diversity

MDPI

Article

Bacterial Diversity Profiles of Desert Sand and Salt Crusts from the Gran Desierto de Altar, Sonora, Mexico

Cristal Ramos-Madrigal [1,2], Esperanza Martínez-Romero [3], Yunuen Tapia-Torres [1] and Luis E. Servín-Garcidueñas [1,*]

[1] Laboratorio de Microbiómica, Escuela Nacional de Estudios Superiores Unidad Morelia, Universidad Nacional Autónoma de México, Morelia 58190, Mexico; cristal.ram.mad@gmail.com (C.R.-M.); ytapia@enesmorelia.unam.mx (Y.T.-T.)
[2] Posgrado en Ciencias Biológicas, Unidad de Posgrado, Ciudad Universitaria, Ciudad de México 04510, Mexico
[3] Centro de Ciencias Genómicas, Universidad Nacional Autónoma de México, Cuernavaca 62210, Mexico; emartine@ccg.unam.mx
* Correspondence: lservin@enesmorelia.unam.mx

Abstract: The Gran Desierto de Altar, located in Sonora, Mexico, represents an arid region that offers an opportunity to study microbial life under extreme conditions. This study analyzed the bacterial diversity present in two distinct types of desert sediments: sand dunes (SDs) and salt crusts (SCs) by culture-dependent and culture-independent methods. Environmental DNA was obtained for 16S rRNA gene amplicon sequencing to obtain taxonomic information using QIIME2. In SD, the bacterial communities comprised 24 phyla, with Actinobacteriota (30–40%), Proteobacteria (22–27%), Bacteroidota (9–11%), Firmicutes (7–10%), and Chloroflexi (3–6%) emerging as the most abundant. Notably, in SC, the archaeal phylum Halobacterota was predominant (37–58%). SC hosted 12 bacterial phyla, the most abundant being Firmicutes (14–30%), Bacteroidota (3–24%), and Proteobacteria (1–12%). Bacteria belonging to the phylum Firmicutes, including *Metabacillus niabensis*, *Bacillus subtilis*, *Bacillus licheniformis*, and *Alkalibacillus haloalkaliphilus*, were isolated using nutrient and saline media. Overall, our findings indicate that the taxonomic composition of the samples analyzed from the Gran Desierto de Altar is consistent with that found in arid environments worldwide. This study provides a basis for future studies focusing on microbial diversity, genetic potentials, and resistance mechanisms of microorganisms from arid environments.

Keywords: microbiota; bacteria; desert; sand; diversity

check for updates

Citation: Ramos-Madrigal, C.; Martínez-Romero, E.; Tapia-Torres, Y.; Servín-Garcidueñas, L.E. Bacterial Diversity Profiles of Desert Sand and Salt Crusts from the Gran Desierto de Altar, Sonora, Mexico. *Diversity* **2024**, *16*, 745. https://doi.org/10.3390/d16120745

Academic Editor: Ipek Kurtboke

Received: 26 September 2024
Revised: 27 November 2024
Accepted: 29 November 2024
Published: 4 December 2024

Copyright: © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https://creativecommons.org/licenses/by/4.0/).

1. Introduction

Deserts are extreme environments characterized by low humidity, extreme temperatures, and high solar radiation [1]. They are classified as arid regions, covering more than one-third of the biomes of the planet, as well as one-fifth of the total surface of the Earth [1]. In addition, a large proportion of the Earth's surface is at risk of desertification. Desertification is a gradual process of soil loss with the deterioration of plant resources due to human activities like overgrazing, deforestation, unsustainable agricultural practices, and fires [2,3], as well as climatic variations, such as droughts or erratic rainfall patterns that affect the biological productivity of the land [4,5].

The Sonoran Desert is one of the driest and hottest deserts in Mexico and contains the largest active sand dune field in North America. Based on regional weather stations, summer temperatures can reach 48 °C (118 °F). A 2021 study published in the Bulletin of the American Meteorological Society revealed that the land surface temperature detected at the Sonoran Desert in Mexico and at the Lut Desert in Iran was 80.8 °C. This temperature is 10 °C higher than the previous world record (70.7 °C) observed in 2005 [6].

The Pinacate and Gran Desierto de Altar Biosphere Reserve, in the Sonoran Desert, is an extremely arid and hot region covering more than 7000 hectares, located in the northwest of Sonora [5]. Its average annual temperature ranges from 18 °C to 22 °C, but in summer it can reach 56.7 °C and in winter it can drop to −8.3 °C [7]. Water in this protected natural area is very scarce; the average annual precipitation is less than 200 mm. Precipitation can range from 164 mm in the northeast to 52 mm in the west. Some places such as the Sierra El Rosario have experienced about 34 months without rain. This Biosphere Reserve contains the driest area within the Sonoran Desert and is one of the driest regions in the world [8].

Soil microorganisms play an important role in the stability and productivity of arid ecosystems, where plants are often scarce [9,10]. Water availability is the main factor controlling bacterial activity, biomass, and diversity in desert soils [11]. However, microbial communities are also affected by other environmental conditions, such as intense radiation doses and high or low temperatures [12] and salinity levels [13]. Desert environments harbor desiccation-resistant and xerophilic microorganisms that thrive under low water activity (aw) levels [14].

There are reports indicating that moisture is an important determinant of bacterial diversity in arid environments, outweighing the influence of other factors such as substrate availability or temperature [10,15]. Endolithic and hypolithic habitats are microenvironments that retain moisture and protect from temperature fluctuations and solar ultraviolet (UV) radiation [16]. Most studies on desert microbial diversity have focused on communities associated with vegetation patches [17,18], shrub islands [19,20], endolithic zones [15,16,21–23], and hypoliths [24–27].

In deserts and arid regions near the sea, such as the Sonoran Desert, the constant evaporation of salt water in flood zones can lead to the formation of salt crusts on the soil or sand. Other arid regions located in low-lying areas, plains, or depressions can also favor the formation of salt crusts, even if rainfall is scarce throughout the year. The microbiota of salt crusts has been studied for the prospects in terms of the bioremediation of saline soils that these halophilic microorganisms may have [28]. Unlike other sediments and soils, salt crusts [29,30] and bare surface soil not associated with plants present more challenging conditions for microorganisms. However, these types of environments have been less studied [31–37].

Organisms from all three domains of life have been described in desert soils worldwide, with those of the bacterial domain being the most abundant [38]. The most abundant bacterial phyla in desert samples correspond to Actinobacteriota, Bacteroidota, Proteobacteria [31,33,36,37,39–41], Gemmatimonadota [42–44], Firmicutes [31,33,36], Cyanobacteria [21,24,27,44,45], Acidobacteriota [31,36], and Chloroflexi [31,36]. At the genus level, some bacteria such as *Geodermatophilus* [37], *Arthrobacter* [31,37], *Microvirga* [31,36,37], *Massilia* [31,37], *Bacillus* [36,37], *Deinooccus* [37], *Planococcus* [37], *Rubrobacter* [37], *Adhaeribacter* [37], and *Roseomonas* [37] have been found in high abundance in most of the studies on desert environments.

In addition to the bacterial community in desert environments, archaea of the phyla Nanohaloarchaeota [46], Euryarchaeota [47], Nanoarchaeota, Thaumarchaeota [36], Crenarchaeota [47], and Halobacterota [48] have been detected.

The study of deserts is of great interest since knowledge of the microorganisms that inhabit them and the mechanisms involved in microbial resistance to these adverse conditions could have important applications in biotechnology, where many processes take place under extreme conditions [49]. Thus, desert microorganisms can help to optimize industrial processes and to discover new, more efficient ones [50].

This study reports on the taxonomic composition and culturable diversity of bacterial communities found on the surface of sand dunes (SDs) and salt crusts (SCs) in the Pinacate and Gran Desierto de Altar Biosphere Reserve in the Sonoran Desert. Archaeal communities were also identified in all samples. In the salt crusts, archaea were more abundant than Bacteria. Our main objective in this initial exploration was to identify key microbial entities in contrasting arid environments within the Sonoran Desert, which includes an

extensive sand dune field unique to North America and salt-rich evaporite regions that have previously received limited attention.

2. Materials and Methods

2.1. Site Description and Sampling

Samples were collected from two distinct sites within the Pinacate and Gran Desierto de Altar Biosphere Reserve, located in the Sonoran Desert (Figure 1). Three samples from the sand dune (SD) region (Figure 2A) were collected and labeled as DUN1 to DUN3. Also, three samples from the salt crust (SC) region (Figure 2B) were obtained and designated as SED1 to SED3. The sand dune samples were collected on 31 January 2022, at coordinates 31°31′40″ N and 113°40′27″ W, and at an altitude of 10 masl (meters above sea level). The ambient temperature was 22 °C. The maximum and minimum daytime temperatures were 23 °C and 6 °C, respectively. These samples were obtained at a depth of no more than 1 cm using a disinfected and flame-sterilized shovel and wearing sterile gloves and face masks. The depth was selected based on the temperature measurements recorded during sampling. While at 1 cm the average surface temperature was 43.8 °C, at 10 cm the temperature dropped to 25.2 °C (average of 3 measurements with a digital laser thermometer). The UV index was 4 during sampling. The initial objective was to obtain the most extreme samples from the surface of the dunes exposed to solar radiation.

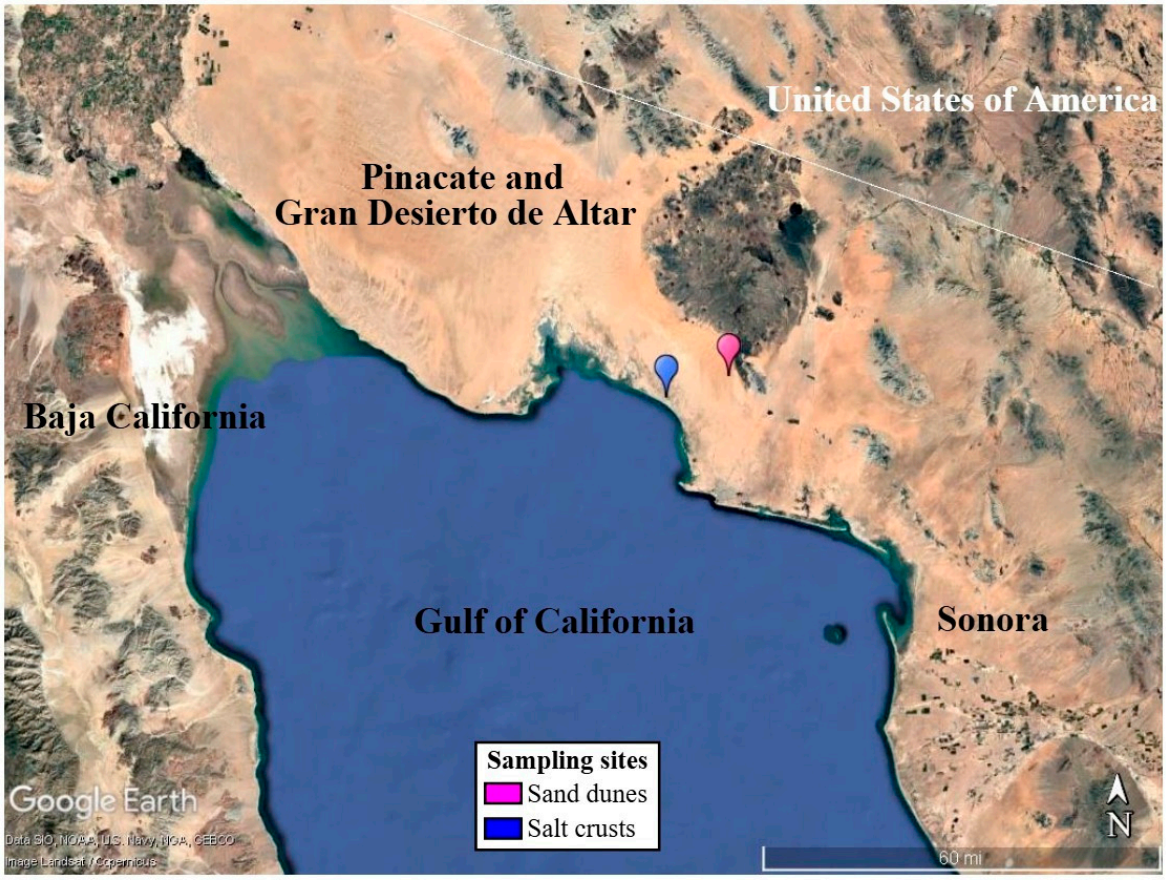


Figure 1. Google Earth map illustrating the sampling sites in Pinacate and Gran Desierto de Altar, Sonora, México. The location of the sand dune (SD) sampling site is indicated with the pink pin. The location of the salt crust (SC) sampling site is indicated with the blue pin.



(**A**) (**B**)

Figure 2. Photographs of the sand dune (**A**) and salt crust (**B**) regions of Pinacate and Gran Desierto de Altar, Sonora, México, during sampling.

Conversely, the salt crust (SC) samples were collected on 30 January 2022, at coordinates 31°31′40″ N and 113°40′27″ W, and at an altitude of 10 masl. The ambient temperature during the sampling was 15 °C. The maximum and minimum temperatures of that day were 22 °C and 7 °C, respectively. The UV index was also 4 during this sampling. Salt crusts were carefully removed from the soil surface to maintain their integrity. These crusts were less than one centimeter thick. All the samples were preserved in sterile 50 mL Falcon tubes, with a total amount of 50 g per sample, and stored in the dark and at room temperature until further processing for DNA extraction.

2.2. DNA Extraction, PCR Amplification, and Library Preparation

DNA extraction was performed using the DNeasy PowerSoil Pro kit (Qiagen, Inc., Germantown, MD, USA) following the manufacturer's instructions. The V3 to V4 region of the bacterial 16S rRNA gene was amplified using the universal primers 341F (59-CCTACGGGNGGCWGCAG-39) and 805R (59-GACTACHVGGGTATCTAATCC-39) [51]. The PCR began with an initial denaturation step at 95 °C for 3 min, followed by 25 cycles consisting of denaturation at 95 °C for 30 s, annealing at 55 °C for 30 s, and extension at 72 °C for 30 s. This was concluded with a final extension step at 72 °C for 5 min. After PCR, the products were purified using AMPure XP beads from Beckman Coulter, Inc. (Fullerton, CA, USA). Library preparation was performed with the Nextera XT index kit from Illumina, and the resultant sample was quantified using the Qubit double-stranded DNA (dsDNA) assay kit from Life Technologies, Carlsbad, CA, USA.

2.3. High-Throughput Sequencing and Statistical Analysis

Sequencing was performed using a MiSeq platform in a 300 bp paired-end format (Macrogen Co., Seoul, Republic of Korea). Following sequencing, reads underwent assessment using FastQC v.0.11.8 with default settings [52], followed by quality filtration (≥Q20 scores) and the removal of adaptor sequences using Trimmomatic v.0.39 [53].

Sequencing data were processed with the QIIME2 software v.2023.7.0 pipeline [54,55]. The q2-dada2 plugin was employed along with the denoise-single method [56] to eliminate noise and chimeric sequences. Amplicon sequence variants (ASVs) were taxonomically assigned using the q2-feature-classifier plugin and the classify-consensus-vsearch method [57] with the SILVA database v.138 SSURef Nr99 [58] as reference.

Alpha and beta diversity were analyzed for all the samples with the rarefied data set due to the differences in sequencing depth (DUN1 = 26,541, DUN2 = 29,903, DUN3 = 26,644, SED1 = 27,908, SED2 = 25,579), and standardized to 25,579. Alpha diversity was measured with the Shannon [59] and Faith's phylogenetic diversity indices [60,61] with the QIIME2 Diversity plugin [62]. Shannon Index of entropy is defined as the degree of uncertainty in

the identity of the species to which an individual randomly selected from the community belongs. A community where all the species have the same abundance will have high entropy, which translates as high diversity [63]. Faith's phylogenetic diversity (Faith's PD or Faith's index) is a phylogenetic alpha diversity metric that not only considers the number and abundance of species, but also the evolutionary relationship between them. This is carried out by considering the lengths of the branches of the phylogenetic tree that connect all the species present in a sample or community [61,64].

Beta diversity was measured using the UNIFRAC weighted method, which measures the distance between species in a phylogenetic tree, weighted by the relative abundance of those species in the samples [65]. The results of this analysis were visualized through a PCoA 2D diagram.

Common bacteria and archaea (at the genus level) shared between the SD and SC samples were determined and a differential abundance analysis was performed between sites using ANCOM [66].

2.4. Microbial Culture Exploration

To complement and corroborate the data obtained by the 16S rRNA gene amplicon sequencing approach, the culturable diversity of microorganisms was explored. Different nutritional and saline media were tested to isolate archaea and bacteria from the SD and SC samples from the Sonoran Desert. The following solid media were used to culture bacteria in triplicate: Luria–Bertani (LB), *Natronococcus occultus* media DSM 3396 (NAT) [67], Halobacterium media DSM 372 (HBA) [68], *Halalkalicoccus jeotgali* media DSM 18796 (HAL) [69], and Sea Salt media (SSM). The samples were pooled, with one set combining DUN1-DUN3 and another set combining SED1-SED3.

To inoculate Petri dishes with sand derived from the SD samples, a strain isolation method previously reported in the desert samples was used. It consists of cultivating grains of sand directly in Petri dishes [70]. For the SC samples, an initial solution of 1 g of SC in 1 mL of sterile distilled water was prepared, and then 1/10 dilutions were prepared and 50 uL were plated in Petri dishes with glass beads. Sterile distilled water (50 uL) was used as a negative control. All the cultures were maintained at a temperature of 37 °C until growth was observed; subsequently, bacterial colonies with different observable morphologies were selected and these were re-cultured to extract and purify DNA. DSM culture media were prepared according to the protocols of the Leibniz Institute DSMZ-German Collection of Microorganisms and Cell Cultures GmbH following the recommended temperatures.

DNA extraction was performed using the DNA Isolation Kit for Cells and Tissues kit from Roche following the manufacturer's recommendations. The amplification of the V1-V3 region of 16S rRNA genes was performed using the primers 27f (5′-AGAGTTTGATCMTGG CTCAG-3′) and 1492r (5′-TACGGYTACCTTGTTACGACTT-3′). The PCR process started with an initial denaturation step at 94 °C for 4 min, followed by 35 cycles consisting of denaturation at 94 °C for 1 min, annealing at 57 °C for 1 min, and extension at 72 °C for 1 min and 40 s. This was concluded with a final extension step at 72 °C for 10 min. After PCR, the products were purified utilizing the GeneJET PCR Purification Kit from Thermo Scientific. The samples of 16S rRNA gene amplicons were sequenced at the UNAM Biotechnology Institute, in Morelos, Mexico using the Sanger sequencing method. The sequencing reads obtained were approximately 1.5 kb in length. The forward and reverse sequences were analyzed in BioEdit v.5.0.9 to align and remove low-quality regions. The sequences were analyzed in the NCBI web version of BLAST-NT to find out the identity of the cultured bacteria or archaea.

3. Results

3.1. Environmental DNA Sequencing and Analysis

The sequencing analysis of the sand dune (SD) and salt crust (SC) samples involved a strict quality control measure, which resulted in high-quality datasets. For the SD samples, a total of 281,822 paired-end raw reads were obtained for the three samples. After filtering,

166,952 high-quality reads were clustered in 1196 valid ASVs for the SD samples. For the SC samples, only two samples passed the initial DNA quality filters and thus were sequenced. For those two SC samples, a total of 207,052 paired-end raw reads were generated. After filtering, 142,592 high-quality reads clustered in 581 valid ASVs for the SC samples.

3.2. Microbial Composition Analysis of Sand Dunes

Taxonomic assignment showed that the predominant phylum in the three SD samples (DUN1, DUN2, and DUN3) was Actinobacteriota (30%, 35%, and 40%), followed by the phyla Proteobacteria (22%, 25%, and 27%), Bacteroidota (9%, 9.5%, and 11%), Firmicutes (10%, 7%, and 7%), and Chloroflexi (6%, 3%, and 4%). The phylum Thermoplasmatota was detected in the SD samples as the only representative of the archaea domain (Figure 3).

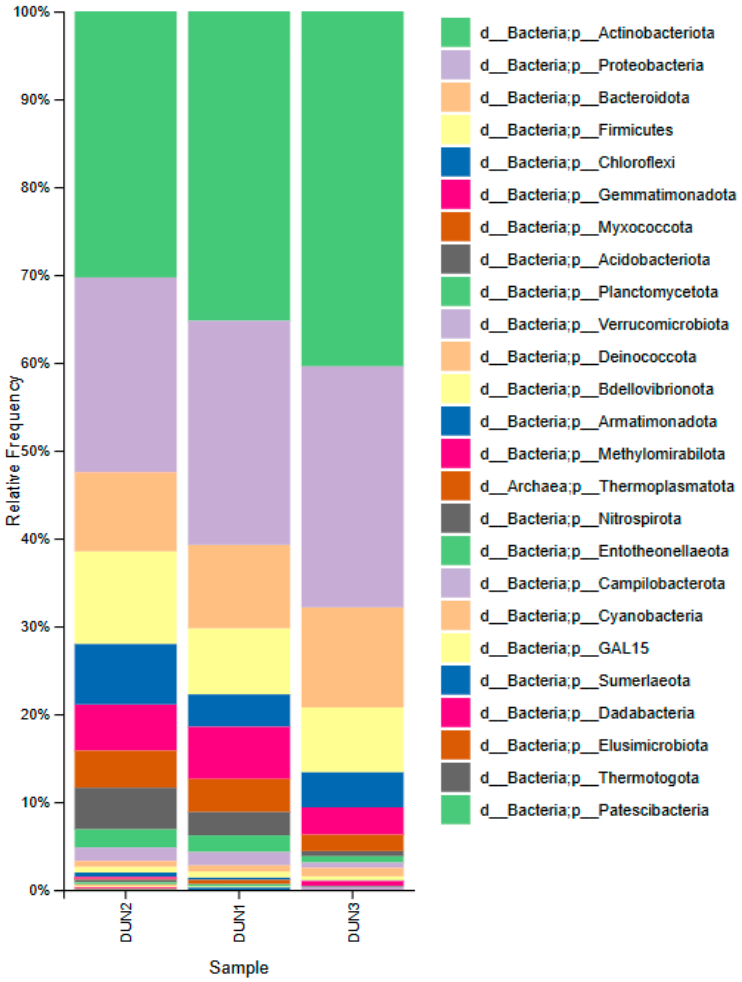


Figure 3. Bar chart showing the relative abundance of bacteria and archaea at the phylum level in the SD samples of Pinacate and Gran Desierto de Altar, Sonora, Mexico (DUN1, DUN2, and DUN3). The bacterial and archaeal communities of the SD samples are composed of 25 different phyla.

At the class level, the highest abundance corresponded to the class Actinobacteriota, Gammaproteobacteria, Bacteroidia, Alphaproteobacteria, Bacilli, Thermoleophilia, Chloroflexia, Acidimicrobiia, and Longimicrobia (Table S1). At the genus level, 103 genera were identified and *Arthrobacter*, *Noviherbaspirillum*, *Massilia*, *Micrococcus*, *Adhaeribacter*, *Flavisolibacter*, and *Nocardioides* stood out with the highest number of sequences and relative abundance (Figure 4 and Table S1). Only four bacteria were identified at the species level in the SD samples: *Micrococcus luteus*, *Massilia armeniaca*, *Staphylococcus aureus*, and *Bacillus weihaiensis* (Table 1).

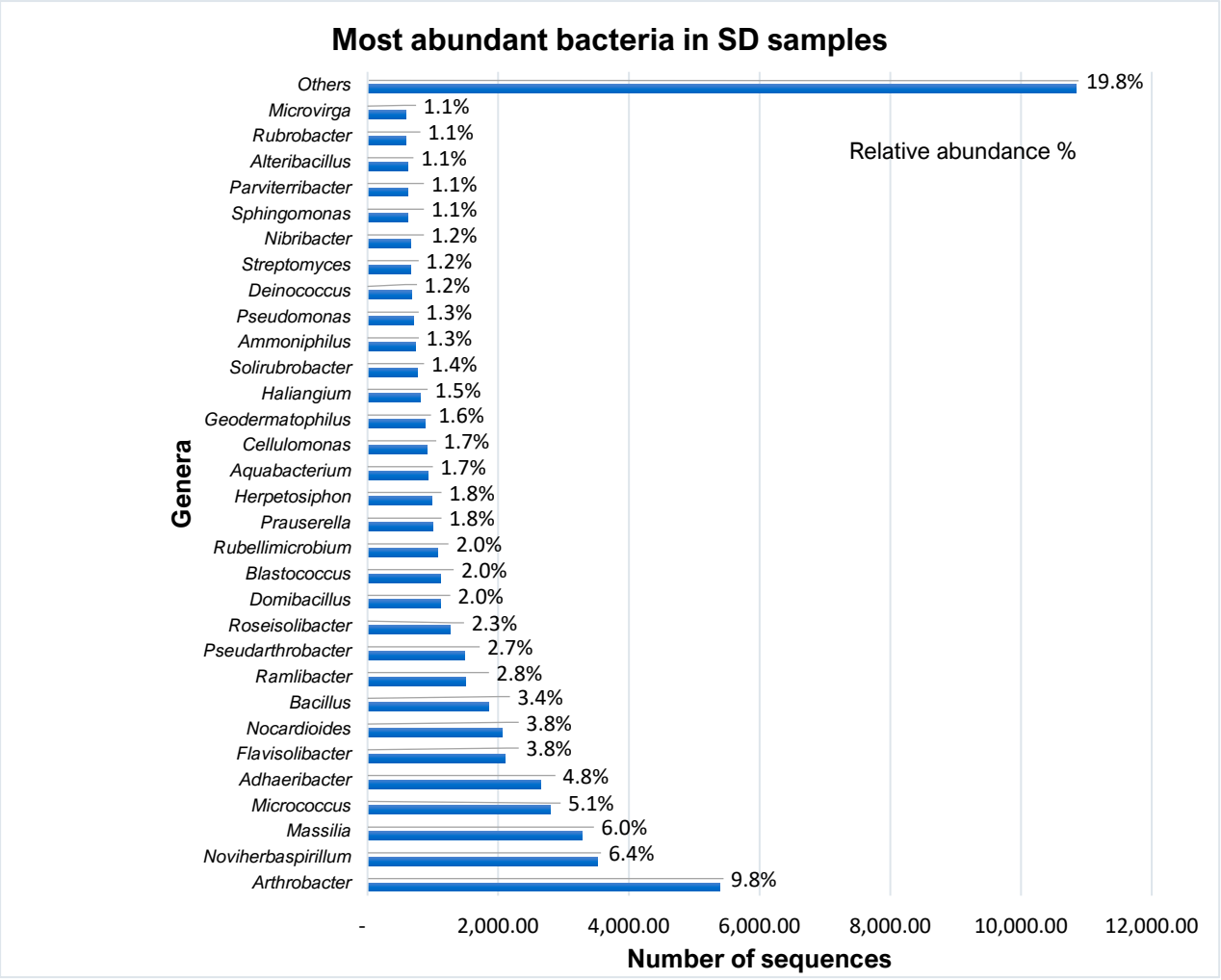


Figure 4. Relative abundance of the 31 most abundant genera in SD samples of Pinacate and Gran Desierto de Altar, Sonora, Mexico. The number of sequences that were assigned to each taxonomic group are shown on the X-axis. Only genera above 1% of the relative abundance are shown.

Table 1. Bacterial species identified in the SD of Pinacate and Gran Desierto de Altar, Sonora, Mexico.

Phylum	Class	Order	Family	Genus	Specie
Actinobacteriota	Actinobacteriota	Micrococcales	*Micrococcaceae*	*Micrococcus*	*M. luteus*
Proteobacteria	Gammaproteobacteria	Burkholderiales	*Oxalobacteraceae*	*Massilia*	*M. armeniaca*
Firmicutes	Bacilli	Staphylococcales	*Staphylococcaceae*	*Staphylococcus*	*S. aureus*
Firmicutes	Bacilli	Bacillales	*Bacillaceae*	*Bacillus*	*B. weihaiensis*

3.3. Microbial Composition Analysis of Salt Crusts

For the two SC samples, taxonomic assignment showed the predominance of the archaea domain. The phylum Halobacterota represented 37% and 58% of the total relative abundance in the two samples, respectively. Then, the bacterial phyla Firmicutes (14% and 30%), Bacteroidota (24% and 3%), and Proteobacteria (12% and 1.5%) were the most abundant (Figure 5).

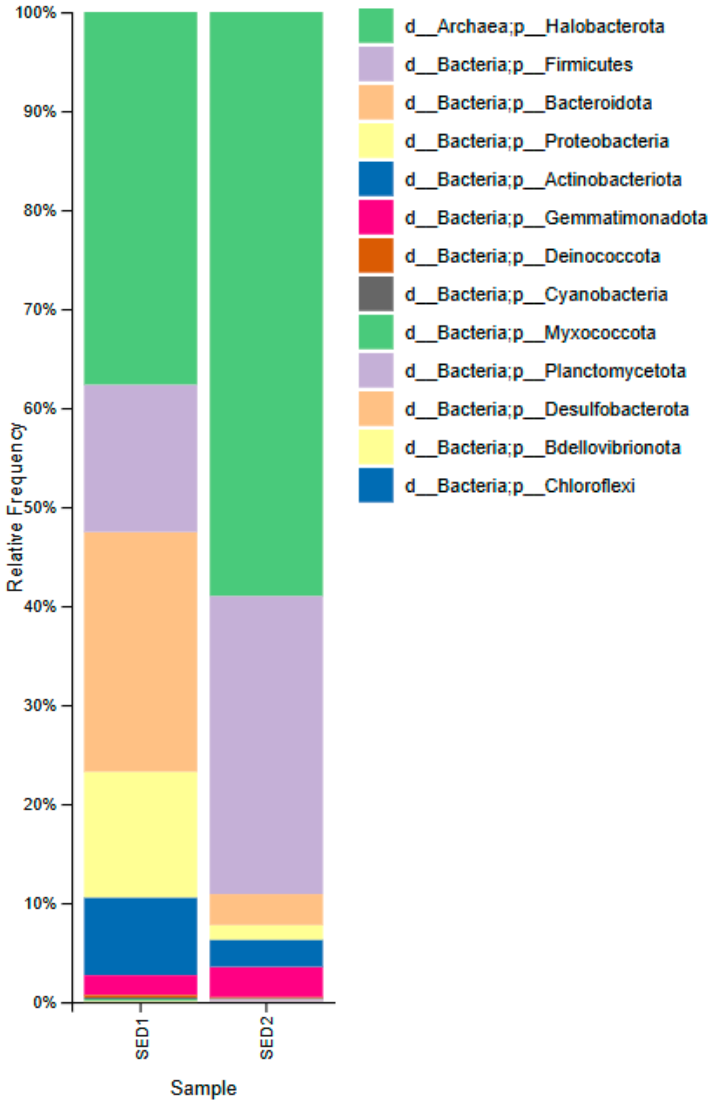


Figure 5. Bar chart showing the relative abundance of bacteria and archaea at the phylum level in the two samples of SC of Pinacate and Gran Desierto de Altar, Sonora, Mexico (SED1 and SED2). The community of bacteria and archaea of the SC samples is composed of members representing 12 different bacteria phyla and only Halobacterota belonging to the Archaea domain.

At the class level, the highest abundance corresponded to the archaeal class Halobacteria, followed by the bacterial Bacilli, Bacteroidia, Actinobacteriota, Alphaproteobacteria, and Gammaproteobacteria (Table S2). At the genus level, 106 bacterial and archaeal genera were identified. Among these, the halophilic archaea of the genera *Natronococcus* and *Halalkalicoccus* occupied nearly 50% of the total sequences (Table S2 and Figure 5).

Archaea genera belonging to the order Halobacterales were detected including *Halorubrum*, *Natronorubrum*, *Natronomonas*, *Natronoarchaeum*, *Halohasta*, *Haloterrigena*, *Haloparvum*, *Halonotius*, *Natrinema*, *Halopiger*, *Halovivax*, *Natrialba*, and others (Table S2, shown in blue and Figure 6). At the species level, two archaea could be identified, *Halalkalicoccus jeotgali* and *Natronococcus occultus*. Also, four bacterial species could be detected, *Bacillus krulwichiae*, *Planococcus kocurii*, *Morganella morgani*, and *Escherichia albertii* (Table 2).

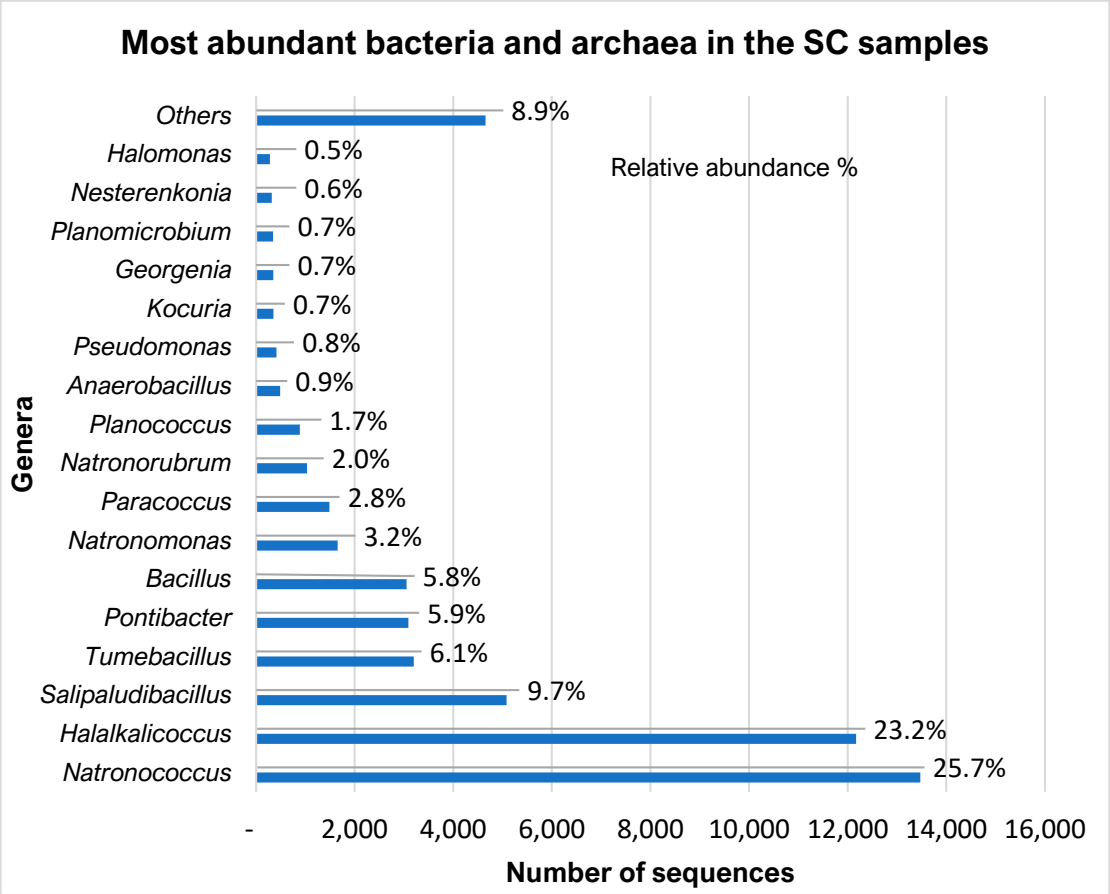


Figure 6. Relative abundance of the 17 most abundant genera in the SC samples from Pinacate and Gran Desierto de Altar, Sonora, Mexico. The number of sequences that were assigned to each taxonomic group is shown on the X-axis. Only genera above 0.5% of the relative abundance are shown.

Table 2. Identified species in the SC of Pinacate and Gran Desierto de Altar, Sonora, Mexico. Archaea are shown in blue.

Phylum	Class	Order	Family	Genus	Specie
Halobacterota	Halobacteria	Halobacterales	*Halococcaceae*	*Halalkalicoccus*	*H. jeotgali*
Halobacterota	Halobacteria	Halobacterales	*Haloferacaceae*	*Natronococcus*	*N. occultus*
Firmicutes	Bacilli	Bacillales	*Bacillaceae*	*Bacillus*	*B. krulwichiae*
Firmicutes	Bacilli	Bacillales	*Planococcaceae*	*Planococcus*	*P. kocurii*
Proteobacteria	Gammaproteobacteria	Enterobacterales	*Morganellaceae*	*Morganella*	*M. morganii*
Proteobacteria	Gammaproteobacteria	Enterobacterales	*Enterobacteriaceae*	*Escherichia*	*E. albertii*

3.4. Diversity Analyses

Although the results of the Kruskal–Wallis's test indicated that there were no significant differences in the alpha diversity measures of SC and SD of the Sonoran Desert (* $p = 0.05$), the alpha diversity indices were similar for the samples of the same origin (Table 3), with the SD samples showing the highest diversity values.

Table 3. Shannon and Faith diversity in SC and SD samples of Pinacate and Gran Desierto de Altar, Sonora, Mexico.

ID	SITE	FAITH'S PD	SHANNON ENTROPY
DUN1	Sand Dunes	20.23	8.083771
DUN2	Sand Dunes	31.70	8.939358
DUN3	Sand Dunes	16.18	7.864047
SED1	Salt Crust	15.02	6.948606
SED2	Salt Crust	9.64	5.407946

Beta diversity was evaluated with the weighted UNIFRAC method [65] (Figure 7) where the first axis accounted for 80.88% of the variance in community composition and discriminated SD and SC, while the second axis explained 10.07% of the variance. The bacterial community composition differed between the SD and SC samples, and the 2D PCoA diagram showed a grouping of the samples by site; the distances between them indicated how different they are from each other. However, the result suggests that there is not enough evidence to affirm that there are significant differences between the groups (Figure 7).

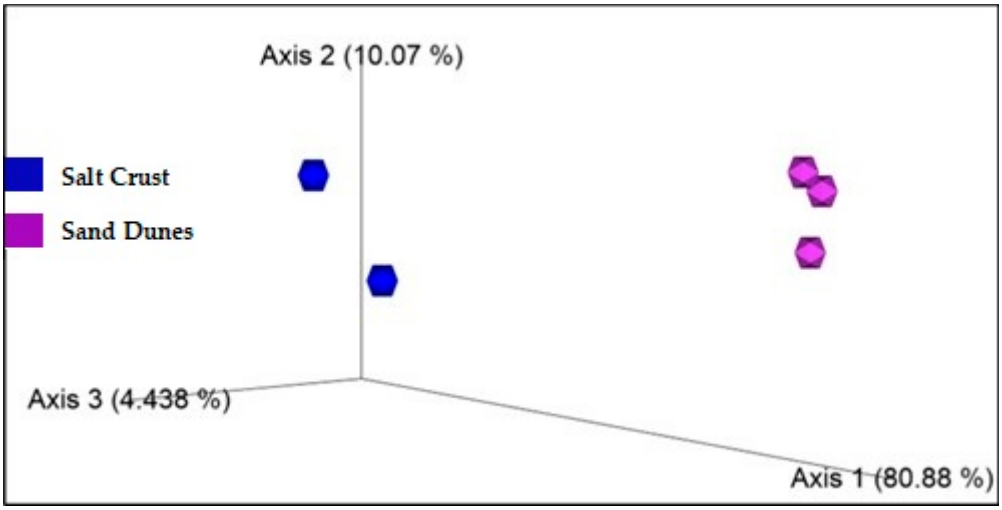


Figure 7. Two-dimensional PCoA diagram obtained from the analysis of the SD and SC samples of Pinacate and Gran Desierto de Altar, Sonora, Mexico, by the weighted UNIFRAC method. Pairwise PERMANOVA results comparing microbial communities between SC and SD samples showed no statistically significant difference between sites ($p = 0.105$, $q = 0.105$). The analysis was based on 999 permutations and revealed a pseudo-F value of 16.148.

3.5. Comparative Analysis

Comparative analyses were performed to evaluate the differences in taxonomic composition among the sample types, focusing on the significant distinctions between the SD and SC samples. A total of 40 bacterial genera were identified as common to both the SD and SC samples (Figure 8). Proteobacteria was the phylum with the most represented shared genera (14), followed by Actinobacteria (9), Firmicutes (6), Bacteroidota (5), and others (Table S3). A Venn diagram was created to illustrate the genera of bacteria or archaea that are present in common, the result being that both sites present a set of bacteria in common consisting of 40 genera. Of these common bacterial genera, Proteobacteria was the phyla with the most members (14), followed by Actinobacteria (9), Firmicutes (6), Bacteroidota (5), Myxococcota (2), Bdellovibrionota (2), Cyanobacteria (1), and Gemmatimonadota (1) (Table S3).

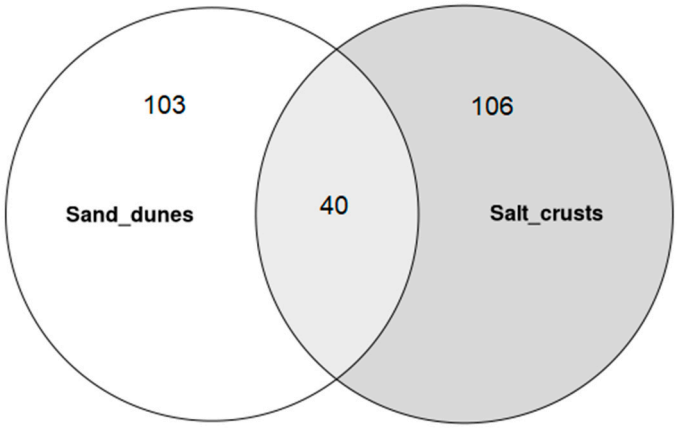


Figure 8. Venn diagram illustrating the relationship between the SD and SC samples from Pinacate and Gran Desierto de Altar, Sonora, Mexico. The diagram indicates the number of shared and unique genera for each sample type.

The results of the ANCOM analysis were represented with a Volcano plot to compare the composition of the SD and SC samples (Figure 9). For the SD and SC samples, the analysis did not show differentially abundant taxa.

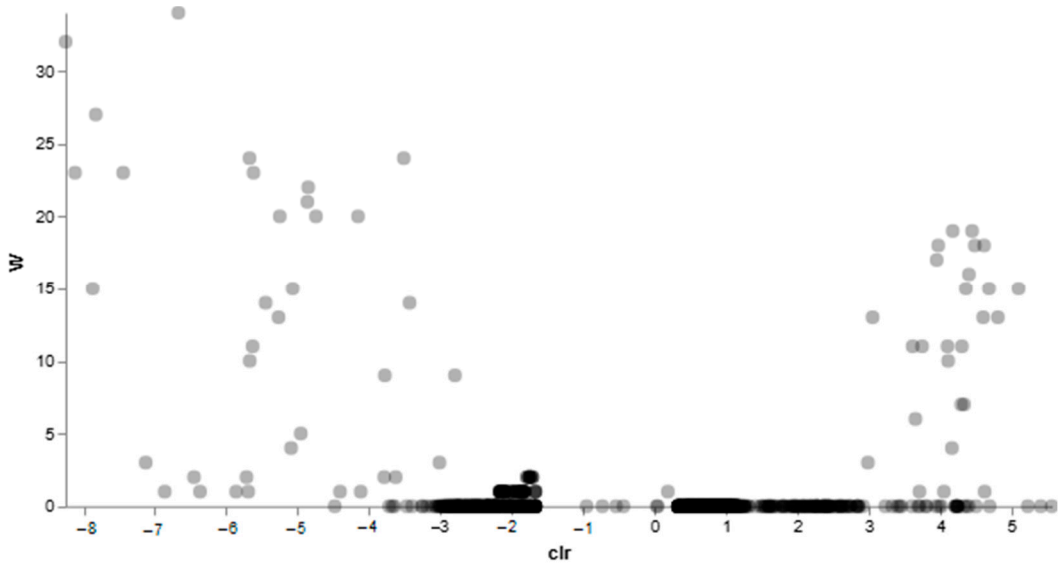


Figure 9. Volcano plot displaying the results of the ANCOM analysis. In this plot, the *y*-axis (W or W score) represents the frequency with which a bacterial taxon (genus in this case) was identified as differentially abundant when compared to the other samples included in the analysis. This value reflects the robustness of the result for each trait. The higher the W value, the stronger the evidence that a bacterial genus has significant differences in abundance between the compared samples. The *x*-axis represents the difference in the relative abundance of the trait between the groups or samples compared on a logarithmic scale. Positive values indicate higher abundance in one group, while negative values indicate higher abundance in the other. The ANCOM statistical results found no significant features between the SD and SC samples of Pinacate and Gran Desierto de Altar, Sonora, Mexico.

3.6. Culturable Bacteria from Sand Dune and Salt Crust Samples

Petri dishes containing the LB, NAT, HBAC, HAL, and SSM culture media were inoculated with independent pools of the SD and SC samples. All the colonies were identified as bacterial isolates. Growth was only observed in the LB, SSM, and NAT media. After 12 h (LB and SSM) and 15 days (NAT), bacterial colonies were obtained and isolated,

which corresponded mostly to *Bacillus* strains with a high identity percentage from 98.67% to 100% to the 16S rRNA genes of the described bacteria (Table 4). No microbial growth was observed in the HAL and HBAC culture media after 20 days of incubation at 37 °C.

Table 4. Bacteria isolated from SD and SC samples from Pinacate and Gran Desierto de Altar, Sonora, Mexico.

Medium	Sample	Specie	Max Score	Total Score	Query Cover	E Value	Ident
SSM	SD	*Metabacillus niabensis*	2492	2492	100%	0	98.99%
LB		*Bacillus subtilis*	2425	2425	100%	0	99.04%
LB		*Bacillus subtilis*	2425	2425	100%	0	99.04%
LB	SC	*Bacillus licheniformis*	2527	2527	100%	0	99.42%
LB		*Bacillus licheniformis*	1515	1515	100%	0	99.40%
NAT		*Alkalibacillus haloalkaliphilus*	2532	2532	100%	0	98.67%
LB		*Bacillus* sp. (*in: firmicutes*)	2580	2580	100%	0	100.00%
LB		*Bacillus subtilis*	2124	2124	100%	0	99.49%

Some of the isolated bacteria exhibited distinctive characteristics in culture. For example, *Alkalibacillus haloalkaliphilus* colonies isolated from the SC samples and cultured in the NAT medium were pink. Also, the *Bacillus subtilis* colonies from the SD samples and cultured in the LB medium presented a mucous consistency. Furthermore, the isolates identified as *Bacillus licheniformis* from the SC samples showed a high adherence to the culture media.

4. Discussion

4.1. Microbial Communities in SD and SC

The taxonomic composition found in the samples analyzed from the Sonoran Desert is consistent with desert sediments and soils worldwide. The predominant microorganisms are bacteria [38], with the most abundant phyla being Actinobacteriota, Bacteroidota, Proteobacteria [31,33,36,37,39–41], Gemmatimonadota [42–44], Firmicutes [31,33,36], and Cyanobacteria [24,27,45], which may be more abundant in this type of soil than in other biomes [71].

Among the genera identified in the SD samples were some of the best-known bacteria in arid environments, such as *Rubrobacter*, *Microvirga*, and *Deinococcus*, three of the genera of bacteria most resistant to ionizing radiation [72]. Actinobacteriota, the most abundant phylum in all three from the SD samples, is known to be dominant in arid environments due to their high sporulation capacity, broad metabolic capacity, competitive advantages, and multiple UV light damage repair mechanisms [73,74] that allow them to withstand extreme environments. In the SD samples, the phylum Thermoplasmatota was identified using the amplicon sequencing method. This phylum contains methanogenic archaea that have been found in peat soils along with other archaeal phyla such as Euryarchaeota and Halobacterota [75]. Members of the phylum Thermoplasmatota have also been found abundantly as planktonic archaea in the sea, together with representatives of Thaumarchaeota [76]. To our knowledge, the presence of Thermoplasmatota is not common in the sand dunes of arid environments. Therefore, the archaeal communities present in the sand dunes of the Sonoran Desert require further investigation and represent a unique opportunity for the description of new archaeal members.

In contrast, the most abundant phylum in the SC samples was Halobacterota, which contains highly halophilic archaea. In a recent study, this archaeal phylum was identified in 0–60 cm surface sediment samples from the Atacama Desert, along with the phyla

Deinococcota and Latescibacterota [48]. The presence of this phylum was also identified in peat [75] and in agricultural soils near mining areas with high content of heavy metals and severe cadmium contamination, which may indicate the ability of some species of this phylum to withstand multiple extreme conditions [55]. *Halalkalicoccus jeotgali* and *Natronococcus occultus*, two halophilic archaea, were the two most abundant identifications in the SC samples (Table 2). Halobacterota is a phylum of extremophilic archaea that depend on high salt concentrations, thus inhabiting extremely saline soils, marshes, lakes, or lagoons [77]. Some halophilic bacteria and archaea have been studied for their ability to degrade contaminant compounds [78]. Protocols to treat brines, salt water, and saline soils contaminated with toxic compounds, heavy metals, hydrocarbons, and aromatic compounds make use of Halobacterota members [77].

The genera *Geodermatophilus*, *Paenibacillus*, *Bacillus*, *Solirubrobacter*, and *Nocardioides* have been widely reported in arid environments to be highly resistant to radiation [24,32,36,37,45]. All these genera were detected in the SD and SC samples. The genera *Bacillus* and *Paenibacillus* were identified in the SD and SC samples (Tables 1, 2, S1, and S2) and are among the most abundant bacterial genera found in desert environments. They have been studied for their ability to form endospores, which facilitate survival under desiccation conditions. Spores of some *Bacillus subtilis* strains have been shown to be able to withstand microgravity conditions in space [79,80] and even simulated Martian atmospheric conditions, such as ultraviolet radiation and dehydration [81,82]. In addition to withstanding stress conditions, most *Bacillus* species are readily grown under mesophilic conditions. In this study, *Bacillus* species were cultured from the SD and SC samples. *Bacillus licheniformis*, for example, is a Gram-positive spore-forming bacterial species of great interest due to its bioactive compounds applicable in multiple areas of biotechnology and industry. In this case, it was isolated from salt crusts (SCs) on the soil surface, directly exposed to high salt concentrations, solar radiation, and temperature fluctuation. One of the genera shared between the SD and SC samples is *Domibacillus*, which was identified in the Cuatro Cienegas basin in Mexico and has recently been found to exhibit altruistic interactions when cultured with *Bacillus* strains [83]. *Bacillus* is well known for its extremophilic capabilities, but its interactions and effects on community structure deserve further investigation in arid environments.

The genus *Paenibacillus* was identified in the SD and SC samples. One strain of this genus, *Paenibacillus* sp. JZ16, is a bacterium that lives inside the roots of the desert plant *Zygophyllum simplex* [84]. In a recent study, this strain was shown to promote salinity stress tolerance in *Arabidopsis thaliana* [84]. These findings demonstrate the applicability that xerophilic organisms can have in such important areas as agriculture. Soil health and microbial activity are crucial for agricultural sustainability [85]. Microorganisms inhabiting arid soils often develop unique adaptations to survive in conditions of water scarcity and high temperatures [86]. Knowing the microorganisms present in arid soils can provide valuable information for the development of agricultural practices adapted to these conditions, improving productivity and soil conservation. Other species, such as *Paenibacillus harenae* [87] and *Paenibacillus gansuensis* [88], were also isolated from sand samples from the desert of the Chinese province of Gansu.

Of the genera shared among the samples, *Arthrobacter* was the most abundant in the SD samples, while *Planomicrobium* was the genus with more sequences in the SC samples (Table S3). On one hand, some *Planomicrobium* strains have been isolated from arid environments such as *Planomicrobium chinense* sp. DX3-12^{T}, isolated from coastal sediment in the East China Sea in Fujian, China [89], and *Planomicrobium iranicum* sp. MX6^{T}, isolated from a hypersaline wetland, both characterized as slightly halophilic [90]. On the other hand, although *Arthrobacter* has been found in mesophilic soils worldwide, it is also one of the genus found in multiple deserts such as the Atacama Desert in Chile [32], the Kyzyl-Kum Desert in Uzbekistan [37], Saudi Arabia Desert [91], the Gobi Desert, and the Taklemaken Desert [35].

4.2. Differences in Microbial Communities

One of the most obvious differences between the two distinct SD and SC samples is the higher presence and abundance of archaea in the SC samples. The pronounced prevalence of the phylum Halobacterota in the SC samples probably contributes to their lower alpha diversity analysis. As discussed above, lower uniformity in taxa abundance correlates with lower diversity indices. Although not conclusive, a trend toward higher diversity is observed in the SD samples (Table 3). Even if the diversity index does not differ too much, the microbial composition between the SD and SC samples is not similar, as can be seen in the Venn diagram (Figure 8). Most of the microbial taxa are not shared between them. In addition, an ANCOM analysis did not find significantly abundant microbial taxa between the SD and SC samples (Figure 9). Although more abundant bacterial groups are observed at some of the sites studied (Table S3), the ANCOM analysis suggests that there is insufficient statistical evidence. However, the statistical power of this test may be limited by the low number of replicates, which could be even more detrimental if the variability in taxa abundances is high as in this case.

4.3. Microbial Dispersal in the Sonoran Desert

During certain months of the year, especially from January to April, the Sonoran Desert presents strong winds that can transport sand particles carrying microorganisms through the air. Conditions (except salinity) such as ambient temperature, aridity, and UV radiation index do not differ considerably from one site to another; this may explain our finding of similar bacteria in both SD and SC samples. The presence of shared bacterial genera among the sites could indicate the tolerance to multiple extreme conditions of these microorganisms. The evident, but not evaluated, salinity conditions of the salt crusts and the high temperatures, aridity, and radiation of the surface samples from the Sonoran Desert dunes are selective pressures that overcome some of these extremophiles.

4.4. Opportunities to Study the Microbial Life of the Sonoran Desert

The study of the adaptations of microbial life in extreme environments can provide valuable information, especially in those environments that are gaining ground and advancing year after year, such as arid ones. Extremophiles have demonstrated versatile applications, such as their use in the production of valuable compounds [92] and their role in bioremediation processes [93]. For astrobiology, extremophiles serve as model organisms to study the survival mechanisms of life in outer space [94]. The existence of microorganisms in extreme environments has continuously expanded the knowledge of the limits of life [95].

In the present study, there are groups of bacteria and archaea that offer the opportunity to learn more about their survival and adaptive capabilities, some of which can even be cultured. In the future, a more robust study that includes a larger number of samples and sampling at different temporalities and at different depths could shed more light on the structure, variability, and fluctuations of the microbial community in this yet underexplored desert. Comparability of samples is somewhat limited due to the difficulty of obtaining DNA from surface sand, as most studies focus on arid soils, yet there are obvious similarities in composition and taxonomic groups that prevail even in the most hostile conditions. A metagenomic study of the samples would provide insight into the genetic potential of the bacteria and archaea found in the Sonoran Desert, as well as the possibility of discovering new strains and species.

5. Conclusions

In this study, the analysis of 16S rRNA gene amplicon data revealed a high level of bacterial diversity in the SD and SC samples of the Sonoran Desert. Shannon and Faith diversity indices showed high values for all the analyzed samples. However, there was a tendency for increased diversity in the SD samples for both indices. No significant differences were observed in diversity between the two systems analyzed. Although the

results of the Kruskal–Wallis's test indicated insufficient evidence to conclude that the SD and SC samples differ in alpha diversity measures, a distinct difference in taxonomic composition between the systems was evident.

The microbiota in the SD samples was dominated by the phyla Actinobacteriota, Proteobacteria, Bacteroidota, Firmicutes, and Chloroflexi, in agreement with the most abundant phyla observed in arid environments worldwide. In contrast, the SC samples were dominated by Archaea from the phylum Halobacterota. Within this archaeal phylum, the genera *Natronococcus* and *Halalkalicoccus* covered around 50% of the relative abundance of the SC samples. In general, a total of 40 bacterial genera were identified as common between the SD and SC samples.

In addition to amplicon sequencing data, bacterial isolates were successfully obtained from the SD and SC samples. Most isolates corresponded to the genus *Bacillus*, which is known to contain polyextremophile species with many potential applications.

This work provides a foundation for future research that could expand our understanding of the microbial diversity present in the extreme environments of the Sonoran Desert.

6. Perspectives

After this initial assessment, it is important to further investigate the microbial community of the Sonoran Desert using additional samples and complementary approaches. Metagenomics would provide a glimpse into the genetic potential of the taxonomic groups identified in this study and could provide genome-wide sequences to further investigate microbial diversity in sand dunes and salt crusts.

Seasonal studies, rainfall simulations, and sampling at different depths could provide information on how communities may change with different temperatures and climatic conditions. Also, a wider range of culture media and experimental conditions promise the isolation of more microorganisms resistant to multiple extreme conditions.

Microorganisms play a fundamental role in carbon, nitrogen, and phosphorus biogeochemical cycles. Hence, understanding microbial communities in arid soils is relevant to better comprehend the functioning of biogeochemical cycles under desert conditions.

Currently, soil salinity is one of the problems that restrict agricultural activities, as it diminishes productivity and adversely impacts vegetation and the environment. The influence of salinity on desertification has been the subject of research, and there are promising prospects for mitigating these issues through the utilization of desert extremophile organisms [96].

Supplementary Materials: The following material is available online at https://www.mdpi.com/article/10.3390/d16120745/s1. Table S1: Identified genera in the SD samples of the Pinacate and Gran Desierto de Altar, Sonora, Mexico. Archaea are shown in blue; Table S2: Identified genera in the SC samples of the Pinacate and Gran Desierto de Altar, Sonora, Mexico. Archaea are shown in blue; Table S3: Common bacteria between SD and SC samples of the Pinacate and Gran Desierto de Altar, Sonora, Mexico.

Author Contributions: Conceptualization, C.R.-M. and L.E.S.-G.; methodology, C.R.-M. and L.E.S.-G.; software, C.R.-M.; validation, C.R.-M. and L.E.S.-G.; formal analysis, C.R.-M.; investigation, C.R.-M.; resources, L.E.S.-G.; data curation, C.R.-M.; writing—original draft preparation, C.R.-M.; writing—review and editing, C.R.-M., E.M.-R., Y.T.-T. and L.E.S.-G.; visualization, C.R.-M.; supervision, C.R.-M., E.M.-R., Y.T.-T., and L.E.S.-G.; project administration, L.E.S.-G.; funding acquisition, L.E.S.-G. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by grants to L.E.S.-G. from PAPIIT-UNAM (IA210617 and IA208019).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Raw sequences are available on the NCBI SRA under the bioproject: PRJNA1077733.

Acknowledgments: C.R.-M. is a student from the Programa de Posgrado en Ciencias Biologicas from the Universidad Nacional Autónoma de México (UNAM), and this paper is part of the requirements for obtaining her Doctoral degree. We thank the Consejo Nacional de Ciencia, Humanidades y Tecnología CONAHCyT-Mexico for funding and for the support of this research through a graduate scholarship to C.R.-M. (number 1084853). The authors are grateful to the three reviewers and the Associate Editor whose constructive comments greatly improved the quality and clarity of an earlier version of this manuscript. We thank Marco A. Rogel-Hernández for his technical support and Jazmín Ramos-Madrigal for her insights and for critically reading the paper.

Conflicts of Interest: The authors declare that they have no conflicts of interest.

References

1. Laity, J.J. *Deserts and Desert Environments*; John Wiley & Sons: Hoboken, NJ, USA, 2009; Volume 3.
2. Foley, J.A.; Defries, R.; Asner, G.P.; Barford, C.; Bonan, G.; Carpenter, S.R.; Chapin, F.S.; Coe, M.T.; Daily, G.C.; Gibbs, H.K.; et al. Global consequences of land use. *Science* **2005**, *309*, 570–574. [CrossRef] [PubMed]
3. Sterk, G.; Stoorvogel, J.J. Desertification–Scientific Versus Political Realities. *Land* **2020**, *9*, 156. [CrossRef]
4. Zhang, L.; Nan, Z.; Yu, W.; Ge, Y. Hydrological Responses to Land-Use Change Scenarios under Constant and Changed Climatic Conditions. *Environ. Manag.* **2015**, *57*, 412–431. [CrossRef]
5. United Nations Convention to Combat Desertification (UNCCD). UNCCD FAQ. Available online: https://www.unccd.int/unccd-faq (accessed on 10 November 2024).
6. Zhao, Y.; Norouzi, H.; Azarderakhsh, M.; AghaKouchak, A. Global Patterns of Hottest, Coldest, and Extreme Diurnal Variability on Earth. *Bull. Am. Meteorol. Soc.* **2021**, *102*, E1672–E1681. [CrossRef]
7. Everardo, G.; Alberto, T.L.; Eva, C. Historia natural y cultural de un geosímbolo de Sonora. *Región Y Soc.* **2012**, *24*, 227–261.
8. IUCN. Mexico's Pinacate Desert Wins World Heritage Status. 2013. Available online: https://iucn.org/content/mexicos-pinacate-desert-wins-world-heritage-status (accessed on 13 November 2024).
9. Belnap, J.; Gardner, J.S. Soil microstructure in soils of the Colorado Plateau: The role of the cyanobacterium Microcoleus vaginatus. *West. N. Am. Nat.* **1993**, *53*, 40–47.
10. Pointing, S.B.; Warren-Rhodes, K.A.; Lacap, D.C.; Rhodes, K.L.; McKay, C.P. Hypolithic community shifts occur as a result of liquid water availability along environmental gradients in China's hot and cold hyperarid deserts. *Environ. Microbiol.* **2007**, *9*, 414–424. [CrossRef]
11. Kieft, T.L. Hot Desert Soil Communities. In *Encyclopedia of Environmental Microbiology*; John Wiley: New York, NY, USA, 2002; pp. 1576–1586.
12. Georgiou, C.D.; Sun, H.J.; McKay, C.P.; Grintzalis, K.; Papapostolou, I.; Zisimopoulos, D.; Panagiotidis, K.; Zhang, G.; Koutsopoulou, E.; Christidis, G.E.; et al. Evidence for photochemical production of reactive oxygen species in desert soils. *Nat. Commun.* **2015**, *6*, 7100. [CrossRef]
13. Zhang, M.; Xing, J.; Long, Q.; Shen, G.; Zhu, D.; Li, Y. Prokaryotic Microbial Diversity Analysis and Preliminary Prediction of Metabolic Function in Salt Lakes on the Qinghai–Tibet Plateau. *Water* **2024**, *16*, 451. [CrossRef]
14. Gargaud, M.; Amils, R.; Quintanilla, J.C.; Cleaves, H.J.; Irvine, W.M.; Pinti, D.L.; Viso, M. *Encyclopedia of Astrobiology*; Springer Science & Business Media: Berlin, Germany, 2011; Available online: https://www.springer.com/gp/book/9783642112744 (accessed on 13 November 2024).
15. Warren, S.D.; Rosentreter, R.; Pietrasiak, N. Biological Soil Crusts of the Great Plains: A Review. *Rangel. Ecol. Manag.* **2021**, *78*, 213–219. [CrossRef]
16. Wierzchos, J.; Ascaso, C.; McKay, C.P. Endolithic cyanobacteria in halite rocks from the hyperarid core of the Atacama Desert. *Astrobiology* **2006**, *6*, 415–422. [CrossRef] [PubMed]
17. Belnap, J.; Rosentreter, R.; Leonard, S.; Kaltenecker, J.; Williams, J.; Eldridge, D. Biological Soil Crusts: Ecology and Management. In *Ecology and Management of Microbiotic Soil Crusts*; USDA: Washington, DC, USA, 2001.
18. Nagy, M.L.; Perez, A.; Garcia-Pichel, F. The prokaryotic diversity of biological soil crusts in the Sonoran Desert (Organ Pipe Cactus National Monument, AZ). *FEMS Microbiol. Ecol.* **2005**, *54*, 233–245. [CrossRef]
19. Aanderud, Z.T.; Shuldman, M.I.; Drenovsky, R.E.; Richards, J.H. Shrub-interspace dynamics alter relationships between microbial community composition and belowground ecosystem characteristics. *Soil Biol. Biochem.* **2008**, *40*, 2206–2216. [CrossRef]
20. Collins, H.P.; Cavigelli, M.A. Soil microbial community characteristics along an elevation gradient in the Laguna Mountains of Southern California. *Soil Biol. Biochem.* **2003**, *35*, 1027–1037. [CrossRef]
21. Vítek, P.; Jehlička, J.; Ascaso, C.; Mašek, V.; Gómez-Silva, B.; Olivares, H.; Wierzchos, J. Distribution of scytonemin in endolithic microbial communities from halite crusts in the hyperarid zone of the Atacama Desert, Chile. *FEMS Microbiol. Ecol.* **2014**, *90*, 351–366. [CrossRef] [PubMed]
22. Gómez-Silva, B.; Vilo-Muñoz, C.; Galetović, A.; Dong, Q.; Castelán-Sánchez, H.G.; Pérez-Llano, Y.; Sánchez-Carbente, M.d.R.; Dávila-Ramos, S.; Cortés-López, N.G.; Martínez-Ávila, L.; et al. Metagenomics of Atacama Lithobiontic Extremophile Life Unveils Highlights on Fungal Communities, Biogeochemical Cycles and Carbohydrate-Active Enzymes. *Microorganisms* **2019**, *7*, 619. [CrossRef] [PubMed]

23. Dong, H.; Rech, J.A.; Jiang, H.; Sun, H.; Buck, B.J. Endolithic cyanobacteria in soil gypsum: Occurrences in Atacama (Chile), Mojave (United States), and Al-Jafr Basin (Jordan) Deserts. *J. Geophys. Res. Biogeosciences* **2007**, *112*, G02030. [CrossRef]
24. Lacap, D.C.; Warren-Rhodes, K.A.; McKay, C.P.; Pointing, S.B. Cyanobacteria and chloroflexi-dominated hypolithic colonization of quartz at the hyper-arid core of the Atacama Desert, Chile. *Extremophiles* **2011**, *15*, 31–38. [CrossRef]
25. Lacap-Bugler, D.C.; Lee, K.K.; Archer, S.; Gillman, L.N.; Lau, M.C.; Leuzinger, S.; Lee, C.K.; Maki, T.; McKay, C.P.; Perrott, J.K.; et al. Global Diversity of Desert Hypolithic Cyanobacteria. *Front. Microbiol.* **2017**, *8*, 867. [CrossRef]
26. Le, P.T.; Makhalanyane, T.P.; Guerrero, L.D.; Vikram, S.; Van de Peer, Y.; Cowan, D.A. Comparative Metagenomic Analysis Reveals Mechanisms for Stress Response in Hypoliths from Extreme Hyperarid Deserts. *Genome Biol. Evol.* **2016**, *8*, 2737–2747. [CrossRef]
27. Makhalanyane, T.P.; Valverde, A.; Lacap, D.C.; Pointing, S.B.; Tuffin, M.I.; Cowan, D.A. Evidence of species recruitment and development of hot desert hypolithic communities. *Environ. Microbiol. Rep.* **2013**, *5*, 219–224. [CrossRef] [PubMed]
28. Pan, Y.; Kang, P.; Zhang, Y.; Li, X. Kalidium cuspidatum colonization changes the structure and function of salt crust microbial communities. *Environ. Sci. Pollut. Res. Int.* **2024**, *31*, 19764–19778. [CrossRef] [PubMed]
29. Li, J.Y.; Jin, X.Y.; Zhang, X.C.; Chen, L.; Liu, J.L.; Zhang, H.M.; Zhang, X.; Zhang, Y.F.; Zhao, J.H.; Ma, Z.S. Comparative metagenomics of two distinct biological soil crusts in the Tengger Desert, China. *Soil Biol. Biochem.* **2020**, *140*, 107637. [CrossRef]
30. Finstad, K.M.; Probst, A.J.; Thomas, B.C.; Andersen, G.L.; Demergasso, C.; Echeverría, A.; Amundson, R.G.; Banfield, J.F. Microbial Community Structure and the Persistence of Cyanobacterial Populations in Salt Crusts of the Hyperarid Atacama Desert from Genome-Resolved Metagenomics. *Front. Microbiol.* **2017**, *8*, 1435. [CrossRef]
31. Ronca, S.; Ramond, J.-B.; Jones, B.E.; Seely, M.; Cowan, D.A. Namib Desert dune/interdune transects exhibit habitat-specific edaphic bacterial communities. *Front. Microbiol.* **2015**, *6*, 845. [CrossRef]
32. Neilson, J.W.; Quade, J.; Ortiz, M.; Nelson, W.M.; Legatzki, A.; Tian, F.; LaComb, M.; Betancourt, J.L.; Wing, R.A.; Soderlund, C.A.; et al. Life at the hyperarid margin: Novel bacterial diversity in arid soils of the Atacama Desert, Chile. *Extremophiles* **2012**, *16*, 553–566. [CrossRef]
33. Ramos-Madrigal, C.; Martínez-Romero, E.; Tapia-Torres, Y.; Servín-Garcidueñas, L.E. Bacterial Diversity Profiling of Desert Sand from Tierra Caliente, Mexico, Based on 16S rRNA Gene Amplicon Sequencing. *Genome Announc.* **2022**, *11*, e0078222. [CrossRef]
34. Prestel, E.; Salamitou, S.; DuBow, M.S. An examination of the bacteriophages and bacteria of the Namib desert. *J. Microbiol.* **2008**, *46*, 364–372. [CrossRef] [PubMed]
35. An, S.; Couteau, C.; Luo, F.; Neveu, J.; DuBow, M.S. Bacterial Diversity of Surface Sand Samples from the Gobi and Taklamaken Deserts. *Microb. Ecol.* **2013**, *66*, 850–860. [CrossRef]
36. Parihar, J.; Parihar, S.P.; Suravajhala, P.; Bagaria, A. Spatial Metagenomic Analysis in Understanding the Microbial Diversity of Thar Desert. *Biology* **2022**, *11*, 461. [CrossRef]
37. Osman, J.R.; Fernandes, G.R.; Kamilova, E.; DuBow, M.S. Genomic microbiome analyses of surface sand samples from the Kyzyl-Kum Desert (Uzbekistan): Characterization and comparative study. *Arch. Microbiol.* **2023**, *205*, 90. [CrossRef] [PubMed]
38. Steven, B.; Gallegos-Graves, L.V.; Yeager, C.; Belnap, J.; Kuske, C.R. Common and distinguishing features of the bacterial and fungal communities in biological soil crusts and shrub root zone soils. *Soil Biol. Biochem.* **2014**, *69*, 302–312. [CrossRef]
39. Chanal, A.; Chapon, V.; Benzerara, K.; Barakat, M.; Christen, R.; Achouak, W.; Barras, F.; Heulin, T. The desert of Tataouine: An extreme environment that hosts a wide diversity of microorganisms and radiotolerant bacteria. *Environ. Microbiol.* **2006**, *8*, 514–525. [CrossRef] [PubMed]
40. Connon, S.A.; Lester, E.D.; Shafaat, H.S.; Obenhuber, D.C.; Ponce, A. Bacterial diversity in hyperarid Atacama Desert soils. *J. Geophys. Res. Bio Geosci.* **2007**, *112*, 2006JG000311. [CrossRef]
41. Kutovaya, O.V.; Lebedeva, M.P.; Tkhakakhova, A.K.; Ivanova, E.A.; Andronov, E.E. Metagenomic characterization of biodiversity in the extremely arid desert soils of Kazakhstan. *Eurasian Soil Sci.* **2015**, *48*, 493–500. [CrossRef]
42. Duan, X.; Li, J.; He, W.; Huang, J.; Xiong, W.; Chi, S.; Luo, S.; Liu, J.; Zhang, X.; Li, J. Microbial diversity and their extracellular enzyme activities among different soil particle sizes in mossy biocrust under N limitation in the southeastern Tengger Desert, China. *Front. Microbiol.* **2024**, *15*, 1328641. [CrossRef]
43. Shen, J.; Wyness, A.J.; Claire, M.W.; Zerkle, A.L. Spatial Variability of Microbial Communities and Salt Distributions Across a Latitudinal Aridity Gradient in the Atacama Desert. *Microb. Ecol.* **2021**, *82*, 442–458. [CrossRef] [PubMed]
44. Mehda, S.; Muñoz-Martín, M.; Oustani, M.; Hamdi-Aïssa, B.; Perona, E.; Mateo, P. Microenvironmental Conditions Drive the Differential Cyanobacterial Community Composition of Biocrusts from the Sahara Desert. *Microorganisms* **2021**, *9*, 487. [CrossRef] [PubMed]
45. Bahl, J.; Lau, M.C.; Smith, G.J.; Vijaykrishna, D.; Cary, S.C.; Lacap, D.C.; Lee, C.K.; Papke, R.T.; Warren-Rhodes, K.A.; Wong, F.K.; et al. Ancient origins determine global biogeography of hot and cold desert cyanobacteria. *Nat. Commun.* **2011**, *2*, 163. [CrossRef]
46. Xie, Y.-G.; Luo, Z.-H.; Fang, B.-Z.; Jiao, J.-Y.; Xie, Q.-J.; Cao, X.-R.; Qu, Y.-N.; Qi, Y.-L.; Rao, Y.-Z.; Li, Y.-X.; et al. Functional differentiation determines the molecular basis of the symbiotic lifestyle of *Ca*. Nanohaloarchaeota. *Microbiome* **2022**, *10*, 172. [CrossRef]
47. Nan, L.; Guo, Q.; Cao, S. Archaeal community diversity in different types of saline-alkali soil in arid regions of Northwest China. *J. Biosci. Bioeng.* **2020**, *130*, 382–389. [CrossRef] [PubMed]

48. Fuentes, B.; Choque, A.; Gómez, F.; Alarcón, J.; Castro-Nallar, E.; Arenas, F.; Contreras, D.; Mörchen, R.; Amelung, W.; Knief, C.; et al. Influence of Physical-Chemical Soil Parameters on Microbiota Composition and Diversity in a Deep Hyperarid Core of the Atacama Desert. *Front. Microbiol.* **2021**, *12*, 794743. [CrossRef] [PubMed]
49. Martin, A.; McMinn, A. Sea ice, extremophiles and life on extra-terrestrial ocean worlds. *Int. J. Astrobiol.* **2018**, *17*, 1–16. [CrossRef]
50. Rampelotto, P. *Biotechnology of Extremophiles: Advances and Challenges*; Springer: Berlin/Heidelberg, Germany, 2016. [CrossRef]
51. Herlemann, D.P.R.; Labrenz, M.; Jürgens, K.; Bertilsson, S.; Waniek, J.J.; Andersson, A.F. Transitions in bacterial communities along the 2000 km salinity gradient of the Baltic Sea. *ISME J.* **2011**, *5*, 1571–1579. [CrossRef]
52. Anders, S. FastQC: A Quality Control Tool for High Throughput Sequence Data. Babraham Bioinformatics. 2010. Available online: https://www.bioinformatics.babraham.ac.uk/projects/fastqc/ (accessed on 1 August 2024).
53. Bolger, A.; Usadel, B.; Lohse, M. Trimmomatic: A flexible trimmer for Illumina sequence data. *Bioinformatics* **2014**, *30*, 2114–2120. [CrossRef] [PubMed]
54. Caporaso, J.G.; Kuczynski, J.; Stombaugh, J.; Bittinger, K.; Bushman, F.D.; Costello, E.K.; Fierer, N.; Gonzalez Peña, A.; Goodrich, J.K.; Gordon, J.I.; et al. QIIME allows analysis of high-throughput community sequencing data. *Nat. Methods* **2010**, *7*, 335–336. [CrossRef]
55. Bolyen, E.; Rideout, J.R.; Dillon, M.R.; Bokulich, N.A.; Abnet, C.C.; Al-Ghalith, G.A.; Alexander, H.; Alm, E.J.; Arumugam, M.; Asnicar, F.; et al. Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. *Nat. Biotechnol.* **2019**, *37*, 852–857. [CrossRef]
56. Callahan, B.J.; Mcmurdie, P.J.; Rosen, M.J.; Han, A.W.; Johnson, A.J.A.; Holmes, S.P. DADA2: High-resolution sample inference from Illumina amplicon data. *Nat. Methods* **2016**, *13*, 581–583. [CrossRef]
57. Rognes, T.; Flouri, T.; Nichols, B.; Quince, C.; Mahé, F. VSEARCH: A versatile open source tool for metagenomics. *PeerJ* **2016**, *2016*, e2584. [CrossRef]
58. Quast, C.; Pruesse, E.; Yilmaz, P.; Gerken, J.; Schweer, T.; Yarza, P.; Peplies, J.; Glöckner, F.O. The SILVA ribosomal RNA gene database project: Improved data processing and web-based tools. *Nucleic Acids Res.* **2013**, *41*, D590–D596. [CrossRef]
59. Shannon, C.E. The mathematical theory of communication. 1963. *MD Comput. Comput. Med. Pract.* **1997**, *14*, 306–317.
60. Armstrong, G.W.; Cantrell, K.; Huang, S.; McDonald, D.; Haiminen, N.; Carrieri, A.P.; Zhu, Q.; Gonzalez, A.; McGrath, I.; Beck, K.L.; et al. Efficient computation of Faith's phylogenetic diversity with applications in characterizing microbiomes. *Genome Res.* **2021**, *31*, 2131–2137. [CrossRef] [PubMed]
61. Faith, D.P. Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* **1992**, *61*, 1–10. [CrossRef]
62. Kruskal, W.H.; Wallis, W.A. Use of Ranks in One-Criterion Variance Analysis. *J. Am. Stat. Assoc.* **1952**, *47*, 583–621. [CrossRef]
63. Moreno, C.E.; Barragán, F.; Pineda, E.; Pavón, N.P. Reanálisis de la diversidad alfa: Alternativas para interpretar y comparar información sobre comunidades ecológicas. *Rev. Mex. Biodivers.* **2011**, *82*, 1249–1261. [CrossRef]
64. Faith, D.P.; Baker, A.M. Phylogenetic diversity (PD) and biodiversity conservation: Some bioinformatics challenges. *Evol. Bioinforma. Online* **2007**, *2*, 121–128. [CrossRef]
65. Lozupone, C.A.; Hamady, M.; Kelley, S.T.; Knight, R. Quantitative and qualitative beta diversity measures lead to different insights into factors that structure microbial communities. *Appl. Environ. Microbiol.* **2007**, *73*, 1576–1585. [CrossRef]
66. Mandal, S.; Van Treuren, W.; White, R.A.; Eggesbø, M.Å.; Knight, R.T.; Peddada, S.D. Analysis of composition of microbiomes: A novel method for studying microbial composition. *Microb. Ecol. Health Dis.* **2015**, *26*, 27663. [CrossRef]
67. Tindall, B.J.; Ross HN, M.; Grant, W.D. Natronobacterium gen. nov. and *Natronococcus* gen. nov., Two New Genera of Haloalkaliphilic Archaebacteria. *Syst. Appl. Microbiol.* **1984**, *5*, 41–57. [CrossRef]
68. Bull, A.T.; Asenjo, J.A.; Goodfellow, M.; Gómez-Silva, B. The Atacama Desert: Technical Resources and the Growing Importance of Novel Microbial Diversity. *Annu. Rev. Microbiol.* **2016**, *70*, 215–234. [CrossRef]
69. Roh, S.W.; Nam, Y.D.; Nam, S.H.; Choi, S.H.; Park, H.S.; Bae, J.W. Complete Genome Sequence of Halalkalicoccus jeotgali B3T, an Extremely Halophilic Archaeon. *J. Bacteriol.* **2010**, *192*, 4528–4529. [CrossRef] [PubMed]
70. Selmani, Z.; Attard, E.; Lauga, B.; Barakat, M.; Ortet, P.; Tulumello, J.; Achouak, W.; Kaci, Y.; Heulin, T. Culturing the desert microbiota. *Front. Microbiol.* **2023**, *14*, 1098150. [CrossRef] [PubMed]
71. Fierer, N.; Leff, J.W.; Adams, B.J.; Nielsen, U.N.; Bates, S.T.; Lauber, C.L.; Owens, S.; Gilbert, J.A.; Wall, D.H.; Caporaso, J.G. Cross-biome metagenomic analyses of soil microbial communities and their functional attributes. *Proc. Natl. Acad. Sci. USA* **2012**, *109*, 21390–21395. [CrossRef]
72. Ferreira, A.C.; Nobre, M.F.; Moore, E.; Rainey, F.A.; Battista, J.R.; da Costa, M. Characterization and radiation resistance of new isolates of Rubrobacter radiotolerans and Rubrobacter xylanophilus. *Extremophiles* **1999**, *3*, 235–238. [CrossRef]
73. Chater, K.F.; Chandra, G. The evolution of development in Streptomyces analysed by genome comparisons. *FEMS Microbiol. Rev.* **2006**, *30*, 651–672. [CrossRef] [PubMed]
74. Ventura, M.; Canchaya, C.; Tauch, A.; Chandra, G.; Fitzgerald, G.F.; Chater, K.F.; van Sinderen, D. Genomics of Actinobacteria: Tracing the evolutionary history of an ancient phylum. *Microbiol. Mol. Biol. Rev. MMBR* **2007**, *71*, 495–548. [CrossRef]
75. Bräuer, L.; Basiliko; Siljanen, M.P.; Zinder, H. Methanogenic archaea in peatlands. *FEMS Microbiol. Lett.* **2020**, *367*, fnaa172. [CrossRef] [PubMed]
76. Li, F.; Leu, A.; Poff, K.; Carlson, L.T.; Ingalls, A.E.; DeLong, E.F. Planktonic Archaeal Ether Lipid Origins in Surface Waters of the North Pacific Subtropical Gyre. *Front. Microbiol.* **2021**, *12*, 610675. [CrossRef]

77. Martínez-Espinosa, R.M. Halophilic archaea as tools for bioremediation technologies. *Appl. Microbiol. Biotechnol.* **2024**, *108*, 401. [CrossRef]
78. Krzmarzick, M.J.; Taylor, D.K.; Fu, X.; McCutchan, A.L. Diversity and Niche of Archaea in Bioremediation. *Archaea* **2018**, *2018*, 3194108. [CrossRef]
79. Morrison, M.D.; Nicholson, W.L. Comparisons of Transcriptome Profiles from Bacillus subtilis Cells Grown in Space versus High Aspect Ratio Vessel (HARV) Clinostats Reveal a Low Degree of Concordance. *Astrobiology* **2020**, *20*, 1498–1509. [CrossRef] [PubMed]
80. Chiang, A.J.; Malli Mohan, G.B.; Singh, N.K.; Vaishampayan, P.A.; Kalkum, M.; Venkateswaran, K. Alteration of Proteomes in First-Generation Cultures of Bacillus pumilus Spores Exposed to Outer Space. *Msystems* **2019**, *4*, e00195-19. [CrossRef] [PubMed]
81. Cortesão, M.; Fuchs, F.M.; Commichau, F.M.; Eichenberger, P.; Schuerger, A.C.; Nicholson, W.L.; Setlow, P.; Moeller, R. Bacillus subtilis Spore Resistance to Simulated Mars Surface Conditions. *Front. Microbiol.* **2019**, *10*, 333. [CrossRef] [PubMed]
82. Schuerger, A.C.; Mancinelli, R.L.; Kern, R.G.; Rothschild, L.J.; McKay, C.P. Survival of endospores of Bacillus subtilis on spacecraft surfaces under simulated martian environments: Implications for the forward contamination of Mars. *Icarus* **2003**, *165*, 253–276. [CrossRef]
83. Aguilera-Najera, D.; Rodriguez-Cruz, U.E.; Vazquez, B.; Fernandez, C.; Martinez-Perez, E.; Tapia-Lopez, R.; Souza, V. Whole genome sequencing of a Domibacillus strain from the Cuatro Ciénegas basin that tends to act as an altruist. *Microbiol. Resour. Announc.* **2024**, *13*, e0023024. [CrossRef] [PubMed]
84. Eida, A.A.; Bougouffa, S.; Alam, I.; Hirt, H.; Saad, M.M. Complete Genome Sequence of *Paenibacillus* sp. JZ16, a Plant Growth Promoting Root Endophytic Bacterium of the Desert Halophyte Zygophyllum Simplex. *Curr. Microbiol.* **2020**, *77*, 1097–1103. [CrossRef]
85. Nadarajah, K.; Abdul Rahman, N.S.N. The Microbial Connection to Sustainable Agriculture. *Plants* **2023**, *12*, 2307. [CrossRef]
86. Kochhar, N.; Kavya, I.K.; Shrivastava, S.; Ghosh, A.; Rawat, V.S.; Sodhi, K.K.; Kumar, M. Perspectives on the microorganism of extreme environments and their applications. *Curr. Res. Microb. Sci.* **2022**, *3*, 100134. [CrossRef]
87. Jeon, C.O.; Lim, J.-M.; Lee, S.S.; Chung, B.S.; Park, D.-J.; Xu, L.-H.; Jiang, C.-L.; Kim, C.-J. *Paenibacillus harenae* sp. nov., isolated from desert sand in China. *Int. J. Syst. Evol. Microbiol.* **2009**, *59*, 13–17. [CrossRef]
88. Lim, J.M.; Jeon, C.O.; Lee, J.C.; Xu, L.H.; Jiang, C.L.; Kim, C.J. *Paenibacillus gansuensis* sp. nov., isolated from desert soil of Gansu Province in China. *Int. J. Syst. Evol. Microbiol.* **2006**, *56 Pt 9*, 2131–2134. [CrossRef]
89. Dai, X.; Wang, Y.-N.; Wang, B.-J.; Liu, S.-J.; Zhou, Y.-G. *Planomicrobium chinense* sp. nov., isolated from coastal sediment, and transfer of *Planococcus psychrophilus* and *Planococcus alkanoclasticus* to *Planomicrobium* as *Planomicrobium psychrophilum* comb. nov. and *Planomicrobium alkanoclasticum* comb. nov. *Int. J. Syst. Evol. Microbiol.* **2005**, *55*, 699–702. [CrossRef] [PubMed]
90. Ramezani, M.; Nikou, M.M.; Pourmohyadini, M.; Spröer, C.; Schumann, P.; Harirchi, S.; Aryaefar, M.; Fazeli, S.A.S.; Amoozegar, M.A.; Ventosa, A. *Planomicrobium iranicum* sp. nov., a novel slightly halophilic bacterium isolated from a hypersaline wetland. *Int. J. Syst. Evol. Microbiol.* **2019**, *69*, 1433–1437. [CrossRef] [PubMed]
91. Yasir, M.; I Azhar, E.; Khan, I.; Bibi, F.; Baabdullah, R.; A Al-Zahrani, I.; Al-Ghamdi, A.K. Composition of soil microbiome along elevation gradients in southwestern highlands of Saudi Arabia. *BMC Microbiol.* **2015**, *15*, 65. [CrossRef] [PubMed]
92. Zhu, D.; Adebisi, W.A.; Ahmad, F.; Sethupathy, S.; Danso, B.; Sun, J. Recent Development of Extremophilic Bacteria and Their Application in Biorefinery. *Front. Bioeng. Biotechnol.* **2020**, *8*, 483. [CrossRef]
93. Donati, E.R.; Sani, R.K.; Goh, K.M.; Chan, K.-G. Editorial: Recent Advances in Bioremediation/Biodegradation by Extreme Microorganisms. *Front. Microbiol.* **2019**, *10*, 1851. [CrossRef]
94. Thombre, R.S.; Vaishampayan, P.A.; Gomez, F. Chapter 7—Applications of extremophiles in astrobiology. In *Physiological and Biotechnological Aspects of Extremophiles*; Salwan, R., Sharma, V., Eds.; Academic Press: Cambridge, MA, USA, 2020; pp. 89–104. [CrossRef]
95. Pikuta, E.V.; Hoover, R.B.; Tang, J. Microbial extremophiles at the limits of life. *Crit. Rev. Microbiol.* **2007**, *33*, 183–209. [CrossRef]
96. Ali, A.M.; Salem, H.M. Salinity-induced desertification in oasis ecosystems: Challenges and future directions. *Environ. Monit. Assess.* **2024**, *196*, 696. [CrossRef]

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.