



Bacterial Communities on the Surface of the Mineral Sandy Soil from the Desert of Maine (USA)

Yang Wang¹ · Jorge R. Osman^{1,2} · Michael S. DuBow¹

Received: 17 April 2019 / Accepted: 7 March 2020 / Published online: 19 March 2020
© Springer Science+Business Media, LLC, part of Springer Nature 2020

Abstract

The Desert of Maine, not a real desert, is a 160,000 m² tourist attraction of glacial silt which resembles a desert, surrounded by a pine forest in the state of Maine located in the northeastern USA. Though not a true desert, the soil of the Desert of Maine has a sandy texture with poor water-holding abilities, nutrient retention capabilities, and a relatively low pH value (pH 5.09). Samples from this site may be of interest to examine the bacterial diversity present on mineral sandy loam soils with an acidic pH, low concentrations of organic materials though surrounded by a pine forest, and compare it with true desert soil microbial populations. Two surface sand samples from the Desert of Maine were obtained, and pyrosequencing of PCR amplified 16S rRNA genes from total extracted DNA was used to assess bacterial diversity, community structure, and the relative abundance of major bacterial taxa. We found that the soil samples from the Desert of Maine displayed high levels of bacterial diversity, with a predominance of members belonging to the *Proteobacteria* and *Actinobacteria* phyla. Bacteria from the most abundant genus, *Acidiphilium*, represent 12.5% of the total 16S rDNA sequences. In total, 1394 OTUs were observed in the two samples, with 668 OTUs being observed in both samples. By comparing Desert of Maine bacterial populations with studies on similar soil environments, we found that the samples contained less *Acidobacteria* than soils from acid soil forests, and less *Firmicutes* plus more *Proteobacteria* than oligotrophic desert soils. Interestingly, our samples were found to be highly similar in their composition to an oak forest soil in France.

Introduction

Bacteria are integral components of soil, where their community structure and diversity have been found to be linked to many soil environmental characteristics, such as the physical and chemical properties of the soil [1, 2]. Traditional microbial cultivation techniques frequently overlook the majority of microbes present in a sample [3], as most bacteria cannot be cultivated under laboratory conditions. During the last two decades, many studies have used high-throughput PCR amplified 16S rDNA sequencing to overcome this difficulty to identify the members of the prokaryotic

community. The 16S rRNA gene is by far the most widely used genetic marker for phylogenetic and microbial community studies, as it has highly conserved regions that permit effective PCR primer design, and sufficient variable regions to allow for accurate taxonomic and phylogenetic identification of community members. Since this gene has been widely sequenced in microbial diversity surveys, there is a large amount of accumulated 16S rDNA sequence data in databases [4] such as the Greengenes, Silva, and RDP databases. The 16S rRNA gene in bacteria includes a total of 9 hypervariable regions (V1–V9), and the V1–V3 regions have been shown to be effective for bacterial identification [5].

The Desert of Maine is a tract of glacial silt with a surface area of 160,000 m², surrounded by a pine forest, in southern Maine in the northeastern USA. The glacial “desert” was once covered by a farm, and exposed because of severe soil erosion due to crop rotation mismanagement (<https://www.desertofmaine.com>). It is not a true desert, as it receives an abundance of precipitation (76–120 cm/year), with a mean annual air temperature of 6–7 °C (<https://websoilsurvey.sc.egov.usda.gov/App/HomePage.htm>, Natural Resources

Yang Wang and Jorge R. Osman contributed equally to this work.

✉ Michael S. DuBow
michael.dubow@u-psud.fr

¹ Institute for Integrative Biology of the Cell (I2BC), CEA, CNRS, Université Paris-Saclay, Univ Paris-Sud, Bâtiment 409, 91405 Orsay, France

² Present Address: Laboratoire de Géologie de Lyon, Université Claude Bernard Lyon-1, UMR5276, Lyon, France

Conservation Service). Although it is a tourist attraction, there is no imported sand nor designer landscaped dunes. This surface area was formed approximately 11,000 years ago, during the end of the last Ice Age of the Pleistocene Period [6]. The parent material of the soil is sandy glaci-fluvial deposits derived from granite and gneiss. Soil and ground rocks were slowly scraped by glaciers into a sandy substance, forming a layer up to 25 m deep. Then, over many centuries, surface soils formed a cap, concealing the “desert sand,” and allowing a forest to grow, followed by the subsequent development of agriculture.

The soil of the Desert of Maine has a sandy texture with poor water-holding abilities, nutrient conservation capabilities, and an acidic pH value. Mineral sandy loam soils contain less organic materials, with a basic pH [7, 8], while low pH soils generally contain more organic materials, such as the soils of forests and some grasslands [9–11]. Soil of the Desert of Maine presents a novel example to identify the bacterial populations that can be present in a mineral sandy loam soil with a relatively low pH and low concentration of organic materials. We used pyrosequencing of PCR amplified 16S rRNA genes from total DNA to assess bacterial diversity, community structure, and the relative abundance of bacterial taxa within two sites of the surface soil from the Desert of Maine, and compared this bacterial community with those from several other sandy desert environments, as well as from other mineral soils.

Materials and Methods

Sampling

Two surface sand samples from the Desert of Maine (Fig. 1) were obtained on September 2, 2011. The two soil samples were collected by scooping surface sand into 50 ml sterile polyethylene conical centrifuge tubes, in an area cordoned off from tourists and without any measurable rainfall for at least 4 days. The average air temperature during the week of sampling was 22 °C. After collection, the samples were treated as previously described [12]. To perform the analyses of selected physicochemical parameters of the sample site soil, samples from the two sites were pooled and sent for analyses using standard methods to the Laboratoire d'Analyses de Sols (Institut National de la Recherche Agronomique, Arras, France).

Sample Preparation

Total DNA was extracted from each sample using the protocol of An et al. [12]. An aliquot of extracted DNA was adjusted to a final DNA concentration of 15 ng/μl in 1/10 TE buffer (1 mM Tris pH 8; 0.1 mM EDTA) using a NanoVue

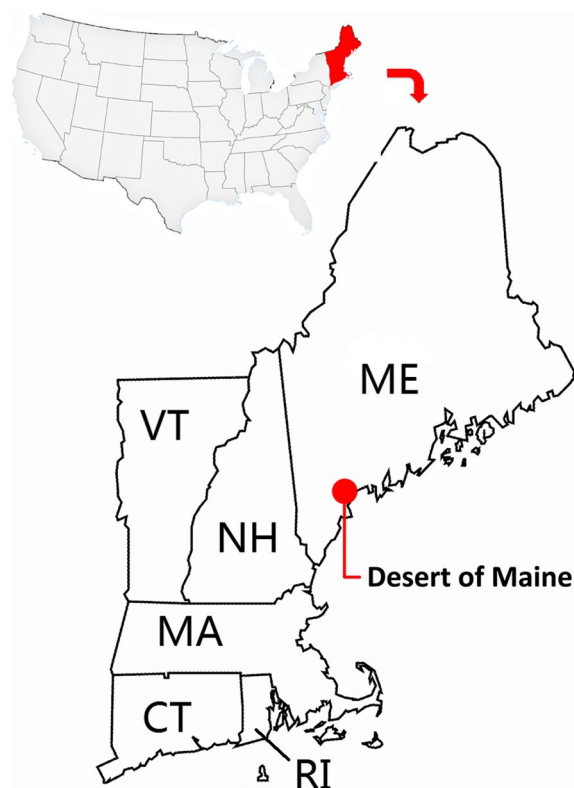


Fig. 1 Location of the Desert of Maine in the northeastern USA

spectrophotometer (GE Healthcare, Little Chalfont, Buckinghamshire, UK), and the concentration verified by ethidium bromide fluorescence after electrophoresis through a 1% agarose gel in TAE buffer (2 mM Tris–acetate pH 8; 5 mM Na-EDTA). PCR reactions were performed in 25 μl reaction volumes. Each reaction contained one of two different thermostable DNA polymerases and their corresponding reaction buffers, 200 μM of each dNTP, 0.5 μM of each primer, and 1 to 10 ng of extracted DNA. The 16S rRNA genes were amplified using universal bacterial primers for pyrosequencing and covering hypervariable regions V1–V3: primer 27F (A adaptor + GAGTTTGATCMTGGCTCAG) and primer 518R (B adaptor + Mid + WTTACCGCGGCTGCTGG), where A and B represent the adaptors using the 454 Roche FLX Titanium pyrosequencing reaction platform. The Mid-sequences are eight nucleotide tags designed for sample identification barcoding according to the 454 protocol. PCR amplification conditions were adapted for the use of two different thermostable DNA polymerases: (A) Phusion High-Fidelity DNA Polymerase (Finnzymes, Finland): 98 °C for 2 min, followed by 28 cycles of 98 °C for 30 s, 54 °C for 20 s and 72 °C for 15 s, and a final elongation step at 72 °C for 5 min; (B) Pfu DNA Polymerase (Fermentas, Canada): 95 °C for 2 min, followed by 30 cycles of 95 °C for 30 s, 48 °C for 30 s and 72 °C for 1 min, and a final elongation step at 72 °C for 5 min. Each DNA sample was

subjected to 3–5 different PCR reactions per DNA polymerase to minimize PCR bias. The PCR products were pooled and subjected to electrophoresis through a 1% agarose gel in TAE buffer. After electrophoresis and visualization of the PCR products by ethidium bromide staining and long-wave UV light illumination, NucleoSpin Extract® kits (Macherey–Nagel, Germany) were used to purify the 16S rDNA PCR products. Then, 40 ng of PCR products from each sample were mixed for pyrosequencing, performed using a 454 Roche FLX Titanium Pyrosequencer (Microsynth AG, Switzerland).

DNA Sequence Data Processing

The raw DNA sequences were first assigned to each sample via their Mid-tag using MOTHUR version 1.33 [13], and reads were removed if at least one of the following criteria was met: (i) length less than 200 nt or longer than 600 nt, (ii) one mismatch to barcode sequences or more than one mismatch to the primer, and (iii) the presence of homopolymers of > 8 bp in length. Adaptor sequences were removed from the sequences using the “Cutadapt” tool [14] implemented in the Galaxy server of the Institut de Génétique et Microbiologie (IGM) of the Université Paris-Sud (<https://galaxy.igmors.u-psud.fr>). Then, the sequences were checked for quality scores by ConDeTri version 2.2 [15], using the criteria that 80% of the nucleotides in a sequence have quality scores > 25. We used UCHIME [16], with reference database Greengenes version 2013_May, and Decipher (through web tools available at <https://decipher.cce.wisc.edu/>) to detect chimera sequences [17]. Sequences detected as chimeras by both programs were removed from the data sets. The raw sequences have been deposited in the GenBank short-read archive (SRA), with accession number SRP056525.

Taxonomy assignments of the remaining 16S rDNA reads were conducted using the Silva NGS website with Silva database release 123 [18, 19]. Sequences classified as Chloroplast, or that could not be classified as belonging to the Bacteria Kingdom, were removed. Diversity analyses were performed using the software package MOTHUR. The relations of the relative abundance of bacterial groups at different taxonomy levels between the two samples were calculated using the Pearson correlation coefficient measure with SPSS Statistics (Version 22). A comparison based on the bacterial relative abundance of the communities from nine different regions was examined using Unweighted Pair Group Method with Arithmetic mean (UPGMA) based on Bray–Curtis distance at 95% similarity. The clean reads were clustered into operational taxonomic units (OTUs) using UPARSE at a cutoff value of 97% sequence identity [20, 21]. The Chao1 and Shannon indices were calculated to estimate taxon richness and diversity [22]. The significance of differences between two bacterial communities was

calculated using Libshuff implemented in MOTHUR [23], with 1500 randomly selected sequences from each sample selected using PANGEA [24].

Results

Chemical and Physical Properties of the Sand Samples

Two areas, separated by 3 m, of the Desert of Maine were sampled on September 2, 2011 (GPS position 43°51'29.46" N, 70° 9'22.97" W). The mean chemical and physical properties of the combined sand samples are shown in Table 1. The mean pH values of the soil at the sampling site was 5.09, indicating an acid soil environment. The levels of total organic carbon and organic material were less than 1 g/kg soil.

Diversity Analyses

The average length of the raw DNA sequences for the two samples was 479 nt (Maine 1) and 480 nt (Maine 2), respectively, while the total number of reads for each sample were 23,405 (Maine 1) and 28,983 (Maine 2), respectively. After bioinformatic cleaning, approximately 95% of the sequences remained (22,320 for Maine 1 and 27,680 for Maine 2). The sequences were further filtered for quality and examined for chimeric sequences, leaving 65% of the total reads (14,776 for Maine 1 and 19,085 for Maine 2). The average length of the sequences after processing was 396 nt for the two samples. The number of reads remaining after each step are presented in Table 2.

The clean sequences were clustered into OTUs at 97% similarity levels, excluding the unclassified sequences at

Table 1 Average chemical and physical properties of the Desert of Maine soil samples

	Mean value
Organic carbon	0.43 g/kg
Total nitrogen	< 0.02 g/kg
Organic material	0.75 g/kg
Aluminum (Al)	4.86 g/100 g
Calcium (Ca)	0.93 g/100 g
Iron (Fe)	1.41 g/100 g
Magnesium (Mg)	0.39 g/100 g
Phosphorous (P ₂ O ₅)	0.08 g/100 g
Potassium (K)	1.97 g/100 g
Sodium (Na)	2.15 g/100 g
Manganese (Mn)	420 mg/kg
pH	5.09

Table 2 Summary of the number of sequences and diversity indices before and after normalization to the same number of reads (14,776)

	Sequence numbers		Diversity Index			Normalized		
	Raw	After cleaning	OTUs ^a	Chao1	Shannon	OTUs ^a	Chao1	Shannon
Maine 1	23405	14776	924	1445	5.57	924	1445	5.57
Maine 2	28983	19085	1139	1693	5.71	1027	1526	5.69

^aOTUs are clustered at 97% sequence identity

the phylum level, and sequences classified as *Chloroplast* were removed. In total, 1394 OTUs were observed in the two samples, and the number of common OTUs observed in both samples was 668. The numbers of core taxons (most abundant OTUs comprising more than 1% of the sequences) were 18 in the Maine 1 sample and 14 in the Maine 2 sample. The core taxons comprised 30% of the bacterial population in the Maine 1 sample and 23% in the Maine 2 sample. We observed no differences between the Shannon diversity indices of the two samples. We also normalized our two samples by subsampling of sequences to the same number of reads (14,776) to perform the analysis based on OTU distribution, and the results after normalization are shown in Table 2.

Classification of DNA Sequences

The sequences from the two samples were classified at 6 taxonomic levels with the Silva NGS database, and comprise at least 22 phyla, 41 classes, 76 orders, 115 families, and 172 genera, plus a number of unclassified sequences at various taxonomic levels. The distribution of sequences at the

phylum level is shown in Fig. 2a. Unclassified sequences at the phylum level represent 2.4% of the sequences in Maine 1 and 3.9% in Maine 2. The community structure at the phylum level shows a similar distribution for the two samples ($R=0.989$) using the Pearson correlation coefficient measure. The significance of the differences between the two bacterial communities was calculated using the Libshuff package in MOTHUR, with a P value <0.01 , indicating that the two bacterial communities do have not the exact same composition. The predominant phyla of the samples represent members of the *Proteobacteria*, *Actinobacteria*, *Chloroflexi*, *Bacteroidetes*, and *Acidobacteria* phyla, at 39.1%, 18.5%, 9.7%, 6.4%, and 5%, respectively, as the average for the two samples, followed by members of the *Cyanobacteria* (4.2%), *Gemmatimonadetes* (3.1%), *Planctomycetes* (2.5%), *Armatimonadetes* (1.9%), and *Deinococcus-Thermus* (0.5%) phyla.

Within the phylum *Proteobacteria*, members of the *Alphaproteobacteria* represent the most abundant group in both samples (68.3% in Maine 1, 63.8% in Maine 2), followed by members of the *Betaproteobacteria* (15.4%, 16.9%), and *Deltaproteobacteria* (14.1%, 15.4%). The bacterial

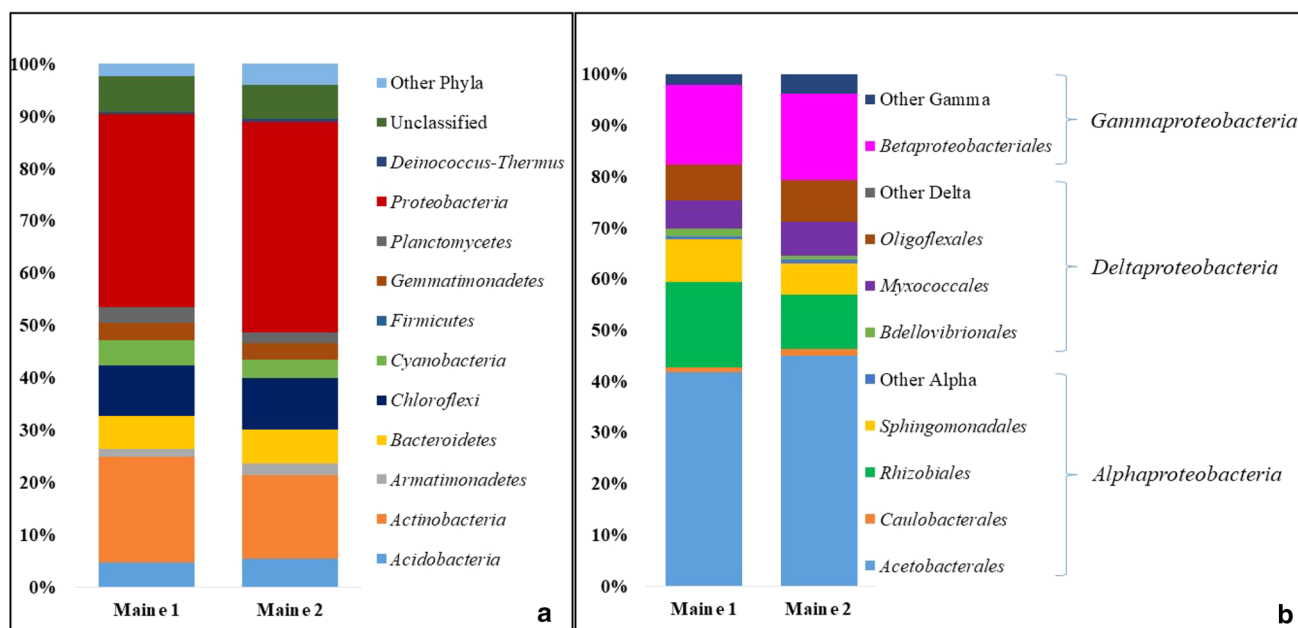


Fig. 2 Relative abundance of bacterial 16S rRNA gene sequences from the two samples at the Phylum (a) and Proteobacteria classes (b) levels. See Materials and Methods for details

community structure at the Class level (Fig. 2b) presents a similar pattern of distribution in the two samples ($R=0.959$) using the Pearson correlation coefficient measure. Examining families, members of the *Sphingobacteriales* family were the predominant members of the *Bacteroidetes* phylum, with an average of 4.8% of the total reads for the two samples. The dominant orders in the two samples were from the *Acetobacterales* (43%), *Rhizobiales* (13%), and *Sphingomonadales* (7.2%) orders.

Among the 172 genera identified in the samples, 69 genera belong to the phylum *Proteobacteria*, 41 genera belong to the phylum *Actinobacteria*, 24 genera belong to the phylum *Bacteroidetes*, and 9 genera belong to the phylum *Acidobacteria*. The most abundant 20 genera in each sample are shown in Table 3. The similarity between the two bacterial communities at the genus level is 0.975 using the Pearson correlation coefficient measure. Each of these abundant genera account for 0.6–11.3% of bacteria identified in the Maine 1 sample and 0.8–13.6% in the Maine 2 sample, with the most abundant genus being *Acidiphilium* (from the phylum *Proteobacteria*) for both samples. Members of the genus *Crinalium* (1.9% average for the two samples) represent a group of phototrophic bacteria belonging to the phylum Cyanobacteria, and species of this genus have been reported to be highly drought-resistant and commonly isolated from coastal sand dunes [25, 26]. Members of the

genus *Arthrobacter* are abundant in both samples (1.4% in average for our two samples), and members of this genus are frequently involved in mineral weathering of soil and can secrete large amounts of oxalic acid [27, 28].

Discussion

In recent years, desert-related environmental effects have been increasing, as global warming and human activities contributing to desertification are increasingly threatening ecosystems around the world (www.unddd.int). Studies concerning microbial colonization and dispersion in deserts have been performed to estimate the function of microbial communities from hot desert sand, which may play an important role in soil stability, nutrient cycles, and environmental health [12, 29–31]. The Desert of Maine was previously productive agriculturally, and was covered by farm land. The underlying mineral soils were exposed because of severe soil erosion due to potato crop rotation mismanagement [6]. In this study, we used pyrosequencing of PCR amplified 16S rRNA genes to assess bacterial diversity and community structure of surface soil from the Desert of Maine. An examination of bacterial populations in samples of surface soil from this unique site can provide an opportunity to investigate bacterial diversity and community structure in a hot desert-like oligotrophic environment, and its relation with those from other soil types, even though it is not a true desert but is, in fact, surrounded by a pine forest.

Previous studies have revealed that many environmental factors, including pH, the concentration of organic material and that of sodium, can have large effects on the presence and distribution of bacterial community members in soil [7, 32, 33]. A large proportion of the variance in soil bacterial diversity and community composition appears to be strongly influenced by pH [34], at local [35] and even continental scales [1]. We thus compared our data on the distribution of the predominant phyla (Fig. 3) with those from studies using 16S rRNA gene pyrosequencing of samples taken from apparently similar soil environments or with similar physicochemical factors. The Desert of Maine is surrounded by a pine forest. Thus, its soil microbiome may be influenced by that of the nearby pine forest environment. Uroz et al. [36] studied the bacterial community of soils from an oak forest of Breuil-Chenue in Morvan (France), and found that members of *Acidobacteria* account for about 36% of the total bacterial population in their sample. Shah et al. [10] examined the sandy, acidic, and relatively nutrient-poor soil of a pine barrens region of Long Island (New York, USA), which is also composed of gravel deposited by the withdrawal of glaciers. This soil had an average pH value of 4.75, total organic carbon of 11.7 g/kg, and 0.13 g/100 g of Al and 0.21 g/100 g of Fe. Samples of surface soil from

Table 3 Relative abundance of the 20 most abundant bacterial genera in the Desert of Maine samples

Genus	Maine1 (%)	Maine2 (%)
<i>Acidiphilium</i>	11.3	13.6
<i>Flavisolibacter</i>	2.4	2.7
<i>Crinalium</i>	2.4	1.3
<i>Methylobacterium</i>	2.2	1.3
<i>Noviherbaspirillum</i> ^a	0.9	2.3
<i>Chthonomonas</i>	1.1	1.6
<i>Amnibacterium</i>	1.6	1.2
<i>Arthrobacter</i>	1.5	1.3
<i>Actinomycetospora</i>	1.3	1.3
<i>Blastocatella</i>	1.1	1.1
<i>Anaeromyxobacter</i>	0.9	1.3
<i>Gemmatimonas</i>	1.0	1.1
<i>Segetibacter</i> ^a	0.7	1.4
<i>Acidobacterium</i>	1.0	1.0
<i>Singulisphaera</i>	0.9	0.7
<i>Lapillicoccus</i>	1.0	0.6
<i>Candidatus_Solibacter</i>	0.6	0.9
<i>Chamaesiphon</i> ^a	1.9	0.5
<i>Spirosoma</i>	0.8	0.7
<i>Hymenobacter</i>	0.6	0.8

^aRepresent genera with >2-fold differences between the two samples

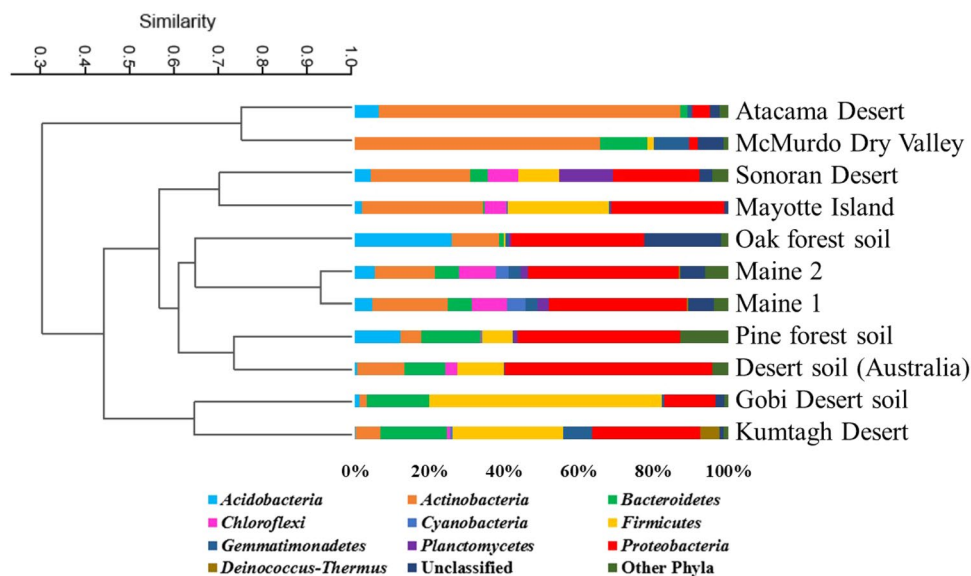


Fig. 3 Comparison of the Desert of Maine bacterial communities with those from other selected soil samples at the Phylum level. UPGMA tree calculated using the Bray–Curtis similarity at 95% based on the relative abundance of bacterial phyla in soil samples from the 2 Desert of Maine samples; An oak forest soil in France [36]; A pine forest soil in the USA [10]; A Gobi desert sand sam-

ple from Mongolia [12]; A sand sample from the Kumtagh Desert in China (data not published); A sand sample from the Australian Desert [37]; A sand sample from the Sonoran Desert [38]; A sand sample from the Atacama Desert in Chile [8]; A sample from the McMurdo Dry Valleys in the Antarctic [39] and a mineralized sandy soil sample from Mayotte [31]

other hot, or cold, deserts were compared with our results including (1) a sand sample (Gobi 1) from the Gobi Desert of Northwestern China [12], which also has a low concentration of organic carbon and organic materials (< 1 g/kg); and (2) a sand sample from the Kumtagh Desert in China, collected in September 2011 (data not published). The samples were treated in the same manner as these from the Desert of Maine; (3) a sand sample from the Australian Deserts [37]; (4) a sample from the Sonoran Desert [38]; (5) a sample (Altamira) from the Atacama Desert in Chile [8]; (6) a sample (Upper Wright Valley) from McMurdo Dry Valleys [39] in the area of the Antarctic continent (a cold desert) and a sample (mineralized sandy soils) from Mayotte, France [31]. All of these studies were performed using pyrosequencing of 16S rDNA amplicons. We used the Pearson correlation coefficient measure to estimate the similarity of the distribution of the predominant phyla among the different sites and a UPGMA tree based on the Bray–Curtis similarity index. The results show that the distribution of the predominant phyla in both samples from Maine are closer to samples from the two forest soils (R values > 0.7), than to samples from either hot or cold desert soils (R values < 0.5). For the Phylum *Proteobacteria*, there is no significant difference between samples from the Desert of Maine and these from the other two forest samples. Moreover, the relative abundance of this phylum in our samples is greater than from the other desert samples ($P < 0.05$). In contrast, the Gobi Desert, Kumtagh, and Mayotte samples contained a much higher proportion of

members of the *Firmicutes* than the others. Samples from the Atacama Desert and the McMurdo Dry Valleys contained a larger population of *Actinobacteria* members when compared with other groups ($P < 0.05$). There is no significant difference in the percentage of *Bacteroidetes* members among the different samples examined here. These results confirm those of earlier studies [7, 8, 40] that suggest that oligotrophic environments with a large mineral component and low levels of organic materials have a relatively large proportion of Gram-positive bacteria, such as those from the *Firmicutes* and *Actinobacteria* phyla. Previous studies [1] indicate that high pH soils typically have a higher relative abundance of members of the *Actinobacteria* and *Bacteroidetes* phyla, with a lower abundance of *Acidobacteria*, when compared with populations from more acidic soils. We did not find significant differences in the percentage of *Acidobacteria* among the different soils we examined, suggesting that other factors may affect the bacterial community structure of these types of soils.

Lauber et al. [1] examined bacterial communities in 88 soils from across North and South America using high-throughput sequencing of PCR amplified 16S rRNA genes, and their results showed that, in soils with pH values of 5–6, the dominant phyla belonged to members of the *Acidobacteria*, *Alphaproteobacteria*, *Actinobacteria*, *Bacteroidetes*, and *Beta/Gammaproteobacteria* [41]. In our samples, which had a similar pH range, we observed a lower proportion of *Acidobacteria* (5.1% vs. 29.7%), and a higher proportion

of *Actinobacteria* (18.5% vs. 8.8%). Our data also reveal a high level (10.3%) of *Chloroflexi* phylum members, which is not commonly found in studies of deserts [42]. A study of the Atacama Desert showed that the non-cyanobacteria phototrophic bacteria *Chloroflexi* was dominant in the hyper-arid core of the desert [43]. Previous studies have shown that members of the *Chloroflexi* may play an important role in soils as soil photoautotrophs that contribute to CO₂ uptake in the surface soil [44, 45]. Members of the family *Acetobacteraceae* were abundant in both samples, comprising 16.8% of total sequences, on average. Members of this family have been described as nitrogen fixing bacteria able to act in plant growth promotion by a variety of mechanisms [46]. Koberl et al. [47] reported a greater proportion of N-fixing bacterial groups in desert soils than in farm soils, and suggest that this could be explained by the fact that plant growth promoting bacteria play an important role as a nitrogen donor in soils without compost treatment.

The most abundant identifiable genera shown in Table 3 demonstrate that the dominant genus in our two samples belongs to members from the genus *Acidiphilium*, accounting for 11.3% of the bacteria in the Maine 1 sample and 13.6% for the Maine 2 sample. *Acidiphilium* is a genus in the phylum *Proteobacteria*, and many species from this genus are acidophilic bacteria isolated from acidic mineral environments [48, 49], which is consistent with the physical characteristics of our sample site. *Acidiphilium* spp. are also involved in the iron cycle, with the function of reducing ferric iron by oxidizing organic matter at low pH [50]. In mineral soils, Fe-oxidizing bacteria are well represented [51, 52]. Lithotrophs, such as members of *Microcoleus* in the phylum *Cyanobacteria*, are typically the dominant microorganisms in the microbial community in hot desert soils (oligotrophic), as well as sulfate-reducing bacteria such as *Desulfobacterales*, but these two groups of bacteria do not appear to be abundant in the Desert of Maine soil [53]. Members of the *Alphaproteobacteria*, *Acidobacteria*, and *Actinobacteria* are ubiquitous in mineral environments, which is consistent with the distribution of bacteria in our samples. We found that the samples contain relatively low levels of mineral weathering bacteria such as members of the *Burkholderia*, *Agrobacterium*, and *Bacillus* genera, and only one abundant genus, *Arthrobacter*, was found to be correlated with mineral weathering [27, 28, 54].

We also observed that 5% of the total OTUs in the dataset contained > 50% of the total sequences, while approximately 80% of the total OTUs were highly diverse and comprised < 20% of the total sequences. The results of taxonomic assignments of the sequences showed that > 30% of the sequences were not able to be classified at the genus level. This situation is frequent in studies of soil bacterial communities using high-throughput DNA sequencing techniques [55–57].

In this study, we used Pyrosequencing of PCR amplified bacterial 16S rRNA genes to reveal a high degree of bacterial diversity and community structure in two soil samples from the Desert of Maine. This small sand-like environment presents unique bacterial community patterns when compared with sand from hot deserts, and also presents differences on the abundance of certain predominant microorganisms within mineral soils, thus aiding in the understand of soil mineralization and, hopefully, helping in land recovery to reverse extreme soil erosion.

Acknowledgements We thank Ginger and Gary Currens from the Desert of Maine for their help in obtaining the sand samples, the Reviewers for their insightful comments and questions, and all the members of the Laboratoire de Génomique et Biodiversité Microbienne des Biofilms (LGBMB) of the Institute for Integrative Biology of the Cell (I2BC) for interesting discussions, comments, and suggestions. YW was a doctoral scholarship recipient from the China Scholarship Council (CSC). JO was a doctoral scholarship recipient from CONICYT Becas Chile. This work was supported by the Centre National de la Recherche Scientifique (CNRS), France.

Compliance with ethical standards

Conflict of interest: The authors declare that they have no conflict of interest.

References

1. Lauber CL, Hamady M, Knight R, Fierer N (2009) Pyrosequencing-based assessment of soil pH as a predictor of soil bacterial community structure at the continental scale. *Appl Environ Microbiol* 75:5111–5120
2. Fierer N, Lauber CL, Ramirez KS, Zaneveld J, Bradford MA, Knight R (2012) Comparative metagenomic, phylogenetic and physiological analyses of soil microbial communities across nitrogen gradients. *ISME J* 6:1007–1017
3. Amann RI, Ludwig W, Schleifer KH (1995) Phylogenetic identification and in situ detection of individual microbial cells without cultivation. *Microbiol Rev* 59:143–169
4. Petrosino JF, Highlander S, Luna RA, Gibbs RA, Versalovic J (2009) Metagenomic pyrosequencing and microbial identification. *Clin Chem* 55:856–866
5. Schloss PD (2010) The effects of alignment quality, distance calculation method, sequence filtering, and region on the analysis of 16S rRNA gene-based studies. *PLoS Comput Biol* 6:e1000844
6. Bahr J (2009) *Amazing and unusual America*. Publications International, Chicago, p 9
7. Griffiths RI, Thomson BC, James P, Bell T, Bailey M, Whiteley AS (2011) The bacterial biogeography of British soils. *Environ Microbiol* 13:1642–1654
8. Crits-Christoph A, Robinson CK, Barnum T, Fricke WF, Davila AF, Jedynek B, McKay CP, Diruggiero J (2013) Colonization patterns of soil microbial communities in the Atacama Desert. *Microbiome* 1:28
9. Nacke H, Thurmer A, Wollherr A, Will C, Hodac L, Herold N, Schoning I, Schrupf M et al (2011) Pyrosequencing-based assessment of bacterial community structure along different management types in German forest and grassland soils. *PLoS ONE* 6:e17000

10. Shah V, Shah S, Kambhampati MS, Ambrose J, Smith N, Dowd SE, McDonnell KT, Panigrahi B et al (2011) Bacterial and archaea community present in the Pine Barrens Forest of Long Island, NY: unusually high percentage of ammonia oxidizing bacteria. *PLoS ONE* 6:e26263
11. Russo SE, Legge R, Weber KA, Brodie EL, Goldfarb KC, Benson AK, Tan S (2012) Bacterial community structure of contrasting soils underlying Bornean rain forests: inferences from microarray and next-generation sequencing methods. *Soil Biol Biochem* 55:48–59
12. An S, Couteau C, Luo F, Neveu J, DuBow MS (2013) Bacterial diversity of surface sand samples from the Gobi and Taklamakan deserts. *Microb Ecol* 66:850–860
13. Schloss PD, Westcott SL, Ryabin T, Hall JR, Hartmann M, Hollister EB, Lesniewski RA, Oakley BB et al (2009) Introducing mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities. *Appl Environ Microbiol* 75:7537–7541
14. Martin M (2011) Cutadapt removes adapter sequences from high-throughput sequencing reads. *EMBnet. J* 17:10–12
15. Smeds L, Kunstner A (2011) ConDeTri—a content dependent read trimmer for Illumina data. *PLoS ONE* 6:e26314
16. Edgar RC, Haas BJ, Clemente JC, Quince C, Knight R (2011) UCHIME improves sensitivity and speed of chimera detection. *Bioinformatics* 27:2194–2200
17. Wright ES, Yilmaz LS, Noguera DR (2012) DECIPHER, a search-based approach to chimera identification for 16S rRNA sequences. *Appl Environ Microbiol* 78:717–725
18. Quast C, Pruesse E, Yilmaz P, Gerken J, Schweer T, Yarza P et al (2013) The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. *Nucleic Acids Res* 41:D590–D596
19. Yilmaz P, Parfrey LW, Yarza P, Gerken J, Pruesse E, Quast C, Schweer T, Peplies J et al (2014) The SILVA and "All-species Living Tree Project (LTP)" taxonomic frameworks. *Nucleic Acids Res* 42:D643–648
20. Edgar RC (2010) Search and clustering orders of magnitude faster than BLAST. *Bioinformatics* 26:2460–2461
21. Edgar RC (2013) UPARSE: highly accurate OTU sequences from microbial amplicon reads. *Nat Methods* 10:996–998
22. Schloss PD, Handelsman J (2008) A statistical toolbox for metagenomics: assessing functional diversity in microbial communities. *BMC Bioinformatics* 9:34
23. Schloss PD, Larget BR, Handelsman J (2004) Integration of microbial ecology and statistics: a test to compare gene libraries. *Appl Environ Microbiol* 70:5485–5492
24. Giongo A, Crabb DB, Davis-Richardson AG, Chauliac D, Moberley JM, Gano KA, Mukherjee N, Casella G et al (2010) PANGEA: pipeline for analysis of next generation amplicons. *ISME J* 4:852–861
25. de Winder B, Matthijs HCP, Mur LR (1990) The effect of dehydration and ion stress on carbon dioxide fixation in drought-tolerant phototrophic micro-organisms. *FEMS Microbiol Lett* 74:33–38
26. de Winder B, Mur LR (1994) The sensitivity for salinity increase in the drought resistant cyanobacterium *Crinallium epipsammum* SAB 22.89. In: Stal L, Caumette P (eds) *Microbial Mats*, NATO ASI Series. Springer, Berlin, pp 117–123
27. Uroz S, Calvaruso C, Turpault MP, Frey-Klett P (2009) Mineral weathering by bacteria: ecology, actors and mechanisms. *Trends Microbiol* 17:378–387
28. Frey B, Rieder SR, Brunner I, Plotze M, Koetzsch S, Lapanje A, Brandl H, Furrer G (2010) Weathering-associated bacteria from the Damma glacier forefield: physiological capabilities and impact on granite dissolution. *Appl Environ Microbiol* 76:4788–4796
29. An S, Sin HH, DuBow MS (2015) Modification of atmospheric sand-associated bacterial communities during Asian sandstorms in China and South Korea. *Heredity* 114:460–467
30. Makhalanyane TP, Valverde A, Gunnigle E, Frossard A, Ramond J, Cowan DA (2015) Microbial ecology of hot desert edaphic systems. *FEMS Microbiol Rev* 39:203–221
31. Osman JR, Fernandes G, Regeard C, Jaubert C, DuBow MS (2018) Examination of the bacterial biodiversity of coastal eroded surface soils from the Dapani (Mayotte Island). *Geomicrobiol J* 35:655–665
32. Rousk J, Baath E, Brookes PC, Lauber CL, Lozupone C, Caporaso JG, Knight R, Fierer N (2010) Soil bacterial and fungal communities across a pH gradient in an arable soil. *ISME J* 4:1340–1351
33. Centeno CM, Legendre P, Beltran Y, Alcantara-Hernandez RJ, Lidstrom UE, Ashby MN, Falcon LI (2012) Microbialite genetic diversity and composition relate to environmental variables. *FEMS Microbiol Ecol* 82:724–735
34. Fierer N, Leff JW, Adams BJ, Nielsen UN, Bates ST, Lauber CL, Owens S, Gilbert JA et al (2012) Cross-biome metagenomic analyses of soil microbial communities and their functional attributes. *Proc Natl Acad Sci USA* 109:21390–21395
35. Osborne CA, Zwart AB, Broadhurst LM, Young AG, Richardson AE (2011) The influence of sampling strategies and spatial variation on the detected soil bacterial communities under three different land-use types. *FEMS Microbiol Ecol* 78:70–79
36. Uroz S, Buee M, Murat C, Frey-Klett P, Martin F (2010) Pyrosequencing reveals a contrasted bacterial diversity between oak rhizosphere and surrounding soil. *Environ Microbiol Rep* 2:281–288
37. Winsley T, van Dorst JM, Brown MV, Ferrari BC (2012) Capturing greater 16S rRNA gene sequence diversity within the domain bacteria. *Appl Environ Microbiol* 78:5938–5941
38. Andrew DR, Fitak RR, Munguia-Vega A, Racolta A, Martinson VG, Dontsova K (2012) Abiotic factors shape microbial diversity in Sonoran Desert soils. *Appl Environ Microbiol* 78:7527–7537
39. Lee CK, Barbier BA, Bottos EM, McDonald IR, Cary SC (2012) The Inter-Valley Soil Comparative Survey: the ecology of Dry Valley edaphic microbial communities. *ISME J* 6:1046–1057
40. Tiao G, Lee CK, McDonald IR, Cowan DA, Cary SC (2012) Rapid microbial response to the presence of an ancient relic in the Antarctic Dry Valleys. *Nat Commun* 3:660
41. Jones RT, Robeson MS, Lauber CL, Hamady M, Knight R, Fierer N (2009) A comprehensive survey of soil acidobacterial diversity using pyrosequencing and clone library analyses. *ISME J* 3:442–453
42. Osman JR, DuBow MS (2018) Bacterial communities on the surface of oligotrophic (nutrient-poor) soils. *Curr Top Biotechnol* 9:31–44
43. Lacap DC, Warren-Rhodes KA, McKay CP, Pointing SB (2011) Cyanobacteria and chloroflexi-dominated hypolithic colonization of quartz at the hyper-arid core of the Atacama Desert, Chile. *Extremophiles* 15:31–38
44. Ley RE, Harris JK, Wilcox J, Spear JR, Miller SR, Bebout BM, Maresca JA, Bryant DA et al (2006) Unexpected diversity and complexity of the Guerrero Negro hypersaline microbial mat. *Appl Environ Microbiol* 72:3685–3695
45. Freeman KR, Pescador MY, Reed SC, Costello EK, Robeson MS, Schmidt SK (2009) Soil CO₂ flux and photoautotrophic community composition in high-elevation, 'barren' soil. *Environ Microbiol* 11:674–686
46. Reis VM, Teixeira KRS (2015) Nitrogen fixing bacteria in the family Acetobacteraceae and their role in agriculture. *J Basic Microbiol* 55:931–949
47. Koberl M, Muller H, Ramadan EM, Berg G (2011) Desert farming benefits from microbial potential in arid soils and promotes diversity and plant health. *PLoS ONE* 6:e24452

48. Harrison PJ (1981) *Acidiphilium cryptum* gen. nov., sp. nov., heterotrophic bacterium from acidic mineral environments. *Int J Syst Bacteriol* 31:327–332
49. Wichlacz PL, Unz RF, Langworthy TA (1986) *Acidiphilium angustum* sp. nov., *Acidiphilium facilis* sp. nov., and *Acidiphilium rubrum* sp. nov.: Acidophilic heterotrophic bacteria isolated from acidic coal mine drainage. *Int J Syst Evol Microbiol* 36:197–201
50. Sanchez-Andrea I, Rodriguez N, Amils R, Sanz JL (2011) Microbial diversity in anaerobic sediments at Rio Tinto, a naturally acidic environment with a high heavy metal content. *Appl Environ Microbiol* 77:6085–6093
51. Kan J, Chellamuthu P, Obraztsova A, Moore JE, Nealon KH (2011) Diverse bacterial groups are associated with corrosive lesions at a Granite Mountain Record Vault (GMRV). *J Appl Microbiol* 111:329–337
52. Wu Y, Tan L, Liu W, Wang B, Wang J, Cai Y, Lin X (2015) Profiling bacterial diversity in a limestone cave of the western Loess Plateau of China. *Front Microbiol* 6:244
53. Pointing SB, Belnap J (2012) Microbial colonization and controls in dryland systems. *Nat Rev Microbiol* 10:551–562
54. Lepleux C, Turpault MP, Oger P, Frey-Klett P, Uroz S (2012) Correlation of the abundance of betaproteobacteria on mineral surfaces with mineral weathering in forest soils. *Appl Environ Microbiol* 78:7114–7119
55. Schutte UM, Abdo Z, Foster J, Ravel J, Bunge J, Solheim B, Forney LJ (2010) Bacterial diversity in a glacier foreland of the high Arctic. *Mol Ecol* 19(Suppl 1):54–66
56. de Gannes V, Eudoxie G, Hickey WJ (2013) Prokaryotic successions and diversity in composts as revealed by 454-pyrosequencing. *Bioresour Technol* 133:573–580
57. Hartmann M, Frey B, Mayer J, Mader P, Widmer F (2015) Distinct soil microbial diversity under long-term organic and conventional farming. *ISME J* 9:1177–1194

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.