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Fertility islands, keys to the establishment of plant and microbial diversity in a highly alkaline hot desert

Kenji Maurice [a,1], Liam Laurent-Webb [b,1], Adeline Dehail [a], Amélia Bourceret [b], Stéphane Boivin [a], Hassan Boukcim [c], Marc-André Selosse [b,d,e], Marc Ducousso [a,*]

[a] CIRAD, UMR082 LSTM, Montpellier Cedex 5, 34398, France
[b] Institut Systématique Evolution Biodiversité (ISYEB), Muséum National d'Histoire Naturelle, CNRS, Sorbonne Université, EPHE, 57 Rue Cuvier, CP39, 75005 Paris, France
[c] Department of Research and Development, VALORHIZ, 1900, Boulevard de la Lironde, PSIII, Parc Scientifique Agropolis, F34980 Montferrier sur Lez, France
[e] Institut Universitaire de France, France
[d] University of Gdańsk, Faculty of Biology, ul. Wita Stwosza 59, 80-308, Gdańsk, Poland

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ABSTRACT

The distribution of plant communities in hot desert ecosystems is discontinuous and resembles the pattern of heterogeneous resource patches, known as "fertility islands". Understanding the key factors that allow plants to establish in these conditions, as well as their associated microbial diversity, is crucial to the comprehension and preservation of these ecosystems. Saudi Arabia in the Arabian Peninsula, is one of the driest regions in the world, with a very low water regime and low soil nutrient contents. The establishment of ecosystems in these arid desert conditions is therefore subject to numerous constraints. Understanding the biotic and abiotic factors linked to the formation of fertility islands, from the perspective of soil composition and its associated microbiome, both in the soil and in the roots of associated plant community, is therefore a fundamental issue for the preservation of these ecosystems. In this study, we analyzed the soil composition between a fertility island and bare soil. The proportions of micro- and macro-elements important for plant nutrition, namely magnesium, phosphorus, potassium and iron were higher in the fertility island. We also observed that soil bacterial and fungal diversity increased in the fertility island. Key taxa such as *Rhizobia* and *Glomeraceae* which play important roles in ecosystem functioning were identified in both the fertility island soil and in the roots of the established plant community. These results confirm that plant establishment is linked to soil conditions, in line with the fertility island hypothesis, and that the microbial community in the fertility island differs both in diversity and in composition from that of the bare soil. Fertility islands soils and the roots of established plant community harbor a microbiome potentially crucial to ecosystem functioning, and are of major interest for conservation and agronomy programs.

1. Introduction

Arid deserts and semi-arid deserts account for more than a third of the world's land surface, with 15% classified as arid and 4% as hyper-arid (Meigs, 1953). These ecosystems host 20% of global plant diversity, play a significant role in carbon storage (Prăvălie, 2016) as well as in net primary production (Millennium Ecosystem Assessment, 2005). In these nutrient-depleted ecosystems, microbial and plant distribution is highly heterogeneous, mirroring the pattern of 'resource islands' or 'fertility islands' (Schlesinger et al., 1995). Plants promote microbial community heterogeneity by improving fertility under their cover (Herman et al., 1995) as they buffer changes in soil temperature and evaporation (Kidron, 2009). By foraging for water deep in the soil, their roots influence the global water cycle and promote inputs of organic matter and nitrogen through litter decomposition and rhizodeposition. The composition of plant communities and their functional traits, such as specific leaf area (SLA) and height, have both direct and indirect effects on the formation of these 'fertility islands', in which microorganisms also play a facilitating role (Ochoa-Hueso et al., 2018). As a result, microbial communities differ in diversity and abundance across these heterogeneous, discontinuous resource patches (Herman et al., 1995; Ochoa-Hueso et al., 2018). A study in the Negev desert found that in

* Corresponding author.
E-mail address: marc.ducousso@cirad.fr (M. Ducousso).
[1] These two authors contributed equally to this work.

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relatively alkaline soil (pH ≈ 8), bacterial biomass, as revealed by bacterial phospholipid fatty acids, was higher in the soil under shrubs (Bachar et al., 2012). Another study in the Negev desert also reported higher bacterial richness and diversity under shrubs (Berg et al., 2015), whereas another in the Mu us desert in China found no difference in bacterial diversity and richness in soil patches under and between shrubs, despite a difference in composition (Sun et al., 2017). Arid conditions stimulate the selection of bacteria that improve plant resistance to abiotic stresses (e.g., drought, water limitation, solar radiation). For example, Marasco et al. (2012) isolated plant growth promoting rhizobacteria (PGPR) strains in the roots of pepper plants in Egypt that were able to enhance photosynthetic activity and biomass synthesis under drought stress. In 2014, Timmusk et al. inoculated wheat with rhizospheric PGPR from harsh environments, and reported five times higher survival rates and 78% more biomass in inoculated plants under drought stress (Timmusk et al., 2014). The aforementioned phenomenon is particularly true for fertility islands, where microorganisms are key to relieving plant abiotic stress. As these microorganisms have coevolved with their host plant in a harsh environment, they are expected to harbor traits that improve plant fitness under local environmental stress (Marasco et al., 2012). Fungal communities, particularly mycorrhizae, can also enhance water uptake, stabilize soil, and provide a wide hyphal network that guarantees water and nutrients are available to all the plants in a specific community (Allen, 2007). Overall, microorganisms in fertility islands directly and indirectly affect the ability of plant communities to recycle nutrients through litter decomposition, rhizodeposition and mineralization of organic matter. Selecting microbial communities that are capable of establishing and interacting positively with plant communities is thus crucial for ecosystem functioning (Alsharif et al., 2020), particularly in arid environments. The extent to which fertility islands affect microbial communities in different ecosystems has been little studied to date.

The Arabian Peninsula is characterized by extreme hot arid desert conditions, including marked temperature fluctuations, scarce rainfall with an annual precipitation range from 25 to 230 mm, and high solar radiation. The arid soils in this region have low organic matter and nitrogen content (Yasir et al., 2015) and higher evapotranspiration than precipitation leads to soil salinization (Shahid et al., 2018). These abiotic stresses are obstacles to the establishment of vegetation and the net primary productivity of the ecosystem. In these conditions, microorganisms play a key role in ecosystem functioning as they are the first soil colonizers (Borin et al., 2010) and control both nutrient cycling and organic matter decomposition (Delgado-Baquerizo et al., 2016). Identifying microbial communities in the context of land aridification and climate change is a major issue as increasing aridity is already reducing both the diversity and abundance of soil microbial communities in drylands (Maestre, et al., 2015). While the number of studies on microbial communities of fertility islands is increasing in hot arid ecosystems (Ewing et al., 2007; Goberna et al., 2007; Li et al., 2021), the identification of the microbial diversity in highly alkaline arid ecosystems is still lacking (Tedersoo et al., 2014).

Despite the harsh conditions, some plant communities are able to establish and form fertility islands, providing favorable microenvironments for microorganisms. The aim of the present study was to identify bacterial and fungal diversity in a 'fertility island' related to a topological micro-environment in a highly alkaline arid natural desert ecosystem, and to test microbial community assembly across bare soil, fertility island soil and roots. We hypothesize that in this highly constrained ecosystem, both microbial diversity and identity are impacted by the soil conditions found in 'fertility islands' and that the response of fungal and bacterial diversity and richness will differ in magnitude between bare soil, fertility island soil and roots. We also hypothesize that the harsh environmental conditions that prevail in this ecosystem result in the selection of potentially highly functional microorganisms for overall ecosystem functioning.

2. Material and methods

2.1. Sampling site

The study site is AlUla, an oasis in north-west Saudi Arabia, 300 km from Medina (GPS coordinates: 26.6922637 N; 37.8687903 E). We studied a plant community in a temporary water flow zone, where water flows only during heavy rainfall events, on average two to four times a year. This flow zone is located at the base of a sandstone rock formation. We compared it to the bare soil outside the flow zone, 10 m from the rock formation, which contained no visible vegetation at the time of sampling (Fig. 1). We sampled soil from: 1) Soil beneath shrubs, where a plant community is established, hereafter termed 'fertility island soil' (FIS), and 2) a sandy zone with no visible vegetation at the time of sampling termed 'bare soil' (BS). A total of 32 samples were taken, nine of which were soil samples, six from the unvegetated dune area (BS) and three from the vegetated fertility island soil (FIS). All soil samples were taken at 30 cm depth and samples for X-ray fluorescence analysis (XRF) consisted of a pool of 4 × 25g samples for each point. Twenty-six root samples that were representative of the plant community were collected from the FIS zone. The plant community mainly comprised *Stipagrostis plumose* Munro ex T. Anderson, *Pergularia tomentosa* L., *Helianthemum lippii* (L.) Dum. Cours. and *Vachellia tortilis* (Forssk.) Galasso & Banfi. All soil samples were sieved to 2 mm and the root samples were stored in a 2% cetrimonium bromide solution. All samples were stored at 4 °C until laboratory analysis.

2.2. Soil chemical composition and pH

The relative abundance of the chemical elements (ranging from magnesium to uranium) in the soil was measured by XRF. Triplicates of each soil sample were pressed at 20 tons for 2 min with 1:3 v:v of Spectroblend (SCP Science). Each pellet was then analyzed in triplicate using an XRF S1 Titan (Bruker). The nine measurements were then averaged and calibrated according to the limit of optical detection (LOD) of each element analyzed (provided by Bruker). The pH was measured using a Knick 766 pH-meter in 1:5 v:v of H_2O and KCl (1 mol.L^{-1}). The difference between the two measurements is an indication of the cation or anion exchange capacity, depending on whether the difference is positive or negative.

2.3. Molecular methods and Illumina MiSeq sequencing

Soil DNA was extracted with the FastDNA Spin kit for soil (MP Biomedicals, Solon, USA), and blank extractions were added as negative controls. The DNA concentrations were assayed by fluorescence with the Picogreen fluorophore (Quant-iT™ PicoGreen™ dsDNA Assay Kits, ThermoFisher scientific, USA). This assay was used to normalize the DNA concentrations to 0.3 ng μL^{-1} before PCR amplification. The primers 479F (5′ CAGCMGCYGCNGTAANAC 3′) and R888 (5′ CCGYCAATTCMTTTRAGT 3′) were used to amplify the V3–V4 hypervariable region of the 16S rRNA gene (Terrat et al., 2015). Primers ITS86F (5′ GTGAATCATCGAATCTTTGAA 3′) and ITS4 (5′ TCCTCCGCTTATTGATATGC 3′) were used to amplify the fungal ITS2 region (Op De Beeck et al., 2014). AMADf (5′ GGGAGGTAGTGACAATAAATAAC 3′) and AMADGr (5′ CCCAACTATCCCTATTAATCAT 3′) were used to amplify the 18S rRNA gene, which is the most suitable for a cross-compartment, survey focused on arbuscular mycorrhizal fungi e.g., soil vs root (Berruti et al., 2017). Reactions were performed in a volume of 20 μL consisting of 10 μL of Buffer Master mix containing Thermo Scientific Phusion™ High-Fidelity DNA Polymerase (ThermoFisher scientific™, USA), 0.5 μL of DMSO, 4.5 μL of DNAse-free water, 3 μL of DNA (0.3 ng μL^{-1}), 1 μL of forward primer and 1 μL of reverse primer, tagged with a short nucleotide sequence. Amplifications were performed with the following conditions: initial denaturation for 10 min, 35 denaturation cycles at 94 °C for 10 s, annealing at 55 °C for 20 s, extension at 72 °C for 20 s and

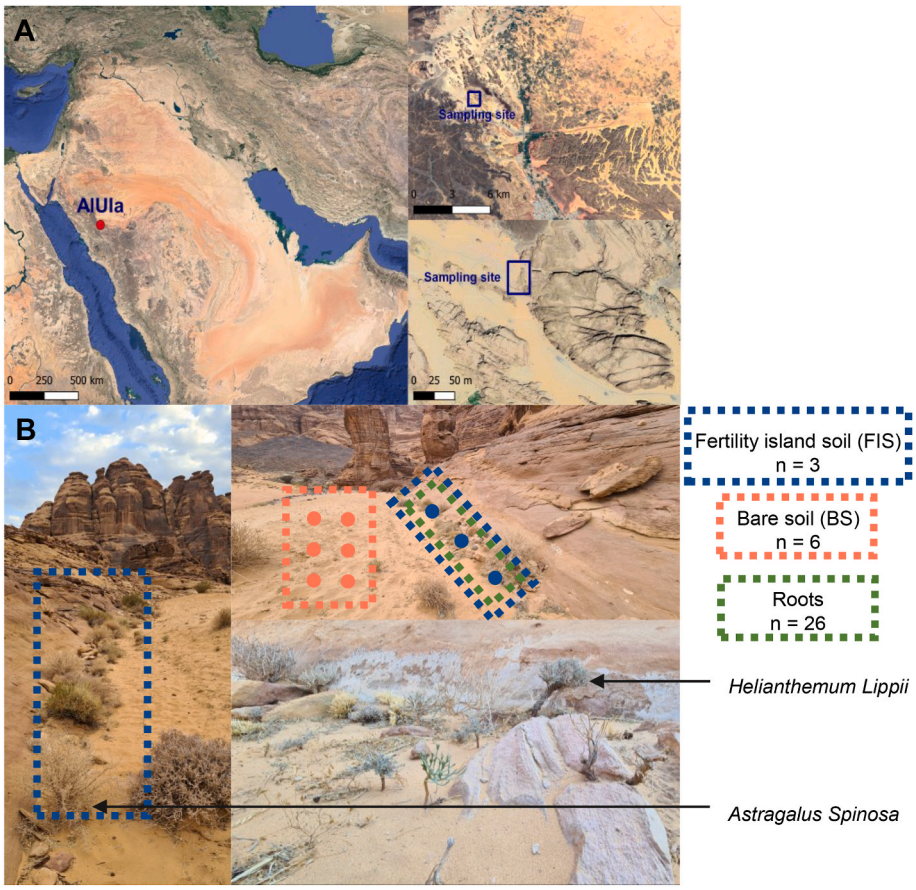

Fig. 1. (A) Sampling site located in the hot arid desert of Saudi Arabia near AlUla oasis (26.6922637 N; 37.8687903 E). (B) Sampling site of the fertility island microenvironment. The different sampling conditions (fertility island soils = FIS, bare soil = BS, and Roots = roots from the plant community established in the fertility island), and the fertility island associated plant community are shown.

a final polymerization extension at 72 °C for 7 min. All the reactions were performed in triplicate with an associated negative control, then pooled before deposition on 2% agarose gel for quality control of the amplifications.

Amplifications of ITS and 18S regions were purified with AMPure XP beads (Beckman Coulter, USA) on a magnetic rack with a 1:1 ratio of AMPure XP for each PCR product. For 16S purification, an additional step of migration of the PCR products on a 2% agarose gel (at 80 V, for 90 min) was performed to separate and recover the band specific to bacterial 16S, and to eliminate the plant chloroplastic 16S DNA (co-amplified during the PCR).

MetaFast library preparation and sequencing were performed on an Illumina 2 × 250 bp MiSeq platform by Fasteris SA (Switzerland). A pipeline based on VSEARCH (Rognes et al., 2016) was used for data processing (Perez-Lamarque et al., 2022). The merged reads were then demultiplexed (assigned to respective samples based on tagged primers) with 0 error accepted in primers or tag sequences, using cutadapt (Martin, 2011). Sequences were clustered into operational taxonomic units (OTUs) with 97% similarity using the VSEARCH algorithm. Chimeras were removed *de novo* (uchime_denovo option of VSEARCH) and the taxonomic assignment of the OTUs was performed (usearch_global option, default parameters) using UNITE V8.3 (Nilsson et al., 2019) and Silva 138.1 (Quast et al., 2012), for ITS2 and for 16S and 18S marker genes, respectively. The OTU tables were filtered to remove contaminants based on comparison with negative controls (blank DNA extractions) using the R package DECONTAM (prevalence method; Davis et al., 2018). Only OTUs with long sequences (>200 bp), assigned to the fungal kingdom and presenting acceptable abundance (≥10 reads) were kept for downstream analyses.

2.4. Statistical analyses

Soil variables measured by XRF are compositional, in percentage, and thus, enclosed in a compositional space called a simplex, where Euclidean distances are not meaningful. To be able to map data into an Euclidean space and perform a multivariate visualization using principal component analysis (PCA) and statistical tests, we applied a centered log ratio transformation (clr) following the recommendations from Reimann et al. (2012). To test for differences of chemical elements composition between fertility island soils and bare soils, we first tested variance equality using F-tests and performed Welch two-sample t-tests on equal variances and t-tests on unequal variances soil variables.

Illumina MiSeq sequencing yielded 631,253 sequences that were clustered into 4276 OTUs for 16S, 15,247,324 sequences that were clustered into 266 OTUs for ITS, and 232,727 sequences that were clustered into 121 OTUs for 18S. Sequencing data were studied using the *microeco* (Liu et al., 2021), *phyloseq* (McMurdie and Holmes, 2013) and *vegan* (Oksanen et al., 2013) packages in R (Team, R. C, 2013). Data were rarefied to 1000 for 16S and 18S and to 20,000 for ITS. To study diversity at the sample level, alpha diversity analyses were performed with the Shannon index and Chao1 estimator. Differences in alpha diversity between bare soil (BS), fertility island soils (FIS) and roots were tested with a Wilcoxon test. Finally, to describe the fungal communities in more detail, we used the FUNGuild database which assigned each out to a trophic type (Nguyen et al., 2016), and Tax4Fun for functional annotation of the bacterial communities. A non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarity distances was performed for each amplicon. In order to test the differences in the structure of the microbial communities between BS, FIS and

roots, we performed Permanovas on Bray-Curtis distances matrix.

In order to identify differentially abundant taxa between bare soil, fertility island soil and plant roots in the fertility island, we used differential abundance analyses using the LEfSe algorithms for bacteria and fungi identified with the ITS region of rRNA (Segata et al., 2011), and Metastat (White et al., 2009) for fungi identified with the 18S region of rRNA. These algorithms, developed in the context of compositional sequencing data, identify which taxa or taxonomic levels are differentially expressed in each condition. The use of two different algorithms is justified by the different number of samples between each amplicon. We reported the LDA score (log of model selection in the linear discriminant analysis of LEfSe) and the relative abundance differences to express the differences in expression between each of our conditions. The higher the LDA score, the more significant the difference.

3. Results

3.1. Soil chemistry in fertility island support plant establishment and nutrition

Overall, our soil samples were characterized by high pH, where fertility island soils were less alkaline (9.23 ± 0.06% for BS and 8.61 ± 0.20% for FIS) and silica content (93.9 ± 1.01% for BS and 82.08 ± 2.94%), reflecting the high proportion of sand in the soil (Table 1, Fig. 2). The main differences between FIS and BS were in the proportion of macro-elements, particularly phosphorus and potassium and micro-elements such as iron and manganese, that were higher in the FIS. The relative proportion of aluminum, which has been shown to be representative of the proportion of clay in the soil, was also higher in the FIS.

3.2. A microbial composition distinct between bare soils, fertility island soils and roots

The fungal communities in the soils and roots were dominated by Ascomycota, representing the majority of OTUs at 94%, 90.7% and 79.6% of relative abundance in the bare soil, FIS, and roots respectively, followed by Basidiomycota (2.1%, 3.6% and 10.5%) (Fig. 3). Amplification of the 18S gene revealed a high proportion of *Glomeromycetes* in the roots, as high as 57.5%, and in the FIS (25.5%), while they represent only 11.8% in the bare soil. ITS rRNA differential abundances revealed the high specificity of OTUs in the FIS. For example, the genus *Archeotomium* and *Naganishia* were significantly more abundant in FIS

Table 1
Fertility islands soils and bare soils have distinct chemistry, where fertility island soils have higher proportion of micro- and macro-elements that support plant nutrition. Mean relative abundance, in percentage (%), and standard deviation for each element is presented according to BS and FIS soils with the associated p-value from t-tests (samples with equal variances) or Welch tests (samples with unequal variances). Tests for micro- and macro-elements (from Si to Al) were performed on centered log ratio transformed values. The difference between pH H_2O and pH KCl correspond to the acidification potential (AP).

	Condition					
	BS		FIS			
	Mean (%)	SD	Mean (%)	SD	**Test type**	**p**
Si	93.9	1.01	82.08	2.94	*t*-test	<.001***
Mg	1.25	0.24	2.09	0.44	*t*-test	<.001***
Mn	0.01	0	0.02	0.01	*t*-test	<.001***
Fe	0.47	0.12	1.53	0.51	*t*-test	<.001***
P	0.02	0.01	0.05	0.01	Welch	<.001***
K	0.13	0.04	0.6	0.16	Welch	<.001***
Ca	0.64	0.23	0.56	0.29	Welch	<.001***
Al	3.33	0.52	12.56	2	Welch	<.001***
pH **(KCl)**	8.82	0.07	7.79	0.33	*t*-test	<.001***
pH **(H_2O)**	9.23	0.06	8.61	0.2	*t*-test	<.001***
AP	0.42	0.1	0.81	0.39	Welch	0.217

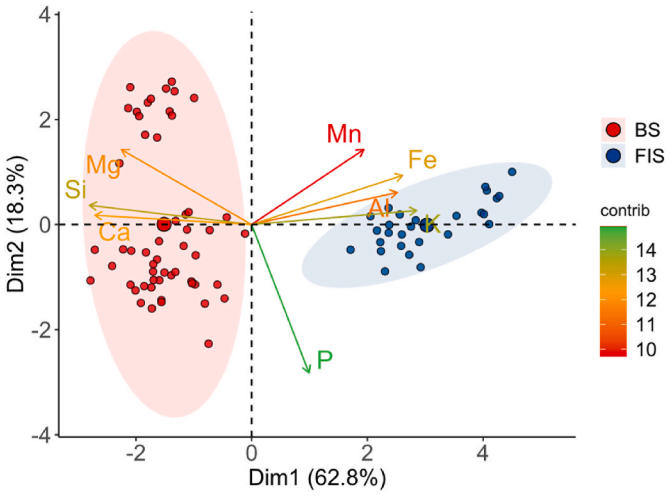

Fig. 2. Fertility island soil is distinct from bare soil and is enriched in micro- and macro-elements that support plant nutrition. Biplot of Principal Component Analysis (PCA) on soil clr transformed XRF technical replicates, dots colors represent the bare soils (BS) and fertility island soils (FIS). The barycenter of the groups is represented by a larger dot. Dimension 1 explains 62.8% of total variation, dimension 2 explains 18.3% of total variation. Vectors are colored according to their relative contribution to the dimensions (contrib).

(Fig. 4). Major bacterial phyla were represented by Actinobacteriota with a mean proportion of 40.0%, 40.2% and 48.7% in the bare soil, FIS and roots, respectively, and Proteobacteria (20.0%, 20.2%, 33.1%). Bacillales were specific to the bare soil, while Thermoleophilia, Gaiellales, Solirubrobacterales and Gemmatimonadota were specific to the FIS.

3.3. Unlike bacteria, the fungal trophic type identified depends on the fertility island effect

Overall, a significant proportion of saprotrophic, symbiotrophic, and pathotrophic fungi, were specific to bare soils, roots, and FIS, respectively. The fungal diversity detected by amplification of the 18S region revealed a high proportion of symbiotrophs in the roots, as high as 60.7%. The potential functions of bacterial communities were mainly linked to metabolism (60.4–60.7%), environmental information processing (20.6–21.5%), genetic information processing (10.6–11.2%), cellular processes (4.6–5.1%) and human diseases (1.8–2.1%), and their proportions remained relatively unchanged (Fig. 5).

3.4. Fertility island soils exhibit higher microbial diversity than bare soils and roots

Shannon diversity and richness were significantly lower in roots for both fungi (ITS rRNA) and bacteria (16S rRNA) while the FIS had significantly higher alpha diversity than bare soil for bacteria, and higher richness for fungi (Fig. 6). Differences in alpha diversity were not significant for 18S. The bacterial and fungal community assemblages were visualized with NMDS, which all clustered according to the three conditions. A clear distinction was observed between soil samples and root samples for bacterial communities, and to a lower extent between FIS and bare soil. The distinction between FIS and bare soils was stronger in the fungal communities highlighted by the ITS rRNA. Overall, bacterial and fungal communities formed distinct clusters according to the soils and roots, as shown in NMDS (Fig. 6), with greater dissimilarity for bacteria than for fungi, as highlighted by ITS and finally by 18S (Permanova 16S, $R2 = 0.279$, $p < 0.001$***; Permanova ITS, $R2 = 0.26$, $p < 0.001$***; Permanova 18S, $R2 = 0.159$, $p < 0.002$**).

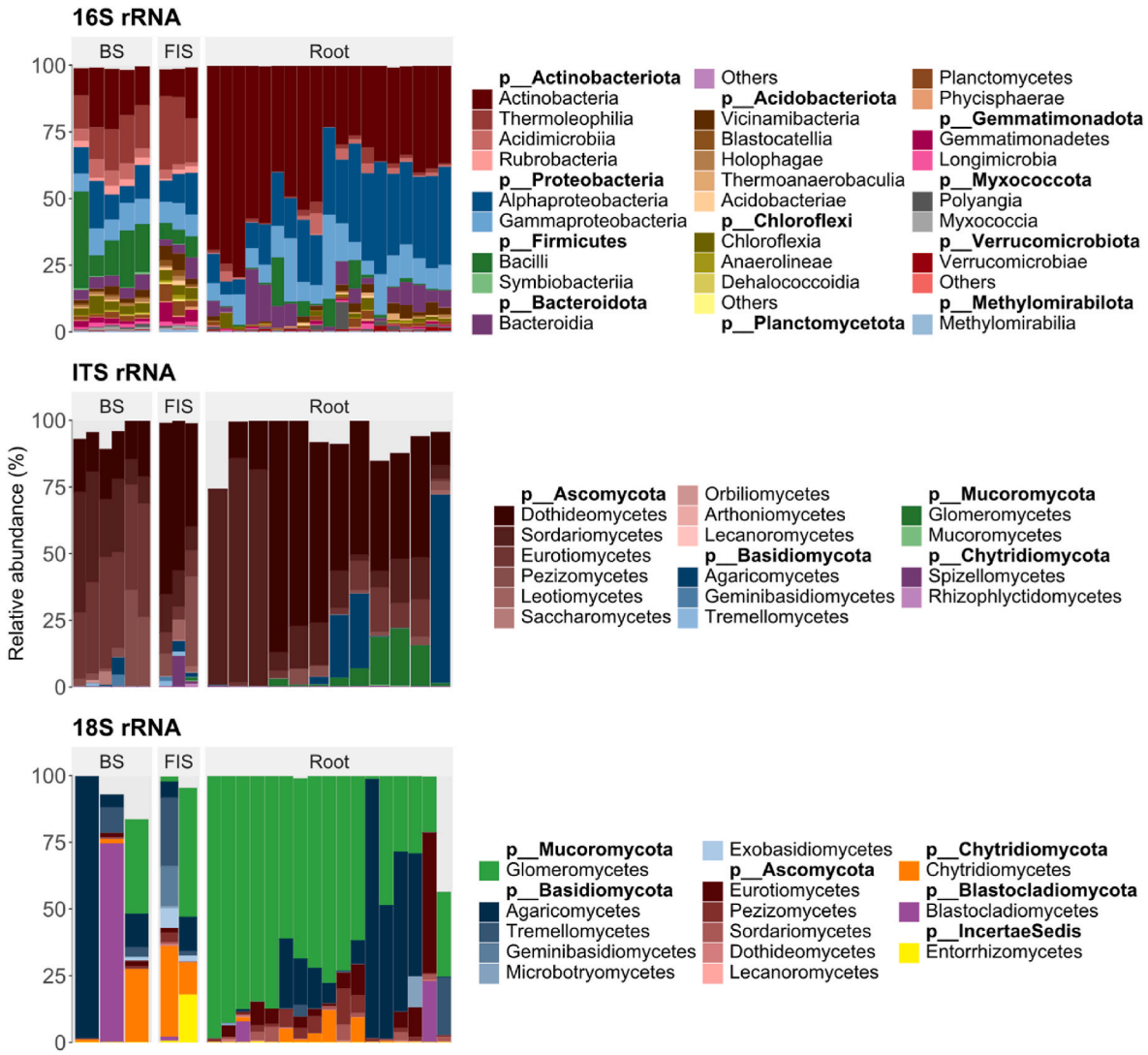

Fig. 3. Fertility islands influence soil microbial compositions, and enrich the proportion of mycorrhizal fungi in the roots of the associated plant community when compared to bare soil. Differences in averaged relative abundances according to the bare soil (BS), fertility island soil (FIS) and, roots of the fertility island plant community (Root) are presented for each amplicon (16S rRNA = bacterial community, ITS rRNA = fungi community, 18S rRNA = mycorrhizal community). Different colors represent different classes (for 16r RNA) and families (for ITS rRNA and 18S rRNA) according to each phyla (p_). Relative abundances were computed after rarefaction of samples to 20,000 for ITS rRNA and to 1000 for 16S rRNA and 18S rRNA amplicon datasets.

4. Discussion

The aim of this study was to investigate differences in soil composition and the associated fungal and bacterial microbiome between a microenvironment called a "fertility island" and the surrounding bare soil in hot arid and highly alkaline desert. We also studied the diversity and composition of the microbiome in the roots of the fertility island's plant community in order to identify putative functional taxa essential to ecosystem functioning and plant development. Our results showed that the fertility island was characterized by changes in soil conditions, such as increased acidity, higher proportions of micro- and macro-elements, and greater water availability and retention reflected by a higher proportion of clay. These parameters probably contributed to the local survival of the plant community. The fertility island also had an effect on the composition and diversity of the microbiome, where the soil associated with plants and their roots hosted a microbiome with a central role in ecosystem functioning.

4.1. A micro-environment within a sand dune

The studied site, with vegetated soil along a topological water flow zone within a dune, exhibits the characteristics of a fertility island, namely an area with, in our case, a greater proportion of micro- and macro-elements that favors plant nutrition. Runoff from the sandstone slab above likely favors the formation of alluvium and colluvium of fine particles loaded with clays and minerals resulting from the degradation of the parent rock. The proportion of Si and Al can be linked to soil texture, as XRF analysis is used to predict soil properties such as texture in a homogeneous environmental setting (Zhu et al., 2011). In our case, higher clr or percentage values of Si corresponded to a higher proportion of sand, and higher clr or percentage values of Al corresponded to a higher proportion of clay. Although the proportion of macro-elements such as P was higher in FIS, phosphorus is mainly available to plants in the form of orthophosphates (HPO_4^{2-} or HPO_4^{-}), which in our study, were not directly measured by XRF. On the other hand, the higher clay content found in FIS soils may support higher nutrition of plants in this ecosystem. Nitrogen-containing organic matter is bound chemically to clay minerals, thereby stabilizing soil organic matter (Kome et al.,

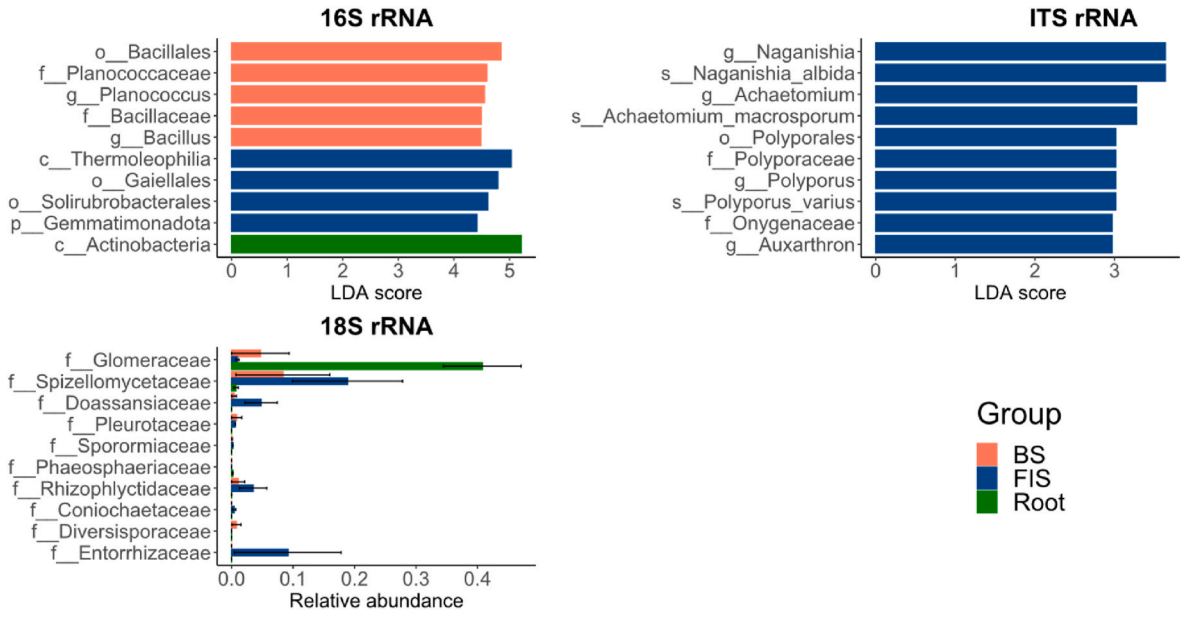

Fig. 4. Differential abundance analysis reveals the specific communities associated to each condition (BS, FIS or Root). LEfSe was run with an alpha threshold of 0.01 for bacterial (16s rRNA) and fungal communities (ITS rRNA), and the LDA score (as the log value of significant taxonomic level identified by the linear discriminant analysis model) is reported for the top 10 differentially abundant taxonomical level (p_ = phylum; c_ = class; o_ = order; f_ = family; s_ = species) at each condition. The higher the LDA score, the higher the significance. For mycorrhizal communities (18S rRNA), significant differential abundances correspond to the Metastat method according to each condition at the family level.

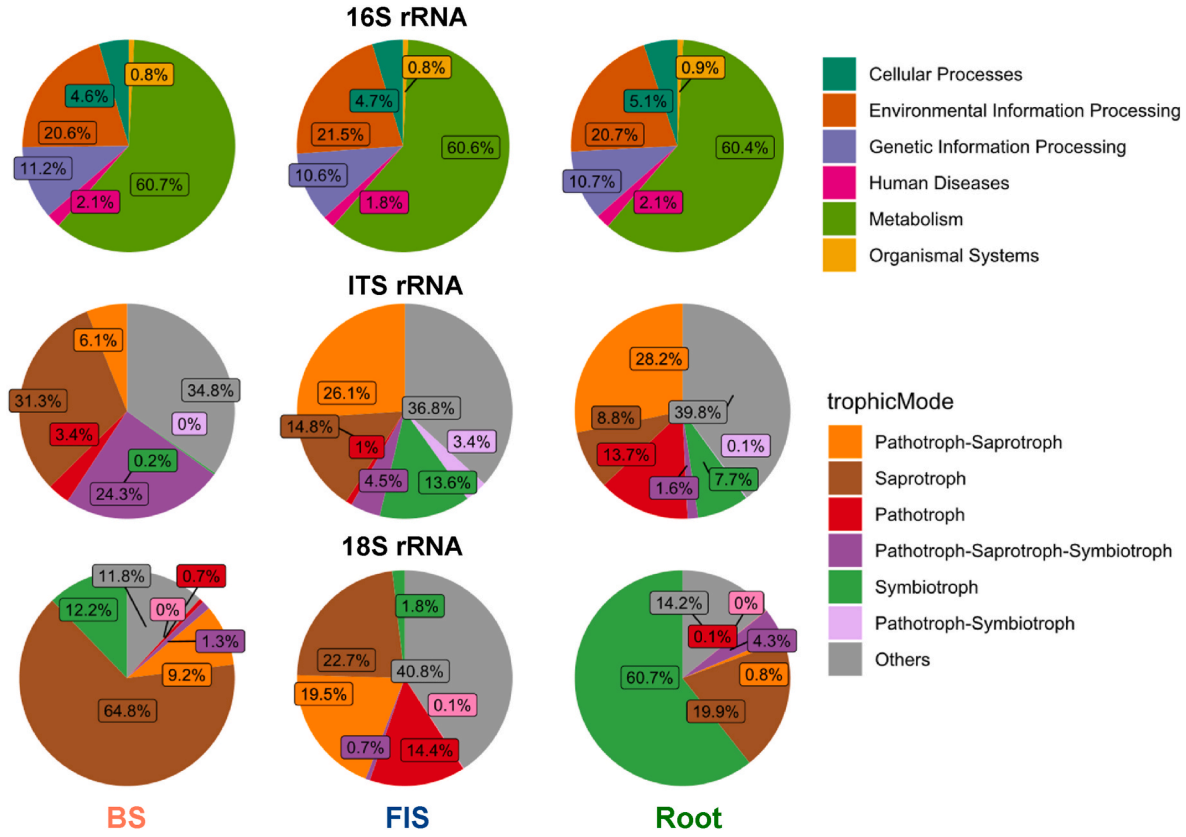

Fig. 5. Root of plants established in the fertility island are enriched with symbiotrophic fungi. Functional assignment from Tax4Fun with the SILVA database for bacteria (16S rRNA) and trophic mode assignment from FunGuild for fungi (ITS rRNA and 18S rRNA) according to the bare soil (BS), fertility island soil (FIS) and, roots of the fertility island plant community (Root) are shown with the associated percentages.

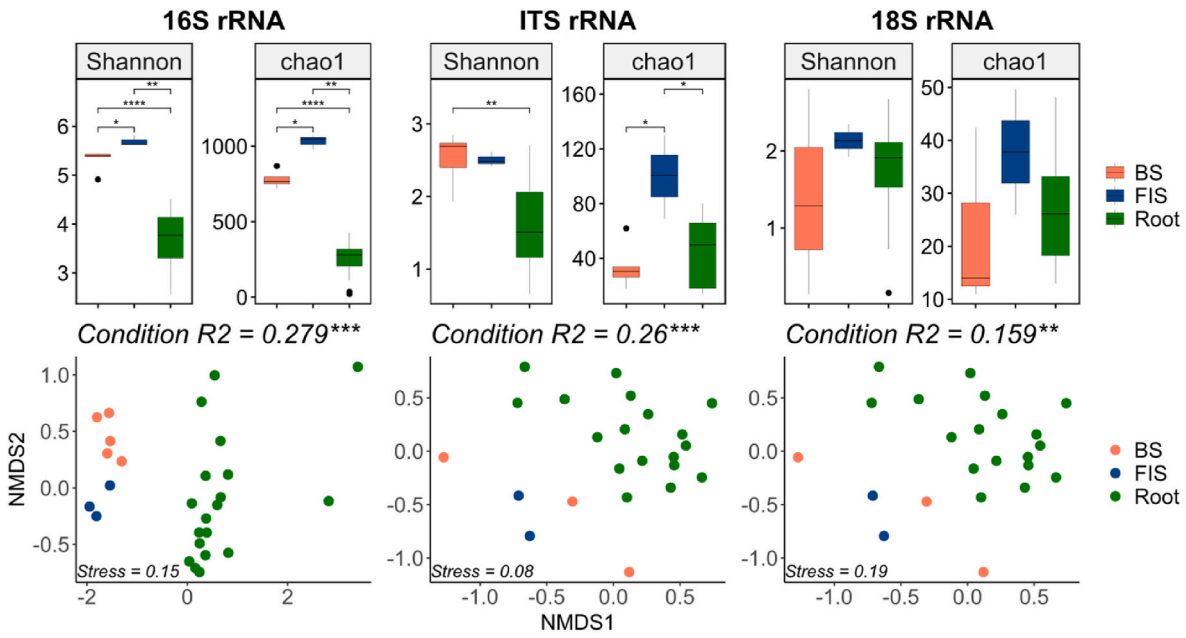

Fig. 6. Microbial communities' compositions are different across soils and roots and alpha diversity is higher in fertility island soils. Alpha diversity indexes are presented for bare soil (BS), fertility island soil (FIS) and roots of the fertility island plant community (Root) according to each amplicon (16S rRNA = bacterial community, ITS rRNA = fungi community, 18S rRNA = mycorrhizal community). Chao1 is the specific richness and Shannon is a species diversity index that considers both richness and evenness. Beta diversity is presented with non-metric multidimensional scaling (NMDS), stress is reported, as well as Permanova of communities' composition with the associate R2 and stars for p-value significance. Samples with less than 1000 reads were discarded and rarefaction was performed at 1000 reads for 16S rRNA and 18S rRNA and 20,000 reads for ITS rRNA.

2019). Clay minerals also influence soil physical properties, where a functional attribute of clay minerals in soil is linked to the formation of microaggregates, which affect phosphorus adsorption and availability (Siebers et al., 2018). A higher proportion of clay in soil also increases soil stability and water retention capacity, favoring seed germination and plant establishment. However, the aforementioned phenomena, along with the assumption that these micro-nutrients are the result of colluvium during rainfall events and accumulate by gravitation, need to be considered from the point of view of the grazing history of the study site. In this micro-environment, the presence of livestock like camels and goats, puts significant herbivory pressure on the ecosystem, and in this case, the fertility island phenomenon could be a byproduct of this herbivory history. Based on 99 case studies in arid or semi-arid ecosystems, Allington and Valone (2014) linked the presence of livestock grazing to the fertility island effect. These authors showed that in cases where herbivory pressure was reported, the presence of livestock grazing was linked to the fertility island pattern with at least one soil nutrient among phosphorus, nitrogen or organic matter. This pattern was inconsistent or non-existent when the zone had not been grazed for more than 30 years. In our case, we assume that the pressure of grazing was less than the pressure caused by soil and climatic conditions, and that the microenvironment is characterized to a greater extent, by the topology-facilitated water flow.

4.2. *Microbial life in a desert: a microbiome composition to alleviate stress*

The diversity found in this hot desert microenvironment was characterized by the ubiquitous bacterial phyla typically found in other environmental studies i.e., dominance of Actinobacteria, Proteobacteria and Firmicutes (Drees et al., 2006; Makhalanyane et al., 2015). The dominance of Actinobacteria is a common feature in desert ecosystems, probably due to their adaptive functional traits that fit desert abiotic stresses such as a mechanism for UV repair, sporulation and competitive advantages (Gao and Garcia-Pichel, 2011). The roots of the plant community were characterized by a high proportion of Rhizobiales that included functional taxa linked to soil fertility and that could play an important role in these nutrient-depleted environments by improving soil fertility (Miao et al., 2020). Proteobacteria may also be functionally indispensable in the desert environment, with taxa involved in bacteriochlorophyll-independent photosynthesis (Boldareva-Nuianzina et al., 2013). The fungi we found in the soils were mainly saprotrophs, mostly represented by Pleosporales, which are key players in recycling organic matter. There was also a high proportion of arbuscular mycorrhizal fungi, represented by the family Glomeraceae, specific to the roots of FIS plants. In these soils with major water and nutrient deficits, enrichment of symbiotic mycorrhizal fungi in roots could therefore be an advantage for plant tolerance and survival (Tedersoo et al., 2020).

4.3. *Microbial communities as a resource for agriculture and land restoration*

Our results show that fertility islands harbor specific and enriched microbial communities, essential for ecosystem functioning. They represent unique patches of microbial resources with functional adaptation to extreme local conditions that are crucial for plant community assembly. These results highlight the potential for isolating the local microbiome in order to harness its plant growth promoting properties as part of the agronomic transition and improve sustainability in the context of increasing desertification and climate change. This is of particular importance in Saudi Arabia and Gulf countries, where water resource is jeopardized. Desert microbial strains can also play an instrumental role in land restoration, and could be a key resource for desert reforestation and desert vegetation programs (Bashan and de-Bashan, 2010). This unique ecological niche is a reservoir of microorganisms with potential agronomic applications were new plant growths promoting strains from arid ecosystems can be isolated (Alsharif et al., 2020). For example, bacteria isolated from the rhizosphere of date palm in Tunisia showed a high potential for promoting plant growth in a large proportion of isolated strains, as they featured auxin production, ammonia synthesis, solubilization of phosphates and siderophore production functional traits (Ferjani et al., 2015). In Saudi Arabia, El-Sayed et al. (2014), isolated plant growth promoting

rhizobacteria from 11 local plant species. Among these, several strains of *Pseudomonas*, *Bacillus* and *Enterobacter* exhibited plant growth promoting traits such as siderophore production, Nitrogen-fixation, mineral phosphate and zinc solubilization. Lytic enzyme traits associated with mitigation of fungal pathogen growth were also identified through the production of protease, chitinase and cellulase. Bacteria belonging to the genus *Bradyrhizobium*, which are abundant in roots, *Azospirillum* in soils, and *Nitrospira* and *Nitrosomonas* were also found in our study. These bacteria play key roles in the nitrogen cycle, and even though their abundances were low, they can be considered as key taxa in ecosystem functioning and can be targeted in agronomical research. However, it is important to note that soil microbial communities are also influenced by plants through their root exudates (Zhalnina et al., 2018) and microbial symbionts (Uroz et al., 2019). Such plant-soil feedback can influence population dynamics and plant identity and phenology should be taken into consideration in future research. In conclusion, future research will benefit from investigating the ability of microbial communities belonging to fertility islands in extreme environments to alleviate abiotic stress, such as drought and low soil nutrient. The unique microbial diversity of this habitat should be considered when developing new agronomic and adaptation strategies, and in conservation programs designed to cope with climate change and prevent desertification.

Credit author statement

Study conception and design: KM, LLW; Sampling: KM, LLW; Laboratory experiments and data collection: KM, AB, SB; Formal analysis: KM, AD; Writing – original draft KM; Writing – review & editing: KM, AB, LLW, SB, HB, MD; Funding acquisition and project supervision: MD, HB, MAS. All the authors discussed the results, contributed to the final manuscript, and approved submission of the final version of the manuscript.

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Declaration of competing interest

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

Data availability

Data will be made available on request.

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