

Title: Diversity and structure of arbuscular mycorrhizal fungal communities and their chemical drivers across dryland habitats in Qatar

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Abstract

Qatar is largely characterized by a hyper-arid climate and low soil fertility, which combine to create a stressful soil environment for arbuscular mycorrhizal (AM) fungi. Here we present a study on AM fungi communities and their relationship to soil chemical characteristics. We used high-throughput sequencing technique for identifying AM fungal diversity and community composition from different habitat types across Qatar. We found 127 AM fungal taxa, of which majority were member of the family *Glomeraceae*. In contrast to what was hypothesized, AM fungi were mainly influenced by soil phosphorus (P) and potassium (K). Chemical soil properties explained 76% of the variation in AM fungi between locations. The lowest AM fungal diversity was observed in barren areas and sand dunes, possibly due to low bioavailability of total nitrogen, while the highest diversity was observed in well-developed grass patches. Present AM fungi in Qatar were not affected by soil salinity and pH; these fungi have likely been exposed to high salinities through their evolutionary history in the region, favoring resistant AM fungi through natural selection. These findings provide baseline information on AM fungal assemblages and their drivers across communities in Qatar. Our data fill a gap of broad scale studies from the Arabian Peninsula, and thus contribute to better understanding of global patterns of AM fungi and their chemical drivers.

Key words: microbiota, arbuscular mycorrhizal fungi, environmental DNA, high-throughput sequencing, soil salinity, heavy metals, dryland

Introduction

Global dryland regions, including those in Qatar, cover approximately one-third of the Earth's surface and therefore play a significant role in the global carbon cycle (Delgado-Baquerizo et al., 2015; Fitter, 2005; Lüneberg et al., 2018; Neilson et al., 2017; Soudzilovskaia et al., 2015; van der Heijden et al., 2015). Given the high variability in rainfall and extended periods of drought in dryland regions, dryland ecosystems are highly susceptible to soil erosion and land degradation caused by climatic variability, and are often depicted as unstable habitats for many microorganisms (Delgado-Baquerizo et al., 2015; Laban et al., 2018; Neilson et al., 2017). However, despite the severe environmental conditions they experience, research has shown dryland ecosystems to be extremely adaptable to environmental changes. For instance, spatial re-establishment of natural grasslands in Africa since 1980 has led to resilience of many dryland microbes by natural selection through their evolutionary history (Reynolds et al., 2007; United Nations, 2011). However, the capacity for dryland microorganisms to adapt to adverse environmental conditions is dependent on abiotic components within the habitat, including adequate soil nutrients and microbiota sustaining the integrity of dryland ecosystems (Jeffries et al., 2003; Laban et al., 2018; Neilson et al., 2017). Due to the adverse conditions in dryland habitats, the extent of mycorrhizal colonization and diversity of soil fungi driven by such ecosystems may be important. Drylands are known to host a large variety of endemic species, including fungal species that exhibit unique adaptations to the harsh conditions presented by drylands (Kamalvanshi et al., 2012; Laban et al., 2018; Neilson et al., 2017; Xu et al., 2018).

Soil biodiversity generally refers to the range of microorganisms that dwell beneath the soil surface. Intracellular colonization of host roots is characteristic of most mycorrhizal associations, with the exception of ectomycorrhizas. Mycorrhizal fungal sheaths enclose the roots

of their host, creating a dense network of intracellular hyphal structure that ultimately results in a mutualistic relationship between the fungal partner and its host (Compant et al., 2010; Fitter, 2005; Kasel et al., 2008; Mandal & Sathyaseelan, 2012). This biological fraction in soil ecosystems comprises less than 0.5% of the total volume of soil, but the biological activity carried out by the microorganisms it contains accounts for over 60% of global ecosystem services and functions, including regulation of nutrient and carbon cycles and decomposition of organic matter (Laban et al., 2018; United Nations, 2011). Among its many functions, arbuscular mycorrhiza (AM) fungal diversity within the global cycle plays an integral part in nutrient cycling and ecosystem functioning. Therefore research pertaining to AM fungal communities is essential as a basis for further understanding complex ecological relations.

Arbuscular mycorrhizal fungi primarily belong to the phylum Glomeromycota and form an obligatory symbiosis with plant roots (Smith & Read, 2008; Tedersoo et al., 2018; van der Heijden et al., 2015). This symbiosis is of a mutualistically beneficial nature, so AM fungi play an important role in plant productivity and stress tolerance (Smith & Read, 2008). The composition of AM fungal communities is highly influenced by edaphic factors (Davison et al., 2015; Dumbrell et al., 2010), Mycorrhizal associations are especially crucial in fragile ecosystems where access to soil resources are limited, and are thus of particular importance in semi-arid and hyper-arid ecosystems (Majid et al., 2016; Villalobos et al., 2016; Zhao et al., 2017). In this regard, the diversity of AM fungi in drylands may be vital for establishing symbiotic associations to maintain ecosystem function (Mahmoudi et al., 2019; Zhao et al., 2017). For instance, belowground mycorrhizal fungi promote carbon sequestration and increase carbon storage in plant litter, which in turn increases net primary production (NPP) in AM-dominated habitats (Jeffries et al., 2003; Soudzilovskaia et al., 2015). However, the extent of mycorrhization depends on the host plant and

symbiotic AM fungal species. Diversity in AM fungi could also enhance ecosystem productivity and function (Delgado & Gómez, 2016; Gerz et al., 2018). The positive effect on ecosystems is particularly important in climate-driven habitats, as potential changes in aridity due to climate change may influence the ability of dryland microbiomes to sustain geochemical cycles and ecosystem functions (Delgado-Baquerizo et al., 2015; Gustafson & Casper, 2006; Majid et al., 2016; Neilson et al., 2017; Zhao et al., 2017). Soil disturbances influenced by agricultural management could positively impact AM fungal diversity if the agro-system management is associated with increasing soil organic matter and organic carbon (Oehl et al., 2010). On the other hand, a disturbance associated with decreasing organic matter will likely reduce fungal diversity (Toljander et al., 2008). The diversity of AM fungal communities is dependent on the chemical nature of the soil environment.

For fungal identification studies, molecular techniques that involve amplification of fungal genes derived from environmental samples have recently become available (Nilsson et al., 2019; Öpik & Davison, 2016). With the development of various next-generation sequencing platforms and a substantial increase in the depth of sequencing (number of sequences per sample), in-depth analysis of abundance and variation in fungal communities is now possible. Platforms like Illumina sequencing have gained increasing recognition in recent fungal diversity research, due to low error rate and enhanced sequencing depth per sample (Nilsson et al., 2019; Shokralla et al., 2012; Tedersoo et al., 2015). The greater sequencing depth of the Illumina MiSeq sequencing platform permits detection of lower AM fungal diversity than is possible with e.g., the 454 sequencing platform (DeBellis et al., 2019; Tedersoo et al., 2015; Vasar et al., 2017). Moreover, the Illumina

platform allows high sequencing recovery, while covering a wider range of phylogenetic clades than other sequencing platforms (Johansen et al., 2016).

This study aims to identify the AM fungal communities along a stress-induced environmental gradient in Qatar. Chemical drivers in the soil were compared with the abundance distribution of AM fungi at various locations. Taxa of AM fungi over a range of habitat types were modeled in order to delineate AM fungal families with respect to chemical characteristics, specifically soil pH, salinity, total carbon (TC), total nitrogen (TN), nitrite (NO_2^-), nitrate (NO_3^-), and concentrations of elements in soil. The general expectation was that differences in the chemical properties of soils between locations and vegetation cover would influence the diversity and composition of AM fungal communities. Specific hypotheses were that: (1) increasing soil salinity and pH reduce the diversity of AM fungal species, as soil conditions become unfavorable for growth of soil fungi; (2) the abundance and diversity of AM fungi are positively associated with concentrations of macronutrients in soil; and (3) presence of cadmium (Cd) and lead (Pb) within the soil environment has significant negative effects on the occurrence and abundance of AM fungal species, due to toxicity effects of these heavy metals on microbial communities.

Materials and Methods

Study Area and Sample Collection

Soil samples were collected from 19 different locations across Qatar (Figure 1). Qatar is located between 24°-27° N and 50°-52° E on the north-eastern coast of the Arabian Peninsula, and occupies a total land surface area of 11,571 km² (Zahlan, 2016). Most of the area in Qatar is covered by barren desert, with a highly arid climate and minimal annual rainfall (<100 mm per year) that typically takes place during the winter months (i.e., December-February). Minimum and

maximum mean monthly temperatures range from 18.5°C in January to 37°C in July. However, maximum daytime temperatures during summer can rise above 40°C, while other periods have more humid days with highs of around 38°C (Mamoon & Rahman, 2016). The topography consists of mainly flat land surfaces, but with hills and undulating sand formations mostly found in the south-east of the country (Abulfatih et al., 2002; Norton et al., 2009). The soils are abundant in calcareous rocks, sand, and gravel. The terrain is low-lying, with natural depressions (*rawdha*) and some small hills with altitude of around 100 m (Mahasneh et al., 2008; Norton et al., 2009). In *rawdha*, the soils are often deeper and richer (Norton et al., 2009).

The sampling sites varied in terms of topography, vegetation coverage, and soil conditions and were classified into one of five habitat types: *rawdha*, saltmarsh, mangrove, barren land (*sabkha*), and areas with natural vegetation (Table 1). Some of the sites were within close proximity to commercial districts and urban areas. At each site (approximately 50 m x 50 m), 20 subsamples were collected from vegetated spots, with each sample being 5 cm in diameter and 5 cm deep in the soil. For each location, a composite sample was prepared by combining approximately 1-1.5 g from each of the 20 subsamples per site. The composite soil samples were air-dried for four days, and thereafter stored in zip-lock plastic bags with silica gels to prevent moisture.

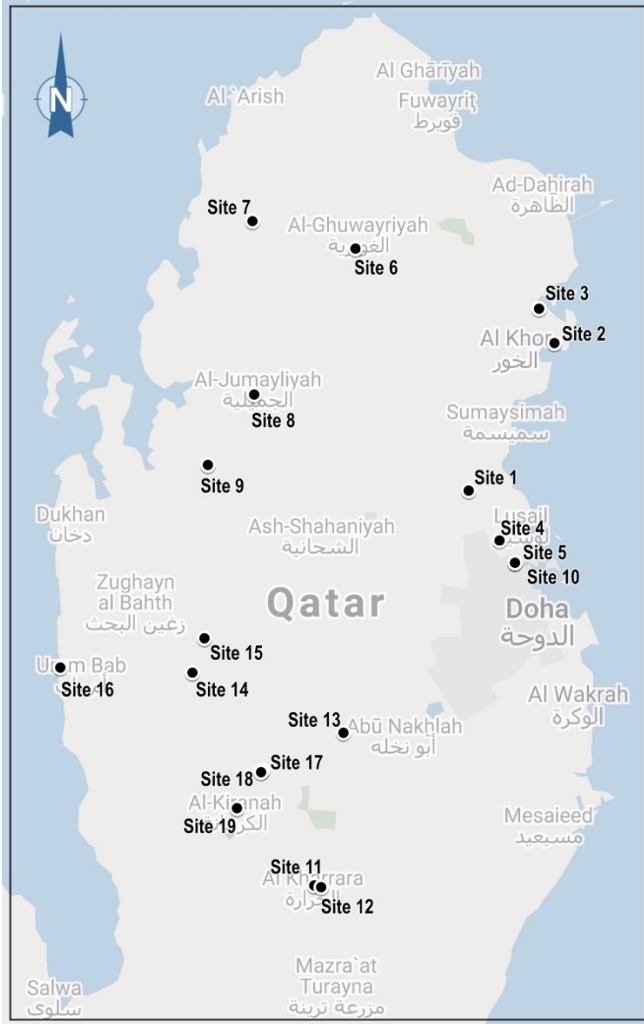


Figure 1. Locations of the 19 study sites across Qatar. Due to close proximity of some study sites, the symbols overlap and are indistinguishable.

Table 1. Description of each sampling location in Qatar

Site no.	Location	Latitude	Longitude	Site description
1	AlSakhama	25.476034 N	51.421473 E	Sandy area with intermittent rocks and patches of vegetation
2	AlKhor	25.687524 N	51.557793 E	Mangrove area with extensive halophytic plants in clay/loam soil
3	AlThakira	25.737380 N	51.534113 E	Saltmarsh with partial vegetation coverage
4	Lusail	25.404546 N	51.470202 E	Wet muddy soil with patches of vegetation as a result of rainfall
5	QU field 1	25.371027 N	51.496573 E	Sabkha area dominated by rocky soil and trees
6	AlGhuwayriyah	25.825498 N	51.239716 E	Sandy area scattered with bushes and trees attributed to rainfall
7	AlNu'man	25.864567 N	51.075506 E	<i>Rawdha</i> area dominated by trees and shrubs
8	AlJumayliyah	25.615461 N	51.078010 E	Slightly moist soil with scattered areas of vegetation and little rocks
9	Khawzan	25.512379 N	51.002956 E	Moist and well packed soil with small plants and patches of grass
10	QU field 2	25.372192 N	51.495583 E	Extensive shrubs with patches of grass
11	AlKharrara 1	24.903225 N	51.173316 E	<i>Rawdha</i> area filled with trees and scattered shrubs. The area is inhabited by grazing animals
12	AlKharrara 2	24.902584 N	51.185224 E	<i>Rawdha</i> area filled with trees and scattered shrubs
13	AlRayyan	25.124299 N	51.221968 E	Largely populated by large bushes, flowering plants and grass patches
14	AlKharsaah 1	25.212063 N	50.979881 E	Grassland with several trees. Likely a disturbed area due to its close proximity with the roadside

15	AlKharsaah 2	25.261641 N	50.998017 E	Rock outcrops with patches of grass
16	Dukhan beach	25.218835 N	50.767926 E	Coastal area dominated by halophytes and fine sandy soil
17	North of Qatar 1	25.06971 N	51.09184 E	Desert area with plain flat soil and minimal vegetation
18	North of Qatar 2	25.06915 N	51.08974 E	Desert area with little to no vegetation
19	AlKiranah	25.01562 N	51.04944 E	Area with dunes and deep sand

Molecular Analyses and Bioinformatics

Environmental DNA was extracted from 0.25 g of homogenized soil sample using the DNeasy PowerSoil Kit (Qiagen GmbH, Hilden, Germany), following the manufacturer's protocol. Total genomic DNA was then quantified and tested for extraction quality using 1% agarose gel electrophoresis. DNA extracts of both composite samples and subsamples were used as templates in subsequent polymerase chain reaction (PCR) amplification. The small-subunit (SSU) ribosomal RNA gene of AM fungal sequences were amplified with using AM fungal specific primers WANDA (Dumbrell et al., 2011) and AML2 (Lee et al., 2008). Each primer was tagged with 12 base multiplex identifier (MID) tags, as described in Tedersoo et al. (2014). PCR was carried out in a total reaction volume of 25 μ L, comprising 1 μ L of template DNA, 0.5 μ L each of forward and reverse primer (20 μ M), 18 μ L of nuclease-free water, and 5 μ L of 5X Hot FIREPol Blend Master Mix (Solis Biodyne, Tartu, Estonia). Optimal PCR conditions used for amplifying fungal communities were as follows: 15 mins at 95°C, followed by 35 cycles of 30s at 95°C, 30s at 55°C, 1 min at 72°C, and a final extension temperature of 72°C for 10 mins. PCR was performed on a GeneAmp PCR System 9700 (Applied Biosystems, Foster City, CA, USA).

The PCR products were pooled into two libraries, at approximately equimolar ratios as determined by the strength of the gel band (1.5% gel electrophoresis). They were then purified using the FavorPrep gel/PCR purification kit (Favorgen Biotech Corp, Ping Tung, Taiwan), following the manufacturer's protocol. Each library was linked with Illumina MiSeq adapters using the TruSeq DNA PCR-free HT Library Prep kit (Illumina Inc., San Diego, CA, USA) and processed by the Illumina MiSeq 2X300 sequencing platform at the Estonian Genome Centre (Tartu, Estonia). A negative control (nuclease-free water instead of template DNA in the PCR mixture) and positive control (DNA extracted from *Plantago ovata* roots) were used throughout the experiment, including sequencing runs.

Illumina paired-end raw sequences were demultiplexed and cleaned using a series of bioinformatics steps following Vasar et al. (2017). Sequences were cleaned by selecting reverse and forward reads with average quality of at least 25, and both reads could have one match in forward and reverse primer sequence. Quality-filtered paired-end reads were combined with FLASH (v1.2.10, Magoč et al., 2011), using the default thresholds (overlap between 10 and 300 bp; overlap identity at least 75%). Sequences were preclustered with 98% identity using VSEARCH (v2.14.1; Rognes et al., 2016) to reduce the computational complexity and time requirement. Cluster information was stored to allow clusters to be mapped back to individual reads. Putative chimeric sequences were removed using the VSEARCH MaarjAM reference database (status February 2020, Öpik et al., 2010) and de novo chimera filtering algorithms. Sequences were clustered into operational taxonomic units (OTU) using 97% identity, which were used as a proxy of species. Obtained cluster centroids were used to get rough estimation of the taxonomy by conducting a BLAST+ search against the MaarjAM database (Öpik et al., 2010). All OTUs represented by a single sequence (singletons) were removed.

Chemical Analyses

Prior to chemical analysis, 29 soil samples, including 19 composite samples, two duplicates and three subsamples, were oven-dried at 60-62°C for 48 hours to prevent decomposition of organic material and enhance the extractability of micronutrients and heavy metals (Erich & Hoskins, 2011). The dried soil was then milled into fine powder in a rotary ball mill (Retsch Mill, Haan, Germany) at a speed of 250 rpm for 40 minutes and passed through a standard sieve of 2 mm mesh, in preparation for downstream chemical analysis. Portions of processed soil used for chemical characterization were analyzed for the parameters: pH, salinity, electrical conductivity (EC), total dissolved solids (TDS), TC, TN, NO₃⁻, NO₂⁻ and concentrations of key elements including Ca, K, Mg, P, Cd, and Pb, following methods validated by the International Organization for Standardization (ISO/IEC 17025).

Soil pH and salinity were measured using a standard probe meter calibrated with 7.0 and 4.0 buffer solutions and 0.01 M of KCl solution, respectively. EC, Total C and TN content in all soil samples and in glycine standard compound were determined by dry combustion in a CHN elemental analyzer (Skalar Analytical, Breda, Netherlands) (Jing et al., 2015). To ensure reliability of the values, the recoveries for theoretical TC and TN in glycine were compared with calculated values for unknown samples, which showed that the values fell within 15% of the EPA criteria. Soil NO₃⁻ and NO₂⁻ were determined by extraction with KCl, followed by UV-Vis spectrophotometry (Fisher Scientific, Waltham, USA) (Wood et al., 1967).

For the quantification of elemental content of soils, the samples were digested in a 54-well digestion hot block (Thomas Scientific, Swedesboro, USA) using a mixture of HNO₃:HF (ratio3:2) (Tighe et al., 2004). About 0.25 g of soil was weighed accurately and placed inside a PTFE Teflon digestion tube followed by the addition of 9.0 ml concentrated nitric acid (69% w/w) and 3.0 ml

concentrated hydrofluoric acid. The tubes were heated gradually to 135°C for approximately 1 hour. Following acid digestion, evaporation was initiated by removing the reflux caps and increasing the temperature to 155°C for an additional hour. Following near complete evaporation, 3.0 ml of nitric acid was added to the remaining residue and diluted to a total volume of 50 ml. Samples were heated until boiling point and consequently, transferred in a 100 ml volumetric flask and diluted with Milli-Q water. Samples solutions along with quality control samples (i.e. blanks, replicate analyses, CRM) were finally analysed by ICP-OES (Perkin Elmer Optima 7300DV System fitted with an S10 autosampler). Samples were analysed for magnesium, potassium, phosphorous, calcium, cadmium and lead. Obtained data was processed using WinLab32 software. To ensure reliability of the data attained, internal standards were included during ICP-OES analysis to avoid potential interferences (Masson et al., 2010). The precision and accuracy of the chemical analyses were assessed using a certified reference material (PACS-3, marine sediment).

Data Analyses

Analyses of AM fungal OTUs

Shannon alpha-biodiversity index was computed to determine the species diversity and richness of identified AM fungal OTUs and genera, and reveal potential trends in AM fungal richness between locations. The frequency of AM fungal occurrence at each location was determined and illustrated as a heat map, according to the OTUs of each genus identified. The indicator species was determined following the method in Dufrêne & Legendre (1997), to compute the indicator index value of AM fungal OTUs for each location sampled.

Chemical Data

Shapiro-Wilk (S-W) normality tests showed that the datasets for salinity, NO₃⁻, and TC were normally distributed at p<0.05 significance level (Table S2). Variables that did not follow a

normal distribution ($p < 0.05$) were normalized by logarithmic transformation prior to ANOVA. The significance (i.e. p-values) between the variable means was less than 0.05 alpha level, indicating that the chemical components differed significantly between locations. Subsequent ANOVA and Tukey HSD comparison used to assess the significance between chemical parameters at 95% confidence interval revealed that soil pH varied least between the study locations (Table S3). ANOVA analyses were conducted using SPSS 19.0 software (SPSS Inc., USA). Principal component analysis (PCA) was used to evaluate different combinations of chemical variables that could explain a common pattern of variation among the locations sampled.

Linking Chemical Variables with AM Fungal Richness

Using the variables obtained from the initial analyses (Figures 2-4), distance-based redundancy analysis (RDA) was carried out (Zhao et al., 2017) to explore potential relationships between the composition of AM fungal community assemblages, soil chemical characteristics, and land type (i.e., mangrove, saltmarsh, *rawdha*, barren land/*sabkha*, and vegetation/shrub patches). Linear regression was conducted to evaluate the relationship between soil characteristics and AM fungal richness. RDA and regression analyses were performed using XLSTAT statistical software (Addinsoft Inc., New York, USA).

Results

AM Fungal Diversity and Relative Abundance

The Illumina 2x300 bp MiSeq platform generated 9,861,189 paired-end reads targeting the SSU region of the rRNA gene (Figure 2). A total of 2,474,899 sequences were quality-filtered and combined, of which 3.3% were determined as putative chimeric reads. Following removal of these chimeric reads, the positive control sample, and singletons ($n=6$), the final dataset comprised 53

OTUs and 1,369,477 sequences from 19 composite soil samples. Each sample comprised 2-62,040 sequences (median 6588 sequences) and 1-28 OTUs (median 7 OTUs). A total of 127 AM fungal OTUs were identified belonging to the following families: *Glomeraceae* (87 OTUs), *Diversisporaceae* (10 OTUs), *Claroideoglomeraceae* (7 OTUs), *Paraglomeraceae* (7 OTUs), *Archaeosporaceae* (7 OTUs), *Acaulosporaceae* (6 OTUs), *Ambisporaceae* (2 OTUs), and *Gigasporaceae* (1 OTU) (Figure 3). The dataset showed that 76% of the AM fungal population was from the *Glomeraceae*, while 13% was from the *Claroideoglomeraceae* (Figure 2).

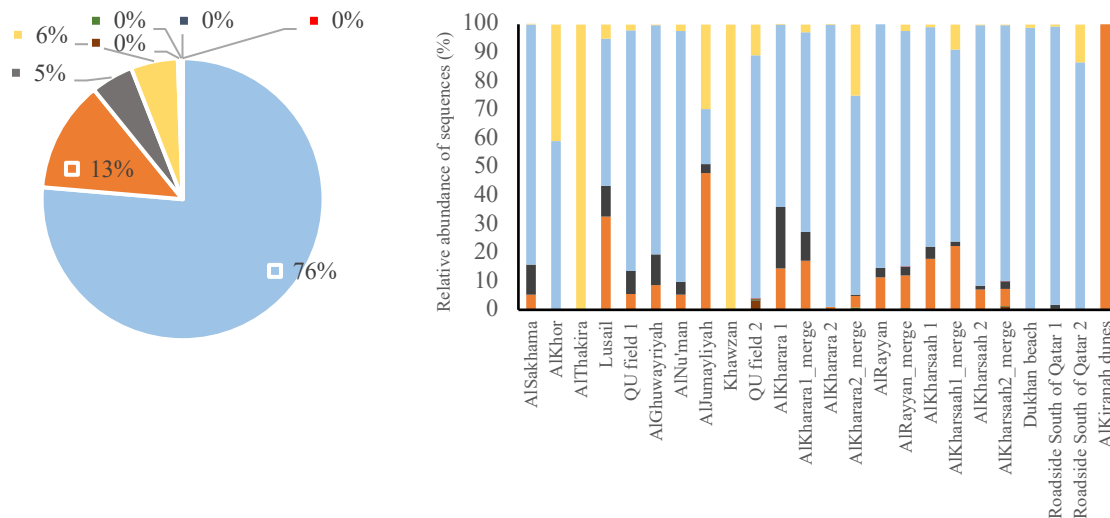


Figure 2. Relative abundance of arbuscular mycorrhizal (AM) fungi families presented across the dataset (pie chart) and per site (bar chart). The AM fungi species were identified by running a BLAST search against the MaarjAM. The abundance of some families was less than 0.1%. AM fungi families are presented in the following colors: *Acaulosporaceae* - ■, *Ambisporaceae* - ■, *Archaeosporaceae* - ■, *Claroideoglomeraceae* - ■, *Diversisporaceae* - ■, *Gigasporaceae* - ■, *Glomeraceae* - ■, *Paraglomeraceae* - ■

Community Composition and Frequency of Occurrence

Arbuscular mycorrhiza fungi indicators (indicator index value >0.25) originated from three main taxa: *Glomeraceae* at 15 sites, *Paraglomeraceae* at two sites, and *Claroideoglomeraceae* at two sites. However, the indicator index value was highest for *Glomeraceae* (13.33) and similar for *Paraglomeraceae* (2.98) and *Claroideoglomeraceae* (2.35) (Table S4). Variation in the composition of AM fungal genera was observed among the soil samples collected from all study locations (Figure 2). The genus *Glomus* was recorded at 80% of sites and was thus the dominant AM fungal taxon in the present study (Figure 3). This was followed by the genera *Paraglomus* (73% of sites), *Claroideoglomus* (67%), and *Diversispora* (67%), while the percentage frequency of occurrence of the remaining AM fungal genera ranged from 13% to 27%. The genus *Glomus* was not recorded in three locations: AlThakira saltmarsh, Khawzan, and AlKiranah sand dunes. Moreover, species from the genera *Acaulospora* and *Archeospora* were mostly found Qatar University (QU) field 2, an area with scattered shrubs within close proximity to a road. The infrequent occurrence of the genera *Acaulospora* and *Archeospora* could imply scarcity of these genera in highly arid regions, which are often restricted in resources (Kamalvanshi et al., 2012; Zerihun et al., 2013).

Taking into account the relative population size of each fungal family, the *Glomeraceae* had the highest species richness and evenness among the locations. AM fungal diversity was also highest for the *Glomeraceae*, and lowest for the families *Ambisporaceae* and *Gigasporaceae* (Table S5). The richness determined for each identified AM fungal family indicated a similar pattern and further established the *Glomeraceae* as the dominant AM fungal family across the dataset. The *Glomeraceae* also displayed the highest species evenness among the locations sampled, while the *Gigasporaceae* showed the lowest species richness (Figure 2).

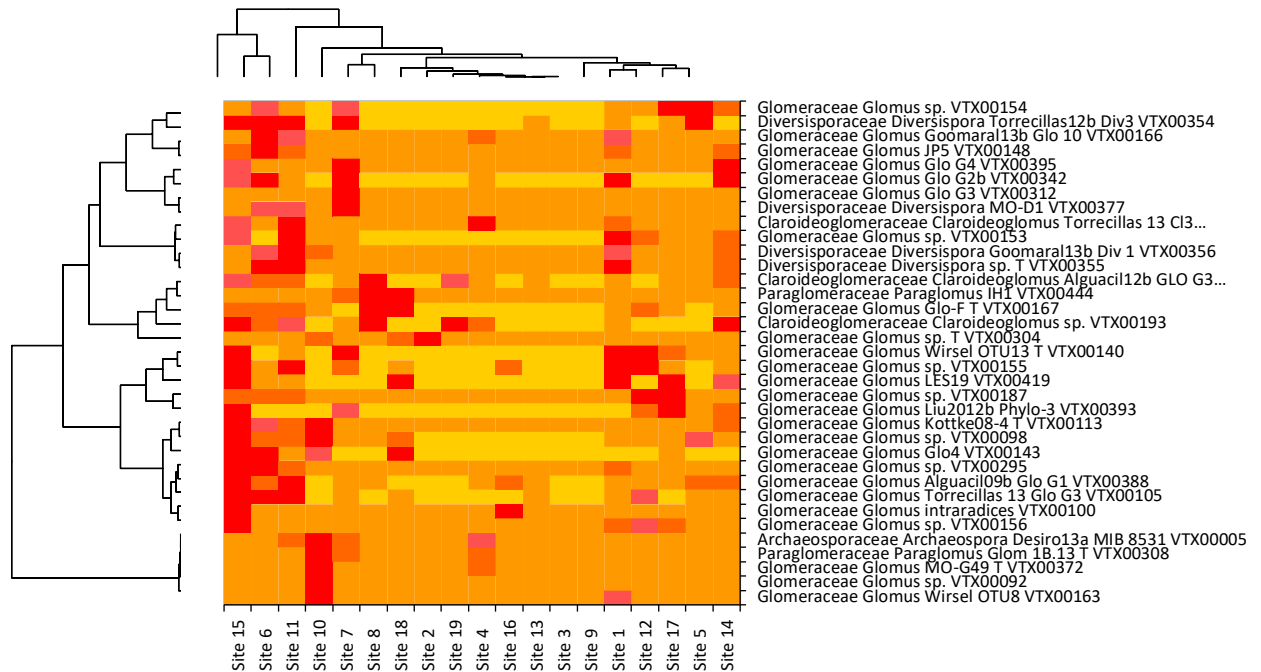


Figure 3. Heat map of operation taxonomic unit (OTUs) of arbuscular mycorrhizal (AM) fungi identified at all study sites. The intensity of color indicates the abundance of AM fungal species present at each sampling location (highest to lowest abundance is illustrated from red to orange to yellow).

Soil Chemical Characteristics

The highest salinities were recorded in AlKhor and AlThakira, in undisturbed areas of mangroves and saltmarshes, respectively, and at Qatar University, where samples were collected from the biology field (lowland coastal area). EC and TDS values were rather similar to salinity and were therefore clustered together (Figure 4). In terms of TC and TN, the absorbance of the 19 composite soil samples were measured and used to extrapolate %TC and %TN for each sampled location. However, the majority of %TN levels were negligible, with values well below the limit of detection. The only measurable TN content was determined in samples taken from the AlKhor

mangrove area, but it was still close to zero (0.014%). The TN measurements were therefore excluded from further analysis. Spectrophotometric measurements of NO_2^- and NO_3^- were made at 543 nm and the results indicated varying concentrations of NO_2^- and NO_3^- for different land types. Soil NO_3^- displayed a wider range of concentrations than soil NO_2^- , for which the values remained relatively constant between the locations (Table 2). The highest quantity of NO_3^- was found in soils from the QU fields, while soil extracts from the AlSakhama (sandy area with intermittent rocks and vegetation patches) had a higher NO_2^- content than other areas, although there were no significant differences in the concentration of NO_2^- and NO_3^- across the dataset. It was initially hypothesized that regions with high soil nutrient content are directly correlated with increasing diversity and abundance of AM fungal communities. The results indicated that availability of nutrients in Qatar's soils were comparatively homogeneous across the country.

Slight alkalinity was detected in soil from AlKhor, AlThakira, Khawzan, and AlJumayliyah (Table 2), which was likely attributable to the large extent of inland saltmarshes, mangroves, and surrounding coastal areas at those sites. The pH levels were rather consistent across the dataset, with soil samples from Dukhan and AlJumayliyah having the highest pH (Table 2). In contrast, the salinity levels fluctuated across the dataset. High salinity levels were found in soil samples from AlKhor mangroves and AlThakira saltmarsh, as a result of highly saline soil depressions predominantly colonized by halophytic plant species, including *Avicennia marina*. A spike in salinity was also observed for QU fields, AlKharrara, and AlRayyan, which may be attributable to influx of coastal waters into these lowland areas, creating inland salt flats that consist of fine silt and high salt content (Abulfatih et al., 2002; Majid et al., 2016). Much of Qatar's central peninsula is composed of a plateau of limestone and sandstone outcrops, contributing to the saline nature of the soil environment (Abulfatih et al., 2002; Babikir, 1990). Overall, the results strongly suggested

that soil habitats in Qatar are relatively saline, with the two-dimensional map indicating three distinct clusters (Figure 4).

Table 2. Statistical summary of soil chemical parameters, measured in triplicate

Location		Mean	Std. Deviation	95% confidence interval for mean		Min.	Max.
				Lower Bound	Upper Bound		
AlSakhama	pH	7.6200	0.04359	7.5117	7.7283	7.59	7.67
	Salinity	0.1333	0.05774	0.0101	0.2768	0.10	0.20
	NO ₃ ⁻	61.5400	0.61612	60.0095	63.0705	60.98	62.20
	NO ₂ ⁻	38.4667	0.64291	36.8696	40.0637	38.00	39.20
AlKhor	pH	8.3167	0.11504	8.0309	8.6024	8.20	8.43
	Salinity	5.4333	0.11547	5.1465	5.7202	5.30	5.50
	NO ₃ ⁻	73.7067	2.00852	68.7172	78.6961	72.00	75.92
	NO ₂ ⁻	36.3600	0.62354	34.8110	37.9090	36.00	37.08
AlThakira	pH	8.9533	0.04163	8.8499	9.0568	8.92	9.00
	Salinity	4.7667	0.05774	4.6232	4.9101	4.70	4.80
	NO ₃ ⁻	133.8567	0.13204	133.5287	134.1847	133.74	134.00
	NO ₂ ⁻	38.0933	0.96443	35.6975	40.4891	37.08	39.00
Lusail	pH	8.8033	0.02517	8.7408	8.8658	8.78	8.83
	Salinity	0.2000	0.00000	0.2000	0.2000	0.20	0.20
	NO ₃ ⁻	111.8733	10.68524	85.3297	138.4170	101.23	122.60
	NO ₂ ⁻	36.3767	0.83164	34.3107	38.4426	35.80	37.33
QU1	pH	8.6967	0.17616	8.2591	9.1343	8.59	8.90
	Salinity	0.4333	0.05774	0.2899	0.5768	0.40	0.50
	NO ₃ ⁻	88.1367	4.47761	77.0137	99.2597	83.40	92.30
	NO ₂ ⁻	34.8400	0.98148	32.4019	37.2781	33.80	35.75
QU2	pH	8.4333	0.20817	7.9162	8.9504	8.20	8.60
	Salinity	4.4667	0.05774	4.3232	4.6101	4.40	4.50
	NO ₃ ⁻	98.1433	1.03036	95.5838	100.7029	97.00	99.00
	NO ₂ ⁻	34.0367	1.42479	30.4973	37.5760	32.40	35.00
AlGhuwayriyah	pH	8.4900	0.06245	8.3349	8.6451	8.44	8.56
	Salinity	0.1333	0.05774	0.0101	0.2768	0.10	0.20
	NO ₃ ⁻	72.2667	0.95521	69.8938	74.6395	71.30	73.21

AlNu'man	NO ₂ ⁻	34.9467	2.45911	28.8379	41.0554	32.33	37.21
	pH	8.3033	0.10263	8.0484	8.5583	8.19	8.39
	Salinity	0.1000	0.00000	0.1000	0.1000	0.10	0.10
AlJumayliyah	NO ₃ ⁻	95.4200	1.51089	91.6667	99.1733	93.88	96.90
	NO ₂ ⁻	39.1833	0.90875	36.9259	41.4408	38.45	40.20
	pH	9.0000	0.10000	8.7516	9.2484	8.90	9.10
Khawzan	Salinity	0.1267	0.04619	0.0119	0.2414	0.10	0.18
	NO ₃ ⁻	91.0667	1.05040	88.4573	93.6760	90.00	92.10
	NO ₂ ⁻	31.8333	1.43727	28.2630	35.4037	30.32	33.18
AlKharrara1	pH	8.9200	0.04583	8.8062	9.0338	8.88	8.97
	Salinity	0.1333	0.05774	0.0101	0.2768	0.10	0.20
	NO ₃ ⁻	83.8767	1.16603	80.9801	86.7733	83.00	85.20
AlKharrara2	NO ₂ ⁻	36.2433	1.20234	33.2565	39.2301	35.00	37.40
	pH	8.7100	0.18248	8.2567	9.1633	8.50	8.83
	Salinity	0.1000	0.00000	0.1000	0.1000	0.10	0.10
AlRayyan	NO ₃ ⁻	72.7133	2.05417	67.6105	77.8162	70.84	74.91
	NO ₂ ⁻	38.1000	1.05357	35.4828	40.7172	37.10	39.20
	pH	8.5000	0.43589	7.4172	9.5828	8.00	8.80
AlKharsaah1	Salinity	3.5000	0.10000	3.2516	3.7484	3.40	3.60
	NO ₃ ⁻	44.2100	3.87586	34.5818	53.8382	40.00	47.63
	NO ₂ ⁻	35.3233	1.51876	31.5505	39.0961	33.87	36.90
AlKharsaah2	pH	9.0733	0.11015	8.7997	9.3470	9.00	9.20
	Salinity	2.1333	0.15275	1.7539	2.5128	2.00	2.30
	NO ₃ ⁻	63.8567	0.82367	61.8106	65.9028	63.28	64.80
Dukhan	NO ₂ ⁻	35.3767	0.66290	33.7299	37.0234	34.82	36.11
	pH	9.0100	0.01000	8.9852	9.0348	9.00	9.02
	Salinity	0.2333	0.05774	0.0899	0.3768	0.20	0.30
Dukhan	NO ₃ ⁻	111.1467	9.18600	88.3274	133.9659	103.46	121.32
	NO ₂ ⁻	35.3933	0.48583	34.1865	36.6002	34.84	35.75
	pH	8.7333	0.11547	8.4465	9.0202	8.60	8.80
Dukhan	Salinity	0.1333	0.05774	0.0101	0.2768	0.10	0.20
	NO ₃ ⁻	135.8033	5.15172	123.0057	148.6009	129.87	139.14
	NO ₂ ⁻	36.8033	1.58935	32.8552	40.7515	35.00	38.00
Dukhan	pH	9.0633	0.05508	8.9265	9.2001	9.00	9.10
	Salinity	0.1000	0.00000	0.1000	0.1000	0.10	0.10
	NO ₃ ⁻	75.9133	0.60616	74.4075	77.4191	75.33	76.54

North Qatar1	NO ₂ ⁻	34.6400	0.65023	33.0247	36.2553	34.00	35.30
	pH	8.9867	0.02517	8.9242	9.0492	8.96	9.01
	Salinity	0.1667	0.11547	0.1202	0.4535	0.10	0.30
North Qatar2	NO ₃ ⁻	165.1800	1.78681	160.7413	169.6187	163.49	167.05
	NO ₂ ⁻	36.9967	1.47690	33.3278	40.6655	35.36	38.23
	pH	9.0300	0.02000	8.9803	9.0797	9.01	9.05
	Salinity	0.1333	0.05774	0.0101	0.2768	0.10	0.20
	NO ₃ ⁻	114.6500	5.61043	100.7129	128.5871	109.08	120.30
AlKiranah	NO ₂ ⁻	36.9400	3.25374	28.8573	45.0227	33.20	39.12
	pH	8.4233	0.04933	8.3008	8.5459	8.39	8.48
	Salinity	0.1000	0.00000	0.1000	0.1000	0.10	0.10
	NO ₃ ⁻	15.9800	1.71616	11.7168	20.2432	14.00	17.04
	NO ₂ ⁻	36.8900	1.64508	32.8034	40.9766	35.00	38.00
Total	pH	8.6877	0.38185	8.5864	8.7890	7.59	9.20
	Salinity	1.1856	1.83424	0.6989	1.6723	0.10	5.50
	NO ₃ ⁻	89.9653	34.09562	80.9185	99.0120	14.00	167.05
	NO ₂ ⁻	36.1496	2.07678	35.5986	36.7007	30.32	40.20

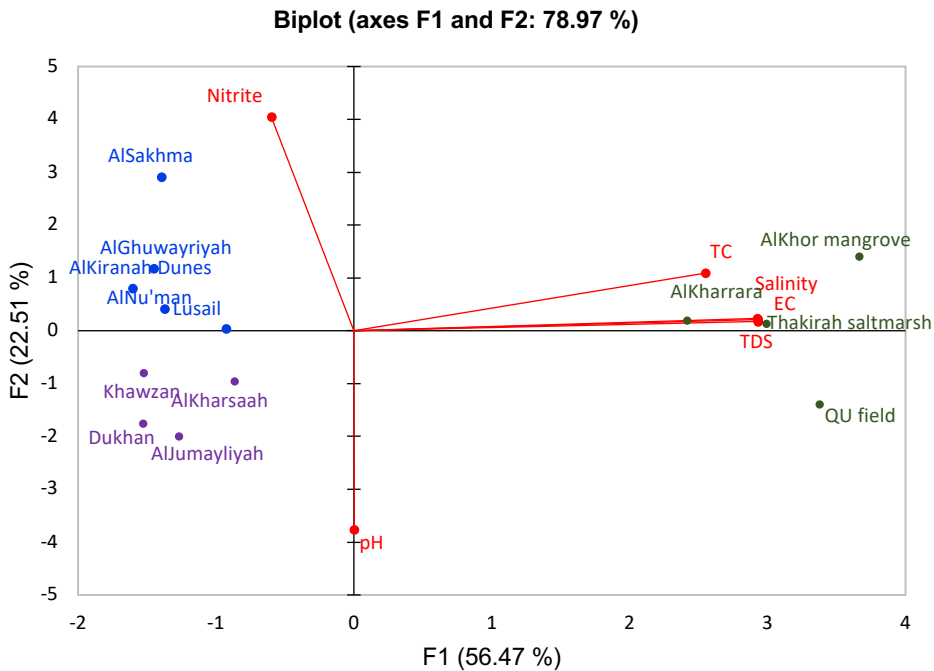


Figure 4. Two-dimensional correlation map computed from principal component analysis (PCA) showing the extent of influence of each chemical factor at the different locations. The significance of influence of a specific chemical factor is indicated by the distance of each location point from that chemical parameter on the graph.

Elemental Composition

The concentrations of Ca and Mg in the soil fluctuated between sites, but were higher in soils in undisturbed areas than in areas in close proximity to a city, urban structure, or road (Table 3). Among the measured elements, Ca showed the highest concentrations in the soils, with values well over 90,000 mg/kg at all 19 locations (Table 3). The lowest measured concentrations were for the heavy metals Cd and Pb, with Cd concentrations that ranged from 0.02 mg/kg to 0.40 mg/kg, and Pb concentrations that ranged from 0.12 mg/kg to 15.29 mg/kg. In quality control of ICP-OES measurements using a certified reference material (PACS3), percentage recovery (%R)

of each metal fell within 15% of the EPA criteria (accuracy 90-106%, n = 6) (Table S1). Two soil samples were prepared in triplicate and two blank samples were used to ensure precision in the data obtained and evaluate potential contamination during sample preparation. In terms of heavy metals, Lusail, AlSakhama, and QU were predominantly influenced by Pb, while AlJumayliyah showed little to no influence of the elements measured in this study (Figure 5). The analyses also indicated that the environmental conditions at AlJumayliyah are unique in a way not directly defined by the basic soil chemistry, but rather by a combination of abiotic components.

Table 3. Concentrations of elements in soil samples from each location

Location	Concentration (mg/kg)					
	Ca	Cd	K	Mg	P	Pb
AlSakhama	141175	0.4	9163	30090	522	8.67
AlKhor	286904	0.11	2393	15153	319	1.7
AlThakira	294279	0.08	2023	20633	269	2.08
Lusail	165214	0.19	6483	26043	305	4.46
QU1	151710	0.29	6250	29404	345	15.29
AlGhuwayriyah	108471	0.35	11713	40469	678	7.32
AlNu'man	101232	0.36	11103	38031	736	9.76
AlJumayliyah	95174	0.27	8592	10271	133	3.18
Khawzan	92467	0.19	7381	14302	140	3.41
QU2	173927	0.07	5542	22595	262	6.35
AlKharrara1	138876	0.27	9046	28272	478	7.34
AlKharrara2	295909	0.1	2355	15426	336	1.4
AlRayyan	276665	0.02	2790	21854	255	0.12
AlKharsaah1	172888	0.22	6485	25924	266	3.4
AlKharsaah2	107655	0.2	8795	19531	278	4.76
Dukhan	74949	0.15	6104	7334	123	2.95
North Qatar1	98698	0.18	8006	15430	173	3.2
North Qatar2	108095	0.14	7617	17552	160	2.96
AlKiranah	100426	0.31	9741	25062	345	5.18
Total Mean	157090.20	0.20	6925.37	22282.87	322.36	4.92
Std. Deviation	75336.29	0.11	2905.34	8726.24	172.62	3.58
First Quartile	100828.75	0.12	5823.05	15427.53	214.10	2.95
Third Quartile	173407.75	0.28	8920.38	27157.64	345.34	6.84
Min.	74948.79	0.02	2022.52	7333.60	122.58	0.12
Max.	295909.03	0.40	11712.75	40469.00	735.77	15.29

The PCA produced eigen values that reflected the quality of variables from the initial number of dimensions ($n = 6$) to a lower number of dimensions. The correlation circle computed from PCA projects the variability of factors (F) in space. Here, F1 and F2 accounted for 68% and 23% of the variation in soil concentrations of elements, respectively (Figure 5). Thus most of the percentage variation in the data was explained by the first dimension (F1), while F1 and F2 combined explained approximately 91% of the total variation. The concentrations of Mg and P were significantly positively correlated (r value close to 1), whereas Ca showed almost no correlation with the other elements (r value close to 0).

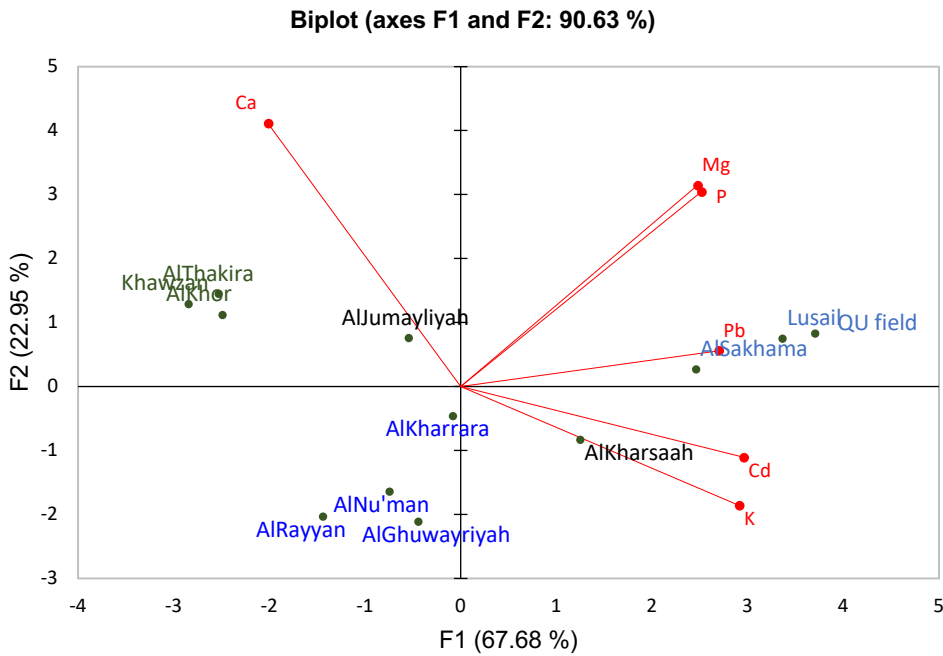


Figure 5. Two-dimensional correlation map computed from principal component analysis (PCA) showing the variation in metal concentrations between sampling locations. The significance of influence of a specific metal is indicated by the distance of each location point from that metal on the graph.

Effect of Chemical Properties and Habitat Type on AM fungal composition and diversity

Approximately 61% of the variation in AM fungal community was explained by six environmental variables: pH, TC, salinity, EC, TDS, and NO_3^- (Figure 6). Approximately 61% of the structure of AM fungi was influenced by these chemical parameters and land types combined (Figure 6). Axis F1 in the diagram indicated the greatest correlation with the explanatory variables salinity, EC and TDS, while the explanatory variables on axis F2 were only positively related to soil pH and negatively related to TC, NO_3^- , salinity, EC, and TDS (Figure 6). The overall effect of soil pH on AM fungal structure was significantly weaker than the relationship between AM fungal communities and nitrate. Sites with extensive vegetation coverage and higher NO_3^- content were mostly associated with AM fungal species from the genera *Claroideoglomus* and *Scutellospora*. The RDA plot also indicated that the effect of chemical parameters was much lower on *Glomus* than on other fungal phyla and species. As a result, the genus *Glomus* was more abundant and widely distributed at the study sites, likely due to its capacity to inhabit a broad range of niches.

The RDA results also showed that the effect of soil elements accounted for approximately 66% of the variation in the AM fungal community in this study. According to the standardized coefficients computed by RDA, axis F1 indicated positive correlations with five explanatory chemical variables: Mg (0.455), P (0.334), Pb (0.309), Ca (0.034), and K (0.033), all of which mostly affected the distribution of *Diversispora*, *Ambispora* and *Glomus* (Figure 6). However, soil Mg content showed the greatest effect on AM fungal distribution on axis F1. On the other hand, the coefficient of variation for Cd (0.478) and K (0.522), shown on axis F2 explained most of the correlation pertaining to distribution of AM fungi. Accordingly, it was apparent that Cd and K had the strongest influence on the distribution of *Diversispora* and *Ambispora*. The effect of the

elements K ($p=0.014$), P ($p=0.043$), and Cd ($p=0.049$) on AM fungal diversity was statistically significant (Table S6).

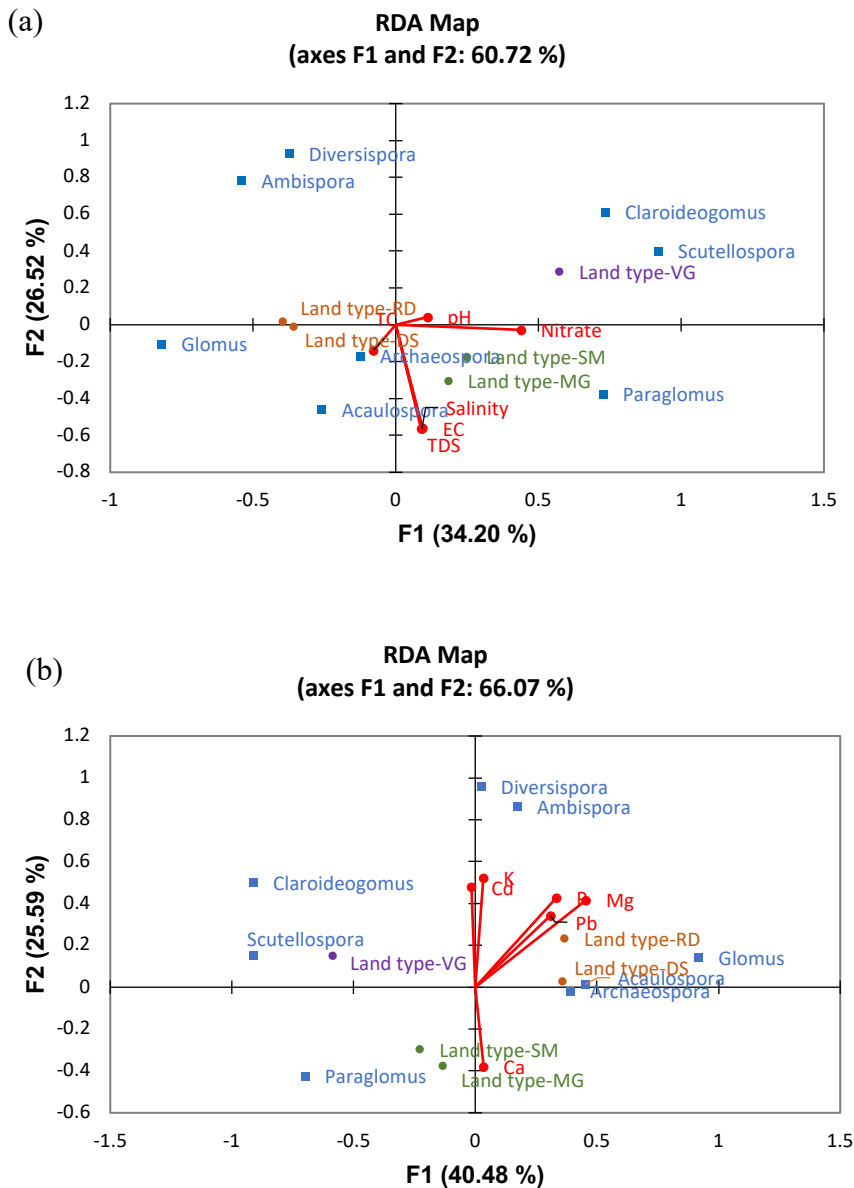


Figure 6. Distance-based redundancy (RDA) plots used to interpret the extent of correlation between different land types and arbuscular mycorrhizal (AM) fungi and (a) soil chemical parameters and (b) metals. Similar land types tend to cluster together in both cases, as they share similarities in soil chemical composition. The land types used in RDA were: vegetation/shrub land (VG), saltmarsh (SM), mangrove (MG), desert/barren land (DS), and *rawdha* (RD).

Discussion

Our results suggest that the *Glomeraceae* is the dominant family group thriving in Qatar's extreme habitat. However, AM fungal families were not evenly distributed among the study sites, as several locations such as AlJumayliyah and AlKiranah dunes were found to be largely populated by *Claroideoglomeraceae*; suggesting that specific AM fungi respond differently to various environmental conditions that allow them to occupy the soil successfully. The hypothesis that pH and salinity have a negative effect on AM fungi was not supported. The hypothesis that AM fungal richness is influenced by availability of macronutrients in soil was only partly supported, since P and K had a significant positive effect on AM fungal richness, while Cd showed a tendency to reduce the richness of AM fungi. Studies on soil fungi in semi-arid China have also found that the richness and abundance of fungal communities is mainly driven by soil P content (Tian et al., 2017; Xu et al., 2018; Zhao et al., 2017). This suggests that the diversity and abundance of fungal communities are generally positively correlated with the concentration of extractable soil P. The importance of soil chemistry and macronutrients to microbial communities has been demonstrated in AM fungal niche studies with similar climatic and environmental conditions to Qatar (e.g., Mendoza et al., 2011; Wang et al., 2017; Xu et al., 2018; Zhang et al., 2017). However, our data do not support the assumption that soil chemistry is the dominant factor controlling AM fungal communities. In our study, we found higher concentrations of soil NO_2^- and NO_3^- in vegetated saltmarshes (AlThakira) and grasslands with shrubs (AlKharsaah). In terms of the elements, we also found that locations with more shrubs, including QU fields, showed higher concentrations of Mg, K, and P than locations with more barren soils. Study sites with vast areas of barren land showed lower concentrations of NO_3^- , NO_2^- , and soil elements. These results indicate that areas

with more vegetation positively influenced soil nutrient conditions, although these nutrients had no effect on AM fungal diversity and richness.

We found that soil salinity had no effect on AM fungal populations. Highly saline soil conditions may cause adverse effects on root colonization, which in turn prevents successful plant-mycorrhizae associations from developing (Becerra et al., 2014). However, the effect of salinity and pH alone on AM fungal abundance was not statistically significant in the present study. It is likely that the AM fungi present in soils in Qatar have been exposed to high salinity levels through their evolutionary history. This prolonged exposure is likely to have favored fungal strains with natural resistance to salinity, through natural selection. Based on the data obtained, soils in lowland areas and regions within close proximity to Qatar's coasts (e.g., AlKhor, AlThakira, Dukhan and AlKiranah) were the most saline, although the salinity exhibited by these coastal areas had no effect on the richness of AM fungi. However, the diversity of AM fungi present in these locations was low, and they were mostly inhabited by species from the genus *Glomus*. *Glomus* also dominated at most sites in the north-east region, which was largely dominated by coastal shores, mangroves, and vegetated land (i.e., AlThakira and AlKhor). Due to their close proximity to Qatar's coasts and low topography, the soils at these sites exhibited higher pH and salinity. However, we found that the diversity of AM fungal families remained unchanged in different soil pH and salinity conditions across Qatar. The analyses showed that the pattern of fungal diversity throughout Qatar was independent of soil pH and salinity, which does not support the suggestion of an association between fungal diversity and richness and abiotic environmental conditions. This contradicts findings in previous studies (Tian et al., 2017; Xue et al., 2018), which highlighted the importance of soil type and chemical components for mycorrhizal communities.

The pH values measured across Qatar were within the range 7.59-9.20, which is similar to the pH range reported in other dryland studies (e.g., Delgado-Baquerizo et al., 2015; Tian et al., 2017; Wang et al., 2016). The highest pH was measured in the coastal areas of Dukhan and AlRayyan, where the sampling sites were mostly barren and without vegetation. However, most sites studied indicated relatively high pH levels, likely as a result of Qatar's arid climate. The majority of the Arabian Peninsula, including Qatar, is characterized by low rainfall and high atmospheric temperatures, contributing to high evapotranspiration rates and minimal leaching capacity. This causes ions such as carbonates and bicarbonates of Ca and Mg to accumulate in the soil, especially in areas at low altitude due to their proximity to seawater (Khanam et al., 2006). Moreover, highly alkaline soils are strongly associated with high, toxic quantities of iron (Fe), carbonate, and bicarbonate, nutrient deficiency, and elevated Na levels (Rengasamy, 2009). The accumulation of exchangeable Na ions in arid soils can potentially reduce the physical stability and overall fertility of the soil, resulting in an inadequate habitat for AM fungal root colonization. However, given the relatively narrow range in soil pH observed across Qatar, the effect of pH on AM fungi in the present study was insignificant.

Locations with higher vegetation coverage can lead to accumulation of plant litter and root exudates, which have been shown to increase TN, NO_3^- , and fungal abundance in the soil environment (Zhang et al., 2017). However, the fungal and chemical data derived in the present study indicated minimal association between TN and NO_3^- and fungal diversity. The results indicated that similar land types share relatively similar soil chemical characteristics, and thus show a comparable pattern to that reported in similar studies in desert habitats (Oyediran et al., 2018; Tian et al., 2017; Wu et al., 2007). Higher occurrence of mycorrhizal associations may be attributed to higher nutrient availability, specifically the composition of organic C, N, P, and K

(Bagyaraj & Revanna, 2017; Datta & Kulkarni, 2012; Gerz et al., 2018; Hossain & Sugiyama, 2011). In the present study, the lowest AM fungal diversity was observed in barren areas, e.g., Kiranah sand dunes and Dukhan, which could potentially be due to low bioavailability of TN, especially in areas with scarce vegetation. The highest diversity of AM fungi was identified in QU field 2, an area that had more developed grass patches than other locations. The data also showed that AM fungi were not affected by the chemical parameters pH, salinity, NO_2^- , NO_3^- , and TC. However, positive correlations were found between P and K and AM fungi, which supports the notion that AM fungi are directly dependent on the amount of bioavailable nutrients within and surrounding their host plant roots. This agrees with previous findings in some studies (Bhat et al., 2014; Timmer & Leyden, 1980), but contradicts those in other studies which reported a negative correlation between AM fungal population and K content (Khanam et al., 2006). Although soil K remains an essential component in AM fungal diversity, it may not be the dominant component, since fungal communities may also be driven by a combination of other environmental factors (Khanam et al., 2006). In addition to K, soil P may have a significant impact on AM fungal community structure, as available P stimulates hyphal development and fungal spore germination (Siles et al., 2015; Wang et al., 2017; Zhao et al., 2017). The positive influence of soil K on AM fungi is likely due to up-regulation in expression of two K-channel genes (*LbKTI* and *LbSKOR*) in plant roots under drought and arid conditions (Zhang et al., 2017). This in turn supports mycorrhizal colonization, explaining the positive influence of soil K and P on AM fungal communities.

The distribution and diversity of fungal families are strongly influenced by heavy metals, in addition to other well-known chemical drivers (i.e., pH, salinity, K, P, and NO_2^-) (Kasel et al., 2008; Lauber et al., 2008; Pan et al., 2020). Heavy metals, particularly Cd, not only alter the soil

chemistry, but also have detrimental effects on soil microbial communities when present even in small quantities, which could lead to losses in diversity and soil fertility (Bååth & Anderson, 2003; Kasemodel et al., 2019; Lin et al., 2019; Lv et al., 2019). AM fungi are generally sensitive to changes in soil conditions, including pH, heavy metals, and micronutrients, and are considered to be useful bioindicators of soil contamination (Dietterich et al., 2017; Kasemodel et al., 2019; Lin et al., 2019; Oehl et al., 2010; Pan et al., 2020; Vyas & Gupta, 2014). However, our results were inconsistent with those presented in other fungal diversity studies (Gaudino et al., 2007; Roupael et al., 2015; Song et al., 2018; Zarei et al., 2010). Throughout Qatar, Cd and Pb contamination of soils did not affect AM fungi, although Cd showed a tendency to influence AM fungal populations ($p=0.049$). However, both Cd and Pb were present at extremely low concentrations and the effect of these heavy metals on belowground fungal communities is generally reported to be largely dependent upon their concentrations. For example, Cd toxicity at the hyphal level in species within the genus *Glomus* has been reported at Cd concentrations above 0.38 mg/kg (Jiang et al., 2016). Given the unaltered diversity of AM fungi in Cd- and Pb-contaminated soils in our study, it is likely that these heavy metals had little to no influence on AM fungi, possibly because concentrations were well below the threshold or marginal effect.

Conclusions

Using the Illumina MiSeq sequencing platform, we identified a total of 127 AM fungal OTUs, eight families, and four orders from the phylum Glomeromycota. The main conclusions are: (1) Among the eight AM fungal families identified, Glomeraceae was the dominant fungal family across Qatar. The genus *Glomus* had the highest species richness (87 OTUs), while the

genus *Scutellospora* had the lowest species richness (1 VT). (2) Variations in the diversity, richness, and abundance of AM fungal OTUs between locations were mainly attributable to the soil P and K availability, while pH, salinity, NO_2^- , NO_3^- and TC had a negligible effect on AM fungal diversity. Thus soil P and K were the dominant driving factors shaping the distribution of AM fungi across Qatar's desert habitat. (3) A linear relationship between Pb and Cd concentrations and AM fungi was found, but was only significant for Cd. Thus Cd has a tendency to influence the diversity and richness of AM fungi, but not as strongly as soil P and K. The chemical parameters analyzed in this study accounted for 76% of the variation in AM fungal, while slight variations in the composition of AM fungi OTUs were independent of soil Mg, Ca, Cd, and Pb content. Overall, AM fungi inhabiting Qatar's desert habitat appear to have a relatively broad environmental niche, as their diversity is not affected by changes in chemical conditions in their soil environment.

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Conflicts of interest

The authors have no competing interest

Availability of data and material

The data have been deposited with links to BioProject accession number PRJNA675322 in the NCBI BioProject database (<https://www.ncbi.nlm.nih.gov/sra/PRJNA675322>)

Code availability

Not applicable

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Authors' Contributions

The study was designed by JMA. SA, JO, AMS, and TA conducted the laboratory work. SA analyzed the data and was the main author of the manuscript. All authors (SA, JO, JMA, AMS, MA, LT, MZ, TA) discussed and contributed to the final version of the manuscript.

Electronic Supplementary Material

Table S1. Concentrations of certified reference materials (PACS) and percentage recovery (%R) in tests to ensure quality control and reliability in the results from ICP-OES.

Table S2. Results of the Shapiro-Wilk normality test used to evaluate the distribution of each variable at 95% confidence interval. Datasets that were not normally distributed ($p < 0.05$) were normalized by logarithmic transformation.

Table S3. Statistical summary data on chemical factors across all sampled locations.

Table S4. Indicator analysis (indicator value > 0.25) calculated based on the abundance of operational taxonomic unit (OTUs) of arbuscular mycorrhizal (AM) fungi for each family identified.

Table S5. Alpha-biodiversity indices determined for each arbuscular mycorrhizal fungi family.

Table S6. Multiple linear regression evaluating the statistical significance ($p < 0.05$) of each chemical component on arbuscular mycorrhizal fungi abundance while all other variables were held constant.

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