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Species Richness of Arbuscular Mycorrhizal Fungi in Heterogenous Saline Environments

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Abstract: Sabkha (inland and coastal—saline beds or saline lands) are widespread in Saudi Arabia and are distinguished by their hypersaline nature. These hypersaline habitats are commonly covered by halophytic vegetation. Moreover, Arbuscular mycorrhizal fungi (AMF) are an essential component of these habitats and exhibit a unique adaptation and contribute significantly to ecosystem variability, diversity, and function. Additionally, AMF from saline habitats are an essential component for the successful rehabilitation of salinity-affected areas. Despite their importance, little is known about the distribution and abundance of AMF along inland and coastal sabkhat of Saudi Arabia. Therefore, the main objective of this study was to investigate the abundance and diversity of AMF in the coastal and inland sabkhat of Saudi Arabia. Five soil samples, each from five randomly selected spots (considering the presence of dominant and co-dominant halophytic species), were collected from every location and were used to assess the AMF abundance and diversity. The study indicated that the highest number of AMF spores was recorded from Jouf, averaging ≈ 346 spores 100 g^{-1} dry soil, and the lowest from Uqair, averaging ≈ 96 spores 100 g^{-1} dry soil. A total of 25 AMF species were identified, belonging to eight identified genera viz., *Acaulospora*, *Diversispora*, *Gigaspora*, *Scutellospora*, *Claroideoglomus*, *Funneliformis*, *Glomus*, and *Rhizophagus* and five families. Of the total identified species, 52% belonged to the family *Glomeraceae*. Moreover, the highest number of species was isolated from the sabkha in Qasab. Additionally, *Glomeraceae* was abundant in all the studied locations with the highest relative abundance in Uqair (48.34%). AMF species *Claroideoglomus etunicatum*, *Funneliformis mosseae*, *Glomus ambisporum*, and *Rhizophagus intraradices* were the most frequently isolated species from all the Sabkha locations with isolation frequency (IF) ≥ 60%, and *Claroideoglomus etunicatum* (Ivi ≥ 50%) was the dominant species in all the studied locations. Furthermore, data on the Shannon–Wiener diversity index showed that the highest AMF species diversity was in Qaseem and Qasab habitats. The highest Pielou's evenness index was recorded in Jouf. Moreover, the soil parameters that positively affected the diversity of identified species included Clay%, Silt%, HCO_3^{1-}, OM, MC, N, and P, while some soil parameters such as EC, Na^+, SO_4^{2-}, and Sand% had a significant negative correlation with the isolated AMF species. This study revealed that AMF can adapt and survive the harshest environments, such as hypersaline sabkhas, and thus can prove to be a vital component in the potential restoration of salinity-inflicted/degraded ecosystems.

Keywords: arbuscular mycorrhizal fungi (AMF); halophytes; diversity; sabkha; salinity

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1. Introduction

Arbuscular mycorrhizal fungi (AMF) are considered one of the prolific soil symbiotic microorganisms [1,2]. They are obligatory symbionts and are said to form an association with the roots of more than 72% of plant species [1,3] around all-natural ecosystems. AMF form a hyphal network in the plant rhizosphere and thus increase the access of roots to soil surface area in multifold, producing spores in the soil and arbuscules and vesicles inside the roots. AMF symbiosis, via this hyphal network, improve the growth of plants by enhancing the uptake of nutrients (N, P, K, C, etc.) and increasing the root hydraulic conductivity and water absorption [4–6]. The plant partner, in exchange, supplies up to 20% of the photosynthetically fixated carbon to the fungus [7]. AMF symbiosis also increases plant resistance to drought, protects against pathogens and pests, and reduces plant sensitivity to toxic substances in the soil [8–10]. They also improve ecosystem sustainability by allowing plants to respond quickly to degradation or other stresses [11]. Several studies have shown that inoculating AMF into degraded soil improves nutrient cycling, increases soil stability, and speeds up the establishment of native plants [8,11–13]. AMF symbiosis has been shown to help plants overcome extreme environmental conditions such as salinity [14,15]. Moreover, a multitude of AMF species have been discovered thriving in saline, both inland and coastal, habitats [8,15,16]. Additionally, several AMF species have been discovered in salt marshes and colonizing the roots of shoreline plants [17–20]. Therefore, as a keystone taxon, the belowground diversity of AMF contributes immensely to the adaptation and maintenance of plant biodiversity and to ecosystem functioning [11,21,22]. As a result, investigating AMF diversity in different ecosystems has become a research focus [23,24].

Sabkha is an Arabic term that is widely used for a salt flat (typically a salt-encrusted mudflat), which is a geological phenomenon that occurs in arid or semi-arid regions [25]. The sabkhat, plural of sabkha, are frequently brine-saturated, and their surfaces are frequently encrusted with several centimeters of thick salt crusts [20]. They have a wide geographical distribution, spanning Southeast Europe, California's siliciclastic coast, Mexico, North Africa from Morocco to Somalia, the Middle East and the Arabian Peninsula, Australia, and Asia [26]. In the Arabian Peninsula, Kinsman and Park [26] classified two major landforms of sabkhat, namely coastal and inland. Coastal sabkhat are low-lying marginal marine salt marshes, while inland sabkhat rise in basins away from the coast and are often surrounded by sand dunes [20]. The inland and coastal sabkhat of Saudi Arabia exhibit significant environmental variation in terms of soil moisture, salinity, light intensity, and temperature fluctuations [27]. Many halophytic species thrive in these ecosystems in specific mosaics [28,29], which are well adapted to these conditions via ecophysiological [30], morphological [31], and genetic variation [32], while certain species may struggle to survive in sabkhas, potentially resulting in barren landscapes. Additionally, these harsh ecosystems harbor a variety of microorganisms, including AMF, which play an important role in maintaining soil health. Fungal and other microbial taxa are among the distinctive biotic communities that exist in these highly saline habitats determined by heterogeneous environmental factors, such as salinity and temperature [33]. These species are highly specialized to adapt to these extreme conditions. These microorganisms significantly increase soil fertility by decomposing organic matter and recycle nutrients such as nitrogen and phosphorous, making them accessible to plants [22]. These microbiota also improve soil water retention and stabilization, reduce soil erosion, and alleviate drought and salinity stress [34]. AMF, in particular, help the plant roots absorb water and nutrients, sequester carbon, and fix nitrogen, which is essential for plant growth and survival in extremely harsh environments [35]. Despite the importance of AMF in their ecological roles among a wide range of environments, including saline habitats [22,36], the information about their abundance and diversity in these challenging sabkhat of Saudi Arabia is scarce [8].

AMF were assigned to the *Glomeromycota*, a newly formed monophyletic group, as a result of extensive research using the morphological and anatomical characteristics of their spores, as well as other modern approaches [37]. They were recently classified as subphylum *Glomeromycotina* in the phylum *Mucoromycota* [38]. Despite the fact that AMF have an ancient origin (400 million years) and played an important role in the evolution of plants, only 334 species have been identified so far [16].

Recent years have seen an increase in understanding the factors that influence the diversity and abundance of AMF in diverse ecosystems around the world. Although AMF diversity has been investigated in saline environments globally, not much has been studied regarding the distribution of AMF and the ecological roles they play in the highly saline coastal and inland sabkhat of Saudi Arabia. Thus, this study aims to address this gap by investigating the diversity and abundance of AMF in both coastal and inland sabkhat of Saudi Arabia. The main objective of this study was to provide the answers to key questions: What is the diversity and abundance of AMF in various inland and coastal sabkhat of Saudi Arabia? What is the impact of edaphic factors on the diversity, richness, and frequency of AMF species in hypersaline environments of Saudi Arabia? By studying these objectives, this study can provide preliminary insights into the AMF ecology and its potential role in the restoration and rehabilitation of fragile saline environments.

2. Materials and Methods

2.1. Description of Study Sites

The study was carried out across five hypersaline regions, encompassing two coastal and three inland sabkhas, each characterized by their ecological features and identified as follows: (1) Salwa, a lowland eastern mudflat coastal sabkha; (2) Uqair, lowland eastern coastal saline bed sabkha; (3) Qasab, Riyadh, inland saline flat sabkha, (4) Aushazia, Qaseem, inland saline flat-bed sabkha, and (5) Domat Aljandal, Jouf, inland flat saline sabkha (Figure 1). Most of the plant taxa cannot grow in sabkha except halophytes. The list of dominant plant species associated with each habitat is presented in Table 1 [28]. These saline ecosystems provide a good opportunity to study the diversity and ecological adaptation of AMF in these extreme conditions [39], thereby enhancing our comprehension of how these fungi support plant life in nutrient-poor and highly saline habitats.

Table 1. List of dominant plant species in the study region.

Qasab	Qaseem	Uqair	Salwa	Jouf
Aeluropus lagopoides (L.) Thwaites	*Aeluropus lagopoides* (L.) Thwaites	*Aeluropus lagopoides* (L.) Thwaites	*Aeluropus lagopoides* (L.) Thwaites	*Aeluropus lagopoides* (L.) Thwaites
Cressa cretica L.	*Cressa cretica* L.	*Zygophyllum album* L.f.	*Zygophyllum album* L.f.	*Cressa cretica* L.
Zygophyllum album L.f.	*Suaeda aegyptiaca* (Hasselq.) Zohary	*Juncus rigidus* Desf.	*Juncus rigidus* Desf.	*Tamarix nilotica* (Ehrenb.) Bunge
Cynodon dactylon (L.) Pers.	*Lycium shawii* Roem. and Schult.		*Phragmites australis* (Cav.) Trin. Ex Steud.	*Zygophyllum album* L.f.
	Salicornia persica L		*Phoenix dactylifera* L.	*Suaeda aegyptiaca* (Hasselq.) Zohary

The climate of Saudi Arabia is predominantly arid, characterized by hot and dry summers and cold rainy winters. It represents 5% of the world's arid region, highlighting its importance in desert ecosystems [40]. The relative humidity is usually low, except in coastal regions, where it can occasionally touch 100%. The average annual temperature during summers is 33 °C and winters is 14 °C, with significant seasonal and diurnal

fluctuations [27,41,42]. The rate of pan evaporation varies from season to season, being low in coastal regions and high in mountain areas, while reaching the highest in interior desert zones due to predominant arid conditions. Climate data for this study over 20 years period (2002–2024) were collected and sourced from https://en.climate-data.org/asia/saudi-arabia-29/ (accessed on 15 December 2024).

Figure 1. Map of Saudi Arabia showing the different Sabkha locations (marked as red) assessed for investigating AMF abundance and diversity. Arabic terms denote the names of the different cities as: الرياض = Riyadh; المدينة المنورة = Medina; جدة = Jeddah; مكة المكرمة = Makkah; دبي = Dubai; مسقط = Muscat; صنعاء = Sana'a; دمشق = Damascus.

2.2. Soil Sampling

For soil sampling, five distinct circular spots (30 × 30 m plots) were randomly selected from each location to ensure the representation of the studied sabkhas. Sampling plots were selected from each location having the maximum density of dominant and co-dominant halophytic species while avoiding barren sparsely vegetated areas. This ensured that the collected soil samples accurately reflect the rhizosphere zone where plant–AMF interactions are most active. From each spot, five soil samples (using soil corer, with a 5 cm diameter) were randomly collected at different points to capture the entire variability in soil and microbial properties of every plot. These five samples were thoroughly mixed to form a single composite sample. The composite sample methodology was chosen to minimize the influence of localized variability, which is common in such environments. So, a total of five pooled samples were collected from each location. Since AMF are highly active in 0–10 cm soil depth [43], all the samples were collected at the same depth (i.e., 10 cm) to have a better comprehension of the mycorrhizal diversity of different locations. All the soil samples were duly labelled and transferred to the Range Science Lab, College of

Food Science and Agriculture, King Saud University, Riyadh, Saudi Arabia. Soil from each sample was divided into sections for AM fungal spore quantification and soil analysis.

2.3. AMF Spore Extraction

For the extraction of AMF spores, the mixed soil samples from different sabkha locations were assessed following the wet-sieving and decanting method of Gerdemann and Nicolson [44] with some modifications by Dhar and Mridha [45]. A total of 100 g soil was taken in a beaker and mixed with 1000 mL of water from each sample. The thoroughly mixed soil–water suspension was left for five minutes for settling down of insoluble, coarse, and heavy particles before passing it through the series of stacked sieves (ASTM-60, ASTM-100, ASTM-270 and ASTM-400) to extract the spores [45]. The process was repeated a couple of times to ensure the collection of most of the spores with minimum loss. The material collected on the sieves were transferred into 50 mL tubes and centrifuged for 5 min (approx. 960× *g*) using a bench-top Hettich® EBA 20 centrifuge. The supernatant was discarded, and the pellet was re-suspended in a 20/60% gradient of sucrose solution. The suspension was centrifuged (approx. 960× *g*) again for 1–2 min. The supernatant in each tube was decanted into smaller sieves. The residues of the individual sieves were washed with tap water and filtered individually through Whatman filter paper No-1. After filtration, the paper was examined under the stereo-binocular microscope at 2.5 × 10 magnification and the number were recorded. Spores with similar morphological characters were grouped and mounted on slides with a mixture of polyvinyl alcohol-lactic acid-glycerol (PVLG) and Melzer's reagent (1:1, *v*/*v*) [46], for identification via already established literatures of [47,48]. International Culture Collection of (Vesicular) Arbuscular Mycorrhizal Fungi (INVAM) guidelines were also followed. After recording the characteristics, the coverslip was pressed gently to observe the internal structures and chemical reaction with mountant, if any.

The total number of spore population in each individual sample was calculated per 100 g dry soil basis. Percent population of AM fungal species was calculated by the following formula:

2.4. Soil Analysis

In the laboratory, a portion from each mixed soil sample was separated and spread out on separate plastic sheet, air-dried at room temperature, filtered through a 2 mm sieve to remove any debris, if any, and stored in a plastic bag until further analysis. The hydrometer method was used to examine the texture of the soil for the sand, silt, and clay fractions [49]. Wet combustion with dichromate at 450 °C was used to measure soil organic matter (OM) [50]. For the estimation of soil electrical conductivity (EC) and pH, soil water extracts (1:5) were made [50]. The titration method was used to evaluate soluble inions (Cl and SO_4^{2-}), while a flame photometer was used to measure soluble cations (Ca, Mg, Na, and K) according to Rhoades [51]. The soil-available phosphorus (AP) was assessed using the Olsen method [52], and available nitrogen (AN) was measured by following the established method of Best [53].

2.5. Statistical Analysis

Ecological measures of diversity used to describe the structure of AMF communities included spore density, species richness, relative abundance, isolation frequency, Shannon–Wiener index of diversity, Simpson's index of dominance, Pielou's index, and the similarity index [54–56]. These parameters were calculated as follows:

a. Spore density reflected the biomass of AMF species, at least to some extent. Direct counts of AMF spores under a binocular stereomicroscope were used to calculate

spore density, and all isolated spores from soil samples were counted, including some spores that lacked distinguishable morphological characteristics.

b. Species richness was defined as the number of species per sample detected in a certain type of habitat.

c. Relative abundance (RA) was defined as the percentage of spore number of a family, genus, or species, which indicated the sporulation ability of different species of AMF.

d. Isolation frequency (IF%) was defined as the percentage of soil samples in which a species occurred, which revealed the extent of distribution of a given AMF species in an ecosystem.

e. The importance value index (Iv*i*) was calculated to assess the dominance of AMF species based on IF and RD as Iv*i* = IF + RA. Species dominance was classified into four levels: the dominant species (Iv$i \geq 50\%$), the most common species ($30\% <$ Iv$i \leq 50\%$), common species ($10\% <$ Iv$i \leq 30\%$), and rare species (Iv$i \leq 10\%$) [56–58].

f. The Shannon–Weiner biodiversity index was used to evaluate the AMF diversity as:

$$H' = -\sum Pi\ ln\ Pi$$

where $Pi = ni/N$, ni = the number of individuals in species i, and N = the total number of individuals in all species.

g. Species evenness (E) was calculated by Simpson's (D) and Pielou's (P) indices as follows:

$$D = \sum[ni/ni - 1)/N(N - 1)]$$
$$P = H'/H_{max}$$

where H_{max} = ln S.

The data were statistically analyzed using analysis of variance (ANOVA) for a factorial design using the program SAS (SAS, v.9.1) and the differences in means was determined by the least significant differences (LSD) ($\alpha = 0.05$) test.

The soil data were subjected to one-way analysis of variance (ANOVA) to evaluate statistical significance among the locations using SAS® 9.2 Software. Upon significance, Tukey's honest significant difference (HSD) tests ($p = 0.05$) were used for pairwise mean comparison and to identify specific locations with statistically distinct soil properties. Heatmap correlation between AMF diversity and soil data was performed using the JMP® Pro 16.0.0 software program. Principal component analysis (PCA) was used to evaluate combinations of soil properties and AMF diversity within each location using JMP® Pro 16.0.0.

3. Results

3.1. AMF Spore Density

The quantified AMF spores from three coastal and two inland sabkhat are shown in Figure 2. As per the results, the production of spore population among all the sabkha habitats showed a significant variation (Figure 2). The highest number of spores was recorded in the samples collected from Jouf (≈346 spores 100 g^{-1} dry soil) and the lowest was displayed in the samples of Uqair (≈96 spores 100 g^{-1} dry soil). Moreover, the spore count of Uqair and Salwa (both coastal habitats) exhibited no significant difference.

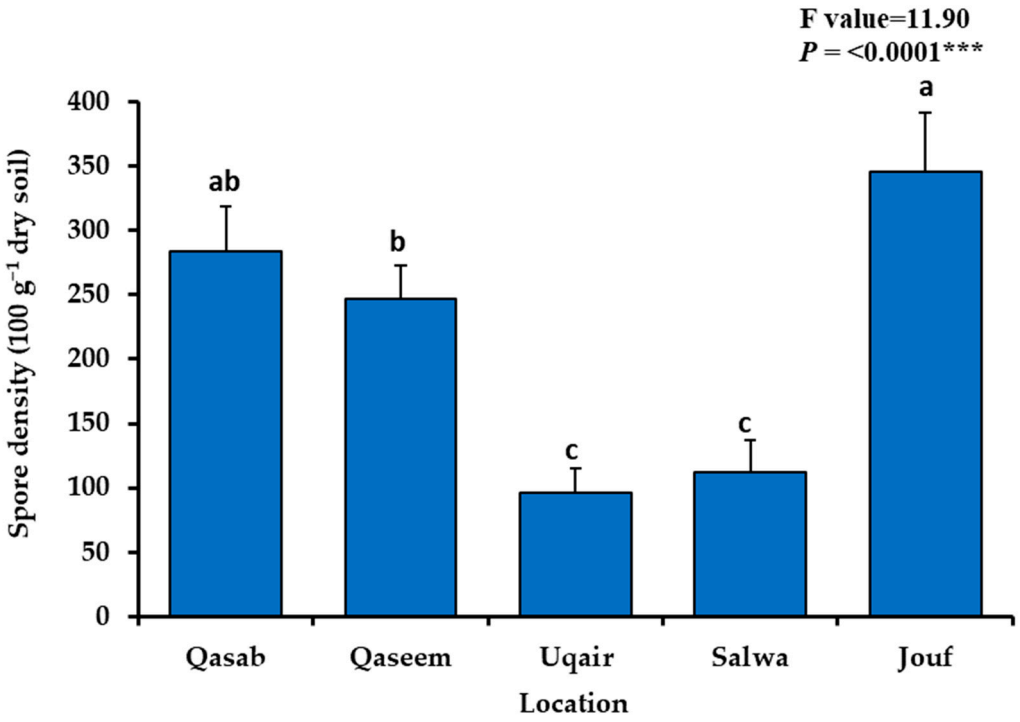

Figure 2. AMF spore density in the samples collected from different inland and coastal sabkha locations around Saudi Arabia. The colored bars represent mean values (n = 5), while the error bars indicate the standard error (SE). Different letters above the error bars represent significant difference (p = 0.05) based on Tukey's test. *** $p < 0.0001$ (Tukey test).

3.2. AMF Composition and Distribution in the Inland and Coastal Sabkhat

There were a total of 25 AMF species, which were subordinated to 8 genera representing 5 families in 2 order levels—*Diversisporales* and *Glomerales* (Table 2). Qaseem was the only location which inhabited all the identified eight genera, i.e., *Acaulospora*, *Diversispora*, *Gigaspora*, *Scutellospora*, *Claroideoglomus*, *Funneliformis*, *Glomus*, and *Rhizophagus*. Genera *Diversispora*, *Claroideoglomus*, *Funneliformis*, *Glomus*, and *Rhizophagus* were present in all the locations, while *Gigaspora* was found to inhabit sabkhat of Qasab and Qaseem. Genus *Acaulospora* and *Scutellospora* were recorded only in Qaseem. The species number among the studied saline habitats showed a marked difference (Table 2). The highest number of species (20 species/location) was identified from the sabkha habitat in Qasab, while the lowest (12 species/location) was recorded from the sabkhat of Uqair and Salwa each.

Of the 25 species, 13 species were identified from the family *Glomeraceae*, which accounted for 52% of the total identified species (Table 2). Moreover, four species belonged to *Diversisporaceae*, three each to *Gigasporaceae* and *Claroideoglomeraceae*. The lowest species count was recorded in the family *Acaulosporaceae*. Moreover, an abundant number of unidentified AMF spores were recorded from all the studied sites. These spores included those with irregular shapes, unusual colors, or structural damage, making morphological identification impossible. These distortions likely resulted from environmental stress, fungal senescence, or sampling conditions, complicating taxonomic classification. Their presence highlights the complexity of AMF communities and the challenges in accurately cataloging fungal diversity.

With regard to species diversity, the genus *Rhizophagus* showed the highest number of species (viz., *R. aggregatus*, *R. intraradices*, *R. fasciculatus*, *R. manihotis*, and *R. morphotype*-not identified to species level) which constituted the 19% of the total (Table 3). Four species each belonged to the genera Diversispora (*D. epigaea*, *D. globifera*, *D. tortousa*, and *D. morphotype*), Funneliformis (*F. coronatum*, *F. geosporum*, *F. mosseae*, and *F. morphotype*) and Glomus

(*G. ambisporum*, *G. hoi*, *G. caledonius*, and *G. morphotype*), with each genus accounted for 15.4% of the species count. Genus *Claroideoglomus* contained three species, including *C. claroideum*, *C. etunicatum*, and *C. morphotype* (not identified to the species level). Two genera *Acaulospora* and *Scutellospora* contained two species (*A. delicata* and *A. morphotype* and *S. calospora* and *S. morphotype*, respectively). Only one species was identified from genus *Gigaspora* (*G. margarita*).

Table 2. The distribution of AMF order, family, genus, and the number of species in soil samples collected from different inland and coastal sabkhat.

Order	Family	Genus	Locations					
			Qasab	Qaseem	Uqair	Salwa	Jouf	Total
Diversisporales	*Acaulosporaceae*	*Acaulospora*	0	2	0	0	0	2
	Diversisporaceae	*Diversispora*	3	1	1	2	2	4
	Gigasporaceae	*Gigaspora*	1	1	0	0	0	1
		Scutellospora	0	2	0	0	0	2
Glomerales	*Claroideoglomeraceae*	*Claroideoglomus*	3	2	2	2	3	3
	Glomeraceae	*Funneliformis*	4	4	3	3	4	4
		Glomus	4	2	2	2	2	4
		Rhizophagus	5	4	4	3	5	5
AMF species richness location^{-1}			20	18	12	12	16	25

Total: Total AMF species.

3.3. Abundance of AMF Species

The AMF communities collected from different sabkha habitats belonged to *Diversisporales* and *Glomerales*, which were further divided into five families and eight genera (Table 2, Figures 3 and 4). *Glomerales* was dominant in all the studied sabkha habitats with relative abundance ranging from 66.09% in Qaseem to 54.17% in Salwa (Figure 3A). Similarly, the family *Glomeraceae* was abundant in all the locations with the highest relative abundance recorded in Uqair 48.34% followed by Qaseem 47.36% (Figure 3B). As per our results, genus *Funneliformis* had the highest relative abundance in Qasab (29.15%), Qaseem (21.97%), and Jouf (34.87%) sabkhat, while genus *Rhizophagus* showed the highest in Uqair (33.81%) and Salwa (23.97%) (Figure 4A). *C. etunicatum* was the dominant species in four of the five studied locations with relative abundance varying from 9.8% in Qaseem to 21.78% in Uqair (Figure 4B).

3.4. Isolation Frequency and Importance Value Index of AMF Species Along the Different Sabkha Habitats

The results in our study show that the AMF species *C. etunicatum*, *F. mosseae*, *G. ambisporum*, and *R. intraradices* were the most frequently isolated species from all the sabkha locations with IF $\geq$ 60% (Table 3), followed by *Claroideoglomus* species and *Funneliformis* species with IF $\geq$ 60% in four of the five studied locations. *F. mosseae* and *R. intraradices* showed isolation frequency of 100% in three of the five studied sabkha habitats. The other species that were most frequently isolated were *D. epigaea*, *F. geosporum*, *R.fasciculatus*, and *R. manihotis* with IF $\geq$ 60% in three studied locations.

Table 3. Isolation frequency (IF%), and important value index (Ivi%) of AMF species collected from the soil samples of sabkhas.

AMF	Qasab		Qaseem		Uqair		Salwa		Jouf	
	IF	Ivi	IF	Ivi	IF	Ivi	IF	Ivi	IF	Ivi
Acaulosporaceae										
Acaulospora delicata	0	0	40	20.9	0	0	0	0	0	0
Acaulospora morphotype	0	0	100	54.7	0	0	0	0	0	0
Claroideoglomeraceae										
Claroideoglomus claroideum	40	20.9	0	0	0	0	0	0	60	31.8
Claroideoglomus etunicatum	100	57.9	100	54.9	100	60.9	100	57.3	100	58.6
Claroideoglomus morphotype	100	52.4	100	52.5	40	21.9	100	54.3	100	51.8
Diversisporaceae										
Diversispora Epigaea	80	43.6	0	0	60	32.5	80	43.6	60	32.5
Diversispora globifera	40	20.7	40	20.8	0	0	80	43.1	0	0
Diversispora tortousa	0	0	0	0	0	0	0	0	40	20.3
Diversispora morphotype	40	20.4	0	0	0	0	0	0	0	0
Glomeraceae										
Funneliformis coronatum	100	53.9	40	21.5	0	0	0	0	40	20.9
Funneliformis geosporum	80	43.7	100	54.1	40	22.1	40	21.7	80	46
Funneliformis mosseae	100	55.6	100	53.8	80	44.6	80	44.4	100	57.7
Funneliformis morphotype	100	51.4	80	41.6	20	10.4	60	31.9	100	52.8
Glomus ambisporum	80	42.1	100	53	80	45.6	80	45.2	80	41.5
Glomus caledonius	20	10.5	0	0	0	0	0	0	0	0
Glomus hoi	40	20.5	0	0	0	0	0	0	0	0
Glomus morphotype	40	20.4	80	41.8	40	21.2	80	42	60	30.5
Rhizophagus aggregatus	100	53.9	40	21.3	0	0	0	0	80	42.3
Rhizophagus intraradices	100	53.1	100	56.6	60	32.3	100	56.9	80	43.5
Rhizophagus fasciculatus	40	21	40	20.4	100	55.8	80	42.8	80	42.5
Rhizophagus manihotis	80	42.4	0	0	100	58.4	80	42.2	80	43.6
Rhizophagus morphotype	80	40.9	60	30.7	20	10.4	0	0	60	31.1
Gigasporaceae										
Gigaspora margarita	40	20.6	100	52.4	0	0	0	0	0	0
Scutellospora calospora	0	0	100	53.4	0	0	0	0	0	0
Scutellospora morphotype	0	0	100	52.5	0	0	0	0	0	0.17

The species in different locations were classified as dominant, most common, common, and rare based on the importance value index (Iv*i*) (Table 3). The data in the results indicate that the highest number of dominant species (ten) were recorded from the sabkha habitat in the Qaseem region, which was followed by sabkha in Qasab with seven dominant species. The sabkhat in Uqair and Salwa revealed an equal and lowest number (three) of dominant species. Similarly, the number of most common species (ten) was found to be highest in the samples collected from the sabkha in Jouf (Table 3). The lowest was recorded from Qaseem. The number of common species (10% < Iv*i* $\leq$ 30%) was highest in Qasab with eight species. The only rare species viz., *Scutellospora morphotype*, was found in Jouf. As per the results, the AMF species *Claroideoglomus etunicatum* was the dominant species in all the

studied locations, with *Claroideoglomus morphotype* in four, and *Funneliformis mosseae* and *Rhizophagus intraradices* in three.

3.5. AMF Diversity of Soil Samples Collected from Different Sabkha Locations

Shannon's, Simpson's, Pielou's, and similarity indices represented the AMF community's diversity, evenness, dominance, richness, and similarity, respectively (Figures 5A–C and 6). The data on the Shannon–Wiener diversity index of AMF isolated from the samples of sabkha habitats are shown in the (Figure 5A). As per the Shannon–Wiener diversity index, the AMF diversity among all the locations did not show a significant difference. The highest AMF diversity was shown in the sabkhat of Qaseem (2.56 ± 0.04) and Qasab (2.44 ± 0.11) followed by Jouf (2.25 ± 0.19). The lowest diversity was recorded in Uqair (2.26).

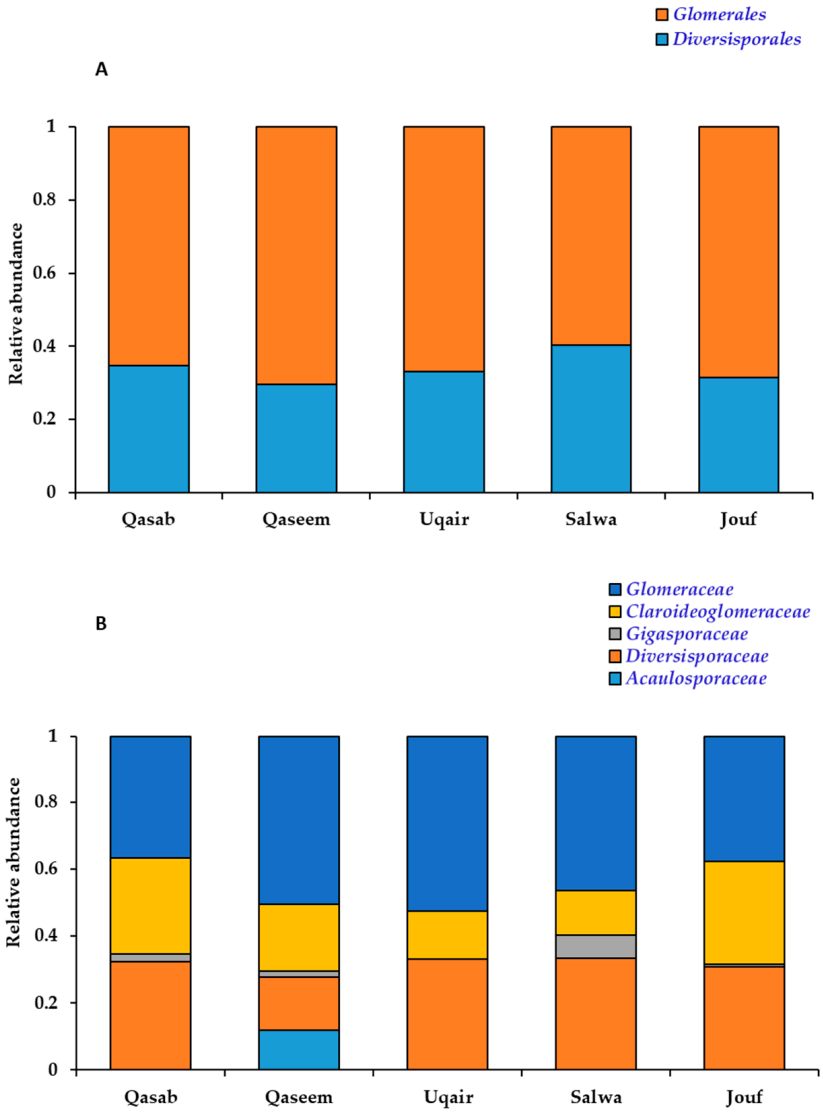

Figure 3. Relative abundance of AMF communities at order (**A**), and family (**B**) level in the soil samples collected from different sabkha habitats.

The data on Simpson's dominance index show that Qaseem and Qasab had the similar and the highest AMF species dominance followed by Salwa and Jouf, which also showed a similar Simpson's species dominance (Figure 5B). The lowest AMF species was recorded in Uqair.

The Pielou's evenness index showed a clear trend of variation among the different sabkha habitats (Figure 5C). Qaseem and Salwa showed the highest Pielou's evenness index while the lowest was recorded in Jouf.

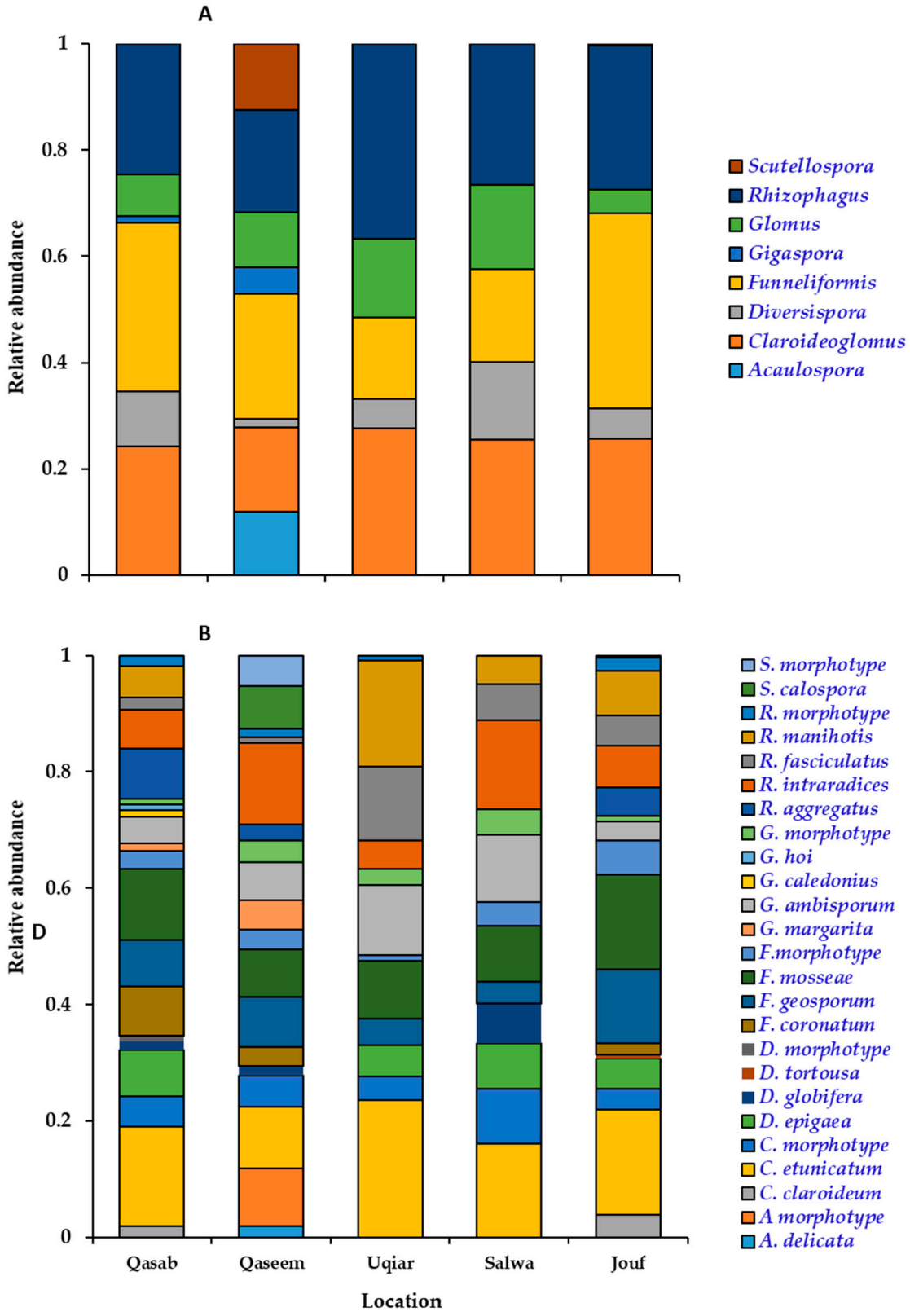

Figure 4. Relative abundance of AMF communities at genus (**A**) and species (**B**) level in the soil samples collected from different sabkha habitats.

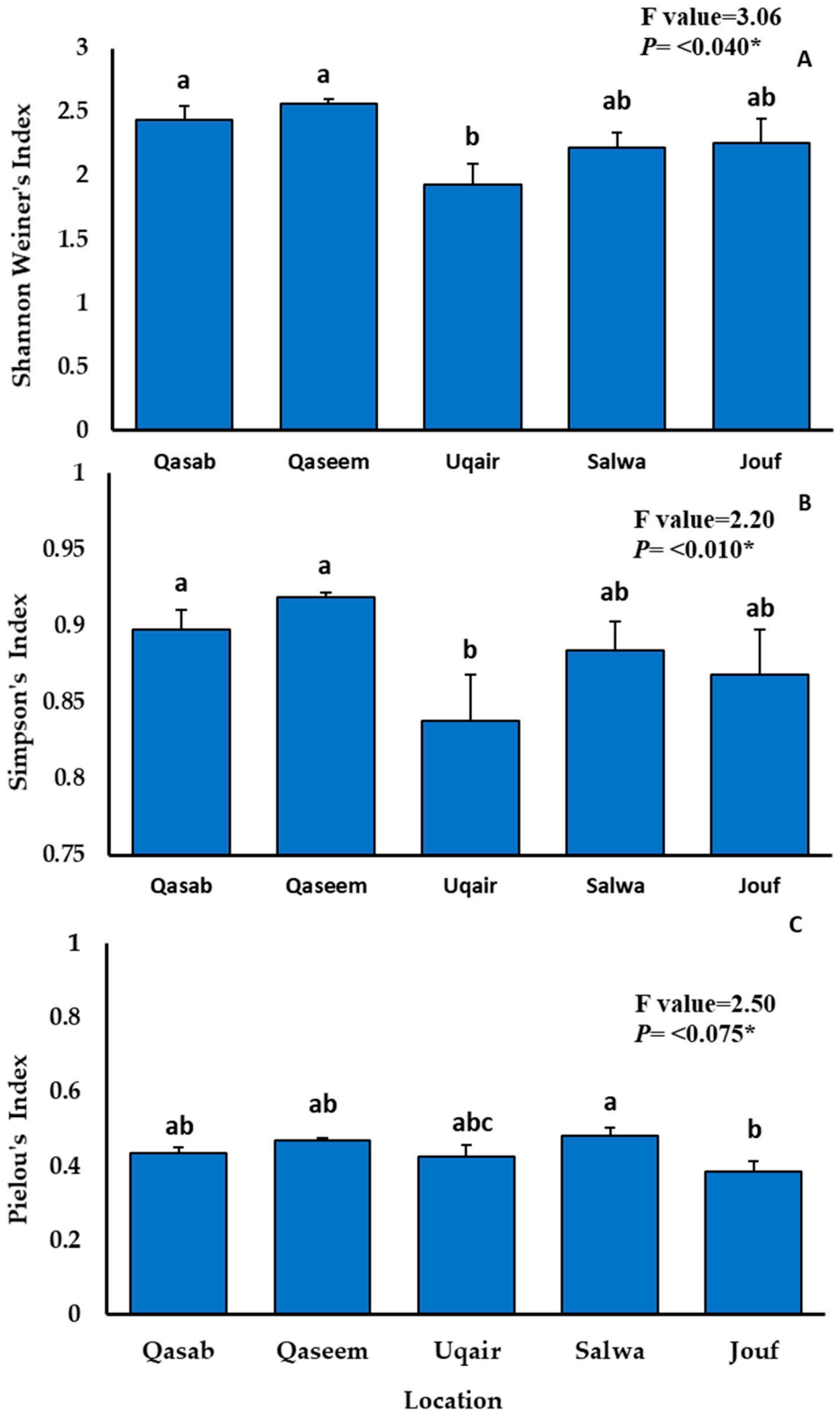

Figure 5. The variation in AMF species among different hypersaline sabkha habitats with the Shannon–Wiener diversity index (**A**); Simpson's dominance index (**B**); and Pielou's evenness index (**C**) of species. Different letters above the error bars represent significant differences ($p = 0.05$) based on Tukey's test. * $p < 0.01$.

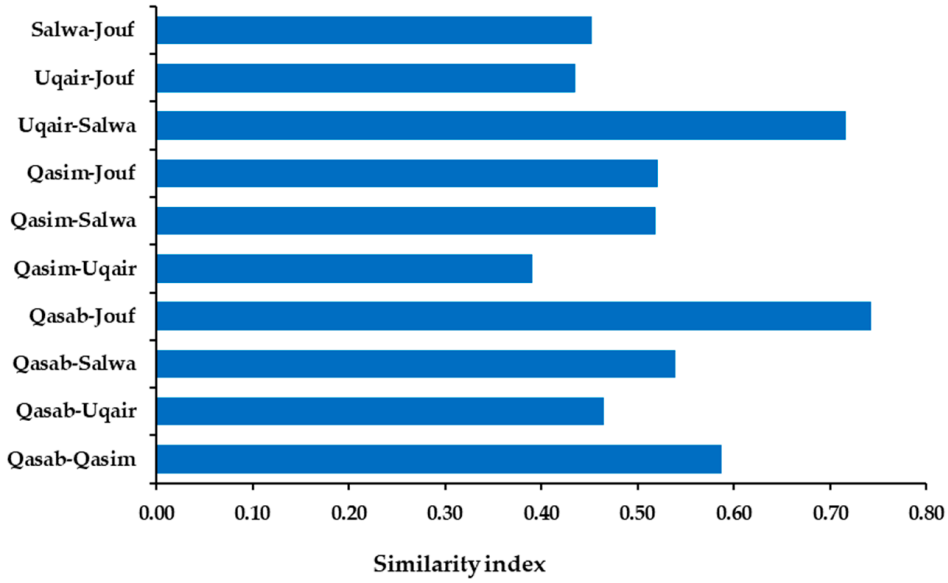

Figure 6. The similarity index of AMF species between different hypersaline sabkha habitats.

The pairwise similarity index based on the richness of AMF species between different sabkha locations is presented in Figure 6. This shows that the highest similarity index was estimated between the Qasab and Jouf regions (0.74). This suggests that both these locations are inland sabkhas and share similar habitat conditions. The similarity in soil physiochemical characteristics and vegetation composition may help to contribute to the presence of comparable AMF species. In contrast, the least similar locations were Qaseem and Uqair (0.39). This difference may be attributed to distinct habitat conditions, one being an inland sabkha and another being a coastal one. The variation in soil properties and associated plant species in their respective habitats significantly influences the distribution and richness of AMF species.

3.6. Soil–AMF Relationship

The texture of the soil differed among the different locations (Table 4). The soil collected from the sabkha in Qasab had sandy loam textures, the texture of the sabkha in Qaseem was sandy clay loam, Uqair was loamy sand, while the sabkhat in Salwa and Jouf had a sandy soil texture.

The analysis of soil physiochemical parameters revealed that studied parameters varied significantly between coastal and inland sabkha locations, except for pH, which was statistically similar in all locations. Moisture content percentage (MC%) of inland sabkhat was significantly higher, with Qaseem showing the highest MC% of 23.23 + 2.09%. The coastal sabkhat Uqair and Salwa did not vary in their MC%. Soils from all the locations were highly alkaline, ranging from 8.16 ± 0.402 for Jouf to 8.88 ± 0.611 for Salwa. The electrical conductivity (Ec) ranged from 9.37 ± 0.432 dS m^{-1} for Jouf to 31.35 ± 1.583 dS m^{-1} for Uqair (Table 4). Statistically, soils from Qasab and Jouf did not show significant difference in their Ec. However, the Ec of Uqair (31.35 ± 1.583 dS m^{-1} and Salwa (29.59 ± 1.40 dS m^{-1})) was significantly higher. The percentage of organic matter (OM%) showed no significant difference with the highest OM% in Qaseem and Qasab, respectively. As per the statistical analysis, available nitrogen (N), phosphorus (P), and potassium (K) were shown to have significant change among all the sabkha locations. The highest P content was recorded in Qasab (120.01 ± 19.687), while the highest K was observed in samples of Qaseem (525.24 ± 51.828). However, N was significantly higher in both Qasab (120.01 + 19.687) and Qaseem (114.16 + 14.005). The cations (Ca^{2+}, Mg^{2+}, Na^{1+}, and K^{1+}) and anions (Cl^{1-}, HCO_3^{1-}, and SO_4^{2-}) also varied significantly among all the sabkhat locations.

Table 4. Physical and chemical properties of soil samples (n = 5) collected from different hypersaline sabkhat locations of Saudi Arabia.

Parameters	Region					F Value	*p*-Value
	Qasab	Qaseem	Uqair	Salwa	Jouf		
MC%	9.06 ±0.861 bc	23.23 ±2.090 a	4.32 ±0.499 c	4.97 ±0.874 bc	9.40 ±1.209 b	47.72	<0.0001 ***
pH	8.22 ±0.426 a	8.49 ±0.210 a	8.56 ±0.368 a	8.87 ±0.611 a	8.16 ±0.402 a	0.47	0.759 ns
EC (dS m^{-1})	12.37 ±1.026 c	24.82 ±1.024 b	31.34 ±1.583 a	28.58 ±1.409 ab	9.37 ±0.432 c	74.5	<0.0001 ***
Ca (meq/L)	35.66 ±4.502 ab	42.43 ±4.683 a	45.29 ±6.196 ab	37.70 ±3.157 ab	22.36 ±1.887 b	4.17	0.012 *
Mg (meq/L)	35.78 ±3.659 ab	46.61 ±5.766 a	36.63 ±2.907 ab	32.96 ±2.502 ab	21.41 ±1.839 b	6.3	0.001 **
Na (meq/L)	50.33 ±5.647 c	143.98 ±11.667 b	206.72 ±13.001 a	212.02 ±10.992 a	44.35 ±2.856 c	71	<0.0001 ***
K (meq/L)	1.87 ±0.376 c	15.19 ±1.976 b	24.53 ±2.147 a	12.89 ±1.063 b	5.59 ±0.627 c	38.3	<0.0001 ***
Cl (meq/L)	102.06 ±10.122 c	209.40 ±15.397 b	274.53 ±15.545 a	264.20 ±15.386 ab	82.08 ±5.684 c	47.5	<0.0001 ***
SO_4(meq/L)	19.27 ±1.756 ab	35.30 ±6.466 a	36.79 ±6.001 a	29.26 ±5.208 ab	9.87 ±1.171 b	5.93	0.002 **
HCO_3 (meq/L)	2.51 ±0.396 ab	3.29 ±0.567 a	1.83 ±0.066 ab	1.66 ±0.240 b	2.35 ±0.273 ab	3.37	0.029 *
OM%	0.50 ±0.041 bc	1.03 ±0.111 a	0.65 ±0.055 bc	0.72 ±0.064 b	0.36 ±0.053 c	13.6	<0.0001 ***
N	120.01 ±19.687 a	114.16 ±14.005 a	80.60 ±4.360 b	70.94 ±6.581 b	82.94 ±6.507 b	3.48	0.025 *
P	4.16 ±0.792 a	0.43 ±0.049 b	3.05 ±0.698 a	2.25 ±0.145 ab	3.55 ±0.391 a	10.6	0.0005 ***
K	213.60 ±30.385 b	525.24 ±51.828 a	517.74 ±51.284 a	363.64 ±33.740 ab	249.49 ±29.155 b	2.36	<0.0001 ***
$CaCO_3$%	9.09 ±1.186 b	9.03 ±0.808 b	4.73 ±0.825 c	16.24 ±1.520 a	2.68 ±0.274 c	26.5	<0.0001 ***
Clay%	14.93 ±2.335 a	14.25 ±1.458 a	11.71 ±1.389 a	14.12 ±2.030 a	17.84 ±2.331 a	1.26	0.317 ns
Silt%	9.56 ±1.539 b	31.85 ±2.142 a	9.32 ±1.197 b	2.77 ±0.534 c	12.00 ±1.668 b	53.1	<0.0001 ***
Sand%	75.51 ±1.539 ab	53.91 ±1.539 c	78.98 ±1.539 ab	83.11 ±1.539 a	70.16 ±1.539 b	14.7	<0.0001 ***

Note: Ec, electrical conductivity (dSm^{-1}); Ca^{2+}, Mg^{2+}, Na^{1+}, and K^{1+} are the cations calculated as meqL^{-1}; and Cl^{1-}, $HCO_3{}^{1-}$, and $SO_4{}^{2-}$ are the anions as meqL^{-1}. Vales in the rows are means (n = 5) followed by (±SE). Different letters within each row (among regions) indicate mean value significance at ($p < 0.05$). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, and "ns" non-significant at $p > 0.05$.

3.7. Relationship Between Soil Characteristics and Species Diversity

The results in Figure 7 indicate that a strong positive correlation was observed between most of the soil parameters (Clay%, Silt%, $HCO_3{}^{1-}$, OM%, MC%, N, and P) and the AMF species (*S. morphotype*, *S. calospora*, *R. manihotis*, *R. intraradices*, *R. aggregatus*, *F. morphotype*, *F. mosseae*, *F. geosporum*, *D. tortousa*, *C. morphotype.*, *C. etunicatum*, and *C. claroideum)*, while some of the species for this group (*R. morphotype*, *R. manihotis*, *R. aggregatus*, *F. morphotype*, *F. mosseae*, *F. geosporum*, *D. tortuosa*, *D. epigaea*, *C. etunicatum*, and *C. claroideum*) were negatively correlated with EC, Na^+, $SO_4{}^{2-}$, and Sand%. These results emphasize the diversities of AMF species' relationship with soil properties, which suggest their unique ecological preference and adaptability.

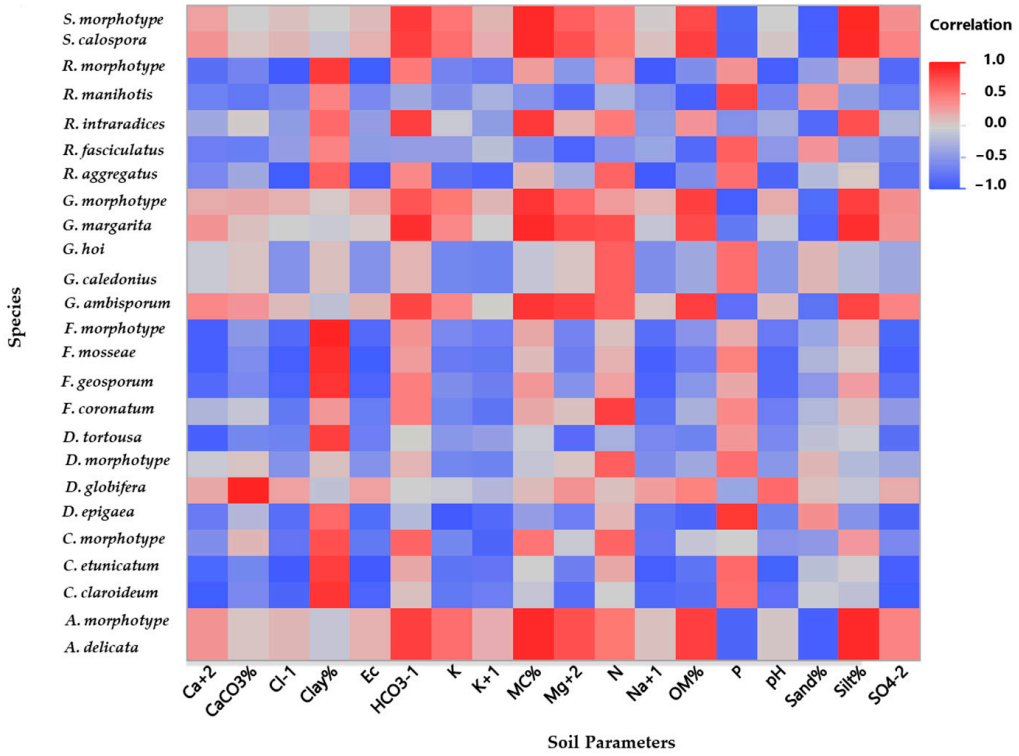

Figure 7. A correlation heatmap of the relationship between soil parameters and the AMF species isolated along different sabkha habitats. Red colors indicate a strong positive correlation while blue indicates a significant negative correlation between species and soil parameters.

PCA was used to determine the relationship between the arbuscular mycorrhizal fungi (AMF) community structure and soil parameters of the studied sabkha regions to capture maximum variation along X and Y axes (Figure 8). PCA showed that two first principal components on X and Y axes accounted for a total of 77.3% variance, with PC1 and PC2 showing a variance of 45.8% and 31.5%, respectively. The analysis showed that the Qaseem and Qasab regions with lower electrical conductivity (Ec), cations and anions, and higher nitrogen (N), organic matter (OM%), moisture content (MC%), silt%, and clay% have a significant number of AMF species, while the Salwa and Uqair regions with higher values of above these soil parameters have significantly low AMF species.

AMF distribution is mostly influenced by MC%, soil texture (silt% and clay%), N, and OM. Spore abundance was positively correlated with clay, silt, MC%, OM%, and negatively correlated with EC, anions, and cations (Ca^{2+}, Na^{+}, and K^{+}). Higher levels of OM%, and available N, along with lower EC and Na^{+} concentrations, correlate with increased species abundance. Conversely, higher EC and Na^{+} levels lead to fewer AMF species.

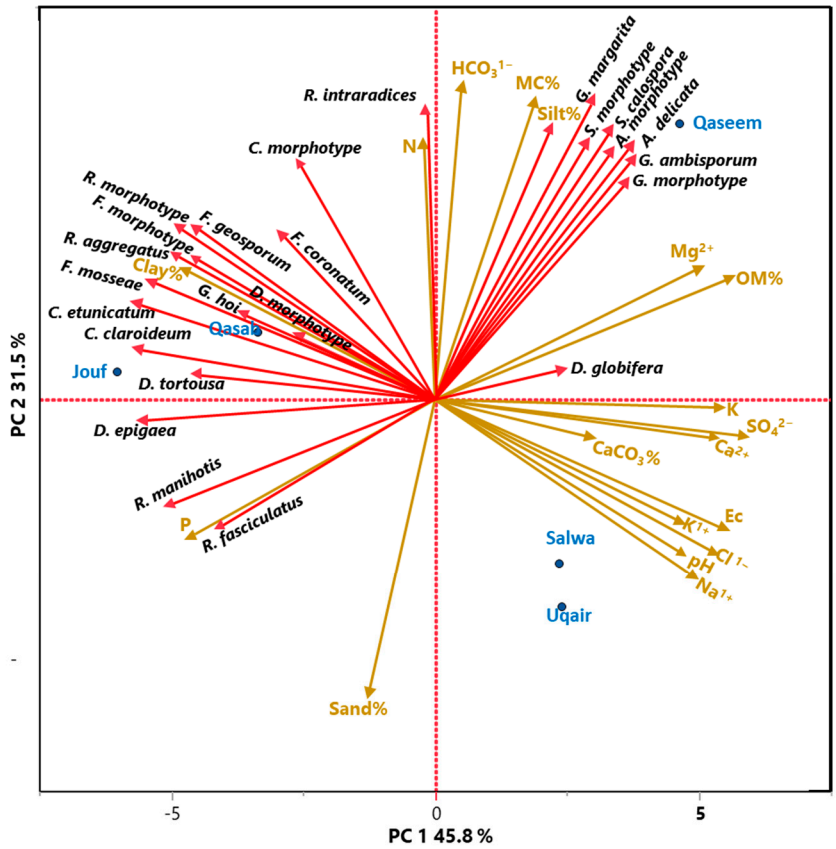

Figure 8. Principal component analysis (PCA) plot showing the associations between soil physiochemical parameters and AMF species along different sabkha locations.

4. Discussion

In recent years, due to the importance of microorganisms, such as AMF, in the functioning of ecosystems, there has been a growing focus on understanding how they react to changes in the environment [59–61]. Understanding the variety of fungus in ecosystems may have predictive consequences for biodiversity and ecosystem evolution processes [62]. Microbiota are driven by both habitat type and edaphic properties. Mycorrhizal symbiosis is essential for plants to cope with adverse environmental conditions [63]. To better understand the function of AMF in hypersaline environments of sabkhat and how they respond to heterogenous environments, the diversity and community distribution of AMF among various inland and coastal sabkhat were studied. Previous studies highlighted the influence of soil properties on mycorrhizal communities [64,65]. In alignment with the previous studies, we found that soil properties are the key factors influencing the diversity of the AMF in the hypersaline environment of inland and coastal sabkhas, particularly in the rhizosphere of halophytes. Despite having low specificity, AM fungi show diverse occurrence and spore density across different habitats which are influenced by soil physicochemical properties and varied climatic conditions [66]. The results of our study show a significant change in the production of the spore population among all the sabkha habitats (Figure 2). This could be due to significantly varied salinity levels in the soils of studied locations or because of other varying physiochemical properties of soil (Table 4).

The electrical conductivity of studied locations ranged from 9.37 ± 0.432 dS m^{-1} for Jouf to 31.35 ± 1.583 dS m^{-1} for Uqair. The sabkha habitats, such as Uqair and Salwa with the highest electrical conductivities of 31.35 ± 1.583 dS m^{-1} and 29.59 ± 1.409 dS m^{-1}, respectively, produced a lesser number of AMF spores and vice versa (Table 4; Figure 2). This study aligns with the previous findings indicating that fungus sporulation and colonization

are negatively correlated with salinity [67], i.e., increasing electrical conductivity inhibits the production of AMF spores, AMF development, and hyphal augmentation [68–73].

Soil properties play an important factor in shaping the AMF community structure [74–76] and our findings partially support the impact of macronutrients on AMF richness. Our results demonstrate that various soil variables, including P, N, Na, $CaCO_3$, and soil texture are significantly correlated with total spore density and species diversity (Figures 6 and 8). In semi-arid regions, soil phosphorous (P) drives the fungal community richness and abundance [77], suggesting a positive correlation between AMF diversity and the concentration of soil phosphorus [78,79]. The overall low AMF species richness observed across all sabkha locations is likely attributed to the physiochemical characteristics of sabkha soils. Soil with a high content of phosphorous (P) appeared to be the main factor, which had a significant direct negative effect on AMF richness [11]. The chemical makeup of the soil in Uqair and Salwa, which has a low species richness, can be attributed to the high available P content in the soil. These results are in line with work by Fall, et al. [80], which showed that there were few AMF morphotypes in several areas with higher levels of available P. However, the Qasab location with higher available P had higher AMF species richness compared to the locations with lower available P. This could be due to the low salinity [73,81] and higher N content [82] observed in the soil of the Qasab region. This suggests that improved soil quality, such as low salinity and higher phosphorous and nitrogen content, could interact to determine AMF richness [83]. This unique condition in Qasab location may have created favorable conditions for AMF abundance.

In general, the composition and distribution of microbial communities is significantly influenced by soil pH [84] and is widely considered as one of the driving factors that determines the diversity of AMF populations [85]. However, the findings in our study contradict this general trend, as no correlation was observed between the soil pH and AMF count. This could be attributed to relatively small variations in soil pH across studied sabkha locations. The pH range of our study sites was very restrictive, ranging from 8.16 ± 0.402 in the Sabkha of Jouf to 8.88 ± 0.611 in Salwa, suggesting minor fluctuation in soil pH was insufficient to significantly influenced soil spore count. The findings of this study are consistent with those of [73,86]. The weak association between AMF and soil pH can also be attributed to species-level pH preferences of different AMF taxa. The distribution and abundance of AMF across various soil conditions are influenced by the optimal pH range for AMF colonization, which varies among species. For example, members of the *Acaulosporaceae* exhibited a negative correlation with pH, while those belonging to the *Glomus* had a positive correlation with pH, according to [76]. These differential responses indicate that some AMF species may grow in alkaline environments, while others may be inhibited. Furthermore, the optimal pH for AMF propagation is slightly in the acidic range, which may account for the low AMF species richness observed in our study This low species richness can also be related to the alkaline nature of soil samples collected from different inland and coastal sabkhat. These results are in line with the work of [80,86]. Soil nutrient sources will undoubtedly facilitate soil biota coexistence and activity in complex saline environments where soil physical and chemical properties, plant eco-physiological adaptation, and temperature –moisture characteristics are all closely related [87]. AMF plays a crucial role in these ecosystems, enhancing plant resilience and aiding in soil health.

A total of 25 AMF species were identified from the field soil samples collected under the rhizosphere of dominant halophytic plants of inland and coastal sabkhat. These species were classified into eight identified genera representing five families across two taxonomic order levels—*Diversisporales* and *Glomerales* (Table 1). The AMF species richness in this study was notably higher than that reported in two saline habitats in the Netherlands

and Northern Germany by [88], who recorded 14, 11, and 10 AMF species under *Aster tripolium*, *Puccinellia distans*, and *Salicornia europaea*, respectively. The difference in AMF diversity may be attributed to variations in sampling time, environmental factors, or the influence of a particular host plant species within the rhizosphere. The interaction of these factors is vital in influencing the composition of AMF diversity and in establishing spore density within the soil environment. Among the genera identified, *Diversispora*, *Claroideoglomus*, *Funneliformis*, *Glomus*, and *Rhizophagus* were the most dominant across all studied habitats. These results are in line with [80,88,89], which showed that these genera along with *Gigaspora*, *Scutellospora*, *Acaulospora*, *Paraglomus*, and *Archaeospora* co-exist in diverse habitats, including saline wetlands. The members of the family *Glomeraceae*, including *Claroideoglomus*, *Funneliformis*, *Glomus*, and *Rhizophagus*, showed complete relative abundance in all the locations. Notably, *Claroideoglomus etunicatum* showed the highest relative abundance and isolation frequency followed in hierarchal order by *F. mosseae*, *R. intraradices*, and *G. ambisporum*. Interestingly, members of the *Gigasporaceae* family were restricted to Qasab and Qasim only while *Acaulospora* was observed in Qasim only. These findings are consistent with previous findings [90,91] which reported a strong dominance of the *Glomeraceae* family in a saline environment. This dominance is likely due to the *Glomeraceae* family's broad ecological range and inherent tolerance to harsh climatic and edaphic conditions. According to some other studies, the species of the *Glomeraceae* family frequently produce vast numbers of spores that can widely disseminate in the rhizospheric soil of associated plant species [92,93]. For natural saline soils, *F. geosporum* and *F. mosseae* have been widely reported as dominant species [72,88]. Furthermore, *C. etunicatum* was discovered in saline soils of Iran's Tabriz Plain [72], while *A. leptoticha* has been identified in the saline–alkaline soils of China's Yellow River Delta [94]. The dominance of these AMF taxa in hypersaline sabkha habitats indicates that their survival and propagation are facilitated by adaptive traits, including tolerance of high salinity, efficient nutrient acquisition, and osmotolerance. Such characteristics may aid in the survival and spread of *Glomeraceae* members, and the development of this phenomenon could also be a result of their adaptation to the specific ecological conditions of saline environments. Thus, the diversity of AMF species in these saline habitats is shaped by both environmental conditions and the adaptation of plant species.

The diversity and distribution of AMF varied significantly among various sabkha locations, suggesting that environmental conditions play a crucial role in shaping the AMF communities. The analysis of AMF diversity indices, such as Shannon, Pielou, Simpson, and Sobs, revealed a parabolic trend, in which diversity increased or decreased based on habitat conditions. AMF community composition is affected by environmental heterogeneity, as shown by the similarity index variation between different sabkhas. Qasab and Jouf have similar salinity gradients, soil pH, and almost the same plant associations that may help analogous AMF species colonize their ecological niches, as AMF communities are often shaped by the dominant and co-dominant host plant species. On the other hand, the low similarity index (0.4) between Qaseem and Uqair suggests ecological divergence as one location being inland sabkha and another one coastal. Different soil salinity, moisture content, and host plant diversity of the habitats may affect the diversity and abundance of AMF species between the two locations. Our study showed that the AMF diversity indices showed an increasing trend with the increasing salinities and P content and vice versa. Therefore, in this study, the AMF diversity varies in different environments with varying soil physiochemical parameters, especially Ec and available P content, which are considered as the main drivers of AMF diversity. Additionally, it has been demonstrated in several studies that AMF diversity and plant richness are closely connected and the above-ground vegetation defines the belowground survival and diversity of AMF [95].

5. Conclusions

This study concluded that AMF community structure in hypersaline sabkha ecosystems is primarily influenced by soil physiochemical characteristics, environmental conditions, and the presence of host plants. However, the relative contribution of each factor may differ across habitats, requiring additional research to determine the primary driver of AMF diversity and distribution. The *Glomeraceae* family has ecological dominance in hypersaline ecosystems, thereby demonstrating their adaptability in extreme environmental conditions. Inoculating degraded soils with AMF taxa may improve plant establishment, nutrient cycling, and soil stability and ecosystem recovery. The ecological significance of these AMF in hypersaline environments requires an understanding of their distributional patterns to evaluate their role in plant adaptation and ecosystem functioning under extreme conditions. Further studies should focus on explaining and understanding the AMF communities by linking their diversity and structure to plant community composition and prevailing environmental conditions. Additionally, long-term field trials could determine the restoration of degraded saline soil and an increase in plant productivity in saline-affected agricultural lands.

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