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Bacterial community structure and predicted function in the rhizosphere of wild and cultivated date palms: Effects of Fertilizers on Composition and Functionality

Dana A. Abumaali [a,b], Sara H. Al-Hadidi [a], Talaat Ahmed [a], Amer Fayad Al-khis [c], Sowaid Ali Al-Malki [c], Mahmoud Yaish [d], Hassan Hassan [a], Roda Al-Thani [b], Juha M. Alatalo [a,*]

[a] Environmental Science Center, Qatar University, Doha, Qatar
[b] Department of Biological and Environmental Sciences, Qatar University, Doha, Qatar
[c] Agricultural Research Department, Ministry of Municipality, Doha, Qatar
[d] Department of Biology, Sultan Qaboos University, Muscat, Oman

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ABSTRACT

This study investigated bacterial diversity in date palm rhizosphere and assessed the influence of different fertilizers on diversity using metagenomics. A total of 6356 Operational Taxonomic Units (OTUs) and 1164425 sequences were analyzed across 27 samples. The findings revealed variations in microbial community phylogeny among similar cultivars from different farms, except for the Khalas cultivar, suggesting minor influence of genotype on microbial community structure. Wild date palms exhibited more unique OTUs, in contrast, cultivated date palms had a higher number of OTUs and diversity. Moreover, different fertilizer treatments had varying effects on bacterial diversity. For example, organic and bio-organic fertilizers positively influenced specific bacterial groups, including delta-proteobacteria, acidobacteria-Gp3, Anaerolinaea, and Clostridia. Conversely, combining high concentrations of chemical fertilizers with other types did not show significant effects. Classes such as *Bacilli*, *Nitrospira*, *Deltaproteobacteria*, *Spartobacteria*, and *Thermomacrobia* exhibited high relative abundances in treatments with high chemical fertilizer concentrations. Our analysis revealed potential pathways related to carbon, nitrogen, phosphorus, phenol, sulfur, and antimicrobial compounds. Interestingly, these pathways and functions varied across different date palm cultivars. Our findings suggest that date palm cultivars shape the rhizosphere by selectively influencing bacterial communities consistently across other locations. These modulated bacterial communities can potentially provide enhanced benefits to the host. Importantly, this study was the first to investigate the soil bacterial diversity of wild date palms, giving valuable insights into the microbial community associated with this specific context.

1. Introduction

In conventional agroecosystems, plants are cultivated in a continuum. They are characterized by frequent crop turnover [1], rich soils, and high microbial diversity levels [2,3]. On the other hand, desert oases face harsh environments and are surrounded by large resource-scarce areas that commonly have low soil phylogenetic and functional microbial diversity [4–8]. As a result, the desert oases host a high plant community diversity featured by a simultaneous multi-cropping system [9], especially in desert regions of North Africa and the Middle East [9–11].

Phoenix dactylifera L., known as "date palm," is one of the oldest plants that are important economically and environmentally, especially in the Middle East. It is estimated that the oldest date palm records are more than 7000 years old [12]. The presence of date palms in the oasis provides shade, decreasing air temperature and maintaining relatively high air humidity, enabling agricultural production [9,13,14]. For their long life cycle (40–50 years of economic life) and long history of cultivation [10], date palm trees are considered to have coevolved with the oasis and its agricultural applications as well as plants growing in natural systems [15].

Plants have a symbiotic relationship with the microbiome that plays

* Corresponding author.
E-mail address: jalatalo@qu.edu.qa (J.M. Alatalo).

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a vital role in fixing atmospheric nitrogen [16], and more than seventy percent of plant rhizosphere bacteria produce auxins [17]. In addition, some bacterial communities apply minimum sensing processes to create specific promoting signals to adjust their activity in the rhizosphere [18, 19]. The diversity of functions performed by organisms within ecosystems has been recognized as a crucial link between biodiversity patterns and ecosystem functions [20–24].

Both abiotic factors and biotic factors influence the distribution and structure of soil microbiomes. The two main factors are soil and plant type that affect soil microbiome diversity structure [25] because of the complexity of the microbial interactions in the soil involving the interactions between microbiome and soil and the interactions between the microbiome and plants [26]. Soil physical-chemical properties (such as pH, nutrients and texture) play a significant role in the microbial structure [27,28] where certain microbial levels, at phylum and class level, have observed a strong correlation with various type of soil physical-chemical properties [29,30]. However, the activity of the soil microbiome alters the physical-chemical properties of soil and soil microenvironment [31]. Improving soil physical and chemical properties led to enhancing plant growth [31]. Many studies recorded that the amount of N in soil reduces the soil microbial diversity [32]. In addition, A high C/N ratio in the soil increases the enrichment of fungi [31]. Soil type could explain 47 and 33% of the variation of rhizosphere bacterial and fungal communities, respectively, followed by genotypes [33]. Furthermore, plant genotype is another main factor affecting the communities and diversity of rhizosphere microbiome [34]. Studies on the rhizosphere have observed a close association of many microbial taxa with the host genotype [35–37]. Recently, studies found that plant genotypes displaying differences to specific pathogenes might drive an increased abundance of specific microbial groupings [38].

Microbial diversity in date palms under arid conditions is high, with recent studies in UAE finding more than 3000 and 5000 bacterial OTUs [39,40]. 20 genera have been identified based on agriculture management and root exudates [41]. Four genera, including *Enterobacter*, *Salinicola*, *Rhizobium*, and *Staphylococcus*, have been found to adapt to arid environments [42]. Only *Labedella* genus was detected as adapted to the oasis environment in plant roots [42–47].

Previous studies showed that applying fertilizers could affect the bacterial community structure in the soil. For example, it was revealed that using organic fertilizer has significantly increased the abundance of beneficial bacteria, such as Proteobacteria and Actinobacteria, in the rhizosphere of maize plants [48]. Similarly, applying nitrogen fertilizer increased the abundance of nitrogen-fixing bacteria in the soil [49]. However, other reports showed the harmful impacts of chemical fertilizers on bacterial communities. For instance, applying chemical fertilizers has substantially decreased the abundance of beneficial bacteria such as *Bacillus* and *Pseudomonas* in the rhizosphere of wheat plants [50], and using urea fertilizer reduced the diversity of bacterial communities in the soil [51].

This paper's project aims to investigate the variations in bacterial functional communities amongst wild date palm populations, cultivars, and within cultivars. The project also seeks to explore the correlation between soil chemical properties and soil bacterial functional diversity within the date palm rhizosphere. Furthermore, it aims to analyze the impact of various fertilizer treatments on the functional diversity of bacteria in the date palm rhizosphere across different cultivars.

2. Materials and methods

2.1. Sample collection

A total of 103 soil samples were collected from the rhizosphere of the date palms. The soils were collected roughly 10 cm below the surface with a high abundance of fine date palm roots. 55 Soil samples in total were from wild-type date palm in Umm Bab (25°13′07.8"N 50°46′04.5"E) and two farms, including Qatar University Farm (25°48′29.8"N, 51°20′47.0"E) and Rowdat Al-Faras Farm (25°49′22.3"N 51°19′58.1"E). Five date palm trees were randomly chosen in Umm Bab. Similarly, five date palm trees were selected from each of the five cultivars (Berhi, Shishi, Nabot Saif, Khalas, and Khenezy) in both farms (Table S1). The collected samples were stored in paper bags during transport to the laboratory. The 48 samples in total were collected under the date palm trees treated with 15 different fertilizer treatments, including organic fertilizer (fermented animal wastes) using 30 kg per tree per year, bio-organic fertilizer (ritual plus fertilizer obtained from BIOGEN company) using 85 g of fertilizer per 100 L of water per 15 days, and chemical fertilizer using N:P: K ration of 1.8:0.8:1 kg/date palm tree (numbers for the 100% treatment) with three replicates for each treatment and the control (Table S1). The soil samples were lifted to dry for 3–4 days to remove moisture. Then samples were ground manually in the bag to prevent contamination.

2.2. Soil chemical analysis

The soil samples (n = 103) were composited as follows: 1g of soil from each replicate from the same cultivar at the same location or from the same treatment, before composite: (5 cultivars * 5 replicates * 2 sites = 50 samples) while after composite sample n = 10 (5 cultivars * 2 sites). 5 samples of wild were composited into 1 sample. In addition, treatment samples (n = 48, 15 treatment + control * 3 replicate) were composited to 16 samples. In total, 27 composite soil samples were obtained. Prior to chemical analysis, 27 composite soil samples were oven dried at 60–62°C for 48hr to avoid the decomposition of organic materials and augment mineral extractability. The dried soil samples were then crushed to a fine powder in a rotary ball mill (Retch Mill, Haan, Germany) at 250 rpm for 40 min, then passed through a 2 mm mesh of a standard sieve. This was used for chemical analysis for various parameters, including pH, salinity, total carbon (TC), total nitrogen (TN), NO_3^-, NO_2^- as well as the concentration of key chemicals elements involving Ca, K, Mg, Cd and Pb using the ESC protocols adapted from EPA method #207 in the ESC ISO 17025-2017 accredited facilities. All chemical analysis were carried out using previously published protocols [52].

2.3. Water chemical analysis

Two water sources were obtained from the Qatar University farm and Rowdat Al-Faras farm, with four replicates for each source. All pH, conductivity, salinity, and TDS were measured directly using meters for all parameters. The procedure for nitrate and nitrite measurement of the soil was the same for the water.

2.4. Sequencing and bioinformatics

Total DNA was extracted from the soil samples using a DNeasy PowerSoil Pro kit (Qiagen, Germany) following the manufacturer's instructions. Using the HiSeq 2500 platform with the sequencing strategy MiSeq-PE300 (MiSeq Reagent Kit), the libraries were sequenced at Begin Genomics Institute (Shenzhen, Guangdong, China). The raw data were filtered to obtain high-quality clean data by removing adaptors and low-quality ambiguous bases. These paired-end reads were added to tags using the Fast Length Adjustment of Short reads program (FLASH, v1.2.11) [53]. These tags overlap with each other and form clusters as OTU with a 97% cutoff value using UPARSE software (v7 0.0.1090) [54], and chimera sequences were compared with the Gold database using UCHIME (v4.2.40) [55]. The Ribosomal Database Project database was used to do taxonomic classifications to the OTU using Ribosomal Database Project (RDP) Classifier v.2.2 with a minimum confidence threshold of 0.6 and trained on the Green genes database v201305 by QIIME v1.8.0 [56]. The OTU-abundance statistics table for each sample was constructed by comparing all tags back to OTU using the USEARCH_global [57]. Based on the OTUs and taxonomic annotation

results, alpha diversity, beta diversity, differential species analysis, and model prediction analysis were done. Alpha diversity at the OTU level was analyzed using MOTHUR (v1.31.2) [58]. Beta diversity at the OTU level was estimated by QIIME (v1.8.0) [56]. The sample cluster was conducted by QIIME (v1.8.0) based on UPGMA. Barplot and heatmap of different classification levels were plotted with R package v3.4.1 and R package "gplots", respectively.

2.5. Function prediction

The microbial functional annotation was predicted, including Kyoto Encyclopedia of Genes and Genomes (KEGG), Clusters of Orthologous Groups (COG) and Metabolic Pathway Database (MetaCyc), metabolic pathways by Phylogenetic Investigation of Communities by Reconstruction of Unobserved States2 (PICRUSt2) (PICRUSt2 v2.3.0-b, R (v3.4.10) [59]. After predicting the function of all samples, the Wilcox test (two groups of samples) or Kruskal test (three groups and above of samples) was used to determine the different functions among all the groups, respectively. CCA-RDA analysis model selection was performed according to the method: Species abundance tables are used to perform DCA analysis to estimate the value of the lengths of gradients. If the value is greater than 4.0, the CCA should be selected. If it is less than 3.0, the RDA and CCA are both available. If it is less than 3.0, the results of RDA are better than that of CCA. R software drew a Spearman correlation heat map between species levels (relative abundance>0.5%). This is shown only when their correlation coefficients are greater than 0.2. Important patterns and relationships among dominant species could be found from the heatmap using R (v3.4.1).

2.6. Statistical analysis

The Shapiro-Wilk (S–W) was applied to analyze the obtained data to evaluate if the data is normally distributed. Minimum, Maximum, Mean, and Standard Deviation was calculated for soil chemical characteristics and metals. T-test of two samples assuming equal variances was used for water samples at a 95% confidence interval. Pearson Correlation Coefficient was obtained by (XLSTAT statistical software; Addinsoft Inc., New York, USA) for soil chemical parameters to check the correlation between parameters. For the principal component, the PCA in OTUs was plotted with XLSTAT to visualize the linkages between the soil microbial communities and the main drivers, soil parameters and sites, and cultivars (farms with cultivated cultivars and wild date palms). Alpha-diversity indices bacterial community based on OTUs were also analyzed to find any distribution patterns of the specific group using MOTHUR (v1.31.2). We applied Shannon and Simpson analyses to estimate bacterial species diversity and richness. We assessed each class's relative abundance (frequency), which was done for each site sampled using XLSTAT. XLSTAT was also used to investigate relationships between the composition of different soil microorganisms' groupings, the chemical parameters in soils, and the different locations sampled. Also, to understand the relationship between different organic fertilizers and the diversity of the bacteria. The Venn plots in OTUs or in taxa were plotted with the R package "Venn Diagram" version (3.1.1). Heatmaps for different cultivars and fertilizer treatments were done concerning the relative abundance of different bacterial classes using XLSTAT.

3. Results and discussion

3.1. Chemical analysis

Among the pH of all composite samples, the Khalas sample at Qatar University farm was the lowest (7.18), and treatment 10 in the fertilizer experiment was the highest (7.89) (Table S2). However, the samples' pH generally ranged from (7.18–7.89), which is weak alkaline and suitable for plant and microorganism growth. However, the observed pH value was lower than the pH range of 7.5–8.1 reported in a previous study (Mlih et al., 2019).

Salinity between samples from the fertilizer experiment had low variation, ranging between 0.4 and 0.6 (Tables S2 and S3). However, other samples, including Khalas and Naboot Saif in RA, had high salinity of 3.13 and 2.55 ppt, respectively. Total suspended solids ranged from 0.59 to 4.59 g/L. Umm Bab sample had a salinity of 1.5. TDS had a positive relationship with salinity, samples with higher salinity had higher TDS, and samples with low salinity had low TDS. The conductivity ranged from 0.74 to 5.44 mS. And it follows the same relationship with TDS and salinity. Total carbon in the soil samples ranged from 3.34 %C to 7.38%C. The interesting result is that the wild date palm in Umm Bab had the highest carbon percentage of 7.38, which was not expected. The total carbon percentage was higher than in a Tunisia study (Mlih et al., 2019). Total nitrogen ranged from 0.045 to 0.810%, which is lower compared to the same study. The total nitrogen percentage ranged from 0.045 in UB to 0.307 in T2, excluding the outlier in sample T1 with a percentage of 0.810 %TN. Nitrite concentration in experimental samples was higher than those from different cultivars, which is expected as they are supplied with fertilizers. Total nitrogen showed a low concentration in all soil compared to the nitrate and nitrite levels. BRA sample had the highest nitrite concentration of 328.4 mg/kg, and the lowest was 14.19 mg/kg in T2 (Tables S2 and S3).

On the contrary, nitrate concentrations were extremely higher in different cultivars and wild samples than in the experimented samples, except Khenezy cultivar from RA because of the fertilizer contents. The nitrate concentration in the soil ranged from 2.4 in T4 to 0.29 in SHRA. Salinity and TDS show a high correlation between each other and salinity and TDS with nitrite (Table S4).

Heavy metals (Mg, Ca, Cd, Pd, K, P) in soil, were analyzed. Calcium concentration in the Umm Bab sample was the highest because the Umm Bab soil composition consists of limestone (Al-Saad, 2005) (Tables S2 and S3). Cadmium concentration varied among samples, with a mean of 0.386 ppm (Table S3). There was a high correlation between phosphorus and cadmium (Table S4). The Umm Bab sample had zero cadmium concentration, and the highest concentration was in the Khenezy cultivar of RA. Magnesium concentration varied from 7264.1 in the Umm Bab sample, and the rest of the samples ranged from 16078.4 32098.7 ppm. Phosphorus concentration was exceptionally low in the wild sample, with 107 ppm compared to the other samples ranging from 1612.1 to 8349.3 ppm. Potassium had a similar phosphorus curve with low concentration in wild samples and close range between other samples. Lead concentration was high in Naboot Saif cultivar, Khenezy of RA, and fertilizer treatment 13 of 30% chemical, 100% organic, and 100% bio-organic fertilizer. However, it was high in treatment 13 (Table S2). The highest bacterial diversity was shown in these samples. A possible explanation is that lead concentration did not reach the level inhibiting bacterial species and their enzymatic functions (Khan et al., 2010).

3.2. Water analysis

Heavy metals in water were analyzed as well (Fig. S1). Noticeably, there was no cadmium detected concentration in both water samples. All other metals were higher in Rowdat Al-Faras water. Besides lead, it was higher in Qatar University farm water. Testing heavy metals in water was done to know if the heavy metal concentration in soil comes from the watering source. The magnesium, calcium, and potassium concentration between the two water sources showed high significance. However, their concentrations in the soil in different cultivars were almost similar, and it is expected as they are watered from the same source. Phosphorus showed no significant difference between both samples. However, lead concentration varied a lot between different cultivars from different farms. The lead concentrations of QU and RA showed no significant difference. It was expected to have a higher lead concentration in QU farm as the watering source had a higher concentration than RA farm. Still, RA farm cultivars showed higher lead concentrations

leading to other contamination possibilities.

3.3. Bacterial community composition of date palm

A total of 1164425 sequences were analyzed across 27 samples. Bacterial biodiversity in date palm soil was represented as OTUs. A total of 6356 OTUs were found in the 27 samples. The bacterial community in date palm soil samples shared 474 OTUs in common after removing OTUs related to archaea and OTUs that were not annotated (Fig. 1). The figure represents that the sample with the highest unique OTUs number reaching 165 OTUs is three times more than the wild sample than the unique number of other samples. This could potentially be explained by the drought stress of Qatari weather and salinity stress near seawater, inducing bacterial diversity in wild date palm soil. In addition, cultivated date palms receive a constant input of water and nutrients (fertilizers) which create more favourable conditions for microbial communities. The other samples, including samples from different cultivars and samples from the fertilizer treatment, ranged between 1 and 49 unique OTUs for each sample. There are a growing number studies regarding the bacterial community of date palm soil using 16S rRNA sequencing for culturable microorganisms and two studies using metagenomics from Tunisia [1,42,60–62], Oman [63–66], Egypt [67], and UAE [39,40,68]. Most studies on date palms focused on isolating growth-promoting bacteria, while, three studies reported on the total number of bacterial OTUs in Tunisia and UAE [1,39,40]. Surprisingly, the study in Tunisia found a considerably lower number (1251 unique OTUs from 105 samples) than we found in Qatar. We had expected that our Qatari samples from date palms would harbour fewer bacterial OTUs than those found in Tunisia due to the harsher environmental conditions in Qatar. In UAE which has similar environmental conditions as Qatar, the total number of bacterial OTUs (3040 and 5155) in the two studies [39,40] was also lower, but closer to what we found in Qatar. To compare with bacterial richness in other habitats in Qatar, a recent study on bacterial diversity across 19 sites in Qatar found 10,628 bacterial OTUs (1,306,756 reads) [69]. Gram-negative bacteria are the dominant bacteria through the phylogenetic identification of date palms in previous studies [42].

3.4. The abundance of Qatari date palm bacterial communities

Relative abundance in the class level showed that all samples except the wild sample had very similar relative abundance (Fig. 2). A recent study from UAE found that Actinobacteriota, Firmicutes, and Proteobacteria had the highest relative abundance in the date palm roots [39], while Actinobacteria, Firmicutes, and Proteobacteria, had the highest relative abundance in soil samples associated with date palms [40]. We found that Actinobacteria and Alphaproteobacteria had the highest relative abundance among the other classes, followed by Gammaproteobacteria and Acidobacteroa_GP16. Nearly 20% of the relative abundance were unidentified "other" classes. These results differ slightly from a study from Tunisia, where Gammaproteobacteria and Pseudomonadaceae dominated the rhizosphere while Acidimicrobia, Actinobacteria and Alphaproteobacteria had the highest relative abundance in bulk soil [1]. Also, the study shared similar classes, including *Deltaproteobacteria*, *Chloroflexi*, *Cytophagia*, *Acidobacteria*, and *Bacilli*, with different percentages. Similarly, another study in Tunisia showed that Gammaproteobacteria had the highest relative abundance percentage at 57%, followed by Actinobacteria and Alphaproteobacteria with 26% and 7%, respectively [42]. The differences between Qatar and Tunisia could either reflect small differences in dominance in bacterial composition between the countries or be due to slightly different sampling [1]. However, overall, the rhizosphere contained similar bacterial groups in

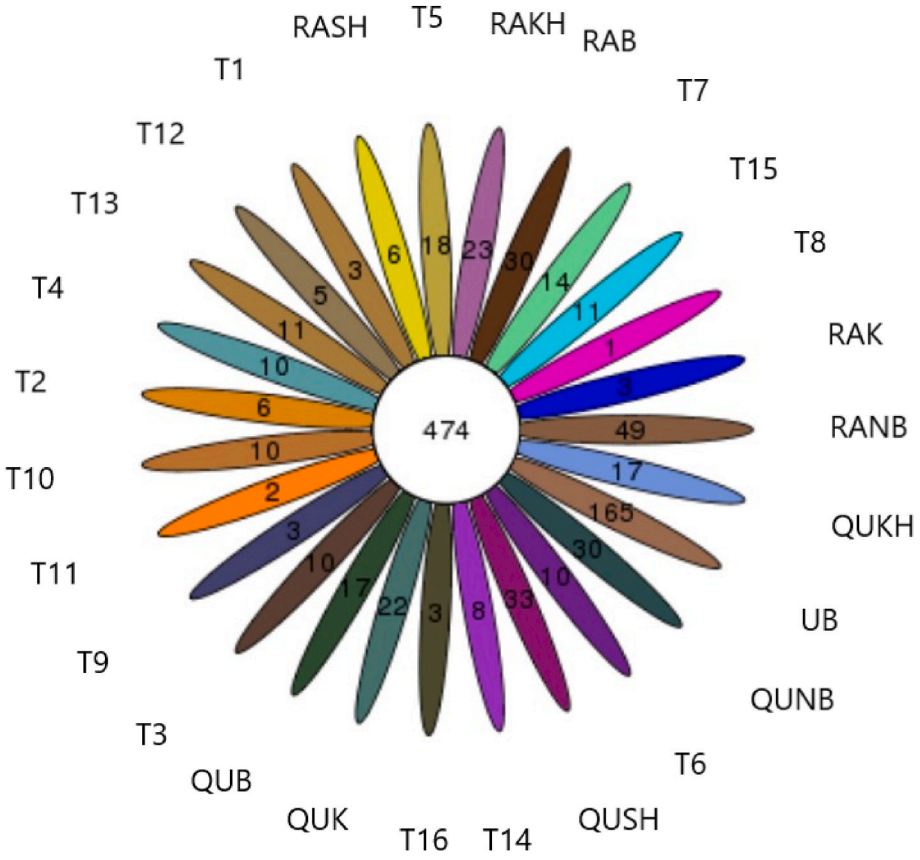

Fig. 1. Core-Pan OTU Plot for soil samples. The middle circle indicates the number of shared OTUs in these samples or groups, and the ellipse outside the center circle indicates the number of OTUs that are unique in each sample (UB = wild date palm). See Table S1 for key of sample IDs.

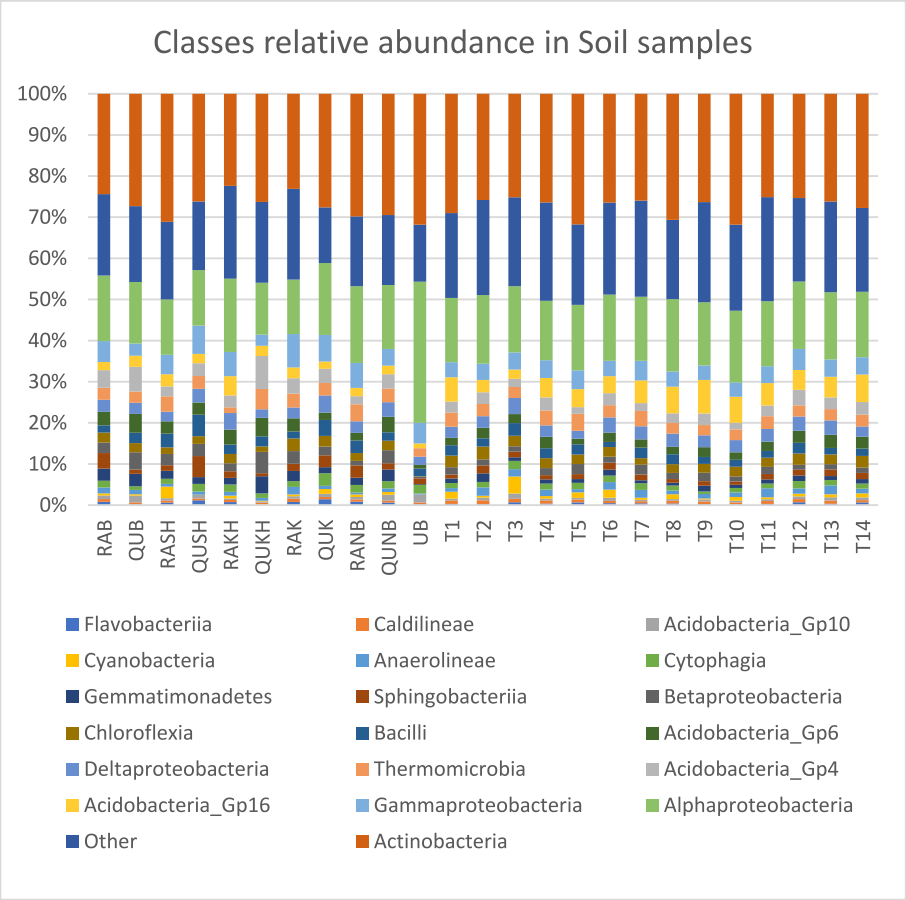

Fig. 2. Class relative abundance of soil samples.

both Qatar and Tunisia.

3.5. Alpha diversity of the bacterial community of date palm in Qatar

The alpha diversity for each sample is presented along with Sobs, Chao, Shannon, and ace indexes (Table 1, Fig. S2). Samples with low

Table 1
Alpha Diversity Statistical Table for Soil Samples (UB = wild date palm), see Table S1 for key for sample IDs.

Sample ID	sobs	chao	ace	Shannon	Simpson	coverage
RAB	3283	3923.8	3949.094	6.890539	0.002432	0.982521
QUB	2673	3232.507	3169.284	6.603998	0.003402	0.98589
RASH	2765	3434.193	3377.223	6.56371	0.004581	0.984159
QUSH	2851	3472.938	3418.266	6.717943	0.00295	0.982974
RAKH	3040	3733.046	3724.189	6.69123	0.003736	0.981047
QUKH	2595	3118.565	3142.816	6.436159	0.005924	0.984834
RAK	2837	3395.324	3431.507	6.516131	0.006064	0.983674
QUK	2810	3382.212	3385.979	6.729371	0.002782	0.982017
RANB	3176	3724.629	3755.691	6.833336	0.002921	0.984084
QUNB	2913	3452.793	3453.922	6.740199	0.003033	0.983538
UB	1850	2202.07	2175.651	5.773418	0.014684	0.989615
T1	2929	3688.242	3653.701	6.570165	0.004517	0.981608
T2	3066	3783.935	3728.129	6.776364	0.003682	0.980286
T3	3174	3813.212	3842.381	6.856839	0.002996	0.980241
T4	3207	3923.723	3924.587	6.83918	0.003061	0.978833
T5	2978	3842.082	3740.258	6.656328	0.003478	0.981195
T6	3292	4052.158	4069.555	6.78985	0.003295	0.981096
T7	3291	4076.164	4060.803	6.751209	0.003903	0.980648
T8	2999	3691.696	3747.255	6.528027	0.004874	0.983186
T9	2952	3610.929	3651.133	6.579999	0.005806	0.981097
T10	2899	3585.327	3631.112	6.58999	0.004084	0.98074
T11	3053	3835.846	3828.928	6.55996	0.005788	0.979829
T12	3039	3830.865	3792.652	6.771292	0.003402	0.978134
T13	3326	4055.338	4032.515	6.806947	0.00385	0.98154
T14	3166	3904.764	3872.007	6.747487	0.003968	0.982084
T15	3168	3867.863	3886.671	6.801862	0.003147	0.982104
T16 (control, fertilizer free)	3117	3824.08	3813.223	6.707876	0.003899	0.982945

sobs (OTU number) and high Shannon index indicates low diversity and Vis versa. Almost all samples have similar values except the UB sample, which is the wild sample with a low Shannon index compared to other samples from different cultivars and the experimented samples (Fig. S1). This result is consistent with the previously published in which salinity affects endophytic bacteria of date palm roots. Salinity stress tends to decrease the OTU number compared to the control [70]. However, one recent study on date palm bacterial microbiome in UAE reported that salinity had no effect on the diversity, but altered the community structure [39]. Regarding the different fertilizer treatments, we found that treatment 13, 100% organic and 30% chemical fertilizer, had the highest richness, followed by treatment 6 (100% organic and 100% bio-organic) and treatment 7 (100% organic, 100% bio-organic, and 100% chemical). This indicates that organic and bio-organic fertilizers support higher bacterial richness than chemical fertilizers. Chemical fertilizer can negatively alter the beneficial bacteria in soil [71]. Also, it may lead to soil degradation, leaching, and degradation of nutrients [72]. On the contrary, organic and bio-organic fertilizers can increase the nutrient availability to microorganisms, enhancing their richness and biodiversity [73].

3.6. Beta diversity of the bacterial community of date palm in Qatar

In (Fig. 3a), the heatmap describes the species' phylogeny under different fertilizer treatments, how they are related to each other through their ancestors, and the relationship between the samples. T8 (70% chemical), T1 (100% chemical), T5 (100% bio-organic 100% chemical), T7 100% chemical, organic and bio-organic), T9 (70% chemical and 100% organic), and T10 (70% chemical and 100% bio-organic) are shown to be closely related to each other, suggesting that there is no major difference or effect on mixing other fertilizer types with a high concentration of chemical fertilizers. *Bacilli, Nitrospira, Deltaproteobacteria, Spartobacteria* and *Thermomacrobia* classes have high relative abundance in the treatments above. The other experimental samples with high organic or bio-organic concentrations are similar. In the control sample, the closely related classes delta-proteobacteria, acidobactria-Gp3, Anaerolinaea, and Clostridia had low relative abundance compared to the sampling sharing the same phylogeny, thus, the organic and bio-organic fertilizers may affect these classes positively. Similarly, a study on date palms in Egypt found that bio-organic fertilizer, including four active strains; *Azotobacter chrococcum* as source of diazotrophs, *Azospirillum brasilense* as a source of nitrogen, *Bacillus megaterium* as a source of potassium, increased the bacteria number in soil compared to control treatment [67].

Compared to the different cultivars samples from the two farms, the wild sample comes from a very different phylogeny, while the cultivars come from similar phylogeny (Fig. 3b). Wild samples have the highest abundance of Actinobacteria, Acidobacteria-Gp10, Deltaproteobacteria, and Cytophagia. The other classes had low relative abundance in the sample. Berhi, Naboot Saif, and Khenezy cultivars from QU farm share close phylogeny to each other with Shishi from RA farm and share a high relative abundance of Nitrospira, Actinobacteria_Gp3, Actinobacteria_Gp4, Actinobacteria_Gp6, Actinobacteria_Gp7, Actinobacteria_Gp16, Actinobacteria_Gp17, Thermoleophilia, Chloroflexia and Betaproteobacteria classes. Berhi, Naboot Saif and Khalas from RA farm share close phylogeny with Shishi and Khalas from QU farm. We expected that similar cultivars from different farms share a close phylogeny, but only Khalas cultivar from both farms shared similar phylogeny. These results indicate that the date palm location has a higher correlation with bacterial biodiversity than the cultivar type. While not totally comparable, a study on the date palm bacterial microbiome across seven oases in Tunisia found that 27% of the OTUs in the rhizosphere were shared among the sites. However, 89% of the relative abundance of OTUs was shared among the sites [1], suggesting high similarity in the dominant bacterial microbiome.

3.7. PCA analysis

A biplot of PCA analysis that includes the samples, soil properties, and bacterial classes showed a correlation between samples of the two farms and salinity, total suspended solids, and conductivity (Fig. 4). F1 and F2 showed higher eigenvalues for PCA (Table S5). The experimental samples showed a high correlation with pH and nitrate concentrations. As they are clustered close to each other, they are highly correlated as they are from the same cultivar, 'Khalas.' Moreover, the wild sample (UB) showed no correlation with other samples but exhibited a correlation with the highest calcium concentration and total carbon percentage. Also, Alphaproteobacteria and Actinobacteria had a higher correlation with the wild sample. Therefore, there might be some relation between the high calcium concentration and the high Alphaproteobacteria relative abundance. Proteobacteria members are predominant in various soil ecosystems involving rhizospheres, saline soils, and semiarid soils [74,75] (Oja et al.). Other studies have found Alphaproteobacteria to be one of the most abundant classes, including soils with high calcium content [74,76,77]. Excessive intake of calcium

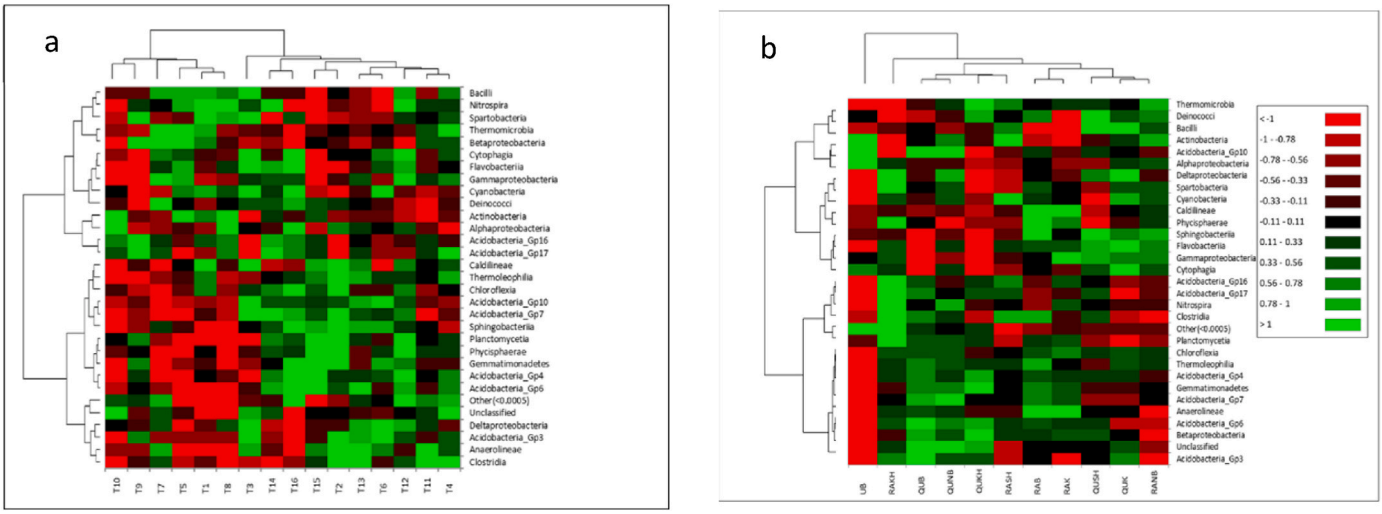

Fig. 3. Heatmap of soil samples under different fertilizers treatment (a) and among different cultivars and wild sample (b).

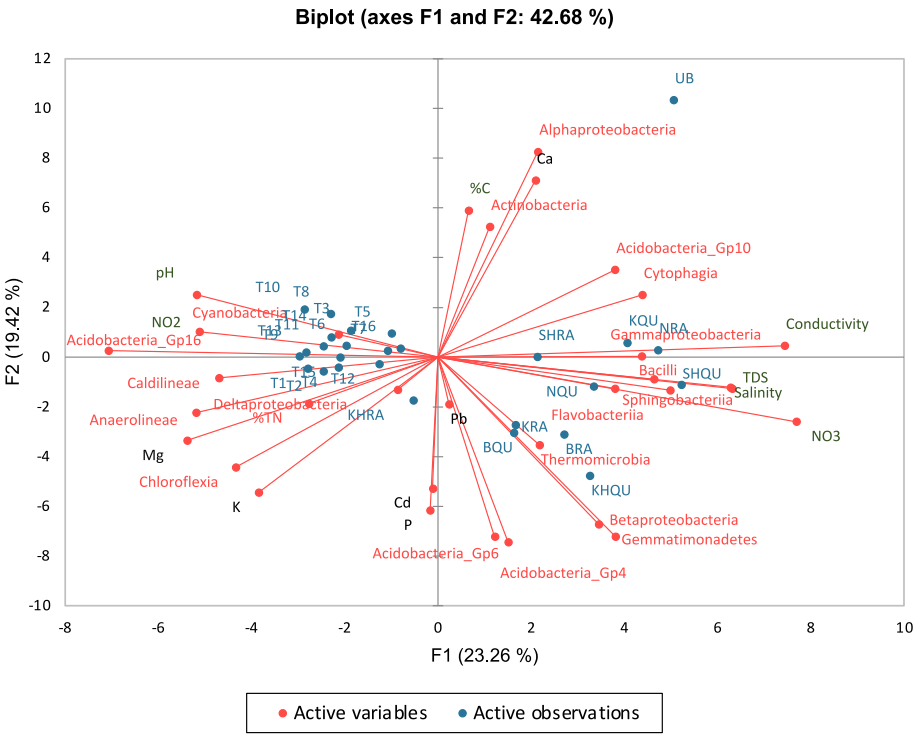

Fig. 4. PCA analysis of soil samples with soil properties and class diversity.

ions leads to severe damage, including the hardening of cell walls, inhibition of cell growth, disruption of energy metabolism, and impairment of the plant cell membrane. These effects decrease photosynthetic and transpiration rates, ultimately resulting in leaf senescence [76,78,79]. Therefore, plants growing in soils with high calcium content have to possess unique physiological adaptation mechanisms, such as a symbiotic bacterial community [76]. In UAE, salinity and pH have been shown to influence the bacterial communities associated with date palms [39,40], while a study across habitats in Qatar found that salinity and soil phosphorus (P) affected soil bacterial diversity [69].

4. Functional analysis

4.1. Predicting the functional capabilities of microbial communities based on the KEGG

The bacterial function prediction analysis was performed to study the effect of the type of land (wild and cultivated), type of cultivar of date palm, and type of fertilizers on soil bacterial functions. Over comparisons with the KEGG database, six classifications of biological metabolic pathways (KO level 1, primary function level) were found involving genetic information processing, organismal systems, cellular processes, cellular processes, environmental information processing, metabolism, and human disease (Fig. 5a). Among these pathways, metabolism (81.8–82.4%), genetic information processing (10.9–12.1%), and cellular processes (3.6–4%) were the primary components. The comparison of rhizosphere bacterial community function predictions among different samples showed that the copy number sequence of the predicted gene in six primary functional layers followed the pattern S (2632962), I (2525324), AA (2522257), K (2507914), W (2041891), respectively. In addition, 32 sub-functions were obtained from analysis of the secondary functional layer of the predicted genes that involved carbohydrate metabolism, amino acid metabolism, metabolism of cofactors and vitamins, metabolism of terpenoids and polyketides, metabolism of other amino acids, lipid metabolism, xenobiotics biodegradation and metabolism (Fig. 5b). The lowest number of sequencing gene copies was recorded with Development (0–1.6) followed by Excretory system (0–5.6), Immune diseases (4–32), and Neurodegenerative (0–1782) categories. The cluster analysis of gene copy numbers (Fig. 5d), revealed that biological replicates from different samples clustered together, indicating good repeatability. The S (treatment 8: 70% chemical) and U (treatment 10: 70% chemical 100% bio-organic) samples were closely grouped, along with the p sample, forming one cluster. Similarly, the Y (treatment 14: 100% bio-organic 30% chemical) sample was close to the R (treatment 7: 100% of chemical, organic and bio-organic) sample, while the G (Khalas cultivar, Rowdat Al-Faras) sample was near the W (treatment 12: 30% chemical) sample. The AA sample (fertilizer-free control) showed similarity to the N sample. Notably, the wild sample (K) was distantly separated from the other samples, indicating that habitat influences soil bacterial community function, and there are discernible differences among various varieties. The annotation analysis classified the functional pathways into 179 level 3 KO categories (Fig. 5c). The paths chosen were associated with carbon, nitrogen, sulfur, phosphorous, phenol, calcium, and antimicrobial production (Table 1a, b). KO terms for the production of antibiotics Clavulanic acid, Penicillin & cephalosporin, Tetracycline, and Streptomycin were different for sequence counts by five date palm cultivars from two locations and wild date palm (Table 2a). Date palm wild was found to have the highest number of sequence counts (72) for Clavulanic acid antibiotic KO terms, while date palm cultivar Nabot Saif was found to have the highest number of sequence counts for Tetracycline (15414) and Streptomycin (40225) antibiotic KO terms from Rowdat Al-Faras farm and Penicillin and cephalosporin (4032) antibiotic KO terms from Qatar university farm

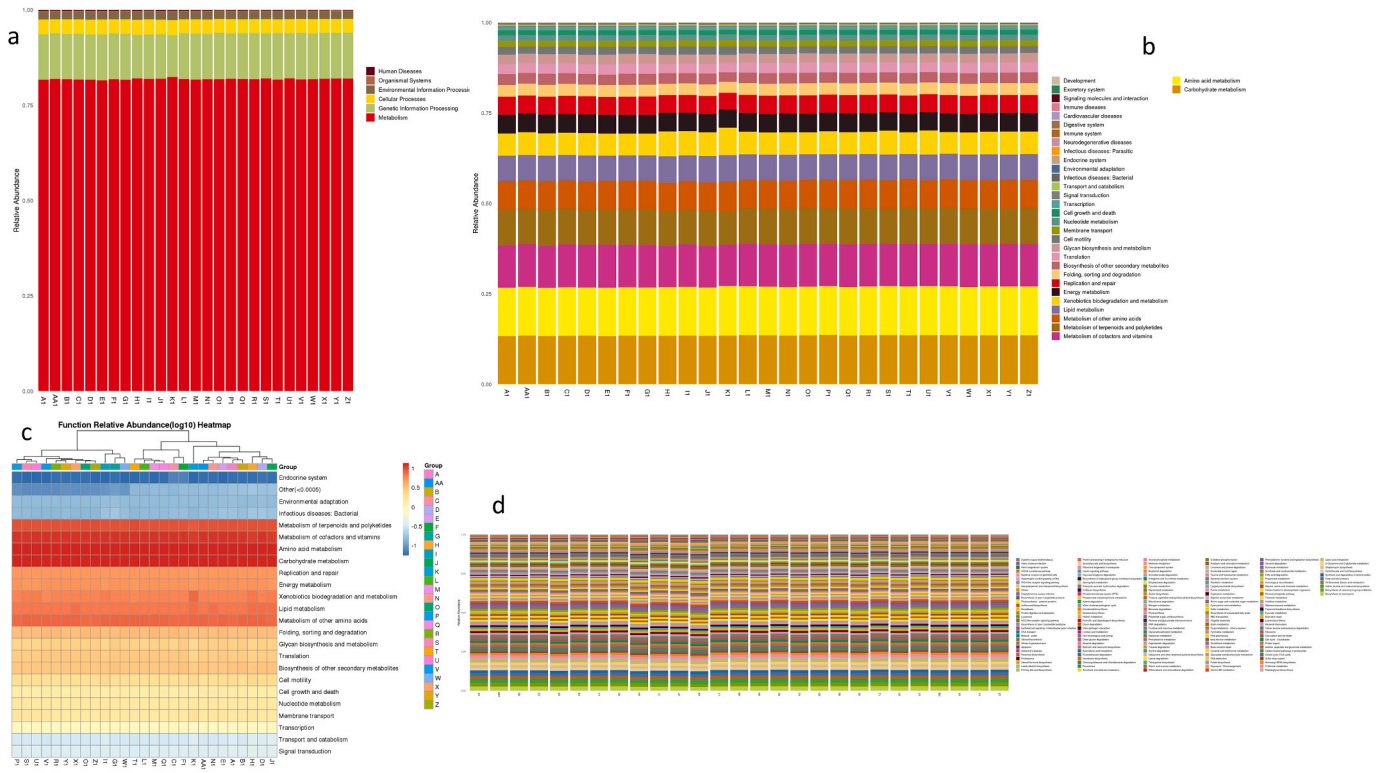

Fig. 5. Kyoto Encyclopedia of Genes and Genomes (KEGG) function prediction. (a) Bar plot group Picrust – KO- level 1, (b) Bar plot group Picrust – KO- level 2 and (c) Bar plot group Picrust – KO- level 3. (d) Heatmap of profile of KEGG secondary metabolic pathway at KO level. Longitudinal clusters indicate the similarity of all Predicted function among different samples, and the horizontal clustering indicates the similarity of certain predicted function among different samples, the closer the distance is and shorter the branch length is, the more similar the predicted function is between the samples. Relative abundance values are log transformed for normalization. If the relative abundance of certain species is 0, the half of the minimum abundance value substitute for it. Functions whose abundance values are less than 0.5% were combined into others.

(Table 2a). Under 15 fertilizer treatment, date palm with 70% chemical fertilizer treatment (treatment 8, Table 2b) was found to have the highest number of sequence counts for antibiotic (Streptomycin), carbon (Starch and sucrose metabolism, Polycyclic aromatic hydrocarbon degradation, Carbon fixation in photosynthetic organisms, Carbon fixation pathways in prokaryotes, C5-Branched dibasic acid metabolism), carbohydrate (Fructose and mannose metabolism, Galactose metabolism), nitrogen (Nitrogen metabolism, Nitrotoluene degradation), Sulfur metabolism, phosphorus (Phosphonate and phosphinate metabolism, Oxidative phosphorylation) and phenol (Phenylalanine metabolism) pathway.

PICRUSt can accurately predict the presence and abundance of genes related to Carbon (C), nitrogen (N), and phosphorus (P) cycles [80–84]. Our results revealed the functional characterization of 179 pathways based on the KEGG database. Additionally, we obtained 234 pathways from the protein cluster analysis of the SQU-1 genome of *Achromobacter xylosoxidans*, a rhizobacterium associated with date palms in Oman [85]. The extracted database of KEGG and the available literature Canonical analysis of principal coordinates (CAP) showed that the KO groups relative to plant growth promotion (PGP) functions, traits carried by date palm bacterial microbiomes in the root and the rhizosphere fractions were not significant by Tunisian oases location [1]. Our findings indicate substantial differences in KO terms related to the production of antibiotics such as Clavulanic acid, Tetracycline, Streptomycin, Penicillin, and cephalosporin, based on sequence counts and date palm cultivar. Similarly, when comparing different wheat cultivars, sequence counts for antibiotic-related KO terms differed among the nine cultivars studied [86]. Some date palm cultivar-associated bacteria identified in the current study may benefit their host.

4.2. *Predicting the functional capabilities of microbial communities based on clusters of orthologous groups (COG)*

The COG pathways were predicted through 16S rRNA sequencing of 27 soil samples. At level one, four classifications of function were found, including information storage and processing, cellular processes and signaling, metabolism, poorly characterized (Fig. 6a). At level two, 25 classifications of function were obtained that included bacterial growth processes (Fig. 6b). Ten COG functional pathways were contained over half of all the acquired pathways involving amino acid transport and metabolism; General function prediction only; Translation, ribosomal structure & biogenesis; Energy production and conversion; Coenzyme transport and metabolism; Cell wall/membrane/envelope biogenesis; Carbohydrate transport and metabolism; transcription; Inorganic ion transport and metabolism and Lipid transport and metabolism, respectively. From the heatmap analysis results of the gene copy number (Fig. 6c), the K sample (date palm wild) was placed in a split branch while the D sample was close to the J sample, and both of them were close to the H sample. W sample was close to E sample. The sample was close to G sample, while b sample was close to F sample. T sample in single branch related to L sample that was close to Y sample. Fertilizer free sample (AA sample, control) was close to c sample. Furthermore, S sample was close to U sample.

A study on the microbiome function in different AM fungal species

combinations used to inoculate to cotton (*Gossypium hirsutum* L.) found that eleven COG functional pathways (amino acid transport and metabolism, cell motility, coenzyme transport and metabolism, general function prediction only, intracellular trafficking, secretion, vesicular transport and transcription, carbohydrate transport and metabolism, defense mechanism, energy production and conversion, secondary metabolite biosynthesis, transport and catabolism and translation, ribosomal structure, and biogenesis) differed between hyperspheres [87]. Importantly, they showed that AM fungi species that colonise plant roots have their own specific microbiome which thus influences trophic interactions [87]. While not focusing on the microbiome of AM fungi, in our result, amino acid transport and metabolism function at COG showed the highest number of gene copies in wild date palm rhizosphere (K sample; 9,716,008) followed by Nabot Saif cultivars (I sample, 9087991) and Barhi cultivars (A sample, 8415404) from Rowdat Al-Faras. While under fertilizer treatment, the highest number of gene copy number was observed in the S sample (70% chemical fertilizer) followed by AA sample (fertilizer-free, control) and Y sample (100% bio-organic and 30% chemical fertilizer). Amino acids are abundant metabolites in plant root exudates and are supposed to shape structures of rhizosphere microbiomes since they act as essential nutrients for particular community members [87]. In Oman, the COG analysis of the date palm rhizosphere revealed that 27.5% of the proteins were classified as essential for metabolism. Categories related to cellular processes and signaling, accounting for 17.9% of the proteins, followed by information storage and processing, comprising 14.7% of the proteins [65].

Table 2a
KO- level 3 for different date palm cultivars rhizosphere soils grown at two farms and wild.

Picrust Function	Date palm cultivars										
	Berhi		Shishi		Khenezy		Khalas		Nabot Saif		wild
	location										
	Rowdat Al-Faras	Qatar University	Rowdat Al-Faras	Qatar University	Rowdat Al-Faras	Qatar University	Rowdat Al-Faras	Qatar University	Rowdat Al-Faras	Qatar University	Umm Bab
antimicrobial											
Clavulanic acid biosynthesis	6	8	1	7	1	18	0	2	3	12	72
Penicillin and cephalosporin biosynthesis	3836.201	3891.353	2925.851	3950.517	2719.933	3348.92	3226.011	3920.751	3371.671	4032.324	3333.089
Tetracycline biosynthesis	15402.83	15091.57	14249.95	13661.2	14404.2	14293.6	13726.09	13370.17	15414.4	14001.57	13795.61
Streptomycin biosynthesis	39681.05	38243.76	39084.65	34587.32	35954.97	35950.29	36635.33	33901.46	40225.3	35710.41	37088.8
carbon											
Starch and sucrose metabolism	14670.17	14212.82	14618.22	13726.12	13046.84	13305.75	13708.72	13635	15167.31	13956.17	13900.99
Polycyclic aromatic hydrocarbon degradation	2114.896	2158.91	1806.977	1968.003	1393.334	1774.165	1660.065	2536.884	2227.661	2353.242	2138.165
Carbon fixation in photosynthetic organisms	27784.97	26713.91	26985.47	24596.79	26194.79	25403.89	25583.41	23959.79	28528.82	25001.13	27313.69
Carbon fixation pathways in prokaryotes	32312.35	31222.19	30897.62	28655.92	29824.46	29591.74	29651.71	28005.22	32765.78	29312.49	30948.09
Fructose and mannose metabolism	12459.46	12089.02	12176.13	11339.31	11554.7	11319.42	11245.85	11306.97	13070.44	11661	13323.9
Galactose metabolism	13073.13	12966.11	13148.99	12105.57	11877.45	12232.79	12275.06	11962.07	13511.92	12437.37	12563.69
C5-Branched dibasic acid metabolism	48572.41	46925.85	48721.18	42623.42	46850.04	45151.11	45967.76	41530.88	51189.86	43564.99	49956.44
nitrogen											
Nitrogen metabolism	10934.93	10654.33	10352.98	9959.556	10024.31	10005.94	10113.34	10450.86	11362.98	10319.86	11559.86
Nitrotoluene degradation	9874.154	9234.786	9943.661	7911.632	10311.19	8614.166	9251.661	10033.03	12403.24	9681.547	12125.61
sulfur											
Sulfur metabolism	18440.54	17621.43	17738.17	17362.74	16320.3	16162.24	16493.29	17693.88	19386.78	17290.04	20656.25
phosphorus											
Phosphonate and phosphinate metabolism	2144.435	1964.936	2088.164	1947.335	2153.498	1711.756	1915.321	2094.627	2507.889	2046.38	2876.934
Oxidative phosphorylation	15356.27	14925.61	14911.8	13704.14	14306.59	14046.07	14077.78	13320.49	15622.63	14025.58	14964.07
phenol											
Phenylalanine metabolism	13217.81	12443.45	12845.79	11748.63	12325.71	11511.32	11787.76	12891.45	15061.84	12672.37	16926.92
calcium											
Calcium signaling pathway	4.7512	1.801	13.3806	6.0896	0	1.694	3.7487	7.4266	5.6194	4.4428	9.7239

Table 2b
KO- level 3 for date palm rhizosphere soils treatment with different type and combination of fertilizer.

Picrust Function	Fertilizer Treatment															
	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11	T12	T13	T14	T15	Control
antimicrobial																
Clavulanic acid biosynthesis	1	6	2	2	1	2	2	0	1	0	10	1	5	2	2	0
Penicillin and cephalosporin biosynthesis	2734.01	2706.989	2776.21	2481.449	2963.67	3064.953	2899.719	3279.103	2431.537	2775.3	2652.516	2588.243	3146.051	2983.179	3036.751	3327.139
Tetracycline biosynthesis	13647.41	12464.31	12915.04	12452.39	13382.28	14379.79	14022.85	15196.33	13085.51	12669.32	12857.86	12654.64	14163.6	14585.55	14022.94	15483.71
Streptomycin biosynthesis	38323.36	34460.96	34645.38	34196.86	38934.5	39499.29	38070.92	42962.91	36010.17	37165.01	35881.53	33360.3	39239.63	39763.75	39308.08	41270.65
carbon																
Starch and sucrose metabolism	14012.53	12673.68	13213.88	12510.57	14729.51	14466.58	14290.56	15866.17	12754.61	13647.83	13112	12379.82	14477.72	14462.55	14106.55	15253.71
Polycyclic aromatic hydrocarbon degradation	1564.53	1526.387	1700.586	1415.815	1826.609	1799.592	1680.002	1975.297	1322.456	1776.761	1411.689	1420.339	1855.451	1786.118	1790.579	1848.863
Carbon fixation in photosynthetic organisms	26596.1	24124.02	24390.8	23930.99	27011.22	27557.01	26951.77	29852.72	24924.48	25753.18	25022.47	23573.13	27276.46	27635.55	26980.41	29041.97
Carbon fixation pathways in prokaryotes	30632.42	28138.75	28052.51	27687.68	30868.37	32131.66	31694.41	34519.51	29018.62	29630.81	29375.83	27136.27	32131.46	32144.56	31765.51	33347.08
Fructose and mannose metabolism	11861.08	10677.94	10939.57	10537.59	12131.55	12177.38	11854.93	13580.07	10819.51	11671.36	10970.43	10543.7	12296.48	12516.97	12031.4	13275.96
Galactose metabolism	12857.23	11613.94	11821.74	11549.71	13396.85	13152.87	12895.63	14453.18	11752.75	12513.99	12002.09	11339.55	13216.93	13212.16	13037.33	13873.39
C5-Branched dibasic acid metabolism	49212.47	43971.59	43544.61	43848.91	49752.59	50281.11	50477.01	55377.37	46710.7	47790.59	46942.36	42427.88	50331.71	51012.06	49739.78	51906.12
nitrogen																
Nitrogen metabolism	10059.27	9100.37	9459.858	8967.252	10383.47	10480.1	10133.79	11612.12	9120.372	9759.091	9233.053	9069.291	10433.91	10572.05	10168.22	11364.95
Nitrotoluene degradation	10963.64	9267.038	8942.82	9081.588	10422.2	10413.19	10256.16	13204.06	9627.93	11116.76	9289.43	8794.106	10859.88	11659.9	10582.89	11313.86
sulfur																
Sulfur metabolism	17110.02	15433.46	16285.86	15013.91	17988.24	17879.22	17581.2	19585.14	15207.26	16871.77	15714.98	15239.56	17810.23	17676.9	17086.63	18945.62
phosphate																
Phosphonate and phosphinate metabolism	2229.426	1939.138	1996.109	1818.611	2413.029	2214.706	2192.774	2668.033	1902.557	2234.974	1950.896	1956.318	2187.471	2245.054	2034.097	2483.952
Oxidative phosphorylation	14585.39	13280.67	13458.16	13093.05	14723.89	15139.93	14922.72	16326.36	13649.62	14017.75	13798.57	12908.56	15088.52	15180.3	14903.19	15812.36
phenol																
Phenylalanine metabolism	12851.41	11294.01	11619.49	10860.08	13340.38	12914.26	12454.5	15332.55	11444.61	13136.44	11392.87	11137.2	12953.61	13437.08	12584.59	14173.77
calcium																
Calcium signaling pathway	2.8981	2.0497	13.0845	2.3494	5.1616	5.2325	0	4.1169	1.9527	2.9228	2.306	3.3034	0	3.1716	3.1754	7.4328

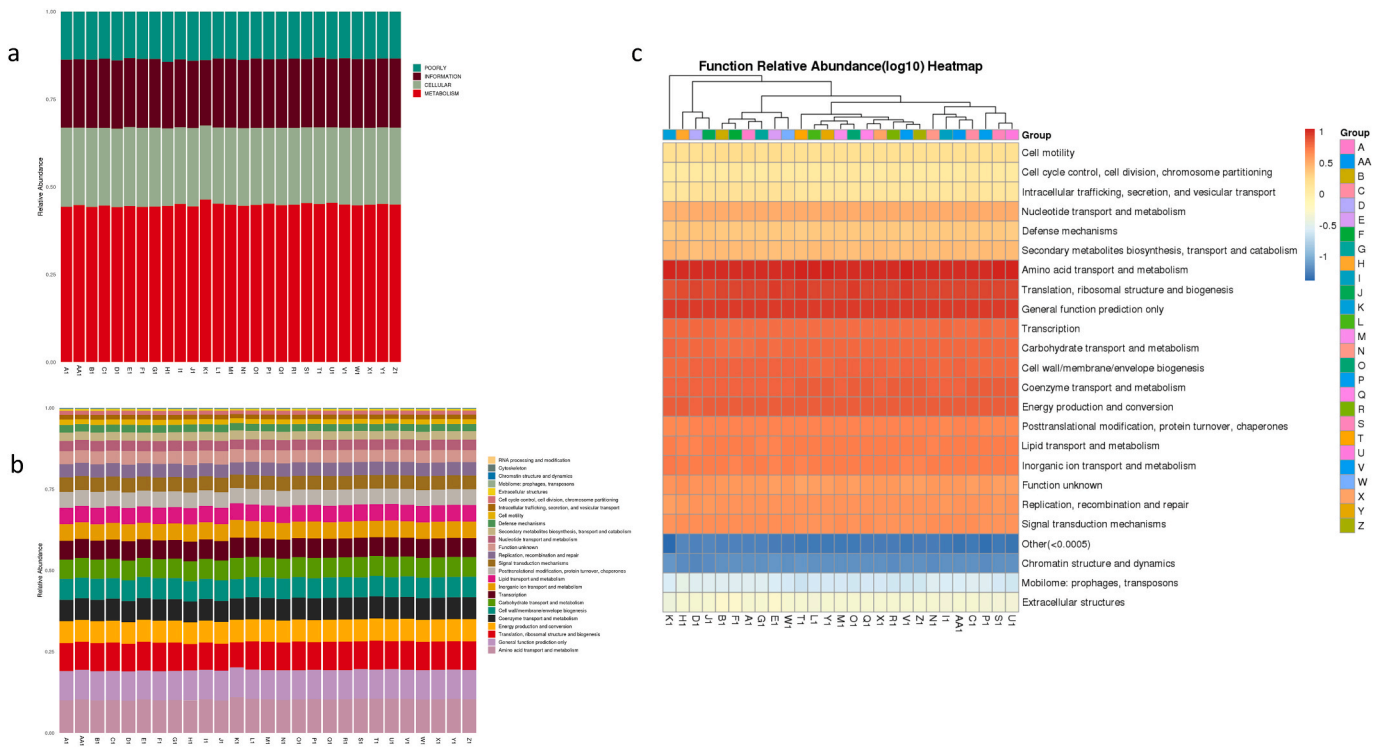

Fig. 6. Cluster of Ortholog Genes (COG) function prediction, based on the gene abundance. (a) Bar plot group Picrust – COG- level 1 (categories: information storage and processing, cellular processes and signaling, metabolism, poorly characterized), (b) Bar plot group Picrust – COG- level 2 and (c) Heatmap of COG functional pathway relative abundance among date palm cultivars (A–J), wild date palm (K), under different fertilizer treatment (L–Z) and control group (AA).

4.3. Predicting the functional capabilities of microbial communities based on the Metabolic Pathway Database (MetaCyc)

A forty-one MetaCyc were predicted at level two through 16S rRNA sequencing of 27 date palm rhizosphere samples. Fig. 7a show that the barplot of picrust of MetaCyc pathways where the highest frequent abundance was 0.29 (others) followed by 0.12 (Amino Acid Biosynthesis), 0.11 (Cofactor, Prosthetic Group, Electron Carrier and Vitamin Biosynthesis), and 0.1 (Nucleoside and Nucleotide Biosynthesis). From Fig. 7b, the heatmap analysis of relative abundance showed that K sample (wild date palm) was placed in a split branch while A sample (Barhi cultivar) was close to I sample (Nabot Sif cultivar, Rowdat Al-Faras). G sample (Khalas cultivar, Rowdat Al-Faras) was close to the cluster, including the AA sample (fertilizer-free, control) and Q sample (100% organic, 100% bio-organic), and cluster involving the N sample (100% bio-organic) and W sample (30% chemical). Whereas F sample (Khenezy, Qatar University) was close to the cluster, including the B sample (Barhi cultivars, Qatar University) and the C sample (Shishi cultivar, Rowdat Al-Faras). In addition, the H sample (Khalas, Qatar University) was close to the cluster, including D (Shishi, Qatar University) sample and the J sample (Nabot Sif, Qatar University).

In the UAE, the MetaCyc functional gene analysis of date palm soil revealed enrichment of fatty acid, cell wall, and starch biosynthesis pathways in soils irrigated with saline groundwater. Furthermore, a significant difference in 54 out of 248 predicted pathways based on bacterial OTU composition was observed between soils under non-saline water and saline groundwater irrigation [39]. However, in the USA, a study comparing the microbial communities in soybean rhizosphere soils between Nebraska and Oklahoma found potential functional differences using MetaCyc analysis. The analysis revealed a higher occurrence of pathways related to cell membrane production in Nebraska, whereas the biosynthesis of aclacinomycin pathways was prominent in Oklahoma (Niraula et al., 2022).

5. Conclusions

The date palm is an important plant species in the Gulf region, providing numerous benefits. Understanding the core microbiota and its functionality in the date palm agroecosystem is crucial to develop agricultural technologies that improve crop production and sustainability in arid environments and combat desertification. The wild date palm (oasis-ecosystem) exhibited a higher number of unique bacterial OTUs, but lower bacterial diversity than cultivated date palms. The addition of organic and bio-organic fertilizers with 100% chemical fertilizer did not have a significant impact on bacterial diversity. However, 100% organic and bio-fertilizers positively affected the relative bacterial abundance of various classes. The correlation between cultivar type and bacterial diversity was weak, except for the Khalas cultivar from both farms, which shared similar phylogeny, indicating a higher correlation between date palm location and bacterial biodiversity. The soil's chemical parameters, such as salinity, total dissolved solids (TDS), and conductivity, correlate highly with bacterial diversity. Therefore, extracting beneficial bacterial classes for date palm production and enhancing the quality and quantity of dates could be a viable approach.

Additionally, the functions of wild sample classes and bacteria with high relative abundance can enhance date palm tolerance to salinity and drought. Therefore, farmers can use different fertilizer treatments based on the bacterial diversity needed to improve date palm yield and quality.

Our findings demonstrate that date palm cultivars significantly shape the rhizosphere by influencing the bacterial community functions. The variations observed in microbial functions among different date palm lines suggest that rhizosphere communities can be manipulated through

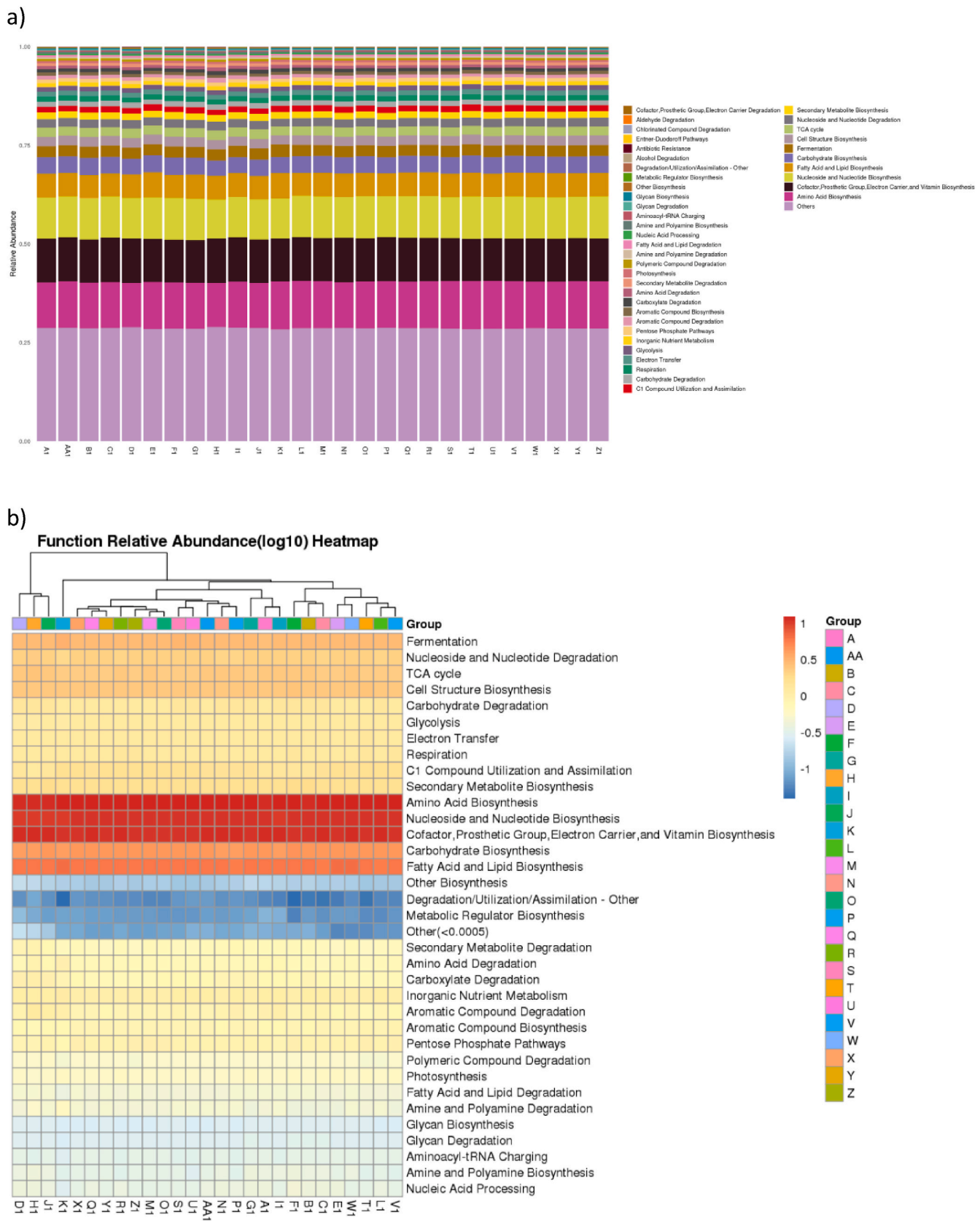

Fig. 7. MetaCyc function prediction. (a) Bar plot group Picrust – MetaCyc- level 2 and (b) Heatmap of MetaCyc functional pathway relative abundance among date palm cultivars (A–J), wild date palm (K), under different fertilizer treatment (L–Z) and control group (AA).

date palm breeding efforts. Moreover, identifying specific community members that respond to other date palm lines can serve as valuable biomarkers for traits associated with community alteration. These findings offer insights into the genetic pathways utilized by date palm hosts in recruiting and supporting beneficial microbial functions, providing breeders with tools to incorporate favourable alleles into commercial production.

Future studies should explore bacterial diversity in date palm soil and its correlation with date palm yield in Qatar. These studies would contribute to a deeper understanding of microbiome diversity and its impact on date palm soil, ultimately enhancing the quality and quantity of date palm yield. In addition, by gaining insights into the role of the microbiome, researchers can identify strategies to promote sustainable date palm production in different environmental conditions.

Compliance with ethical requirements

This article does not contain any studies with human or animal subjects.

CRediT authorship contribution statement

Dana A. Abumaali: Investigation, Writing – original draft, Writing – review & editing. **Sara H. Al-Hadidi:** Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Talaat Ahmed:** Methodology, Supervision, Writing – review & editing. **Amer Fayad Al-khis:** Investigation, Methodology. **Sowaid Ali Al-Malki:** Investigation, Methodology. **Mahmoud Yaish:** Writing – review & editing. **Hassan Hassan:** Supervision, Writing – review & editing. **Roda Al-Thani:** Supervision, Writing – review & editing. **Juha M. Alatalo:** Conceptualization, Supervision, Writing – review & editing, Funding acquisition, Methodology.

Declaration of competing interest

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

Data availability

The sequence datasets generated and/or analyzed during the current study are available in the NCBI repository: https://www.ncbi.nlm.nih.gov/sra/PRJNA978392.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.egg.2023.100195.

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