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The Microbiome of *Suaeda monoica* and *Dipterygium glaucum* From Southern Corniche (Saudi Arabia) Reveals Different Recruitment Patterns of Bacteria and Archaea

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Soil and plant interact differently in response to the same stress (e.g., salinity) and recruit certain bacteria. The southern corniche (Saudi Arabia) has limited plant growth, which could be due to the high temperature and salinity. The study aimed to determine the soil microbiome of selected plants and the interactions between soil and these plants. *Suaeda monoica* and *Dipterygium glaucum* soil samples were collected from the crust (surface) and rhizosphere, while soil with no plant growth from the nearby area was used as control. High-throughput hypervariable V3–V4 region of the 16S rRNA gene was used to evaluate the shifts in soil microbiome due to growth of plant growth. The analysis detected up to 16% archaeal strains in *S. monoica*-associated samples, while *D. glaucum* and control samples contained 100% bacterial strains. The top 10 phyla composition of the soil samples were Proteobacteria, Actinobacteria, Firmicutes, Gemmatimonadota, Bacteroidota, Halobacterota, Cyanobacteria, Cloroflexi, Planctomycetota, and Myxococcota. The V3–V4 region analysis successfully clustered the 5 samples into 3 clusters (control, *D. glaucum*, and *S. monoica*) at higher-order classification but not at the species level due to unidentified bacteria. The main differences between soil samples were due to halophyte *S. monoica* samples containing high amounts of halophilic archaea and halophilic bacteria. This showed that selected plants interacted differently with the soil. EC- and KO-based analyses of functional genes and pathways showed that 5 pathways

were specific to control, 11 pathways were observed only in *D. glaucum* samples, 12 pathways were expressed in *S. monoica* samples only, and 9 pathways were common in all samples. The study also detected numerous relatively novel genera in high abundance such as *Aliifodinibius*, *Pontibacter*, and *Lacunisphaera*. This showed that the soil in the sampling area is not well explored and that novel species could be isolated from the soil samples and used for future research.

Keywords: soil, microbiome, V3–V4, Suaeda monoica, *Dipterygium glaucum*

1 INTRODUCTION

The southern corniche (Jeddah, Saudi Arabia) is located in the coastal area of the Red Sea and hosts various attractions and tourism spots. In several sections of this long corniche, there is very limited plant growth, which could be due to the high temperature and salinity. The selected sampling area was a good site to explore the soil microbiome and try to understand the interactions between soil and plant. Two plants, namely, *Suaeda monoica* and *Dipterygium glaucum*, were found to grow nearby and surrounded by a large empty area.

S. monoica is a well-studied coastal halophyte that grows in marine environments (Devadatha et al., 2018). It was reported to possess various actives such as antiviral, antioxidant, wound healing (Rajathi et al., 2014), phytoremediation (Joshi et al., 2020), and antimicrobial activities (Muthazhagan et al., 2014). As a halophyte, it has also been used in the reclamation of salt-affected agricultural lands due to its ability to absorb sodium chloride (Ayyappan et al., 2013). A previous study on *S. monoica* in Saudi Arabia reported that this plant is used to treat various other diseases such as rheumatism, paralysis, asthma, and snakebites (Al-Said et al., 2017). A recent study identified novel marine fungi associated with *S. monoica* in India, which indicates that its microbiome is still under discovery (Devadatha et al., 2018).

D. glaucum Decne. is a monotypic genus with one species belonging to the family Capparidaceae, a slender, shrubby plant with small yellow flowers (Batanouny and Baeshin, 1982; Altwaty et al., 2016; Alzahrani et al., 2020). It is commonly distributed along the Arabian Gulf coast, and Saudi Arabia (in Wadi beds), especially after seasonal rain (Batanouny and Baeshin, 1983). This species suffers from the rarity of water and the very high temperature, which affect its phenotypic characteristics. However, this traditional plant, with multiple medicinal uses, is popular for the treatment of miss-breathing troubles. Previous phytochemical studies on *D. glaucum* revealed its antioxidant, antimicrobial, and antispasmodic activities (Altwaty et al., 2016; Shaheen et al., 2017).

Hence, this study aimed to compare the bacterial communities in saline soil with limited plant growth and evaluate the shifts in soil microbiome due to the growth of plants such as *S. monoica* and *D. glaucum*. The study also evaluated soil samples taken from the crust (surface) as well as rhizosphere of selected plants and compared them with control (no plant growth) samples.

2 MATERIAL AND METHODS

2.1 Site Description

Soil samples were collected from Southern corniche (Jeddah, Saudi Arabia), which is a saline sandy area where very few plants grow (GPS: 21.2181995–39.1756291). Sc samples were collected from crust soil of *S. monoica*, Sr samples were collected from rhizosphere soil of *S. monoica*, Dc samples were collected from crust soil of *D. glaucum*, and Dr samples were collected from rhizosphere soil of *D. glaucum*. A control sample (c) was also collected from soil samples where no plant growth was observed (**Figure 1**).

2.2 DNA Extraction

FastDNA™ Spin Soil Kit (MP Biomedicals, Santa Ana, CA, USA) was used to extract total genomic DNA for the next-generation sequencing (NGS) according to the manufacturer's instructions (Furtak et al., 2019). The DNA was visualized on 1% TAE agarose gel to assess DNA quality. DNA quality was measured using nanodrop (Implen NanoPhotometer® N60/N50) and fluorometric quantification using iQuant™ Broad Range dsDNA Quantification Kit. Extracted gDNA was diluted in sterile water to 10 ng μl^{-1} and stored at −20°C until further processing.

2.3 PCR Amplification and Next-Generation Sequencing

The purified gDNA were proceeded with NGS by amplifying the hypervariable V3–V4 region of the 16S rRNA gene using 341F (5′ CCTACGGGNGGCWGCAG3′) and 785R (5′GACTACHVGG GTATCTAATCC3′) primers (Furtak et al., 2019). PCRs were carried out with REDiant 2× PCR Master Mix (1st BASE, Kuala Lumpur, Malaysia). Library construction was carried out in 2 steps where selected regions (16S V3–V4) were amplified using locus-specific sequence primers with forward (5′ TCGTCGGCAGC GTCAGATGTGTATAAGAGACAG) and reverse (5′ GTCTCG TGGGCTCGGAGATGTGTATAAGAGACAG) overhang adapters. PCRs were carried out with KOD-Multi & Epi-® (Toyobo, Osaka, Japan) (1st BASE). In the second step, dual indices were attached to the amplicon PCR using Illumina (San Diego, CA, USA) Nextera XT Index Kit v2 following the manufacturer's protocols. The quality of the libraries was measured using Agilent (Santa Clara, CA, USA) Bioanalyzer 2100 System by Agilent DNA 1000 Kit and fluorometric quantification by Helixyte Green™ Quantifying Reagent. The libraries were normalized and pooled according to Illumina-suggested protocols, and sequencing was done using MiSeq platform using

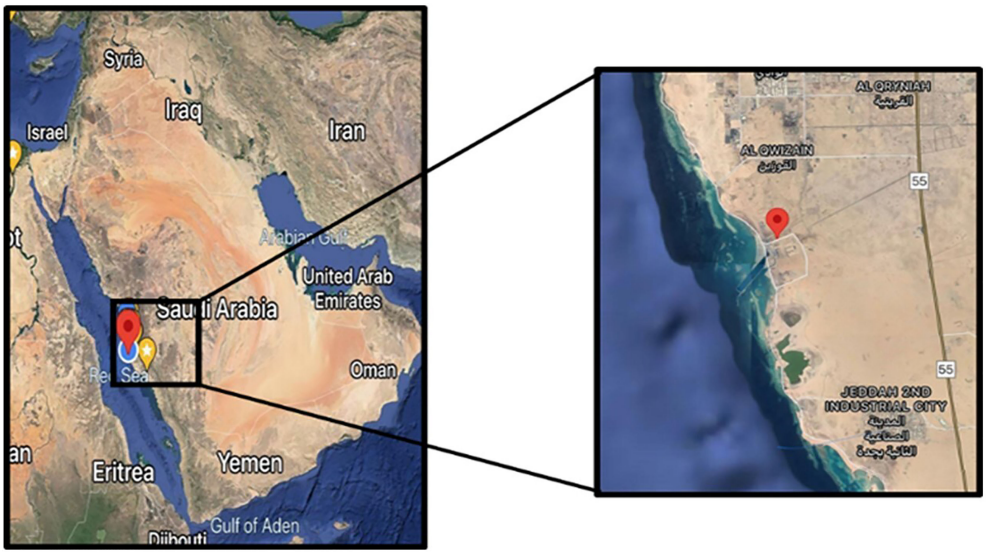

FIGURE 1 | Sampling site.

300 PE (1st BASE). Primers and adapters were removed followed by the merging of forward and reverse reads. Sequences shorter than 150 bp were removed, and the reads were made even before the data were proceeded with operational taxonomic unit (OTU) clustering using SILVA, GreenGenes, RDP, UNITE, and other databases for taxonomic assignments.

2.4 Statistical Analysis

One-way ANOVA was used for multiple comparisons of the 5 samples. For α-diversity, Chao1, Shannon, Simpson, InvSimpson, and Fisher diversity indices were used to estimate richness and diversity. Rarefaction curves were also generated based on the average number of observed OTUs to compare the relative levels of OTU diversity. For β-diversity, UniFrac distant matrix, principal coordinates analysis (PCoA), multidimensional scaling/non-metric multidimensional scaling (MDS/NMDS), canonical correspondence analysis/redundancy analysis (CCA/RDA), and UPGMA-Tree were used. PCoA plots were prepared based on weighted and unweighted UniFrac distance metrics to observe the similarities between soil samples and the clustering of the different soil groups. Multivariate parametric analysis (DESeq) was used to analyze parametric data, while analysis of similarity (ANOSIM) was used to analyze the non-parametric data. Venn diagram and double dendrogram clustered heatmaps were generated to visualize the data and observe how the soil samples will cluster.

2.5 Prediction of Bacterial Community Function

Phylogenetic Investigation of Communities by Reconstruction of Unobserved States (PICRUSt) was used to predict functional composition in the metagenome of the 5 soil samples generated using the GreenGenes database (Wu et al., 2019; Yurgel et al., 2019). PICRUSt metagenome inferences were carried out based on Kyoto Encyclopedia of Genes and Genomes (KEGG) orthologs (KO) and Enzyme Commission numbers (EC numbers). A dendrogram with a heatmap was generated to visualize the data and observe how the soil samples will cluster.

3 RESULTS

3.1Composition

The 16s V3–V4 region analysis detected archaeal strains in Sc and Sr samples with an abundance of 12% and 16%, respectively, while other samples (C, Dc, and Dr) contained 100% bacterial strains (**Figure 2**). A total of 19–23 phyla were found in the studied soil samples with diverse compositions, which showed the richness of the soil samples and interactions with plants. Using 1% as a threshold, a total of 19 phyla, 34 classes, and 76 orders were detected, which showed the richness of the soil microbiome. Top 10 composition analysis of soil samples was carried out, and the results showed an interaction between soil microbiome and plants (**Supplementary Figure 1**). For instance, the composition of the control sample was relatively even among typical soil bacteria, while samples associated with plants showed diverse distribution and the rise of new phyla, namely, Euryarchaeota (Halobacterota).

The top 10 phyla composition of the soil samples was Proteobacteria (23% ± 6%), Actinobacteria (19% ± 12%), Firmicutes (19% ± 8%), Gemmatimonadota (9% ± 4%), Bacteroidota (6% ± 4%), Halobacterota (6% ± 8%), Cyanobacteria (6% ± 6%), Cloroflexi (5% ± 3%), Planctomycetota (3% ± 2%), and Myxococcota (3% ± 2%). The highest variation between soil samples was in halophilic archaea Halobacterota and

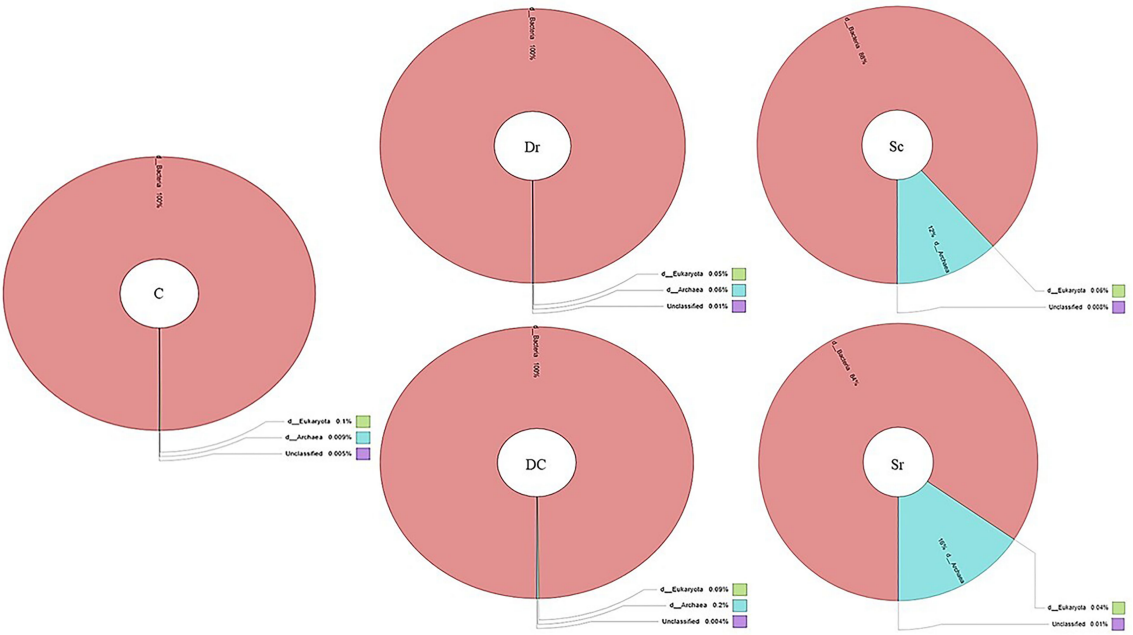

FIGURE 2 | Krona chart of domains detected in soil samples (C, Dc, Dr, Sc, and Sr).

Cyanobacteria composition, while Proteobacteria percentage was the most similar. Halobacterota, which is from archaea, was only present in *S. monoica*-associated soil samples (Sc and Sr), while Cyanobacteria was almost absent in *D. glaucum* samples (Dc and Dr). Myxococcota was also mainly present in plant-associated soil samples (Dc, Dr, S, c, and Sr).

The top 10 class composition of the soil samples was Bacilli (22% ± 9%), Alphaproteobacteria (17% ± 5%), Actinobacteria (17% ± 11%), Gammaproteobacteria (12% ± 6%), Longimicrobia (8% ± 4%), Halobacteria (7% ± 9%), Cyanobacteria (6% ± 8%), Acidimicrobiia (5% ± 5%), Bacteroidia (4% ± 3%), and Planctomycetes (3% ± 2%). The highest variation was observed in Halobacteria and Cyanobacteria classes, while the highest similarity was observed in the Alphaproteobacteria class. All the top 10 classes showed high variations with a coefficient of variation (CV) of more than 30%.

Order composition showed a similar trend to phyla and class compositions where the highest variation was observed in Halobacteriales and Cyanobacteriales orders. The top 10 order composition of the soil samples was Bacillales (28% ± 13%), Longimicrobiales (12% ± 6%), Frankiales (10% ± 8%), Halobacteriales (9% ± 14%), Rhizobiales (9% ± 6%), Burkholderiales (9% ± 8%), Paenibacillales (7% ± 2%), Cytophagales (6% ± 4%), Rhodobacterales (5% ± 3%), and Cyanobacteriales (5% ± 7%). The highest similarity between soil samples was observed in the Paenibacillales order.

The top 10 family compositions showed high variations (CV% > 30) in 9 out of 10 families. The highest variations were observed in Micrococcaceae, Balneolaceae, and Nostocaceae. Other differences observed were that Sr samples contained almost twice Bacillaceae as Sc. The top 10 family composition was Bacillaceae (33% ± 15%), Longimicrobiaceae (15% ± 8%), Geodermatophilaceae (10% ± 8%), Paenibacillaceae (8% ± 1%), Sphingomonadaceae (7% ± 5%), Rhodobacteraceae (7% ± 4%), Beijerinckiaceae (7% ± 4%), Micrococcaceae (6% ± 6%), Balneolaceae (4% ± 9%), and Nostocaceae (4% ± 7%). The highest similarity between soil samples was observed in the Paenibacillaceae family.

The top 10 genera composition also showed high variations (CV % > 30) in 9 out of 10 genera. The highest variation was observed in the *Sphaerospermopsis* genus, which was mainly present in Sc and absent in Dc and Dr. *Pontibacter* was mainly present in the control sample and absent in Sr, while *Halomonas* was mainly present in Sr and absent in Dc and Dr. *Geodermatophilus* genus was absent in Sr and present at low abundance (1%) in Sc. The top 10 genera composition of the soil samples was *Bacillus* (36% ± 14%), *Longimicrobiaceae* (19% ± 11%), *Geodermatophilus* (8% ± 7%), *Microvirga* (7% ± 5%), *Ammoniphilus* (7% ± 2%), *Rubellimicrobium* (6% ± 5%), *Blastococcus* (5% ± 3%), *Halomonas* (5% ± 10%), *Pontibacter* (4% ± 5%), and *Sphaerospermopsis* (3% ± 6%). The highest similarity between soil samples was observed in the *Ammoniphilus* genus.

3.2 Clustering

3.2.1 Operational Taxonomic Units and Diversity Indices

Figure 3 highlights the relationships, overlaps, and differences between studied soil samples (C, Dc, Dr, Sc, and Sr).

Sc had less OTUs and lower diversity as compared to the control sample (C), while Dr showed the highest number of OTUs and diversity. All α-diversity indices determined Sc as the sample with the lowest diversity and richness (**Figure 4**).

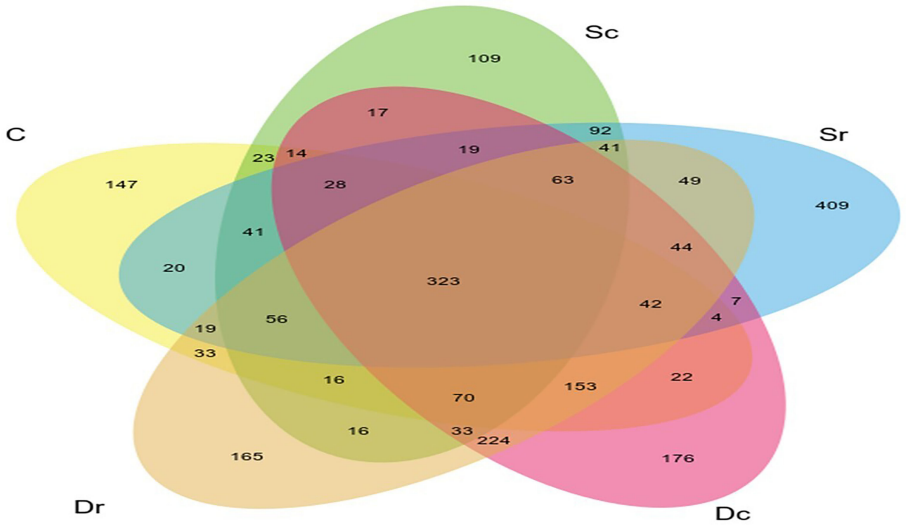

FIGURE 3 | Venn diagram of the relationships between soil samples (C, Dc, Dr, Sc, and Sr).

However, the ranking for other samples varied across different indices. Sr and Dc had similar OTUs but showed different results in α-diversity indices. Most of the variation in α-diversity indices was in Simpson and InvSimpson indices. For instance, Dr was the richest sample in all indices except in Simpson and InvSimpson. The highest variations across all indices were observed in Sr, which ranged from being ranked 4th in diversity (Simpson and InvSimpson indices) to being ranked 2nd (Chao1 and Fisher). *D. glaucum* samples showed higher diversity than *S. monoica* at the family level, and Balneolaceae and Nostocaceae were only present in *S. monoica*; however, they were present in small amounts. For example, in the top 10 families, Balneolaceae and Nostocaceae made up 16% and 20% in Sr and Sc, respectively; however, they only made up <10% of all the families detected in *S. monoica* samples. In terms of sample type, rhizosphere-related samples showed higher diversity than crust-related samples.

In β-diversity, several analysis methods (CCA, RDA, NMDS, MDS, and PCoA) were carried out to compare the 5 samples (**Figure 5**). The control sample (C) was often clustered separately, while Dc and Dr were always clustered together. Sample Sc and Sr clustered differently between different methods. NMDS and RDA showed the highest sensitivity and clustered the 5 samples into 4 clusters, while PCoA and MDS

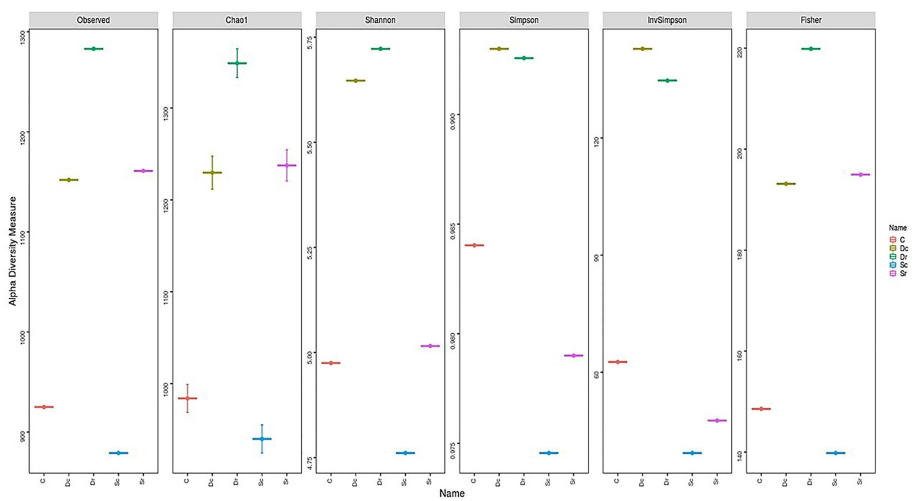

FIGURE 4 | Alpha (α) diversity indices of soil samples (C, Dc, Dr, Sc, and Sr).

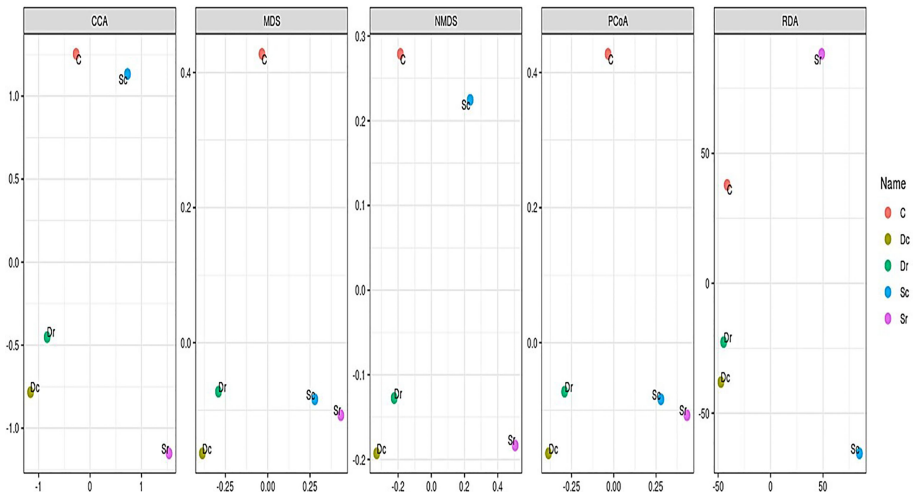

FIGURE 5 | Beta (β) diversity indices of soil samples (C, Dc, Dr, Sc, and Sr).

produced the most accurate clusters by showing 3 clusters (C, Dc and Dr, and Sc and Sr).

3.2.2 Heatmaps and Phylogenetic Investigation of Communities by Reconstruction of Unobserved States Analysis

Heatmap-based clustering of *S. monoica*, *D. glaucum*, and control samples showed that at phylum, class, order, and family levels, all 3 samples clustered separately, with *D. glaucum* being closer to control than *S. monoica*. At genus and species levels, the rhizosphere sample of *S. monoica* (Sr) became a unique cluster, while the crust of *S. monoica* (Sc) clustered with the control sample. Aside from numerous unidentified or uncultured species, this unique Sr cluster was due to the dominance of halophilic bacteria that belong to *Halomonas* and *Halofilum* genera (**Supplementary Figure 2**).

EC- and KO-based analyses of functional genes and pathways showed that *S. monoica*, *D. glaucum*, and control samples all clustered separately, which showed the significant difference between different groups of samples. The results also showed that 5 pathways were specific to control, 11 pathways were observed only in *D. glaucum* samples, 12 pathways were expressed in *S. monoica* samples only, and 9 pathways were common in all samples. Interestingly, 19 pathways were mainly observed in *D. glaucum*, while a total of 37 pathways were observed mainly in *S. monoica*. **Table 1** summarizes the unique pathways detected in various samples and their functions, while **Table 2** summarizes the pathways that were upregulated in certain samples and their functions (**Supplementary Figure 3**).

4 DISCUSSION

Proteobacteria, Actinobacteria, Bacteroidetes, Chloroflexi, Acidobacteria, and Firmicutes are dominant phyla in soil (Dube et al., 2019; Wolińska, 2019). The results of this study

TABLE 1 | Unique pathways detected in various samples and their functions.

Sample	Organisms	Reference	Function
Only in control soil (no plant growth)			
Biphenyl degradation	Firmicutes	Selesi and Meckenstock, 2009	Biodegradation
Benzoyl-CoA degradation II	Proteobacteria	Harwood et al., 1998	Biodegradation
Toluene degradation VI	Proteobacteria	Rabus et al., 2016	Biodegradation
Anaerobic aromatic compound degradation	Proteobacteria	Rabus et al., 2016; Harwood et al., 1998	Biodegradation in anoxic environments
Only in *Dipterygium glaucum*-associated soil			
Chondroitin sulfate degradation I	Proteobacteria, Bacteroidetes, Actinobacteria, and Firmicutes	Wang et al., 2020	Chondroitin sulfate catabolism and many other biological and pathophysiological activities
Superpathway of methanogenesis	*Archaea*, Proteobacteria	Ferry 2011; Kurth et al., 2020; Zhang et al., 2020	Biomethanation (C cycle)
Only in *Suaeda monoica*-associated soil			
UTP and CTP dephosphorylation I	All organisms	Wang et al., 2020	Nucleotide biosynthesis

TABLE 2 | Pathways that were upregulated in certain samples and their functions.

Sample	Organisms	Reference	Function
Upregulated in control soil (no plant growth)			
Superpathway of polyamine biosynthesis III	Proteobacteria	(Karatan et al., 2005)	Biosynthesis of spermidine
Methanogenesis from acetate	Archaea	(Abbanat and Ferry, 1990; Bologna et al., 2010)	Fermentation products
Superpathway of taurine degradation	Bacteria	(Cook and Denger, 2002)	Bile acid conjugation, detoxification, taurine degradation
Biotin biosynthesis II	Bacteria	(Manandhar and Cronan, 2017)	Biotin biosynthesis
Superpathway of sulfolactate degradation	Bacteria	(Denger and Cook, 2010)	Sulfolactate degradation
Peptidoglycan biosynthesis IV (*Enterococcus faecium*)	Firmicutes	(Bellais et al., 2006)	Cell wall biosynthesis, peptidoglycan biosynthesis
3-Hydroxypropanoate cycle	Chloroflexi	(Klatt et al., 2007)	Degradation, utilization, assimilation
Glyoxylate assimilation	Archaea, Chloroflexi	(Friedmann et al., 2006)	Glyoxylate assimilation
Upregulated in *Dipterygium glaucum* associated soil			
Superpathway of pyrimidine ribonucleosides degradation	Archaea, Bacteria	(Löffler et al., 2005)	Nucleoside degradation, pyrimidine nucleobase degradation
Superpathway of mycolyl–arabinogalactan–peptidoglycan complex biosynthesis	Actinobacteria	(Alderwick et al., 2006)	Carbohydrate biosynthesis
Reductive TCA cycle II	Aquificae	(Aoshima and Igarashi, 2006)	Biosynthesis of sugars
Nitrifier denitrification	Bacteria	(Campbell et al., 2011)	Aerobic denitrification
Androstenedione degradation	Bacteria	(Campbell et al., 2011)	Inorganic nutrient metabolism, anaerobic respiration
Benzoyl-CoA degradation I (aerobic)	Bacteria	(Teufel et al., 2010)	Aromatic compound degradation
Superpathway of methylglyoxal degradation	Bacteria	(Ahmad et al., 2020)	Aldehyde degradation
Mannosylglycerate biosynthesis I	Archaea, Bacteria	(Empadinhas and da Costa, 2006)	Metabolic regulator biosynthesis
Neopentalenoketolactone and pentalenate biosynthesis	Actinobacteria	(Jiang et al., 2009)	Antibiotic biosynthesis
Mannan degradation	Bacteria	(Kawaguchi et al., 2014)	Polysaccharide degradation
D-Mannuronate biosynthesis	Bacteria	(Shoji et al., 2014)	Sugar biosynthesis
L-Arabinose degradation IV	Archaea	(Brouns et al., 2006)	Carbohydrate degradation
Upregulated in *Suaeda monoica*-associated soil			
L-Rhamnose degradation II	Bacteria, Fungi	(Watanabe et al., 2008)	Carbohydrate degradation, sugar degradation
Glucose degradation (oxidative)	Bacteria	(Basu and Phale, 2006)	Secondary metabolite degradation
Sitosterol degradation to androstenedione	Bacteria	(Malaviya and Gomes, 2008)	Fatty acid and lipid degradation
7-(3-Amino-3-carboxypropyl)-wyosine biosynthesis	Archaea	(Umitsu et al., 2009)	Nucleic acid processing
Tetrahydromethanopterin biosynthesis	Proteobacteria	(Shaw et al., 2010)	Amine and polyamine biosynthesis
Flavin biosynthesis II (archaea)	Archaea	(Haase et al., 2013)	Vitamin biosynthesis
Entner-Doudoroff pathway III (semi-phosphorylative)	Euryarchaeota, Archaea	(Kim and Lee, 2006)	Carbohydrate degradation
Phosphopantothenate biosynthesis III	Archaea	(Yokooji et al., 2009)	Cofactor, carrier, and vitamin biosynthesis
Adenosine nucleotides degradation IV	Bacteria	(Bærentsen et al., 2019)	Adenosine nucleotide degradation
Archaetidylinositol biosynthesis	Archaea	(Koga and Nakano, 2008)	Fatty acid and lipid biosynthesis
CDP-archaeol biosynthesis	Archaea	(Koga and Nakano, 2008)	Phospholipid biosynthesis
Mevalonate pathway II (archaea)	Chloroflexi, Euryarchaeota	(Azami et al., 2014)	Isopentenyl diphosphate biosynthesis
Cob(II)yrinate *a*,*c*-diamide biosynthesis I (early cobalt insertion)	Archaea, Bacteria	(Frank et al., 2005)	Enzyme cofactor biosynthesis
Allantoin degradation IV (anaerobic)	Bacteria	(Blank et al., 2014)	Allantoin degradation
Nitrate reduction VI (assimilatory)	Archaea	(Nunn et al., 2010)	Sugar degradation
Factor 420 biosynthesis	Archaea	(Bashiri et al., 2019)	Electron carrier biosynthesis
NAD salvage pathway II	Bacteria	(Lin et al., 2004)	Vitamin biosynthesis
Superpathway of geranylgeranyldiphosphate biosynthesis I (via mevalonate)	Bacteria, Eukaryota	(Johnson et al., 2005)	Terpenoid biosynthesis, diterpenoid biosynthesis

were similar, as the top 5 phyla detected in soil samples were Proteobacteria (23% ± 6%), Actinobacteriota (19% ± 12%), Firmicutes (19% ± 8%), Gemmatimonadota (9% ± 4%), and Bacteroidota (6% ± 4%). Gemmatimonadota was present in high concentrations and was previously established as a typical soil phylum (Lena and Suda, 2018). Proteobacteria phylum and Paenibacillaceae belonging to Firmicutes phylum were the most common in all soil samples. Proteobacteria and Firmicutes are known to be dominant phyla in soil (Dube et al., 2019). This can be observed in the control samples where aside from the overall evenness of the phyla's distribution, the percentages of Proteobacteria, Actinobacteria, and Firmicutes were similar, while soil samples associated with plants showed unevenness. In this study, the top 10 phylum analysis of *S. monoica* showed that both Proteobacteria and Actinobacteriota were low, which could be due to the abundance of halophilic archaea belonging to

Halobacterota phylum (14.2% ± 1.4). Archaea contains the conserved region 16s V3–V4 as reported by recent studies (Lena & Suda, 2018; McGovern et al., 2018; Bukin et al., 2019; Willis et al., 2019). These halophilic methanogenic archaea are known to be common in soil; however, they are less tolerant to desiccation and oxygen exposure (Conrad, 2020). This can be supported by the fact Halobacterota content in the rhizosphere samples, which are more protected from heat and oxygen, was higher than in crust samples. In addition, the detection of archaea in the crust and rhizosphere of *S. monoica* samples only showed that soil microbes respond to differences in soil chemistry, which was in line with Dube et al. (2019), who studied the effect of long-term agriculture activities on the bacterial diversity in the soil.

Previous research also suggested that bacteria in the soil and their plant host interact differently in response to the same stress (e.g., salinity) (Kearl et al., 2019). Other studies also reported that plants excrete certain chemicals to recruit certain soil bacteria or suppress others to increase their resistance to diseases (Berendsen et al., 2018; Liu and Brettell, 2019). Myxococcota has been recently proposed as a new phylum and was mainly present in plant-associated soil samples (Dc, Dr, Sc, and Sr). The phylum was proposed due to the unique "pack hunting" predatory strategy of Myxococcota in which they feed on other bacteria by swarming and secreting lytic enzymes (Waite et al., 2020). The results also showed that when Chloroflexi was high in *D. glaucum*, cyanobacteria were low. Chloroflexi is considered light-harvesting (Thweatt et al., 2019) and was previously found to outcompete cyanobacteria in nitrogen fixation (Lacap et al., 2011) and is capable of carbon fixation (Ward et al., 2018). Rhizosphere of halophytes was reported to have diverse bacterial communities that promote plant growth by increasing the uptake of organic and minerals from the soil (Mehnaz et al., 2017; Kearl et al., 2019). In this study, rhizosphere-related samples showed slightly higher diversity than crust-related samples. The average number of phyla was 13 and 14 in rhizosphere and crust samples, respectively. The average number of classes was 38 and 36 in rhizosphere and crust samples, respectively. Overall, the maximum identified difference was observed at the genus level where *S. monoica*'s crust was high in *Sphaerospermopsis*, rhizosphere of *S. monoica* was high in *Halomonas* and *Bacillus*, and control was high in *Pontibacter*. Halophilic bacteria stimulate plant growth *via* many mechanisms such as increasing photosynthesis, reducing sodium uptake from the soil, and creating biofilms to trap water and nutrients (Kearl et al., 2019). In this study, the rhizosphere of *S. monoica* contained *Halomonas* genus, which was previously found to be common in the root and rhizosphere of halophytes and stimulated the growth of plants such as alfalfa in high-salinity conditions (Kearl et al., 2019). A recent study also reported that high salinity significantly reduced Actinobacteria (−0.99) and increased Firmicutes (0.88) (Kuznetsova et al., 2020). This can be supported by the fact that in *D. glaucum*, where Firmicutes was low, Actinobacteria was high. In terms of *Sphaerospermopsis* abundance in *S. monoica*'s crust, Cyanobacteria from *Sphaerospermopsis* BCCUSP55 genus could be related to nitrogen fixation at the soil surface. *Sphaerospermopsis* genus was previously reported to be closely related to a well-known nitrogen-fixing cyanobiont bacteria known as *Nostoc* (Gunawardana, 2020). This can be supported by the fact that at the family level, Nostocaceae cyanobacteria were abundant in *S. monoica*-associated samples, especially *S. monoica*'s crust, while Balneolaceae was abundant in Sr. Another species, *Sphaerospermopsis aphanizomenoides*, was reported to not only grow faster than other Nostocales families in high temperature but also to be correlated with phytoplankton (Budzyńska et al., 2019).

V3–V4 region was found to produce high richness and diversity (García-López et al., 2020). In this study, variations at the species level were high; however, it was mostly unidentified or uncultured species, which indicated that the V3–V4 region is efficient for higher-order classification. A similar issue was encountered in this study where V3–V4 region results of genus composition of *D. glaucum* also contained up to 3% unidentified *Sphingomonas* spp. This genus is well studied, and the ambiguity of these species could be due to the V3–V4 region limitation as the genus that we studied. *Rubellimicrobium* (7%) and *Kocuria* (6%) are also well-studied, yet their species were not determined. A previous study also reported that the *Rubellimicrobium* genus completely disappeared once plants grew on the soil (Köberl et al., 2013), despite *Kocuria* species being known to tolerate salinity, promote plant growth, and increase their ability to resist disease (Goswami et al., 2014). Recent studies recommended accurate species classification in other regions such as V2–V3 (Bukin et al., 2019) or other newer methods such as sFL16S (Jeong et al., 2021). However, some of the observed unidentified species could be due to the novelty of the species, as many belonged to relatively new genera and families. For instance, the rhizosphere of *S. monoica* contained a relatively high amount of unidentified *Aliifodinibius* spp. belonging to the Balneolaceae family. *Aliifodinibius* genus was described in 2013 (Wang et al., 2013) and currently contains only 6 known species, namely, *Aliifodinibius roseus* (identified 2013), *Aliifodinibius sediminis* (identified 2013), *Aliifodinibius halophilus* (identified 2016), *Aliifodinibius salicampi* (identified 2017), *Aliifodinibius salipaludis* (identified 2020), and *Aliifodinibius saliphilus* (identified 2020) (Zhao et al., 2020). The genus composition of *D. glaucum* also contained up to 3% of a relatively new genus called *Lacunisphaera*, which was described in 2017 (Rast et al., 2017). New genera under the same family (Opitutaceae) have also been proposed as recently as 2018 (Rochman et al., 2018). Other highly unclassified bacteria were observed mainly in the control sample, which was *Pontibacter* (7%). *Pontibacter* genus is relatively new, described in 2005, and novel species are being added as recently as *Pontibacter oryzae* and *Pontibacter chitinilyticus* in 2019 (Chhetri et al., 2019a; Chhetri et al., 2019b), while *Pontibacter pudoricolor* and *Pontibacter russatus* were described in 2020 (Maeng et al., 2020). Hence, novel halophilic *Aliifodinibius* spp. and *Lacunisphaera* spp. could be isolated from the sample or site. *Pontibacter* genus was recently found to be extremely tolerant to physiochemical and environmental stresses (Belov et al., 2019).

In terms of OTUs and diversity indices, the rhizosphere of *S. monoica* showed the highest variations across different indices ranging from being ranked 4th in diversity (Simpson and InvSimpson indices) to being ranked 2nd (Chao1 and Fisher). Most variations in ranking can be attributed to Simpson and InvSimpson in terms of indices and rhizosphere of *S. monoica* in terms of samples. Diversity indices measure and are influenced by richness, commonly measured by the Shannon index, and evenness, commonly measured by the Simpson index (MacDonald et al., 2017). An inverse relationship between species richness and evenness was also reported previously where detection of rare/less abundant species decreased evenness and increases richness (MacDonald et al., 2017). In this study, OTU numbers correlated with richness, Chao1, and Fisher indices only and not Shannon, while Simpson and InvSimpson indices gave similar results to Pielou's evenness. Additionally, the rhizosphere soil of *D. glaucum* was the richest except in Simpson, InvSimpson, and Pielou's evenness, while the rhizosphere of *S. monoica*'s and *D. glaucum*'s crust has similar OTUs but showed different results in α-diversity indices. These 2 samples (Sr and Dc) had significantly different composition at phylum, order, and family levels, which showed that OTUs alone is not a good indicator of diversity. This complexity and varying rankings of studied samples have been previously addressed and linked with varying richness (total number of species), the proportion of each species between different samples, detection of rare species, and other statistical differences between the indices (MacDonald et al., 2017; Daly et al., 2018). Considering that majority of the species were not identified, the Simpson index could be more accurate because they are less sensitive to minor/rare species (Morris et al., 2014); hence, *D. glaucum* samples showed higher diversity than *S. monoica*. Additionally, heatmap results showed that *S. monoica*, *D. glaucum*, and control samples showed that at phylum, class, order, and family levels, all 3 samples clustered separately. This is also supported by ordination analysis by PCoA that clustered the 5 samples into 3 clusters representing the 3 main soil samples (control, *D. glaucum*, and *S. monoica*).

EC- and KO-based analyses of functional genes and pathways showed that *S. monoica*, *D. glaucum*, and control samples all clustered separately, which showed the significant difference between different groups of samples. However, the differences in the pathways could be due to the difference in species compositions. For example, control samples that have the least species diversity showed the least unique pathways (n = 5), while *D. glaucum* samples and *S. monoica* samples showed more than 10 unique pathways each. This was expected, as the microbiome composition of *D. glaucum* samples and *S. monoica* samples contained archaeal species. **Table 1** shows the unique pathway predicted in the studied samples. Control samples expressed mainly aromatic compound degradation pathways such as biphenyl degradation, benzoyl-CoA degradation, and toluene degradation, which free up nutrients (Harwood et al., 1998; Rabus et al., 2016; Selesi and Meckenstock, 2009). On the contrary, *S. monoica* appeared to prefer nucleoside and nucleotide degradation pathways as sources of nutrients and energy (Wang et al., 2020). Interestingly, the chondroitin sulfate degradation I pathway, which is produced to degrade animal carcass tissues to provide nutrients for the plant, was predicted in *D. glaucum*, which is known to be extremely poisonous to mammals, causing paralysis in cattle (Manners et al., 1998).

Table 2 summarizes the pathways predicted to be upregulated in the studied samples. Control samples showed the upregulation of very few stress-related pathways such as superpathway of polyamine biosynthesis III, which is linked with spermidine synthesis. Spermidine is produced by Proteobacteria as a stress tolerance mechanism (Barbagallo et al., 2011). Unlike control samples, plant-associated soil samples expressed numerous plant-promoting trains such as the acquisition of nitrogen, phosphorus, and essential minerals (e.g., vitamins) and the production of antibiotics to combat pathogens (Ahemad and Kibret, 2014). For example, *D. glaucum* samples showed increased expression of superpathway of mycolyl–arabinogalactan–peptidoglycan complex biosynthesis and neopentalenoketolactone and pentalenate biosynthesis, which could be due to the abundance of Actinobacteria order (Crick and Brennan, 2008). Superpathway of mycolyl–arabinogalactan–peptidoglycan complex biosynthesis is also a cell wall biosynthesis. This indicated a bacterial growth promotion, which is supported by the high diversity observed in *D. glaucum*. In terms of *S. monoica*, the predicted pathways were the upregulation of L-rhamnose degradation, glucose degradation, and nitrate reduction, which could be due to the abundance of halotolerant strains such as *Halomonas elongata*. Previous studies reported that *Halomonas* strains contain high quantities of glucose, mannose, and rhamnose and express nitrate reductases (Maheshwari and Saraf, 2016; Joulak et al., 2021). Moreover, several lipid biosynthesis pathways were upregulated such as archaetidylinositol and CDP-archaeol biosynthesis pathways. Previous studies also linked the abundance of lipids with the presence of archaea (Maheshwari and Saraf, 2016; Caforio and Driessen, 2017). The major differences between soil samples could be explained by the associated plant species; however, a number of differences in terms of predicted pathways were also observed. The main pattern observed in rhizosphere samples was the expression of sugar synthesis and degradation pathways. For example, L-rhamnose, lactose, galactose, and glucose degradation pathways were predicted in *S. monoica* rhizosphere. The high expression of sugar synthesis and degradation pathways was expected, as the rhizosphere is known to be a sugar-rich habitat that promotes the growth of the associated microbiome (Jha and Subramanian, 2018). Taken together, predicted expression pathways were correlated with the species composition, as all samples were collected from geographically adjacent sites.

CONCLUSION

The most common phyla in soil samples were Proteobacteria, Actinobacteriota, Firmicutes, Gemmatimonadota, and

Bacteroidota, which is a typical bacterial community found in the soil microbiome. The control sample that was taken from the soil with no plant growth showed a relatively even distribution of major phyla, while plant-associated samples showed a significant increase in certain phyla as well as the growth of archaea. The V3–V4 region analysis gave a good background on the general and higher-order classification. It successfully clustered the 5 samples into 3 clusters (control, *D. glaucum*, and *S. monoica*) at phylum, class, order, and family levels. In terms of genus and species levels, future research can be carried out on amplifying the V2–V3 region to get a more accurate lower classification. The soil composition of *S. monoica*-associated samples contained relatively high amounts of halophilic archaea such as *Salarchaeum japonicum* and *Halococcus hamelinensis*, halophilic bacteria such as *Halomonas elongata*, and unidentified cyanobacteria such as *Sphaerospermopsis* spp. This could explain why *S. monoica* had lower diversity than *D. glaucum* and control samples. The soil composition of *D. glaucum* contained up to 3% each for *Lacunisphaera* spp. and *Sphingomonas* spp. Few relatively novel genera were detected in high abundances such as *Aliifodinibius*, *Pontibacter*, and *Lacunisphaera*. This indicated that novel species could be isolated from the soil samples and used for future research. Predicted pathways indicated that most of the differences between soil samples were due to the associated plant species and microbiome composition.

DATA AVAILABILITY STATEMENT

The data presented in the study are deposited in the NCBI repository, accession number PRJNA821426, PRJNA821365 and PRJNA821368.

AUTHOR CONTRIBUTIONS

RJ, RA and NasB: Data collection and project administration, HS: Statistical analyses and original draft writing, MAl: Project administration and original draft writing, AS: Funding acquisition, AA and MR: Software and formal analysis, LB, AF and MAr: Final draft writing, NabB: Conceptualization and Design of the study, MB: Design of the study and activities supervision. All authors contributed to manuscript revision, read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.865834/full#supplementary-material

REFERENCES

Abbanat, D. R., and Ferry, J. G. (1990). Synthesis of Acetyl Coenzyme A by Carbon Monoxide Dehydrogenase Complex From Acetate-Grown *Methanosarcina Thermophila*. *J. Bacteriol.* 172 (12), 7145–7150. doi: 10.1128/jb.172.12.7145-7150.1990

Ahemad, M., and Kibret, M. (2014). Mechanisms and Applications of Plant Growth Promoting Rhizobacteria: Current Perspective. *J. King. Saud. Univ-Sci.* 26 (1), 1–20. doi: 10.1016/j.jksus.2013.05.001

Ahmad, M., Anjum, N. A., Asif, A., and Ahmad, A. (2020). Real-Time Monitoring of Glutathione in Living Cells Using Genetically Encoded FRET-Based Ratiometric Nanosensor. *Sci. Rep.* 10 (1), 992. doi: 10.1038/s41598-020-57654-y

Alderwick, L. J., Seidel, M., Sahm, H., Besra, G. S., and Eggeling, L. (2006). Identification of a Novel Arabinofuranosyltransferase (AftA) Involved in Cell Wall Arabinan Biosynthesis in Mycobacterium Tuberculosis. *J. Biol. Chem.* 281 (23), 15653–15661. doi: 10.1074/jbc.M600045200

Al-Said, M. S., Siddiqui, N. A., Mukhair, M. A., Parvez, M. K., Alam, P., Ali, M., et al, et al. (2017). A Novel Monocyclic Triterpenoid and a Norsesquaterpenol From the Aerial Parts of *Suaeda Monoica* Forssk. Ex JF Gmel With Cell Proliferative Potential. *Saudi Pharm. J.* 25, 1005–1010. doi: 10.1016/j.jsps.2017.03.008

Altwaty, N. H., El-Sayed, O. E., Aly, N. A., Baeshen, M. N., and Baeshen, N. A. (2016). Molecular and cytogenetic assessment of dipterygium glaucum genotoxicity. *Anais da Academia Bras. Cienc.* 88, 623–634. doi: 10.1590/0001-3765201620150208

Alzahrani, D., Albokhari, E., Yaradua, S., and Abba, A. (2020). Complete plastome genome of dipterygium glaucum, dipterygieae, cleomaceae. *Mitochondrial DNA Part B* 5 (2), 1872–1873. doi: 10.1080/23802359.2020.1750978

Aoshima, M., and Igarashi, Y. (2006). A Novel Oxalosuccinate-Forming Enzyme Involved in the Reductive Carboxylation of 2-Oxoglutarate in *Hydrogenobacter Thermophilus* TK-6. *Mol. Microbiol.* 62 (3), 748–759. doi: 10.1111/j.1365-2958.2006.05399.x

Ayyappan, D., Balakrishnan, V., and Ravindran, K. (2013). Potentiality of *Suaeda Monoica* Forsk. A Salt Marsh Halophyte on Restoration of Saline Agricultural Soil. *World Appl. Sci. J.* 28, 2026–2032. doi: 10.5829/idosi.wasj.2013.28.12.2136

Azami, Y., Hattori, A., Nishimura, H., Kawaide, H., Yoshimura, T., and Hemmi, H. (2014). (R)-Mevalonate 3-Phosphate Is an Intermediate of the Mevalonate Pathway in *Thermoplasma Acidophilum*. *J. Biol. Chem.* 289 (23), 15957–15967. doi: 10.1074/jbc.M114.562686

Bærentsen, R. L., Brodersen, D. E., and Zhang, Y. E. (2019). Evolution of the Bacterial Nucleosidase PpnN and Its Relation to the Stringent Response. *Microbial Cell (Graz Austria)* 6 (9), 450–453. doi: 10.15698/mic2019.09.692

Barbagallo, M., Di Martino, M. L., Marcocci, L., Pietrangeli, P., De Carolis, E., Casalino, M., et al. (2011). A New Piece of the Shigella Pathogenicity Puzzle: Spermidine Accumulationby Silencing of the speG Gene. *PloS One* 6 (11), e27226. doi: 10.1371/journal.pone.0027226

Bashiri, G., Antoney, J., Jirgis, E. N. M., Shah, M. V., Ney, B., Copp, J., et al. (2019). A Revised Biosynthetic Pathway for the Cofactor F420 in Prokaryotes. *Nat. Commun.* 10 (1), 1558. doi: 10.1038/s41467-019-09534-x

Batanouny, K. H., and Baeshin, N. A. (1982). Studies on the flora of Arabia, II. The Medina-badr road Saudi Arabia. *Bull. Fac. Sci.* 6, 1–26.

Batanouny, K. H., and Baeshin, N. A. (1983). Plant communities along the Medina-badr road across the hejaz mountains, Saudi Arabia. *Vegetatio* 53 (1), 33–43. doi: 10.1007/BF00039769

Basu, A., and Phale, P. S. (2006). Inducible Uptake and Metabolism of Glucose by the Phosphorylative Pathway in *Pseudomonas Putida* CSV86. *FEMS Microbiol. Lett.* 259 (2), 311–316. doi: 10.1111/j.1574-6968.2006.00285.x

Bellais, S., Arthur, M., Dubost, L., Hugonnet, J.-E., Gutmann, L., van Heijenoort, J., et al. (2006). Aslfm, the D-Aspartate Ligase Responsible for the Addition of D-Aspartic Acid Onto the Peptidoglycan Precursor of *Enterococcus Faecium*. *J. Biol. Chem.* 281 (17), 11586–11594. doi: 10.1074/jbc.M600114200

Belov, A. A., Cheptsov, V. S., Vorobyova, E. A., Manucharova, N. A., and Ezhelev, Z. S. (2019). Stress-Tolerance and Taxonomy of Culturable Bacterial Communities Isolated From a Central Mojave Desert Soil Sample. *Geosciences* 9 (4), 166. doi: 10.3390/geosciences9040166

Berendsen, R. L., Vismans, G., Yu, K., Song, Y., de Jonge, R., Burgman, W. P., et al. (2018). Disease-Induced Assemblage of a Plant-Beneficial Bacterial Consortium. *ISME J.* 12, 1496–1507. doi: 10.1038/s41396-018-0093-1

Bhat, B. A., Mir, W. R., Sheikh, B. A., Rather, M. A., and Mir, M. A. (2022). In Vitro and in Silico Evaluation of Antimicrobial Properties of *Delphinium Cashmerianum* L., a Medicinal Herb Growing in Kashmir, India. *J. Ethnopharmacol.* 291, 115046. doi: 10.1016/j.jep.2022.115046

Blank, D., Wolf, L., Ackermann, M., and Silander, O. K. (2014). The Predictability of Molecular Evolution During Functional Innovation. *Proc. Natl. Acad. Sci. U. S. A.* 111 (8), 3044–3049. doi: 10.1073/pnas.1318797111

Bologna, F. P., Campos-Bermudez, V. A., Saavedra, D. D., Andreo, C. S., and Drincovich, M. F. (2010). Characterization of Escherichia Coli EutD: A Phosphotransacetylase of the Ethanolamine Operon. *J. Microbiol. (Seoul Korea)* 48 (5), 629–636. doi: 10.1007/s12275-010-0091-0

Brouns, S. J. J., Walther, J., Snijders, A. P. L., van de Werken, H. J. G., Willemen, H. L. D. M., Worm, P., et al. (2006). Identification of the Missing Links in Prokaryotic Pentose Oxidation Pathways: Evidence for Enzyme Recruitment. *J. Biol. Chem.* 281 (37), 27378–27388. doi: 10.1074/jbc.M605549200

Budzyńska, A., Rosińska, J., Pełechata, A., Toporowska, M., Napiórkowska-Krzebietke, A., Kozak, A., et al. (2019). Environmental Factors Driving the Occurrence of the Invasive Cyanobacterium *Sphaerospermopsis Aphanizomenoides* (Nostocales) in Temperate Lakes. *Sci. Total Environ.* 650, 1338–1347. doi: 10.1016/j.scitotenv.2018.09.144

Bukin, Y. S., Galachyants, Y. P., Morozov, I., Bukin, S., Zakharenko, A., and Zemskaya, T. (2019). The Effect of 16S rRNA Region Choice on Bacterial Community Metabarcoding Results. *Sci. Data* 6, 1–14. doi: 10.1038/sdata.2019.7

Caforio, A., and Driessen, A. J. (2017). Archaeal Phospholipids: Structural Properties and Biosynthesis. *Biochim. Biophys. Acta (BBA)-Mol. Cell Biol. Lipids* 1862 (11), 1325–1339. doi: 10.1016/j.bbalip.2016.12.006

Campbell, M. A., Nyerges, G., Kozlowski, J. A., Poret-Peterson, A. T., Stein, L. Y., and Klotz, M. G. (2011). Model of the Molecular Basis for Hydroxylamine Oxidation and Nitrous Oxide Production in Methanotrophic Bacteria. *FEMS Microbiol. Lett.* 322 (1), 82–89. doi: 10.1111/j.1574-6968.2011.02340.x

Chhetri, G., Kim, J., Kim, H., Kim, I., and Seo, T. (2019a). *Pontibacter Oryzae* Sp. Nov., a Carotenoid-Producing Species Isolated From a Rice Paddy Field. *Antonie Van Leeuwenhoek* 112, 1705–1713. doi: 10.1007/s10482-019-01298-0

Chhetri, G., Kim, J., Kim, I., Kim, M. K., and Seo, T. (2019b). *Pontibacter Chitinilyticus* Sp. Nov., a Novel Chitin-Hydrolysing Bacterium Isolated From Soil. *Antonie Van Leeuwenhoek* 112, 1011–1018. doi: 10.1007/s10482-019-01235-1

Conrad, R. (2020). Methane Production in Soil Environments—Anaerobic Biogeochemistry and Microbial Life Between Flooding and Desiccation. *Microorganisms* 8, 881. doi: 10.3390/microorganisms8060881

Cook, A. M., and Denger, K. (2002). Dissimilation of the C2 Sulfonates. *Arch. Microbiol.* 179 (1), 1–6. doi: 10.1007/s00203-002-0497-0

Crick, D. C., and Brennan, P. J. (2008). Biosynthesis of the Arabinogalactan-Peptidoglycan Complex of *Mycobacterium Tuberculosiss*. *Mycobacterial Cell Envelope*, 25–40. doi: 10.1093/glycob/11.9.107r.

Daly, A. J., Baetens, J. M., and De Baets, B. (2018). Ecological Diversity: Measuring the Unmeasurable. *Mathematics* 6, 119. doi: 10.3390/math6070119

Denger, K., and Cook, A. M. (2010). Racemase Activity Effected by Two Dehydrogenases in Sulfolactate Degradation by *Chromohalobacter Salexigens*: Purification of (S)-Sulfolactate Dehydrogenase. *Microbiol. (Read. Engl.)* 156 (Pt 3), 967–974. doi: 10.1099/mic.0.034736-0

Devadatha, B., Sarma, V. V., Ariyawansa, H., and Jones, E. G. (2018). Deniquelata Vittalii Sp. Nov., a Novel Indian Saprobic Marine Fungus on *Suaeda Monoica* and Two New Records of Marine Fungi From Muthupet Mangroves, East Coast of India. *Mycosphere* 9, 565–582. doi: 10.5943/mycosphere/9/3/8

Dube, J. P., Valverde, A., Steyn, J. M., Cowan, D. A., and Van der Waals, J. E. (2019). Differences in Bacterial Diversity, Composition and Function Due to Long-Term Agriculture in Soils in the Eastern Free State of South Africa. *Diversity* 11, 61. doi: 10.3390/d11040061

Empadinhas, N., and da Costa, M. S. (2006). Diversity and Biosynthesis of Compatible Solutes in Hyper/Thermophiles. *Int. Microbiol.* 9 (3), 199–206. doi: 10.2436/20.7010.01.65

Ferry, J. G. (2011). Fundamentals of Methanogenic Pathways that Are Key to the Biomethanation of Cbiomass. *Curr. Opin. Biotechnol.* 22 (3), 351–357.

Frank, S., Brindley, A. A., Deery, E., Heathcote, P., Lawrence, A. D., Leech, H. K., et al. (2005). Anaerobic Synthesis of Vitamin B12: Characterization of the Early Steps in the Pathway. *Biochem. Soc. Trans.* 33 (Pt 4), 811–814. doi: 10.1042/BST0330811

Friedmann, S., Alber, B. E., and Fuchs, G. (2006). Properties of Succinyl-Coenzyme A:D-Citramalate Coenzyme A Transferase and Its Role in the Autotrophic 3-Hydroxypropionate Cycle of *Chloroflexus Aurantiacus*. *J. Bacteriol.* 188 (18), 6460–6468. doi: 10.1128/JB.00659-06

Furtak, K., Grządziel, J., Gałązka, A., and Niedźwiecki, J. (2019). Analysis of Soil Properties, Bacterial Community Composition, and Metabolic Diversity in Fluvisols of a Floodplain Area. *Sustainability* 11, 3929. doi: 10.3390/su11143929

García-López, R., Cornejo-Granados, F., Lopez-Zavala, A. A., Sánchez-López, F., Cota-Huízar, A., Sotelo-Mundo, R. R., et al. (2020). Doing More With Less: A Comparison of 16S Hypervariable Regions in Search of Defining the Shrimp Microbiota. *Microorganisms* 8, 134. doi: 10.3390/microorganisms8010134

Gardner, D., Ralphs, M., Turner, D., and Welsh, S. (2002). Taxonomic Implications of Diterpene Alkaloids in Three Toxic Tall Larkspur Species (*Delphinium* Spp.). *Biochem. Syst. Ecol.* 30, 77–90. doi: 10.1016/S0305-1978(01)00120-X

Goswami, D., Pithwa, S., Dhandhukia, P., and Thakker, J. N. (2014). Delineating *Kocuria Turfanensis* 2M4 as a Credible PGPR: A Novel IAA-Producing Bacteria Isolated From Saline Desert. *J. Plant Interact.* 9, 566–576. doi: 10.1080/17429145.2013.871650

Gunawardana, D. (2020). An in Silico Study of Two Transcription Factors Controlling Diazotrophic Fates of the Azolla Major Cyanobiont *Trichormus Azollae*. *Bioinf. Biol. Insights* 14, 1177932220977490. doi: 10.1177/1177932220977490

Haase, I., Sarge, S., Illarionov, B., Laudert, D., Hohmann, H.-P., Bacher, A., et al. (2013). Enzymes From the Haloacid Dehalogenase (HAD) Superfamily Catalyse the Elusive Dephosphorylation Step of Riboflavin Biosynthesis. *Chembiochem* 14 (17), 2272–2275. doi: 10.1002/cbic.201300544

Harwood, C. S., Burchhardt, G., Herrmann, H., and Fuchs, G.. (1998). Anaerobic Metabolism of Aromatic Compounds via the Benzoyl-CoA Pathway. *FEMS Microbiol. Rev.* 22 (5), 439–458.

Jeong, J., Yun, K., Mun, S., Chung, W. H., Choi, S. Y., Nam, Y. D., et al. (2021). The Effect of Taxonomic Classification by Full-Length 16S rRNA Sequencing With a Synthetic Long-Read Technology. *Sci. Rep.* 11, 1–12. doi: 10.1038/s41598-021-90067-z

Jha, Y., and Subramanian, R. B. (2018). "Effect of Root-Associated Bacteria on Soluble Sugar Metabolism in Plant Under Environmental Stress," in *Plant Metabolites and Regulation Under Environmental Stress* (UK: Academic Press), 231–240.

Jiang, J., Tetzlaff, C. N., Takamatsu, S., Iwatsuki, M., Komatsu, M., Ikeda, H., et al. (2009). Genome Mining in *Streptomyces Avermitilis*: A Biochemical Baeyer-Villiger Reaction and Discovery of a New Branch of the Pentalenolactone Family Tree. *Biochemistry* 48 (27), 6431–6440. doi: 10.1021/bi900766w

Johnson, C. D., Chary, S. N., Chernoff, E. A., Zeng, Q., Running, M. P., and Crowell, D. N. (2005). Protein Geranylgeranyltransferase I Is Involved in Specific Aspects of Abscisic Acid and Auxin Signaling in Arabidopsis. *Plant Physiol.* 139 (2), 722–733. doi: 10.1104/pp.105.065045

Joshi, A., Kanthaliya, B., Rajput, V., Minkina, T., and Arora, J. (2020). Assessment of Phytoremediation Capacity of Three Halophytes: *Suaeda Monoica*, *Tamarix*

Indica and *Cressa Critica*. *Biol. Futura* 71, 301–312. doi: 10.1007/s42977-020-00038-0

Joulak, I., Concórdio-Reis, P., Torres, C. A., Sevrin, C., Grandfils, C., Attia, H., et al. (2021). Sustainable Use of Agro-Industrial Wastes as Potential Feedstocks for Exopolysaccharide Production by Selected Halomonas Strains. *Environ. Sci. Poll Res.* 29 (15), 22043–22055. doi: 10.1007/s11356-021-17207-w.

Karatan, E., Duncan, T. R., and Watnick, P. I. (2005). NspS, a Predicted Polyamine Sensor, Mediates Activation of *Vibrio Cholerae* Biofilm Formation by Norspermidine. *J. Bacteriol.* 187 (21), 7434–7443. doi: 10.1128/JB.187.21.7434-7443.2005

Kawaguchi, K., Senoura, T., Ito, S., Taira, T., Ito, H., Wasaki, J., et al. (2014). The Mannobiose-Forming Exo-Mannanase Involved in a New Mannan Catabolic Pathway in Bacteroides Fragilis. *Arch. Microbiol.* 196 (1), 17–23. doi: 10.1007/s00203-013-0938-y

Kearl, J., McNary, C., Lowman, J. S., Mei, C., Aanderud, Z. T., Smith, S. T, et al. (2019). Salt-Tolerant Halophyte Rhizosphere Bacteria Stimulate Growth of Alfalfa in Salty Soil. *Front. Microbiol.* 10, 1849. doi: 10.3389/fmicb.2019.01849

Kim, S., and Lee, S. B. (2006). Characterization of *Sulfolobus Solfataricus* 2-Keto-3-Deoxy-D-Gluconate Kinase in the Modified Entner-Doudoroff Pathway. *Biosci. Biotechnol. Biochem.* 70 (6), 1308–1316. doi: 10.1271/bbb.50566

Klatt, C. G., Bryant, D. A., and Ward, D. M. (2007). Comparative Genomics Provides Evidence for the 3-Hydroxypropionate Autotrophic Pathway in Filamentous Anoxygenic Phototrophic Bacteria and in Hot Spring Microbial Mats. *Environ. Microbiol.* 9 (8), 2067–2078. doi: 10.1111/j.1462-2920.2007.01323.x

Köberl, M., Schmidt, R., Ramadan, E. M., Bauer, R., and Berg, G. (2013). The Microbiome of Medicinal Plants: Diversity and Importance for Plant Growth, Quality and Health. *Front. Microbiol.* 4, 400. doi: 10.3389/fmicb.2013.00400

Koga, Y., and Nakano, M. (2008). A Dendrogram of Archaea Based on Lipid Component Parts Composition and Its Relationship to rRNA Phylogeny. *Systematic Appl. Microbiol.* 31 (3), 169–182. doi: 10.1016/j.syapm.2008.02.005

Kurth, J. M., Op denCamp, H. J., and Welte, C. U (2020). Several Ways One Goal —Methanogenesis From Unconventional Substrate. *Appl. Microbiol. Biotechnol.* 104 (16), 6839–6854.

Kuznetsova, A.I., Ivanova, E. A., Samylina, O. S., Kurbanova, F. G., Gruzdev, D. S., Kanapatskiy, T. A, et al. (2020). Prokaryotic Communities in Saline Soils of the Lake Elton Area in a Soil Catena Along the Khara River. *Microbiology* 89, 670–684. doi: 10.1134/S0026261720060119

Lacap, D. C., Warren-Rhodes, K. A., McKay, C. P., and Pointing, S. B. (2011). Cyanobacteria and Chloroflexi-Dominated Hypolithic Colonization of Quartz at the Hyper-Arid Core of the Atacama Desert, Chile. *Extremophiles* 15, 31–38. doi: 10.1007/s00792-010-0334-3

Lena, T., and Suda, W. (2018). "Mapping the Environmental Microbiome," in *Encyclopedia of Bioinformatics and Computational Biology*. Eds. S. R, M. G, K. N and C. S (Netherlands: Elsevier B.V.), pp. 17–28.

Lin, S.-J., Ford, E., Haigis, M., Liszt, G., and Guarente, L. (2004). Calorie Restriction Extends Yeast Life Span by Lowering the Level of NADH. *Genes Dev.* 18 (1), 12–16. doi: 10.1101/gad.1164804

Liu, H., and Brettell, L. E. (2019). Plant Defense by VOC-Induced Microbial Priming. *Trends Plant Sci.* 24, 187–189. doi: 10.1016/j.tplants.2019.01.008

Löffler, M., Fairbanks, L. D., Zameitat, E., Marinaki, A. M., and Simmonds, H. A. (2005). Pyrimidine Pathways in Health and Disease. *Trends Mol. Med.* 11 (9), 430–437. doi: 10.1016/j.molmed.2005.07.003

Looman, J. (1984). Biological Flora of Canada. 5. *Delphinium Glaucum* Watson, Tall Larkspur. *Can. Field-Nat.* 98 (3), 345–361.

MacDonald, Z. G., Nielsen, S. E., and Acorn, J. H. (2017). Negative Relationships Between Species Richness and Evenness Render Common Diversity Indices Inadequate for Assessing Long-Term Trends in Butterfly Diversity. *Biodiversity Conserv.* 26, 617–629. doi: 10.1007/s10531-016-1261-0

Maeng, S., Park, Y., Lee, S. E., Han, J. H., Cha, I. T., Lee, K. E, et al. (2020). *Pontibacter Pudoricolor* Sp. Nov., and *Pontibacter Russatus* Sp. Nov. Radiation-Resistant Bacteria Isolated From Soil. *Antonie Van Leeuwenhoek* 113, 1361–1369. doi: 10.1007/s10482-020-01446-x

Maheshwari, D. K., and Saraf, M. (2016). *Halophiles: Biodiversity and Sustainable Exploitation (Sustainable Development and Biodiversity, 6) (Softcover Reprint of the Original. 1st ed. 2015 ed* Vol. 6 (Switzerland: Springer).

Malaviya, A., and Gomes, J. (2008). Androstenedione Production by Biotransformation of Phytosterols. *Bioresource Technol.* 99 (15), 6725–6737. doi: 10.1016/j.biortech.2008.01.039

Manandhar, M., and Cronan, J. E. (2017). Pimelic Acid, the First Precursor of the Bacillus Subtilis Biotin Synthesis Pathway, Exists as the Free Acid and Is Assembled by Fatty Acid Synthesis. *Mol. Microbiol.* 104 (4), 595–607. doi: 10.1111/mmi.13648

Manners, G. D., Panter, K. E., Pfister, J. A., Ralphs, M. H., and James, L. F. (1998). The Characterization and Structure– Activity Evaluation of Toxic Norditerpenoid Alkaloids From Two Delphinium Species. *J. Nat. Prod.* 61, 1086–1089. doi: 10.1021/np980013e

McGovern, E., Waters, S. M., Blackshields, G., and McCabe, M. S. (2018). Evaluating Established Methods for Rumen 16S rRNA Amplicon Sequencing With Mock Microbial Populations. *Front. Microbiol.* 9, 1365. doi: 10.3389/fmicb.2018.01365

Mehnaz, D., Mukhtar, S., Ishaq, A., Hassan, S., Abdulla, K., and Mirza, M. S. (2017). Comparison of Microbial Communities Associated With Halophyte (*Salsola Stocksii*) and Non-Halophyte (*Triticum Aestivum*) Using Culture-Independent Approaches. *Pol. J. Microbiol.* 66 (3), 375–386. doi: 10.5604/01.3001.0010.4866

Morris, E. K., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T. S, et al. (2014). Choosing and Using Diversity Indices: Insights for Ecological Applications From the German Biodiversity Exploratories. *Ecol. Evol.* 4, 3514–3524. doi: 10.1002/ece3.1155

Muthazhagan, K., Thirunavukkarasu, P., Ramanathan, T., and Kannan, D. (2014). Studies on Phytochemical Screening, Antimicrobial and Anti Radical Scavenging Effect Coastal Salt Mash Plant of a *Suaeda Monoica*. *Res. J. Phytochem.* 8, 102–111. doi: 10.3923/rjphyto.2014.102.111

Nunn, C. E. M., Johnsen, U., Schönheit, P., Fuhrer, T., Sauer, U., Hough, D. W., et al. (2010). Metabolism of Pentose Sugars in the Hyperthermophilic Archaea *Sulfolobus Solfataricus* and *Sulfolobus Acidocaldarius*. *J. Biol. Chem.* 285 (44), 33701–33709. doi: 10.1074/jbc.M110.146332

Rabus, R., Boll, M., Heider, J., Meckenstock, R. U., Buckel, W., Einsle, O., et al. (2016). Anaerobic Microbial Degradation of Hydrocarbons: From Enzymatic Reactions to the Environment. *Microb. Physiol.* 26 (1–3), 5–28.

Rajathi, F. A. A., Arumugam, R., Saravanan, S., and Anantharaman, P. (2014). Phytofabrication of Gold Nanoparticles Assisted by Leaves of *Suaeda Monoica* and Its Free Radical Scavenging Property. *J. Photochem. Photobiol. B.: Biol.* 135, 75–80. doi: 10.1016/j.jphotobiol.2014.03.016

Rast, P., Glöckner, I., Boedeker, C., Jeske, O., Wiegand, S., Reinhardt, R., et al. (2017). Three Novel Species With Peptidoglycan Cell Walls Form the New Genus *Lacunisphaera* Gen. Nov. In the Family Opitutaceae of the Verrucomicrobial Subdivision 4. *Front. Microbiol.* 8, 202. doi: 10.3389/fmicb.2017.00202

Rochman, F. F., Kim, J. J., Rijpstra, W. I.C., Damsté, J. S. S., Schumann, P., Verbeke, T. J., et al. (2018). *Oleiharenicola Alkalitolerans* Gen. Nov., Sp. Nov., a New Member of the Phylum Verrucomicrobia Isolated From an Oilsands Tailings Pond. *Int. J. Syst. Evol. Microbiol.* 68, 1078–1084. doi: 10.1099/ijsem.0.002624

Selesi, D., and Meckenstock, R. U.. (2009). Anaerobic Degradation of the Aromatic Hydrocarbon Biphenyl by a Sulfate-Reducing Enrichment Culture. *FEMS Microbiol. Ecol.* 68 (1), 86–93.

Shaheen, U., Shoeib, N. A., Temraz, A., and Abdelhady, M. I. (2017). Flavonoidal constituents, antioxidant, antimicrobial, and cytotoxic activities of dipterygium glaucum grown in kingdom of Saudi Arabia. *Pharmacogn. Mag.* 13 (Suppl 3), S484. doi: 10.4103/pm.pm_44_16

Shaw, F. L., Elliott, K. A., Kinch, L. N., Fuell, C., Phillips, M. A., and Michael, A. J. (2010). Evolution and Multifarious Horizontal Transfer of an Alternative Biosynthetic Pathway for the Alternative Polyamine Sym-Homospermidine. *J. Biol. Chem.* 285 (19), 14711–14723. doi: 10.1074/jbc.M110.107219

Shoji, M., Sato, K., Yukitake, H., Naito, M., and Nakayama, K. (2014). Involvement of the Wbp Pathway in the Biosynthesis of *Porphyromonas Gingivalis* Lipopolysaccharide With Anionic Polysaccharide. *Sci. Rep.* 4, 5056. doi: 10.1038/srep05056

Teufel, R., Mascaraque, V., Ismail, W., Voss, M., Perera, J., Eisenreich, W., et al. (2010). Bacterial Phenylalanine and Phenylacetate Catabolic Pathway Revealed. *Proc. Natl. Acad. Sci. U. S. A.* 107 (32), 14390–14395. doi: 10.1073/pnas.1005399107

Thweatt, J. L., Canniffe, D. P., and Bryant, D. A. (2019). Biosynthesis of Chlorophylls and Bacteriochlorophylls in Green Bacteria. *Adv. Bot. Res.* 90, 35–89. doi: 10.1016/bs.abr.2019.03.002

Umitsu, M., Nishimasu, H., Noma, A., Suzuki, T., Ishitani, R., and Nureki, O. (2009). Structural Basis of AdoMet-Dependent Aminocarboxypropyl Transfer Reaction Catalyzed by tRNA-Wybutosine Synthesizing Enzyme, TYW2. *Proc. Natl. Acad. Sci. U. S. A.* 106 (37), 15616–15621. doi: 10.1073/pnas.0905270106

Waite, D. W., Chuvochina, M., Pelikan, C., Parks, D. H., Yilmaz, P., Wagner, M., et al. (2020). Proposal to Reclassify the Proteobacterial Classes Deltaproteobacteria and Oligoflexia, and the Phylum Thermodesulfobacteria Into Four Phyla Reflecting Major Functional Capabilities. *Int. J. Syst. Evol. Microbiol.* 70, 5972–6016. doi: 10.1099/ijsem.0.004213

Wang, Y. X., Liu, J. H., Xiao, W., Ma, X. L., Lai, Y. H., Li, Z. Y, et al. (2013). *Aliifodinibius Roseus* Gen. Nov., Sp. Nov., and *Aliifodinibius Sediminis* Sp. Nov., Two Moderately Halophilic Bacteria Isolated From Salt Mine Samples. *Int. J. Syst. Evol. Microbiol.* 63, 2907–2913. doi: 10.1099/ijs.0.043869-0

Wang, W., Shi, L., Qin, Y., and Li, F.. (2020). Research and Application of Chondroitin Sulfate/dermatan Sulfate-Degrading Enzymes. *Front. Cell Dev. Biol.* 1435.

Ward, L. M., Hemp, J., Shih, P. M., McGlynn, S. E., and Fischer, W. W. (2018). Evolution of Phototrophy in the Chloroflexi Phylum Driven by Horizontal Gene Transfer. *Front. Microbiol.* 9, 260. doi: 10.3389/fmicb.2018.00260

Watanabe, S., Piyanart, S., and Makino, K. (2008). Metabolic Fate of L-Lactaldehyde Derived From an Alternative L-Rhamnose Pathway. *FEBS J.* 275 (20), 5139–5149. doi: 10.1111/j.1742-4658.2008.06645.x

Welsh, S., and Ralphs, M. (2002). Some Tall Larkspurs (*Delphinium-Ranunculaceae*) a Taxonomic Review. *Biochem. Syst. Ecol.* 2, 103–112. doi: 10.1016/S0305-1978(01)00122-3

Willis, C., Desai, D., and LaRoche, J. (2019). Influence of 16S rRNA Variable Region on Perceived Diversity of Marine Microbial Communities of the Northern North Atlantic. *FEMS Microbiol. Lett.* 366, fnz152. doi: 10.1093/femsle/fnz152

Wolińska, A. (2019). Metagenomic Achievements in Microbial Diversity Determination in Croplands: A Review. *Microb. Diversity Genom. Era*, 15–35. doi: 10.1016/B978-0-12-814849-5.00002-2

Wu, X., Li, J., Ji, M., Wu, Q., Wu, X., Ma, Y., et al. (2019). Non-Synchronous Structural and Functional Dynamics During the Coalescence of Two Distinct Soil Bacterial Communities. *Front. Microbiol.* 10, 1125. doi: 10.3389/fmicb.2019.01125

Yokooji, Y., Tomita, H., Atomi, H., and Imanaka, T. (2009). Pantoate Kinase and Phosphopantothenate Synthetase, Two Novel Enzymes Necessary for CoA Biosynthesis in the Archaea. *J. Biol. Chem.* 284 (41), 28137–28145. doi: 10.1074/jbc.M109.009696

Yurgel, S. N., Nearing, J. T., Douglas, G. M., and Langille, M. G. (2019). Metagenomic Functional Shifts to Plant Induced Environmental Changes. *Front. Microbiol.* 10, 1682. doi: 10.3389/fmicb.2019.01682

Zhao, X., Miao, S., Sun, Y., Gong, Q., Zhao, J., Wang, J, et al. (2020). *Aliifodinibius Salipaludis* Sp. Nov., Isolated From Saline-Alkaline Soil. *Curr. Microbiol.* 77, 1328–1333. doi: 10.1007/s00284-019-01863-w

Zhang, C. J., Pan, J., Liu, Y., Duan, C. H., and Li, M. (2020). Genomic and Transcriptomic Insights Into Methanogenesis Potential of Novel Methanogens from Mangrove Sedimentsl. *Microbiome* 8 (1), 1–12.

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