



UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
INSTITUTO DE BIOLOGÍA
Biología evolutiva

TÍTULO DEL PROYECTO

**METAANÁLISIS DE LOS PATRONES MACROGEOGRÁFICOS DE
CUATRO REGIONES EN LA COMPOSICIÓN DE LAS
COMUNIDADES BACTERIANAS Y ARQUEANAS ASOCIADAS A
LAS RIZÓSFERAS DE HALÓFITAS Y XERÓFITAS.**

(POR ARTÍCULO CIENTÍFICO)

**Meta-analysis of Community Composition Patterns of Halophyte and Xerophyte
Rhizosphere Associated Bacteria**

QUE PARA OPTAR POR EL GRADO DE:
MAESTRO EN CIENCIAS BIOLÓGICAS

PRESENTA:
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COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLÓGICAS

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ASUNTO: Oficio de Jurado

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P r e s e n t e

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el 20 de junio del 2022, se aprobó el siguiente jurado para el examen de grado de **MAESTRO EN CIENCIAS BIOLÓGICAS** en el campo de conocimiento de **BIOLOGÍA EVOLUTIVA** del alumno **COLCHADO LÓPEZ GIOVANI JOEL** con número de cuenta **312068374** por la modalidad de graduación de **tesis por artículo científico** titulado: “**Meta-analysis of Community Composition Patterns of Halophyte and Xerophyte Rhizosphere Associated Bacteria**”, que es producto del proyecto realizado en la maestría que lleva por título: “**Metaanálisis de los patrones macrogeográficos de cuatro regiones en la composición de las comunidades bacterianas y arquenas asociadas a las rizósferas de halófitas y xerófitas**”, ambos realizados bajo la dirección del **DR. ULISES YNUÉN ROSAS LÓPEZ**, quedando integrado de la siguiente manera:

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Sin otro particular, me es grato enviarle un cordial saludo.

A T E N T A M E N T E
“POR MI RAZA HABLARÁ EL ESPÍRITU”
Ciudad Universitaria, Cd. Mx., a 31 de agosto de 2022

COORDINADOR DEL PROGRAMA


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Índice

I. Resumen en español	1
II. Abstract	2
III. Introducción general	3
IV. Sobretiro del artículo	7
Título	7
Abstract	7
Keywords	8
1. Introduction	8
2. Materials and methods	11
Data provenance and accessions	11
Bioinformatic processing	12
Data visualization and statistical analyses	13
3. Results	14
The taxonomic composition of the prokaryote microbial communities in xerophyte and halophyte rhizospheres display an enormous diversity	14
Alpha diversity analyses can be explained by host species and geographical site	17
Beta diversity confirms that host taxonomic identity and local bioclimatic features both explain rhizosphere microbiome composition	18
4. Discussion and conclusions	21
Author contributions	24
Acknowledgements	25
Declaration of competing interests	25
V. Supplementary Material	26
VI. Discusión general y conclusiones	60
VII. Referencias bibliográficas	64

Resumen en español

Las interacciones planta-procarionte en el entorno de la raíz han sido ampliamente estudiadas en todo el mundo, debido a que en su mayoría estas tienen un impacto benéfico para la supervivencia y el crecimiento vegetal. Lo anterior, como resultado de la explotación por parte de las plantas de los procesos bioquímicos microbianos, tales como la fijación de nitrógeno y la secreción de Sustancias Poliméricas Extracelulares (EPS, por sus siglas en inglés). Dichos procesos bioquímicos son influenciados como legado de las condiciones climáticas y edafológicas que estructuran al acervo bacteriano del suelo, que forman una fuente importante a partir de la cual las plantas adquieren su microbioma rizosférico. Dado que las halófitas y las xerófitas experimentan condiciones ambientales extremas, las interacciones raíz-procarionte son indispensables para el establecimiento y la supervivencia de las plantas, sobre todo en un escenario de mayor escasez de agua por efectos del cambio climático; aun así, conocemos poco sobre los patrones a escala macrogeográfica que ocurren en las comunidades raíz-microbio de ambientes áridos. En este trabajo, presento un metaanálisis para comparar los patrones de composición de las comunidades de procariontes asociadas a la rizósfera de halófitas y xerófitas de ambientes áridos usando datos de 13 especies de angiospermas en cinco países (E.E.U.U., México, Namibia, Pakistán y Túnez), analizados en Qiime 2. En términos taxonómicos, las comunidades rizosféricas son diversas e incluyen clases cosmopolitas como Alphaproteobacteria, Bacilli y Gammaproteobacteria, así como algunos grupos endémicos de algunos sitios como las clases halinófilas Haloarchaea, y PAUC43, estas últimas encontradas sólo en E.E.U.U. La diversidad alfa (ACE, Faith PD y Shannon) y beta (Jaccard) sugieren que los factores que dominan en la estructuración de las comunidades microbianas son la familia de la planta hospedera y sus estrategias ecológicas, así como el medio abiótico (variables bioclimáticas, pH del suelo y total de bases intercambiables). Sin embargo, la estrategia fenológica (caducifolias vs. perennifolias) no tienen un efecto significativo. En resumen, este trabajo representa una primera aproximación al estudio de los patrones macrogeográficos que gobiernan a los microbiomas rizosféricos en ambientes áridos.

Resumen en inglés (Abstract)

In plant roots, prokaryote-plant interactions have been extensively studied worldwide due to the benefits for plant survival and growth that result from the exploitation of microbial biochemical processes, such as nitrogen fixation and secretion of Extracellular Polymeric Substances (EPS). Climatical and edaphic forces structure the soil bacterial pool, from which plants acquire a large share of their rhizosphere microbiome. As halophyte and xerophyte plants are subject to extreme environmental conditions, prokaryote-root interactions could be pivotal for plant establishment and survival, even more under the imminent scenario of climate change and increased water scarcity; yet, we have a limited understanding on large-scale patterns for root-microbe communities in arid environments. Here, we present a meta-analysis approach to compare composition patterns of the prokaryotic community associated to the rhizospheres of halophytes and xerophytes from 'arid' environments, representing 13 angiosperm plant species from five countries (Mexico, Namibia, Pakistan, Tunisia, and USA), using a Qiime2 pipeline. In taxonomic terms, rhizosphere prokaryotic communities are diverse and include cosmopolitan classes like Alphaproteobacteria, Bacilli, and Gammaproteobacteria, as well as some site-specific groups like haline-thriving Haloarchaea, and PAUC43f which was found only in the USA samples. Alpha (ACE, Faith PD y Shannon) and beta (Jaccard) diversity estimates suggested that the main factors structuring microbial communities are host plant family, plant ecological strategy and abiotic environment (bioclimatic variables, soil pH and total exchangeable bases). Furthermore, life history strategy (i.e. deciduous vs. perennial phenology) is not significant. This work presents an early sketch on the macro-geographical patterns driving rhizosphere microbiomes in arid environments.

Introducción general

Los ambientes áridos ocupan cerca del 40% de la superficie terrestre, aunque se espera un aumento entre el 11 y 23% en la distribución de las condiciones de aridez como resultado del cambio climático, lo que conllevaría al cambio de la dinámica ecológica en varias regiones del mundo (Huang *et al.*, 2015; Sherwood y Fu, 2014). Informalmente, ‘aridez’ y ‘árido’ son términos utilizados para un gradiente de ambientes que van de subhúmedo a hiperárido, cuya característica definitoria es que la media anual de precipitación sea menor a la tasa de evapotranspiración lo que conlleva a un fuerte estrés hídrico en los seres biológicos que habitan estos sitios. En estos ambientes, la aridez es un factor clave que afecta a la composición de las comunidades (Armas *et al.*, 2011; Xiong, *et al.*, 2020). Para lidiar con el estrés ambiental, las plantas que habitan los ambientes áridos muestran una gran cantidad de estrategias que han evolucionado convergentemente entre linajes de las Spermatophyta, lo cual incluye el desarrollo de rasgos morfológicos (ej. xerófitas y halófitas) y diversas estrategias fenológicas (es decir, caducifolias y perennifolias), las cuales les permiten la supervivencia en ecosistemas áridos (Duarte *et al.*, 2014; Hashem y Mohamed, 2020; He *et al.*, 2021; Jarvis *et al.*, 2014; Rudgers *et al.*, 2019). Además de las estrategias directas de las plantas, su supervivencia también depende de su habilidad para reclutar microbios del ambiente para satisfacer sus necesidades ecológicas como la adquisición de nitrógeno (N) y fósforo (P), y la aminoración del estrés hídrico (Flores-Núñez *et al.*, 2020; Oburger *et al.*, 2009; Liu *et al.*, 2018). Se ha demostrado que los rasgos de las plantas, así como su identidad filogenética, son importantes para el reclutamiento microbiano y estos en conjunto con los factores abióticos modelan a las comunidades nativas desde las cuales el microbioma es adquirido (Emmett *et al.*, 2017; Thiergart *et al.*, 2020). Por lo tanto, explorar las variaciones en la composición entre comunidades microbianas y cómo éstos interactúan con las diferentes estrategias de las plantas y sus afinidades filogenéticas, así como los factores del medio abiótico desde una perspectiva macrogeográfica son necesarias para entender las interacciones planta-microbio en ambientes áridos.

El microbioma que se establece sobre las raíces de las plantas es reclutado principalmente del suelo, en una región que es dominada por los perfiles de

exudación vegetal y que se conoce como ‘rizosfera’. En la rizosfera, los exudados de la raíz actúan como ‘bienes’ que favorecen el reclutamiento de comunidades microbianas benéficas compuestas por miembros de los distintos dominios (aunque principalmente dominadas por Bacteria); también ayudan a la planta a controlar la proliferación de patógenos (Durán *et al.*, 2018; Rey y Jacquet, 2018). Los principales servicios proveídos por las comunidades rizosféricas incluyen favorecer el establecimiento y crecimiento de las plantas mediante la bioerosión controlada por microorganismos (López y Bacilio, 2020), la fijación de N (Flores-Núñez *et al.*, 2020; Li *et al.*, 2017), el flujo de carbono vía la descomposición de raíces (Ling *et al.*, 2022; Whitford, 1996), el aumento en la disponibilidad de P y minerales (Gómez Garrido *et al.*, 2018; Oburger *et al.*, 2009) y la producción de aminoácidos osmoprotectores y sustancias poliméricas extracelulares (Taketani *et al.*, 2015). Además, la comunidad microbiana de la rizosfera ayuda a consolidar la formación de la rizovaina (conocida como *rhizosheath* en inglés), una estructura descrita en las xerófitas y conformada por agregados densos de suelo firmemente adherido a las raíces por interacciones entre el suelo, las biopelículas microbianas y los exudados. La rizovaina actúa como un reservorio que ayuda a las plantas a resistir la escasez de agua y nutrientes durante las épocas de secas (Dos Santos Silva *et al.*, 2019; Liu *et al.*, 2018). Debido a todos estos servicios que los microbiomas rizosféricos proveen, es evidente que estudiar la composición microbiana a nivel funcional y taxonómico es fundamental para entender los procesos y las necesidades ecológicas de las plantas.

El *metabarcoding* es una técnica independiente de cultivo que permite estudiar la composición taxonómica de las comunidades microbianas a partir de muestras ambientales como suelos, tejidos u otros medios lo cual la hace muy adecuada para el estudio de las comunidades rizosféricas. Para conseguirlo, este método aprovecha las tecnologías de secuenciación de alto rendimiento aplicado a un gen específico que servirá como el identificador de los elementos presentes en la comunidad microbiana, usualmente alguna región del 16S rRNA en el caso de procariotas, y usa recursos bioinformáticos para analizar dicha información. Estudios que usan *metabarcoding* han arrojado información sobre los factores que afectan a las comunidades microbianas, lo que incluye al genotipo de la planta hospedera

(Hernández-Terán *et al.*, 2020), el ambiente abiótico (Ma *et al.*, 2016), y la interacción entre ambos factores (Durán *et al.*, 2018; Qiao *et al.*, 2017). Con base en este tipo de estudios se ha sugerido que el efecto del hospedero es menos determinante que los factores abióticos, que son los que guían dominantemente a la composición microbiana. Además, otros estudios sugieren que el reclutamiento microbiano desde las comunidades nativas del suelo a la rizosfera es un proceso conducido principalmente por factores estocásticos y con una marcada redundancia funcional (Hu *et al.*, 2020). Sin embargo, existen diferencias entre las comunidades del suelo y las rizosféricas que pueden ser explicadas por el linaje de la planta hospedera, como Wang y Sugiyama (2020) hicieron constar en niveles taxonómicos superiores (órdenes de plantas) para algunas familias bacterianas como Burkholderiaceae y Streptomycetaceae; esto parece mostrar que las plantas ejercen una señal filogenética sobre las comunidades procariotas de las raíces, aunque otro estudio sugiere que este efecto es mínimo y restringido principalmente a la endosfera de la raíz (Fitzpatrick *et al.*, 2018). Así mismo, las plantas también exhiben plasticidad en términos de la selección de microbiomas rizosféricos bajo condiciones estresantes como la sequía (Karray *et al.*, 2020) y la enfermedad (Bejarano-Bolívar *et al.*, 2021).

Debido a las condiciones ambientales extremas a las cuales están expuestas las halófitas y las xerófitas, las interacciones raíz-procarionte resultan indispensables para el establecimiento y la supervivencia de las plantas. Por lo tanto, entender las interacciones raíz-procarionte a nivel rizosfera es importante para combatir las inminentes amenazas que son el cambio climático y una mayor escasez de agua a escala global. A pesar de ello, tenemos un entendimiento limitado de los patrones globales de variación presente en las comunidades microbianas de las raíces de plantas de ambientes áridos. Debido a las complejas interacciones entre el hospedero y el ambiente, podría ser útil vislumbrar los factores más importantes que estructuran a los microbiomas de la rizosfera de especies vegetales en regiones áridas. Por lo cual, las principales hipótesis con relación a las diferencias en la estructuración de las relaciones planta-procarionte en ambientes áridos para probar son: i) la variación observada en las comunidades de procariontes asociadas a la rizosfera de las diferentes especies hospederas son influenciadas principalmente –en términos de

diversidad– por el ambiente abiótico, más que por la proximidad evolutiva de las plantas hospederas; ii) las diferencias entre los microbiomas se relacionan mayoritariamente con las estrategias ecológicas (es decir, las estrategias halófitas que favorecen la resistencia a altas concentraciones iónicas en los suelos o las estrategias xerófitas que invierten en la resistencia a la desecación) y fenológicas en lugar de la proximidad filogenética. Con este trabajo, busco bosquejar los patrones ecológicos en la interacción raíz-microorganismos que ocurren en los ambientes áridos.

Meta-analysis of Community Composition Patterns of Halophyte and Xerophyte Rhizosphere Associated Bacteria

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Abstract

In plant roots, prokaryote-plant interactions have been extensively studied worldwide, demonstrating their importance for plant survival and growth, through the exploitation of microbial metabolic processes, such as nitrogen fixation and Extracellular Polymeric Substances (EPS). Climatic and edaphological forces structure the soil bacterial pool from which plants acquire a large share of their rhizosphere microbiome. As halophyte and xerophyte plants are subject to extreme environmental conditions, prokaryote-root interactions could be pivotal for plant establishment and survival, even more under the imminent scenario of climate change and increased water scarcity; yet, we have a limited understanding on large-scale geographical patterns of root-microbe communities in arid environments. Here, we used a meta-analysis approach to compare prokaryotic community composition associated to the

rhizospheres of halophytes and xerophytes from ‘arid’ environments, representing 13 angiosperm plant species from five countries (Mexico, Namibia, Pakistan, Tunisia and USA), using a Qiime2 pipeline. In taxonomic terms, rhizosphere prokaryotic communities are diverse and include cosmopolitan classes like Alphaproteobacteria, Bacilli, and Gammaproteobacteria, as well as some site-specific groups like haline-thriving Haloarchaea, and PAUC43f which was found only in Pakistan samples. Alpha (ACE, Faith PD y Shannon) and beta (Jaccard) diversity estimates suggested that the main factors modeling microbial communities are host plant family, plant ecological strategy and the abiotic environment (bioclimatic variables, soil pH and total exchangeable bases). Furthermore, life history strategy (deciduous vs. perennial) is not significant for these communities’ structure. Thus, this work presents an early sketch on the macro-geographical patterns driving rhizosphere microbiomes in arid environments.

Keywords

Arid environments, halophytes, rhizosphere microbiome, root biology, xerophytes.

1. Introduction

Arid environments occupy circa 40% of the world surface, though an increase in aridity distribution is predicted due to climatic change, thus shifting the ecological dynamics across various regions worldwide (Sherwood & Fu, 2014). Informally, ‘arid’ is a term used for a gradient of environments ranging from dry sub-humid to hyper-aridity, distributed across the continental landmasses and polar latitudes, though all these environments share the trait that mean precipitation rates are far exceeded by evapotranspiration rates.. In these environments, aridity is a key factor affecting community composition (Armas et al., 2011; Xiong, et al., 2020).

To deal with environmental stress characteristic of arid environments, plants exhibit various strategies which have evolved convergently in multiple lineages among the Spermatophyta such as diverse life history strategies (i.e. deciduous and perennial lifestyles) and the development of morphophysiological traits (hereafter referred to as ‘ecological strategies’) to cope with different environmental stresses (Duarte et al., 2014; Hashem & Mohamed, 2020; He et al., 2021; Jarvis et al., 2014; Rudgers et al.,

2019). Such ecological strategies involve, but are not limited to, traits that enable the plants to establish themselves and survive in saline soils with high concentrations of diverse types of ions (halophytes), or morphophysiological traits that help them to efficiently store water and survive the severe droughts of the long dry seasons (xerophytes). Besides, plant survival depends on the ability to recruit microbes from the environment to fulfill particular ecological needs such as nitrogen (N) and phosphorous (P) acquisition, and stress alleviation (Flores-Núñez et al., 2020; Oburger et al., 2009; Liu et al., 2018). It has been shown that plant traits and phylogenetic identity play a major role in microbial recruitment together with abiotic factors that shape the native community from which this microbiome is acquired (Emmett et al., 2017; Thiergart et al., 2020). Therefore, to understand arid environments' plant-microbe ecology it is important to explore compositional variations among microbial communities at the large geographical scale, in order evaluate how these variations are related to different plant life strategies, phylogenetic affinities, and abiotic factors.

The plant microbiome is mainly recruited from bulk soil, into a region dominated by plant exudation profile, which is known as 'rhizosphere'. In the rhizosphere, root exudates act as environmental goods that favor the recruitment of multi-kingdom (though mainly Bacteria-dominated) beneficial microbial communities, while controlling against pathogenic species, often using the same developmental mechanisms to accomplish both processes as has been previously suggested to occur in the common symbiosis signaling pathway (CSSP) that controls for both, immunity against pathogens and mycorrhizae recruitment (Durán et al., 2018; Rey & Jacquet, 2018). The main services provided by these rhizosphere communities include supporting plant establishment and growth through microbial bioerosion (López & Bacilio, 2020), N fixation (Flores-Núñez et al., 2020; Li et al., 2017), carbon recycling through root litter decomposition (Ling et al., 2022; Whitford, 1996), P and metal mining for roots availability (Gómez Garrido et al., 2018; Oburger et al., 2009); and production of osmoprotective amino acids and extracellular polymeric substances (Taketani et al., 2015). In addition, rhizosphere communities help to consolidate the rhizosheath formation, a structure described in xerophytes conformed by densely packed soil

attached to roots by means of soil-biofilm-exudate interactions. The rhizosheath acts as a reservoir to alleviate water and nutrient depletion during dry seasons (Dos Santos Silva et al., 2019; Liu et al., 2018). Due to all of these services that the rhizosphere microbiome provides, it becomes evident that studying rhizosphere microbial composition, at least at the taxonomical level, is fundamental to understand plant ecological processes and necessities.

Metabarcoding is a culture-independent method that allows the study of microbial taxonomic composition using high-throughput sequencing and bioinformatic pipelines. This approach has allowed the identification of , multiple factors affecting the microbiome rhizosphere such as host plant genotype (Hernández-Terán et al., 2020), abiotic environment (Ma et al., 2016), and the interaction between both factors (Durán et al., 2018; Qiao et al., 2017). In general, host effect is less determinant while abiotic factors largely drive rhizosphere microbial composition. Microbial recruitment from bulk soil to the rhizosphere is primarily driven by stochastic factors and functional redundancy (Hu et al., 2020), yet there are noticeable differences between bulk soil and rhizosphere communities driven by the host population (Wang & Sugiyama, 2020). At higher taxonomic levels, plants' phylogenetic identity seems to influence the assembly patterns of their root prokaryotic communities, although this effect may be restricted to the root endosphere (Fitzpatrick et al., 2018). Plants also exhibit plasticity in terms of rhizosphere microbiome selection under stressful conditions such as drought (Karray et al., 2020) and disease (Bejarano-Bolívar et al., 2021).

As halophyte and xerophyte plants are subject to extreme environmental conditions, prokaryote-root interactions could be pivotal for plant establishment and survival, even more under the imminent scenario of climate change and increased water scarcity; yet, we have a limited understanding on the global variation patterns of root-microbe communities in arid environments. Due to the complex interactions between host and environment, it would be useful to elucidate the environmental (i.e. edaphological and climatic) and hosts' ecology factors that play a key role in shaping the variations that occur in the rhizosphere of plants from arid environments at a transcontinental scale. Previous works have summarized the factors accounting for root microbiome variation, which include plant taxonomic identity and ecological traits, as well as the

environmental factors that these plants inhabit such as soil and climatic characteristics (see Fierer, 2017; Dastogeer et al., 2020). For this purpose, here we present a meta-analysis of published datasets derived from metabarcoding technology. The main hypotheses are i) the structure of prokaryotic communities associated to the rhizosphere of different host species is mainly influenced –in terms of diversity– by the abiotic environment rather than by the evolutionary proximity of their host plants; ii) differences across microbiomes can be related to ecological (i.e., xerophyte or halophyte strategies) and life history traits (i.e. deciduous vs perennial) of their hosts rather than by their phylogenetic proximity. With this, we aim to sketch the ecological patterns that shape the variation of arid environments' root-soil interface.

2. Materials and methods

Data provenance and accessions

For this meta-analysis, data from five previously published studies produced by other research groups were used, which together analyzed 13 species' rhizosphere microbial communities. The main criterium was that data provenance came from continental environments under the 'arid' umbrella. Therefore, multiple 'arid' environments were included (Figure 1), though the regions sampled differed in terms of bioclimatic and edaphological features. The species were: *Myrtillocactus geometrizans* (Mart. ex Pfeiff.) Console (Cactaceae, Caryophyllales) and *Opuntia robusta* H.L.Wendl. ex Pfeiff (Cactaceae, Caryophyllales), both xerophytes from central Mexico (Fonseca-García et al., 2016); *Opuntia ficus-indica* (L.) Mill (Cactaceae, Caryophyllales), an invader xerophyte sampled across Tunisia (Karray et al., 2020); *Allenrolfea occidentalis* (S.Watson) Kuntze (Amaranthaceae, Caryophyllales), *Salicornia rubra* A.Nelson (Amaranthaceae, Caryophyllales) and *Sarcocornia utahensis* Tidestr. (Amaranthaceae, Caryophyllales), three native halophytes from Utah (Kearl et al., 2019); *Cladoraphis spinosa* (L.F.) S.M. Phillips (Poaceae, Poales), *Stipagrostis sabulicola* (Pilg.) De Winter (Poaceae, Poales), *Stipagrostis seelyae* De Winter (Poaceae, Poales) from sand dunes in the Namib Desert (Marasco et al., 2018); and *Atriplex amnicola* Paul G.Wilson (Amaranthaceae, Caryophyllales), *Kochia*

indica Wight – synonym of *Bassia indica* (Wight) A.J.Scott – (Chenopodiaceae, Caryophyllales), *Salsola stocksii* Boiss. – synonym of *Seidlitzia stocksii* (Boiss.) Assadi – (Chenopodiaceae, Caryophyllales) and *Urochloa mutica* (Forssk.) T.Q.Nguyen (Poaceae, Poales), halophytes from the Khewra salt mine in Pakistan (Mukhtar et al., 2018). Information about these plant species and their environments is available in Table S1. Data is publicly available in SRA at NCBI under the following accession numbers: SRR3108963, SRR3108968-69, SRR3108988-89, SRR3108991, SRR3108994, and SRR3108998 (Fonseca-García et al., 2016), SRR8365816-17, SRR8365826-29, SRR8365832-34, SRR8365849-56 and SRR8365867-68 (Karray et al., 2020), SRR9660293-300 (Kearl et al., 2019); SRR7527033-47, SRR7527049-81, SRR7527086-93, SRR7527096-101 (Marasco et al., 2028); and SRR14654853-59, SRR14654865, SRR14654870-77 (Mukhtar et al., 2018). Other datasets were initially considered in our meta-analysis, but they were dropped as the quality of the data did not pass our quality cutoffs for fair comparisons between datasets.

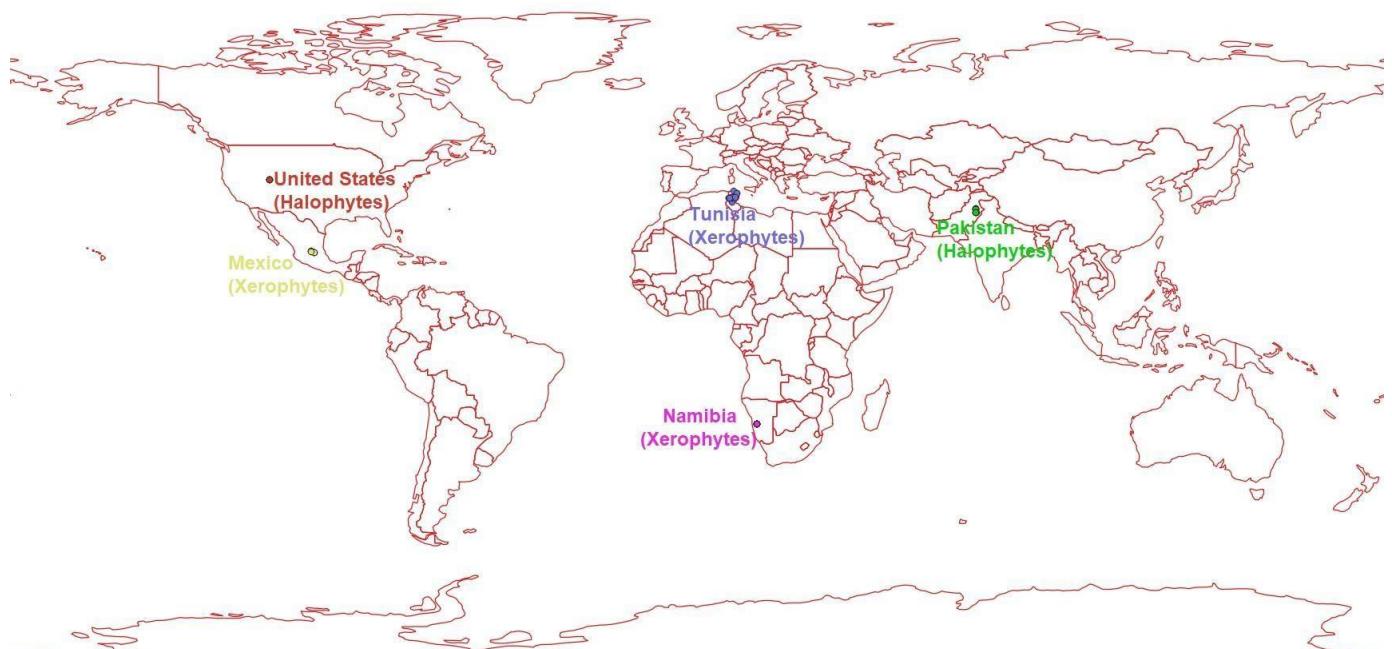


Figure 1. Geographical location of the datasets used for this metanalysis. In parentheses, the plant ecological community is shown.

Bioinformatic processing

Sequences from the rhizosphere samples were obtained using the SRAToolKit 2.10.5 CentOS ‘fasterq-dump’ function (SRA Toolkit Development Team, 2020:

<https://trace.ncbi.nlm.nih.gov/Traces/sra/sra.cgi?view=software>). Then, they were processed using the Qiime2 2021.4 software (Bolyen et al., 2019) for sequence summarization, quality control, taxonomic classification and diversity indices estimation. In order to increase reproducibility, we decided to characterize the communities as ASVs (amplicon sequence variant) instead of OTUs (operational taxonomic unit), as commonly used. As sequences were originally obtained from different primers sets covering the 16S rRNA V3/V4 regions, the ‘cutadapt’ plugin (Marcel, 2011) was used to trim the sequences according to primers 515F ('--p-front-f GTGCCAGCAGCGSGCGGWAA') and 806R ('--p-front-r NACTACNVGGGTWTCTAATCC'). Later, sequences were denoised and merged using DADA2 (Callahan et al., 2016) ('--p-chimera-method pooled', '--p-max-ee-r 4'); on average, 70-85% of the sequences were retained as non-chimeric. A total of 36,384 ASVs were obtained from 113 samples after trimming sequences and performing QC-filtering with DADA2. Samples were rarefied using ‘rarefy’ with a ‘--p-sampling-depth’ of 13,200 (ca. 90% of the counts of the lowest sample used); three samples with counts lesser than this number were discarded. The plot of rarefaction for the remaining samples is shown in Figure S1, where the samples from Pakistan reached the asymptote earlier than the rest of the samples. Finally, taxonomic classification was done using the SILVA 138 database (Quast et al., 2013) trained for the 505F/806R primer set aforementioned, and filtered with ‘--p-exclude mitochondria,chloroplast,Unassigned,Eukaryota’ to remove undesirable groups. We recognize that the primer pair described beforehand (ie. 515F/806R) may only be accurate for Bacteria, and thus our Archaea data may be propense to artifacts, yet we decided not to remove these ASVs for the sake of comparison with the original research works that we used, where this data is also reported (e.g. Fonseca-García et al., 2016; Mukhtar et al., 2018). Using this filtered taxonomy dataset, a phylogeny was reconstructed using Fasttree (Price et al., 2009) and rooted using the ‘midpoint-root’ function for downstream estimation of phylogenetic diversity metrics.

Data visualization and statistical analyses.

Alpha and beta diversity indexes were calculated using ‘core-metrics-

phylogenetics' and 'alpha-diversity' (for ACE) plug-ins from Qiime2. Further graphical and statistical analyses were done using R 4.0.1 (R Core Team, 2020). Packages 'ggplot2' and 'cowplot' were used to create plots and arrange them into panels, respectively. Kruskal-Wallis test and Tukey-HSD post-hoc were performed using the 'kruskal()' function from package 'agricolae' (De Mendiburu & Yaseen, 2020), while ANOSIM was performed using 'anosim()' function from 'vegan' (Oksanen et al., 2022). For the NMDS and PCA calculation, a value of 'set.seed(120)' was used; functions 'envfit()' and 'metaMDS()' from the 'vegan' package were used to obtain the NMDS analysis, along with stressplot() from that same package; while 'cor()', 'eigen()' and 'scale()' from 'base' package were used to create the PCA. For the PCA, only data significantly correlated with the NMDS ordination were used. Data corresponding to bioclimatic variables was extracted using QGIS and WorldClim 2 geographical layers (Fick & Hijmans, 2017), while soil was obtained from the Harmonized World Soil Database 1.2 (Fischer et al., 2008). Venn diagrams were obtained using the functions 'phyloseq()' from the homonymous package (McMurdie & Holmes, 2013), and 'venn()' from 'eulerr' package (Larsson, 2021). Finally, functions 'vegdist()' and 'decostand()' from 'vegan' were used to generate a correlation matrix using Bray-Curtis distances and to normalize thereafter, respectively; these functions together with 'hclust()' from 'stats', 'heatmap.2()' from 'gplots' package, and 'color_branches()' (from 'dendextend' package; Galili, 2015) were used to create a heatmap plot with dendrogram.

3. Results

The taxonomic composition of the prokaryote microbial communities in xerophyte and halophyte rhizospheres display an enormous diversity

A total of 36,384 ASVs were obtained from 113 samples. The taxonomic structure of rhizosphere microbiome communities per host species and family (Figure 2A-B), as annotated by SILVA, shows that the main bacterial families are Bacillaceae, Burkholderaceae, Pseudonodocardiaceae, Rhizobiaceae and Streptomycetaceae; while the classes Alphaproteobacteria, Actinobacteria, Bacilli and Gammaproteobacteria were the most abundant, in accordance with the original published works (Fonseca-García et al., 2016; Karray et al., 2020; Kearl et al., 2019;

Marasco et al., 2028; Mukhtar et al., 2018)., while an archaean class (Halobacteria, preferably named Haloarchaea according to DasSarma, P. & DasSarma, S., 2008) was also observed in high relative abundance (circa 10%) in the rhizosphere of plants from the Utah Desert. Additionally, some genera previously identified as plant growth promoting bacteria (PGPB; Ahemad & Kibret, 2014) were found universally in all the sites analyzed, though varying in their relative frequencies. These genera include Acinetobacter, Arthrobacter, Bacillus, Bradyrhizobium, Methylobacterium, Paenibacillus and Pseudomonas. Also, the halophile PGPB genus Halomonas was found in the samples from Utah, as was previously reported (Kearl et al., 2019).

A Kruskal-Wallis analysis showed that classes were statistically different ($p<0.05$, Table S2) between hosts' rhizospheres with the exception of Chloroflexia (Chloroflexi), which showed differences between hosts at the species level ($p=0.0324$) but not at the family level ($p=0.265$). Interestingly, the taxonomic annotation also captured the marine class PAUC43f, only for the halophytes from the United States. This class thrives in marine environments (Bergo et al., 2020; Hardoim et al., 2021) but has also been described in continental environments in saline sediments such as salt pans and ephemeral salt lakes (Aerts et al., 2019; Genderjahn et al., 2018), so its presence in the Utah Desert may not be that surprising; yet literature so far, including the original research paper from where these sequences came from, have not previously described this class presence associated to terrestrial plants, only to rhodophytes (Abdullah, 2020). If this observation is genuine or an artifact caused by the bioinformatic pipeline cannot be clarified in the present meta-analysis but rather further research focused on addressing this issue is required (Table S3).

To visualize convergence patterns across hosts, we made a heatmap with Bray-Curtis clustering (Fig. 2C). This analysis shows that, at microbial family-level composition, there are ordination patterns that clearly reflect the geographical provenance of the samples among hosts of different taxonomic affinity. The most dissimilar locality is the halophytic community from the USA, while the halophytes from Pakistan cluster in the same group as the xerophytes. Altogether, these results suggest that abiotic environmental factors are pivotal to the microbiome assembling

processes, rather than host's evolutionary relationships.

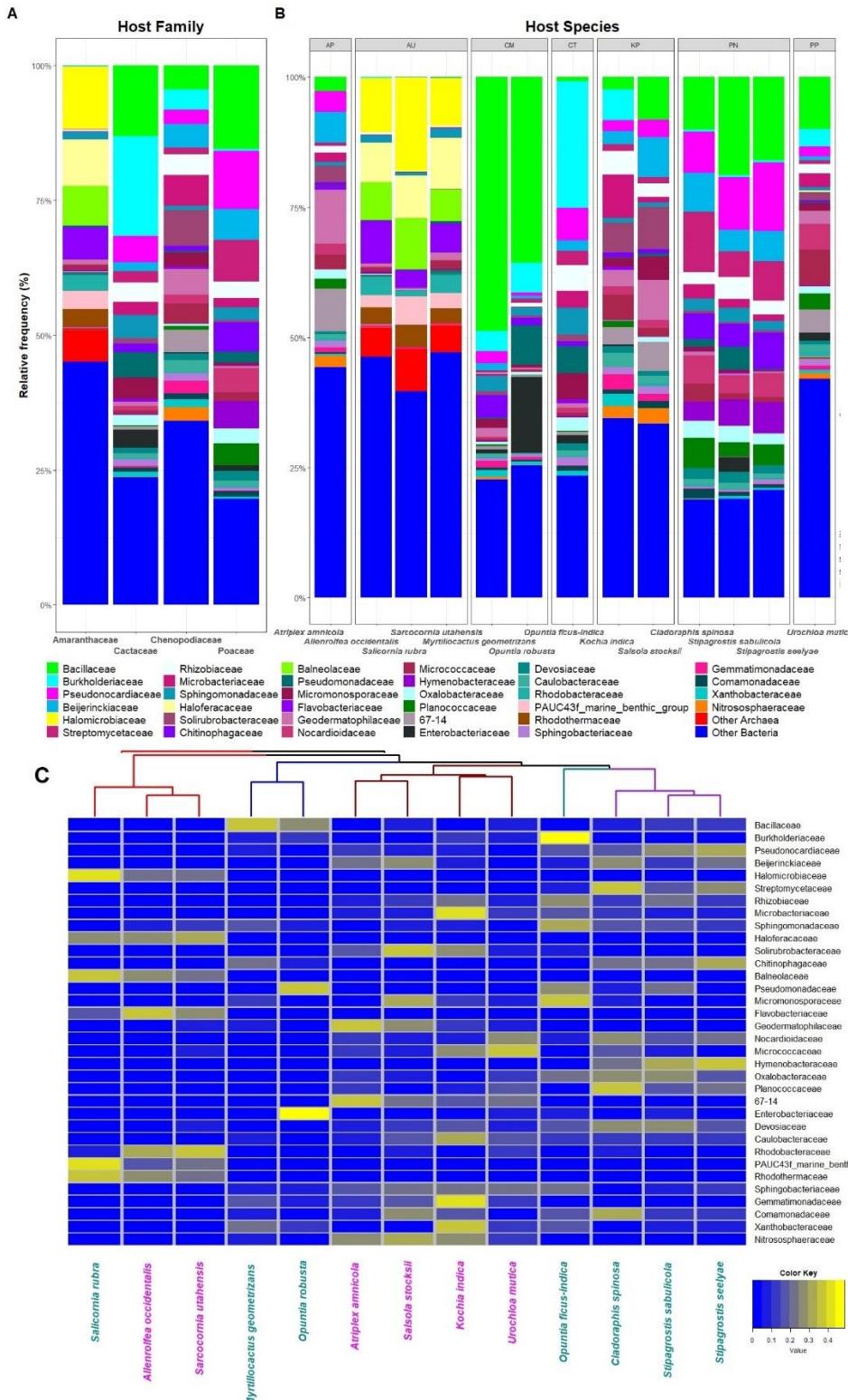


Figure 2. Relative frequencies of the 34 main bacterial and archaeal families according to the host taxonomic classification: host family (A) and host species (B). Abbreviations in facets (panel B) indicate host species family and provenance as follows: Amaranthaceae from Pakistan (AP), Amaranthaceae from the US (AU), Cactaceae from Mexico (CM), Cactaceae from Tunisia (CT), Chenopodiaceae from Pakistan (KP), Poaceae from Namibia (PN) and Poaceae from Pakistan (PP). A heatmap analysis with Bray-Curtis clustering (C) displays weak correlations at prokaryotic family-level. For host species (columns), magenta names are halophytes while cyan names are xerophytes. In dendrogram, each branch color corresponds to a macro-geographical site (country).

Alpha diversity analyses can be explained by host species and geographical site

To visualize the alpha diversity of each sample according to its host species or geographical country of provenance, three indices were calculated: the ACE Richness Estimator (Figure 3A-B), Faith Phylogenetic Distance (Figure 3C-D) and Shannon Evenness (Figure 3E-F). Statistical differences were obtained for each of these indices according to a Kruskal-Wallis test for host species identity (ACE: $p=5.641E-05$; Faith PD: $p=3.910E-04$; Shannon: $2.299E-03$) and country (ACE: $p=2.348E-07$; Faith PD: $p=1.872E-06$; Shannon: $1.612E-05$). Altogether, these results indicate that the local diversity of each rhizosphere community displays differences related to the host species and the environment in which they thrive. In contrast, there were no statistical differences for alpha diversity according to the host ecological and life history strategies were not significant for every index ($p>0.05$, Figure S2) with Shannon evenness being the only exception, displaying differences between deciduous and perennial hosts ($p=0.038$, Figure S1).

According to these indices, the ASVs alpha diversity seems to be more similar among xeric environments (Mexico, Namibia and Tunisia) than between the haline sites (Pakistan and USA). In particular, both halophyte communities display extremely contrasting values for richness (Figure 3B), and moderately yet evident differences regarding the PD and evenness (Figure 3D, F), with the Utah microbiomes having the highest values among all sites for all three estimators, while the Khewra Salt Mine displays the lowest median ASVs richness and PD, and the second-lowest evenness. In contrast, xerophyte sites seem highly alike (Figure 3B, D, F) in terms of their richness, PD and evenness; this similarity among xerophytes microbiomes could be caused by the close phylogenetic affinity of the sampled hosts, as all species from both sites are members of the Cactaceae family.

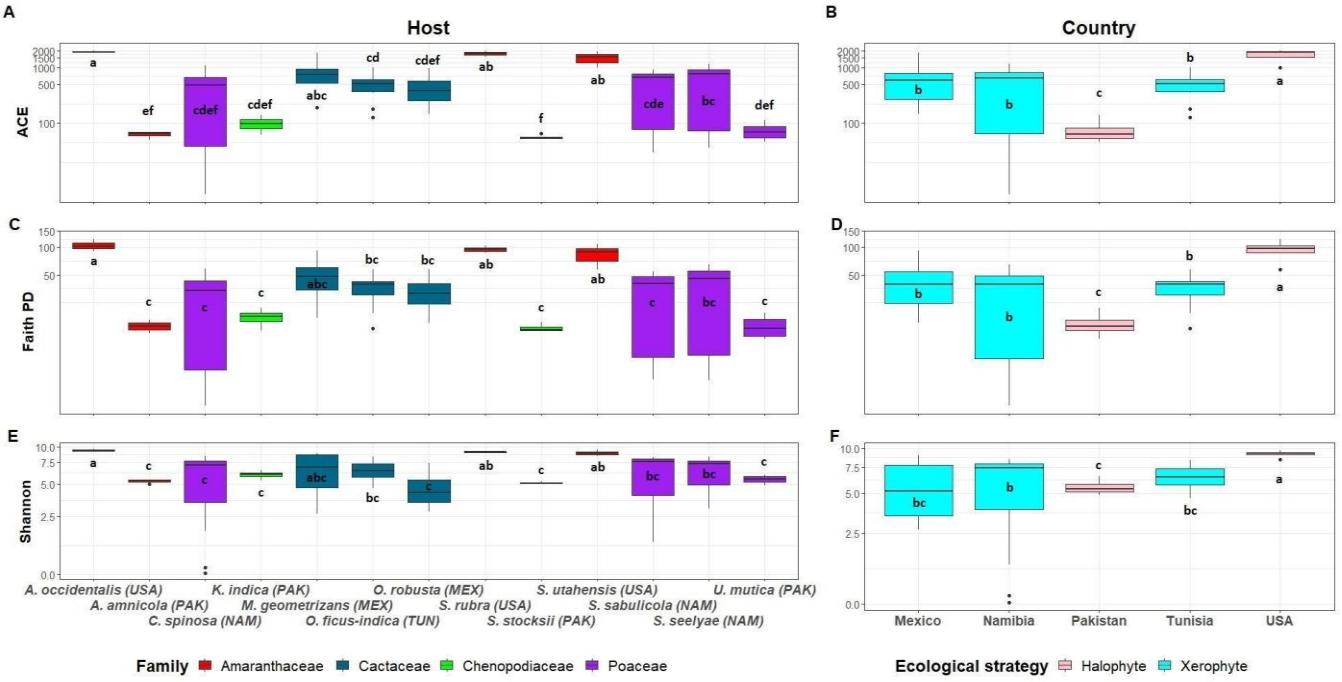


Figure 3. Boxplots for three alpha diversity estimators: ACE richness (A-B), Faith phylogenetic distance (C-D) and Shannon evenness (E-F). Left panels display the indices' values according to the host species (A, C, E), boxes' colors correspond to the family-level identity of the host. Right panels show the indices' values with respect to the country of sampling (B, D, F), boxes are coloured according to the host species ecological strategy. In all cases, there were statistically significant differences according to a Kruskal-Wallis test ($p<0.05$). Letters indicate statistically homogeneous groups according to a Tukey HSD post-hoc test.

Beta diversity confirms that host taxonomic identity and local bioclimatic features both explain rhizosphere microbiome composition

Non-metric dimensional scaling (NMDS) was calculated using Jaccard distance to evaluate the beta diversity among samples (Figure 4A). A stress value of 0.125 (S) was observed for this NMDS, indicating a good data fitness to a bidimensional ordination; similar results were obtained when using Bray-Curtis dissimilarity (Figure S3). According to this analysis, halophytes and xerophyte communities were evidently different between them, with halophytes communities from Pakistan and the USA also being noticeably distinct. Additionally, the xerophyte communities were also spatially separated in this ordination, yet more alike. The more similar localities were Mexico and Tunisia. This could be due to the close phylogenetic distance between the host plants from both localities, as they are Cactaceae. Further, Namibia was projected near both of these localities, yet still separated. However, it is noticeably that in this location two subgroups were recovered, which correspond to communities from the

outer and inner rhizosphere (or rhizosheath), respectively. This observation suggests that proximity to the root is determinant for microbiome composition. In terms of the main abiotic variables governing the differential microbiome composition, axis NMDS1 was negatively correlated to pH, silt content, rainy season precipitation and total exchangeable bases (TEB), while soil density was positively correlated to this axis. Electrical conductivity (EC), organic C content and dry season precipitation were highly positively correlated to axis NMDS2, while annual mean temperature and cation exchange capacity (CEC) were negatively correlated to this axis.

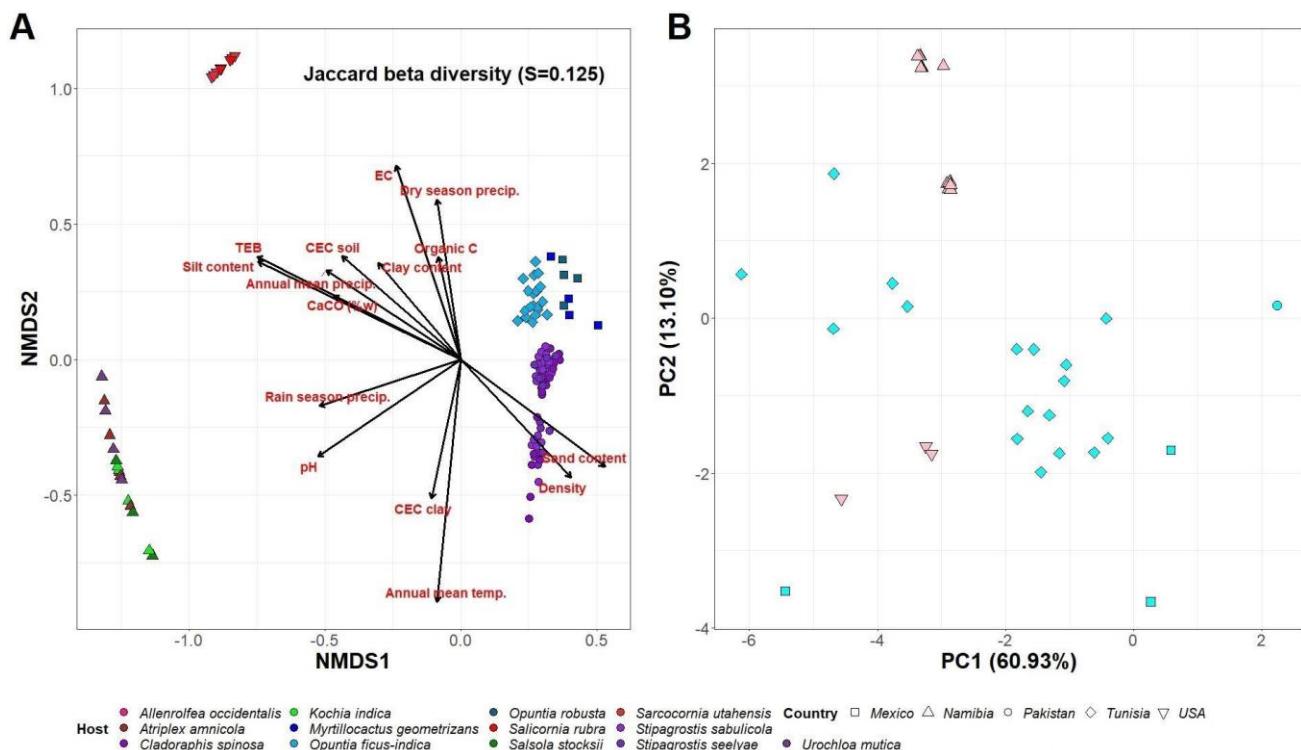


Figure 4. Multivariate analysis of beta diversity and abiotic conditions. A) NMDS biplot for Jaccard distance-based beta diversity ($S=0.0853$). Dot shape indicates the country of provenance for samples, while color indicates the host species. Additionally, colors also represent the family affinity of hosts: Amaranthaceae (red shades), Cactaceae (blue shades), Chenopodiaceae (green shades) and Poaceae (purple shades). Vectors indicate the main environmental variables correlated to NMDS axes. B) PCA ordination of localities according to the main environmental variables (shown in panel A). In this panel, cyan represents xerophyte communities while pink are halophyte communities. Shape indicates country of origin. Eigenvalues and eigenvectors for PCA are reported in Table S4.

To further evaluate the influence on microbial community composition, an ANOSIM test was conducted using the host taxonomic identity, environment, and ecological and life history traits (Table 1). All these variables were significantly related to the observed differences in rhizosphere community structure, yet host ecological strategy and the

country from which each community was obtained were the most important factors explaining the observed beta diversity, in accordance with the aforementioned NMDS analysis. Further analysis to account for convergences between core microbial members in the rhizospheres showed that there are no shared core prokaryotes between countries nor plant families, the only exception being Tunisia and Mexico which shared 5 core elements, all associated to Cactaceae (Figure S4). Altogether, these results suggest that the abiotic features rule both, the host recruitment strategies and thus the composition of microbial communities inhabiting soils. Also, our results suggest that, at family level, host plants are selective of the microbial communities that colonize their rhizosphere in arid environments.

A Kruskal-Wallis test using the rasters' data suggests that significant differences are found between both xerophytic communities' climatic conditions. To further confirm this, a Principal Component Analysis (PCA) was conducted using the bioclimatic and soil factors that had a significant effect on the NMDS ordination (Figure 4B). This PCA shows that both xerophytic communities overlap in terms of abiotic environmental conditions along the PC1 (60.93%) axis which correlates to climatic conditions, while they are highly dissimilar along the PC2 (13.10%) that correlates to pH and CEC. Further, PCA separates the Namibia and Pakistan communities from all others while approaching Mexico, Tunisia and the USA communities. Both, PC and NMDS analyses suggest that phylogenetic affinity does influence the prokaryote community composition by reducing their dispersion differences, as was the case for the Cactaceae-only communities of Mexico and Tunisia that were different in terms of abiotic environment but nevertheless displayed highly similar microbial communities. Furthermore, the proximity displayed in the PCA for the Tunisia (Cactaceae-associated) and USA (Amaranthaceae-associated) communities, despite their evident different microbial communities (as shown by the NMDS) suggest that the phylogenetic distance between their hosts –at family level– may be the reason behind the differences on their microbiome assemblages, proving that both genotype and environment influence the microbial composition in arid rhizospheres, though abiotic environment still dominates community structure.

Table 1. ANOSIM test for factor effects on the observed structure of microbial communities. 999 free permutations were used for this analysis using Jaccard distance matrix.

Factor	R	p	
Host species	0.6797	<0.001	***
Host family	0.7017	<0.001	***
Country	0.8451	<0.001	***
Ecological strategy	0.9535	<0.001	***
Life history strategy	0.6872	<0.001	***

4. Discussion and conclusions

Our meta-analysis shows that there is a large degree of variation in the microbial communities associated with the rhizosphere of plants from arid environments. Although the variation has multiple underlying factors (some of them addressed here), these differences seem to be mainly driven by the variation of abiotic factors at a large geographical scale (transcontinental, in this work), rather than to biological traits of the host plants. In particular, climate, pH and soil cation exchange capability seem more determinant in governing the soil microbiome, possibly affecting in a top-down fashion the rhizosphere microbial recruitment. These findings are consistent with previously reported results (Hernández-Terán et al., 2020; Hu et al., 2020; Ma et al., 2016; Qiao et al., 2017): as rhizosphere prokaryote communities are assembled from the microbial pool inhabiting bulk soil, plants are limited to select from native soil communities that are influenced-modeled/structured by abiotic factors. Furthermore, at the finer scale rhizosphere microbiome is selected by the host, influenced by its genotype-specific exudation profile and root architecture, aiming to control the establishment of microbial communities that fulfill their nutritional needs while also restricting antagonists from colonizing the rhizosphere and inner root compartments (a process suggested previously by Forte et al. (2017) as the ‘ecosystem on a leash’ model). Further, other factors such as exudation profiles or specific ion/salt concentrations in soils could better explain the differences observed in other works, but such data we are lacking as of now. Besides, though hosts exert some control on microbial acquisition, exudation profiles can also be induced by the microbiome that colonizes the rhizosphere (Korenblum et al., 2020); therefore, studying the feedback dynamics between

microbial functionality and plant metabolic processes is necessary to understand the complexity that governs the host-microbe interactions.

In particular, factors related to aridity (i.e. temperature and precipitation) were found to be the key climatic drivers guiding microbial community structure, as has been previously shown along an aridity gradient (Karray et al., 2020). Also, soil properties were highly related to microbiome composition. Our results highlighted pH as one of the most significant factors being determinant to microbiome functionality as it affects microbial physiological and exo-enzymatic processes (Fan et al., 2018; Puissant et al., 2019). Other physicochemical properties such as CEC and soil particle content have also been previously identified to affect microbial communities (Nuccio et al., 2016), in line with our results.

Plant traits do not seem to be the main key factors governing microbiome assemblage; though some traits may influence on this process such as occurs with plant ecological strategy (i.e. xerophyte or halophyte) which according to our ANOSIM test showed a significant and highly correlated relation to beta diversity; while, Contrarily to our initial hypothesis, the plants' phylogenetic affinity seemed to be less correlated to the observed variation in microbiome composition. We hypothesize that these results stem from the fact that plant ecological strategy is also finally governed by abiotic factors, thus the differences observed are a result of both types of communities growing at different sites (xerophytes were exclusive from Mexico and Tunisia, while halophytes came from Pakistan and the US). We suggest that an experimental design sampling using both types of plants growing in the same location or under common garden conditions could solve the true effect an ecological strategy exerts on the rhizosphere microbiome. Though some works suggest that host life history influences root microbiome (Emmett et al., 2017), our results show this trait to be poorly related to microbiome variation in arid environments and most of the effect observed may be derived from host plant phylogenetic effects. As establishment in arid environments is difficult due to water and salt related stresses, it would also be interesting to test the effect of other biological variables (such as the host developmental stage – see İnceoğlu et al., 2013 –, and exudation profiles) on the rhizosphere microbiome for plants from these environments and the turnovers that occur along host developmental

gradients and its feedback with microbial communities (Lu et al., 2018).

We recognize that our work meets some limitations. Firstly, though there are other works using metabarcoding to describe the rhizosphere microbiome of xerophytes in other regions, these were not used, as the sequences were either unavailable at public databases, the metadata was miss-annotated (as in Coleman-Derr et al., 2016), the sequences did not overlap with the 16S rRNA region we used or presented low quality, generally displaying a high number of chimeric sequences (Dai et al., 2019; Mukhtar et al., 2021). We suggest that researchers increase data availability so that massive data analyses can be conducted to reveal the broad patterns of variation that occur across microbial communities. Furthermore, our works focuses on so-called ‘prokaryote’ communities (ie. Archaea and Bacteria domains), thus it fails to picture the whole microbiome as it excludes the important Eukarya members of these microbial communities. This omission results from the general lack of works assessing eukaryotes in the rhizosphere, and though there is research on arid environments’ fungal communities, these are notoriously fewer than those works on bacterial and archaeal communities. We also acknowledge that metabarcoding techniques for eukaryotes are highly biased: most of the protocols currently widely used only describe fungal and, to a lesser extent, metazoan communities; so even using these data would not give us a complete description of the microbial community of arid plants rhizosphere. Even more difficult, both technically and financially, would be to also include metabarcoding information for viral sequences given their reduced genome size and higher genetic variability. Additionally, microbe-microbe (and cross-kingdom) interactions may also play a major role on the assemblage patterns of the microbiome, as has been previously observed (Horn et al., 2017). Though not analyzed in this meta-analysis, these factors should be considered for further insight in the processes that drive rhizosphere microbial assemblages and host-microbe interaction patterns across arid environments worldwide, as these inter-microbial interactions could have significant effects on the whole plant-microbe system survival (Thiergart et al., 2020; Bi et al., 2021). Therefore, it would be very useful for future research to develop protocols that attempt to describe these ignored elements of microbial communities, both functionally and taxonomically, as they have been suggested to be pivotal for

structuring rhizosphere ecological processes (Gao et al., 2019).

To the best of our knowledge, our work is the first macro-geographical description of arid environments' rhizosphere communities variation patterns. Interest in these regions have been growing as a result of higher global aridity due to climate change, so we hope that this meta-analysis fits as a useful sketch to visualize plant-microbe ecological processes in arid environments. Future works will be important to increase the taxonomical and the functional knowledge of the ecological processes that occur in arid regions, and will help us cast light upon the finer processes governing these ecosystems. One possible explanation is that, in arid environments, plant ecological strategies have a less selective effect on the bulk soil community recruitment, as host plants tend to adopt a generalist rhizosphere control strategy where both cooperation and recruitment plasticity may be the more determinant factors impacting plant-microbe survival rather than specificity, given the limited amount of nutritional and hydric resources available. We believe it is important to carry out experiments to assess these hypotheses by growing the same ecotype in different soils and analyzing the potential changes in microbial activity and plant productivity. Also, it may be possible that due to the essential functional processes that microbes provide, they are the key resource that plants compete for, so under extreme aridity conditions, plants which are less selective on their rhizosphere microbiome and invest the less resources on exudation (which is metabolically costly) thrive better than specialist plants. To address these questions, researching the patterns of variation across species- and family-level divergences could be useful, such as the characterization of microbial communities associated with spatially and evolutionarily close species, yet thriving under different environmental constraints and needs. Furthermore, research on the evolutionary constraints that guide these processes could be useful to elucidate the role microbiome specificity has on plant survival and, ultimately, provide data that allows us to alleviate the effects of the worldwide aridity expansion scenario.

Author contributions

JCL and UR planned the work and designed the research strategy. JCL worked on the bioinformatic, statistical and graphical analyses presented in this work. JCL is also credited for leading the manuscript writing process, with major manuscript writing and

feedback contributions from AR, PV and UR. UR was responsible for funding acquisition.

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Declaration of competing interests

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.

SUPPLEMENTARY MATERIAL

sample-id	BioProject	BioSample	Center Name
SRR9660293	PRJNA553550	SAMN12238117	BRIGHAM YOUNG UNIVERSITY
SRR9660294	PRJNA553550	SAMN12238116	BRIGHAM YOUNG UNIVERSITY
SRR9660295	PRJNA553550	SAMN12238115	BRIGHAM YOUNG UNIVERSITY
SRR14654870	PRJNA309754	SAMN04419098	FORMAN CHRISTIAN COLLEGE
SRR14654871	PRJNA309754	SAMN04419097	FORMAN CHRISTIAN COLLEGE
SRR14654872	PRJNA309754	SAMN04419096	FORMAN CHRISTIAN COLLEGE
SRR14654873	PRJNA309754	SAMN04419095	FORMAN CHRISTIAN COLLEGE
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SRR3108968	PRJNA308956	SAMN04418126	USDA-ARS
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SRR9660298	PRJNA553550	SAMN12238112	BRIGHAM YOUNG UNIVERSITY
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SRR3108968	public	desert	Soil	SRX1537278	Mexico	<i>Mytillocactus geometrizans</i>	
SRR3108969	public	desert	Soil	SRX1537279	Mexico	<i>Mytillocactus geometrizans</i>	
SRR3108998	public	desert	Soil	SRX1537308	Mexico	<i>Mytillocactus geometrizans</i>	
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			Root system			
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SRR7527046	public	Sandy desert	Root system	SRX4395418	Namibia	<i>Stipagrostis seelyae</i>
SRR7527047	public	Sandy desert	Root system	SRX4395417	Namibia	<i>Stipagrostis seelyae</i>
SRR7527050	public	Sandy desert	Root system	SRX4395414	Namibia	<i>Cladoraphis spinosa</i>
SRR7527053	public	Sandy desert	Root system	SRX4395411	Namibia	<i>Cladoraphis spinosa</i>
SRR7527055	public	Sandy desert	Root system	SRX4395409	Namibia	<i>Stipagrostis seelyae</i>
SRR7527060	public	Sandy desert	Root system	SRX4395404	Namibia	<i>Cladoraphis spinosa</i>
SRR7527061	public	Sandy desert	Root system	SRX4395403	Namibia	<i>Cladoraphis spinosa</i>
SRR7527063	public	Sandy desert	Root system	SRX4395401	Namibia	<i>Stipagrostis sabulicola</i>
SRR7527065	public	Sandy desert	Root system	SRX4395399	Namibia	<i>Stipagrostis seelyae</i>
SRR7527066	public	Sandy desert	Root system	SRX4395398	Namibia	<i>Cladoraphis spinosa</i>
SRR7527068	public	Sandy desert	Root system	SRX4395396	Namibia	<i>Stipagrostis seelyae</i>
SRR7527071	public	Sandy desert	Root system	SRX4395393	Namibia	<i>Stipagrostis sabulicola</i>
SRR7527075	public	Sandy desert	Root system	SRX4395389	Namibia	<i>Cladoraphis spinosa</i>
SRR7527077	public	Sandy desert	Root system	SRX4395387	Namibia	<i>Cladoraphis spinosa</i>
SRR7527079	public	Sandy desert	Root system	SRX4395385	Namibia	<i>Stipagrostis seelyae</i>
SRR7527080	public	Sandy desert	Root system	SRX4395384	Namibia	<i>Stipagrostis sabulicola</i>
SRR7527081	public	Sandy desert	Root system	SRX4395383	Namibia	<i>Stipagrostis sabulicola</i>
SRR7527087	public	Sandy desert	Root system	SRX4395377	Namibia	<i>Stipagrostis sabulicola</i>
SRR7527089	public	Sandy desert	Root system	SRX4395375	Namibia	<i>Stipagrostis sabulicola</i>
SRR7527091	public	Sandy desert	Root system	SRX4395373	Namibia	<i>Stipagrostis sabulicola</i>
SRR7527092	public	Sandy desert	Root system	SRX4395372	Namibia	<i>Stipagrostis sabulicola</i>
SRR7527093	public	Sandy desert	Root system	SRX4395371	Namibia	<i>Stipagrostis sabulicola</i>
SRR7527096	public	Sandy desert	Root system	SRX4395368	Namibia	<i>Stipagrostis seelyae</i>
SRR7527097	public	Sandy desert	Root system	SRX4395367	Namibia	<i>Stipagrostis seelyae</i>

sample-id	Family	Order	Life trait	Instrument	Lat. Lon.
SRR9660293	Amaranthaceae	Caryophyllales	Deciduous	Illumina HiSeq 2500	39.9517 N 111.9008 W
SRR9660294	Amaranthaceae	Caryophyllales	Deciduous	Illumina HiSeq 2500	39.9517 N 111.9008 W
SRR9660295	Amaranthaceae	Caryophyllales	Deciduous	Illumina HiSeq 2500	39.9517 N 111.9008 W
SRR14654870	Amaranthaceae	Caryophyllales	Perennial	454 GS FLX Titanium	73.00 N 32.41 E
SRR14654871	Amaranthaceae	Caryophyllales	Perennial	454 GS FLX Titanium	73.04 N 32.36 E
SRR14654872	Amaranthaceae	Caryophyllales	Perennial	454 GS FLX Titanium	73.03 N 32.39 E
SRR14654873	Amaranthaceae	Caryophyllales	Perennial	454 GS FLX Titanium	73.06 N 32.34 E
SRR14654855	Chenopodiaceae	Caryophyllales	Perennial	454 GS FLX Titanium	73.07 N 31.49 E
SRR14654856	Chenopodiaceae	Caryophyllales	Perennial	454 GS FLX Titanium	73.02 N 31.43 E
SRR14654857	Chenopodiaceae	Caryophyllales	Perennial	454 GS FLX Titanium	73.03 N 31.47 E
SRR14654858	Chenopodiaceae	Caryophyllales	Perennial	454 GS FLX Titanium	73.08 N 31.38 E
SRR3108963	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	21.05 N 100.17 W
SRR3108968	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	21.40 N 101.02 W
SRR3108969	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	21.40 N 101.02 W
SRR3108998	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	21.05 N 100.17 W
SRR8365816	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	35.39 N 9.28 E
SRR8365817	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	35.38 N 9.3 E
SRR8365826	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	36.50 N 10.52 E
SRR8365827	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	34.15 N 9.17 E
SRR8365828	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	34.15 N 9.17 E
SRR8365829	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	35.55 N 10.17 E
SRR8365832	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	37.12 N 9.54 E
SRR8365833	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	36.50 N 10.43 E
SRR8365834	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	36.50 N 10.41 E
SRR8365849	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	35.31 N 9.27 E
SRR8365850	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	35.22 N 8.46 E
SRR8365851	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	35.29 N 8.66 E
SRR8365852	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	35.22 N 8.46 E
SRR8365853	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	35.17 N 9.27 E
SRR8365854	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	35.31 N 9.21 E
SRR8365855	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	35.4 N 10 E
SRR8365856	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	35.21 N 8.47 E
SRR8365867	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	35.22 N 8.46 E
SRR8365868	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	35.21 N 8.48 E
SRR3108988	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	21.05 N 100.17 W
SRR3108989	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	21.10 N 101.02 W
SRR3108991	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	21.05 N 100.17 W
SRR3108994	Cactaceae	Caryophyllales	Perennial	Illumina MiSeq	21.10 N 101.02 W
SRR9660299	Amaranthaceae	Caryophyllales	Perennial	Illumina HiSeq 2500	39.9517 N 111.9008 W
SRR9660300	Amaranthaceae	Caryophyllales	Perennial	Illumina HiSeq 2500	39.9517 N 111.9008 W
SRR14654853	Chenopodiaceae	Caryophyllales	Deciduous	454 GS FLX Titanium	73.01 N 32.38 E
SRR14654854	Chenopodiaceae	Caryophyllales	Deciduous	454 GS FLX Titanium	73.02 N 32.32 E
SRR14654874	Chenopodiaceae	Caryophyllales	Deciduous	454 GS FLX Titanium	73.04 N 32.35 E
SRR14654875	Chenopodiaceae	Caryophyllales	Deciduous	454 GS FLX Titanium	73.07 N 32.33 E
SRR9660296	Amaranthaceae	Caryophyllales	Deciduous	Illumina HiSeq 2500	39.9517 N 111.9008 W

SRR9660297	Amaranthaceae	Caryophyllales	Deciduous	Illumina HiSeq 2500	39.9517 N 111.9008 W
SRR9660298	Amaranthaceae	Caryophyllales	Deciduous	Illumina HiSeq 2500	39.9517 N 111.9008 W
SRR14654859	Poaceae	Poales	Perennial	454 GS FLX Titanium	73.05 N 31.41 E
SRR14654865	Poaceae	Poales	Perennial	454 GS FLX Titanium	73.09 N 31.48 E
SRR14654876	Poaceae	Poales	Perennial	454 GS FLX Titanium	73.01 N 31.40 E
SRR14654877	Poaceae	Poales	Perennial	454 GS FLX Titanium	73.07 N 31.42 E
SRR7527036	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527041	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527043	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527045	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527049	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527051	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527052	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527054	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527056	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527057	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527058	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527059	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527062	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527064	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527067	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527069	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527070	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527072	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527073	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527074	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527076	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527078	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527086	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527088	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527090	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527098	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527099	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527100	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527101	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527033	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527034	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527035	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527037	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527038	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527039	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527040	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527042	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527044	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527046	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E
SRR7527047	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E

SRR7527050	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
SRR7527053	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
SRR7527055	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
SRR7527060	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
SRR7527061	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
SRR7527063	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
SRR7527065	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
SRR7527066	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
SRR7527068	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
SRR7527071	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
SRR7527075	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
SRR7527077	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
SRR7527079	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
SRR7527080	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
SRR7527081	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
SRR7527087	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
SRR7527089	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
SRR7527091	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
SRR7527092	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
SRR7527093	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
SRR7527096	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
SRR7527097	Poaceae	Poales	Perennial	Illumina MiSeq	23.73 S 15.77 E	
Lat.		Library		Mean		
sample-id	dec.	Lon. dec.	Layout	SRA Study	Altitude (m)	temp.
SRR9660293	39.9517	111.9008	PAIRED	SRP213895	1387	10.29167
SRR9660294	39.9517	111.9008	PAIRED	SRP213895	1387	10.29167
SRR9660295	39.9517	111.9008	PAIRED	SRP213895	1387	10.29167
SRR14654870	32.41	73	SINGLE	SRP321293	199	23.375
SRR14654871	32.36	73.04	SINGLE	SRP321293	201	23.38333
SRR14654872	32.39	73.03	SINGLE	SRP321293	201	23.35833
SRR14654873	32.34	73.06	SINGLE	SRP321293	201	23.375
SRR14654855	31.49	73.07	SINGLE	SRP321293	185	23.86667
SRR14654856	31.43	73.02	SINGLE	SRP321293	180	23.99583
SRR14654857	31.47	73.03	SINGLE	SRP321293	181	23.79583
SRR14654858	31.38	73.08	SINGLE	SRP321293	185	23.8875
SRR3108963	21.05	-100.17	PAIRED	SRP068631	2175	18.3
SRR3108968	21.4	-101.02	PAIRED	SRP068631	2089	17
SRR3108969	21.4	-101.02	PAIRED	SRP068631	2089	17
SRR3108998	21.05	-100.17	PAIRED	SRP068631	2175	18.3
SRR8365816	35.39	9.28	PAIRED	SRP174342	593	18.28333
SRR8365817	35.38	9.3	PAIRED	SRP174342	513	18.7625
SRR8365826	36.5	10.52	PAIRED	SRP174342	169	18.77917
SRR8365827	34.15	9.17	PAIRED	SRP174342	221	20.06667
SRR8365828	34.15	9.17	PAIRED	SRP174342	221	20.06667

SRR8365829	35.55	10.17	PAIRED	SRP174342	77	19.57083
SRR8365832	37.12	9.54	PAIRED	SRP174342	13	17.975
SRR8365833	36.5	10.43	PAIRED	SRP174342	292	17.9875
SRR8365834	36.5	10.41	PAIRED	SRP174342	255	18.06667
SRR8365849	35.31	9.27	PAIRED	SRP174342	474	19.04583
SRR8365850	35.22	8.46	PAIRED	SRP174342	1130	14.55417
SRR8365851	35.29	8.66	PAIRED	SRP174342	692	17.11667
SRR8365852	35.22	8.46	PAIRED	SRP174342	1130	14.55417
SRR8365853	35.17	9.27	PAIRED	SRP174342	400	19.49583
SRR8365854	35.31	9.21	PAIRED	SRP174342	564	18.40417
SRR8365855	35.4	10	PAIRED	SRP174342	123	19.67083
SRR8365856	35.21	8.47	PAIRED	SRP174342	1164	14.39583
SRR8365867	35.22	8.46	PAIRED	SRP174342	1130	14.55417
SRR8365868	35.21	8.48	PAIRED	SRP174342	1137	14.52083
SRR3108988	21.05	-100.17	PAIRED	SRP068631	2175	18.3
SRR3108989	21.1	-101.02	PAIRED	SRP068631	2089	17
SRR3108991	21.05	-100.17	PAIRED	SRP068631	2175	18.3
SRR3108994	21.1	-101.02	PAIRED	SRP068631	2089	17
	-	-	-	-	-	-
SRR9660299	39.9517	111.9008	PAIRED	SRP213895	1387	10.29167
	-	-	-	-	-	-
SRR9660300	39.9517	111.9008	PAIRED	SRP213895	1387	10.29167
SRR14654853	32.38	73.01	SINGLE	SRP321293	200	23.39167
SRR14654854	32.32	73.02	SINGLE	SRP321293	198	23.45833
SRR14654874	32.35	73.04	SINGLE	SRP321293	200	23.39167
SRR14654875	32.33	73.07	SINGLE	SRP321293	201	23.37083
	-	-	-	-	-	-
SRR9660296	39.9517	111.9008	PAIRED	SRP213895	1387	10.29167
	-	-	-	-	-	-
SRR9660297	39.9517	111.9008	PAIRED	SRP213895	1387	10.29167
	-	-	-	-	-	-
SRR9660298	39.9517	111.9008	PAIRED	SRP213895	1387	10.29167
SRR14654859	31.41	73.05	SINGLE	SRP321293	185	24.18333
SRR14654865	31.48	73.09	SINGLE	SRP321293	184	23.94167
SRR14654876	31.4	73.01	SINGLE	SRP321293	179	23.88333
SRR14654877	31.42	73.07	SINGLE	SRP321293	186	24.2375
SRR7527036	-23.73	15.77	PAIRED	SRP153940	923	19.83333
SRR7527041	-23.73	15.77	PAIRED	SRP153940	923	19.83333
SRR7527043	-23.73	15.77	PAIRED	SRP153940	923	19.83333
SRR7527045	-23.73	15.77	PAIRED	SRP153940	923	19.83333
SRR7527049	-23.73	15.77	PAIRED	SRP153940	923	19.83333
SRR7527051	-23.73	15.77	PAIRED	SRP153940	923	19.83333
SRR7527052	-23.73	15.77	PAIRED	SRP153940	923	19.83333
SRR7527054	-23.73	15.77	PAIRED	SRP153940	923	19.83333
SRR7527056	-23.73	15.77	PAIRED	SRP153940	923	19.83333
SRR7527057	-23.73	15.77	PAIRED	SRP153940	923	19.83333
SRR7527058	-23.73	15.77	PAIRED	SRP153940	923	19.83333

SRR7527091	-23.73	15.77	PAIRED	SRP153940	923	19.83333		
SRR7527092	-23.73	15.77	PAIRED	SRP153940	923	19.83333		
SRR7527093	-23.73	15.77	PAIRED	SRP153940	923	19.83333		
SRR7527096	-23.73	15.77	PAIRED	SRP153940	923	19.83333		
SRR7527097	-23.73	15.77	PAIRED	SRP153940	923	19.83333		
		Precip. dry			N (ug g-1)	P (ug g-1)		
sample-id	Precip. rain season	season	pH	C (%)	1)	1)	K (ug g-1)	
SRR9660293		92	60	7.8 na	na	na	na	
SRR9660294		92	60	7.56 na	na	na	na	
SRR9660295		92	60	7.56 na	na	na	na	
SRR14654870		257	21	8.25	33.39	12.87	3.29	0.55
SRR14654871		258	21	8.25	33.39	12.87	3.29	0.55
SRR14654872		259	21	8.25	33.39	12.87	3.29	0.55
SRR14654873		260	21	8.25	33.39	12.87	3.29	0.55
SRR14654855		235	18	8.16	32.95	13.12	2.56	0.45
SRR14654856		232	16	8.16	32.95	13.12	2.56	0.45
SRR14654857		232	17	8.16	32.95	13.12	2.56	0.45
SRR14654858		235	16	8.16	32.95	13.12	2.56	0.45
SRR3108963		355	130	5.79	3.97	8.76	18.11	64.35
SRR3108968		136.5	68	6.25	0.71	12.65	4.53	251.7
SRR3108969		136.5	68	6.25	0.71	12.65	4.53	251.7
SRR3108998		355	130	5.79	3.97	8.76	18.11	64.35
SRR8365816		96	38	6.65	1.34	0.56	13.33	98.48
SRR8365817		90	36	6.68	0.52	0.46	1.3	88.29
SRR8365826		192	24	7.88	1.72	0.39	22.7	86.19
SRR8365827		53	8	8.22	2.224	0.61	3.16	131.03
SRR8365828		53	8	8.22	2.224	0.61	3.16	131.03
SRR8365829		111	23	8.34	1.96	0.57	6.64	131.03
SRR8365832		270	24	7.43	4.44	0.45	13.01	78.88
SRR8365833		204	29	7.36	0.99	0.545	13.92	94.91
SRR8365834		200	29	6.85	0.26	0.7	5.14	103.63
SRR8365849		87	35	8	1.44	0.46	0.92	170.45
SRR8365850		126	60	7.61	0.54	0.7	1.21	50.75
SRR8365851		95	49	6.74	0.59	0.4	0.72	50.75
SRR8365852		126	60	6.42	0.74	0.88	1	51.84
SRR8365853		81	31	8.19	1.21	0.51	2.15	170.45
SRR8365854		90	36	7.99	0.95	0.65	1.88	163.68
SRR8365855		100	22	6.61	0.47	0.52	3.48	88.29
SRR8365856		126	60	7.82	1.69	1.56	1.14	79.09
SRR8365867		126	60	7.61	0.54	0.7	1.21	50.75
SRR8365868		125	59	5.74	0.6	1.41	1.49	91.52
SRR3108988		355	130	5.79	3.97	8.76	18.11	64.35
SRR3108989		136.5	68	6.25	0.71	12.65	4.53	251.7
SRR3108991		355	130	5.79	3.97	8.76	18.11	64.35
SRR3108994		136.5	68	6.25	0.71	12.65	4.53	251.7
SRR9660299		92	60	7.8 na	na	na	na	
SRR9660300		92	60	7.56 na	na	na	na	

SRR14654853	256	21	8.46	37.55	16.11	3.82	0.62
SRR14654854	255	21	8.46	37.55	16.11	3.82	0.62
SRR14654874	256	21	8.46	37.55	16.11	3.82	0.62
SRR14654875	260	21	8.46	37.55	16.11	3.82	0.62
SRR9660296	92	60	7.8 na	na	na	na	na
SRR9660297	92	60	7.74 na	na	na	na	na
SRR9660298	92	60	7.74 na	na	na	na	na
SRR14654859	234	17	8.05	35.31	12.56	2.91	0.53
SRR14654865	236	17	8.05	35.31	12.56	2.91	0.53
SRR14654876	233	16	8.05	35.31	12.56	2.91	0.53
SRR14654877	234	16	8.05	35.31	12.56	2.91	0.53
SRR7527036	77	2	7.43 na	2.49	0.24		6.4
SRR7527041	77	2	7.43 na	2.49	0.24		6.4
SRR7527043	77	2	7.43 na	2.49	0.24		6.4
SRR7527045	77	2	7.43 na	2.49	0.24		6.4
SRR7527049	77	2	7.43 na	2.49	0.24		6.4
SRR7527051	77	2	7.43 na	2.49	0.24		6.4
SRR7527052	77	2	7.43 na	2.49	0.24		6.4
SRR7527054	77	2	7.43 na	2.49	0.24		6.4
SRR7527056	77	2	7.43 na	2.49	0.24		6.4
SRR7527057	77	2	7.43 na	2.49	0.24		6.4
SRR7527058	77	2	7.43 na	2.49	0.24		6.4
SRR7527059	77	2	7.43 na	2.49	0.24		6.4
SRR7527062	77	2	7.43 na	2.49	0.24		6.4
SRR7527064	77	2	7.43 na	2.49	0.24		6.4
SRR7527067	77	2	7.43 na	2.49	0.24		6.4
SRR7527069	77	2	7.43 na	2.49	0.24		6.4
SRR7527070	77	2	7.43 na	2.49	0.24		6.4
SRR7527072	77	2	7.43 na	2.49	0.24		6.4
SRR7527073	77	2	7.43 na	2.49	0.24		6.4
SRR7527074	77	2	7.43 na	2.49	0.24		6.4
SRR7527076	77	2	7.43 na	2.49	0.24		6.4
SRR7527078	77	2	7.43 na	2.49	0.24		6.4
SRR7527086	77	2	7.43 na	2.49	0.24		6.4
SRR7527088	77	2	7.43 na	2.49	0.24		6.4
SRR7527090	77	2	7.43 na	2.49	0.24		6.4
SRR7527098	77	2	7.43 na	2.49	0.24		6.4
SRR7527099	77	2	7.43 na	2.49	0.24		6.4
SRR7527100	77	2	7.43 na	2.49	0.24		6.4
SRR7527101	77	2	7.43 na	2.49	0.24		6.4
SRR7527033	77	2	7.43 na	2.49	0.24		6.4
SRR7527034	77	2	7.43 na	2.49	0.24		6.4
SRR7527035	77	2	7.43 na	2.49	0.24		6.4
SRR7527037	77	2	7.43 na	2.49	0.24		6.4
SRR7527038	77	2	7.43 na	2.49	0.24		6.4
SRR7527039	77	2	7.43 na	2.49	0.24		6.4

SRR7527040	77	2	7.43	na	2.49	0.24	6.4
SRR7527042	77	2	7.43	na	2.49	0.24	6.4
SRR7527044	77	2	7.43	na	2.49	0.24	6.4
SRR7527046	77	2	7.43	na	2.49	0.24	6.4
SRR7527047	77	2	7.43	na	2.49	0.24	6.4
SRR7527050	77	2	7.43	na	2.49	0.24	6.4
SRR7527053	77	2	7.43	na	2.49	0.24	6.4
SRR7527055	77	2	7.43	na	2.49	0.24	6.4
SRR7527060	77	2	7.43	na	2.49	0.24	6.4
SRR7527061	77	2	7.43	na	2.49	0.24	6.4
SRR7527063	77	2	7.43	na	2.49	0.24	6.4
SRR7527065	77	2	7.43	na	2.49	0.24	6.4
SRR7527066	77	2	7.43	na	2.49	0.24	6.4
SRR7527068	77	2	7.43	na	2.49	0.24	6.4
SRR7527071	77	2	7.43	na	2.49	0.24	6.4
SRR7527075	77	2	7.43	na	2.49	0.24	6.4
SRR7527077	77	2	7.43	na	2.49	0.24	6.4
SRR7527079	77	2	7.43	na	2.49	0.24	6.4
SRR7527080	77	2	7.43	na	2.49	0.24	6.4
SRR7527081	77	2	7.43	na	2.49	0.24	6.4
SRR7527087	77	2	7.43	na	2.49	0.24	6.4
SRR7527089	77	2	7.43	na	2.49	0.24	6.4
SRR7527091	77	2	7.43	na	2.49	0.24	6.4
SRR7527092	77	2	7.43	na	2.49	0.24	6.4
SRR7527093	77	2	7.43	na	2.49	0.24	6.4
SRR7527096	77	2	7.43	na	2.49	0.24	6.4
SRR7527097	77	2	7.43	na	2.49	0.24	6.4
sample-id	Strategy	Soils	Sand (%)	Silt (%)	Clay (%)	Texture	Density (kg/dm3)
SRR9660293	Halophyte	RG	43	35	22	loam	1.4
SRR9660294	Halophyte	RG	43	35	22	loam	1.4
SRR9660295	Halophyte	RG	43	35	22	loam	1.4
SRR14654870	Halophyte	CL	40	37	23	loam	1.31
SRR14654871	Halophyte	CL	40	37	23	loam	1.31
SRR14654872	Halophyte	CL	40	37	23	loam	1.31
SRR14654873	Halophyte	CL	40	37	23	loam	1.31
SRR14654855	Halophyte	CL	39	37	24	loam	1.46
SRR14654856	Halophyte	CL	39	37	24	loam	1.46
SRR14654857	Halophyte	CL	40	37	23	loam	1.31
SRR14654858	Halophyte	CL	39	37	24	loam	1.46
SRR3108963	Xerophyte	PH	25	35	40	light clay	1.18
SRR3108968	Xerophyte	CL	78	15	7	loam	1.53
SRR3108969	Xerophyte	CL	78	15	7	loam	1.53
SRR3108998	Xerophyte	PH	25	35	40	light clay	1.18
						sandy	
SRR8365816	Xerophyte	CL	74	13	13	loam	1.4
						sandy	
SRR8365817	Xerophyte	CL	74	13	13	loam	1.4

SRR8365826	Xerophyte	RG	69 18	13	sandy loam	1.22
SRR8365827	Xerophyte	LP	52 28	20	loam	1.3
SRR8365828	Xerophyte	LP	52 28	20	loam heavy	1.3
SRR8365829	Xerophyte	SN	5 32	63	clay	1.47
SRR8365832	Xerophyte	VR	18 30	52	light clay	1.55
SRR8365833	Xerophyte	VR	33 24	43	light clay	1.4
SRR8365834	Xerophyte	VR	33 24	43	light clay sandy	1.4
SRR8365849	Xerophyte	CL	74 13	13	loam sandy	1.4
SRR8365850	Xerophyte	RG	57 28	15	loam heavy	1.34
SRR8365851	Xerophyte	VR	7 22	71	clay sandy	1.21
SRR8365852	Xerophyte	RG	57 28	15	loam	1.34
SRR8365853	Xerophyte	FL	46 33	21	loam	1.39
SRR8365854	Xerophyte	FL	46 33	21	loam sandy	1.39
SRR8365855	Xerophyte	RG	57 28	15	loam sandy	1.34
SRR8365856	Xerophyte	RG	57 28	15	loam sandy	1.34
SRR8365867	Xerophyte	RG	57 28	15	loam sandy	1.34
SRR8365868	Xerophyte	RG	57 28	15	loam	1.34
SRR3108988	Xerophyte	PH	25 35	40	light clay	1.18
SRR3108989	Xerophyte	CL	78 15	7	loam	1.53
SRR3108991	Xerophyte	PH	25 35	40	light clay	1.18
SRR3108994	Xerophyte	CL	78 15	7	loam	1.53
SRR9660299	Halophyte	RG	43 35	22	loam	1.4
SRR9660300	Halophyte	RG	43 35	22	loam	1.4
SRR14654853	Halophyte	CL	40 37	23	loam	1.31
SRR14654854	Halophyte	CL	40 37	23	loam	1.31
SRR14654874	Halophyte	CL	40 37	23	loam	1.31
SRR14654875	Halophyte	CL	40 37	23	loam	1.31
SRR9660296	Halophyte	RG	43 35	22	loam	1.4
SRR9660297	Halophyte	RG	43 35	22	loam	1.4
SRR9660298	Halophyte	RG	43 35	22	loam	1.4
SRR14654859	Halophyte	CL	39 37	24	loam	1.46
SRR14654865	Halophyte	CL	39 37	24	loam	1.46
SRR14654876	Halophyte	CL	39 37	24	loam	1.46
SRR14654877	Halophyte	CL	39 37	24	loam loamy	1.46
SRR7527036	Xerophyte	RG	81 14	5	sand loamy	1.68
SRR7527041	Xerophyte	RG	81 14	5	sand	1.68
SRR7527043	Xerophyte	RG	81 14	5	loamy	1.68

SRR7527045	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527049	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527051	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527052	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527054	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527056	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527057	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527058	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527059	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527062	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527064	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527067	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527069	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527070	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527072	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527073	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527074	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527076	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527078	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527086	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527088	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527090	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527098	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527099	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527100	Xerophyte	RG	81 14	5	sand loamy sand loamy	1.68
SRR7527101	Xerophyte	RG	81 14	5	loamy	1.68

						sand	
SRR7527033	Xerophyte	RG	81	14	5	loamy	
SRR7527034	Xerophyte	RG	81	14	5	sand	1.68
SRR7527035	Xerophyte	RG	81	14	5	loamy	
SRR7527037	Xerophyte	RG	81	14	5	sand	1.68
SRR7527038	Xerophyte	RG	81	14	5	loamy	
SRR7527039	Xerophyte	RG	81	14	5	sand	1.68
SRR7527040	Xerophyte	RG	81	14	5	loamy	
SRR7527042	Xerophyte	RG	81	14	5	sand	1.68
SRR7527044	Xerophyte	RG	81	14	5	loamy	
SRR7527046	Xerophyte	RG	81	14	5	sand	1.68
SRR7527047	Xerophyte	RG	81	14	5	loamy	
SRR7527050	Xerophyte	RG	81	14	5	sand	1.68
SRR7527053	Xerophyte	RG	81	14	5	loamy	
SRR7527055	Xerophyte	RG	81	14	5	sand	1.68
SRR7527060	Xerophyte	RG	81	14	5	loamy	
SRR7527061	Xerophyte	RG	81	14	5	sand	1.68
SRR7527063	Xerophyte	RG	81	14	5	loamy	
SRR7527065	Xerophyte	RG	81	14	5	sand	1.68
SRR7527066	Xerophyte	RG	81	14	5	loamy	
SRR7527068	Xerophyte	RG	81	14	5	sand	1.68
SRR7527071	Xerophyte	RG	81	14	5	loamy	
SRR7527075	Xerophyte	RG	81	14	5	sand	1.68
SRR7527077	Xerophyte	RG	81	14	5	loamy	
SRR7527079	Xerophyte	RG	81	14	5	sand	1.68
SRR7527080	Xerophyte	RG	81	14	5	loamy	
SRR7527081	Xerophyte	RG	81	14	5	sand	1.68

							sand
							loamy
							sand
SRR7527087	Xerophyte	RG	81	14	5		1.68
SRR7527089	Xerophyte	RG	81	14	5		1.68
SRR7527091	Xerophyte	RG	81	14	5		1.68
SRR7527092	Xerophyte	RG	81	14	5		1.68
SRR7527093	Xerophyte	RG	81	14	5		1.68
SRR7527096	Xerophyte	RG	81	14	5		1.68
SRR7527097	Xerophyte	RG	81	14	5		1.68
sample-id	Organic_C (%w)	CEC_clay (cmol/kg)	CEC_soil (cmol/kg)	Saturation (%)	TEB (cmol/kg)	CaCO (%w)	Gypsum (%w)
SRR9660293	0.77	40	17	100	31.1	15	0
SRR9660294	0.77	40	17	100	31.1	15	0
SRR9660295	0.77	40	17	100	31.1	15	0
SRR14654870	0.56	93	18	100	33.2	9	0.4
SRR14654871	0.56	93	18	100	33.2	9	0.4
SRR14654872	0.56	93	18	100	33.2	9	0.4
SRR14654873	0.56	93	18	100	33.2	9	0.4
SRR14654855	0.37	45	15	100	24	26	0.1
SRR14654856	0.37	45	15	100	24	26	0.1
SRR14654857	0.56	93	18	100	33.2	9	0.4
SRR14654858	0.37	45	15	100	24	26	0.1
SRR3108963	2.74	21	18	90	16.2	0.2	0.1
SRR3108968	0.26	83	6	100	6	8.4	0.1
SRR3108969	0.26	83	6	100	6	8.4	0.1
SRR3108998	2.74	21	18	90	16.2	0.2	0.1
SRR8365816	1	8	5	100	5	43.4	0.2
SRR8365817	1	8	5	100	5	43.4	0.2
SRR8365826	0.45	37	7	90	6	0	1
SRR8365827	0.22	62	13	89	11.6	5	0.1
SRR8365828	0.22	62	13	89	11.6	5	0.1
SRR8365829	0.38	44	29	100	28.7	29.1	2
SRR8365832	1.63	37	25	100	25	2.3	0.1
SRR8365833	1.25	56	28	100	28.3	7.6	0.2
SRR8365834	1.25	56	28	100	28.3	7.6	0.2
SRR8365849	1	8	5	100	5	43.4	0.2
SRR8365850	0.2	64	10	100	10.3	8.5	0.9
SRR8365851	1.2	68	52	100	52	17.5	0.2
SRR8365852	0.2	64	10	100	10.3	8.5	0.9
SRR8365853	0.65	49	13	89	11.2	0.4	0.2
SRR8365854	0.65	49	13	89	11.2	0.4	0.2
SRR8365855	0.2	64	10	100	10.3	8.5	0.9

SRR8365856	0.2	64	10 100	10.3	8.5	0.9
SRR8365867	0.2	64	10 100	10.3	8.5	0.9
SRR8365868	0.2	64	10 100	10.3	8.5	0.9
SRR3108988	2.74	21	18 90	16.2	0.2	0.1
SRR3108989	0.26	8.3	6 100	6	8.4	0.1
SRR3108991	2.74	21	18 90	16.2	0.2	0.1
SRR3108994	0.26	8.3	6 100	6	8.4	0.1
SRR9660299	0.77	40	17 100	31.1	15	0
SRR9660300	0.77	40	17 100	31.1	15	0
SRR14654853	0.56	93	18 100	33.2	9	0.4
SRR14654854	0.56	93	18 100	33.2	9	0.4
SRR14654874	0.56	93	18 100	33.2	9	0.4
SRR14654875	0.56	93	18 100	33.2	9	0.4
SRR9660296	0.77	40	17 100	31.1	15	0
SRR9660297	0.77	40	17 100	31.1	15	0
SRR9660298	0.77	40	17 100	31.1	15	0
SRR14654859	0.37	45	15 100	24	26	0.1
SRR14654865	0.37	45	15 100	24	26	0.1
SRR14654876	0.37	45	15 100	24	26	0.1
SRR14654877	0.37	45	15 100	24	26	0.1
SRR7527036	0.14	62	4 100	4	3	0.1
SRR7527041	0.14	62	4 100	4	3	0.1
SRR7527043	0.14	62	4 100	4	3	0.1
SRR7527045	0.14	62	4 100	4	3	0.1
SRR7527049	0.14	62	4 100	4	3	0.1
SRR7527051	0.14	62	4 100	4	3	0.1
SRR7527052	0.14	62	4 100	4	3	0.1
SRR7527054	0.14	62	4 100	4	3	0.1
SRR7527056	0.14	62	4 100	4	3	0.1
SRR7527057	0.14	62	4 100	4	3	0.1
SRR7527058	0.14	62	4 100	4	3	0.1
SRR7527059	0.14	62	4 100	4	3	0.1
SRR7527062	0.14	62	4 100	4	3	0.1
SRR7527064	0.14	62	4 100	4	3	0.1
SRR7527067	0.14	62	4 100	4	3	0.1
SRR7527069	0.14	62	4 100	4	3	0.1
SRR7527070	0.14	62	4 100	4	3	0.1
SRR7527072	0.14	62	4 100	4	3	0.1
SRR7527073	0.14	62	4 100	4	3	0.1
SRR7527074	0.14	62	4 100	4	3	0.1
SRR7527076	0.14	62	4 100	4	3	0.1
SRR7527078	0.14	62	4 100	4	3	0.1
SRR7527086	0.14	62	4 100	4	3	0.1
SRR7527088	0.14	62	4 100	4	3	0.1
SRR7527090	0.14	62	4 100	4	3	0.1
SRR7527098	0.14	62	4 100	4	3	0.1

SRR7527099	0.14	62	4 100	4	3	0.1
SRR7527100	0.14	62	4 100	4	3	0.1
SRR7527101	0.14	62	4 100	4	3	0.1
SRR7527033	0.14	62	4 100	4	3	0.1
SRR7527034	0.14	62	4 100	4	3	0.1
SRR7527035	0.14	62	4 100	4	3	0.1
SRR7527037	0.14	62	4 100	4	3	0.1
SRR7527038	0.14	62	4 100	4	3	0.1
SRR7527039	0.14	62	4 100	4	3	0.1
SRR7527040	0.14	62	4 100	4	3	0.1
SRR7527042	0.14	62	4 100	4	3	0.1
SRR7527044	0.14	62	4 100	4	3	0.1
SRR7527046	0.14	62	4 100	4	3	0.1
SRR7527047	0.14	62	4 100	4	3	0.1
SRR7527050	0.14	62	4 100	4	3	0.1
SRR7527053	0.14	62	4 100	4	3	0.1
SRR7527055	0.14	62	4 100	4	3	0.1
SRR7527060	0.14	62	4 100	4	3	0.1
SRR7527061	0.14	62	4 100	4	3	0.1
SRR7527063	0.14	62	4 100	4	3	0.1
SRR7527065	0.14	62	4 100	4	3	0.1
SRR7527066	0.14	62	4 100	4	3	0.1
SRR7527068	0.14	62	4 100	4	3	0.1
SRR7527071	0.14	62	4 100	4	3	0.1
SRR7527075	0.14	62	4 100	4	3	0.1
SRR7527077	0.14	62	4 100	4	3	0.1
SRR7527079	0.14	62	4 100	4	3	0.1
SRR7527080	0.14	62	4 100	4	3	0.1
SRR7527081	0.14	62	4 100	4	3	0.1
SRR7527087	0.14	62	4 100	4	3	0.1
SRR7527089	0.14	62	4 100	4	3	0.1
SRR7527091	0.14	62	4 100	4	3	0.1
SRR7527092	0.14	62	4 100	4	3	0.1
SRR7527093	0.14	62	4 100	4	3	0.1
SRR7527096	0.14	62	4 100	4	3	0.1
SRR7527097	0.14	62	4 100	4	3	0.1

Table S1. Summary of the metadata used in this meta-analysis. Information for bioclimatic variables was extracted from the WorldClim Bioclimatic variables raster (30s) while the values for the edaphic variables were obtained from the Harmonized World Soil Database.

Class	p (species)	Alloc	Atrarn	Claspi	Kchind	Myrgeo	Opufin	Opurob	Slirub	Slssto	Saruta	Stisab	Stisee	Uromut
Gammaproteobacteria	<0.001	bcd	f	cd	def	cde	a	a	cdef	ef	bc	b	bcd	ef
Actinobacteria	<0.001	abc	c	ab	bc	abc	ab	abc	abc	c	abc	ab	a	c
Alphaproteobacteria	<0.001	abc	c	ab	c	abc	ab	bc	abc	c	abc	ab	a	c
Bacilli	<0.001	c	c	a	bc	a	b	a	bc	c	bc	a	a	bc
Halobacteria	<0.001	a	c	c	c	c	c	c	a	c	a	c	c	b
Bacteroidia	<0.001	ab	c	abc	c	bc	bc	bc	abc	c	ab	ab	a	c
Rhodothermia	<0.001	a	bc	bc	c	c	c	c	a	c	a	bc	c	ab
Acidobacteriae	<0.001	abc	bc	abc	bc	a	a	a	abc	c	abc	abc	ab	bc
Anaerolineae	<0.01	a	c	bc	c	c	c	c	ab	c	ab	bc	abc	bc
Thermoleophilia	<0.01	b	b	b	b	ab	a	ab	b	b	b	b	b	b
PAUC43f	<0.001	a	c	c	c	c	c	c	a	c	a	c	c	b
Planctomycetes	<0.001	a	b	ab	ab	ab	b	ab	a	b	a	ab	ab	b
Verrucomicrobiae	<0.01	a	b	ab	b	a	a	ab	ab	b	a	ab	a	b
Acidimicrobia	<0.001	a	cd	bcd	cd	bcd	bc	cd	ab	d	a	cd	bc	cd
BD2-11	<0.001	c	b	c	c	c	bc	c	a	c	a	bc	c	b
Phycisphaerae	<0.001	ab	d	cd	d	abc	d	abcd	abc	d	a	cd	bcd	d
Polyangia	<0.01	a	b	ab	b	ab	ab	ab	ab	b	a	ab	ab	ab
Nitrososphaeria	<0.001	a	bc	d	ab	abc	d	a	ab	ab	a	d	d	c
Saccharimonadia	<0.001	abcd	d	abc	d	abcd	a	bcd	abcd	d	abcd	ab	ab	cd
Chloroflexia	<0.05	ab	b	ab	b	b	a	b	ab	b	ab	b	ab	b
Desulfuromonadia	<0.001	a	b	b	b	b	b	b	a	b	a	b	b	a
Other. Archaea														
Other. Bacteria														

Class	p (family)	AMAR	CACT	CHEN	POAC									Abbreviations:
Gammaproteobacteria	<0.001	c	a	c	b		AMAR							Amaranthaceae (<i>Caryophyllales</i>)
Actinobacteria	<0.001	b	a	b	a		Alloc							<i>Allenrolfea occidentalis</i>
Alphaproteobacteria	<0.001	bc	ab	c	a		Atrarn							<i>Atriplex amnicola</i>
Bacilli	<0.001	c	b	c	a		Slirub							<i>Salicornia rubra</i>
Halobacteria	<0.001	a	b	b	b		Saruta							<i>Sarcocornia utahensis</i>
Bacteroidia	<0.001	ab	b	c	a		CACT							Cactaceae (<i>Caryophyllales</i>)
Rhodothermia	<0.001	a	b	b	b		Myrgeo							<i>Myrtillocactus geometrizans</i>
Acidobacteriae	<0.001	c	a	c	b		Opufin							<i>Opuntia ficus-indica</i>
Anaerolineae	<0.01	a	c	c	b		Opurob							<i>Opuntia robusta</i>

Table S2. Homogeneous statistical groups for host species and family classification according to the relative abundance of the 21 main bacterial and archaeal classes. p-values result from a Kruskal-Wallis test. Letters were obtained using a post-hoc Tukey HSD test.

Feature ID	Class	Confidence	Sequence
02f4dfba89fe831569 ead167995452d2	PAUC43f_marine_b	1	AACGGAGGGAGCAAGCGTTGCCGAATTACTGGGCGTACAG AGCGCGTAGGCAGGTGAGTCGTATGTGAAAGGCCGGG

	enthic_group		CTCAACCCGGGCATGCCATGCGATACTGCCCTGGCTCGAGGCCG GCAGGGGCCAGTGGATTCCGGTAGCGGTGGAATGCGTAG ATATCAGGAGGAACACCAGCGCGAAGGCGACTGGCTGGCC GGACCTGACGCTGCAGCGCAAAGCGTGGGATCAAACAGG
032538e6af79a29d7 614f31139018702	PAUC43f_marine_b enthic_group	0.99410478	TACGGAGGGAGCGAGCGTTGCCAATCACTGGCGTAAAGG GCGCGTAGGCGGCCGCGTAAGTCGCGTGTGAAAGGCCGGGG CTCAACCCCGCGCATGACACGCGAAACTGCTCGGCTGGAGAGA GGTAGGGCGAGCGGAATTCCGGTAGCGGTGGAATGCGT AGATATCAGGAGGAACACTCGTGGCGAAGGCGGCTCGCTGGG CCTCTCTGACGCTGAAGCGCGAAAGCGTGGGAGCAAACAGG
0585d0c24c272c3fe bee2519c2055fba	PAUC43f_marine_b enthic_group	0.98710047	TACGGAGGGTGCAAGCGTTATCCGAATCACTGGCGTAAAGG GCGCGTAGGCGGCCGCGTAAGTCGCGTGTGAAAGGCCGGGG TCAACCCCGTGATGGCACGCGATACTGCGCGGCTGGAGAAAG GTAGGGCGAGCGGAATTCCGGTAGCGGTGGAATGCGTA GATATCAGGAGGAACACCGTGGCGAAGGCGGCTCGCTGGG CTTCTGACGCTGAAGCGCGAAAGCGTGGGAGCAAACAGG
0687ad322d40e6b9 e69e5b1a555b9681	PAUC43f_marine_b enthic_group	0.99532254	TACGGAGGGAGCGAGCGTTGCCAATTACTGGCGTAAAGG GCGCGTAGGCGGCCGCGTAAGTCGCGTGTGAAAGGCCGGGG TCAACTCCGTGCATTGCATTGATACTGCTGGCTAGAGAAAGG TAGAGGCAGCGGAATTCCGGTAGCGGTGGAATGCGTAGA TATCGGGAAAGAACACCTGCGCGAAGGCGGCTCGCTGGGCCT TTCTGACGCTGAAGCGCGAAAGCGTGGGAGCAAACAGG
08f10298d84e838bf c86c164f571654a	PAUC43f_marine_b enthic_group	0.99999942	TACGGAGGGAGCGAGCGTTGCCAATCACTGGCGTAAAGG GCGCGTAGGCGGCCGCGTAAGTCGCGTGTGAAAGGCCGGGG CTCAACCCGAGTATTGCATGCGATACTGCCCTGGCTGGAGACAG GTAGAGGCAGCGGAATTCCGGTAGCGGTGGAATGCGTAG ATATCAGGAGGAACACTCGTGGCGAAGGCGGCTCGCTGGGC GTTCTGACGCTGAAGCGCGAAAGCGTGGGAGCAAACAGG
107f6fee39386b95c b37f5d5e9aa6988	PAUC43f_marine_b enthic_group	0.99999939	AACGGAGGGAGCGAGCGTTGCCAATTACTGGCGTAAAGG GCGCGTAGGCGGCCGCGTAAGTCGCGTGTGAAAGGCCGGGG CTTAACCCCGTGATGGCATGCGATACTGCGTGGCTAGAGACAG GCAGGGCGAGCGGAATTCCGGTAGCGGTGGAATGCGTA GATATCAGGAGGAACACCGTGGCGAAGGCGGCTCGCTGGG CTCGTCTGACGCTGAAGCGCGAAAGCGTGGGAGCAAACAGG
115df018323bca886 fb99db0c580916d	PAUC43f_marine_b enthic_group	0.99997241	AACGGAGGGAGCAAGCGTTGCCAATTACTGGCGTAAAGG GCGCGTAGGCGGCCGCGTAAGTCGCGTGTGAAAGGCCGGGG CTCAACCCGAGTATTGCATGCGATACTGCGAAGGCTAGAGACAG GTAGGGCGAGCGGAATTCCGGTAGCGGTGGAATGCGTA GATATCAGGAGGAACACCGTGGCGAAGGCGGCTCGCTGGG CTGTTCTGACGCTGAAGCGCGAAAGCGTGGGAGCGAACAGG
129fdd563215e52b9 ebc2bac8541d7f9	PAUC43f_marine_b enthic_group	0.99999994	AACGGAGGGAGCGAGCGTTGCCAATTACTGGCGTACAG GCGCGTAGGCGGCCGCGTAAGTCGCGTGTGAAAGGCCGGGG CTCAACCCGGAGGTGCGAGCGAAACTGCTGGCTGGAGCTA GGTAGAGGCAGCGGAATTCCGGTAGCGGTGGAATGCGTA GATATCAGGAGGAACACCGACGGCGAAGGCGACTCGCTGGAC CTGTTCTGACGCTGAAGCGCGAAAGCGTGGGAGCGAACAGG
13f4b88d1eaaba769 ea32bf0efeb07e9	PAUC43f_marine_b enthic_group	0.99982748	TACGGAGGGAGCGAGCGTTGCCAATTACTGGCGTAAAGG GCGCGTAGGCGGCCGCGTAAGTCGCGTGTGAAAGGCCGGGG TCAACCCCGAGCATTGCGACGCGATACTGCGTGGCTAGAGAAAG GTAGGGGTGAGCGGAATTCCGGTAGCGGTGGAATGCGTAG

			ATATCGGGAGGAACACTCGTGGCGAAGGCCGCTACTGGGCCT TTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
1597f9c210ce1c30fa c380db61fad100	PAUC43f_ marine_b enthic_group	0.99999951	AACGGAGGGAGCGAGCGTTGCCGAATTACTGGCGTAAAG GGCGCGTAGGCAGCCGCGTGAGTCGTATGTGAAAGGCCGGGG CTAACCCCGTCATGGCATGCATACTGCGTGGCTAGAGACAG GTAGGGCGAGCGGAATTCCCGGTAGCGGTGGAATGCGTA GATATCGGGAGGAACACCCGTGGCGAAGGCCGCTCGCTGGC CTCGTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
1655c225966dafe4b abb9c8761d637a7	PAUC43f_ marine_b enthic_group	0.99943044	CACGGGGGAGCAAGCGTTGCCGAATTACTGGCGTGCAG GGCGCGTAGGCAGCCGATAAGTCGTGTGAAACCCATGGC TCAACTGTGGAGAGCCACGCATACTGTCGGCTAGAGACAGG CAGGGCGAGCGGAACCTCCGGTGTAGCGGTGGAATGCGTAG ATATCGGGAGGAACACCCGTGGCGAAGGCCGCTCGCTGGC GTGCTGACGCTGAAGCGCAAAGCGTGGGAGCGAACAGG
1a603ccb26c75f2ef5 1a2f7a0c3ca5b9	PAUC43f_ marine_b enthic_group	0.99999992	AACGGAGGGAGCGAGCGTTGCCGAATTACTGGCGTAAAG AGTGCCTAGGCAGCCATGTAAGTCGTGTGAAAGGCCGGGG TTAACCCCGTGTATGGCATACGATACTGCATGGCTGGAGACAG TAGGGCGAGCGGAATTCCCGGTAGCGGTGGAATGCGTAGA TATCGGGAGGAACACCACTGGCGAAGGCCGCTCGCTAGGC GATCTGACGCTGAAGCACGAAAGCGTGGGAGCAAACAGG
1cb58995ca92a710a 9baf0ed12c7edae	PAUC43f_ marine_b enthic_group	0.98780194	TACGGAGGGAGCAAGCGTTTCGAATTACTGGCGTAAAGG GCGCGTAGGCAGCCGATAAGTCGTGTGAAAGGCCGGGG TCAACCCCGAGCATGGCACGCATACTGTCGGCTGGAGAGAG GTAGAGGCAGCGGAATTCCCGGTAGCGGTGGAATGCGTAG ATATCGGGAGGAACACCCGCGCGAAGGCCGCTCGCTGGC TTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
1cba4563829a4fc7 d60e567319140cd	PAUC43f_ marine_b enthic_group	0.89109621	TACGGAGGGAGCAAGCGTTTCGAATTACTGGCGTAAAGG GCGCGTAGGCAGCCGCTGTAACTGCAATGTGAAATGCCGGGG CAACTCCGTGCACTGCATCCGATACTGCATGGCTAGAGAAAGGT AGAGGCAGCGGAATTCCCGGTAGCGGTGGAATGCGTAGAT ATCGGGAGGAACACCCGTGGCGAAGGCCGCTCGCTGGC TTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
1fd4821395451eea1 a369e737495e599	PAUC43f_ marine_b enthic_group	0.99999935	AACGGAGGGAGCGAGCGTTGCCGAATTACTGGCGTAAAG GGCGCGTAGGCAGCCGCGTGAGTCGTATGTGAAAGGCCGGGG CTAACCCCGTCATGGCATGCATACTGCGTGGCTAGAGACAG GCAGGGCGAGCGGAATTCCCGGTAGCGGTGGAATGCGTA GATATCGGGAGGAACACCCGTGGCGAAGGCCGCTCGCTGGAC CTCGTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
2459ac22af01d26ea 99f6f0902d2db85	PAUC43f_ marine_b enthic_group	0.99999992	AACGGAGGGAGCAAGCGTTGCCGAATTACTGGCGTAAAG AGCGCGTAGGCAGCCGCTGTAACTGCGTATGTGAAAGGCCGGGG TTAACCCCGGTATGGCATACGATACTGCATGGCTGGAGACAGG TAGGGCGAGCGGAATTCCCGGTAGCGGTGGAATGCGTAGA TATCGGGAGGAACACCACTGGCGAAGGCCGCTCGCTAGGC GTTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
25e52ec5289a428df ca24ff8d15ce7d1	PAUC43f_ marine_b enthic_group	0.99999974	AACGGAGGGAGCGAGCGTTGCCGAATTACTGGCGTAAAG GGCGCGTAGGCAGCCGCGTGAGTCGTATGTGAAAGGCCGGGG CTAACCCCGTCATGGCATGCATACTGCGTGGCTAGAGACAG GCAGGGCGAGCGGAATTCCCGGTAGCGGTGGAATGCGTA GATATCGGGAGGAACACCCGTGGCGAAGGCCGCTCGCTGGC CTGGTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG 7

2632c8c42e3c181ad0bb85a4d0ff8a97	PAUC43f_marine_benthic_group	0.99933031	TACGGAGGGAGCAAGCGTTCTCGAATTACTGGCGTAAAGG GCGCGTAGGCAGCCTGGTAAGTCGCTGTGAAAGGCCGGGC TCAACCCCGAGCATTGCATGCATACTGCCTGGCTAGAGAGAG GTAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTA GATATCAGGAAGAACACCTGTGGCGAAGGCCGGCTCGCTGGACC TCTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
2706df0cf3f714c1a9d4c7828eb0a86a	PAUC43f_marine_benthic_group	0.99990656	TACGGAGGGAGCAAGCGTTCTCGAATTACTGGCGTAAAGG GCGCGTAGGCAGCCTGGTAAGTCGCTGTGAAAGGCCGGGC TCAACCCCGAGCATTGCACGCATACTGCCTGGCTAGAGAAAG GTAGGGTGAGCGGAATCCCGGTAGCGGTGGAATGCGTAG ATATCAGGAAGAACACCTGTGGCGAAGGCCGGCTCGCTGGACC TTTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
2713349995bf1df88cb0f251a7689df0	PAUC43f_marine_benthic_group	0.99933193	CACGGGGGAGCAAGCGTTCTCGAATCACTGGCGTGCAG GGCAGTAGGCAGCCTGGTAAGTCGCTGTGAAATCCCATGGC TCAACTGTGGAGAGCCACGCATACTGCCTGGCTAGAGACAGG CAGGGCGAGCGGAACTCCCGGTAGCGGTGGAATGCGTAG ATATCAGGAAGAACACCTGTGGCGAAGGCCGGCTCGCTGGACC GAACTGACGCTGAAGCGCAAAGCGTGGGAGCGAACAGG
2b4ddc33052303fbb2d632311b79d0c4	PAUC43f_marine_benthic_group	0.99999975	AACGGAGGGAGCGAGCGTTCTCGAATCACTGGCGTAAAGG AGCGCGTAGGCAGCCTGGTAAGTCGCTGTGAAAGGCCGGGC TTAACCCCGCTATTGCATGCATACTGCATGGCTAGAGACAGG CAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTAG ATATCAGGAAGAACACCTGTGGCGAAGGCCGGCTCGCTGGACC CGTCTGACGCTGCAGCGCAAAGCGTGGGAGCAAACAGG
31270d9d40428f8084381da0ca8e54bb	PAUC43f_marine_benthic_group	0.98928831	TACGGAGGGAGCGAGCGTTCTCGAATTACTGGCGTAAAGG GCGCGTAGGCAGCCTGGTAAGTCGCTGTGAAAGGCCGGGC TCAACCCCGAGCATTGCACGCATACTGCCTGGCTGGAGAGAG GTAGAGGCAGCGGAATCCCGGTAGCGGTGGAATGCGTAG ATATCAGGAAGAACACCCCGCGCGAAGGCCGGCTCGCTGGACC TTTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
42aa2e30f05cb270137b9b1694f6b362	PAUC43f_marine_benthic_group	1	TACGGAGGGAGCGAGCGTTCTCGAATTACTGGCGTAAAGG GCGCGTAGGCAGCCTGGTAAGTCGCTGTGAAAGGCCGGGC CAACTCCGTGCACTGCATTCGATACTGCCTGGCTAGAGAAAGGT AGAGGCAGCGGAATCCCGGTAGCGGTGGAATGCGTAGAT ATCAGGAAGAACATCTCGCGCGAAGGCCGGCTCGCTGGCTTT TCTGACGCTGAAGCGCGAAAGCGTGGGAGCAAACAGG
432b704a935cc49044a290aa7493cbd2	PAUC43f_marine_benthic_group	0.99957154	TACGGAGGGAGCAAGCGTTCTCGAATTACTGGCGTAAAGG GCGCGTAGGCAGCCTGGTAAGTCGCTGTGAAAGGCCGGGC TCAACCCCGAGCATTGCACGCATACTGCCTGGCTAGAGAGAG GTAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTA GATATCAGGAAGAACACCTGTGGCGAAGGCCGGCTCGCTGGACC TTTCTGACGCTGAAGCGCGAAAGCGTGGGAGCAAACAGG
44bd32c61ff96c8702563c1da1d7feec	PAUC43f_marine_benthic_group	0.99670828	TACGGAGGGAGCGAGCGTTCTCGAATTACTGGCGTAAAGG CGCGTAGGCAGCCTGGTAAGTCGCTGTGAAAGGCCGGGC CTCAACCCCGCTATGACACGCATACTGCATGGCTGGAGATAG GTAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTA GATATCAGGAAGAACACCTGTGGCGAAGGCCGGCTCGCTGGACC CTATTCTGACGCTGAAGCGCGAAAGCGTGGGAGCAAACAGG
5169ff82500fc624136e76aae186bcf2	PAUC43f_marine_b	0.99999469	AACGGAGGGAGCGAGCGTTCTCGAATTACTGGCGTAAAGG GCGCGTAGGCAGCCTGGTAAGTCGCTGTGAAAGGCCGGGC CTCAACCCGAGTATTGCATGCATACTGCAAGGCTAGAGACAG

	enthic_group		GTAAGGGCGAGCGGAATTCCCGGTAGCGGTGGAATCGTA GATATCDDGAAGAACACCGGTGGCGAAGGCCTCGCTGGC CTGTTCTGACGCTGAAGCGCAAAGCGTGGGAGCGAACAGG
5522d158893e82c63 3c07789902454b8	PAUC43f_marine_b enthic_group	0.99998816	TACGGAGGGAGCAAGCGTTTCGGAATTACTGGCGTAAAGG GCGCGTAGGCCGGCGGTAAAGTCGCGTGTGAAAGGCCGGGG TCAACCCCGAGTATTGCATGCGATACTGCCTGGCTGGAGACAGG TAGAGGCAGCGGAATTCCCGGTAGCGGTGGAATCGTAGA TATCGGGAGGAACACTGTGGCGAAGGCCTCGCTGGCCT GTTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
567eec98ae584597 80a9fb5ce6392ae	PAUC43f_marine_b enthic_group	0.99912584	TACGGAGGGAGCAAGCGTTTCGGAATTACTGGCGTAAAGG GCGCGTAGGCCGGCGGTAAAGTCGCGTGTGAAAGGCCGGGG TCAACCCCGAGCACTGCATGTGATACTGCCTGGCTAGAGAGAG TAGAGGGCGAGCGGAATTCCCGGTAGCGGTGGAATCGTAGA GATATCDDGAAGAACACCTGTGGCGAAGGCCTCGCTGGACC TCTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
56a66cc5dbdf6d873 a41d3a2f6d47567	PAUC43f_marine_b enthic_group	1	AACGGAGGGAGCAAGCGTTTCGGAATTACTGGCGTACAG AGCGCGCAGGCCAGGTAAGTCGTATGTGAAAGGCCGGG CTCAACCCGGCATGCCATGCGATACTGCCTGGCTAGAGGCCG GCAGGGGCCAGTGGAAATTCCCGGTAGCGGTGGAATCGTAG ATATCGGGAGGAACACCAGCGCGAAGGCAGTGGCTGGGCC GGACCTGACGCTGCAGCGCAAAGCGTGGGATCAAACAGG
5aaf83ee881e128ff8 228d703655d58b	PAUC43f_marine_b enthic_group	1	AACGGAGGGAGCAAGCGTTTCGGAATTACTGGCGTACAG AGCGCGTAGGCCAGGTAAGTCGTATGTGAAAGGCCGGG CTCAACCCGGCATGCCATGCGATACTGCCTGGCTAGAGGCCG GCAGGGGCCAGTGGAAATTCCCGGTAGCGGTGGAATCGTAG ATATCGGGAGGAACACCAGCGCGAAGGCAGTGGCTGGGCC GGACCTGACGCTGCAGCGCAAAGCGTGGGATCAAACAGG
5fcac520749b33dfd9 f28ee6447be0f3	PAUC43f_marine_b enthic_group	0.78735693	TACGGAGGGAGCGAGCGTTTCGGAATTACTGGCGTAAAGG GCGCGTAGGCCGGCGGTAAAGTCGAATGTGAAATGCCGGGG CAACTCCGTGCACTGCATCCGATACTGCATGGCTAGAGAAAGGT AGAGGCAGCGGAATTCCCGGTAGCGGTGGAATCGTAGAT ATCGGGAGGAACACCCGTGGCGAAGGCCTCGCTGGCCTT TTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
682a5c5c329d2933d 8598a834b151d5e	PAUC43f_marine_b enthic_group	1	AACGGAGGGAGCAAGCGTTTCGGAATTACTGGCGTACAG AGCGCGTAGGCCAGGTAAGTCGTATGTGAAAGGCCGGG CTCAACCCGGCATGCCATGCGATACTGCCTGGCTAGAGGCCG CAGGGGCCAGTGGAAATTCCCGGTAGCGGTGGAATCGTAGA TATCGGGAGGAACACCAGCGCGAAGGCAGTGGCTGGGCC GACCTGACGCTGCAGCGCAAAGCGTGGGATCAAACAGG
6846f5fae6edd3d53 a8e7f672448824f	PAUC43f_marine_b enthic_group	0.99936962	CACGGGGGAGCAAGCGTTTCGGAATTACTGGCGTGCAG GGCGCGTAGGCCAGGTAAGTCGTATGTGAAACCCATGGC TCAACTGTGGAGAGCCACGCGATACTGTTGGCTAGAGACAGG CAGGGGCCAGCGGAATTCCCGGTAGCGGTGGAATCGTAG ATATCGGGAGGAACACCCGTGGCGAAGGCCTCGCTGGCCT GTGCTGACGCTGAAGCGCAAAGCGTGGGAGCGAACAGG
70e0b2fac1e61be4c ee380d58ac04cca	PAUC43f_marine_b enthic_group	0.99999813	AACGGAGGGAGCGAGCGTTTCGGAATTACTGGCGTAAAG AGCGCGTAGGCCAGGTAAGTCGTATGTGAAAGGCCGGGG CTTAACCCCGCTATGGCATACGATACTGCATGGCTAGAGACAG GTGGGGCGAGCGGAATTCCCGGTAGCGGTGGAATCGTAG GATATCGGGAGGAACACCAGTGGCGAAGGCCTCGCTAGGC CTGTTCTGACGCTGTAGCGCAAAGCGTGGGAGCAAACAGG

75a5a9267ec2a6b8a326e1a1c2c282d0	PAUC43f_marine_benthic_group	0.84163359	TACGGAGGGAGCAAGCGTTCCGAATTACTGGCGTAAAGG GCGCGTAGGC GGCGCTGTAAAGTCGCGTGAAATGCCGGGCT CAACCCCGCTGCACTGCACGCATACTGCATGGCTGGAGAGAG GTAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTA GATATCDDGAAGAACACCTGTGGCGAAGGC GGCTCGCTGGACC TTTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
765c246a568dd41ebfc9ce935575a222	PAUC43f_marine_benthic_group	0.99975134	AACGGAGGGAGCGAGCGTTCCGAATCACTGGCGTACAG GGC CGTAGGC GGCGATCAGTCGTGTGAAGACCCCCGGG CTCAACCCGGAGGGCAGCGATACTGTCGGCTGGAGACA GGCAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTA AGATATCDDGAAGAACACCCGGTGGCGAAGGC GGCTCGCTGGG CCTGATCTGACGCTGAGGC CGCAAAGCGTGGGAGCGAACA
771a9b7ec90659ab3a68984c6087c6a1	PAUC43f_marine_benthic_group	0.99999988	AACGGAGGGAGCGAGCGTTCCGAATTACTGGCGTAAAG AGCGCGTAGGC GGCCATGTAAGTCGTGTGAAGAGCCGGG CTAAACCCCGTGTATGGCATACGATACTGCATGGCTAGAGACAG GTAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTA GATATCDDGAAGAACACCCAGTGGCGAAGGC GGCTCGCTAGGC CTGTTCTGACGCTGTAGCGCAAAGCGTGGGAGCAAACAGG
778740c10e17b465e149223c267a5943	PAUC43f_marine_benthic_group	0.99999999	AACGGAGGGAGCAAGCGTTCCGAATTACTGGCGTACAG AGCGCGTAGGC GGCCATGTAAGTCGTGTGAAGAGCCGGG CTAAACCCCGTGTATGGCATACGATACTGCATGGCTAGAGACAG GTAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTA GATATCDDGAAGAACACCCAGTGGCGAAGGC GGCTCGCTAGGC CTGATCTGACGCTGCAGCGCAAAGCGTGGGAGCAAACAGG
7b2e850a955112c2a100a3778f984b7d	PAUC43f_marine_benthic_group	0.99999995	AACGGAGGGAGCGAGCGTTCCGAATTACTGGCGTAAAG AGCGCGTAGGC GGCCATGTAAGTCGTGTGAAGAGCCGGG CTAAACCCCGTGTATGGCATACGATACTGCATGGCTAGAGACAG GTAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTA GATATCDDGAAGAACACCCAGTGGCGAAGGC GGCTCGCTAGGC CTGTTCTGACGCTGTAGCGCAAAGCGTGGGAGCAAACAGG
7db9d2040f25d9226d67df57e55e1b12	PAUC43f_marine_benthic_group	0.99999743	AACGGAGGGAGCGAGCGTTCCGAATTACTGGCGTAAAGG GCGCGTAGGC GGCGCTGTAGCGTATGTGAAGAGCCAGGG CTAAACCCGGCATTGCA TGCGATACTGCGTGGCTAGAGACAGG TAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTAGA TATCGGGAGGAACACCCGTGGCGAAGGC GGCTCGCTGGCCT GTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
8185d2e1bf616f1d33a8362b3805f955	PAUC43f_marine_benthic_group	0.99952853	TACGGAGGGAGCAAGCGTTCCGAATTACTGGCGTAAAGG GCGCGTAGGC GGCGCTGTAAAGTCGCA TGCGATACTGCCTGGCTAGAGAGAGG TAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTAGA TATCGGGAGGAACACCTGTGGCGAAGGC GGCTCGCTGGACCTT TTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
859571cf22de06d1bb3bc860bfcd68b6	PAUC43f_marine_benthic_group	0.99999923	CACGGGGGGAGCAAGCGTTCCGAATTACTGGCGTGCAG GGC CGTAGGC GGCGATAAGTCGCGTGTGAAGAGCCACGG CTCAACTGTGGACGCCACGTGATACTGTCGGCTAGAGACAG GCAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTA GATATCDDGAAGAACACCTGTGGCGAAGGC GGCTCGCTGGG CTGTCGCTGACGCTGAAGCGCAAAGCGTGGGAGCGAACAGG
8703683fcc3663fdad837b7e9a3e0317	PAUC43f_marine_b	0.99999949	AACGGAGGGAGCGAGCGTTCCGAATTACTGGCGTAAAGG AGCGCGTAGGC GGCCATGTAAGTCGTATGTGAAGAGCCGGGCTTAACCCCGTATTGCA TGCGATACTGCATGGCTAGAGACAGG

	enthic_group		CAGGGGCGAGCGGAATCCCGGTAGCGGTGGAATCGTAG ATATCGGAGGAACACCGTGGCAAGGGCTCGTAGACCT CGTCTGACGCTCAGCGAAAGCGTGGGAGCAAACAGG
87e2862bd2142f436 5e67576a7923c15	PAUC43f_marine_b enthic_group	0.99999995	AACGGAGGGAGCAAGCGTTGCCGAATTACTGGCGTAAAG AGCGCGTAGGCCCATGTAAGTCGTGTGAAAGGCCGGGG CTAACCCCGTGTATGGCATACGATACTGCATGGCTGGAGACAG GTAGGGCGAGCGGAATCCCGGTAGCGGTGGAATCGTA GATATCGGAGGAACACCGTGGCAAGGCCTCGCTAGGC CTGTTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
8830189070633e39a 941ddddda16f8c8	PAUC43f_marine_b enthic_group	0.99999601	CACGGGGGAGCGAGCGTTGCCGAATCACTGGCGTGCAG GGCGCGTAGGCCGGGGTAAGTCGTGTGAAAGGCCACGG CTAACCCGTGGACGCCACGCGATACTGCCTGGCTAGAGACAG GCAGGGCGAGCGGAACTCCCGGTAGCGGTGGAATCGTA GATATCGGAGGAAGAACACCCGTGGCAAGGCCTCGCTGGGC CTGACTGACGCTGAAGCGCAAAGCGTGGGAGCGAACAGG
93ce7b3d849921776 26073740beb3191	PAUC43f_marine_b enthic_group	0.99986885	TACGGAGGGAGCAAGCGTTTCGGAATTACTGGCGTAAAGG GCGCGTAGGCCGGGGTAAGTCGTGTGAAAGGCCGGGGC TCAACCCCGAGCATGGCATGCGATACTGCCTGGCTAGAGAAAG GTAGGGGTAGCGGAATCCCGGTAGCGGTGGAATCGTAG ATATCGGAGGAACACTCGTGGCAAGGCCTCGCTGGGC TTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
9908c2115b46524eb 866d6c59163ca4c	PAUC43f_marine_b enthic_group	0.99982172	TACGGAGGGAGCGAGCGTTTCGGAATTACTGGCGTAAAGG GCGCGTAGGCCGGGGTAAGTCGTATGTGAAAGGCCGGGGC TCAACCCCGAGCATGGCATGCGATACTGCCTGGCTGGAGAAAG GTAGAGGCAGCGGAATCCCGGTAGCGGTGGAATCGTAG ATATCGGAGGAAGAACACCTCGGGCAAGGCCTCGCTGGGC TTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
a2d207d7dbeccdd4 6f3974449ebe138	PAUC43f_marine_b enthic_group	0.9999998	AACGGAGGGAGCGAGCGTTGCCGAATCACTGGCGTAAAG AGCGCGTAGGCCGGGGTAAGTCGTATGTGAAAGGCCGGGG CTAACCCCGGTATTGCGATACTGCCTGGCTAGAGACAG GCAGGGCGAGCGGAATCCCGGTAGCGGTGGAATCGTA GATATCGGAGGAACACCGTGGCAAGGCCTCGCTAGGC CTAGTCTGACGCTGAGCGCAAAGCGTGGGAGCAAACAGG
a30c9302723cd6008 96a2ca15e0a641f	PAUC43f_marine_b enthic_group	0.99758315	TACGGAGGGAGCGAGCGTTTCGGAATTACTGGCGTAAAGG GCGCGTAGGCCGGGGTAAGTCGTGTGAAAGGCCGGGGC TCAACCCCGAGCATGGCATGCGATACTGCCTGGCTAGAGAAAG GTAGAGGCAGCGGAATCCCGGTAGCGGTGGAATCGTAG ATATCGGAGGAAGAACACCTCGGGCAAGGCCTCGCTGGGC TTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
a5280adb7c6c9ec64 eb65c34a3540a69	PAUC43f_marine_b enthic_group	0.99946587	CACGGGGGAGCAAGCGTTGCCGAATCACTGGCGTGCAG GGCGCGTAGGCCGGGGTAAGTCGTGTGAAACCCCATGGC TCAACTGTGGAGAGCCACGCGATACTGTTGGCTAGAGACAGG CAGGGCGAGCGGAATCCCGGTAGCGGTGGAATCGTAG ATATCGGAGGAAGAACACCCGTGGCAAGGCCTCGCTGGGC GTACTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
a96ffdb2c1f22a562f 133f334a12b95d	PAUC43f_marine_b enthic_group	0.8261967	TACGGAGGGAGCGAGCGTTTCGGAATTACTGGCGTAAAGG GCGCGTAGGCCGGGGTAAGTCGAATGTGAAATGCCGGGGC CAACTCCGCGCACTGCATCCGATACTGCATGGCTAGAGAAAGGT AGAGGCAGCGGAATCCCGGTAGCGGTGGAATCGTAGAT ATCGGAGGAAGAACACCCGTGGCAAGGCCTCGCTGGGC TTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG

b4b27cbcbd64b2495 1d6b81d577b11b6	PAUC43f_marine_benthic_group	0.99999968	AACGGAGGGAGCGAGCGTTGCCGAATTACTGGCGTACAG GGCGCGTAGGCAGCCATGTAAGTCACGTGAAAGGCCGGGG CTCAACCCCGTATTGCACGTGATACTGCATGGCTGGAGACAG GTAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTA GATATCAGGAGGAACACCCGTGGCGAAGGCAGCTGCTGGGC CTCGTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
bbc8308fb6a1e5eda ff1c824efbba471	PAUC43f_marine_benthic_group	0.99999939	AACGGAGGGAGCGAGCGTTGCCGAATTACTGGCGTAAAG GGCGCGTAGGCAGCCGTAGTCGCTGTGAAAGGCCGGGG CTCAACCCGAGTATTGCATGCATACTGCCTGGCTGGAGACAG GTAGAGGCAGCGGAATCCCGGTAGCGGTGGAATGCGTAG ATATCAGGAGGAACACTCGTGGCGAAGGCAGCTGCTGGGC GTTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
bc84a1334fdb1f793 d5d93faa5c78ff3	PAUC43f_marine_benthic_group	0.99999984	AACGGAGGGAGCGAGCGTTGCCGAATTACTGGCGTAAAG AGCGCGTAGGCAGCCATGTAAGTCGTTGTGAAAGGCCGGGG CTTAACCCGTGTATGGCATACGATACTGCATGGCTGGAGACAG GTAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTA GATATCAGGAGGAACACCCAGTGGCGAAGGCAGCTGCTAGGC CTGTTCTGACGCTGTAGCGCAAAGCGTGGGAGCAAACAGG
bd6224755bf967096 ea6da7c4689d4f6	PAUC43f_marine_benthic_group	0.99999971	AACGGAGGGAGCGAGCGTTGCCGAATCACTGGCGTAAAG GGCGCGTAGGCAGCCGTAGTCGTATGTGAAAGGCCGGGG CTTAACCCGTGCATGGCATACGATACTGCCTGGCTAGAGACAG GCAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTA GATATCAGGAGGAACACCCGTGGCGAAGGCAGCTGCTGGGC CTCGTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
bea1ea32b5fa1a6afd b437015c1aa90c	PAUC43f_marine_benthic_group	0.90501484	TACGGAGGGAGCAAGCGTTGCCGAATTACTGGCGTAAAGG GCGCGTAGGCAGGTAGTCGAATGTGAAATGCCGGGGCT CAACTCCCGCACTGCATCCGATACTGCATGGCTAGAGAAAGGT AGAGGCAGCGGAATCCCGGTAGCGGTGGAATGCGTAGAT ATCAGGAGGAACACCCGTGGCGAAGGCAGCTGCTGGCCTT TTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
bf5cd635d8c1b5b78 10438b622c1a80c	PAUC43f_marine_benthic_group	0.99988175	TACGGAGGGAGCGAGCGTTGCCGAATTACTGGCGTAAAGG GCGCGTAGGCAGGTAGTCGTGTGAAAGGCCGGGGCT TCAACCCGAGCATTGCACGCATACTGCCTGGCTAGAGAGAAG GTAGGGGTAGCGGAATCCCGGTAGCGGTGGAATGCGTAG ATATCAGGAGGAACACTCGTGGCGAAGGCAGCTGCTGGCCTT TTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
bfd1181a8ebfb38e6 edcd429242c61e2	PAUC43f_marine_benthic_group	0.99975486	TACGGAGGGAGCAAGCGTTGCCGAATTACTGGCGTAAAGG GCGCGTAGGCAGGTAGTCGTATGTGAAAGGCCGGGGCT CAACCCGAGCATTGCACGCATACTGCCTGGCTAGAGAGAAG TAGGGGCAGCGGAATCCCGGTAGCGGTGGAATGCGTAGA TATCAGGAGGAACACCTGTGGCGAAGGCAGCTGCTGGACCTT TTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
c2fe6a702ad8801b2 c06d2a70051c3c9	PAUC43f_marine_benthic_group	0.9999982	AACGGAGGGAGCGAGCGTTGCCGAATTACTGGCGTAAAGG AGCGCGTAGGCAGGTAGTCGATGTGAAAGGCCGGGG CTTAACCCCGTATTGCATGCATACTGCCTGGCTAGAGACAG GGAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTA GATATCAGGAGGAACACCCAGTGGCGAAGGCAGCTGCTAGGC CTCGTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
c4a6a868e8863abea 0377ca64f360c84	PAUC43f_marine_b	0.99999498	CACGGGGGGAGCAAGCGTTGCCGAATCACTGGCGTGCAG GGCGCGTAGGCAGGTAGTCGCTGTGAAAGGCCACGG CTCAACCGTGGACGCCACGCATACTGTCCGGCTAGAGACAG

	enthic_group		GCAGGGGCGAGCGGAACCTCCGGTGTAGCGGTGGAATGCGTA GATATCGBGAAGAACACCCGTGGCGAAGGCGGCTCGCTGGC CTGATCTGACGCTGAAGCGCAAAGCGTGGGAGCGAACAGG
c523b601cb3590761 3ecfe8cf5145aa2	PAUC43f_marine_b enthic_group	0.99997046	AACGGAGGGAGCGAGCGTTGTCGGAATTACTGGCGTAAAG GGCGCGTAGGCAGGCCCTGTAAGTCGATGTGAAAGGCCGGGG CTCAACCCGAGTATTGATCGCATGCGATACTGCAAGGCTAGAGACAG GTAGGGGCGAGCGGAATTCCGGTGTAGCGGTGGAATGCGTA GATATCGBGAAGAACACCCGTGGCGAAGGCGGCTCGCTGGC CTGATCTGACGCTGAAGCGCAAAGCGTGGGAGCGAACAGG
c8ba58f429a1378ac ea808cab6e39fc3	PAUC43f_marine_b enthic_group	0.99881792	TACGGAGGGAGCAAGCGTTGTCGGAATTACTGGCGTAAAG GCGCGTAGGCAGGCCCTGTAAGTCGATGTGAAAGGCCGGGG CAACCCGAGCAGTGCATGCGATACTGCGTAGAGAGAGG TAGGGGCGAGCGGAATTCCGGTGTAGCGGTGGAATGCGTA TATCGGAAGAACACCTGTGGCGAAGGCGGCTCGCTGGACCTC TTCTGACGCTGAAGCGCAAAGCGTGGGAGCGAACACAGG
d2331784ee005073f 655bb033b3255f0	PAUC43f_marine_b enthic_group	0.99997648	TACGGAGGGAGCGAGCGTTGTCGGAATTACTGGCGTAAAG GGCGCGTAGGCAGGCCCTGTAAGTCGATGTGAAAGGCCGGGG CTCAACCCGAGCATTGATCGCATGCGATACTGCGTAGAGAAA GGTAGGGGTGAGCGGAATTCCGGTGTAGCGGTGGAATGCGTA GATATCGBGAAGAACACCTGTGGCGAAGGCGGCTCGCTGGC CTTTCTGACGCTGAAGCGCAAAGCGTGGGAGCGAACACAGG
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d3dcde194617df844 84b19fd8f56da4a	PAUC43f_marine_b enthic_group	0.99999998	AACGGAGGGAGCGAGCGTTGTCGGAATTACTGGCGTACAG AGCGCGTAGGCAGGCCATGTAAGTCGATGTGAAAGGCCGGGG CTCAACCCGTGTATGGCATACGATACTGCGTAGGCTGGAGACAG GTAGGGGCGAGCGGAATTCCGGTGTAGCGGTGGAATGCGTA GATATCGBGAAGAACACCAAGTGGCGAAGGCGGCTCGCTAGGC CTGATCTGACGCTGCAGCGCAAAGCGTGGGAGCGAACACAGG
d3ee25b689cd31fe3 3438c368dcff4f3	PAUC43f_marine_b enthic_group	0.99999995	AACGGAGGGAGCGAGCGTTGTCGGAATTACTGGCGTAAAG AGCGCGTAGGCAGGCCATGTAAGTCGATGTGAAAGGCCGGGG CTAACCCCGTGTATGGCATACGATACTGCGTAGGCTAGAGACAG GTAGGGGCGAGCGGAATTCCGGTGTAGCGGTGGAATGCGTA GATATCGBGAAGAACACCAAGTGGCGAAGGCGGCTCGCTAGGC CTGATCTGACGCTGCAGCGCAAAGCGTGGGAGCGAACACAGG
d905eed080271289 8f748814c321b793	PAUC43f_marine_b enthic_group	0.99998291	TACGGAGGGAGCGAGCGTTGTCGGAATTACTGGCGTAAAG GGCGCGTAGGCAGGCCATGTAAGTCGATGTGAAAGGCCGGGG CTAACCCGAGCATTGATCGCATGCGATACTGCGTAGAGAAA GGTAGGGGTGAGCGGAATTCCGGTGTAGCGGTGGAATGCGTA GATATCGBGAAGAACACCAAGTGGCGAAGGCGGCTCGCTAGGC CTTTCTGACGCTGAAGCGCAAAGCGTGGGAGCGAACACAGG
da8d3394223b6e6e 54f61392b9ef0b4f	PAUC43f_marine_b enthic_group	0.99999957	AACGGAGGGAGCGAGCGTTGTCGGAATTACTGGCGTAAAG AGCGCGTAGGCAGGCCATGTAAGTCGATGTGAAAGGCCGGGG CTAACCCCGTGTATGGCATACGATACTGCGTAGGCTAGAGACAG GCAGGGGCGAGCGGAATTCCGGTGTAGCGGTGGAATGCGTA GATATCGBGAAGAACACCAAGTGGCGAAGGCGGCTCGCTAGGC CTAGTCTGACGCTGCAGCGCAAAGCGTGGGAGCGAACACAGG

db7507bc4a3650269 8b1f846d04e8c54	PAUC43f_marine_benthic_group	0.99999974	AACGGAGGGAGCGAGCGTTGCCGAATCACTGGCGTAAAG GGCGCGTAGGC GGCGCGTGAGTCGTATGTGAAAGGCCGGGG CTAACCCCGTGTATTGCATGCATACTGCCTGGCTAGAGACAG GCAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTA GATATCAGGGAGGAACACCGTGGCGAAGGC GGCTCGCTGGGC CTCGTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
e253e678589d61bf3 c0d039bfb5cb673	PAUC43f_marine_benthic_group	0.99999674	AACGGGGGGAGCGAGCGTTGCCGAATCACTGGCGTATAAG GGCGCGTAGGC GGCGCGTGAGTCGTATGTGAAAGGCCACGGC TCAACC GTGGAGAGCCATGCATACTGCCTGGCTAGAGACAGG CAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTAG ATATCAGGGAGGAACACCTGTGGCGAAGGC GGCTCGCTGGGC GATCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
e2f950524a4fc5fec0f b855b2091660e	PAUC43f_marine_benthic_group	0.99267286	TACGGAGGGAGCAAGCGTTTCGAATTACTGGCGTAAAGG GCGCGTAGGC GGCGCTGGTAAGTCGTGTGAAAGGCCGGGG TCAACCCCGAGCACTGCACCGATACTGCCTGGCTGGAGAGAG GTAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTA GATATCAGGGAGGAACACCTGTGGCGAAGGC GGCTCGCTGGACC TTTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
e61b8069ae1b20f8e 12eb848afa0869b	PAUC43f_marine_benthic_group	0.99971317	AACGGAGGGAGCGAGCGTTGCCGAATTACTGGCGTAAAG GGCGCGTAGGC GGCGCGTAAGTCGTGTGAAAGGCCGGGG CTCAACCCCGTGTGGCATGCACCGATACTGCCTGGCTGGAGAAA GGTAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGT AGATATCAGGGAGGAACACCGTGGCGAAGGC GGCTCGCTGGG CCTTTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAG G
ec7588e44fda1d359 37c48c7edf3f3ba	PAUC43f_marine_benthic_group	0.99999976	AACGGAGGGAGCGAGCGTTGCCGAATTACTGGCGTAAAG AGTGC GTAGGC GGCCATGTAAGTCGTGTGAAAGGCCGGGG TTAACCCCGCGTATTGCATGCATACTGCCTGGCTAGAGACAGG CAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTAG ATATCAGGGAGGAACACCACTGTGGCGAAGGC GGCTCGCTAGGC CGTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
ef813dd28c29a6ee6 65c590fa2da29c0	PAUC43f_marine_benthic_group	0.99998961	AACGGAGGGAGCGAGCGTTGCCGAATTACTGGCGTAAAG AGCGCGTAGGC GGCTACGTAAGTCGTGTGAAAGGCCGGGG CTAACCCCGCGTATTGCATGCATACTGCCTGGCTAGAGACAG GCAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTA GATATCAGGGAGGAACACCACTGTGGCGAAGGC GGCTCGCTAGGC CTCGTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
f171b6dd237f56afc2 ed7d634ce3c4ac	PAUC43f_marine_benthic_group	0.9999998	AACGGAGGGAGCGAGCGTTGCCGAATTACTGGCGTAAAG AGCGCGTAGGC GGCCATGTAAGTCGTGTGAAAGGCCGGGG CTAACCCCGCGTATTGCATACGATACTGCATGGCTAGAGACAG GTAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTA GATATCAGGGAGGAACACCACTGTGGCGAAGGC GGCTCGCTAGGC CTGCTCTGACGCTGTAGCGCAAAGCGTGGGAGCAAACAGG
f27d92f608f221dbb1 7c18cef8c0d4e5	PAUC43f_marine_benthic_group	0.99983927	AACGGAGGGAGCGAGCGTTGCCGAATTACTGGCGTACAG GGCGCGTAGGC GGCGCGTGTGGCTGTGAAATCCCGGG TCAACCCGGGAGGTGCAGGC GAAACTGTCCGGCTGGAGACAG GTAGAGGC GAGCGGAATCCCGGTAGCGGTGGAATGCGTAG ATATCAGGGAGGAACACCACTACGGCGAAGGC AGCTCGCTGGGC CGTCTGACGCTGAAGCGCAAAGCGTGGGAGCAAACAGG
f2df23dd314f087a06 7027786bb31876	PAUC43f_marine_b	0.99999993	AACGGAGGGAGCGAGCGTTGCCGAATTACTGGCGTACAG GGCGCGTAGGC GGCGCGATAGTCGTGTGAAAGCCCCGGG

	enthic_group		CTCAACCCGGGAGGTGCAGGCCAAACTGTCCGGCTGGAGTCAGTAGAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTAAATCGGGAGGAACACCGACGGCGAAGGCAGCTCGCTGGGCCTGTTCTGACGCTGAAGCGCAGCGCAAAGCGTGGGATCAAACAGG
f3035edcf60ac13e5a7715ec162df936	PAUC43f_marine_benthic_group	1	AACGGAGGGAGCAAGCGTTGCCGAATTACTGGCGTACAGAGCGCGCAGGCCCGCAGGTAGTCGTATGTGAAAGGCCCGGCTCAACCCGGCATGCCATGCGATACTGCCTGGCTAGAGGCCGCGAGGGGCCAGTGGAAATCCCGGTAGCGGTGGAATGCGTAGATATCGGGAGGAACACCCAGCGCGAAGGCAGCTGGCTGGGCCGGACCTGACGCTGCAGCGCAAAGCGTGGGATCAAACAGG
f512b711f50781778c61cae5065ef4b6	PAUC43f_marine_benthic_group	0.99994056	TACGGAGGGAGCGAGCGTTGCCGAATTACTGGCGTAAAGGGCGTAGGCCCGCCTGTAAGTCGCGTGTGAAAGGCCGGGCTCAACCCGTGCACTGCGATACTGCCTGGCTGGAGAAAAGTAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTAGATATCGGGAGGAACACCCGGTGGCGAAGGCAGCTCGCTGGGCCCTTCTGACGCTGAAGCGCAGCGCAAAGCGTGGGAGCAAAACAGG
f5f1de14ec35241e6cf60099d61216c7	PAUC43f_marine_benthic_group	0.99903168	TACGGAGGGAGCGAGCGTTGCCGAATTACTGGCGTAAAGGGCGTAGGCCCGCCTGTAAGTCGCGTGTGAAAGGCCGGGCTCAACCCGTGATGACACCGCAGTACTGCCTGGCTAGAGATAGTAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTAGATATCGGGAGGAACACTCGTGGCGAAGGCAGCTCGCTGGGCCCTTCTGACGCTGAAGCGCAGCGCAAAGCGTGGGAGCAAAACAGG
f63d5f3d5410e83151619780651e1178	PAUC43f_marine_benthic_group	0.99839251	TACGGAGGGAGCAAGCGTTGCCGAATTACTGGCGTAAAGGGCGTAGGCCCGCCTGTAAGTCGCGTGTGAAAGGCCGGGCTCAACCCGAGCACTGCATGCGATACTGCATGGCTAGAGAGAGGTTAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTAGATATCGGGAGGAACACCCGGTGGCGAAGGCAGCTCGCTGGACCTTTCTGACGCTGAAGCGCAGCGCAAAGCGTGGGAGCAAAACAGG
fe507232ac9b3ad84c3950b7051d7251	PAUC43f_marine_benthic_group	0.99995128	TACGGAGGGAGCAAGCGTTGCCGAATTACTGGCGTAAAGGGCGTAGGCCCGCCTGTAAGTCGCGTGTGAAAGGCCGGGCTCAACCCGAGTATTGCATGCGATACTGCAGGCTAGAGACAGGTAGGGCGAGCGGAATCCCGGTAGCGGTGGAATGCGTAGATATCGGGAGGAACACCCGGTGGCGAAGGCAGCTCGCTGGCCTGTTCTGACGCTGAAGCGCAGCGCAAAGCGTGGGAGCGAACAGG
02f4dfba89fe831569ead167995452d2	PAUC43f_marine_benthic_group	1	AACGGAGGGAGCAAGCGTTGCCGAATTACTGGCGTACAGAGCGCGTAGGCCCGCAGGTAGTCGTATGTGAAAGGCCCGGCTCAACCCGGCATGCCATGCGATACTGCCTGGCTCGAGGCCGCGAGGGGCCAGTGGAAATCCCGGTAGCGGTGGAATGCGTAGATATCGGGAGGAACACCCAGCGCGAAGGCAGCTGGCTGGGCCGGACCTGACGCTGCAGCGCAAAGCGTGGGATCAAACAGG

Table S3. List of ASVs identified as members of class PAUC43f. Taxonomic information and confidence of assignment were obtained using QIIME2 annotated with SILVA for 16S rRNA (v4 region) sequences.

	PC1	PC2	PC3
Eigenvalues	15.46671700	6.48802300	2.57893400
Ann. mean temp.		-	-
	0.07412014	0.31011471	0.29024054
Ann. mean precip.	0.52358969	0.01365311	0.03951500
Precip. rainy season	0.06911353	0.10692148	0.09242221
Precip. dry season	-0.42505070	0.02173096	0.11768470
pH	0.38033900	0.10741840	0.32687160
Electric conductivity	-0.40232931	0.05813941	0.12861521
Sand content	-0.10969910	0.02094065	0.45963115
Silt content	0.09536237	0.36473611	0.46710354
Clay content	-0.24949631	0.20618923	0.02466118
Soil density	0.29312182	0.24167142	0.02169672
Gravel content	-0.01322169	0.52978613	0.30414347
Clay CEC	0.06886618	0.49231458	0.31514987
Soil CEC	-0.14842120	0.28796760	0.19193120
Saturation	0.17916060	0.14535630	0.32951310
Total exch. bases	-	-	-
	0.00461990	0.12033774	0.00876504
CaCO content	-0.00508872	0.02910592	0.02406517

Table S4. Table S3. List of ASVs identified as members of class PAUC43f. Taxonomic information and confidence of assignment were obtained using QIIME2 annotated with SILVA for 16S rRNA (v4 region) sequences.

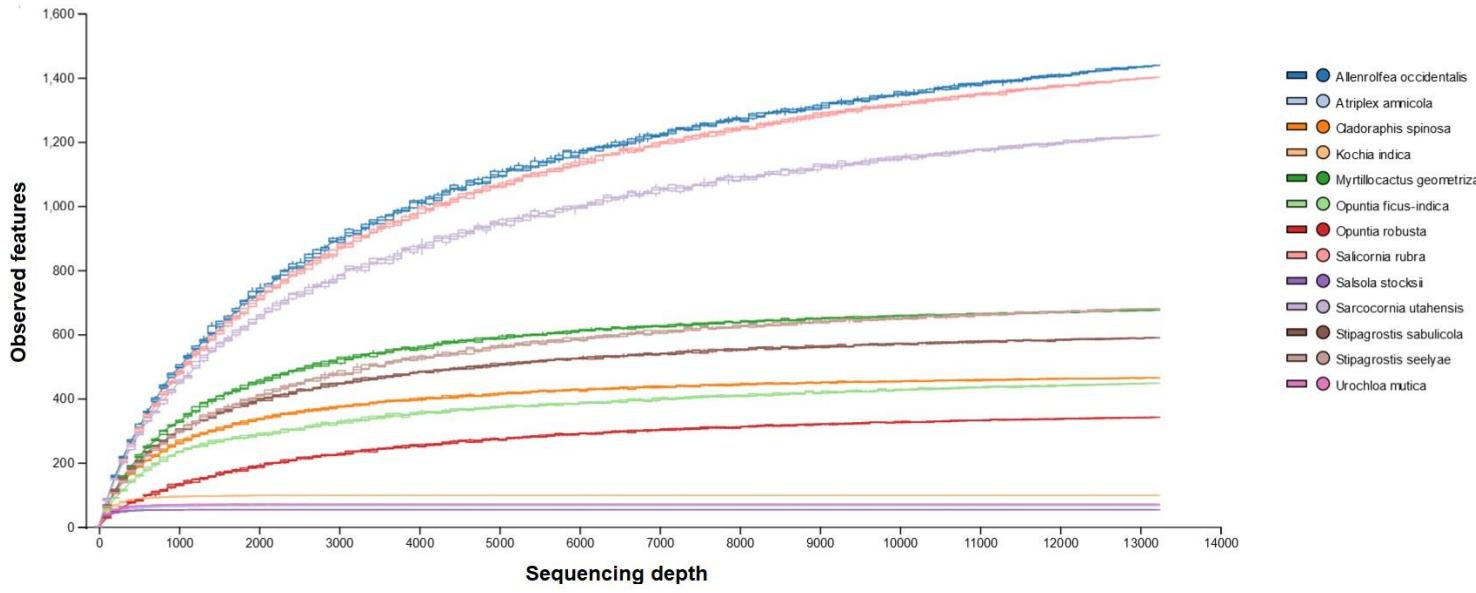


Figure S1. Table S4. Table S3. List of ASVs identified as members of class PAUC43f. Taxonomic information and confidence of assignment were obtained using QIIME2 annotated with SILVA for 16S rRNA (v4 region) sequences.

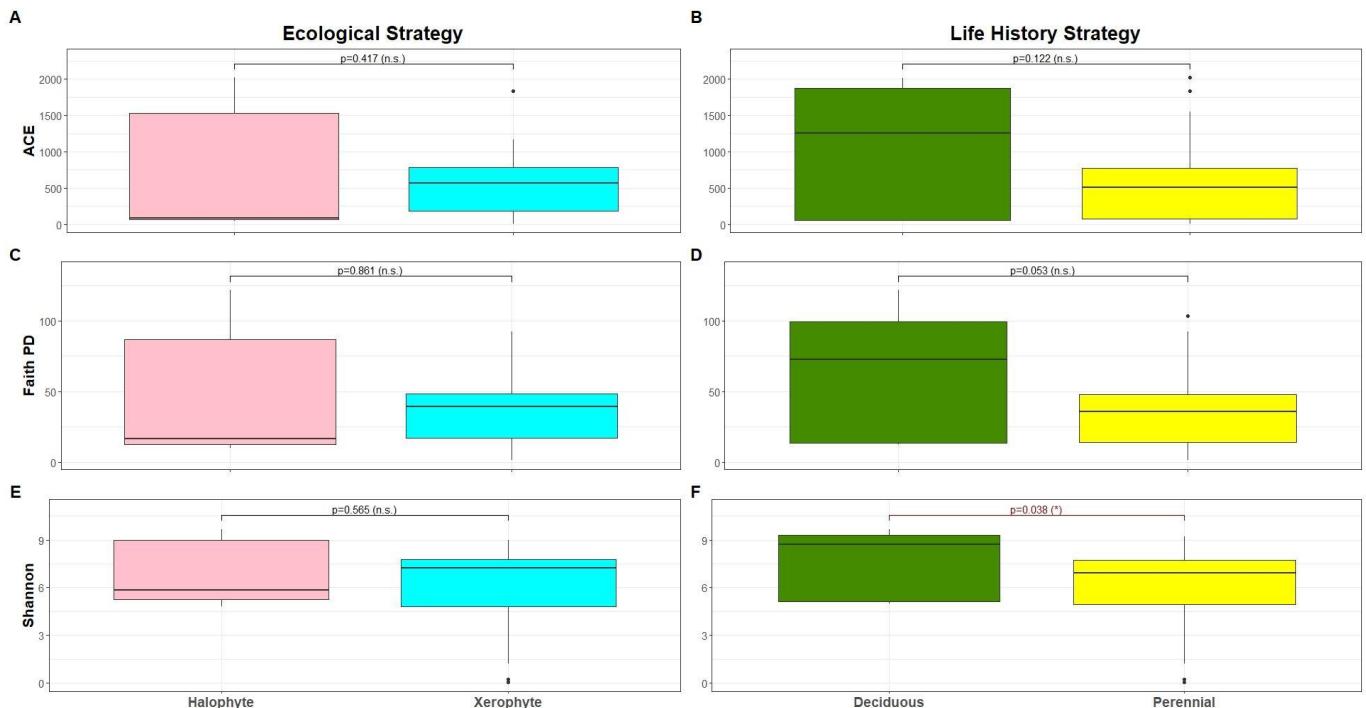


Figure S2. Boxplots for three alpha diversity estimators: ACE richness (A-B), Faith phylogenetic distance (C-D) and Shannon evenness (E-F). Left panels display the indices' values according to the host ecological strategy (A, C, E). Right panels show the indices' values with respect to the host life history strategy (B, D, F). In all cases, there were no statistically significant differences according to a Kruskal-Wallis test ($p>0.05$), with Shannon evenness for life history strategy being the only exception (F, $p=0.038$).

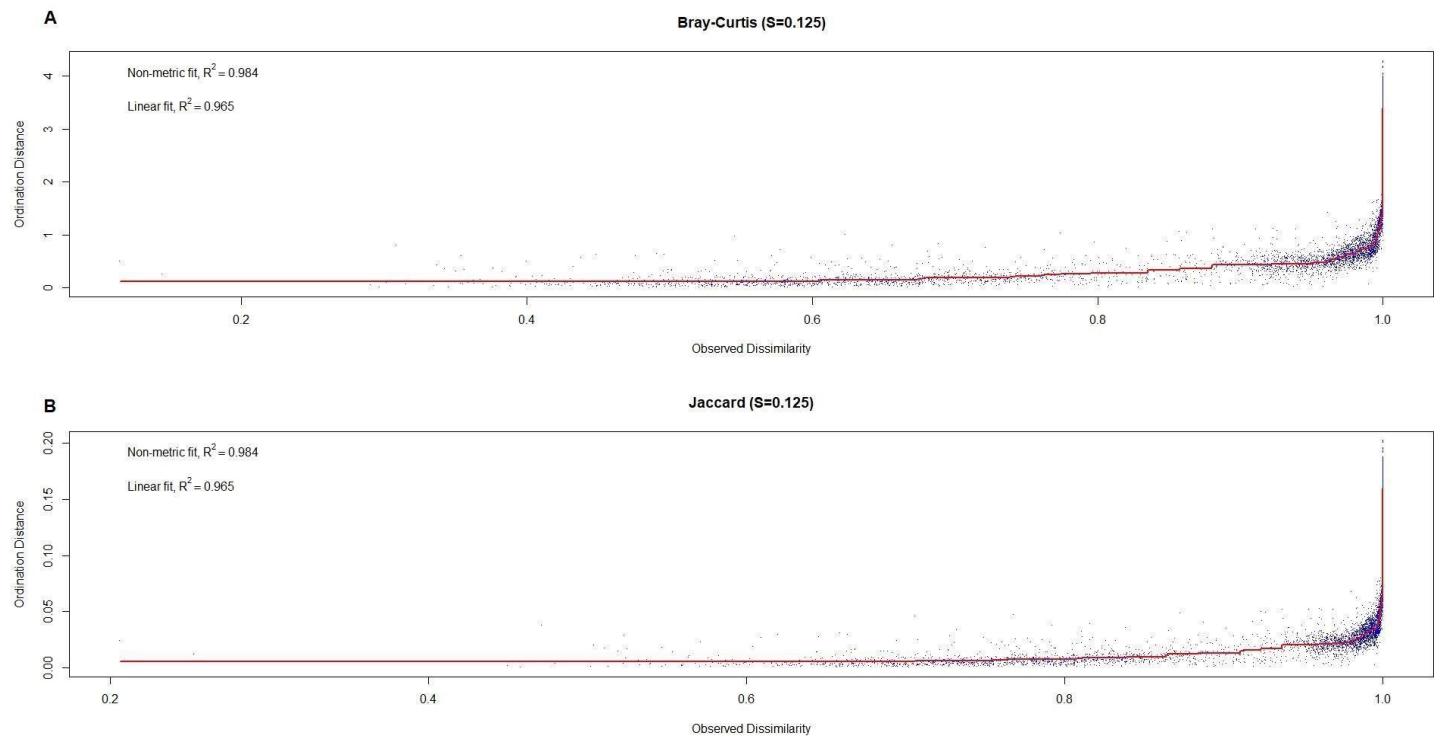


Figure S3. Stressplot for Bray-Curtis (A) and Jaccard (B) dissimilarity indices. Stress value ($S=0.125$), non-metric fit ($R^2=0.964$) and linear fit ($R^2=0.905$) for both indices were identical.

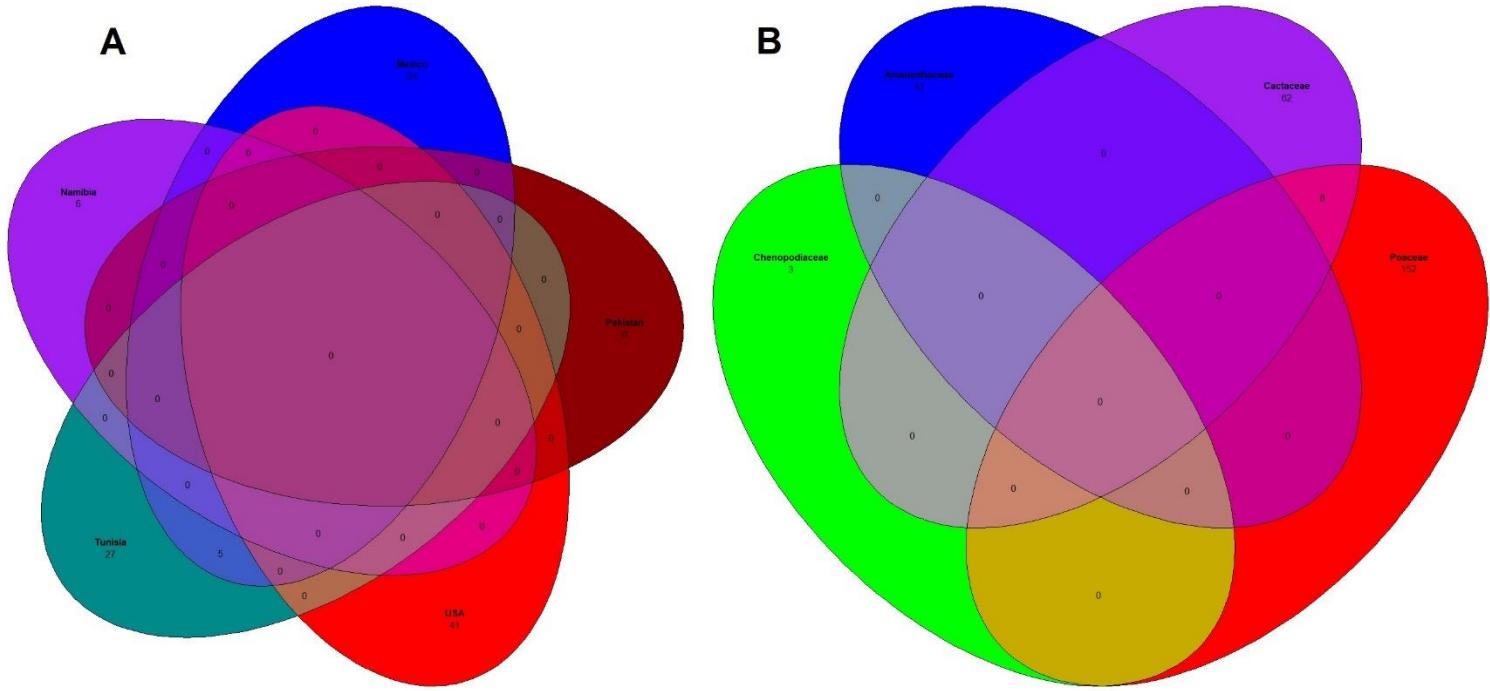


Figure S4. Venn diagrams for the core elements according to (A) Country and (B) Host plant family.

Discusión general y conclusiones

Los resultados que se presentan indican que tanto las variables edáficas, bioclimáticas y la identidad filogenética del hospedero –en especial a nivel familia– son los arquitectos de la estructura de los microbiomas entre especies vegetales que habitan en ambientes áridos. Estos hallazgos son consistentes con resultados previamente publicados de sitios específicos que resaltan la importancia de los factores abióticos en el estructuramiento de las comunidades rizosféricas, lo que incluye a los ambientes áridos (Hernández-Terán et al., 2020; Hu et al., 2020; Ma et al., 2016; Qiao et al., 2017).

Con base en los resultados obtenidos, se puede sugerir que el papel de los factores bioclimáticos relacionados con la aridez (es decir, la temperatura y la precipitación) son los que están más vinculados con la variación en la estructura de las comunidades microbianas, algo previamente ya reportado a través de un gradiente de aridez (Karray et al., 2020). Además, las propiedades edáficas también están fuertemente relacionadas con la composición microbiana; principalmente el pH, que tiene efectos directos en la funcionalidad microbiana pues afecta a los procesos fisiológicos y la actividad exo-enzimática de los organismos (Fan et al., 2018; Puissant et al., 2019). Otras propiedades fisicoquímicas de los suelos que fueron relevantes incluyen la capacidad de intercambio catiónico, que influye en la capacidad del suelo para retener nutrientes, y la textura del suelo, la cual afecta las dinámicas cinéticas de los microorganismos y los nutrientes disponibles en el suelo. Ambos factores ya han sido previamente descritos como importantes en la estructuración de los microbiomas del suelo (Nuccio et al., 2016).

Ahora bien, los rasgos del hospedero tienen un efecto importante en la estructuración del microbioma, aunque su efecto pudiera estar a su vez influenciado por los factores abióticos del ambiente. Por una parte, parece que la estrategia ecológica (es decir, ser halófita o xerófita) sí juega un papel en la variación observada; si bien los análisis de diversidad alfa no sugieren un efecto significativo de estas estrategias en los valores observados para la diversidad local de las comunidades asociadas según los estimadores empleados, la

diversidad beta – la cual es útil para comparar entre la estructura de comunidades de diferentes sitios – a través de una prueba de ANOSIM sí muestra una alta correlación con este factor. Una posibilidad al respecto es que las estrategias ecológicas de los hospederos también son gobernadas por los factores abióticos que afectan a las comunidades microbianas. Por lo tanto, las diferencias observadas pueden ser el resultado de ambos tipos de comunidades creciendo en sitios abióticamente diferentes. Aunque nuestros resultados sugieren que este rasgo está pobremente relacionado a la variación del microbioma en ambientes áridos, y gran parte del efecto observado puede deberse a los otros atributos del hospedero (ecología, afinidad filogenética); por lo cual, para probar esta idea sería interesante disponer de plantas halófitas y xerófitas creciendo en una misma localidad o bajo condiciones climáticas similares (ej. experimento de jardín común), con el objeto de conocer cuál es el verdadero efecto de la estrategia ecológica en el microbioma de la rizósfera. Por otra parte, aunque algunos trabajos sugieren que la estrategia de historia de vida del hospedero puede influir en el microbioma de la raíz (Emmett et al., 2017), nuestros resultados sugieren que este rasgo está menormente relacionado a la variación del microbioma en comparación a otros atributos del hospedero (ecología, afinidad filogenética). Dado que el establecimiento en las regiones áridas es complicado debido a los estreses relacionados con la escasez de agua y la concentración de sales en los suelos, sería interesante también probar otras variables biológicas (como la etapa ontogénica del hospedero – ver İnceoğlu et al., 2013 –, y los perfiles de exudación), y sus efectos en el microbioma rizosférico para plantas de estos ambientes, así como las dinámicas que ocurren a través de los gradientes de desarrollo de los hospederos y sus relaciones con las comunidades microbianas (Lu et al., 2018).

Dado que las comunidades procariotas que son reclutadas por la rizosfera se adquieren mayoritariamente de aquellas nativas del suelo, las plantas se encuentran condicionadas a escoger de asociaciones con microorganismos de comunidades que son moldeadas por los factores abióticos que gobiernan los suelos. El microbioma que es seleccionado por la rizosfera está principalmente

influenciado por los perfiles de exudación y la arquitectura de la raíz, específicos a cada hospedero, lo cual se considera una estrategia cuya finalidad es controlar el establecimiento microbiano para promover a las especies benéficas y restringir la proliferación de antagonistas, para que así puedan suplirse sus necesidades nutrimentales y proteger los compartimentos internos de la raíz (un proceso sugerido previamente por Forter *et al.* (2017) como el modelo del ‘ecosistema en correa’). Aunque los hospederos ejercen cierto control sobre la adquisición del microbioma, este no es un proceso unilateral –, los microorganismos pioneros de la rizosfera también pueden influir en los perfiles de exudación que la planta usa para reclutar al microbioma, lo que genera un filtro en la comunidad microbiana que se establece en la rizosfera (Korenblum *et al.*, 2020); por lo tanto, para entender por completo la complejidad que existe en las interacciones planta-microbio, también es necesario desarrollar estudios enfocados en las dinámicas de retroalimentación entre el metabolismo vegetal y la funcionalidad microbiana.

Aunque este metaanálisis pudiera ser relevante para visualizar la variación que ocurre en los microbiomas procariontes de las rizosferas en zonas áridas, también deben reconocerse sus limitantes. Primero, los trabajos incluidos no son los únicos desarrollados para plantas de ambientes áridos pero varios tuvieron que ser excluidos debido a cuatro limitantes principales: i) los datos de *metabarcoding* no estaban disponibles en acervos públicos, ii) los metadatos asociados no están adecuadamente anotados, haciendo imposible separar las secuencias de la rizósfera de aquellas del suelo u otros compartimentos vegetales (ej. interior de la raíz), iii) las secuencias obtenidas no se sobrelapan con la región del 16S rRNA analizada en este metaanálisis, o iv) los datos eran de pobre calidad, presentando una gran cantidad de secuencias químéricas. Esto destaca la necesidad de aumentar la disponibilidad de los datos, curar adecuadamente los metadatos asociados y estandarizar las técnicas de análisis dentro del campo para poder realizar análisis más finos sobre la variación que ocurre en las comunidades microbianas.

Es necesario destacar que este trabajo se centró únicamente en las comunidades procariontes, por lo que tiene serias limitaciones para describir la estructura del

microbioma entero al carecer de los miembros eucariontes. La razón para esta omisión es la falta de trabajos incluyendo datos de las comunidades eucarióticas de la rizósfera pues los trabajos con *metabarcoding* para las comunidades fungales de ambientes áridos son muy escasos, en especial al compararlos con los datos disponibles para procariontes. Además, existe un gran sesgo dentro del estudio de las comunidades eucariontes; debido a las complicaciones al desarrollar *primers* que describan adecuadamente su diversidad y al interés focalizado en algunos grupos por sobre otros como Fungi y, en menor medida, Metazoa, poco se conoce del papel de los otros grupos de eucariontes tradicionalmente agrupados como Protista. Por lo tanto, en el mejor de los casos sólo se tiene una imagen incompleta de las comunidades microbianas que hay en la rizósfera de especies vegetales que habitan en ambientes áridos. Aún más complicado, técnica y financieramente, sería incluir la información de secuencias virales o similares dentro de la descripción de los microbiomas, en gran parte debido a la inmensa variabilidad genética que ocurre en estos grupos. Además, obtener sólo una visión descriptiva en términos taxonómicos puede ser insuficiente para explicar los patrones observados entre comunidades microbianas, pues es posible que las interacciones microbio-microbio (y entre reinos) jueguen un rol importante en la estructuración del microbioma, como ha sido previamente observado por Horn et al. (2017), y podrían tener un efecto significativo en la supervivencia del sistema planta-microbios (Bi et al., 2021; Gao et al., 2019; Thiergart et al., 2020).

En conclusión y con base en lo anterior, se puede resaltar que este trabajo es la primera descripción macrogeográfica de los patrones de variación de las comunidades rizosféricas de ambientes áridos. Esto es importante pues el interés en estas regiones ha aumentado como resultado de una mayor aridez global por el cambio climático, por lo que espero que este trabajo sirva como un punto de inicio para visualizar a escala global los procesos ecológicos que ocurren en estos ambientes. Para ello es también indispensable aumentar nuestro conocimiento taxonómico y funcional de estas comunidades microbianas.

Referencias bibliográficas

Abdullah, N.S.A.B. Bacterial diversity associated with red seaweeds, *Gracilaria manilaensis* & *Laurencia* sp., found in peninsular Malaysia. PhD Thesis, International Islamic University Malaysia, Malaysia, November 2020.

Aerts, J.W.; van Spanning, R.J.M.; Flahaut, J.; Molenaar, D.; Bland, P.A.; Genge, M.J.; Ehrenfreund, P.; Martins, Z. Microbial communities in sediments from four mildly acidic ephemeral salt lakes in the Yilgarn Craton (Australia) – Terrestrial analogs to ancient Mars. *Front. Microbiol.* 2019, 10, 779. doi:10.3389/fmicb.2019.00779

Ahemad, M; Kibret, M. Mechanisms and applications of plant growth promoting rhizobacteria: Current perspective. *J. King Saud Univ. Sci.* 2014, 26, 1–20. doi:10.1016/j.jksus.2013.05.001

Armas, C.; Rodríguez-Echeverría, S.; Pugnaire, F.I. A field test of the stress-gradient hypothesis along an aridity gradient. *J. Veg. Sci.* 2011, 22, 818–27. doi:10.1111/j.1654-1103.2011.01301.x

Bejarano-Bolívar, A.A.; Lamelas, A.; Aguirre von Wobeser, E.; Sánchez-Rangel, D.; Méndez-Bravo, A.; Eskalen, A.; Reverchon, F. Shifts in the structure of rhizosphere bacterial communities of avocado after *Fusarium* dieback. *Rhizosphere*. 2021, 18, 10033. doi:10.1016/j.rhisph.2021.100333

Bergo, N.M.; Bendia, A.G.; Ferreira, J.C.N.; Murton, B.J.; Brandini, F.P.; Pellizari, V.H. Microbial diversity of deep-sea ferromanganese crust field in the Rio Grande Rise, Southwestern Atlantic Ocean. *Microb. Ecol.* 2020, 82, 344–55. doi:10.1007/s00248-020-01670-y

Bi, L.; Yu, D.T.; Du, S.; Zhang, L.M.; Zhang, L.Y.; Wu, C.F.; Xiong, C.; Han, L.L.; He, J.Z. Diversity and potential biogeochemical impacts of viruses in bulk and rhizosphere soils. *Environ. Microbiol.* 2021, 23, 588–99. doi:10.1111/1462-2920.15010

Bolyen, E.; Rideout, J.R.; Dillon, M.R.; Bokulich, N.A.; Abnet, C.C.; Al-Ghalith, G.A.; Alexander, H.; Alm, E.J.; Arumugam, M.; Asnicar, F.; Bai, Y.; Bisanz, J.E.; Bittinger, K.; Brejnrod, A.; Brislawn, C.J.; Brown, C.T.; Callahan, B.J.; Caraballo-

Rodríguez, A.M.; Chase, J.; Cope, E.K.; Da Silva, R.; Diener, C.; Dorresteijn, P.C.; Douglas, G.M.; Durall, D.M.; Duvallet, C.; Edwardson, C.F.; Ernst, M.; Estaki, M.; Fouquier, J.; Gauglitz, J.M.; Gibbons, S.M.; Gibson, D.L.; Gonzalez, A.; Gorlick, K.; Guo, J.; Hillmann, B.; Holmes, S.; Holste, H.; Huttenhower, C.; Huttley, G.A.; Janssen, S.; Jarmusch, A.K.; Jiang, L.; Kaehler, B.D.; Kang, K.B.; Keefe, C.R.; Keim, P.; Kelley, S.T.; Knights, D.; Koester, I.; Koscioletk, T.; Kreps, J.; Langille, M.G.I.; Lee, J.; Ley, R.; Liu, Y.X.; Loftfield, E.; Lozupone, C.; Maher, M.; Marotz, C.; Martin, B.D.; McDonald, D.; McIver, L.J.; Melnik, A.V.; Metcalf, J.L.; Morgan, S.C.; Morton, J.T.; Naimey, A.T.; Navas-Molina, J.A.; Nothias, L.F.; Orchanian, S.B.; Pearson, T.; Peoples, S.L.; Petras, D.; Preuss, M.L.; Pruesse, E.; Rasmussen, L.B.; Rivers, A.; Robeson, M.S.; Rosenthal, P.; Segata, N.; Shaffer, M.; Shiffer, A.; Sinha, R.; Song, S.J.; Spear, J.R.; Swafford, A.D.; Thompson, L.R.; Torres, P.J.; Trinh, P.; Tripathi, A.; Turnbaugh, P.J.; Ul-Hasan, S.; van der Hooft, J.J.J.; Vargas, F.; Vázquez-Baeza, Y.; Vogtmann, E.; von Hippel, M.; Walters, W.; Wan, Y.; Wang, M.; Warren, J.; Weber, K.C.; Williamson, C.H.D.; Willis, A.D.; Xu, Z.Z.; Zaneveld, J.R.; Zhang, Y.; Zhu, Q.; Knight, R.; Caporaso, J.G. Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. *Nat. Biotechnol.* 2019, 37, 852–7. doi:10.1038/s41587-019-0209-9

Callahan, B.J.; McMurdie, P.J.; Rosen, M.J.; Han, A.W.; Johnson, A.J.A.; Holmes, S.P. DADA2: High resolution sample inference from Illumina amplicon data. *Nat. Methods.* 2016, 13, 581–3. doi:10.1038/nmeth.3869

Coleman-Derr, D.; Desgarennes, D.; Fonseca-García, C.; Gross, S.; Clingenpeel, S.; Woyke, T.; North, G.; Visel, A.; Partida-Martínez, L.P.; Tringe, S.G. Plant compartment and biogeography affect microbiome composition in cultivated and native Agave species. *New Phytol.* 2016, 209, 798–811. doi:10.1111/nph.13869

Dai, L.; Zhang, G.; Yu, Z.; Ding, H.; Xu, Y.; Zhang, Z. Effect of drought stress and developmental stages on microbial community structure and diversity in peanut rhizosphere soil. *Int. J. Mol. Sci.* 2019, 20, 2265. doi:10.3390/ijms20092265

DasSarma, P.; DasSarma, S. On the origin of prokaryotic "species": the taxonomy of halophilic Archaea. *Saline Syst.* 2008, 4, 5. doi:10.1186/1746-1448-4-5

De Mendiburu, F.; Yaseen, M. *agricolae: Statistical Procedures for Agricultural Research.* R package version 1.4.0. 2020, , <https://myaseen208.github.io/agricolae/><https://cran.r-project.org/package=agricolae>

Dastogeer, K.M.G.; Tumpa, F.H.; Sultana, A.; Akter, M.A.; Chakraborty, A. Plant microbiome—an account of the factors that shape community composition and diversity. *Curr. Plant Biol.* 2020, 3, 100161. doi:10.1016/j.cpb.2020.100161

Dos Santos Silva, C.; Da Silva, J.M.; Lima de Oliveira, J.U.; Guimarães Verçosa de Araújo; R.; Bento de Lima, J.R.; Ferreira Guedes, E.L.; dos Santos, M.T.; Coentro Montao, Y.; Carvalho dos Santos, T.M. Bioprospecting rhizobacteria associated to cacti to water stress resistance and biofilm formation. *Rev. Bras. Gest. Amb. Sustent.* 2019, 6, 873–81. doi:10.21438/rbgas.061417

Duarte, B.; Sleimi, N.; Caçador, I. Biophysical and biochemical constraints imposed by salt stress: learning from halophytes. *Front. Plant Sci.* 2014, 12, 746. doi:10.3389/fpls.2014.00746

Durán, P.; Thiergart, T.; Garrido-Oter, R.; Agler, M.; Kemen, E.; Schulze-Lefert, P.; Hacquard, S. Microbial interkingdom interactions in roots promote *Arabidopsis* survival. *Cell.* 2018, 175, 973–83. doi:10.1016/j.cell.2018.10.020

Emmett, B.D.; Youngblut, N.D.; Buckley, D.H.; Drinkwater, L.E. Plant phylogeny and life history shape rhizosphere bacterial microbiome of summer annuals in an agricultural field. *Front. Microbiol.* 2017, 12, 2414. doi:10.3389/fmicb.2017.02414

Fan, K.; Weisenhorn, P.; Gilbert, J.A.; Shi, Y.; Bai, Y.; Chu, H. Soil pH correlates with the co-occurrence and assemblage process of diazotrophic communities in rhizosphere and bulk soils of wheat fields. *Soil Biol. Biochem.* 2018, 121, 185–192. doi:10.1016/j.soilbio.2018.03.017

Fick, S.E.; Hijmans, R.J. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Clim.* 2017, 37, 4302–15.

Fierer, N. Embracing the unknown: disentangling the complexities of the soil microbiome. *Nat. Rev. Microbiol.* 2017, 15, 579–90. doi:10.1038/nrmicro.2017.87

Fischer, G.; Nachtergael, F.; Prieler, S.; van Velthuizen, H.T.; Verelst, L.; Wiberg, D. 2008. Global Agro-ecological Zones Assessment for Agriculture (GAEZ 2008). IIASA, Laxenburg, Austria and FAO, Rome, Italy.

Fitzpatrick, C.R.; Copeland, J.; Wang, P.W.; Guttman, D.S.; Kotanen, P.M.; Johnson, M.T.J. Assembly and ecological function of the root microbiome across angiosperm plant species. *PNAS.* 2018, 115, e1157–65. doi:10.1073/pnas.1717617115

Flores-Núñez, V.M.; Fonseca-García, C.; Desgarennes, D.; Eloe-Fadrosh, E.; Woyke, T.; Partida-Martínez, L.P. Functional signatures of the epiphytic prokaryotic microbiome of Agaves and Cacti. *Front. Microbiol.* 2020, 10, 3044. doi:10.3389/fmicb.2019.03044

Fonseca-García, C.; Coleman-Derr, D.; Garrido, E.; Visel, A.; Tringe, S.G.; Partida-Martínez, L.P. The Cacti Microbiome: Interplay between habitat-filtering and host-specificity. *Front. Microbiol.* 2016, 7, 150. doi:10.3389/fmicb.2016.00150

Foster, K.R.; Schluter, J.; Coyte, K.Z.; Rakoff-Nahoum, S. The evolution of the host microbiome as an ecosystem on a leash. *Nature.* 2017, 548, 43–51. doi:10.1038/nature23292

Galili, T. dendextend: an R package for visualizing, adjusting, and comparing trees of hierarchical clustering. *Bioinformatics.* 2015, 31, 3718–20. doi:10.1093/bioinformatics/btv428

Gao, Z.; Karlsson, I.; Geisen, S.; Kowalchuk, G.; Jousset, A. Protists: Puppet masters of the rhizosphere microbiome. *Trends in Plant Sci.* 2019, 24, 165–76. doi:10.1016/j.tplants.2018.10.011

Genderjahn, S.; Alawi, M.; Mangelsdorf, K.; Horn, F.; Wagner, D. Desiccation- and saline-tolerant Bacteria and Archaea in Kalahari pan sediments. *Front. Microbiol.* 2018, 9, 2082. doi:10.3389/fmicb.2018.02082

Gómez Garrido, M.; Mora Navarro, J.; Murcia Navarro, F.J.; Faz Cano, Á. The chelating effect of citric acid, oxalic acid, amino acids and *Pseudomonas*

fluorescens bacteria on phytoremediation of Cu, Zn, and Cr from soil using *Suaeda vera*. Int. J. Phytoremediation. 2018, 20, 1033–42. doi:10.1080/15226514.2018.1452189

Hardoim, C.C.P.; Ramaglia, A.C.M.; Lôbo-Hajdu, G.; Custódio, M.R. Community composition and functional prediction of prokaryotes associated with sympatric sponge species of southwestern Atlantic coast. Sci. Rep. 2021, 11, 9576. doi:10.1038/s41598-021-88288-3

Hashem, H.A.; Mohamed, A.H. 2020. Strategies for drought tolerance in xerophytes. In: Hasanuzzaman, M. (eds). Plant Ecophysiology and Adaptation under Climate Change: Mechanisms and Perspectives. Springer, Singapore. pp. 269–93. doi:10.1007/978-981-15-2156-0_9

He, J.; Lyu, R.; Luo, Y.; Lin, L.; Yao, M.; Xiao, J.; Xie, L.; Wen, J.; Pei, L.; Yan, S.; Cheng, J.; Li, J.; Li, L. An updated phylogenetic and biogeographic analysis based on genome skimming data reveals convergent evolution of shrubby habit in Clematis in the Pliocene and Pleistocene. Mol. Phylogenet. Evol. 2021, 164, 107259. doi:10.1016/j.ympev.2021.107259

Hernández-Terán, A.; Navarro-Díaz, M.; Benítez, M.; Lira, R.; Wegier, A.; Escalante, A.E. Host genotype explains rhizospheric microbial community composition: the case of wild cotton metapopulations (*Gossypium hirsutum* L.) in Mexico. 2020, 96, fiaa109. doi:10.1093/femsec/fiaa109

Horn, S.; Hempel, S.; Verbruggen, E.; Rillig, M.C.; Caruso, T. Linking the community structure of arbuscular mycorrhizal fungi and plants: a story of interdependence?. ISME J. 2017, 11, 1400–11. doi:10.1038/ismej.2017.5

Hu, J.; Wei, Z.; Kowalchuk, G.A.; Xu, Y.; Shen, Q.; Jousset, A. Rhizosphere microbiome functional diversity and pathogen invasion resistance build up during plant development. Environ. Microbiol. 2020, 22, 5005–18. doi:10.1111/1462-2920.15097

İnceoğlu, Ö.; Van Overbeek, L.S.; Falcão Salles, J., Van Elsas, J.D.. Normal operating range of bacterial communities in soil used for potato cropping. Appl. Environ. Microbiol. 2013, 79, 1160–70. doi:10.1128/AEM.02811-12 The normal

operating range of bacterial communities in soil used for potato cropping.

Jarvis, D.E.; Ryu, CH.; Beilstein, M.A.; Schumaker, K.S. Distinct roles for SOS1 in the convergent evolution of salt tolerance in *Eutrema salsugineum* and *Schrenkia parvula*. *Mol. Biol. Evol.* 2014, 31, 2094–107. doi:10.1093/molbev/msu152

Karray, F.; Gargouri, M.; Chebaane, A.; Mhiri, N.; Mliki, A.; Sayadi, S. Climatic aridity gradient modulates the diversity of the rhizosphere and endosphere bacterial microbiomes of *Opuntia ficus-indica*. *Front. Microbiol.* 2020, 11, 1622. doi:10.3389/fmicb.2020.1622

Kearl, J.; McNary, C.; Lowman, J.S.; Mei, C.; Aanderud, Z.T.; Smith, S.T.; West, J.; Colton, E.; Hamson, M.; Nielsen, B.L. Salt-tolerant halophyte rhizosphere bacteria stimulate growth of alfalfa in salty soil. *Front. Microbiol.* 2019, 10, 1849. doi:10.3389/fmicb.2019.01849

Korenblum, E.; Dong, Y.; Szymanski, J.; Panda, S.; Jozwiak, A.; Massalha, H.; Meir, S.; Rogachev, I.; Aharoni, A. Rhizosphere microbiome mediates systemic root metabolite exudation by root-to-root signaling. *Proc. Natl. Acad. Sci. USA.* 2020, 117, 3874–83. doi:10.1073/pnas.1912130117

Larsson, J. *eulerr*: Area-Proportional Euler and Venn Diagrams with Ellipses. R package version 6.1.1. 2021. <https://CRAN.R-project.org/package=eulerr>

Li, H.B.; Singh, R.K.; Singh, P.; Song, Q.Q.; Zing, Y.X.; Yang, L.T.; Li, Y.R. Genetic diversity of nitrogen-fixing and plant growth promoting *Pseudomonas* species isolated from sugarcane rhizosphere. *Front. Microbiol.* 2017, 7, 1268. doi:10.3389/fmicb.2017.01268

Ling, N.; Wang, T.; Kuzyakov, Y. Rhizosphere bacteriome structure and functions. *Nat. Commun.* 2022, 13, 836. doi:10.1038/s41467-022-28448-9

Liu, T.Y.; Ye, N.; Song, T.; Cao, Y.; Gao, B.; Zhang, D.; Zhu, F.; Chen, M.; Zhang, Y.; Xu, W.; Zhang, J. Rhizosheath formation and involvement in foxtail millet (*Setaria italica*) root growth under drought stress. *J. Int. Plant Biol.* 2018, 61, 449–62. doi:10.1111/jipb.12716

López, B.R.; Bacilio, M. Weathering and soil formation in hot, dry environments

mediated by plant-microbiome interactions. *Biol. Fertil. Soils.* 2020, 56, 447–59. doi:10.1007/s00374-020-01456-x

Lu, T.; Ke, M.; Jin, Y.; Fan, X.; Zhang, Z.; Fu, Z.; Sun, L.; Gillings, M.; Peñuelas, J.; Qian, H.; Zhu, Y.G. Rhizosphere microorganisms can influence the timing of plant flowering. *Microbiome.* 2018, 6, 231. doi:10.1111/nph.13697

Ma, B.; Wang, H.; Dsouza, M.; Lou, J.; He, Y.; Dai, Z.; Brookes, P.C.; Xu, J.; Gilbert, J.A. Geographic patterns of co-occurrence network topological features for soil microbiota at continental scale in eastern China. *ISME J.* 2016, 10, 1891–901. doi:10.1038/ismej.2015.261

Marasco, R.; Mosqueira, M.J.; Fusi, M.; Ramond, J.B.; Merlino, G.; Booth, J.M.; Maggs-Kölling, G.; Cowan, D.A.; Daffonchio, D. Rhizosheath microbial community assembly of sympatric desert speargrasses is independent of the plant host. *Microbiome.* 2018, 6, 215. doi:10.1186/s40168-018-0597-y

Marcel, M. Cutadapt removes adapter sequences from high-throughput sequencing reads. *EMBnet J.* 2011, 17, 10–2. doi:10.14806/ej.17.1.200

McMurdie, P.J.; Holmes, S. phyloseq: An R package for reproducible interactive analysis and graphics of microbiome census data. *PLoS ONE.* 2013, 8, e61217. doi:10.1371/journal.pone.0061217

Mukhtar, S.; Mirza, B.S.; Mehnaz, S.; Mirza, M.S.; McLean, J.; Malik, K.A. Impact of soil salinity on the microbial structure of halophyte rhizosphere microbiome. *World J. Microbiol. Biotechnol.* 2018, 9, 136. doi:10.1007/s11274-018-2509-5

Mukhtar, S.; Mehnaz, S.; Malik, K.A. Comparative study of the rhizosphere and root endosphere microbiomes of Cholistan desert plants. *Front. Microbiol.* 2021, 12, 618742. doi:10.3389/fmicb.2021.618742

Nuccio, E.E.; Anderson-Furgeson, J.; Esteria, K.Y.; Pett-Ridge, J.; de Valpine, P.; Brodie, E.L.; Firestone, M.K. Climate and edaphic controllers influence rhizosphere community assembly for a wild annual grass. *Ecology.* 2016, 97, 1307–18. doi:10.1890/15-0882.1

Oburger, E.; Kirk, G.J.D.; Wenzel, W.W.; Puschenreiter, M.; Jones, D.L.

Interactive effects of organic acids in the rhizosphere. *Soil Biol. Biochem.* 2009, 41, 449–57. doi:10.1016/j.soilbio.2008.10.034

Oksanen, J.; Simpson, G.; Blanchet, F.; Kindt, R.; Legendre, P.; Minchin, P.; O'Hara, R.; Solymos, P.; Stevens, M.; Szoecs, E.; Wagner, H.; Barbour, M.; Bedward, M.; Bolker, B.; Borcard, D.; Carvalho, G.; Chirico, M.; De Caceres, M.; Durand, S.; Evangelista, H.; FitzJohn, R.; Friendly, M.; Furneaux, B.; Hannigan, G.; Hill, M.; Lahti, L.; McGlinn, D.; Ouellette, M.; Ribeiro Cunha, E.; Smith, T.; Stier, A.; Ter Braak, C.; Weedon, J. *vegan: Community Ecology Package.* R package version 2.6-2. 2022, <https://CRAN.R-project.org/package=vegan>

Price, M.N.; Dehal, P.S.; Arkin, A.P. *FastTree: Computing large minimum evolution trees with profiles instead of a distance matrix.* *Mol. Biol. Evol.* 2009, 26, 1641–50. doi:10.1093/molbev/msp077

Puissant, J.; Jones, B.; Goodall, T.; Mang, D.; Blaud, A.; Gweon, H.S.; Malik, A.; Jones, D.L.; Clark, I.M.; Hirsch, P.R.; Griffiths, R. The pH optimum of soil exoenzymes adapt to long term changes in soil pH. *Soil Biol. Biochem.* 2019, 138, 107601. doi:10.1016/j.soilbio.2019.107601

Qiao, Q.; Wang, F.; Zhang, J.; Chen, Y.; Zhang, C.; Liu, G.; Zhang, H.; Ma, C.; Zhang, J. The variation in the rhizosphere microbiome of cotton with soil type, genotype and developmental stage. *Sci. Rep.* 2017, 7, 3940. doi:10.1038/s41598-017-04213-7

Quast, C.; Pruesse, E.; Yilmaz, P.; Gerken, J.; Schweer, T.; Yarza, P.; Peplies, J.; Glöckner, F.O. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. *Nucl. Acids. Res.* 2013, 41, D590-D596. doi:10.1093/nar/gks1219

R Core Team. *R: A language and environment for statistical computing.* R Foundation for Statistical Computing. 2020. Available at: <https://www.r-project.org/>.

Rey, T.; Jacquet, C. Symbiosis genes for immunity and vice-versa. *Curr. Opin. Plant Biol.* 2018, 44, 64–71. doi:10.1016/j.pbi.2018.02.010

Rudgers, J.A.; Hallmark, A.; Baker, S.R.; Baur, L.; Hall, K.M.; Litvak, M.E.;

Muldavin, E.H.; Pockman, W.T.; Whitney, K.D. Sensitivity of dryland plant allometry to climate. *Funct. Ecol.* 2019, 33, 2290–303. doi:10.1111/1365-2435.13463

Sherwood, S.; Fu, Q. A Drier Future? *Science.* 2014, 343, 737–9. doi:10.1126/science.1247620

Taketani; R.G.; Kavamura, V.N.; Mendes, R.; Melo, I.S. Functional congruence of rhizosphere microbial communities associated to leguminous tree from Brazilian semiarid region. *Environ. Microbiol. Rep.* 2015, 7, 95–101. doi:10.1111/1758-2229.12187

Thiergart, T.; Durán, P.; Ellis, T.; Vannier, N.; Garrido-Oter, R.; Kemen, E.; Roux, F.; Alonso-Blanco, C.; Ågren, J.; Schulze-Lefert, P.; Hacquard, S. Root microbiota assembly and adaptive differentiation among European *Arabidopsis* populations. *Nat. Ecol. Evol.* 2020, 4, 122–31. doi:10.1038/s41559-019-1063-3

Wang, B.; Sugiyama, S. Phylogenetic signal of host plants in the bacterial and fungal root microbiomes of cultivated angiosperms. *Plant J.* 2020, 104, 522–31. doi:10.1111/tpj.14943

Whitford, W.G. The importance of the biodiversity of soil biota in arid ecosystems. *Biodivers. Conserv.* 1996, 5, 185–95. doi:10.1007/BF00055829

Xiong, D.; Wei, C.Z.; Jasper Wubs, E.R.; Veen, G.F.; Liang, W.; Wang, X.; Li, Q.; Van der Putten, W.H.; Han, X. Nonlinear responses of soil nematode community composition to increasing aridity. *Global Ecol. Biogeogr.* 2020, 29, 117–26. doi:10.1111/geb.13013