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BACTERIOME ASSOCIATED WITH *Rhizophora mangle* SEDIMENTS WITHIN BRAZIL SEMI-ARID MANGROVES

Bacteriomas associados aos sedimentos de *Rhizophora mangle* em manguezais semiáridos do Brasil

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ABSTRACT

Microorganisms play important roles in nutrient cycling in mangrove ecosystems and knowledge on the plant/microorganism association is essential to better understand the functioning of this environment. *Rhizophora mangle* is the dominant tree species within Brazilian mangroves and little information is available on the microbiota associated with this plant species. In this context, the aim of this study was to survey the taxonomic diversity of bacteria in the *R. mangle* root zones in mangroves within the semi-arid region of Northeast Brazil submitted to different human disturbances, intending to determine the bacterial fingerprint associated with this habitat. The total DNA extracted from sediments of different mangroves was pooled and used for construction of 16S rDNA cloning libraries, which resulted in 663 sequences with an average size of 809 bp. All mangroves were rich in different phyla of the Bacteria domain, with Acidobacteria, Bacteroidetes, Chloroflexi, and Proteobacteria being detected in all locations. Proteobacteria was dominant in all mangroves, and it was mainly represented by Alpha, Delta, and Gammaproteobacteria. The greatest richness was found in the Timonha river mangrove, with 13 phyla, a location considered more preserved compared to other mangroves. The lowest richness was found in Ceará river mangrove, with only seven phyla. This mangrove is threatened by intense urbanization. The results clearly showed that the taxonomic diversity of bacteria from mangroves subjected to intense urbanization have decreased, highlighting the risks of these changes for the functioning of important microbe-mediated processes and related ecosystem services.

Keywords: Brazilian mangroves, semi-arid, *Rhizophora mangle*, rRNA 16S, clone library.

RESUMO

Os microrganismos desempenham papéis importantes na ciclagem de nutrientes em ecossistemas de mangue e o conhecimento da associação planta/microrganismo é essencial para melhor compreender o funcionamento desse ambiente. Rhizophora mangle é a espécie de árvore dominante dentro dos manguezais brasileiros e pouca informação está disponível sobre os micro-organismos associados a essa espécie de planta. Nesse contexto, o objetivo deste estudo foi realizar um levantamento da diversidade taxonômica de bactérias nas zonas radiculares de R. mangle em manguezais da região semiárida do Nordeste do Brasil, submetidos a diferentes distúrbios antrópicos, visando determinar a impressão digital bacteriana associada a esse habitat. O DNA total extraído dos sedimentos de diferentes manguezais foi utilizado para a construção de bibliotecas de clones de rDNA 16S, que resultou em 663 sequências com tamanho médio de 809 pb. Todos os manguezais exibidos eram ricos em diferentes filos de Bacteria, com Acidobacteria, Bacteroidetes, Chloroflexi e Proteobacteria, sendo detectados em todos os locais. Proteobacteria foi dominante em todos os manguezais, tendo sido representado principalmente por Alpha, Delta e Gammaproteobacteria. A maior riqueza foi encontrada no manguezal do rio Timonha, com 13 filos, local considerado mais preservado em comparação com outros manguezais. A menor riqueza foi encontrada no manguezal do rio Ceará, com apenas sete filos. Esse manguezal é ameaçado por intensa urbanização. Os resultados mostraram claramente que a diversidade taxonômica de bactérias de manguezais submetida à intensa urbanização diminuiu, evidenciando os riscos dessas alterações para o funcionamento de importantes processos mediados por micro-organismos e serviços ecossistêmicos relacionados.

Palavras-chave: *manguezais brasileiros, semiárido, Rhizophora mangle, rRNA 16S, biblioteca de clones.*

INTRODUCTION

Vegetation that is exclusively found in mangroves comprises about 73 species within 28 genera, which present a number of different adaptations allowing them to survive in this salty, muddy and anoxic coastal environment (Duke *et al.*, 2006; Lo *et al.*, 2014). In Brazil, this exclusive vegetation is represented by the genera *Avicennia, Laguncularia* and *Rhizophora*, with the latter prevailing throughout the coastal zone (Spalding; Kainuma & Collins, 2010).

Rhizophora is the predominant and the most widespread genus of the family Rhizophoraceae (Lo *et al.*, 2014). Although globally distributed, only six species and approximately an equal number of hybrids have been described for this genus: *R. apiculata, R. mucronata* and *R. stylosa* in Indo-West Pacific, and *R. mangle, R. racemosa* and *R. samoensis* in Atlantic-East Pacific mangroves (Lo *et al.*, 2014).

R. mangle, also known as red mangrove, is the dominant species in tropical coastal areas of the Atlantic Ocean, Pacific America and in several tropical islands at the South-Western Pacific Ocean (Duke *et al.*, 2006; Lo *et al.*, 2014; Spalding; Kainuma & Collins, 2010). The red mangrove has an intricate prop root system that supports its fixation in muddy soils, and its respiration and aeration during periods of complete submersion (Duke *et al.*, 2006).

Since the red mangrove is predominant in tropical mangroves, it is assumed that this plant might have an essential role for the ecosystem, and it has been hypothesized that

microbial community inhabiting this environment is very specific due to selection over time (Cleary *et al*., 2012; Dias *et al*., 2012). Despite that intimate association, plant effects on microbial diversity and vice-versa is little understood in mangroves (Gomes *et al*., 2010). In terrestrial plants, such interaction is recognized as the rhizospheric effect; i.e., the effect caused by plants providing nutrient-rich exudates (Höflich; Wiehe & Kühn, 1994) and therefore select for certain taxa and/or functional groups of microorganisms (Kumar *et al*., 2007). On the other side, microorganisms are essential for plant growth, protection against pathogen and organic matter turnover (Narula; Kothe & Behl, 2009).

Soil bacteriomes associated to *R. mangle* of the semi-arid coast of Brazil were reported as rich and complex repositories of diversity and complexity when compared with *R. mangle* forests in the North or South of Brazil (Tavares *et al*., 2021). The semi-arid coast displays important features that can explain such findings, such as water deficit caused by low rainfall, water impoundment by dams, and elevate evapotranspiration. Those features contribute to saline intrusion and landward migration of such mangrove forests, a temporal trend recently reported by Godoy and Lacerda (2015). Considering that the composition of sediment microbial communities can also suffer the influence of plant diversity and genotype related to rhizodeposits types and amounts, root architecture, and plant physiological activity (Craig *et al*., 2020; Philippot *et al*., 2013), the analysis of the *R. mangle* associated microbiota can help to understand how variable those communities are in a spatial scale and to discern among abiotic drivers of variation.

This study aimed to conduct the first survey of the benthic bacterial community under *Rhizophora mangle* forests *across* eight mangroves within the semi-arid coast of Northeast Brazil, intending to determine the bacterial fingerprint associated with that habitat. This knowledge traces a baseline regarding the bacterial diversity associated with *R. mangle*, which can help future studies associated with ecosystem monitoring of the effects of anthropogenic actions, such as the impacts of oil spills, which recently reached the coast of Brazil (Soares *et al*., 2020). Knowing those communities is strategic to use microbial diversity with creativity in a science-based manner to deal with Anthropocene's problems in our changing biosphere.

MATERIALS AND METHODS

Sediment samples were taken from eight mangroves across the 573 km of Ceará state's coastal zone, on the semi-arid coast of Brazil (Fernandez *et al*., 2019). The study comprised samples from Icapuí (ICA), Malcozinhado (MAL), Cocó (COC), Ceará (CEA), Aracatiaçu (ARA), Acaraú (ACA), Coreaú (COR) and Timonha (TIM) mangroves. CEA, COC, and MAL are located in the metropolitan region of Fortaleza, the biggest city of the State of Ceará, and are intensively subjected to urbanization and sewage disposal. ARA, ACA, and COR are located on the west coast of the state and are threatened mostly by shrimp farming. TIM was considered as the reference mangrove, since it is located in the environmental protection area of the Parnaiba River, at the extreme west of the State of Ceará. ICA is located on the extreme east coast in a risk area for oil spills due to its proximity to petroleum exploitation reservoirs.

Sediments were collected within the prop roots of *R. mangle* in the 0-20 cm superficial layer, at low tide (0.0-0.2 m), during the wet season (between March and May 2010). For the molecular analysis, samples were stored in sterile flasks, labeled, and placed in an ice-

cooled box. Sediments for physicochemical analyses were packaged in plastic bags and taken to the laboratory. Salinity and pH were measured in the sediment interstitial water. The remaining samples were dried for organic matter and particle size analyses.

Organic matter content (OMC) was analyzed by the loss on ignition protocol (Schulte & Hopkins, 1996). In order to perform the particle size analysis, samples of dry sediments were weighed (100 g) in triplicates and washed in a 0.062 mm mesh sieve to remove the silt-clay from the sand fraction. The sand retained on the sieve was recovered, oven-dried, and re-weighed. The silt-clay content was calculated by subtracting the final and initial weights. PC-ORD (Mccune & Mefford, 2011) was used to generate the cluster analysis of the abiotic factors based on Euclidian distance. The variables were also analyzed by ANOVA with $p < 0.001$ and Tukey *a posteriori* test.

The metagenomic DNA was isolated from 0.5 g of sediments using the PowerSoil™ DNA Isolation kit (MoBio, Carlsbad, CA, USA). 20 ng of purified DNA was amplified by PCR using the universal primers 27F and 1525R (Lane, 1991), covering nearly the entire 16S rRNA gene (*E. coli* 16S rRNA gene sequence). The *amplicons* for each mangrove were cloned into the pGEM-T easy cloning vector (Promega, Madison, WI, USA) and introduced into *Escherichia coli* Top10F' (Invitrogen, Carlsbad, CA, USA) by electroporation, according to the protocol provided by the manufacturer. The plasmids containing the 16S rRNA gene were extracted from the clones by the alkaline lysis method (Sambrook & Russel, 2001) and sequenced by Macrogen Inc. (Seoul, Korea) using the universal primer T7 promoter in an ABI 3730 (Applied Biosystems) with ABI PRISM BigDyeTM terminator cycle sequencing kit and AmpliTaq DNA polymerase (Applied Biosystems, Foster City, CA, USA), following the protocols supplied by the manufacturer.

Electropherograms were analyzed, and sequences were trimmed and selected for high-quality sequences at Ribosomal Data Project Pipeline (rdp.cme.msu.edu). Sequences longer than 300 bp and with more than 80% of bases with Phred > 20 were selected to constitute the final dataset. Sequences were assigned to operational taxonomic units (OTU) with Mothur software (version 1.32.0) (Schloss *et al.*, 2009), using a naïve Bayesian classification based on the reconstructed SILVA SEED database (release 111) (Quast *et al.*, 2013) as a reference dataset for classifying sequences from the phylum to genus level. A similarity of 98% between sequences was considered to assemble them into OTU at the species level (Nemergut *et al.*, 2011). Chimera checking was performed using the chimera. uchime algorithm (Edgar *et al.*, 2011) with Mothur and SILVA-Gold as the references. A set of 663 sequences passed the quality filtering steps and was used to calculate the richness estimators and diversity indexes. Mothur was also used to build clusters based on relative abundance at different hierarchical levels.

RESULTS AND DISCUSSION

Physicochemical characteristic of semi-arid mangrove sediments

In the present study, we examined the geographic distribution of benthic bacterial communities associated with red mangrove over 573 km of the coastal zone under the semi-arid climate of Northeast Brazil. The eight studied mangroves were chosen taking into consideration local environmental characteristics and the main anthropic impacts

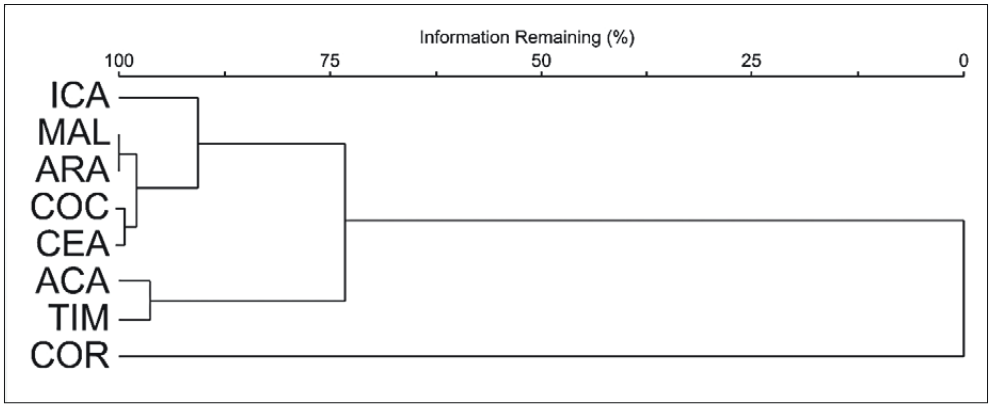
acting on each habitat. The environmental variables (pH and salinity), sediment characteristics (organic matter and silt+clay contents), and GPS coordinates of the eight sampling sites are shown in Table I. The variables were analyzed by ANOVA with $p < 0.001$ and Tukey *a posteriori* test, which exhibited a statistically significant difference of the silt+clay and organic matter contents between COR and the other mangroves. Also, silt+clay content was shown to increase from the east (ICA) to the west (TIM), probably due to the regional drift current that flows predominantly from the east to the west. Organic matter was mostly related to silt+clay contents, and this fact was clearly seen in COR, where both were higher. Figure 1 shows the clustering based on Euclidean distance for the abiotic variables, where COR is separated from the other mangroves. Also, ACA and TIM clustered together, with 73% of similarity, separating themselves from the group formed by the other mangroves.

Table I – Main characteristics of mangroves and environmental sediments variables in *R. mangle* habitats of the mangroves of Ceará, NE, Brazil

Mangrove	Code†	Municipality	Population‡	Sampling location		Main anthropic changes§	Mangrove area# (ha)	Shrimp farm area†† (ha)	pH	Salinity‡‡	O.M. (g/ kg)	Silt + Clay (%)
				Latitude	Longitude							
Icapuí	ICA	Icapuí	18,392	S04°41.514′	W37°21.195′	Salterns, shrimp farming	62	494.21	7.1	39	66.20[a]	29.2[a]
Malcozinhado	MAL	Cascavel	66,142	S04°03.787′	W38°11.341′	Urbanization	26	0	7.8	34	84.99[b]	49.4[c]
Cocó	COC	Fortaleza	2,452,185	S03°46.482′	W38°26.552′	Intense urbanization, littering, sewage	526	0	7.2	35	82.83[b]	39[b]
Ceará	CEA	Fortaleza /Caucaia	2,777,626	S03°42.135′	W38°35.849′	Intense urbanization, littering, sewage	881	0	7.1	42	84.49[b]	39[b]
Aracatiaçu	ARA	Amontada /Itarema	76,703	S03°0.405'	W39°42.475'	Shrimp farming	778	344.62	7.3	36	82.58[b]	52.4[c]
Acaraú	ACA	Acaraú	57,551	S02°50.976'	W40°7.650'	Shrimp farming	1,557	705.53	7.5	31	87.79[bc]	77.9[d]
Coreú	COR	Camocim /Granja	112,803	S02°53.567′	W40°49.902′	Shrimp farming	3,530	904.08	7.3	43	158.54[d]	95.2[e]
Timonha	TIM	Barroquinha /Chaval	27,091	S02°56.585′	W41°19.073′	Pristine	5,011	76.92	7.0	39	96.93[c]	84.1[d]

† Three letter code of each mangrove used in this work; ‡ IBGE census 2010 (http://censo2010.ibge.gov.br/) – population of the cities adjacent to the mangrove; § According to Lacerda *et al.*, 2008; # Remote sensing (Maia *et al.*, 2006); †† Semace archives – shrimp farming areas in the reference cities (Soares *et al.*, 2020); ‡‡ Salinity values expressed in Practical Salinity Units. Different letters represent significant differences ($p < 0.001$) demonstrated by variance analysis with Tukey's post-test.

Figure 1 - Cluster analysis of environmental variables (pH, salinity, silt-clay, and organic matter content) of sediments of *Rhizophora mangle* root zones of mangroves at Ceará State (NE, Brazil) based on Euclidian distance



Phylum-level bacterial taxonomic composition

After quality checking, 663 sequences (Phred > 20) of 16S rRNA partial gene were obtained, reaching an average of 83 sequences per sample, with a mean size of 809 bp (NCBI PopSet 846337277) (Table II). Richness (Chao1 estimator) and diversity (Shannon index) were highest in TIM, a pristine mangrove, and lowest in the most urbanized mangrove (CEA). According to the observed OTUs and Chao1 richness estimator, there are significant differences between the more preserved and urban mangroves ($p < 0.05$). The ecological indexes showed that those more altered urban mangroves presented lower richness and diversity when compared to the preserved mangrove, signaling an urgent need for conservation actions.

The retrieved sequences were affiliated to at least 19 phyla with remarkable dominance (> 1% relative abundance): Proteobacteria, Acidobacteria, Actinobacteria, Bacteroidetes, Chloroflexi, Planctomycetes, Deferribacteres, and Firmicutes in all mangroves. Members of these eight phyla make up an average of 94.75% of the libraries. In addition, members of other phylum-level lineages with relative abundance lower than 1%, such as Chlamydiae, Chlorobi, Cyanobacteria, Lentisphaerae, Nitrospira, Gemmatimonadetes, Spirochaetes, Synergistetes, Tenericutes, Verrucomicrobia, and WS3, were detected in the dataset. Only 6.38% of total sequences could not be affiliated to any known bacterial group, evidencing that the study dataset possesses sequences with high quality and length, which provided good coverage of the 16S rRNA gene enabling the classification of a great part of the sequences.

TIM and COR exhibited 13 phyla, followed by ICA (12 phyla), COC and MAL (10 phyla each), and CEA (seven phyla). The preserved mangrove (TIM) shared 10 phyla with its neighbor COR (threatened by intense shrimp farming), and both shared nine phyla with ICA, located in the extreme of the east coast. The adjacent mangroves ARA and ACA, which are quite threatened by shrimp farming, shared seven out of the total of nine phyla found in each. Proteobacteria, Acidobacteria, Bacteroidetes, and Chloroflexi were detected in all locations, comprising at least 71.6% of total phyla relative abundance. Proteobacteria alone ranged from 40 up to 78% in ICA and CEA, respectively.

Table II – Estimated OTU richness and diversity indexes for 16S rRNA clone libraries of mangrove sediment samples associated with *Rhizophora mangle*

	NS†	OTUs‡	bp	Chao1§	Shannon§	Good's Coverage at 0.02#	Good's Coverage at 0.2††
ICA	91	79	812	493[ab]	4.30	0.22	0.90
MAL	86	80	853	635[ab]	4.35	0.13	0.94
COC	78	75	853	714[b]	4.30	0.08	0.87
CEA	86	78	917	346[a]	4.10	0.19	0.88
ARA	89	83	977	501[ab]	4.40	0.14	0.97
ACA	84	81	801	831[b]	4.38	0.07	0.96
COR	62	61	654	946[bc]	4.33	0.03	0.73
TIM	93	90	606	1025[c]	4.49	0.06	0.88

† NS - Number of sequences for each library; ‡Calculated with Mothur at the 0.02 distance; § Chao1 richness estimator and Shannon diversity index calculated using Mothur (0.02 distance); # Good's coverage estimator at distances; # 0.02 (species level) and †† 0.2 (phylum level).

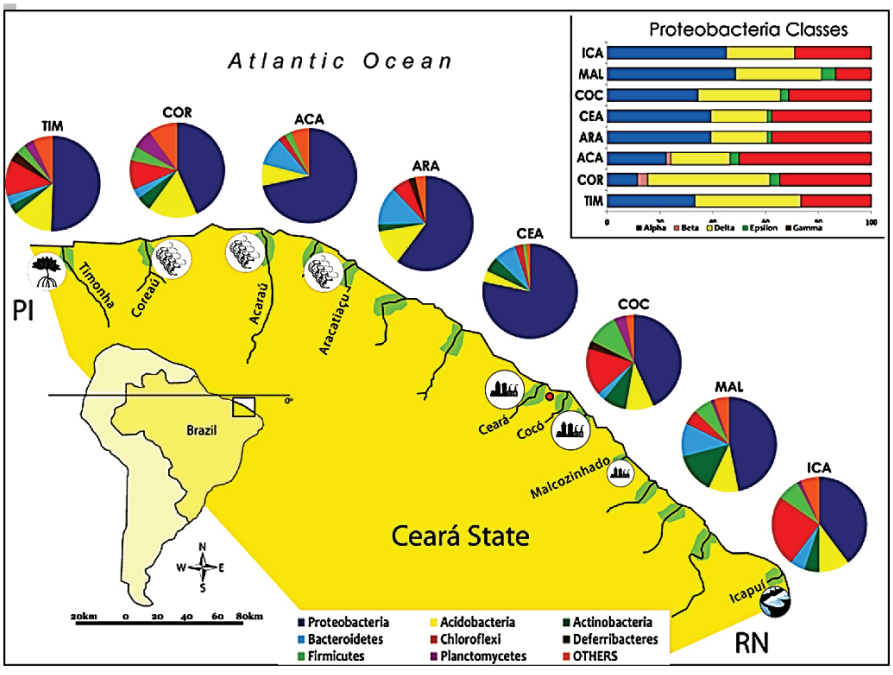
The dominance of Proteobacteria in mangrove sediments is remarkable, regardless of the methodology applied in the study or of the pressures to which the environment is subjected (Figure 2). This dominance was reinforced by Illumina 16S rRNA gene amplicon sequencing, which pointed to the dominance of Proteobacteria (mainly by Deltaproteobacteria and Gammaproteobacteria, which are part of the core microbiome of mangroves worldwide) in the soil associated with *R. mangle* in the North, Northeast, and South of Brazil (Tavares *et al.*, 2021). Although the high throughput sequencing used by those authors revealed the presence of other phyla, such as Euryarchaeota and Epsilonbacteraeota, in mangroves from the North and South of Brazil as well as in Icapui mangrove (ICA in the present study), the dominance of Proteobacteria is unquestionable. Andreote and colleagues (2012) obtained similar results at phylum-level analyzing sediments from different areas of mangroves in the Southeast region of Brazil (Cananeia and Bertioga, SP), where the relative abundance of Proteobacteria ranged from 47.1 to 56.3%. Pureza *et al.* (2013) also reported a similar phylum-core in a mangrove from Amazonia (Bragança, PA), and Ghosh *et al.* (2010) showed that the relative abundance of Proteobacteria was greater than 50% in an Indian mangrove (Ghosh *et al.*, 2010; Pureza *et al.*, 2013). Fierer *et al.* (2012) has pointed out that Proteobacteria are ubiquitous in soils, and only their relative abundances and their specific representatives tend to vary between different ecosystems (Fierer *et al.*, 2012).

The most representative classes in the eight semi-arid mangroves were Alphaproteobacteria (18.9%), Gammaproteobacteria (18.1%), and Deltaproteobacteria (15.5%), followed by Acidobacteria classes (Figure 2). A similar distribution of those classes was reported in previous studies in Brazilian mangroves (Andreote *et al.*, 2012; Dias *et al.*, 2010; Gomes *et al.*, 2010; Nogueira *et al.*, 2015; Santos *et al.*, 2011). Changes in that pattern have been reported in hydrocarbons contaminated mangroves, where Betaproteobacteria is frequently dominant (Ghosh *et al.*, 2010; Nogueira *et al.*, 2015; Peixoto *et al.*, 2011).

Members of Acidobacteria are phylogeneic and physiologically diverse and ubiquitous in soils, with few described strains (Jones *et al.*, 2009; Wang *et al.*, 2012). In this study, Acidobacteria ranged from 3.8 to 12% (CEA and ARA, respectively), which contrast with the low abundance previously reported in mangroves from Southeastern Brazil (Andreote *et al.*, 2012). Studies suggest that the abundance of this phylum is significantly

increased when pH is lower than 5.5, although in this study the pH variation has ranged around 7.0. Wang and colleagues (2012) reported the abundance of Acidobacteria ranging between 4 up to 6% in no acidic freshwater samples and suggested that not only pH drives the abundance of this group. Previous studies reported a higher abundance of Acidobacteria (29% and 54%) in the Brazilian Atlantic forest (Bruce *et al.*, 2010), and in pasture soils (7% and 14%) (Rocha *et al.*, 2013). Therefore, *R. mangle* from the semi-arid region of Brazil emerges as a new habitat for Acidobacteria prospection. Within the classes of Acidobacteria, Gp10, Gp17, Gp21, and Gp23 were the most representative in our dataset, although other subdivisions were also found. Studies point out that subdivisions Gp1, Gp3, Gp4, Gp6, and Gp18 are enriched in freshwater environments, while subdivisions Gp10, Gp21, Gp22, and Gp26 are more abundant in marine sediments (Orcutt *et al.*, 2011; Zhang *et al.*, 2015). When analyzing soils and sediments collected across different continents, Jones *et al.* (2009) realized that subdivision Gp1 was responsible for almost 7.5% of all bacterial sequences. These results indicate that Acidobacteria is relatively abundant in sediments, including semi-arid mangrove sediments, although more studies are required for understanding the role of specific subgroups detected in mangroves.

Figure 2 – Spatial distribution of bacterial phyla associated with *Rhizophora mangle* in mangroves from the semi-arid coastal zone of Brazil. "OTHERS" encompass: Chlamydiae, Chlorobi, Cyanobacteria, Lentisphaerae, Nitrospira, Gemmatimonadetes, Spirochaetes, Synergistetes, Tenericutes, Verrucomicrobia, and WS3



Bacteroidetes are found in numerous environments ranging from animal guts and skins to sediments and seawater (Thomas *et al.*, 2011), always under anaerobic conditions. The ability of Bacteroidetes to occupy a variety of environments is mainly because they are recognized specialists in the degradation of high molecular weight organic matter, from polysaccharides to proteins. Some studies correlate the presence of Bacteroidetes with substrate pH, being significantly higher in alkali medium (Lauber *et al.*, 2009). Although there was no significant difference in the pH of the studied mangroves, the relative

abundance of this group was higher (11.4%) in MAL (pH 7.8) and lower (3.4%) in TIM (pH 7.0), confirming their preference for alkali habitats.

Few studies report an expressive presence of Chloroflexi in mangrove sediments (Liang *et al.*, 2007; Pureza *et al.*, 2013; Zhang *et al.*, 2015), although in this study it represents 9% of the detected phyla. It was among the four phyla that were detected in all mangroves, being the second most abundant phylum in ICA (24%). In mangrove sediments from Shenzhen Bay, China, the relative abundance of Chloroflexi reached 28%, whereas Proteobacteria was the second most abundant phylum (Zhang *et al.*, 2015). In mangroves from Southeastern Brazil, the relative abundance of that phylum varied from 5.4% to 1.3%, with the lowest value detected in contaminated mangroves (Andreote *et al.*, 2012). Similarly, in this study, CEA mangrove showed the lowest relative abundance of green non-sulfur bacteria (Chloroflexi phylum), confirming this trend.

Diversity of bacterial genera

A total of 188 bacterial genera were identified among the 663 sequences from our dataset. So far, only 26 of these genera had been reported in mangroves (Baba *et al.*, 2011; Basak *et al.*, 2014; Chakraborty *et al.*, 2015; Fan *et al.*, 2012; Flores-Mireles; Winans & Holguin, 2007; Gao; Xu & Ruan, 2014; Gomes *et al.*, 2010; Guo *et al.*, 2011; Khatri *et al.*, 2012; Mishra *et al.*, 2012; Santos *et al.*, 2011; Soto-Ramírez *et al.*, 2008; Zhang *et al.*, 2008; Zhao & Ruan, 2011). A great amount of randomly selected clones of this study was affiliated with groups that encompassed marine and/or estuarine anaerobic bacteria. The large inputs of organic matter support high rates of heterotrophic metabolism and, since oxygen is usually depleted below a few millimeters in mangrove sediments, even where the sediment surface is exposed to air, anaerobic metabolism predominates with decomposition mediated primarily by fermentative and sulfate-reducing bacteria (Alongi, 2010).

At least 33 genera were related to sulfur metabolism, comprising 25 genera of sulfate-reducing bacteria (SRB) and eight genera of sulfur-oxidizing bacteria (Figure 3). Among the sulfur-oxidizing bacteria, the majority belongs to purple sulfur bacteria (Chromatiales), a group of anaerobic microorganisms that obtain energy from anoxygenic photosynthesis, i.e., oxidizing hydrogen sulfide to sulfite and sulfate. *Ectothiorhodosinus* was the most abundant genus of purple sulfur bacteria. Only one genus (*Ignavibacterium*) was assigned to green sulfur bacteria.

The sulfate-reducing bacteria (SRB) were mostly assigned to Deltaproteobacteria, as expected (Figure 3). The most representative orders were Desulfobacterales (mainly represented by the genera *Desulfonema*, *Desulfopila*, *Desulfosalsimonas*, *Desulfobacterium*, and *Desulfosarcina*) and Syntrophobacteriales (*Desulfoglaeba*, *Desulfovirga*, and *Desulfosoma*). The other orders detected were Desulfovibrionales (*Desulfocurvus* and *Desulfonauticus*) and Desulfarculales (*Desulfarculus*), although in minor amounts. The occurrence of *Dethiobacter* (Firmicutes) and *Thermodesulfovibrio* (Nitrospirae) was also noticed, which are also sulfate-reducing bacteria.

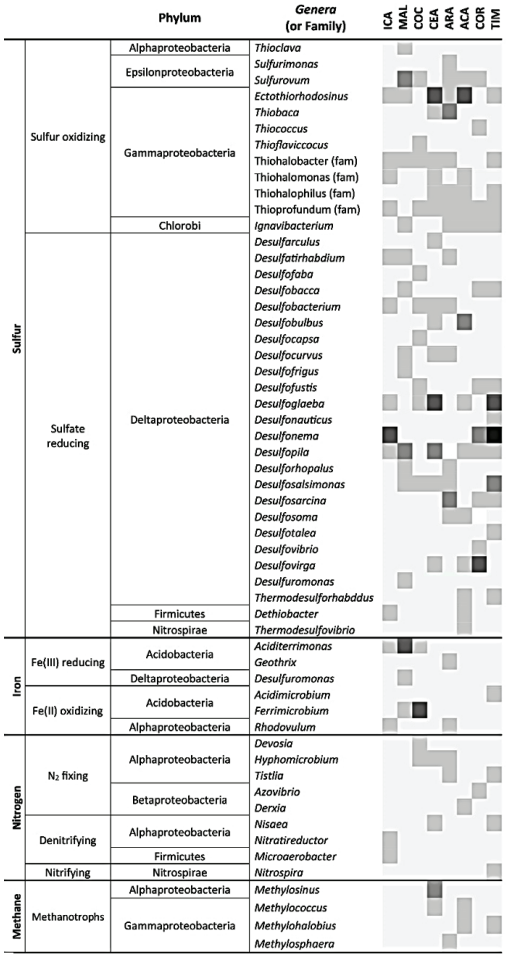
The iron cycle in mangroves is dynamic and closely linked with the sulfur cycle (Alongi, 2010). Iron and sulfur are important elements in the biogeochemistry of estuarine sediments because microbial groups related to both cycles play important roles in the decomposition of organic matter (Nóbrega *et al.*, 2013). Sequences affiliated to Acidobacteria and related to iron metabolism were detected (Figure 3). *Aciditerrimonas* and *Geothrix*

reduce ferric iron (III), whereas *Acidimicrobium* and *Ferrimicrobium* oxidize ferrous iron (II). Rhodobacteraceae, a highly diverse family within the class Alphaproteobacteria, known as a phototrophic iron oxidizer (Hedrich *et al.*, 2011), was also well represented in the studied mangroves.

Within Alphaproteobacteria, groups related to the nitrogen cycle were abundant in the red mangrove habitats (Figure 3). The most frequent genera were *Tistlia*, *Devosia, Hyphomicrobium* (nitrogen-fixing bacteria), *Nitratireductor,* and *Nisaea* (denitrifying), as well as *Derxia* and *Azovibrio* (Betaproteobacteria), *Microaerobacter* (Firmicutes), and *Nitrospira* (Nitrospira), which are all related to the N cycle.

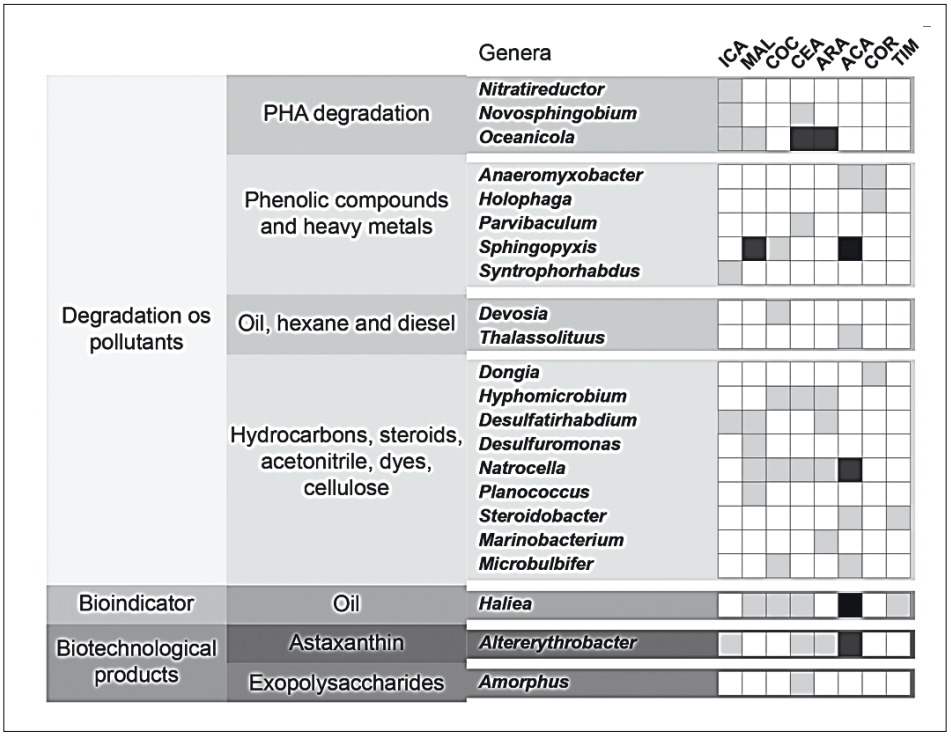
Besides the above-mentioned bacterial genera, this study reports the presence of well-known genera related to the degradation of aromatic compounds, petroleum, and several contaminants (Figure 4). The genera *Nitratireductor*, *Oceanicola,* and *Novosphingobium*, associated with pyrene and naphthalene degradation (Lai *et al.*, 2011; Suzuki & Hiraishi, 2007; Yuan *et al.*, 2009), were detected in ICA, MAL, CEA, and ARA. Furthermore, bacteria belonging to the genera *Anaeromyxobacter*, *Holophaga*, *Parvibaculum*, *Sphingopyxis*, and *Syntrophorhabdus*, all related to degradation of phenolic compounds (Godoy *et al.*, 2003; Liesack *et al.*, 1994; Qiu *et al.*, 2008; Sanford; Cole & Tiedje, 2002; Schleheck *et al.*, 2004), were detected in six of the eight studied mangroves (ACA, COR, MAL, COC, CEA, and ICA). The species *Anaeromyxobacter dehalogenans*, which is already extensively used in the bioremediation of uranium (Wu; Sanford & Löffler, 2006), was detected in ACA and COR. The genera *Devosia* and *Thalassolituus*, encompassing bacteria related to the oil (Choi & Cho, 2013), hexane, and diesel (Ryu *et al.*, 2008; Verma *et al.*, 2009) degradation, were detected in COC and ACA. OTUs affiliated to *Dongia*, *Hyphomicrobium* (Alphaproteobacteria), *Desulfatirhabdium*, *Desulfuromonas* (Deltaproteobacteria), *Nantrocella*, *Planococcus*, and *Steroidobacter* (Gammaproteobacteria), related to the degradation of other hydrocarbons such as dyes, acetonitrile, dichloromethane, and steroid hormones (Balk *et al.*, 2008; Engelhardt *et al.*, 2001; Fahrbach *et al.*, 2008; Liu *et al.*, 2010; Sung *et al.*, 2003), were found in all studied mangroves. The genus *Haliea*, previously reported by Santos *et al.* (2011) as a possible bioindicator for oil contamination in mangroves, was found in MAL, COC, CEA, ACA, and TIM, being more abundant in ACA (Figure 4). *Altererythrobacter* and *Amorphous* (Alphaproteobacteria), two genera of marine bacteria, were found in ICA, CEA, ARA, and ACA (Figure 4). Some species belonging to these genera have been reported as producers of useful

Figure 3 - Bacterial genera related to sulfur, iron, and nitrogen cycles detected by 16S rDNA cloning library of sediments collected in *Rhizophora mangle* root zones in mangroves (ICA, MAL, COC, ARA, ACA, COR, and TIM) from Northeast, Brazil



enzymes and compounds such as epoxide hydrolase (Kumar *et al.*, 2007), astaxanthin (Matsumoto *et al.*, 2011), and exopolysaccharides (Wawonng *et al.*, 2010). These results highlight the genetic potential of the bacterial community for biotechnological applications.

Figure 4 - Bacterial genera related to the metabolism of different compounds in the studied mangroves (ICA, MAL, COC, ARA, ACA, COR, and TIM) from Northeast, Brazil



Undoubtedly, researches undertaken in Brazil are at the forefront of studies on bioremediation and restoration of mangroves (Angelim *et al.*, 2013; Santos *et al.*, 2011; Sodré *et al.*, 2013; Machado *et al.*, 2019). However, knowing the mangrove microbiomes is essential to take further steps in this direction. The taxonomic characterization of those microbiomes allows us to (1) understand how environmental modifications related to specific anthropogenic impacts or related to climate change can alter those communities as well as make conclusions regarding their resistance and resilience, and (2) explore this bacterial composition in a strategic way to provide biotechnological tools to bioremediate and restore altered ecosystems (Allard *et al.*, 2020).

CONCLUSIONS

The successive oil spills that occurred on the Brazilian coast in 2019 and 2020 illustrate quite well how important it is to know our biodiversity. Taking into consideration the bacterial diversity, this study provided a baseline to evaluate how it affected those coastal ecosystems, as well as provided tools that are being studied for the bioremediation of damaged mangroves.

Our dataset provides an important overview of the sediment bacteriome throughout the coastal zone in the semi-arid region of Brazil, comprising preserved and anthropized

mangroves. The results endorsed a general pattern, a core of bacteria phylum-groups in mangroves, regardless of the local environment characteristics, and high redundancy of bacterial genera involved in the sulfur metabolism, especially sulfate-reducing bacteria. These organisms proliferate in habitats rich in partially oxidized substrates and anaerobic conditions, typically found inside red mangrove habitats. Furthermore, our study presents the identification of a signature of bacterial genera inside red mangrove habitats in the Northeastern Brazilian mangroves.

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REFERENCES

Allard, S.M. *et al*. Introducing the mangrove microbiome initiative: identifying microbial research priorities and approaches to better understand, protect, and rehabilitate mangrove ecosystems. *mSystems,* v. 5, p. 20, 2020.

Alongi, D.M. Dissolved iron supply limits early growth of estuarine mangroves. *Ecology*, v. 91, n. 11, p. 3229-3241, 2010.

Andreote, F.D. *et al.* The microbiome of Brazilian mangrove sediments as revealed by metagenomics. *PLoS One*, v. 7, n. 6, 2012.

Angelim, A.L. *et al.* An innovative bioremediation strategy using a bacterial consortium entrapped in chitosan beads. *J. Environ. Manage.*, v. 127, p. 10-17, 2013.

Baba, A.; Miyazaki, M.; Nagahama, T. & Nogi, Y. Microbulbifer chitinilyticus sp. nov. and microbulbifer okinawensis sp. nov., chitin-degrading bacteria isolated from mangrove forests. *Int. J. Syst. Evol. Microbiol.*, v. 61, n. 9, p. 2215-2220, 2011.

Balk, M. *et al.* Desulfatirhabdium butyrativorans gen. nov., sp. nov., a butyrate-oxidizing, sulfate-reducing bacterium isolated from an anaerobic bioreactor. *Int. J. Syst. Evol. Microbiol.*, v. 58, p. 110-115, 2008.

Basak, P. *et al.* Spatiotemporal analysis of bacterial diversity in sediments of sundarbans using parallel 16S rRNA gene tag sequencing. *Microb. Ecol.*, v. 69, n. 3, p. 500-511, 2014.

Bruce, T. *et al.* Bacterial community diversity in the Brazilian Atlantic Forest Soils. *Microb. Ecol.*, v. 60, n. 4, p. 840-849, 2010.

Chakraborty, A. *et al.* Changing bacterial profile of Sundarbans, the world heritage mangrove: impact of anthropogenic interventions. *World J. Microbiol. Biotechnol.*, v. 31, n. 4, p. 593-610, 2015.

Choi, A. & Cho, J.C. Thalassolituus marinus sp. nov., a hydrocarbon-utilizing marine bacterium. *Int. J. Syst. Evol. Microbiol.*, v. 63, Is. 6, 2013.

Cleary, D.F.R.; Smalla, K.; Mendonça-Hagler, L.C.S. & Gomes, N.C.M. Assessment of variation in bacterial composition among microhabitats in a mangrove environment using DGGE fingerprints and barcoded pyrosequencing. *PloS One*, v. 7, n. 1, p. e29380, jan. 2012.

Craig, H.; Kennedy, J.P.; Devlin, D.J.; Bardgett, R.D. & Rowntree, JK. Effects of maternal genotypic identity and genetic diversity of the red mangrove Rhizophora mangle on associated soil bacterial communities: A field-based experiment. *Ecol. Evol.*, v. 10, p. 13957-13967, 2020.

Dias, A.C.F. *et al.* Interspecific variation of the bacterial community structure in the phyllosphere of the three major plant components of mangrove forests. *Braz. J. Microbiol.*, p. 653-660, 2012.

Dias, A.C.F. *et al.* The bacterial diversity in a Brazilian non-disturbed mangrove sediment. *Anton. Leeuw. Int. J. G.*, v. 98, n. 4, p. 541-551, 2010.

Duke, N.C. & Allen, J.A. Rhizophora mangle, R. samoensis, R. racemosa, R. x harrisonii, *in* Elevitch, C.R. (ed.). *Species profiles for pacific island agroforestry*. 2.1. ed. Hōlualoa, Hawaii, USA: Permanent Agriculture Resources (PAR), 2006.

Edgar, R.C. *et al.* UCHIME improves sensitivity and speed of chimera detection. *Bioinformatics*, v. 27, n. 16, p. 2194-2200, 2011.

Engelhardt, M.A. *et al.* Isolation and characterization of a novel hydrocarbon-degrading, Gram-positive bacterium, isolated from intertidal beach sediment, and description of Planococcus alkanoclasticus sp. nov. *J. Appl. Microbiol.*, v. 90, n. 2, p. 237-247, 2001.

Fahrbach, M. *et al.* Steroidobacter denitrificans gen. nov., sp. nov., a steroidal hormone-degrading gammaproteobacterium. *Int. J. Syst. Evol. Microbiol.*, v. 58, n. Pt 9, p. 2215-2223, 2008.

Fan, L.F.; Tang, S.L.; Chen, C.P. & Hsieh, H.L. Diversity and composition of sulfate-and sulfite-reducing prokaryotes as affected by marine-freshwater gradient and sulfate availability. *Microb. Ecol.*, v. 63, n. 1, p. 224-237, 2012.

Fernandez, G.B. *et al*. Natural landscapes along Brazilian coastline, *in* Salgado, A.A.R.; Santos, L.J.C. & Paisani, J.C. (ed.). *The physicol geography of Brazil: environment, vegetation and landscape*. Cham: Springer, p. 199-218, 2019.

Fierer, N. *et al.* Cross-biome metagenomic analyses of soil microbial communities and their functional attributes. *Proc. Natl. Acad. Sci. U. S. A.*, v. 109, n. 52, p. 21390-21395, 2012.

Flores-Mireles, A.L.; Winans, S.C. & Holguin, G. Molecular characterization of diazotrophic and denitrifying bacteria associated with mangrove roots. *Appl. Environ. Microbiol.*, v. 73, n. 22, p. 7308-7321, 2007.

Gao, Z.M.; Xu, X. & Ruan, L.W. Enrichment and characterization of an anaerobic cellulolytic microbial consortium SQD-1.1 from mangrove soil. *App. Microb. Biotech.*, v. 98, n. 1, p. 465-474, 2014.

Ghosh, A. *et al.* Culture independent molecular analysis of bacterial communities in the mangrove sediment of Sundarban, India. *Saline Syst.*, v. 6, n. 1, p. 11, 2010.

Godoy, M.D.P. & Lacerda, L.D. Mangroves response to climate change: a review of recent findings on mangrove extension and distribution. *An. Acad. Bras. Ciênc.*, v. 87, p. 651-667, 2015.

Godoy, F. *et al.* Sphingopyxis chilensis sp. nov., a chlorophenol-degrading bacterium that accumulates polyhydroxyalkanoate, and transfer of Sphingomonas alaskensis to Sphingopyxis alaskensis comb. nov. *Int. J. Syst. Evol. Microbiol.*, v. 53, n. 2, p. 473-477, 2003.

Gomes, N.C.M. *et al.* Taking root: enduring effect of rhizosphere bacterial colonization in mangroves. *PLoS One*, v. 5, n. 11, p. 1-10, jan. 2010.

Gomes, N.C.M. & Cleary, D.F.R. Impacts of mangrove roots on bacterial composition, *in* Bruijin, F.J. (ed.). *Molecular microbial ecology of the Rhizosphere*. [s.l.] John Wiley & Sons, 2013, p. 1083-1088.

Guo, C.; Ke, L.; Dang, Z. & Tam, N.F. Temporal changes in Sphingomonas and Mycobacterium populations in mangrove sediments contaminated with different concentrations of polycyclic aromatic hydrocarbons (PAHs). *Mar. Pollut. Bull.*, v. 62, n. 1, p. 133-139, 2011.

Höflich, G.; Wiehe, W. & Kühn, G. Plant growth stimulation by inoculation with symbiotic and associative rhizosphere microorganisms. *Experientia*, v. 50, p. 897-905, 1994.

Jones, R.T. *et al.* A comprehensive survey of soil acidobacterial diversity using pyrosequencing and clone library analyses. *ISME J.*, v. 3127, n. 10, p. 442-453, 2009.

Khatri, I. *et al.* Draft genome sequence of *rhodovulum* sp. Strain PH10, a phototrophic alphaproteobacterium isolated from a soil sample of mangrove of namkhana, India. *J. Bacteriol. Res.*, v. 194, n. 22, p. 6363, 2012.

Kumar, R. *et al.* Establishment of azotobacter on plant roots: chemotactic response, development and analysis of root exudates of cotton (Gossypium hirsutum L.) and wheat (Triticum aestivum L.). *J. Basic Microbiol.*, v. 47, n. 5, p. 436-439, 2007.

Lacerda, L.D.; Molisani, M.M.; Sena, D. & Maia, L.P. Estimating the importance of natural and anthropogenic sources on N and P emission to estuaries along the Ceará State Coast NE Brazil. *Environ. Monit. Assess.*, v. 141, n. 1-3, p. 149-164, 2008.

Lai, Q. *et al.* Nitratireductor pacificus sp. nov., isolated from a pyrene-degrading consortium. *Int. J. Syst. Evol. Microbiol.*, v. 61, n. 6, p. 1386-1391, 2011.

Lane, D.J. 16S/23S rRNA sequencing, *in* Stackebrandt, E. & Goodfellow, M. (ed.). *Nucleic acid techniques in bacterial systematics.* Chichester, United Kingdom: Wiley and Sons, 1991, p. 115-175.

Lauber, C.L.; Hamady, M.; Knight, R. & Fierer, N. Pyrosequencing-based assessment of soil pH as a predictor of soil bacterial community structure at the continental scale. *Appl. Environ. Microbiol.*, v. 75, n. 15, p. 5111-5120, 2009.

Liang, J.B. *et al.* Recovery of novel bacterial diversity from mangrove sediment. *Mar. Biol.*, v. 150, n. 5, p. 739-747, 2007.

Liesack, W.; Bak, F.; Kreft, J.-U. & Stackebrandt, E. Holophaga foetida gen. nov., sp. nov., a new, homoacetogenic bacterium degrading methoxylated aromatic compounds. *Arch. Microbiol.*, v. 162, n. 1-2, p. 85-90, 1994.

Liu, Y.; Jin, J.H.; Liu, Y.H.; Zhou, Y.G. & Liu, Z.P. Dongia mobilis gen. nov., sp. nov., a new member of the family Rhodospirillaceae isolated from a sequencing batch reactor for treatment of malachite green effluent. *Int. J. Syst. Evol. Microbiol.*, v. 60, n. Pt 12, p. 2780-2785, 2010.

Machado, L.F. *et al.* Tracking mangrove oil bioremediation approaches and bacterial diversity at different depths in an *in situ* Mesocosms System. *Front. Microbiol.*, v. 10, p. 2107, 2019.

Maia, L.P.; Lacerda, L.D.; Monteiro, L.H.U. & Souza, G.M. *Atlas dos manguezais do Nordeste do Brasil*. Fortaleza, CE: Semace, 2006.

Matsumoto, M. *et al.* Altererythrobacter ishigakiensis sp. nov., an astaxanthin-producing bacterium isolated from a marine sediment. *Int. J. Syst. Evol. Microbiol.*, v. 61, n. Pt 12, p. 2956-2961, 2011.

Mccune, B. & Mefford, M.M. *PC-ORD: multivariate analysis of ecological data version 6 user's booklet*. Gleneden Beach, Oregon: USAMJM Software, 2011.

Mishra, R.R.; Swain, M.R.; Dangar, T.K. & Thatoi, H. Diversity and seasonal fluctuation of predominant microbial communities in Bhitarkanika, a tropical magrove ecosystem in India. *Rev. Biol. Trop.*, v. 60, n. 2, p. 909-924, 2012.

Narula, N.; Kothe, E. & Behl, R.K. Role of root exudates in plant-microbe interactions. *J. Appl. Bot. Food Qual.*, v. 82, n. 2, p. 122-130, 2009.

Nemergut, D.R. *et al.* Global patterns in the biogeography of bacterial taxa. *Environ. Microbiol.*, v. 13, n. 1, p. 135-144, 2011.

Nóbrega, G.N.; Ferreira, T.O.; Romero, R.E.; Marques, A.G.B. & Otero, X.L. Iron and sulfur geochemistry in semi-arid mangrove soils (Ceará, Brazil) in relation to seasonal changes and shrimp farming effluents. *Environ. Monit. Assess.*, v. 185, n. 9, p. 7393-7407, 2013.

Nogueira, V.L.R. *et al.* Microbiomes and potential metabolic pathways of pristine and anthropized Brazilian mangroves. *Reg. Stud. Mar. Sci.*, v. 2, p. 56-64, 2015.

Orcutt, B.N.; Sylvan, J.B.; Knab, N.J. & Edwards, K.J. Microbial ecology of the dark ocean above, at, and below the seafloor. *Microbiol. Mol. Biol. Rev.*, v. 75, n. 2, p. 361-422, 2011.

Peixoto, R. *et al.* Bacterial communities reflect the spatial variation in pollutant levels in Brazilian mangrove sediment. *Antonie van Leeuwenhoek*, v. 99, n. 2, p. 341-354, 2011.

Philippot, L.; Raaijmakers, J.M.; Lemanceau, P. & Van der Putten, W.H. Going back to the roots: the microbial ecology of the rhizosphere. *Nat. Rev. Microbiol.*, v. 11, p. 789-799, 2013.

Pureza, L.M. *et al.* Bacterial diversity in an Amazonian mangrove ecosystem. *Aquatic Sci. Technol.*, v. 1, n. 1, p. 66-85, 2013.

Qiu, Y.L. *et al.* Syntrophorhabdus aromaticivorans gen. nov., sp. nov., the first cultured anaerobe capable of degrading phenol to acetate in obligate syntrophic associations with a hydrogenotrophic methanogen. *Appl. Environ. Microbiol.*, v. 74, n. 7, p. 2051-2058, 2008.

Quast, C. *et al.* The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. *Nucleic Acids Res.*, v. 41, n. Database issue, p. D590-D596, 2013.

Rocha, U.N.; Plugge, C.M.; George, I.; Van Elsas, J.D. & Van Overbeek, L.S. The rhizosphere selects for particular groups of Acidobacteria and Verrucomicrobia. *PLoS One*, v. 8, n. 12, p. 16-20, 2013.

Ryu, S.H. *et al.* Devosia geojensis sp. nov., isolated from diesel-contaminated soil in Korea. *Int. J. Syst. Evol. Microbiol.*, v. 58, n. Pt 3, p. 633-636, 1º mar. 2008.

Sambrook, J. & Russel, D.W. *Molecular cloning: a laboratory manual.* 3. ed. Cold Spring HArbor, NY: Cold Springer Harbor Laboratory Press, 2001.

Sanford, R.A.; Cole, J.R. & Tiedje, J.M. Characterization and description of Anaeromyxobacter dehalogenans gen. nov., sp. nov., an aryl-halorespiring facultative anaerobic myxobacterium. *Appl. Environ. Microbiol.*, v. 68, n. 2, p. 893-900, 2002.

Santos, H.F. *et al.* Mangrove bacterial diversity and the impact of oil contamination revealed by pyrosequencing: bacterial proxies for oil pollution. *PloS One*, v. 6, n. 3, p. e16943, 2011.

Schleheck, D.; Tindall, B.J.; Rosselló-Mora, R. & Cook, A.M. Parvibaculum lavamentivorans gen. nov., sp. nov., a novel heterotroph that initiates catabolism of linear alkylbenzenesulfonate. *Int. J. Syst. Evol. Microbiol.*, v. 54, n. Pt 5, p. 1489-1497, 2004.

Schloss, P.D. *et al.* Introducing mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities. *Appl. Environ. Microbiol.*, v. 75, n. 23, p. 7537-7541, 2009.

Schulte, E.E. & Hopkins, B.G. Estimation of soil organic matter by weight loss-on- ignition, *in Soil organic matter: analysis and Interpretation.* Madison, Wiscosin, USA: Soil Science Society of America, Inc., v. 49, p. 21-31, 1996.

Soares, M.O.; Teixeira, C.E.P.; Bezerra, L.E.A.; Rossi, S.; Tavares, T.C.L. & Cavalcante, R.M. Brazil oil spill response: time for coordination. *Science*, v. 367, n. 6474, p. 155, 2020.

Sodré, V. *et al.* Physiological aspects of mangrove (*Laguncularia racemosa*) grown in microcosms with oil-degrading bacteria and oil contaminated sediment. *Environ. Pollut.* (Barking, Essex: 1987), v. 172, p. 243-249, 2013.

Soto-Ramírez, N. *et al.* Halobacillus mangrovi sp. nov., a moderately halophilic bacterium isolated from the black mangrove Avicennia germinans. *Int. J. Syst. Evol. Microbiol.*, v. 58, n. 1, p. 125-130, 2008.

Spalding, M.; Kainuma, M. & Collins, L. *World Atlas of Mangroves*. London-Washington, DC: Earthscan, v. 39, 2010.

Sung, Y. *et al.* Characterization of two tetrachloroethene-reducing, acetate-oxidizing anaerobic bacteria and their description as Desulfuromonas michiganensis sp. nov. *Appl. Environ. Microbiol.*, v. 69, n. 5, p. 2964-2974, 2003.

Suzuki, S. & Hiraishi, A. Novosphingobium naphthalenivorans sp. nov., a naphthalene-degrading bacterium isolated from polychlorinated-dioxin-contaminated environments. *J. Gen. Appl. Microbiol.*, v. 53, n. 4, p. 221-228, 2007.

Tavares, T.C.L.; Bezerra, W.M.; Normando, L.R.O.; Rosado, A.S. & Melo, V.M.M. Brazilian semi-arid mangroves-associated microbiome as pools of richness and complexity in a changing world. *Front. Microbiol.*, v. 12, p. 2485, 2021.

Thomas, F.; Hehemann, J.H.; Rebuffet, E.; Czjzek, M. & Michel, G. Environmental and gut bacteroidetes: the food connection. *Front. Microbiol.*, v. 2, n. MAY, p. 1-16, 2011.

Verma, M.; Kumar, M.; Dadhwal, M.; Kaur, J. & Lal, R. Devosia albogilva sp. nov. and Devosia crocina sp. nov., isolated from a hexachlorocyclohexane dump site. *Int. J. Syst. Evol. Microbiol.*, v. 59, p. 795-799, 2009.

Wang, Y.; Sheng, H.F.; He, Y.; Wu, J.Y.; Jiang, Y.X.; Tam, N.F.Y. & Zhou, H.W. Comparison of the levels of bacterial diversity in freshwater, intertidal wetland, and Mmrine sediments by using millions of illumina tags. *Appl. Environ. Microbiol.*, v. 78, n. 23, 2012.

Wu, Q.; Sanford, R.A. & Löffler, F.E. Uranium(VI) reduction by Anaeromyxobacter dehalogenans strain 2CP-C. *Appl. Environ. Microbiol.*, v. 72, n. 5, p. 3608-3614, 2006.

Yuan, J. *et al.* Oceanicola pacificus sp. nov., isolated from a deep-sea pyrene-degrading consortium. *Int. J. Syst. Evol. Microbiol.*, v. 59, n. Pt 5, p. 1158-1161, 2009.

Zhang, S. *et al.* Microbial diversity of mangrove sediment in Shenzhen Bay and gene cloning, characterization of an isolated phytase-producing strain of SPC09 B. cereus. *Appl. Microbiol. Biotechnol.*, v. 99, n. 12, p. 5339-5350, 2015.

Zhang, Y.; Dong, J.; Yang, Z.; Zhang, S. & Wang, Y. Phylogenetic diversity of nitrogen-fixing bacteria in mangrove sediments assessed by PCR-denaturing gradient gel electrophoresis. *Arch. Microbiol.*, v. 190, n. 1, p. 19-28, 2008.

Zhao, C. & Ruan, L. Biodegradation of enteromorpha prolifera by mangrove degrading micro-community with physical-chemical pretreatment. *Appl. Microbiol. Biotechnol.*, v. 92, n. 4, p. 709-716, 2011.