



# Mangrove microbiota along the urban-to-rural gradient of the Cayenne estuary (French Guiana, South America): Drivers and potential bioindicators

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## ABSTRACT

The microbial communities inhabiting the Atlantic-East Pacific (AEP) mangroves have been poorly studied, and mostly comprise chronically polluted mangroves. In this study, we characterized changes in the structure and diversity of microbial communities of mangroves along the urban-to-rural gradient of the Cayenne estuary (French Guiana, South America) that experience low human impact. The microbial communities were assigned into 50 phyla. Proteobacteria, Chloroflexi, Acidobacteria, Bacteroidetes, and Planctomycetes were the most abundant taxa. The environmental determinants found to significantly correlated to the microbial communities at these mangroves were granulometry, dieldrin concentration, pH, and total carbon (TC) content. Furthermore, a precise analysis of the sediment highlights the existence of three types of anthropogenic pressure among the stations: (i) organic matter (OM) enrichment due to the proximity to the city and its wastewater treatment plant, (ii) dieldrin contamination, and (iii) naphthalene contamination. These forms of weak anthropogenic pressure seemed to impact the bacterial population size and microbial assemblages. A decrease in Bathyarchaeota, “*Candidatus Nitrosopumilus*”, and *Nitrospira* genera was observed in mangroves subjected to OM enrichment. Mangroves polluted with organic contaminants were enriched in Desulfobacteraceae, Desulfarculaceae, and Acanthopleuribacteraceae (with dieldrin or polychlorobiphenyl contamination), and Chitinophagaceae and Geobacteraceae (with naphthalene contamination). These findings provide insights into the main environmental factors shaping microbial communities of mangroves in the AEP that experience low human impact and allow for the identification of several potential microbial bioindicators of weak anthropogenic pressure.

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## 1. Introduction

Tropical and subtropical intertidal zones are occupied by iconic mangrove forests ecosystems, extending approximately 137,000 km<sup>2</sup> along the shores of 123 countries (Bunting et al., 2018). Within latitudes of around 32°N and 38°S, mangroves harbor significant biodiversity distributed in two distinct floristic realms (Spalding, 2010), the AEP and the Indo–West Pacific (IWP) (Duke, 1992). These forests are assemblages of salt-tolerant trees and shrubs that grow on soft sediments in places where freshwater mixes with seawater (e.g., estuarine margins and coastal marine environments). Mangroves are well adapted to dynamic environments (salinity fluctuations, periodic flooding, and anoxia of sediment) and are among the most productive ecosystems in tropical coastal areas (Donato et al., 2011). They carry out functions of great ecological importance (e.g., carbon and nutrient recycling, provision of breeding and feeding areas), and they also provide valuable ecosystem services such as coastal protection (Massel et al., 1999) and climate change mitigation (Laffoley and Grimsditch, 2009; Walcker et al., 2018). Despite the numerous services they provide, mangroves are being degraded by anthropogenic activities and lost at an alarming rate in some areas (Carugati et al., 2018).

The benthic microbiota plays a fundamental role in mangrove functioning because it processes most of the energy flow and nutrients. It is responsible for OM degradation and nutrient recycling (Alongi, 1994). Mangrove microorganism biodiversity has been the subject of numerous studies, which have deepened our understanding of the microbial communities inhabiting the mangrove rhizosphere (Gomes et al., 2014) and mangrove sediments (Jiang et al., 2013; Mendes et al., 2012; Nogueira et al., 2015; Rocha et al., 2016; Santana et al., 2019). However, most of the studies were mainly focused on mangroves in the IWP region. Most of the studies conducted in the AEP region have been within the Eastern American subregion and dealt with coastal mangroves in southern Brazil (Dias et al., 2010, 2011; Peixoto et al., 2011; Rigonato et al., 2013) and Colombia (Torres et al., 2019). In these countries, the anthropogenic pressure on mangroves is very strong in some areas due to the proximity of big industrial cities and sites of offshore oil exploitation. Because microorganisms are stress-sensitive, several microbial bioindicators of pollution were identified in Brazilian and Colombian mangroves (Peixoto et al., 2011; Torres et al., 2019).

Apart from chemical contaminants (Matturro et al., 2016; Sheng et al., 2016; Zhang et al., 2014), the microbial structure and composition of prokaryotic communities in soils and sediments are known to be shaped by several physicochemical factors such as carbon and nitrogen concentration (Liu et al., 2012), redox potential (DeAngelis et al., 2010), pH (Aciego Pietri and Brookes, 2008; Wardle, 1992), and salinity (Chambers et al., 2016). Compared to the IWP mangroves and the human-impacted AEP mangroves, relatively little is known about the factors shaping the distribution of the microbial communities in low-human impacted AEP mangroves. Within the Eastern American subregion of the AEP zone, the mangrove coastline of the Guianas (between the Oyapock and Orinoco Rivers estuaries) appears to be an exception, as the mangroves here experience low-level human impact (Diop et al., 2016; Michelet et al., 2021). In French Guiana (FG), mangroves occupy about 80% of the coastal line with a total extent of about 70,000 ha (Fromard et al., 2004). Due to their localization, near the Amazon's mouth (Brazil), FG mangroves are very dynamic and are under the influence of one of the world's largest sediment discharge systems (Anthony et al., 2010; Marchand et al., 2006).

In order to better understand which environmental drivers are important to explain the compositional changes of mangrove microbiota in the AEP, an analysis of the microbial diversity in Guiana's mangroves was carried out.

Based on the same sedimentary cores used by Michelet et al. (2021) and considering the different sedimentary layers, we assessed the microorganism response to low human pressure along the Cayenne estuary and defined the main environmental drivers shaping the structure and diversity of communities.

Finally, an exploration of the changes in the relationship between mangrove microbiota diversity and the abiotic environment, according to sediment depth and the urban-to-natural gradient, allowed us to identify potential microbial bioindicators of mangrove health.

## 2. Materials and methods

### 2.1. Study area and sampling strategy

The location of the study area was the Cayenne estuary in FG (South America; Fig. 1). Three stations (S1, S2, and S3) were selected on the edge of the estuary (<5 m) and at an increasing distance from Cayenne city, which is the largest city and the capital of FG (61,268 inhabitants; INSEE 2017), along an urban-to-natural gradient. Station 1 (S1) is located at the Crique Fouillée tributary creek (4°54'53.208" N, 52°20'15.9324" W; Fig. 1), draining urban waters and the effluents of the wastewater treatment plant of Cayenne city (urban, commercial, and industrial waters). Station 2 (S2) is located near the confluence of the Cayenne and Montsinery Rivers, which flow in the Cayenne estuary (4°53'49.2288" N, 52°22'27.714" W; Fig. 1). This station receives water from the suburban Cayenne drainage basin. Station 3 (S3) is located southeast of Cayenne city, 11.7 km from S1 and 4.7 km from S2, along the Cayenne River (4°51'31.9716" N, 52°23'59.5248" W; Fig. 1) in a natural area farther from human activities.

At each station, three sediment cores (A, B and C) were collected at low tide, within a 10 m<sup>2</sup> plot and located 2 m away from each other, with plexiglass tubes (internal diameter 10.4 cm, height 20 cm) between November 19 and 21, 2017 (spring tides, dry season). The sediment cores were sliced in 0.5 cm thick layers around the two first centimeters, then 1 cm thick layers until the end of the core. The obtained layers were randomly subsampled to create 3 pools of sediments: 0 to 2 cm, 2 to 10 cm, and 10 cm to the end of the core.

During subsampling, the pH and redox potential (Eh) were immediately measured with a multiparameter probe (WTW Multi 3500i). The slices were then subsampled for characterization of environmental parameters: granulometry, TC, total nitrogen (TN), trace metals and metalloids (TMM), organic contaminants, and microbial analysis. Subsamples were immediately frozen and stored at –80 °C (for TC, TN, TMM, organic contaminants, and microbial analyses) or 4 °C (for granulometry analysis).

### 2.2. Treatment

#### 2.2.1. Measurement of TC and TN and determination of granulometry

Sediments were freeze-dried over 24 h, crushed to powder, and homogenized for sediment analysis. TC and TN were measured by combustion at 930 °C using a CHN carbon analyzer (Flash-2000; Thermo Fisher Scientific Inc., Milan, Italy). In FG, the total organic carbon and TC appeared to be very well correlated, due to the lack of carbonates (Marchand et al., 2004). Thus, TC can be considered as a proxy for carbon organic content in the sediments. Granulometry analysis was realized using a laser beam diffraction analyzer (Partica LA-950V2; Horiba Instruments, Inc.).

#### 2.2.2. Contaminants and TMM analysis

Five groups of organic contaminants—15 polycyclic aromatic hydrocarbons (PAHs), some of which are frequently monitored according

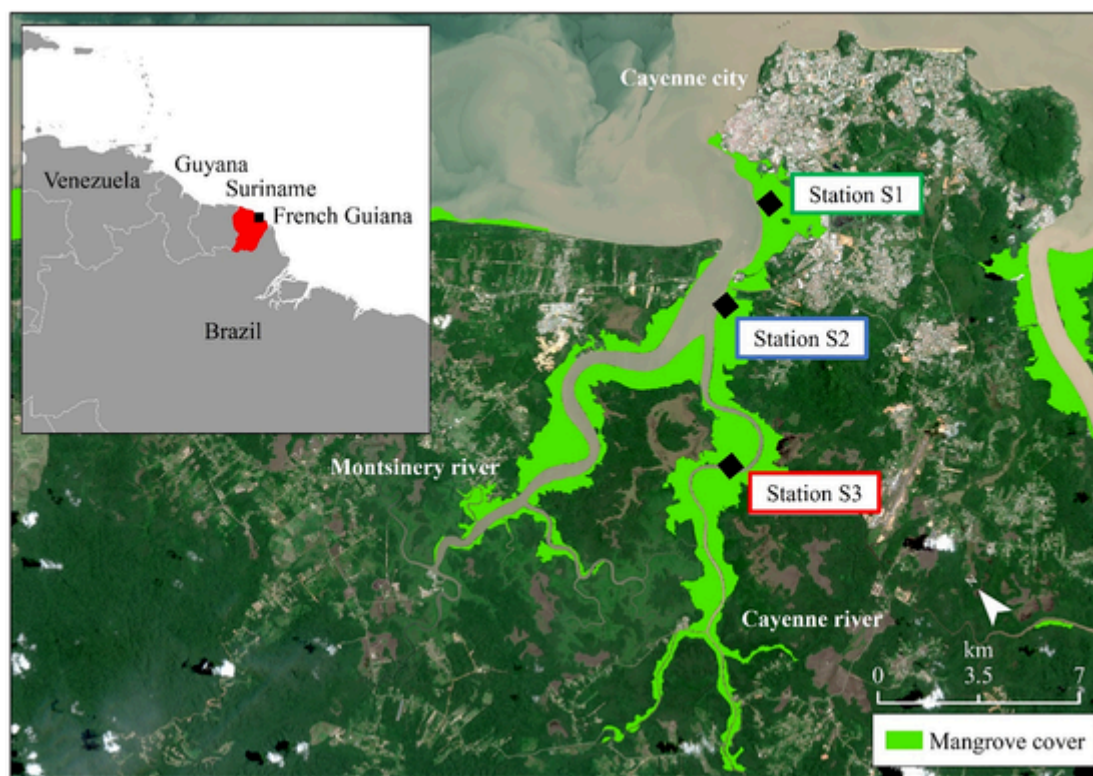


Fig. 1. Location of mangrove sampling stations in FG (South America). S1 is located near Cayenne city, S2 at the confluence of Cayenne and Montsinery Rivers, and S3 along the Cayenne River. Mangrove cover is represented in green. (Modified from Michelet et al., 2021). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

to recommendations by the European Union and the US Environmental Protection Agency (acenaphthene, acenaphthylene, anthracene, benzo [ghi]perylene, benzo[a]anthracene, benzo[b]fluoranthene, benzo [b + k]fluoranthene, benzo[thiophene, biphenyl, chrysene, dibenzothiophene, fluoranthene, fluorene, naphthalene, phenanthrene, and pyrene), 11 polychlorinated biphenyls (PCB-7, PCB-28, PCB-52, PCB-101, PCB-105, PCB-118, PCB-138, PCB-153, PCB-156, PCB-169, and PCB-180), 12 organochlorine pesticides (2,4-DDT, 2,4-DDD, 2,4-DDE, 4,4-DDD, 4,4-DDE, 4,4-DDT, aldrin, chlordecone, dieldrin, endrin, hexachlorobenzene (HCB), and isodrin), 6 phthalates (DMP, DEP, DBP, BBP, DEHA, and DEHP), and 7 polybromodiphenylethers (BDE 28, BDE 47, BDE 99, BDE 100, BDE 153, BDE 154, and BDE 183) were extracted from the sediments and analyzed (Michelet et al., 2021). For PAHs, PCB, and pesticides quantification, naphthalene  $d_8$ , biphenyl  $d_{10}$ , phenanthrene  $d_{10}$ , pyrene  $d_{10}$ , chrysene  $d_{12}$ , benzo(a)pyrene  $d_{12}$ , benzo (g,h,i)perylene  $d_{12}$  were used as standards. For the plastic additives, di (2-ethylhexyl) phthalate- $d_4$  and BDE 77 were respectively used as standards. All standards were obtained from LGC Standard (Wesel, Germany) and Interchim (Montluçon, France). In order to discriminate the sources of PAHs, the ratios Flt/(Flt + Pyr) and Ant/(Ant/Phe) (Flt, fluoranthene; Pyr, pyrene; Ant, anthracene; Phe, phenanthrene) were calculated and compared to the published cut-off values (at  $>0.5$ , PAHs are likely to occur from biomass burning) (Brändli et al., 2007; Katsoyiannis et al., 2007).

Twenty-seven TMM were quantified in each sample such as lead (Pb), chromium (Cr), nickel (Ni), copper (Cu), zinc (Zn), manganese (Mn), mercury (Hg), arsenic (As) and molybdenum ( $^{95}\text{Mo}$ ). Extraction and analysis protocols are presented in detail in Michelet et al. (2021). To check the accuracy of the TMM measurements, the certified reference material MESS-4 (National Research Council Canada) was run before starting the measurements and many times per analytical batch (Supplementary Data A). The analytical recovery was within 10% compared to certified concentration. Freeze-dried sediment (Christ Gamma

1-16 LSCplus) were analyzed for particulate Hg using a CV-AAS (LECO AMA 254) equipped with a low Hg optical cell. The method detection limit was 2 pg (3 times the standard deviation of the blank samples). The measured values were always within  $\pm 5\%$  of the recommended values.

#### 2.2.3. Total DNA extraction and quantification

Sediments were freeze-dried for 48 h and crushed to powder using a sterilized mortar and pestle. Total DNA was then extracted from 0.25–0.30 g dry sediment with the DNeasy PowerSoil Kit (Qiagen) according to the manufacturer's protocol. The DNA extracts were quantified by fluorometric dosage with a Quantifluor dsDNA system kit (Promega) according to the supplier's recommendations. The total DNA measurement (molecular microbial biomass) was used as a proxy for the microbial biomass.

#### 2.2.4. Quantitative polymerase chain reaction (qPCR)

To determine the bacterial and archaeal abundances in the sediments, 16S rRNA genes (*rrs*) were quantified by qPCR. The GoTaq qPCR Master Mix (Promega) was used following the supplier's recommendations, using specific archaeal (931F: 5'-AGGAATTGGCGGGGAGCA-3' and m1100R: 5'-BTGGGTCTCGCTCGTTRCC-3') and bacterial (300F: 5'-GCCTACGGGAGGCAGCAG-3' and univ516R: 5'-GTDTTACCGCGGCKGCTGRCA-3') primer sets (for a review, see Klindworth et al., 2013). The qPCR cycles for archaea consisted of initial denaturation (3 min at 98 °C), followed by 35 cycles of denaturation for 10 s at 98 °C, primer hybridization for 10 s at 62 °C, and elongation for 20 s at 72 °C. For bacteria, the first step of initial denaturation lasted 2 min at 98 °C, followed by 30 cycles of initial denaturation for 5 s at 58 °C, primer hybridization for 10 s at 55 °C, and elongation for 12 s at 72 °C.



### 2.2.5. 16S rRNA gene amplification and sequencing

To characterize the structure and composition of the bacterial and archaeal communities, hypervariable regions V4–V5 of the 16S rRNA genes were amplified by PCR using the 515f (5'-TGT GYC AGC MCG CGC GGT A-3') and 928r (5'-CCG YCA ATT CMT TTR AGT-3') primer sets (Parada et al., 2016). Each 25  $\mu$ L reaction mix contained 2  $\mu$ L of DNA ( $\sim$ 0.5–5 ng  $\mu$ L<sup>-1</sup>), 10  $\mu$ M of 515f forward primer, 10  $\mu$ M of 928r reverse primer, 10 mM of dNTPs, 0.4  $\mu$ L of Pfu DNA polymerase (Promega), and 2.5  $\mu$ L of Pfu buffer (Promega). The PCR cycles consisted of initial denaturing for 2 min at 94 °C, followed by 35 cycles composed of denaturation for 20 s at 94 °C, primer hybridization for 20 s at 50 °C, and elongation for 25 s at 72 °C in a T100 thermal cycler (Bio-Rad). PCR products were verified by agarose gel electrophoresis (1.5% w/v). Amplicon purification was performed using the Agencourt AMPure XP system, and quantification, with QuantIT PicoGreen. Primers containing the Illumina adapters flanked by floating tails complementing those on amplicons and 5  $\mu$ L of purified amplicons were added for the second round of amplification. The PCR cycling started at 94 °C for 2 min, followed by 12 cycles of amplification (94 °C for 1 min, 55 °C for 1 min, 68 °C for 1 min), and a final extension step at 68 °C for 10 min. The purified amplicons were sequenced on an Illumina MiSeq platform (Genotoul, Toulouse, France).

### 2.2.6. Sequence analysis

The raw data were processed using the dada2 package (v.3.9) in R studio interface (v3.2.3) following the workflow described by Callahan et al. (2016). The raw sequence datasets are available in the National Center for Biotechnology Information database under the PRJNA735070 BioProject. For taxonomic assignment, amplicon sequence variants (ASVs) were compared with the Silva database (Silva v\_132) (Quast et al., 2013). All non-assigned reads at the phylum level and reads belonging to chloroplasts and mitochondria were removed from the dataset. To compare the diversity index (specific richness and Shannon index), the samples were rarefied at an even number of sequences (4180 reads) with the phyloseq package (v3.9) (McMurdie and Holmes, 2013).

### 2.3. Statistical analysis

Statistical analyses were performed with R studio software (v3.2.3). As described by Michelet et al. (2021), a multiple factor analysis (MFA) (Escofier and Pagès, 1994) constituted by four variable groups (physicochemical parameters, OM, organic contaminants, and TMM) was performed using FactoMineR (Lê et al., 2008) and factoextra (Kassambara and Mundt, 2020) packages to compare microbiota and environmental parameters in the three stations and depths (statistical individuals). Only variables with a large contribution to one of the axes ( $\cos^2 > 0.5$ ) were plotted (Fig. 2). Differences in environmental parameters and relative abundance of each taxonomic group were tested and displayed by the Scheirer–Ray–Hare test and Wilcoxon pairwise test in the R companion package (Mangiafico, 2021). A forward selection and a permutation test (vegan package) (Oksanen et al., 2020) were performed on the noncollinear variables (lattice package) (Sarkar, 2008) to determine the environmental drivers of the microbial community composition. This selection was followed by permutational multivariate analysis of variance (PERMANOVA) in the vegan package in order to test the differences in prokaryotic composition between samples. The top 30 phyla Z-scores were calculated in the ComplexHeatmap package (Gu et al., 2016), and these analyses were completed with pairwise Spearman correlation ( $r_s$ ) to determine the correlations between taxa and environmental factors.

## 3. Results and discussion

### 3.1. Sampling stations characteristics and specificities

The physicochemical parameters (pH, Eh, granulometry), organic matter characteristics (TC, TN, TC:TN), TMM levels, and organic contaminant concentrations of sediments from three sampling sites (S1, S2, and S3) and three depths (0–2, 2–10, and > 10 cm) are recorded in Table 1 and in Supplementary Tables B. In addition, multivariate analysis (MFA) was used to determine the sediment characteristics and specificities (Fig. 2).

Axis 1 shows a separation between stations, mainly explained by variations in granulometry, TC, TN, TC:TN, and TMM concentrations (Fig. 2B). All sediments were dominated by the silt fraction (74–89%), but a higher sand value is shown for S1 (18–21%;  $p > 0.05$ ), situated closer to the ocean (Fig. 2B, Supplementary Data B). At this station, higher TC (2–6%) was also measured ( $p < 0.001$ ; Fig. 2B; Supplementary Data B), while the TC levels in the sediment at S2 and S3 (1–2%) were lower and similar to those of nearby mangroves (Marchand et al., 2006). A slight enrichment in nitrogen was also observed in the surficial sediment at S1 (TN  $\sim$ 0.3%; Fig. 2B, Supplementary Data B). The slight OM enrichment observed was likely due to the proximity with Cayenne city (urban runoff) and its wastewater treatment plant. Higher TC:TN ratios were also observed at S1 at all depths (15.1 to 17.9;  $p < 0.001$ ; Fig. 2B, Supplementary Data B). This ratio is usually used as a proxy to determine the source and fate of OM in water (e.g., Gordon and Goni, 2003; Ramanathan et al., 2008; Wu et al., 2007). The measured values in S1 are in line with TC:TN ratio generally observed for terrigenous OM (e.g., mangrove tree leaves and roots), which is known to be poorly degradable by microorganisms (Marchand et al., 2003). The OM characteristics (TN, TC, and TC:TN ratio) were very similar at S2 ( $10.3 \pm 1.2$ ) and S3 ( $9.5 \pm 0.4$ ). S1 was also characterized by 1.2 times higher Hg concentration than the two other stations ( $p < 0.01$ ; Table 1, Fig. 2B). A positive correlation was found between Hg and TC ( $r_s = 0.76$ ;  $p < 0.001$ ). Previous studies have shown that OM content probably promotes Hg storage in mangrove sediments (Marchand et al., 2006; Lei et al., 2019). The Hg concentrations measured in the Cayenne estuary correspond to natural background levels observed in mangrove estuarine sediments in FG (Marchand et al., 2006) and were below the NOAA ERL sediment quality guidelines (low effects range) (Burton, 2002). The concentrations of <sup>95</sup>Mo (2.6–1.8  $\mu$ g g<sup>-1</sup>) and <sup>111</sup>Cd (0.07–0.08  $\mu$ g g<sup>-1</sup>) were also higher at S1 ( $p < 0.001$ ; Table 1, Fig. 2B). On the contrary, Cr, Zn, Al, and Mn concentrations were lower at S1 ( $p < 0.01$ ). At S2 and S3, the Cr content (84.5  $\mu$ g g<sup>-1</sup>) was slightly higher than the NOAA ERL values (80  $\mu$ g g<sup>-1</sup>) (Burton, 2002) and higher than the range already observed in FG (Marchand et al., 2006). At S3, the Zn concentration (155.5  $\mu$ g g<sup>-1</sup>) in the sediments was also slightly higher than the ERL value (150  $\mu$ g g<sup>-1</sup>). As concluded by Marchand et al. (2006), even if the origin of metals is difficult to clearly define, metals in FG mangrove sediments most probably result from diagenetic processes rather than anthropogenic inputs. Observed differences between stations are probably related to the differences in granulometry (e.g., sand content) and TC contents.

The second axis of the MFA discriminated the samples based on pH, redox potential, and organic contaminant concentration (Fig. 2B). The pH of sediment pore water was 6.2 on average (min 5.7, max 6.5), but clear differences in pH profiles were observed between stations. Notably, pH gradients existed within the sedimentary columns at S1 and S3, where increases and decreases greater than 0.5 pH units were observed, respectively. The sediments were dominated by aerobic redox conditions in S1 and S3 (Eh  $\sim$ 100–200 mV) and were more reduced in S2 (Eh  $\sim$ –100 mV) (Fig. 2B, Supplementary Data B). Significant differences in pesticide, PCB, and PAH concentrations were also observed between stations ( $p < 0.05$ ; Fig. 2B, D). Although organochlorine pesticides (HCB, ddd24, dieldrin) and PCBs were detected at S1, the highest

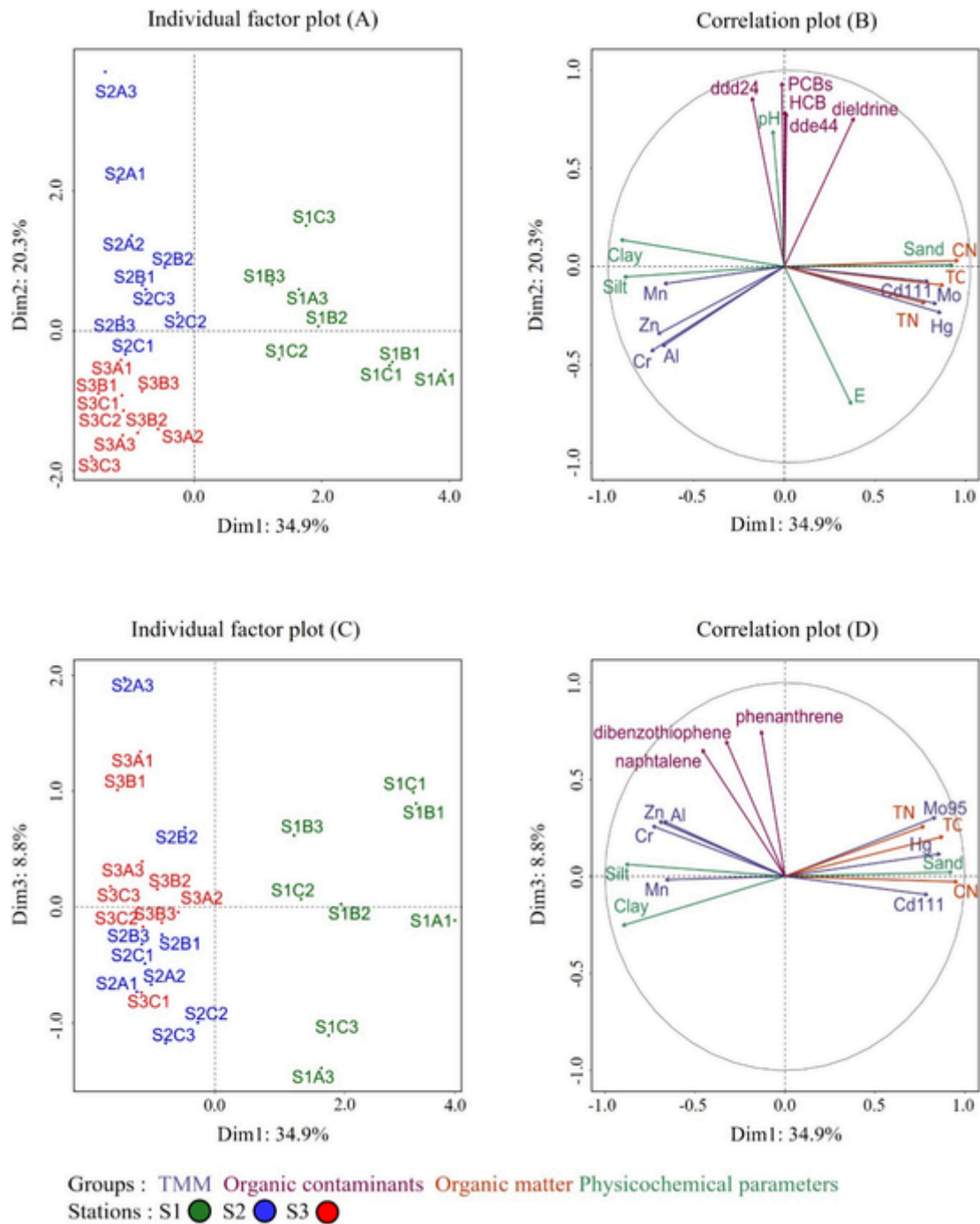


Fig. 2. Multiple factor analysis of data obtained from different stations with four groups of variables ( $\cos^2 > 0.5$ ): physicochemical parameters (green), OM (orange), organic contaminants (purple), and TMM (blue). Graphs represent (A, C) individual factor plots and (B, D) correlation plots on axes 1 and 2 (A, B) and 1 and 3 (C, D). Dots correspond to 26 samples from three sampling stations: S1 (green), S2 (blue), S3 (red). A, B, C indicate replicates; 1: 0–2 cm; 2: 2–10 cm; 3: > 10 cm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

concentrations were observed at S2 (Table 1, Fig. 2B). These compounds are among the 12 most persistent organic pollutants (POPs) according to the Stockholm Convention on POPs (2001) and are also listed as priority chemicals in the EU Water Framework Directive 2013/39/EC (European Union, 2013). Among these compounds, dieldrin was the only one to show values close to or slightly higher than the ERL ( $2 \text{ ng g}^{-1}$ ) for about half of the samples at S2 (Table 1). This pesticide was used extensively in agriculture as an alternative to DDT until its use was forbidden by the French government in 1972. Measured HCB concentrations (up to  $5.7 \text{ ng g}^{-1}$ ) were under the no-effect concentration value of  $20 \text{ ng g}^{-1}$  for chronic exposure of benthic organisms (OSPAR

ERL value) (Long et al., 1995). However, the quality of the sediment could be poor (class 3) according to the environmental quality classification of sediment in Norway (Bakke et al., 2010). Following this classification, considering the sum of DDT, the sediments would be considered as good (class 2) or even, for some samples, as background (class 1) (Long et al., 1995). The maximum value of the sum of PCBs ( $6.8 \text{ ng g}^{-1}$ ; Table 1) was far from the sediment ERL guideline value of  $23 \text{ ng g}^{-1}$  (Long et al., 1995). The maximum value of the sum of PCBs ( $6.8 \text{ ng g}^{-1}$ ; Table 1) was far from the sediment ERL guideline value of  $23 \text{ ng g}^{-1}$  (Long et al., 1995). By contrast, compared to the other two stations, S3 was characterized by elevated concentrations of naphtha-

**Table 1**Levels of organic contaminants and metals in sediments at three depths (0–2, 2–10, > 10 cm) at three sampling stations (mean  $\pm$  SD,  $n = 3$ ).

Depth	Station 1			Station 2			Station 3		
	0–2 cm	2–10 cm	> 10 cm	0–2 cm	2–10 cm	> 10 cm	0–2 cm	2–10 cm	> 10 cm
Organic contaminants concentrations (ng g <sup>-1</sup> d.w.)									
ddd24	0.1 $\pm$ 0.1	0	0.3 $\pm$ 0.3	0.3 $\pm$ 0.5	0.2 $\pm$ 0.1	0.5 $\pm$ 0.5	0	0	0
dde44	0.1 $\pm$ 0.1	0	0.3 $\pm$ 0.3	0.1 $\pm$ 0.2	0.2 $\pm$ 0.2	0.2 $\pm$ 0.3	0	0	0
DBT	0	2.8 $\pm$ 3.9	2.4 $\pm$ 4.2	4.4 $\pm$ 7.6	2.4 $\pm$ 4.1	10.1 $\pm$ 17.4	11.2 $\pm$ 12.6	1.4 $\pm$ 2.4	6.4 $\pm$ 1.6
Dieldrin	1.6 $\pm$ 0.3	1.7 $\pm$ 0.3	1.8 $\pm$ 0.3	1.9 $\pm$ 0.2	1.9 $\pm$ 0.3	<b>2.0 <math>\pm</math> 0.1</b>	0	0	0
HCB	1.1 $\pm$ 1.0	0.7 $\pm$ 0.1	1.4 $\pm$ 0.9	1.9 $\pm$ 2.2	0.6 $\pm$ 0.4	2.8 $\pm$ 2.6	0	0	0
Naphthalene	0	0	0	0	28.1 $\pm$ 48.6	<b>227.5 <math>\pm</math> 394.1</b>	<b>274.1 <math>\pm</math> 191.6</b>	<b>110.5 <math>\pm</math> 33.6</b>	<b>232.2 <math>\pm</math> 33.4</b>
PCBs	1.2 $\pm$ 0.5	1.1 $\pm$ 0.1	2.2 $\pm$ 0.9	1.4 $\pm$ 4.3	3.2 $\pm$ 0.9	3.4 $\pm$ 3.0	0.1 $\pm$ 0.1	0	0
Phenanthrene	8.5 $\pm$ 1.2	12.5 $\pm$ 5.0	6.7 $\pm$ 6.9	7.3 $\pm$ 4.8	8.1 $\pm$ 5.1	14.1 $\pm$ 13.5	17.0 $\pm$ 18.9	6.0 $\pm$ 1.6	9.3 $\pm$ 1.3
TMM concentrations ( $\mu$ g g <sup>-1</sup> d.w.)									
Al (mg g <sup>-1</sup> )	109.3 $\pm$ 5.8	113.2 $\pm$ 1.5	107.8 $\pm$ 5.0	115.8 $\pm$ 3.7	115.0 $\pm$ 3.7	114.7 $\pm$ 6.0	118.3 $\pm$ 1.5	117.9 $\pm$ 0.5	116.9 $\pm$ 6.0
<sup>111</sup> Cd	0.09 $\pm$ 0.02	0.08 $\pm$ 0.01	0.08 $\pm$ 0	0.07 $\pm$ 0	0.07 $\pm$ 0.01	0.07 $\pm$ 0	0.07 $\pm$ 0	0.06 $\pm$ 0	0.07 $\pm$ 0
Cr	78.1 $\pm$ 5.0	82.5 $\pm$ 3.5	77.2 $\pm$ 4.5	<b>84.4 <math>\pm</math> 3.6</b>	<b>84.3 <math>\pm</math> 2.3</b>	<b>84.9 <math>\pm</math> 4.4</b>	<b>87.5 <math>\pm</math> 1.4</b>	<b>87.7 <math>\pm</math> 0.5</b>	<b>87.2 <math>\pm</math> 4.5</b>
Hg (ng g <sup>-1</sup> )	64.2 $\pm$ 5.0	56.3 $\pm$ 2.3	57.5 $\pm$ 4.4	44.7 $\pm$ 0.8	48.4 $\pm$ 1.2	47.9 $\pm$ 0.3	48.8 $\pm$ 1.3	53.2 $\pm$ 0.6	50.9 $\pm$ 3.4
Mn	436.7 $\pm$ 44.0	434.4 $\pm$ 225.6	424.3 $\pm$ 68.4	1328.4 $\pm$ 404.2	696.7 $\pm$ 291.3	560.0 $\pm$ 80.0	1136.6 $\pm$ 100.5	999.2 $\pm$ 227.2	840.0 $\pm$ 224.3
<sup>95</sup> Mo	2.6 $\pm$ 0.2	1.8 $\pm$ 0.1	1.9 $\pm$ 0.6	1.2 $\pm$ 0.2	1.5 $\pm$ 0.3	1.2 $\pm$ 0.1	1.3 $\pm$ 0.1	1.6 $\pm$ 0.1	1.4 $\pm$ 0.1
Zn	131.7 $\pm$ 13.3	149.20 $\pm$ 4.18	134.5 $\pm$ 14.2	149.4 $\pm$ 5.2	147.8 $\pm$ 6.8	146.6 $\pm$ 8.0	<b>160.2 <math>\pm</math> 4.2</b>	<b>154.0 <math>\pm</math> 2.6</b>	<b>152.4 <math>\pm</math> 6.8</b>

Bold numbers correspond to values superior to OSPAR ERL or NOAA threshold.

lene (96.4 to 468.9 ng g<sup>-1</sup>; Table 1), one of the 16 PAHs considered to be priority pollutants by the EPA (Bojes and Pope, 2007). According to the values of the Flt/(Flt + Pyr) ratio, usually used to discriminate the sources of PAHs, hydrocarbons detected in Cayenne River sediments are from diesel and wood combustion (Pereira et al., 2019; Pichler et al., 2021). When present in the sediments, naphthalene levels were always higher than the NOAA threshold effect level (34.57 ng g<sup>-1</sup>), and for some samples, were above the NOAA ERL value (160 ng g<sup>-1</sup>) (MacDonald et al., 2000).

The study of Michelet et al. (2021) on the same cores showed low averaged concentrations of the sum of the different organic contaminants measured (PAHs, organochlorine pesticides) in the whole sedimentary cores that were under the regulatory thresholds. By considering the mean individual concentrations of compounds at each depth layers (0–2 cm; 2–10 cm; > 10 cm), it clearly appears however that some compounds were above the regulatory thresholds in some layers at stations 2 et 3 (i.e. dieldrin and naphthalene, respectively).

### 3.2. Prokaryotic community of mangrove sediments of Cayenne estuary

#### 3.2.1. Estimations of community size

The total DNA extracted from the sediments (the molecular microbial biomass) was used to estimate the size of the microbial pool at the sampling stations (Dequiedt et al., 2011; Terrat et al., 2012). This proxy includes the prokaryotic communities and micro eukaryotic inhabitants of mangrove sediments (e.g., fungi and meiofauna). At stations 1 and 3, molecular microbial biomass was 3.1  $\pm$  0.4  $\mu$ g g<sup>-1</sup> d.w. and 3.98  $\pm$  0.52 g<sup>-1</sup> d.w., respectively (Supplementary Data C). Higher values were observed in the surface layer at station 2 ( $p = 0.05$ ; 7.3  $\pm$  0.8  $\mu$ g g<sup>-1</sup> d.w.). These molecular microbial biomass values correspond well to values reported in other mangrove sediments (~11–20  $\mu$ g g<sup>-1</sup>) (Fernandes et al., 2014; Jiang et al., 2011).

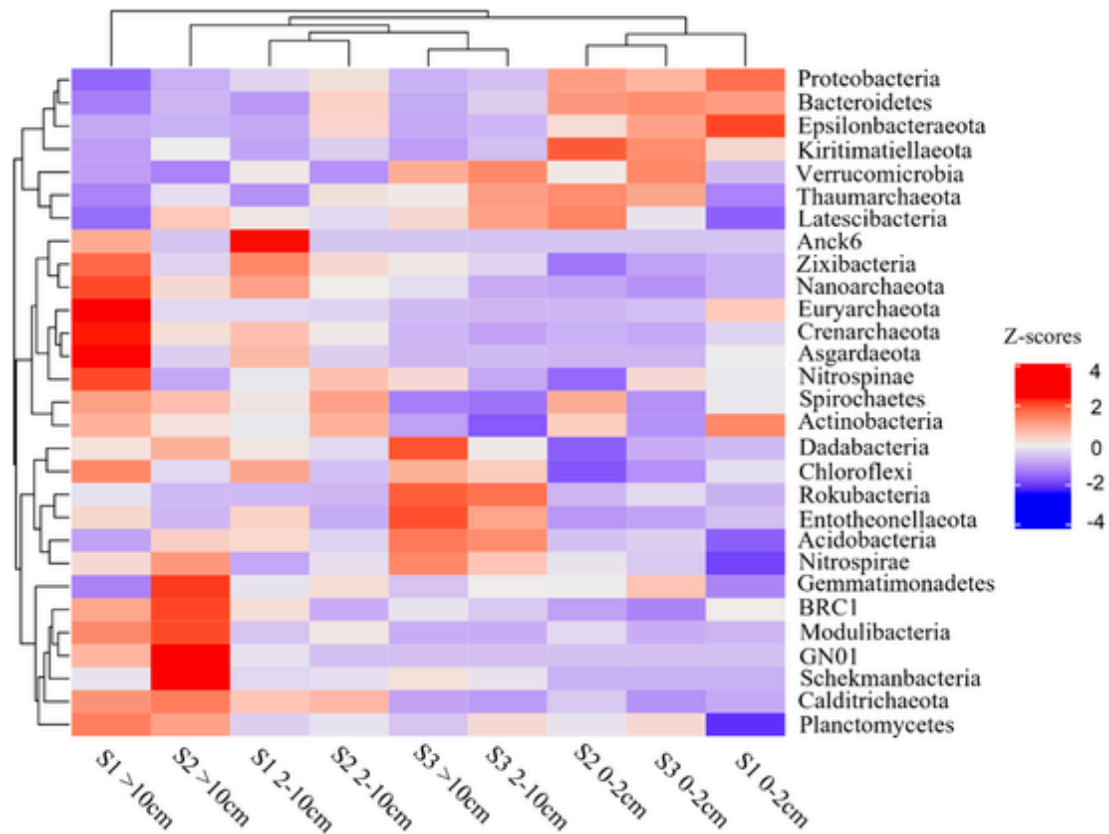
Within the microbial communities, differences were only observed in the size of the bacterial populations in the surface layer ( $p < 0.001$ ). Indeed, the number of bacterial 16S rRNA gene copies was higher at station 1 than at stations 2 and 3 ( $p < 0.01$ ) on the surface and reached 7.9  $\times 10^9$  copies g<sup>-1</sup> d.w. vs. 1.4  $\times 10^9$  and 4.9  $\times 10^5$  copies g<sup>-1</sup> d.w., respectively (Supplementary Data C). The environmental conditions at station 1 and, notably, the higher OM content (1.5- to 4-fold more than other stations), seemed to promote bacterial growth (TC and TN  $r_s = 0.7$ ,  $p < 0.01$ ) (Kaiser and Guggenberger, 2003; Rocha et al.,

2016). By contrast, the archaeal abundance was not significantly different between the three stations at any depth ( $p > 0.05$ ; 5.8  $\times 10^6$  copies g<sup>-1</sup> sediment d.w.; Supplementary Data C) and corresponded to values earlier observed for other mangrove sediments (Li et al., 2019; Zhou et al., 2017).

#### 3.2.2. Structure and composition of mangrove microbiota

After the filtering and trimming processes, 7759 ASVs were assigned (465  $\pm$  167 ASVs by sample; Supplementary Data C), and 650 ASVs that were not assigned, representing 0.6% of the community, were removed. There was no significant difference in alpha diversity between stations ( $p > 0.05$ ); specific richness and Shannon index fluctuated between 220 and 817 ASVs and 5.1 to 6.3, respectively (Supplementary Data C). By contrast to the soil microbiomes in Brazilian mangroves, microbiota associated with the Cayenne estuary's mangroves seems less diverse (Tavares et al., 2021).

The taxonomic composition of the mangrove microbiota encompassed 50 phyla (Supplementary Data D). These communities were predominantly composed of members of Proteobacteria (40–58%), Chloroflexi (9.0–22.3%), Acidobacteria (4.7–13.1%), Bacteroidetes (3.5–13.1%), Planctomycetes (3.7–6.9%), Crenarchaeota (1.0–9.4%), Thaumarchaeota (0.7–4.7%), Gemmatimonadetes (2.3–4.7%), and Nitrospirae (0.65–3.6%) (Fig. 3). The observed prevalence of the most abundant phyla (> 3% of relative abundance) is in accordance with the literature (Andreote et al., 2012; Huergo et al., 2018; Tavares et al., 2021) suggesting that Proteobacteria, Chloroflexi, Acidobacteria, Bacteroidetes, and Planctomycetes constitute the core microbiome of mangrove sediments in the AEP region. Differences in community composition were observed between depths and stations (PERMANOVA,  $p < 0.05$ ). At the phylum level, the heatmap clustering analysis highlighted several microbial patterns (Fig. 3). In the surface mangrove sediment of the three stations, the relative abundance of the major phyla Proteobacteria, Bacteroidetes, Epsilonbacteraeota, and Kiritimatiellaeota was higher. Bacteroidetes and Kiritimatiellaeota are regarded as specialists in the degradation of macromolecules, such as complex polysaccharides and proteins, to obtain carbon, amino acids, and sulfur (McBride, 2014; Sackett et al., 2019). Both phyla could have a pivotal role in initiating the mineralization of high-molecular-weight organic matter in mangrove sediments. Within the Proteobacteria, Desulfobacteraceae (1.1–6.4%), Desulfobulbaceae (1.8–4.4%), and Desulfarcuaceae (0.4–2.2%) were dominant (Supplementary Data E). These three



**Fig. 3.** Z-score heatmap of top 30 phyla (representing 94.3% of total community) at three sampling stations (S1, S2, S3). Red indicates higher Z-scores (higher relative abundance compared to mean of abundance of that phylum) and blue indicates lower Z-scores (lower relative abundance). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

families are strictly anaerobic and chemoorganoheterotrophic, and they belong to the group of sulfate-reducing bacteria (Kuever, 2014). They are commonly observed in mangroves (Huerger et al., 2018; Gong et al., 2019). Mangrove sediments contain high levels of OM and sulfates and frequently experience anaerobic conditions (Correia and Guimarães, 2017), creating favorable conditions for sulfate reduction (Gros et al., 2018; Fernández-Cadena et al., 2020). Within the Epsilonbacteraeota, sulfur-oxidizing bacteria *Sulfurimonas* (Thiovulaceae) and *Sulfurovum* (Sulfurovaceae) were the most abundant. These aerobic bacteria oxidize the sulfide produced by anaerobic sulfate-reducing bacteria, suggesting transitions between oxic and anoxic conditions in the surface sediment, probably related to tidal cycles and benthic infaunal activities. Changes of the prokaryotic communities were observed between the surficial sediment and the other sedimentary layers. Among the most abundant phyla, Planctomycetes and Caldithrichaeota were found to be enriched in deeper sediments at S1 and S2 (Fig. 3 and Supplementary Data D). Moreover, a significant increase in the relative abundance of Crenarchaeota and Gemmatimonadetes was observed at S1 and S2, respectively. Planctomycetes phylum comprises members related to Planctomycetia and Phycisphaerae, but surprisingly no known anaerobic ammonia-oxidizing microorganisms belonging to “*Candidatus* Brocardiales” were observed. Caldithrichaeota was mostly represented by the genus *Calorithrix*, but the genus *Caldithrix* is specifically observed in deeper sediments at S1 and S2. The cultured Caldithrichaeota are anaerobic, chemoorganoheterotrophic, and are able to degrade detrital proteins through the use of extracellular peptidases (Marshall et al., 2017). Members of the phylum Gemmatimonadetes are characteristically detected in the soil and mangrove microbiomes (Takayasu et al., 2019; Zhang et al., 2019). Despite their widespread distribution, their physiology and ecology are poorly described (Zeng et al., 2021). Finally, a strong vertical stratification was observed for Crenarchaeota at S1 with

higher relative abundances in the deeper sediments than in surficial sediments. Identified members of Crenarchaeota belong exclusively to Bathyarchaeota, a taxon of global generalists that are widespread in anoxic sediments (Zhou et al., 2018). Sediment depth is known to be one of the determinants in the structuration of the archaeal communities in mangrove sediment, principally due to the biogeochemical zonation along with depth profile (Zhou et al., 2017). Crenarchaeota and Lokiarchaeota usually dominate the archaeal communities in subsurface sediments, while Thaumarchaeota and Euryarchaeota dominate in surface sediments.

A different trend in the vertical stratification of the microbial communities was observed at S3. In this station, Nitrospirae, Acidobacteria, and Chloroflexi were found to be enriched in the subsurface layers. Within the phylum Nitrospirae, *Nitrospira* and *Thermodesulfobacterium* were particularly abundant at S3. *Nitrospira* plays a pivotal role in the second step of nitrification as nitrite-oxidizing bacteria (NOB) in diverse natural ecosystems (Daebeler et al., 2014) or in wastewater treatment plants (Daims et al., 2011). They are often associated with ammonia oxidizing archaea (AOA) for the two-step process of nitrification. *Nitrospira* members seem also to be able to achieve complete ammonia oxidation (comammox; Daims et al., 2015). This genus is adapted to oligotrophic conditions (Daims and Wagner, 2018; Koch et al., 2019) but little is known about potential factors driving niche specialization between comammox and canonical ammonia oxidizers. *Thermodesulfobacterium* representatives occur in anaerobic environments, where they contribute to the degradation of organic compounds and indirectly to the production of methane (Daims, 2014). Among the less abundant phyla, Latescibacteria (family Latescibacteriaceae), Entothaeonellaeota (family Entothaeonellaceae) Dadabacteria (order Dadabacteriales), Rokubacteria (order Rokubectiales) were also more abundant in the deepest layer at S3 (Fig. 3; Supplementary Data D).



Some studies have shown that factors such as pH, TC, TN, and granulometry could modulate the observed microbial patterns in mangrove sediments (Colares and Melo, 2013; Zhang et al., 2019; Li et al., 2021). The complex distributions that can be observed are notably the results of the microbial lifestyles (e.g., heterotroph or oligotroph, anaerobe or aerobe) with respect to the local environmental conditions.

### 3.2.3. Drivers of mangrove microbiota in the Cayenne estuary

Differences in microbial community composition among the sediment samples were found to have significant correlations with four environmental factors (granulometry, dieldrin, pH, and TC), together explaining  $R^2_{adj} = 31.2\%$ : sand percentage ( $p < 0.01$ ,  $R^2_{adj} = 0.12$ ), dieldrin ( $p < 0.01$ ,  $R^2_{adj} = 0.11$ ), pH ( $p < 0.01$ ,  $R^2_{adj} = 0.04$ ), and TC ( $p < 0.01$ ,  $R^2_{adj} = 0.04$ ).

Several studies reported the effects of clay, sand, and silt contents on the microbial communities in soils (e.g., Dequiedt et al., 2011) and mangrove sediments (Colares and Melo, 2013). Sessitsch et al. (2001) studied the effect of soil particle size fractions on microbial population structures. These authors demonstrated that the microbial structure was significantly affected by particle size, with higher diversity observed for microbiota inhabiting soil composed of smaller size fractions. The authors hypothesized that the low nutrient availability, protozoan grazing, and competition with microbes (i.e., fungi) could explain the reduced diversity in larger size fractions. Colares and Melo (2003) studied the relationship between microbial community structure and environmental factors in Brazilian mangrove sediments. Their redundancy analysis revealed that the silt-clay percentage was the most important factor controlling the microbial profiles. Particle size fractions (sand, silt, and clay) differ in mineralogical composition (Acosta et al., 2011). They have specific surface reactivity yielding the formation of organomineral complexes with different concentration, composition, and availability of associated OM (Christensen, 2001). As a consequence, these fractions represent various microenvironments in terms of organic substrates, but also oxygenation, accessible water, and nutrients, promoting the development of specific communities.

An unexpected outcome in this study was the identification of dieldrin as one of the main drivers of the distribution of microbial communities in the Cayenne estuary. To date, studies showing a shift in microbial communities as a result of organochlorine pesticides are scarce (Sangwan et al., 2012; Tejada et al., 2015; Wu et al., 2018). The effect of dieldrin on microbial communities was observed in the gastrointestinal system of zebrafish (Hua et al., 2021), with an increased abundance of members belonging to Verrucomicrobia and a decrease in Clostridia and Betaproteobacteria. Organochlorines can also induce shifts in microbial functions in soils, such as through suppression of nitrogen-fixing bacteria that have a pivotal role in replenishing natural nitrogen fertilizer in soil (Poltera, 2007).

In biogeography studies, pH was recognized as another factor determining the microbiota structure of soils in terms of richness, diversity, and composition (Fierer and Jackson, 2007; Lauber et al., 2009; Dequiedt et al., 2011). Chen et al. (2016) and Li et al. (2021) showed that in mangroves, pH is also one of the main factors explaining the microbial community composition in sediments regardless of the season or developmental stage of the mangrove forest. pH was also shown to be the best predictor of community structure and the relative abundance of major dominant lineages at the continental scale in North and South America (Lauber et al., 2009). Most microorganisms have a low tolerance to pH variations that affect biogeochemical processes and their activities and related biogeochemical processes (Nicol et al., 2008).

Other studies have shown that mangrove microbiota composition responds strongly to other physicochemical properties of the sediment, such as TC content (Colares and Melo, 2003; Zhang et al., 2019; Li et al., 2021). Colares and Melo (2003) highlighted a significant correlation between microbial community structure and OM content in Brazil-

ian mangroves. Zhang et al. (2019) characterized the microbiota from six Chinese mangroves and showed that mean annual precipitation and TC were the main factors explaining the distribution of the community. Tidal cycles (Zhang et al., 2018) and variables associated with the vegetation above (e.g., Jiang et al., 2013; Gomes et al., 2014; Luis et al., 2019) have also been reported to be drivers of the distribution and structure of bacterial communities of mangrove soils and sediments.

### 3.3. Potential microbial bioindicators of anthropogenic pressures

Potential microbial bioindicators of anthropogenic pressure were found based on the correlations between specific taxa and the variables associated with the three types of anthropogenic pressure identified along the urban-to-rural gradient of the Cayenne estuary (OM enrichment and organochlorine and naphthalene contamination).

#### 3.3.1. Microbial signature of slight OM enrichment in mangrove

Several microbial taxa exhibited a negative or positive correlation with OM enrichment (TC), making them serious candidates for bioindication purposes (Fig. 4).

This is the case of the Bathyarchaeota class, formerly known as the Miscellaneous Crenarchaeotal Group (MCG), (0.93–8.1%), which was positively correlated with TC ( $r_s = 0.6$ ,  $p < 0.01$ ; Fig. 4A, Supplementary Data F). In mangrove sediments, Bathyarchaeota is the dominant archaeal taxon (Zhou et al., 2017, 2018), its abundance was suggested to be mainly correlated with total organic carbon content (Xiang et al., 2017; Yu et al., 2017). This observation may be associated with their heterotrophic lifestyle and their ability to anaerobically use detrital proteins, fatty acids/aromatic compounds, polymeric carbohydrates, and other OM (Lazar et al., 2016; Meng et al., 2014). Despite the diversity of Bathyarchaeota (over 25 subgroups) (Zhou et al., 2018) and their environmental preferences, the abundance of the overall population seems to be a good indicator of OM enrichment in mangrove.

The levels of Euryarchaeota (0–1.6%) and Asgardaeota (0–0.88%), both highly abundant in anaerobic marine sediments (Hoshino et al., 2020), were also correlated with TC (both  $r_s = 0.7$ ,  $p < 0.01$ ; Fig. 4A). Almost all the ASVs in the phylum Euryarchaeota were included in the Thermoplasmata sublineage, especially in the anaerobic heterotrophic MBG-D archaeal group (newly named Thermoprofundales). In recent years, single-cell genomic and metagenomic approaches have shown that MBG-D archaea are capable of exogenous protein mineralization and acetogenesis in marine sediment (Lazar et al., 2017; Lloyd et al., 2013). In mangrove sediments, these archaea appear to be capable of transporting and assimilating peptides and generating acetate and ethanol through fermentation (Zhou et al., 2019). In the phylum Asgardaeota, the majority of ASVs belong to Lokiarchaeota, which vary in their metabolic activity, and their in situ activities are still largely unknown (Yin et al., 2021).

By contrast, Nitrospirae ( $r_s = -0.7$ ;  $p < 0.01$ ), Acidobacteria ( $r_s = -0.6$ ;  $p < 0.01$ ), Thaumarchaeota ( $r_s = -0.6$ ;  $p < 0.01$ ), and Latescibacteria ( $r_s = -0.6$ ;  $p < 0.01$ ) were negatively correlated with TC (Fig. 4A). The majority of Thaumarchaeota ASVs (38 ASVs) belong to “*Candidatus Nitrosopumilus*”, which are mesophilic, autotrophic, and aerobic AOA. Some groups of Thaumarchaeota are recognized as major contributors of ammonia oxidation (the first step in nitrification) in marine oligotrophic ecosystems (Pester et al., 2011; Wang et al., 2019) and could be dominant in some ecosystems, such as in the Amazon River and its plume (Pinto et al., 2020). Ammonia oxidation is known to be inhibited by several parameters, notably organic carbon content (Pester et al., 2012), OM quality (Strauss and Lamberti, 2000), and the TC:TN ratio (Bates et al., 2011). AOA are adapted to low ammonium concentrations and are outcompeted by bacteria when concentrations become higher (Nakagawa and Stahl, 2013). Sensitivity to slight OM enrichment was also observed for the *Nitrospira* genus (19 ASVs; 0–0.9%;  $r_s = -0.68$ ;  $p < 0.05$ ), the NOB and comammox bacteria. Latescibacte-



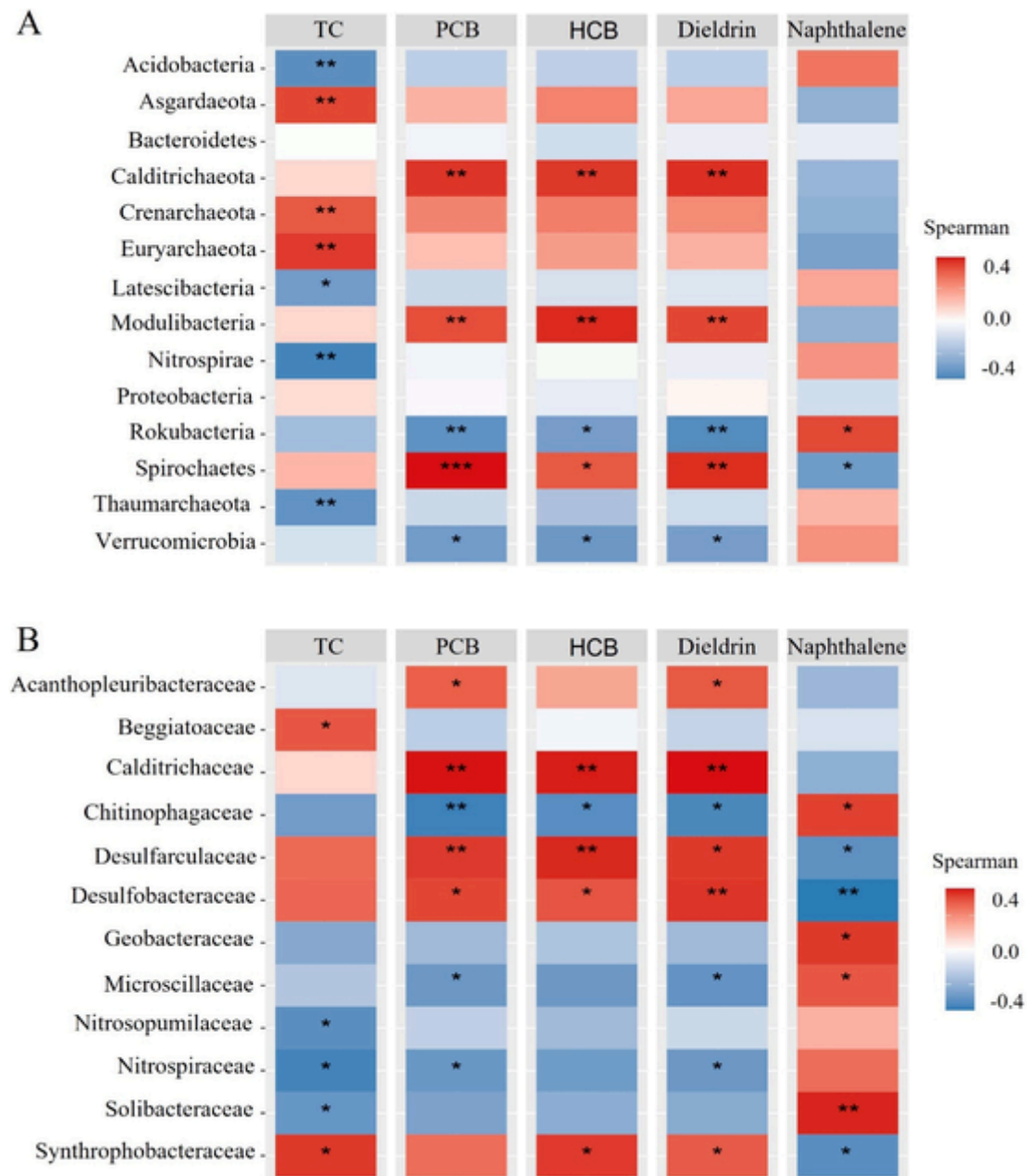


Fig. 4. Spearman's rank correlation coefficient heatmap showing relationships between environmental variables and interesting taxa. A: phylum level; B: family level. Statistically significant Spearman correlations are highlighted (\* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ ).

ria (formerly WS3) represents a ubiquitous phylum found in terrestrial, aquatic, and marine environments (Youssef et al., 2015). Metabolic reconstruction suggests a saprophytic lifestyle for this candidate phylum, with a marked capacity for decomposition of OM (proteins, lipids, and polysaccharides) predominant in plant, bacterial, fungal, crustacean, and eukaryotic algal cell walls (Farag et al., 2017; Youssef et al., 2015). Finally, a negative correlation between Acidobacteria abundance and TC content was observed in our dataset (Fig. 4A), as it was also in terrestrial ecosystems, leading to the conclusion that members of this taxon may be oligotrophic bacteria (Fierer et al., 2007).

### 3.3.2. Taxa sensitive to organochlorine compounds

Correlations between several microbial taxa and organochlorine (dieldrin, PCB, and HCB) concentrations were observed (Fig. 4; Supplementary Data F).

Calditrichaeota (Calditrichaceae family) and Spirochaetes (*Spirochaeta* genus) were significantly correlated ( $r_s < 0.7$ ;  $p < 0.05$ ) with PCB, HCB, and dieldrin content (Fig. 4). Spirochaetes are indigenous to sulfide-rich mud or sediments (Tanner et al., 2000; Leschine et al., 2006) and are typically found in PCB-contaminated waters (Dong et al., 2018) or contaminated sediments (Quero et al., 2015). Calditrichaeota and Spirochaeta are known to be very diversified and to have a wide range of ecological niches (Leschine et al., 2006; Marshall et al., 2017). Until now, these organisms have never been associated with dechlorination of organochlorine compounds; however, our results suggest that Calditrichaeota and *Spirochaeta* could have a role in the degradation of PCB, HCB, and dieldrin, or at least could be tolerant to these compounds. Future experimental studies are needed to validate this finding (e.g., biodegradation assays). “*Candidatus Modulibacteria*” phylum (previously named KS3B3 or GN03) was also positively correlated with the three organochlorine compounds. By con-

trast, “*Candidatus Rokubacteria*” (0–1.5%; previously named SPAM or candidate division NC10) was negatively correlated with PCB ( $r_s = -0.6$ ;  $p < 0.05$ ), HCB ( $r_s = -0.6$ ;  $p < 0.001$ ), and dieldrin ( $r_s = -0.7$ ;  $p < 0.01$ ). This phylum is found in diverse terrestrial ecosystems such as alpine soil, crop soil, or copper mine soil (Becraft et al., 2017), and this is the first time that it is identified in a marine ecosystem. The lack of knowledge on “*Candidatus Modulibacteria*” and “*Candidatus Rokubacteria*”, two phyla without cultivable representatives, does not allow us to explain the significant correlations with organochlorine compounds in this study. The relative abundance of the Verrucomicrobia phylum was significantly higher at S3 than at S1 and S2 (0.49%;  $p < 0.05$ ). This taxon is related to the Planctomycetes–Verrucomicrobia–Chlamydia superphylum, has diverse metabolism capabilities (such as methanogenesis and degradation of sulfated polysaccharides) (Freitas et al., 2012; Van Vliet et al., 2019), and is typically found in mangrove sediments (Liang et al., 2007; Nogueira et al., 2015). It was negatively correlated with PCB ( $r_s = -0.6$ ;  $p < 0.05$ ), HCB ( $r_s = -0.6$ ;  $p < 0.05$ ), and dieldrin ( $r_s = -0.5$ ;  $p < 0.05$ ), suggesting that Verrucomicrobia is sensitive to the organochlorine compounds in mangrove sediments.

At the family level, some taxa seem particularly interesting in their response to PCB pressure, notably in the Desulfobacterota (formerly Deltaproteobacteria) phylum. Two families were significantly correlated with PCB content (Fig. 4B): Desulfobacteraceae ( $r_s = 0.6$ ;  $p < 0.05$ ) and Desulfurculaceae ( $r_s = 0.6$ ;  $p < 0.001$ ). These Desulfobacterota are strictly anaerobic and sulfate-reducing bacteria, and are indirectly implicated in PCB dechlorination by promoting organohalide respiration of PCB dechlorinating bacteria (Praveckova et al., 2016; Matturro et al., 2020). The Acanthopleuribacteraceae family (Acidobacteria) is known to degrade PCB and is considered very useful in remediating polluted environments (Falkiewicz-Dulik et al., 2015). The significant response of Acanthopleuribacteraceae ( $r_s = 0.6$ ;  $p < 0.01$ ) to the low quantity of PCBs measured makes this taxon a particularly interesting bioindicator of PCB contamination.

### 3.3.3. Bacterial signature of naphthalene contamination in mangrove

Although naphthalene content was above the regulatory threshold, it was not identified as one of the main drivers of mangrove microbiota along the estuary. However, the levels of some taxa were positively correlated with naphthalene content, such as uncultured Rokubacteria phylum ( $r_s = 0.5$ ,  $p < 0.05$ ; Fig. 4A). As seen previously, Rokubacteria are not well described, but their diversified genome reveals a potential implication in the nitrogen, methane, and sulfur cycles (Hug et al., 2013; Becraft et al., 2017). However, a meta-analysis of the rokubacterial MAGS conducted by Kroeger et al. (2018) showed that taxa members have several features involved in metabolizing long and short hydrocarbons in soil via two enzymes, cytochrome P450 and alkane 1-monooxygenase, respectively. Cytochrome P450 has been described as one of the enzymes involved in the naphthalene biodegradation (Mohapatra and Phale, 2021) which may explain the observed positive correlation. These details can explain the positive correlation observed in this study. Within the Acidobacteria, the Solibacteraceae family was also positively correlated with naphthalene ( $r_s = 0.7$ ;  $p < 0.01$ ; Fig. 4B). Members of this family possess some functional genes that allow them to degrade branched hydrocarbons such as pristane (Wang et al., 2016), yet it has not been proven if they can degrade PAHs.

A correlation between the Chitinophagaceae family and naphthalene was observed ( $r_s = 0.6$ ;  $p < 0.05$ ). Strains of this family have been isolated from freshwater sediments and soil contaminated with petroleum (Blanco-Enríquez et al., 2018). Members of Chitinophagaceae are known to be able to degrade biopolymers (Gomes et al., 2010) and to belong to microbial consortia that remove PAHs. Specifically, some members of Chitinophagaceae have the capacity to degrade pyrene and benzo[a]pyrene in water (Blanco-Enríquez et al., 2018), but no significant correlation was found in this study between Chitinophagaceae and these two compounds, which were barely detected in the samples.

No direct link between Chitinophagaceae and naphthalene degradation is reported in the literature. Similarly, Geobacteraceae, a sulfur-reducing and iron-reducing Desulfobacterota bacteria (Kleindienst et al., 2012) were positively correlated with naphthalene ( $r_s = 0.6$ ;  $p < 0.01$ ; Fig. 4B). Some studies have shown that this family has the capacity to degrade aromatic compounds and PAHs (Coates et al., 2001; Holmes et al., 2004; Durante-Rodríguez et al., 2018), and it was used in the bioremediation of organic contaminants in the soil subsurface (Holmes et al., 2004).

## 4. Conclusion

Our study shows that estuarine mangroves of the Cayenne River are globally exposed to low anthropogenic pressures. However, we detected low OM enrichment, and organochlorine and pyrolytic PAH pollution derived from human activities, mainly at the stations closest to the city of Cayenne (S1 and S2). The core microbial taxa are similar to the one observed in Brazil mangroves, which are more impacted by human activities. Granulometry, dieldrin concentration, pH, and TC content appear to drive the mangrove microbiota. Taxa of interest were identified that are correlated to OM enrichment and organochlorine (dieldrin, PCB and HCB) and naphthalene contamination, represent potential bioindicators of the health status of the mangrove ecosystem. However, much more research is needed to assess the structural, spatial, and temporal distributions of microbial communities in mangroves as well as their response to growing anthropogenic pressures in an overall still relatively preserved environment.

## Data availability statement

The data presented in this study are openly available in <https://doi.org/10.5281/zenodo.4592299> [<https://doi.org/10.5281/zenodo.4592299>].

## Uncited reference

OSPAR, 2009

## CRediT authorship contribution statement

**Maud Fiard:** Conceptualization, Software, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Philippe Cuny:** Conceptualization, Methodology, Resources, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Léa Sylvi:** Resources, Investigation. **Cédric Hubas:** Conceptualization, Methodology, Software, Resources, Writing – review & editing. **Ronan Jézéquel:** Investigation. **Dominique Lamy:** Conceptualization, Methodology, Resources, Writing – review & editing. **Romain Walcker:** Conceptualization, Methodology, Investigation, Resources, Writing – review & editing, Visualization, Project administration, Funding acquisition. **Amonda El Houssainy:** Investigation, Writing – review & editing. **Lars-Eric Heimbürger-Boavida:** Investigation, Writing – review & editing. **Tony Robinet:** Writing – review & editing. **Isabelle Bihannic:** Resources, Investigation. **Franck Gilbert:** Conceptualization, Methodology, Writing – review & editing, Funding acquisition. **Emma Michaud:** Conceptualization, Methodology, Resources, Writing – review & editing, Project administration, Funding acquisition. **Guillaume Dirberg:** Conceptualization, Methodology, Resources, Writing – re-

view & editing, Project administration, Funding acquisition. **Cécile Milton:** Conceptualization, Methodology, Formal analysis, Resources, Writing – original draft, Writing – review & editing, Supervision.

## Declaration of competing interest

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.150667>.

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