

Functional profiling of coastal microbial mats from the Yucatan Peninsula: methane, nitrogen and sulfur metabolism

Miriam Carrillo-Díaz de León

Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional Unidad Mérida

Santiago Cadena-Rodríguez

Instituto de Ciencias del Mar y Limnología

Ma Leopoldina Aguirre-Macedo

Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional Unidad Mérida

José Q. García-Maldonado

`jose.garcia@cinvestav.mx`

Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional Unidad Mérida

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Abstract

Methane, sulfur, and nitrogen metabolism are key processes in microbial mats that directly regulate greenhouse gas emissions, nutrient availability, and ecosystem productivity. Previous studies have identified microbial mats along the coastline of the Yucatan Peninsula, revealing a diverse array of microbial macrostructures associated with mangrove ecosystems. However, a metagenomic analysis for the understanding of these metabolisms is not yet available. This study aimed to explore the functional diversity of microbial mats in coastal lagoons of the Yucatan Peninsula, focusing on methane, nitrogen, and sulfur metabolism, through shotgun sequencing. Results indicated that methanogenic communities were dominated by *Methanosarcina*, and that the main pathway was acetoclastic, whereas the methanotrophic communities were dominated by *Methylobacterium*. Flat mats from Ría Lagartos and Progreso presented greater potential for methane oxidation, whereas pustular mats from Progreso and floating mats from Sisal presented greater potential for methane production. Sulfur-related microorganisms (3.11–4.23%) were dominated by *Desulfosarcina* and *Pseudodesulfovibrio*. Total gene counts revealed a greater potential for dissimilatory sulfate reduction and sulfate oxidation in flat mats from Ría Lagartos, whereas assimilatory sulfate reduction metabolism predominated in the other mats. Nitrogen-related communities were highly abundant (21.8–28.8%), dominated by *Streptomyces* and *Pseudomonas*. Total gene count revealed greater potential for nitrogen fixation and nitrification in mats from Progreso, whereas mats from Ría Lagartos and Sisal presented a greater potential for denitrification, implying higher N₂O emissions. These findings underscore the functional heterogeneity of microbial mats and their influence on greenhouse gas dynamics and nutrient cycling in coastal ecosystems on the Yucatan Peninsula.

Introduction

Microbial mats are multilayered biofilms, self-sustaining ecosystems, with complex stratified communities that drive some of the most fundamental biogeochemical processes on Earth [1]. Within just a few millimeters, microbial mats exhibit steep redox gradients that generate highly distinct microenvironments. These gradients create sharp transitions in chemical conditions, allowing specialized microbial communities to thrive in each niche. As a result, mats support the complete cycling of essential elements such as carbon, nitrogen, and sulfur, with different microorganisms performing complementary metabolic processes. Despite their small physical size, these mats act as biogeochemical hotspots, concentrating intense chemical activity and nutrient transformations that are disproportionate to the spatial scale they occupy. In the upper oxic layers, photosynthetic microorganisms fix carbon and produce oxygen, whereas in the deeper anoxic layers, fermentation of organic matter provides substrates that fuel methanogenesis. Methanogenic archaea, represented by a minor fraction of the community, produce methane through hydrogenotrophic, acetoclastic, and methylotrophic pathways, and are sensitive to environmental drivers such as salinity, temperature and organic matter availability [2]. Sulfur cycling is one of the most active processes in coastal and hypersaline environments where sulfate is abundant. In the anoxic layers, sulfate-reducing bacteria use sulfate as a terminal electron acceptor to oxidize organic matter, producing hydrogen sulfide. This

process is energetically favorable and often outcompetes methanogenesis for shared substrates such as acetate and hydrogen, although both processes can cooccur when substrates are available [3]. Nitrogen cycling in microbial mats is remarkably complete, with evidence of nitrogen fixation, nitrification, denitrification, dissimilatory nitrate reduction to ammonium (DNRA), and sometimes anammox occurring within the same thin community [4]. Nitrogen fixation by cyanobacteria and heterotrophic diazotrophs provides a critical input of bioavailable nitrogen, which is particularly important in nutrient-limited coastal environments. Nitrification converts ammonium to nitrate, fueling denitrification, which returns nitrogen to the atmosphere as N_2 or the greenhouse gas N_2O .

Coastal mats have been commonly reported in a wide range of extreme environments such as hypersaline lagoons, intertidal zones, and coastal wetlands. More recently, some studies have pointed out the potential association of mats with mangrove ecosystems, since mangroves thrive in floodplains along the shoreline, where high microbial activity influences productivity, anaerobic decomposition, sulfate reduction, and nitrogen transformations that sustain these ecosystems [5]. The Yucatan Peninsula harbors extensive mangrove ecosystems distributed along its coastline characterized by a karst landscape. Previous studies have documented the presence of diverse microbial mat formations, including floating, flat, and pustular mat types associated with different mangrove conditions, in coastal lagoons in this region. These mats represent structurally and functionally distinct microbiomes, yet their specific ecological roles in biogeochemical cycling remain poorly understood. While 16S rRNA gene-based studies have characterized the taxonomic composition of these communities, the functional potential encoded in their metagenomes has not been explored. This study aimed to explore the functional diversity of microbial mats from coastal lagoons of the Yucatan Peninsula, with an emphasis on methane, nitrogen, and sulfur metabolism, through shotgun sequencing. Understanding the metabolic potential of these communities will contribute to a better assessment of their role in greenhouse gas dynamics and nutrient cycling and may impact future mangrove conservation and restoration strategies.

Methods

Sampling and physicochemical characterization

In May 2019, coastal microbial mat samples were collected from Sisal, Progreso, and Ría Lagartos in Yucatan, Mexico. Floating microbial mats from Sisal (SFI) and flat mats from Progreso (PF) were associated with degraded mangroves, pustular mats from Progreso (PP) with restored mangroves, and flat mats from Ría Lagartos (RLF) with a mangrove-free coastal area. At each site, triplicate surficial cores of 8 cm in width by 8 cm in length and 3–5 cm in depth were collected and three subcores (1 cm × 1 cm, upper centimeter) were taken per core, yielding 9 samples per locality. The subcores were immediately stored in liquid nitrogen. At each site, interstitial water and physicochemical data were collected as previously described [5]. The detailed study sites and physicochemical variables are reported in Cadena *et al* 2025 [5].

DNA extraction and shotgun sequencing

DNA extraction and shotgun sequencing

DNA was extracted from 0.25 g of each mat sample ($n = 9$ per locality) via the PowerSoil DNA Isolation Kit (Mo Bio Laboratories, Carlsbad, CA, USA) [5]. All the 9 DNA samples from each site were pooled equally for shotgun sequencing, with a minimum of 200 ng in 20 μ l, and A260/A280 ratios ranging from 1.8–2.0. These pools were submitted to Novogene Corporation Inc. (Sacramento, CA) for shotgun library preparation and sequencing. The genomic DNA was subjected to random fragmentation. The resulting fragments were end-repaired, an adenine (A) tail was added, and the fragments were subsequently ligated with Illumina adapters. The resulting adapter-ligated fragments were size-selected, amplified via PCR, and purified. The libraries were quantified via Qubit and qPCR. The sequences were subsequently pooled and sequenced on the Illumina NovaSeq X Series system (2 $\times$ 150 bp paired-end reads). The resulting sequences are available in the National Center for Biotechnology Information repository, under the BioProject number PRJNA1455683.

Bioinformatic processing of shotgun sequences

Shotgun reads were analyzed via the MetaWRAP pipeline [6]. Quality was assessed with FastQC before and after trimming via the read_qc module, removing adapters, low-quality reads ($Q < 20$), reads with $> 10\%$ undetermined bases, sequencing artifacts, and human DNA contamination. Clean reads were assembled into contigs via Megahit.

Taxonomic and functional annotation of contigs

Contigs were taxonomically assigned via Kraken2, diversity analyses were conducted with KrakenTools, and the classification results were visualized in Pavian. The relative abundances of methane-, sulfur- and nitrogen-related communities were plotted in R (4.4.2) using ggplot2, tidyr, and dplyr libraries [7–9]. The functional annotation of contigs was performed with DRAM1 [10] with default parameters to retrieve sulfur- and nitrogen-cycling genes, which were normalized by total sum scaling (relative abundance). Methane-cycling genes were identified using MCycDB [11], with a 50 million random reads subsampling. The results were visualized as heatmaps and abundance graphs with tidyverse and pheatmap libraries [12, 13].

Results

Shotgun sequencing summary and diversity

Between 87–140 million reads passed quality control and were assembled into 121,109–224,346 contigs per sample, which were used for taxonomic assignments, diversity and functional analyses. The assemblies showed good continuity with N50 values ranging from 2,343–2,893 bp, and L50 values

ranging from 24,178–42,305. The Shannon index was consistently above 5, indicating high diversity (Table S1). Bray-Curtis dissimilarity analysis (beta diversity) revealed that the microbial communities from Progreso were the most similar (dissimilarity = 0.21), whereas those from RLF and SFI mats were the most distinct (dissimilarity = 0.43) (Fig. 1). The microorganisms identified from the contigs belonged to bacteria (80–98%), archaea (0.4–18%), fungi (0.3–0.5%), protists (0.12–0.2%), and viruses (0.04–0.06%) (Fig. S1). For each sample, between 58–67 phyla, 117–144 classes, 245–345 orders, 597–637 families, 2,175–2,406 genera, and 8,551–10,099 species were assigned.

Taxonomic and functional diversity of microbial mats

• Methane-cycling genes and communities

Methanogenic archaea comprised 36 genera representing 0.095–0.25% of the microbial communities found in mats (Fig. 2a). The highest methanogen abundance was detected in PP mats (0.25%), and the lowest in SFI mats (0.095%), whereas RLF mats presented the highest richness (35 genera). All mats exhibited representatives of all methanogenic metabolisms. Hydrogenotrophic genera predominated (23/36), followed by methylotrophic (8/36). Versatile *Methanosarcina* was the most abundant genus across all the sites, followed by hydrogenotrophic *Methanobacterium* in PF and PP mats, and methylotrophic *Methanlobus* in RLF and SFI mats. The hydrogenotrophic genus *Methanobrevibacter* also had a high abundance in all sites, whereas other genera presented differential abundances between sites. For example, PP mats showed high abundances of *Methanothrix*, *Methanofollis*, and *Methanoregula*; PF mats showed a high abundance of *Methanocella*; RLF mats showed a high abundance of *Methanocaldococcus*, and SFI mats showed a high abundance of *Methanomethylovorans*.

A total of 25 genera of methanotrophic bacteria were detected, representing 1.07–1.41% of the communities (Fig. 2b), all of which were shared across sites. The total abundance of aerobic methanotrophs was greater than that of methanogens in all mats. All types of methanotrophs (I, II, X) were found, with a greater diversity of type I (Gammaproteobacteria) (14/25) and type II (Alphaproteobacteria) (9/25). The most abundant genus at all sites was *Methylobacterium* (type II), followed by *Methylomonas* (type I) in PF and PP mats, *Methylocystis* (type II) in RLF mats, and *Methylococcus* (type I) in SFI mats. Together with *Methylobacterium* (type II), these five genera dominated methanotrophic communities across all mats. No anaerobic methanotrophs (ANME) were detected at contig level in this study.

Between 238 and 248 methane-cycling genes were detected per sample, with 227 shared across all four samples. Key gene families for methanogenesis and aerobic oxidation of methane were selected for further analysis and comparison between samples [11] (Fig. 3a, 3b). All sites presented genes for hydrogenotrophic (*fwdBCEFGH*, *ptr*, *mch*, *mta*(AB), *hmd*, *mer*), acetoclastic (*acsACD*, *ackA*, *pta*, *cdhABCDE*, *cooSF*), and methylotrophic (*mtaABC*, *mtbABC*, *torACDYZ*, *mttABC*, *mtmBC*) methanogenesis, as well as serine (*glyA*, *hprA*, *gck*, *eno*, *ppc*, *mtkAB*, *mcl*, *mdh*, *serABC*, *thrH*, *psp*), RuMP (*fae-hps*, *hxlAB*, *pfk*(AB), *fbaAB*, *fbp*) and xylulose (*fbp*, *fbp3*, *glpX*) methanotrophic pathways.

Acetoclastic pathway genes (*acsACD*, *pta*, and *ackA*) were the most abundant at all sites, which was consistent with the dominance of *Methanosarcina*. PF and PP mats presented greater overall methanogenic gene abundances than RLF and SFI mats, except for hydrogenotrophic genes *mch* and *mer*, which were enriched in RLF mats, and methylotrophic gene *torACDYZ*, which was enriched in SFI mats (Fig. 3c). For aerobic methanotrophy, serine cycle genes dominated across all sites, with high abundances of *glyA* and *serA* suggesting the prevalence of type II methanotrophs. The abundances of RuMP and xylulose pathway genes were generally low, except for *pfk(AB)* and *fbaAB* genes (Fig. 3d).

Total gene reads indicated a dominance of the serine pathway (93,852–10,830) for methanotrophy (Table S2) and the acetoclastic pathway (54,165–58,102) for methanogenesis, both peaking at RLF mats and lowest at SFI mats (Table S3). The methylotrophic, hydrogenotrophic, and RuMP pathways were most abundant in PF mats, whereas the xylulose pathway was most abundant in RLF mats (Fig. 4a).

Although key genes for methanogenesis (*mcrA*) and aerobic methanotrophy (*pmoA* and *mmoX*) were detected at low abundance across all sites, their relative distributions revealed distinct metabolic potentials (Fig. 4b). PP and SFI mats presented increased methane production potential, with SFI mats exhibiting the highest *mcrA:pmoA* gene ratio (21:4). In contrast, PF and RLF mats presented greater methane oxidation potential. RLF mats had higher abundance of *pmoA* but lacked *mmoX*, whereas PF mats showed higher *mmoX* abundance, implying that methane oxidation is primarily mediated by the soluble methane monooxygenase (sMMO).

• Sulfate-cycling genes and communities

86 sulfur-related genera were detected, corresponding to sulfate-reducing bacteria (SRB), sulfur-oxidizing bacteria (SOB), and sulfur-disproportionating bacteria (SDP), comprising 3.11–4.23% of the communities (Fig. 5). The highest abundance was detected in RLF mats (4.32%), and the highest richness was detected in PF mats (81 genera), whereas SFI mats presented the lowest abundance and richness (3.11%, 77 genera). *Desulfosarcina* and *Pseudodesulfovibrio* were the most abundant genera at all sites, followed by *Desulfococcus* and *Sulfitobacter*. PP mats were characterized by a great abundance of *Desulfuromonas*, whereas RLF mats were characterized by a high abundance of *Desulfobacter*.

Key genes involved in the sulfur cycle were selected for comparison (Fig. 6a). All sites possessed genes for dissimilatory sulfate reduction (DSR) (*dsrAB*, *aprAB*, *sat*), assimilatory sulfate reduction (ASR) (*cysNC*, *cysJHINCD*, *sir*, *sat*), sulfate oxidation (*soxABCDXYZ*), thiosulfate reduction (*phsA/psrA*), and the sulfur relay system (*TST/MPST/sseA*) (Table S4). The *TST/MPST/sseA* gene was highly abundant across all sites, particularly in SFI mats (27%), indicating a potential for sulfur compound detoxification. DSR genes were also abundant across all sites, whereas the gene for thiosulfate reduction (*phsA/psrA*) was low in abundance, and gene for tetrathionate reduction (*ttrA*) was absent, suggesting that these intermediary pathways are not major routes in these communities. The lack of the eukaryotic *PAPSS* gene, coupled with the presence of the bacterial genes *cysNC* and *cysC/N/D*, confirms a prokaryotic-driven processing of sulfate in these environments. Moreover, RLF mats presented the highest abundance of *soxABCDXYZ*

(28%), and *dsrAB* (11%) genes, but also presented the lowest abundance of some ASR genes, such as *cysH* and *sat*. PF mats presented the lowest abundance of *soxABCDXYZ* (2%) and the highest abundance of *cysND* (14%), indicating a greater potential for ASR at this site (Fig. 6b).

Total gene count revealed greater potential for ASR than DSR at all sites, except for RLF mats, which also presented the highest sulfate oxidation potential. PF mats presented the highest potential for ASR and the lowest for sulfate oxidation. All sites had a low thiosulfate reduction potential. SFI mats had the highest potential for the sulfur relay system (Fig. 6c).

• Nitrogen-cycling genes and communities

67 nitrogen related genera were detected, including nitrifiers, denitrifiers and nitrogen-fixing bacteria, accounting for 21.8–28.8% of the communities (Fig. 7). The highest abundance was found in PP mats (28.8%), whereas RLF mats had the lowest abundance (21.8%), but the highest richness, along with PF mats, with 65 genera each. The lowest richness was found on SFI mats, with 59 genera. The most abundant nitrogen cycling genera at all sites were *Streptomyces* (nitrifier) and *Pseudomonas* (nitrifier/denitrifier), followed by *Bradyrhizobium* (nitrogen-fixing) in PF, PP and RLF mats, whereas SFI mats presented high abundances of *Synechococcus* (nitrogen-fixing) and *Paracoccus* (denitrifier). *Flavobacterium* (denitrifier) was also highly abundant at all sites, and PP mats were characterized by a higher abundance of *Rhizobium* and *Mesorhizobium*, both of which are nitrogen-fixing bacteria.

Key genes involved in the nitrogen cycle were selected for comparison (Fig. 8a). All the studied microbial mats possessed genes for nitrogen fixation (*nifDHK*), denitrification (*narGHI*, *napAB*, *nirKS*, *norBC*, *nosZ*), nitrification (*hao*, *narGH*), assimilatory nitrate reduction (ANR) (*nasBC*, *nirA*, *nark/nrtP/nasA*), dissimilatory nitrate reduction (DNR) (*narGHI*, *napAB*, *nrfAH*) and anammox (*nirKS*) (Table S5).

Genes encoding the complete denitrification pathway were detected across all sites, except for *napAB* gene, which was not detected in PF mats, and fungal nitric oxide reductase (*CYP55*), which was not detected at any site. This suggests that denitrification is primarily mediated by bacteria and is a robust process in these environments. Within nitrification, while genes for hydroxylamine oxidation (*hao*) and nitrite oxidation to nitrite (*narGHI*) were present at all sites, the absence of *amoA* suggests that the process is truncated, with no detected potential for complete ammonia oxidation. This disparity indicates greater genetic potential for denitrification than for nitrification. We did not find evidence of anammox at these sites because of the absence of key genes such as *hdh* and *hzs*. Nitrogen fixation appears to proceed via the conventional pathway, as all sites possessed *nifDHK* but lacked the alternative *vnfDKGH* and *anfG* genes. For ANR, only *nark/nrtP/nasA* gene was present at all sites, whereas *nasBC* gene was present only in PP and SFI mats, and gene *nirA* was present in PF, RLF, and SFI mats; both genes presented low abundances. For DNR, *narGHI* and *nrfAH* genes were present at all sites, whereas *napAB* gene was absent in PF mats. In contrast, PF mats presented the highest abundance of *nifDHK* (27%) and *nrfAH* (20%), while PP mats presented a low abundance of the latter; RLF mats were

distinguished by the greatest abundance of *napAB* (11%); and PP mats presented the highest abundance of *hao* (27%). All sites presented similar abundances of *norBC*, *nosZ* and *narGHI* genes (Fig. 8b).

Total gene count indicated a higher capacity for DNR than ANR in these mats. All sites presented a low potential for anammox. PF mats presented greater potential for N fixation and the lowest potential for denitrification. RLF and SFI mats had a greater potential for denitrification than nitrification, whereas PP mats had the opposite. PF mats presented similar abundances for both processes (Fig. 8c).

Discussion

This study provides a systematic metagenomic characterization of the functional diversity of microbial mats from coastal lagoons of the Yucatan Peninsula, with emphasis on methane, sulfur, and nitrogen cycling. The four mat types examined, floating mats from Sisal, flat and pustular mats from Progreso, and flat mats from Ría Lagartos, shared a core microbial community involved in all three biogeochemical cycles, but presented distinct functional profiles that reflected differences in mat morphology, mangrove conditions, and environmental variables, particularly salinity.

Coastal microbial mats are among the most diverse ecosystems known [14], harboring hundreds of microbial species within the top millimeters of sediment [15]. The microbial mats examined in this study exhibited high diversity (Table S1), although the Shannon diversity indices were similar across sites, the highest value was recorded in Ría Lagartos, despite it being the most hypersaline site. This contrasts with studies reporting a negative correlation between salinity and microbial diversity [16]. Instead, the Ría Lagartos mats presented an increase in archaeal abundance of up to 18% (Fig. S1), suggesting strong adaptations to salinity, irradiation, and desiccation. Beta diversity analyses revealed that flat and pustular mats from Progreso were the most similar in community composition, whereas flat mats from Ría Lagartos and floating mats from Sisal represented the most distinct communities (Fig. 1). The fact that Sisal and Ría Lagartos had the lowest and highest salinities, respectively, is consistent with a previous study identifying salinity as the environmental variable that explained most of the taxonomic variation in these microbial mats [5].

Composition and functional potential of methanogens and methanotrophs

In this study, we found a high diversity of methanogenic archaea and methanotrophic bacteria (Fig. 2), reporting genera not previously detected with sequencing of the molecular marker *mcrA* [17]. These groups are seldom studied, since they are part of the rare biosphere in these environments [18], although methanogenesis and methanotrophy are microbial-mediated processes that dictate methane emission from the soil to the atmosphere in coastal environments such as mangroves [19, 20]. All mats were dominated by the genus *Methanosarcina*, which is consistent with other studies in coastal ecosystems [19, 21, 22]. This genus can utilize a diverse array of substrates, including hydrogen, acetate and methylated compounds, and adapts well to different conditions, including high salt concentrations and

oxygen exposure [23]. Other representative taxa found in similar environments include methylotrophic *Methanlobus* and hydrogenotrophic *Methanobacterium* [19, 24, 25], both of which were abundant in this study.

Aerobic methanotrophs were detected in all four microbial mats, and their relative abundance was higher than that of methanogens across sites. To our knowledge, this is the first study to report the diversity of methanotrophic bacteria in coastal areas of the Yucatan Peninsula. These communities were dominated by *Methylobacterium* (type II), *Methylomonas* (type I), *Methylocystis* (type II), and *Methylococcus* (type I), which is consistent with findings from other studies in mangrove sediments [19, 26]. Notably, this contrasts with findings from the well-studied hypersaline microbial mats of Guerrero Negro, Baja California, where aerobic methanotrophs are largely absent [27]. Regarding anaerobic methane oxidation (AOM), although genes shared with the methanogenesis pathway were detected, no genera known to mediate AOM were identified. This suggests that these organisms are either present in extremely low abundances or restricted to deeper zones of the microbial mats.

In all microbial mats we detected genes belonging to all the methanogenic and methanotrophic pathways (Fig. 3), as well as the molecular markers *mcrA*, *pmoA* and *mmoX* (Fig. 4). This confirms the capacity for both methane production and oxidation in these sites. The gene abundance of methanogenic pathways revealed that the acetoclastic route is predominant. This finding is noteworthy since methylotrophic methanogenesis is considered to dominate in highly saline environments, such as those studied here, where methylated compounds accumulate as compatible solutes in response to osmotic stress [28]. Recent studies have indicated that methane generation in restored estuarine mangroves primarily occurs through acetate fermentation and CO₂ reduction, reflecting the high availability of acetate and hydrogen produced during the fermentation of abundant mangrove-derived organic matter [28]. Conversely, the elevated abundance of serine cycle genes, suggests a greater prevalence of type II methanotrophs. These methanotrophs are typically dominant in resource-limited environments because of their high affinity for nutrients and substrates, as well as greater tolerance to environmental stress [29, 30].

Based on the *mcrA*:*pmoA* ratio, which has been used as a predictor of methane emissions [24, 31], and the *mmoX*, which is particularly important in environments where *Methylocella* (type II) might be relatively abundant [32], the floating mats from Sisal showed greater potential for methane production. This observation aligns with reports that degraded mangroves—such as those in Sisal—emit more methane than undisturbed systems do [33]. Additionally, low salinity has been correlated with greater methane production [34], and floating mats in wetlands have been shown to increase anaerobic decomposition, thereby increasing the surface diffusive flux of methane [35]. In contrast, the flat mats from Progreso and Ría Lagartos presented greater potential for methane oxidation. Although these sites are also degraded or without mangroves, higher salinity may limit methane production, thereby favoring oxidation processes. Ría Lagartos presented a higher abundance of *pmoA*, but no *mmoX* was detected, possibly because this gene is present at low abundances. In contrast, Progreso presented a greater abundance of *mmoX*, implying that methane oxidation here is primarily mediated by sMMO, which is

consistent with a greater abundance of *Methylocella* than in the other mats. Given these functional differences, flat mats represent a better choice for the isolation of methanotrophs that could be used in methane mitigation strategies.

Microbial sulfur-cycling communities and metabolic potential

The highest abundance of SRB together with SOB and SDB was found in flat mats from Ría Lagartos (Fig. 5), whereas the lowest was observed in floating mats from Sisal, again indicating that salinity and sulfate are major drivers of microbial composition. The most abundant genera across all mats were SRB *Desulfosarcina* and *Pseudodesulfovibrio*. These genera are not typically the most abundant SRB reported in similar ecosystems. Members of *Desulfosarcina* have been implicated in syntrophic associations with archaea that mediate anaerobic methane oxidation [36] and are also capable of hydrocarbon degradation [37]. *Pseudodesulfovibrio* is found mainly in marine habitats, and some members can survive under extreme temperature and salinity [38]. The SRB *Desulfococcus* and SOB *Sulfitobacter* were also highly abundant across all sites. *Desulfococcus* is commonly reported in microbial mats, even in oxic surface layers [19, 26, 39]. *Sulfitobacter* has been described as a significant contributor to the organic sulfur cycle in marine habitats, including sediments, where it is widely distributed [40]. Together these genera were the main contributors to sulfur metabolism in mats from the Yucatan Peninsula. Other genera may reflect adaptations to the conditions of each mat. For example, *Desulfuromonas* was more abundant in pustular mats, whereas *Desulfobacter* was more abundant in the flat mats from Ría Lagartos.

As expected, sulfur cycling is a core metabolic feature in all these mats, regardless of mat type or mangrove condition. All microbial mats presented a high abundance of DSR genes. However, except for flat mats from Ría Lagartos, there is a greater potential for ASR over DSR (Fig. 6). In ASR, sulfate is used to synthesize sulfur-containing amino acids, whereas in DSR, sulfate serves to generate energy and as an electron acceptor [41]. This indicates that in most mats sulfur is primarily used for biomass, not for energy generation. The hypersaline conditions found in the flat mats from Ría Lagartos could favor DSR due to high sulfate concentrations, prevalent anoxia, and the high abundance of SRB that thrive under such conditions [42]. Accordingly, these mats showed the highest potential for DSR, as well as the highest potential for sulfate oxidation. This combination indicates efficient sulfur cycling, where sulfide produced by SRB is reoxidized to sulfate. In contrast, flat mats from Progreso presented the highest potential for ASR and the lowest for sulfate oxidation, indicating a less dynamic sulfur cycle. All sites had a low potential for thiosulfate reduction, indicating that sulfur cycling is dominated by direct sulfate-sulfide transformations, with intermediates playing a minimal role. However, the presence of SDB, such as *Desulfolithobacter* and *Thermosulfurimonas* at low abundances (not shown) suggests that such intermediates may still occur at low levels within localized microenvironments. Floating mats from Sisal presented the highest potential for the sulfur relay system, pointing towards a more stress-related sulfur metabolism primarily involved in the detoxification of sulfur compounds [43, 44] rather than in energy-conserving cycling.

Microbial nitrogen-cycling communities and metabolic potential

Nitrogen-related communities are among the dominant groups in mats from the Yucatan Peninsula, accounting for nearly 30% of the relative abundance (Fig. 7). Their highest abundance was observed in pustular mats from a restored mangrove zone. These findings indicate that bacteria involved in nitrogen transformation are relevant and more abundant in vegetated soils than in those without plants [45]. The most abundant genera in all mats were *Streptomyces* and *Pseudomonas*. *Streptomyces* are commonly found in both terrestrial and marine environments, where they play an important role in the turnover of organic material, using nitrogen sources to obtain energy [46]. *Pseudomonas* are capable of both nitrification and denitrification, showing strong adaptability to fluctuating environments such as coastal microbial mats [47]. Additionally, both genera possess biotechnological importance, with *Streptomyces* as a source of bioactive compounds, and *Pseudomonas* having the ability to degrade a wide range of organic compounds [47, 48], highlighting the potential of these microbial mats for bioprospection. Other main genera in these mats included different nitrogen-fixing bacteria, such as *Bradyrhizobium*, which was highly abundant in mats from Progreso and Ría Lagartos, and *Synechococcus*, which was highly abundant in mats from Sisal. In pustular mats, nitrogen-fixing genera such as *Rhizobium* and *Mesorhizobium* were more abundant, suggesting that these mats serve as valuable nutrient sources for plants. Collectively, these patterns point to functional redundancy within the mats, where the same process (nitrogen fixation) is carried out primarily by different genera. Floating mats also presented a high abundance of *Paracoccus*, a denitrifying bacterium capable of biofilm formation, a trait particularly advantageous in this dynamic environment [49].

All genes involved in the denitrification pathway were detected in the microbial mats, indicating that this pathway is important at these sites (Fig. 8). A previous study at some of these sites, particularly Progreso, revealed that the sediments are characterized by low total nitrogen, indicating potential N-loss via denitrification [17]. Denitrification is regarded as the primary pathway for nitrogen loss in mangrove sediments, releasing the greenhouse gases N_2O and N_2 [50]. When denitrification dominates over DNRA, higher N_2O emissions can result [51], which was the case for all except flat mats from Progreso. However, N_2O emissions have not yet been studied in microbial mats or mangrove ecosystems of the Yucatan Peninsula, and this knowledge gap should be addressed in future research.

Flat mats in Progreso presented greater potential for N fixation, followed by pustular mats, and the lowest potential for denitrification. High rates of N fixation in mangroves have been correlated with dead and decomposing leaves, pneumatophores and soil [45]. Moreover, mats from Ría Lagartos and Sisal had greater potential for denitrification than nitrification, whereas pustular mats had the opposite. This suggests greater potential nitrogen retention in mats from Progreso and higher potential greenhouse gas emissions in mats from Sisal and Ría Lagartos. All mats were also characterized by a greater potential for DNR than ANR. DNR uses nitrate as an external electron acceptor for energy production, reducing it to nitrite, ammonia, or gaseous nitrogen, often in anaerobic environments. This process is

also important for recycling nitrogen, which supports the high productivity of mangrove ecosystems [19, 26].

Another N-loss pathway is anammox. We did not find evidence of this process in the microbial mats because of the absence of key functional genes. However, we detected only two candidate genera belonging to this metabolism—*Brocadia* and *Kuenenia*—in extremely low abundances (not shown) [52]. Similarly, within the nitrification pathway, we found no metagenomic evidence that the mat communities are capable of ammonia oxidation, a finding that is consistent with other studies [53]. Ammonia-oxidizing bacteria typically belong to genera such as *Nitrosomonas*, *Nitrospira*, and *Nitrosococcus* [54], which were present in low abundances in these mats (not shown). It remains possible that these processes occur in low abundances or in deeper areas of the mats.

Conclusions

This study provides a comprehensive understanding of the biochemical cycles and diversity of communities associated with methane, sulfur and nitrogen in microbial mats from the Yucatan Peninsula. Overall, microbial mats from the Yucatan Peninsula share a core community of microbes involved in methane, nitrogen, and sulfur metabolism, with the dominant genera consistently present across all mats. However, their genetic potential varies depending on the mat type and location. Acetoclastic methanogenesis was the dominant methane-producing pathway in these mats, whereas the serine pathway was dominant for aerobic methane oxidation. Flat mats from Ría Lagartos and Progreso presented greater potential for aerobic methane oxidation, acting as better sinks for greenhouse gases, whereas floating mats from Sisal presented greater potential for methane production, which should be addressed in future studies to mitigate methane emissions. In sulfur metabolism, the flat mats from Ría Lagartos exhibited efficient sulfur cycling driven by hypersaline conditions, indicating high potential for both DSR and sulfate oxidation. The other mats were characterized primarily by ASR metabolism, and the floating mats from Sisal presented high potential for sulfur detoxification. In nitrogen metabolism, mats from Progreso presented greater potential for nitrogen fixation and nitrification, indicating efficient nitrogen retention. In contrast, mats from Ría Lagartos and Sisal presented greater potential for denitrification, implying higher N₂O emissions. The identification of dominant metabolic pathways in these microbial mats can aid in the development of mangrove restoration strategies and efforts to mitigate greenhouse gas emissions. Future research should focus on metatranscriptomic analyses to understand metabolically active functions and their contributions to biogeochemical cycling, while also accounting for seasonal variations, since changes in environmental conditions across different seasons may significantly influence microbial activity and metabolic fluxes.

Declarations

Competing interests

The authors declare no competing interests.

Ethics approval

Not applicable.

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Author Contribution

Conceptualization: M.C.D., J.Q.G.M.; Methodology: M.C.D.; Formal analysis and investigation: M.C.D.; Writing - original draft preparation: M.C.D.; Writing - review and editing: J.Q.G.M., S.C.R., M.L.A.M.; Funding acquisition: J.Q.G.M.; Resources: J.Q.G.M., S.C.R., M.L.A.M.; Supervision: J.Q.G.M., S.C.R., M.L.A.M.

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Data Availability

The shotgun raw sequences reported are available in the NCBI Sequence Read Archive under the BioProject PRJNA1455683.

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Figures

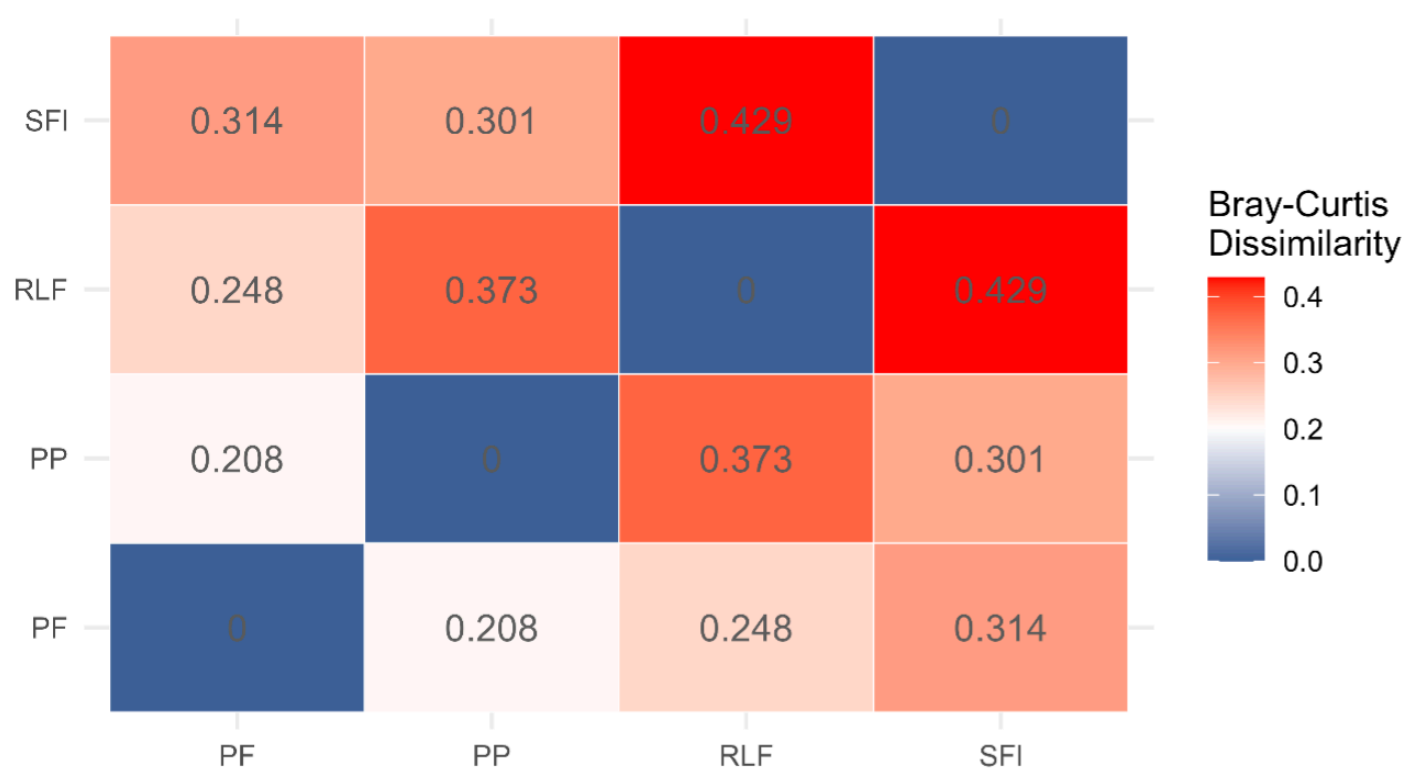
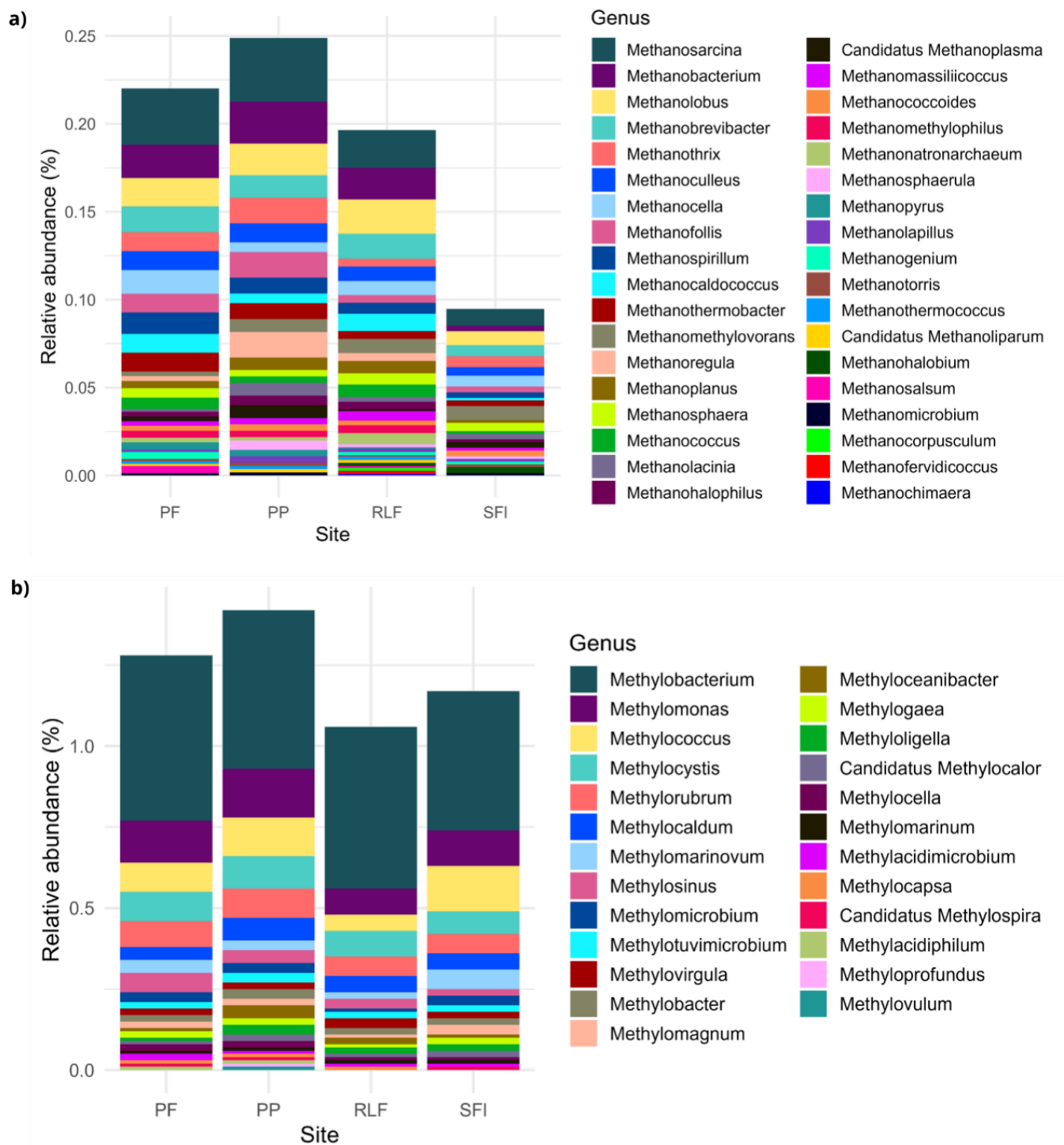


Figure 1

Heatmap of Bray-Curtis dissimilarity between microbial mat communities from the four sampling sites. PF= Progreso flat, PP= Progreso pustular, RLF= Ría Lagartos flat, SFI= Sisal floating



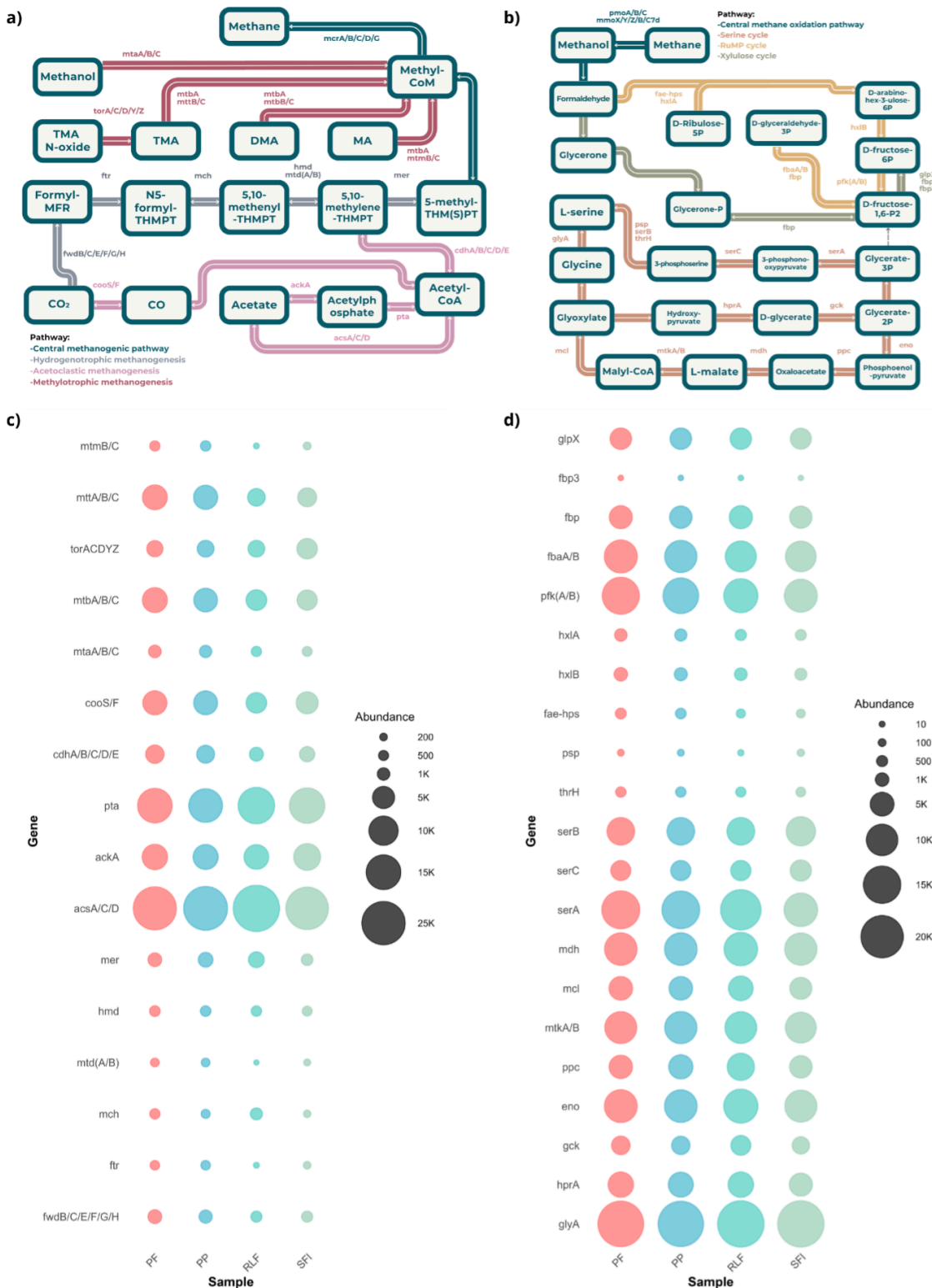


Figure 3

Genes involved in the different methanogenic (a) and methanotrophic pathways (b). Abundance of genes involved in the different methanogenic (c) and methanotrophic (d) pathways in microbial mats from the Yucatan Peninsula. PF= Progreso flat, PP= Progreso pustular, RLF= Ría Lagartos flat, SFI= Sisal floating

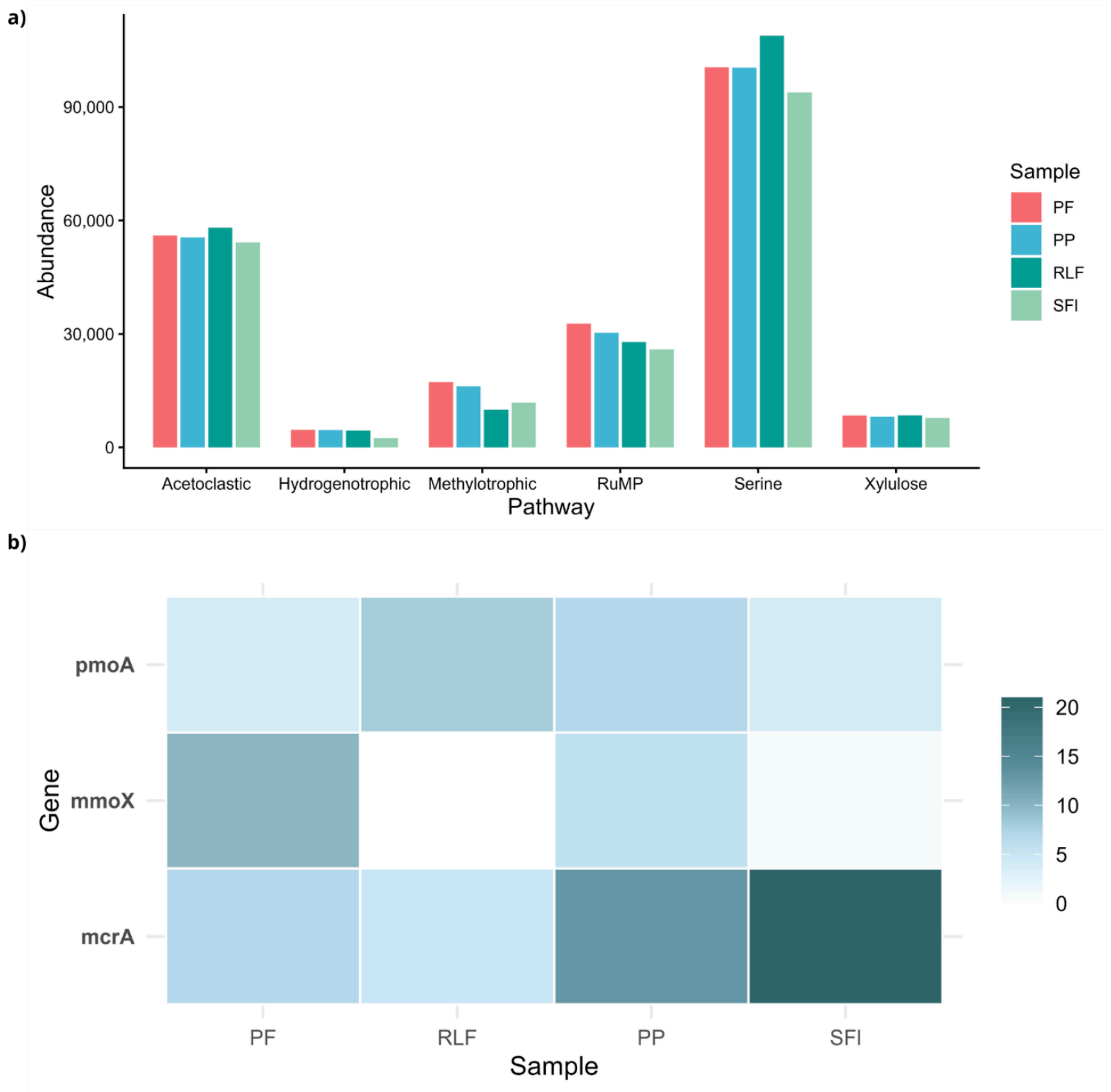


Figure 4

Total gene abundance of methanogenic and methanotrophic pathways (a). Heatmap showing the abundance of key gene markers for methanogenesis (*mcrA*) and aerobic oxidation of methane (*pmoA* and *mmoX*) (b) in microbial mats from the Yucatan Peninsula. PF= Progreso flat, PP= Progreso pustular, RLF= Ría Lagartos flat, SFI= Sisal floating

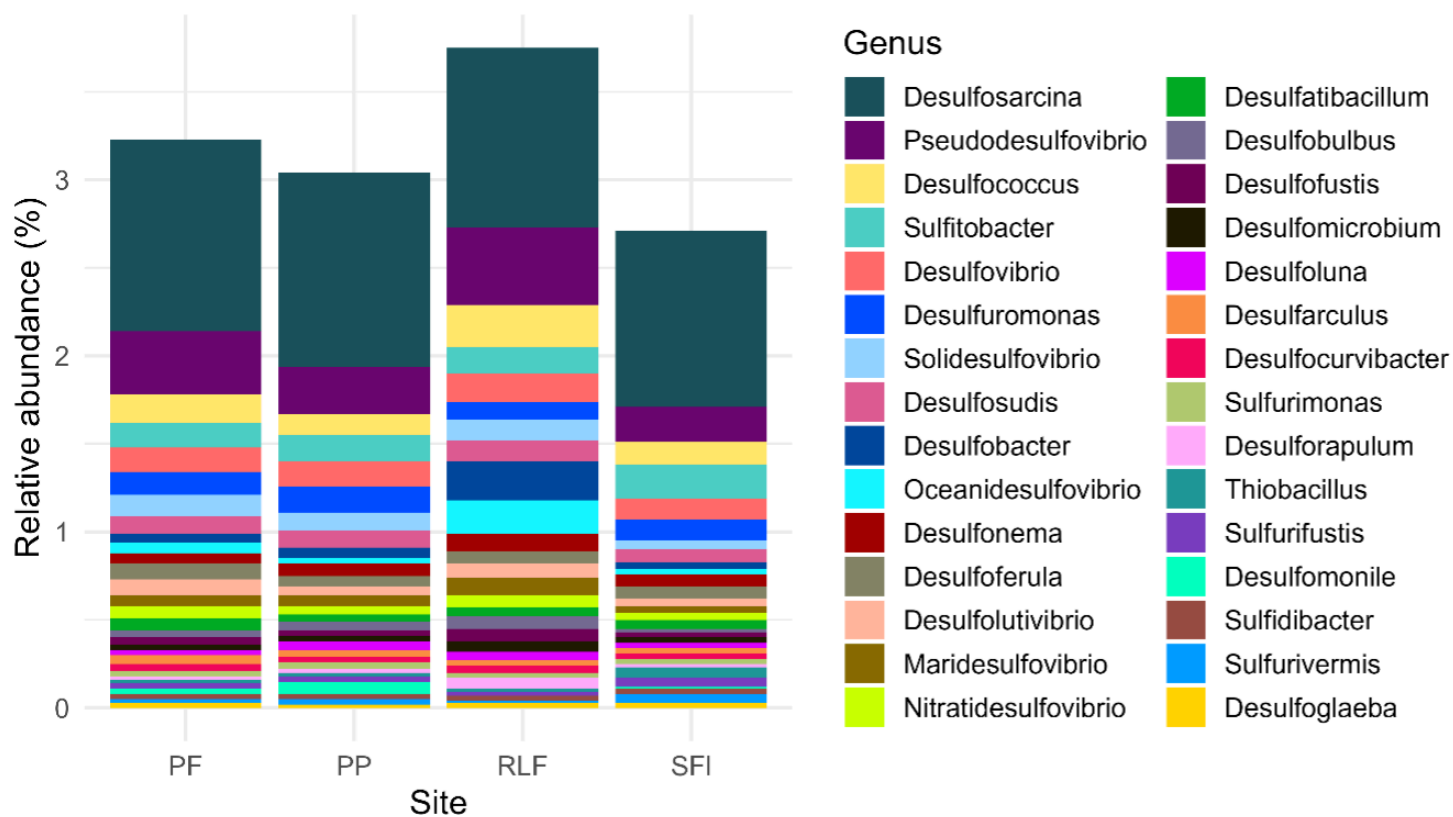


Figure 5

Relative abundance of the 30 most abundant sulfur-related genera in microbial mats from the Yucatan Peninsula. PF= Progreso flat, PP= Progreso pustular, RLF= Ría Lagartos flat, SFI= Sisal floating

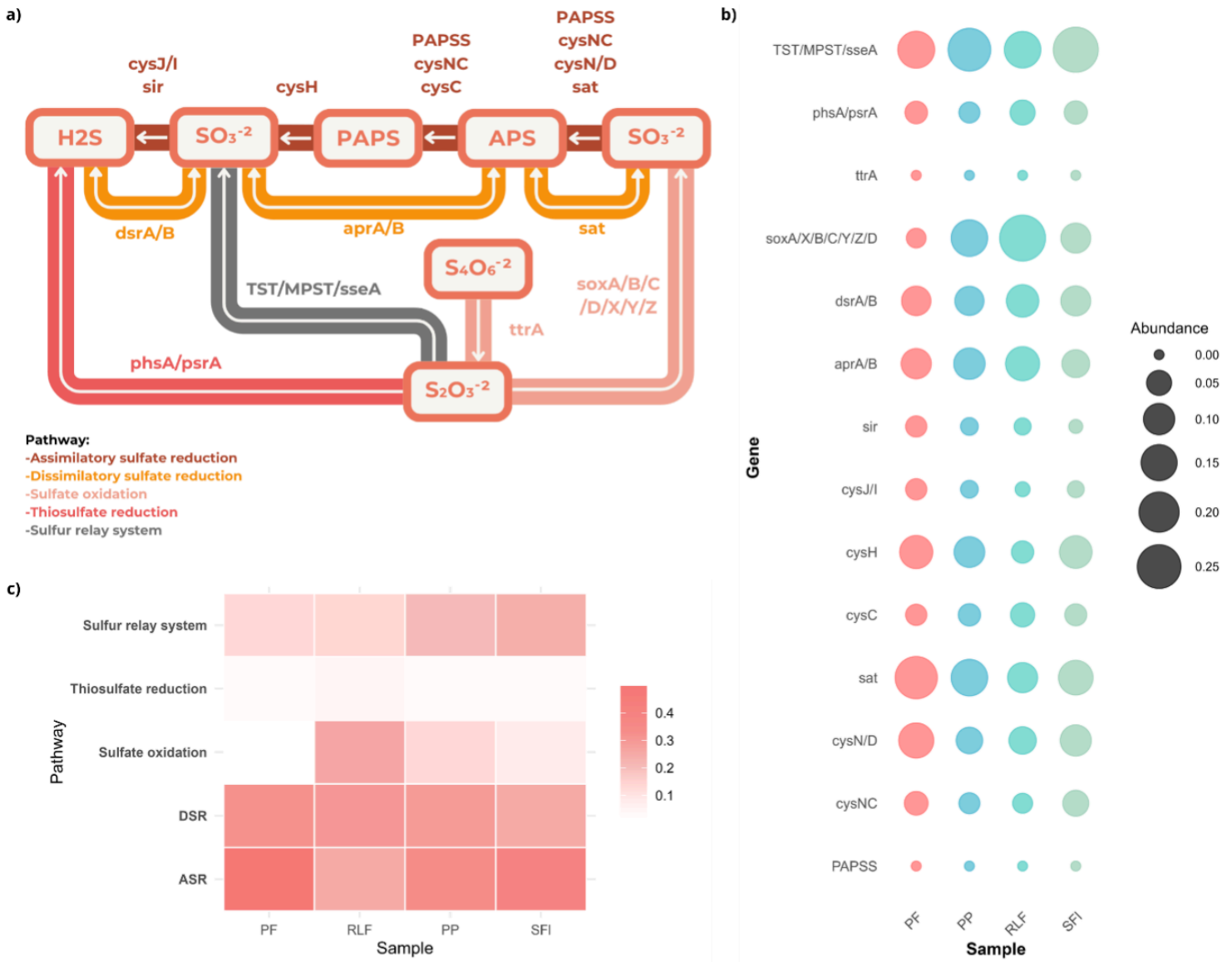


Figure 6

Genes involved in different pathways of the sulfur cycle (a). Abundance of genes involved in the sulfur cycle across the samples (b). Heatmap showing the total gene abundance of the sulfur cycle pathways in microbial mats from the Yucatan Peninsula (c). PF= Progreso flat, PP= Progreso pustular, RLF= Ría Lagartos flat, SFI= Sisal floating. ASR= assimilatory sulfate reduction, DSR= dissimilatory sulfate reduction

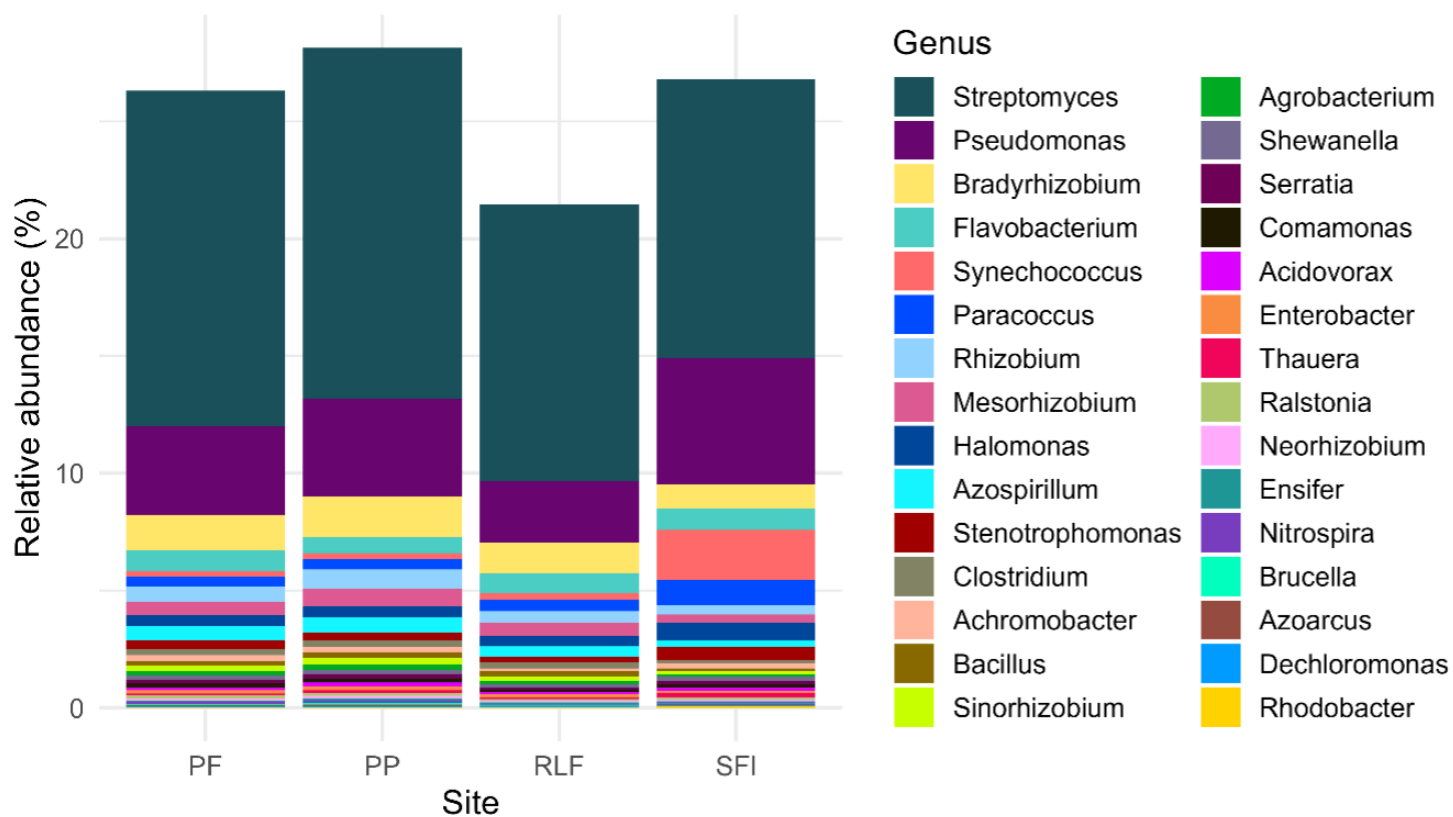


Figure 7

Relative abundance of the 30 most abundant nitrogen-related genera in microbial mats from the Yucatan Peninsula. PF= Progreso flat, PP= Progreso pustular, RLF= Ría Lagartos flat, SFI= Sisal floating

