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# Community and functional shifts in sediment microbiomes driven by coral-algal proximity in the Northern Red Sea

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Coral-algal interfaces are hotspots of biogeochemical activity, yet the structure and functional roles of sediment microbiomes associated with these habitats remain poorly resolved, particularly in the environmentally extreme northern Red Sea. This study characterizes how microbial community composition and functional potential vary with coral-algal proximity across three coastal sites (Alshreah, Saweehal, Marwan Cave). Shotgun metagenomic sequencing was performed on 18 sediment samples collected from two contrasting habitats at each site: (i) far-from-algae zones ( $\geq 500$  m) and (ii) close-to-algae zones ( $\leq 10$  m). Across all locations, eight dominant bacterial species structured the sediment microbiome, including *Shewanella algae*, *Arenibacter algicola*, *Vibrio algicola*, *Zobellia alginiliquefaciens*, and *Prochlorococcus marinus*. Species-level patterns showed strong spatial heterogeneity, with Marwan Cave consistently dominated by *S. algae*, while other sites exhibited clear habitat-dependent shifts. *A. algicola* and *S. algae* were more abundant near coral-algal habitats, whereas *V. algicola* was more prevalent in distant sediments. Further analysis indicated that both geographic location and algal proximity contributed to community structuring, with proximity effects most apparent at Alshreah and Saweehal. Functional profiles revealed clear habitat partitioning. Close-to-algae sediments were enriched in genes for chemotaxis, glycerol transport, and anaerobic metabolism, indicative of bacterial exploitation of algal exudates and low-oxygen microzones, while far-from-algae sediments showed higher representation of ABC transport systems, amino-acid metabolism, and stress-response pathways, reflecting nutrient-limited and more environmentally variable conditions. Overall, proximity to coral-algal assemblages emerged as a major ecological gradient shaping both the taxonomic and functional attributes of Red Sea sediment microbiomes,

operating alongside strong site-level environmental differences. These findings highlight the biogeochemical influence of benthic algae and provide baseline insights into microbial processes that may reinforce coral–algal regime shifts in warming reef systems.

#### KEYWORDS

algae-associated bacteria, benthic microbiome, coral–algal proximity, environmental gradients, metagenomics, Northern Red Sea, sediment microbiome

## Highlights

- Sediment microbiomes differed between far-from- and close-to-coral-algal habitats.
- Close-to-coral-algae sites were enriched in *Shewanella algae* and *Arenibacter algicola*.
- Far-from-coral-algae sites showed more *Vibrio algicola* and oligotrophic indicators.
- Functional shifts included chemotaxis, nutrient transport, and metal detoxification.

## 1 Introduction

Algae are foundational primary producers in marine ecosystems, sustaining food webs and driving global biogeochemical cycles. Both microalgae (e.g., *Chlorella*, *Nannochloropsis*, *Phaeodactylum tricornutum*) and macroalgae (e.g., *Ulva*, *Gracilaria*, *Porphyra*, *Corallina*) coexist with dense and taxonomically diverse microbial communities on their surfaces and within their tissues (Ramanan et al., 2016; Field et al., 1998). These microbial partners influence algal physiology through nutrient provisioning, vitamin synthesis, and degradation of complex polysaccharides (Egan et al., 2013; Dittami et al., 2016; Moran, 2015). Such interactions span mutualistic to opportunistic associations and can enhance algal productivity or contribute to disease and physiological stress (Fuhrman, 2009). Algae–microbe consortia are also a major source of industrially significant hydrocolloids, including carrageenan from *Kappaphycus alvarezii* and *Euचेuma denticulatum*, and agar/agarose from *Gracilaria* and *Gelidium* species (Rhein-Knudsen et al., 2015).

Beyond their roles in algal biology, microbial interactions with benthic algae influence broader reef ecosystem processes. Coral reefs function as holobiont systems in which corals, algae, and microbes collectively maintain nutrient recycling, energy flow, and resilience (Ainsworth et al., 2010; Thompson et al., 2014; Peixoto et al., 2017; Worden et al., 2015). Transitions from coral to algal dominance disrupt these interactions and are often reinforced by microbial feedback. Algal exudates enrich heterotrophic bacteria, alter coral-associated microbiomes and promote competitive imbalances that favor algal proliferation (Nelson et al., 2013; Smith et al., 2006). These microbial processes contribute to coral–

algal phase shifts observed across degraded reefs, such as the post-bleaching macroalgal expansion documented in the Seychelles (Wilson et al., 2012).

Environmental gradients, particularly temperature, nutrients, and turbidity modulate coral–algal–microbe dynamics and can destabilize the holobiont under stress. Heat stress reduces beneficial microbial taxa and alters host metabolism, weakening coral and algal resilience (Marangon et al., 2024; Pogoreutz et al., 2022). Conversely, some microbial communities can buffer hosts against stressors and support holobiont stability (Peixoto et al., 2017). These context-dependent outcomes emphasize the need for high-resolution metagenomic analyses to disentangle ecological drivers shaping benthic microbial assemblages (Nelson et al., 2013; Barott et al., 2012).

Sediments represent a critical but understudied component of coral reef ecosystems, functioning as dynamic reservoirs of organic matter, microbial activity, and biogeochemical cycling. Microbial communities in reef sediments respond sensitively to environmental gradients such as nutrient inputs, redox shifts, and benthic primary producer cover, including macroalgae. Unlike algal surface microbiomes, sediment microbiomes integrate both water-column inputs and benthic organic deposition, making them strong indicators of reef environmental status. Despite this importance, little is known about how sediment microbial assemblages change along coral–algal interfaces, where shifts in dissolved organic carbon, oxygen microgradients, and algal exudates may drive major reorganization of microbial structure and function. This study addresses this knowledge gap by examining how proximity to coral–algal habitats shapes both the taxonomic and functional profiles of benthic sediment microbiomes in the northern Red Sea.

Sediments represent a critical yet understudied component of this reef–benthos continuum. Reef sediments act as biogeochemical reactors where organic matter deposition, oxygen gradients, and benthic primary producer inputs shape highly dynamic microbial communities. Because sediment microbiomes integrate both water-column influences and benthic organic sources, they respond sensitively to microenvironmental changes associated with macroalgal cover, dissolved organic carbon release, and redox fluctuations (Nelson et al., 2013; Barott et al., 2012). Despite this central role, little is known about how sediment microbial communities reorganize along coral–algal interfaces, where sharp

chemical and metabolic gradients can restructure microbial diversity and function. This study addresses this gap by investigating how proximity to coral–algal habitats affect the taxonomic and metabolic profiles of benthic sediment microbiomes in the northern Red Sea.

Despite increasing recognition of coral–algal–microbe interactions, major knowledge gaps remain regarding their functional and ecological significance within Red Sea reef ecosystems. The Red Sea hosts unique environmental extremes in temperature, salinity, and nutrient availability, yet algae-associated and sediment-associated microbiomes remain insufficiently characterized. To address this, the present study applies metagenomic and taxonomic profiling to characterize sediment microbiomes along gradients of algal proximity in the northern Red Sea (Tabuk, Saudi Arabia). Specifically, we assess community composition, spatial structure, and functional attributes to elucidate how algal–microbial interactions shape the ecological dynamics and resilience of Red Sea reef sediments.

## 2 Materials and methods

### 2.1 Explored sites and soil sampling

Sediment samples were collected from three coastal locations along the northern Red Sea in the Tabuk region of Saudi Arabia: Alshreah, Saweehal, and Marwan Cave (Figure 1). Each site features

distinct coral–algal benthic habitats characteristic of the warm, saline northern Red Sea. Sediments were sampled from two contrasting habitat zones at each location: (1) far-from-algae zones, situated approximately  $\geq 500$  m from visible coral–algal associations, and (2) close-to-algae zones, located within  $\sim 10$  m of active coral–algal reefs. A total of 18 sediment samples were collected (six per site; three replicates per habitat). Sampling depths ranged between 10 and 20 m, and site-specific environmental parameters (temperature, salinity, pH, turbidity, and dissolved oxygen) were measured *in situ* to contextualize sediment microbial composition (Table 1).

GPS coordinates of the sampling sites were: Alshreah (E34°52′32.0″; N29°06′41.7″), Saweehal (E34°39′22.1″; N28°01′52.3″), and Marwan Cave (E34°50′50.4″; N29°01′33.7″). To maintain clarity, sample IDs were coded based on site, habitat, and replicate number. Site codes were R = Alshreah, S = Saweehal, and M = Marwan Cave. Habitat codes were 1 = far-from-algae and 2 = close-to-algae, while replicates were denoted as A, B, and C. For example, R1A refers to Alshreah, far-from-algae, replicate A; while R2C refers to Alshreah, close-to-algae, replicate C. The complete sample set included R1ABC, R2ABC, S1ABC, S2ABC, M1ABC, and M2ABC.

All samples were collected using hand-held basic sediment-corer with cylindrical tube attached at the end of the corer, in sterile plastic containers (approximately 1 kg sediment sample from each point) transported on ice, and processed at the Biodiversity Genomics Unit, Faculty of Science, University of Tabuk, Saudi Arabia.

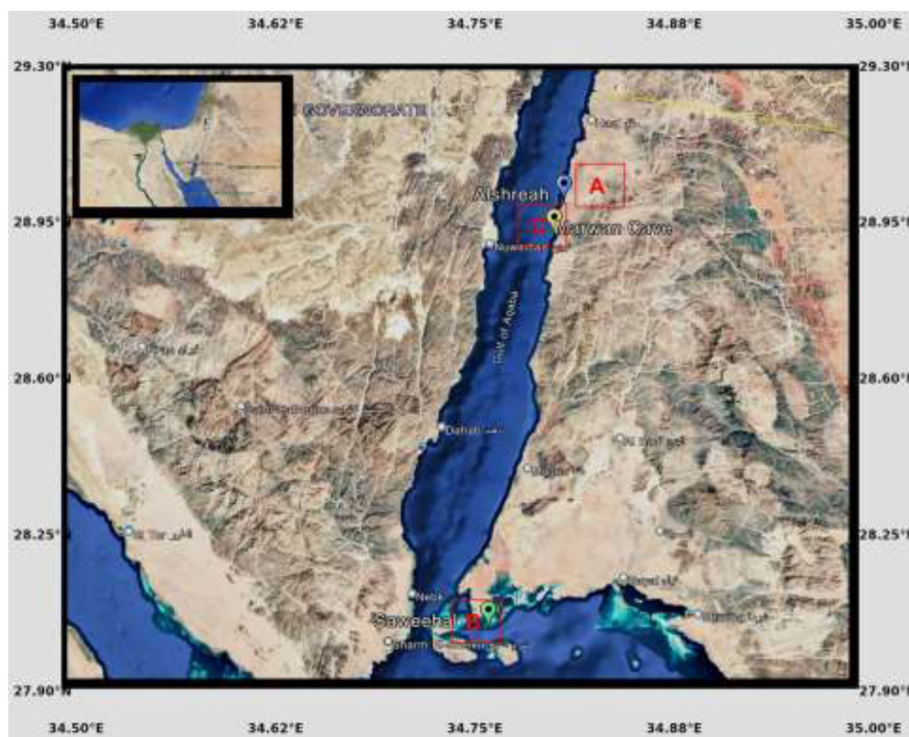


FIGURE 1

The sampling locations for this study along the coast of northern Red Sea in Tabuk, Saudi Arabia. The image shows the location of three sampling locations: (A) Alshreah (E34°52′32.0″; N29°06′41.7″), (B) Saweehal (E34°39′22.1″; N28°01′52.3″), and (C) Marwan Cave (E34°50′50.4″; N29°01′33.7″).

TABLE 1 The physicochemical characteristics of the study locations\*.

Characteristics of Water	Alshreah (R1)	Alshreah (R2)	Saweehal (S1)	Saweehal (S2)	Marwan Cave (M1)	Marwan Cave (M2)
Temperature	28.7	28.4	29.7	29.3	29.8	29.4
pH	8.1	8.3	8.0	8.3	8.4	7.2
Salinity ppt	44.5	43.3	43.6	44.4	44.0	44.3
Turbidity (NTU)	13	16	12	13	11	14
DO (mg/l)	3.36	3.54	3.31	3.72	3.46	3.33

\*Comparative analysis of key physicochemical water parameters—temperature, pH, salinity, turbidity, and dissolved oxygen (DO) before collection of sediments associated with Alshreah (R1, R2), Saweehal (S1, S2), and Marwan Cave (M1, M2). Data reflect median values from triplicate sampling points at each site Alshreah (R1, R2), Saweehal (S1, S2), and Marwan Cave (M1, M2) where 1 represents “far from coral-algae” and 2 represents “close to coral-algae”.

Environmental metadata (temperature, salinity, turbidity, and dissolved oxygen) were recorded at each sampling site to contextualize sediment-associated microbial communities. A multiparameter water quality meter (MPG-6099 Plus) was used to record turbidity, pH, dissolved oxygen, temperature, and salinity directly at the sampling point. Each sensor was calibrated according to the manufacturer’s protocols to ensure accuracy and reproducibility. Specifically, the pH electrode was standardized using NIST-traceable buffer solutions (pH 4.00, 7.00, and 10.00), the turbidity sensor was calibrated with formazin standards (0 NTU, 20 NTU, and 100 NTU), dissolved oxygen was calibrated using the water-saturated air method (100% saturation) and sodium sulphite solution (0% oxygen), conductivity/salinity was calibrated with potassium chloride solutions of known conductivity, and the temperature sensor was verified against a certified thermometer. Calibration checks were performed prior to each field campaign, and verification logs were maintained to ensure traceability and to minimize instrument drift.

## 2.2 Environmental DNA isolation and preparation of library

eDNA was extracted from sediment samples using the DNeasy PowerSoil Pro Kit (Qiagen, Cat. No. 47014; Germantown, MD, USA) following the manufacturer’s protocol. The quality and quantity of the extracted eDNA were assessed with a NanoDrop 1000 spectrophotometer (Thermo Scientific, Waltham, MA, USA). Libraries were prepared using the Illumina DNA Prep Kit (Illumina, San Diego, CA, USA) according to the manufacturer’s instructions. Library concentrations were measured with a Qubit Fluorometer (Thermo Fisher Scientific, Waltham, MA, USA), and quality was assessed using an Agilent 2100 Bioanalyzer (Agilent Technologies, Santa Clara, CA, USA).

## 2.3 Metagenomic sequencing

Sequencing was performed on the Illumina NovaSeq 6000 platform with paired-end 150 bp reads, generating an average of

~10 million raw reads per sample. Raw sequences were demultiplexed and converted into FASTQ format using bcl2fastq (Illumina). Taxonomic classification was performed with Kraken2 v2.2.2 (Wood et al., 2019), using the Kraken2 Soil (K2So) database for bacteria and fungi. The Kraken2 output was converted into BIOM format with kraken2biom and into Metaphlan (mpa) format using kreport2mpa.py and combine\_mpa.py utilities. Lineage-level heatmaps were produced using the Phyloseq R package (McMurdie and Holmes, 2013).

## 2.4 Metagenome assembly and gene prediction

Paired-end reads were assembled using MEGAHIT v1.2.9 (Li et al., 2015). Contigs were separated into prokaryotic and eukaryotic bins using EukRep v0.6.6 (West et al., 2018). Annotation of bacterial contigs was performed with the SqueezeMeta pipeline v2.3.0 (Tamames and Puente-Sánchez, 2019). Taxonomic classification of 16S rRNA sequences was performed with the RDP classifier (Wang et al., 2007). Aragorn v1.2.41 was used to predict tRNA/tmRNA sequences (Laslett and Canback, 2004). Gene prediction was performed using Prodigal v2.6.3 (Hyatt et al., 2010), and redundancy was reduced using CD-HIT, clustering sequences at  $\geq 90\%$  identity and  $\geq 90\%$  coverage to generate a non-redundant gene catalogue.

## 2.5 Genome binning and taxonomic assignment

Metagenome-assembled genomes (MAGs) were assessed using CheckM v2.2.3 for completeness and contamination (Chaumeil et al., 2020). Taxonomic identification was carried out with GTDB-Tk v2.4.0 (Chaumeil et al., 2020; Parks et al., 2018; Figueroa-González et al., 2024), using the Genome Taxonomy Database. Kaiju (standalone, Greedy mode) was employed for taxonomic annotation against the NCBI NR database (Menzel et al., 2016). Gene abundances were normalized as transcripts per million (TPM), with species-level abundance calculated by summing TPM values across genes assigned to the same species.

## 2.6 Data visualization and statistical analyses

All statistical analyses were conducted in R v4.3.2 (R Core Team, 2023). Data wrangling and visualization were carried out using tidyverse v2.0.0 (Wickham et al., 2019), ggplot2 v3.4.4 (Wickham, 2016), and ComplexHeatmap v2.18.0 (Gu et al., 2016). Community ecology analyses, including diversity indices and PCA, were performed using vegan v2.6-6 (Oksanen et al., 2013) and phyloseq v1.48.0 (McMurdie and Holmes, 2013). Alpha diversity was calculated using Simpson, ACE, Shannon, and Chao1 indices. Biological groups constituting less than 5% of the total sample were excluded from downstream analyses to enhance statistical power and minimize the influence of rarely represented categories that may compromise predictive stability and reliability.

## 2.7 Principal component analysis

Beta-diversity patterns were examined by PCA on a Bray-Curtis dissimilarity matrix of species abundance. Dimensionality reduction was performed with the prcomp function in R, and biplots were generated with samples differentiated by location and by proximity to algal reefs.

## 3 Results

### 3.1 Physicochemical characteristics of sampling sites

During sampling, the surrounding marine sediments exhibited distinct physicochemical conditions across sites (Table 1). A total of

18 sediment samples (collected adjacent to coral-algae habitat and away from coral-algae habitat) were obtained from three locations in the northern Red Sea (NRS) of the Tabuk region, at depths ranging from 10 to 20 m. Temperature values ranged from 28.4 to 29.8°C, while pH averaged between 7.2 and 8.4. Salinity varied from 43.0 to 44.5, and turbidity ranged between 11 and 16 NTU. Dissolved oxygen concentrations were relatively low, ranging from 3.3 to 3.7 mg/L. These parameters reflect the characteristically warm, saline environment of the northern Red Sea, which plays a central role in shaping benthic algal habitats and their associated microbial communities.

### 3.2 Taxonomic composition

Metagenomic sequencing and taxonomic classification were performed to identify operational taxonomic units (OTUs). Taxonomic assignments were carried out using Kaiju (standalone version), and gene abundances were quantified as transcripts per million (TPM) with SOAPaligner. Species-level abundances were inferred by summing the abundances of genes classified under each species. After redundancy filtering, a total of 2,505,200 predicted genes were obtained, of which 1,811,793 (71.7%) open reading frames (ORFs) were successfully annotated against the NR database.

Across taxonomic ranks, the proportion of annotated sequences was as follows: kingdom (84.42%), phylum (70.42%), class (75.24%), order (70.68%), family (65.09%), genus (44.98%), and species (34.15%). The relative abundance of bacterial communities at the phylum level revealed clear differences among sediment samples collected from the three coastal sites (Figure 2). Across all 18 sediment samples, the dominant bacterial phyla included Proteobacteria, Bacteroidota, Verrucomicrobiota, Firmicutes, and Cyanobacteria. However, their distribution differed markedly between habitats. Near-algae

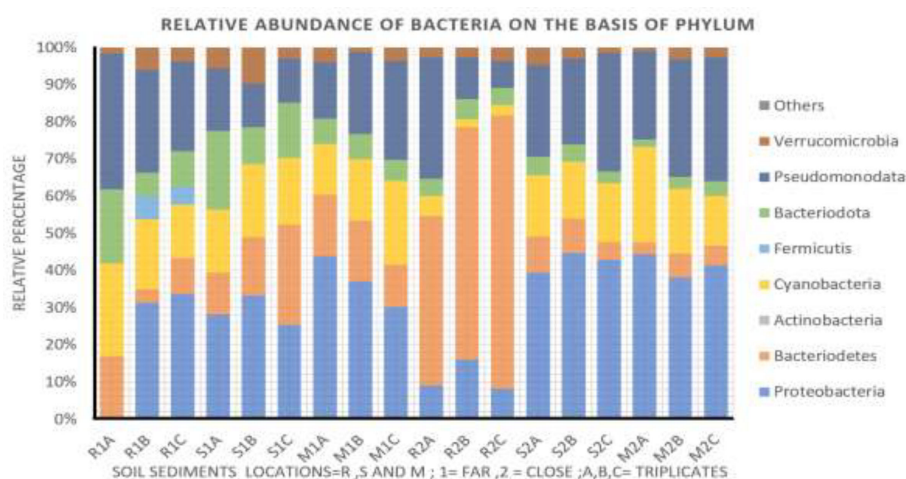


FIGURE 2

Relative abundance of bacterial phyla across sediment samples from three sites in the northern Red Sea of Tabuk region. Sediment samples were collected from three sites (Alshreah = R, Saweehal = S, Marwan Cave = M), two habitats at each site: far from algae-coral associations (coded as 1) and close to algae-coral associations (coded as 2), with three replicates (A-C) per habitat. Taxonomic classification was performed at the phylum level using Bray-Curtis sample clustering analysis.

sediments showed higher relative abundances of copiotrophic lineages such as *Vibrio*, *Pseudoalteromonas*, *Halomonas*, and members of Rhodobacteraceae, consistent with their capacity to exploit algal-derived dissolved organic carbon. In contrast, far-from-algae sediments were enriched in oligotrophic taxa including *Woeseia*, *Nitrosopumilus*, *Marinimicrobia*, and lineages of Planctomycetota, indicating adaptation to more recalcitrant and spatially diffuse carbon pools.

Sediments from Alshreah (R) were characterized by a mixed community. In samples collected far from algae (R1A–R1C), Bacteroidota and Cyanobacteria were relatively abundant, whereas close-to-algae sediments (R2A–R2C) exhibited striking enrichment of Bacteroidota, particularly in replicates R2B and R2C.

At Saweehal (S), the microbial profile was more balanced. Far-from-algae sediments (S1A–S1C) showed higher proportions of Firmicutes and Cyanobacteria, while close-to-algae samples (S2A–S2C) displayed increased Proteobacteria dominance, accompanied by moderate levels of Bacteroidota and Cyanobacteria.

In contrast, Marwan Cave (M) sediments were dominated by Proteobacteria, both in far-from-algae (M1A–M1C) and close-to-algae (M2A–M2C) samples. However, the relative abundance of Bacteroidota was notably lower in Marwan sediments, with particularly low representation in sample M2A. Firmicutes and Cyanobacteria contributed consistently across replicates, while Verrucomicrobia appeared sporadically in both Saweehal and Marwan sediments at low levels.

Overall, the taxonomic distribution indicates that algal proximity influences bacterial community composition, with Bacteroidota enriched near algal-associated sediments at Alshreah, whereas Proteobacteria dominated Marwan sediments regardless of algal proximity.

### 3.3 Species-specific distribution of algae-associated microbiomes

The analysis of algae-associated microbial abundance (AMA) revealed eight dominant bacterial species across all sediment samples: *Arenibacter algicola*, *Shewanella algae*, *Vibrio algicola*, *Zobellia alginiliquefaciens*, *Prochlorococcus marinus*, *Pseudoceanicola algae*, *Parasphingopyxis algicola*, and *Algicella marina* (Figure 3). *Prochlorococcus marinus* contributed modest but consistent abundances across all sites, reflecting its role as a background primary producer, while less abundant taxa such as *Pseudoceanicola algae*, *Parasphingopyxis algicola*, and *Algicella marina* likely participated in algal organic matter breakdown and nutrient recycling. Species abundances of these dominant taxa varied widely, ranging from 6 to 70% across replicates, indicating strong spatial heterogeneity in community composition.

Clear location- and proximity-based shifts were observed: in Alshreah (R), far-from-algae samples (R1) were enriched in *Vibrio algicola*, reflecting the polluted status of this site, whereas close-to-algae samples (R2) showed a predominance of *Arenibacter algicola*. In Saweehal (S), *Zobellia alginiliquefaciens* dominated the far-from-algae samples (S1), while *Shewanella algae* prevailed in close-to-algae samples (S2). In Marwan cave (M), both far-from- (M1) and close-to-algae (M2) samples exhibited consistently high levels of *Shewanella algae*, alongside relatively stable contributions of *Vibrio algicola* and other taxa. The persistence of *Shewanella algae* at this site is particularly notable, as this species is known to promote algal growth, inhibit fungal infections, and detoxify arsenic, thereby reducing its bioavailability in aquatic ecosystems.

Notably, sediments collected near coral-algae habitats exhibited higher representation of *Arenibacter algicola* and *Shewanella algae*,

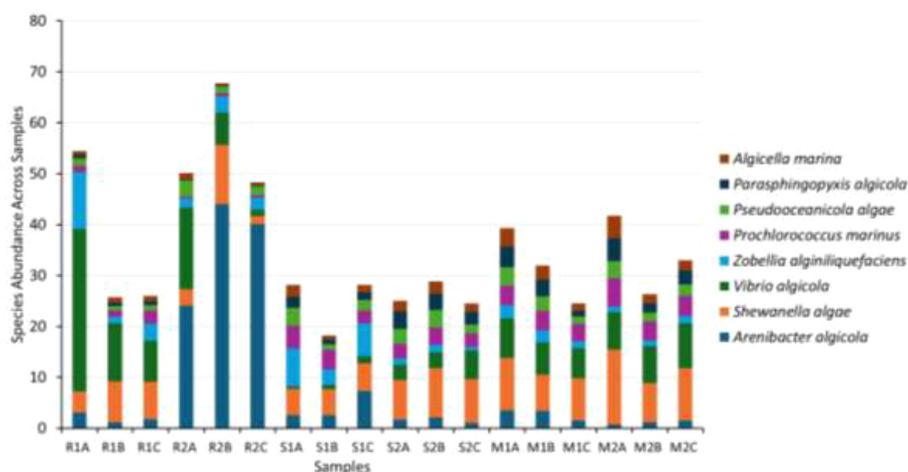


FIGURE 3

Species-level relative abundance across sediment samples from three sites in the northern Red Sea of Tabuk region. Sediment samples were collected from three sites (Alshreah = R, Saweehal = S, Marwan Cave = M), two habitats at each site: far from algae–coral associations (coded as 1) and close to algae–coral associations (coded as 2), with three replicates (A–C) per habitat. Bars represent summed TPM-normalized gene abundances for the eight most abundant taxa detected: *Arenibacter algicola*, *Shewanella algae*, *Vibrio algicola*, *Zobellia alginiliquefaciens*, *Prochlorococcus marinus*, *Pseudoceanicola algae*, *Parasphingopyxis algicola*, and *Algicella marina*. Taxonomy was assigned with Kaiju and abundances derived from read mapping to the non-redundant gene catalogue (TPM).

suggesting that proximity to algal hosts plays a critical role in shaping species-level microbiome structure.

### 3.4 Geographic and proximity-driven structuring of bacterial communities

The species-level dissimilarities analysis revealed a clear spatial structuring of sediment microbiomes across the three northern Red Sea locations and between proximity categories (Figure 4). The first two principal components explained 68.68% of the total variance, indicating strong underlying gradients in community composition. The dissimilarity analysis revealed that the samples are separated primarily by geographic location (PC1, 58.84%), with Alshreah, Saweehal, and Marwan forming three distinct clusters (Figure 4). This indicates that geographic heterogeneity is the dominant source of community variation, consistent with the site-specific physicochemical conditions including temperature, pH, salinity, turbidity and dissolved oxygen.

Dissimilarities associated with proximity to coral–algal habitats are also evident along PC2 (17.84%). In both Alshreah and Saweehal, close-to-algae sediments formed distinct clusters separate from their respective far-from-algae groups, demonstrating that algal proximity is a strong driver of within-site microbial variation. These proximity-linked shifts are concordant with the species-level changes described above, including the enrichment of *Shewanella* algae and *Arenibacter algicola* in close-to-algae sediments. In contrast, Marwan Cave samples showed minimal separation by proximity, forming a tight cluster regardless of distance to algae. This reduced within-site variation aligns with the uniform dominance of *Shewanella* algae at

this location, suggesting strong local structuring that overrides proximity effects.

Together, the PCA results demonstrate that site-level environmental conditions primarily structure the sediment microbiome, and algal proximity imposes an additional, consistent shift within sites where spatial heterogeneity exists. The observed patterns clearly demonstrate that algal proximity contributes to within-site differentiation, while geographic location accounts for the majority of between-site variance.

### 3.5 Functional annotation of metagenomic genes from MAGs

Clusters of Orthologous Groups (COG) were assigned to predicted proteins using annotation criteria of amino acid identity > 40%, overlap length  $\geq 23$  amino acids, and E-value < 0.1. High-quality reads were mapped to the non-redundant gene catalog using SOAP-aligner, and average TPM (Transcripts Per Million) values across replicates were used to summarize functional profiles. The resulting COG distribution highlighted distinct functional signatures between microbial communities associated with algae and those located far from algae (Table 2).

Close-to-algae samples: Several functional groups were enriched in algae-associated sediments. These included chemotaxis and methyl-accepting proteins (COG0840; TPM 3,990–6,604), suggesting enhanced microbial responses to algal chemical gradients; NAD-dependent aldehyde dehydrogenases (COG1012), implicated in detoxification of reactive aldehydes produced during algal photosynthesis or stress; and glycerol

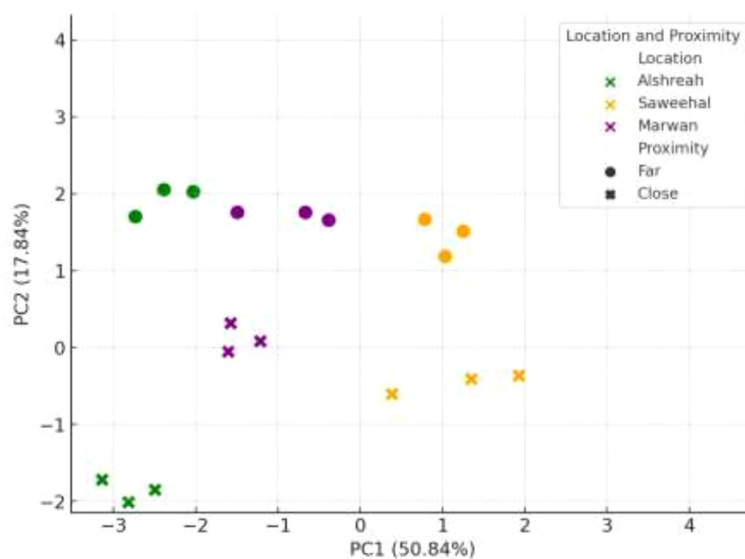


FIGURE 4

Principal component analysis (PCA) of species-level composition of algal-associated bacterial communities. Points are colored by location (Alshreah = green; Saweehal = orange; Marwan = purple) and shaped by proximity to algae (far-from-algae = circles; close-to-algae = crosses). The first two principal components explain 68.68% of the variance (PC1 = 50.84%, PC2 = 17.84%). PC1 mainly separates samples by geographic location, while PC2 captures differences associated with algal proximity.

TABLE 2 Dominant taxa and functional characteristics of close-to-algae vs. far-from-algae sediment microbiomes.

Category	Close-to-algae sediments	Far-from-algae sediments
Dominant Species	<i>Shewanella algae</i> , <i>Arenibacter algicola</i> , <i>Vibrio algicola</i> (variable), <i>Zobellia alginiliquefaciens</i> (site-dependent)	<i>Vibrio algicola</i> , <i>Zobellia alginiliquefaciens</i> , <i>Prochlorococcus marinus</i> , minor taxa ( <i>Pseudoceanicola</i> , <i>Parasphingopyxis</i> , <i>Algicella</i> )
Key Functional Enrichments	Chemotaxis receptors (COG0840); glycerol uptake permeases (COG0580); anaerobic reductases (nitrate, DMSO/arsenate); polysaccharide degradation	ABC transporters; amino-acid and polyamine transporters; stress-response pathways (oxidative stress genes elevated)
Ecological Interpretation	Adapted to high DOC from algae; strong resource-sensing; biofilm formation; microaerophilic niche beneath algal mats	Adapted to dilute, oligotrophic conditions; generalist metabolism; increased need for broad-stress tolerance
Microhabitat Drivers	Algal exudates, localized oxygen depletion, enriched labile carbon	Lower organic inputs; stable oxygenation; fewer algal-derived metabolites

uptake permeases (COG0580), consistent with microbial utilization of dissolved organic carbon and osmoregulation. Energy production pathways were also prominent, such as anaerobic dehydrogenases (COG0243) and nitrate reductases (COG5013), reflecting adaptation to oxygen-deficient niches near algal mats. Signal transduction genes (COG0642; TPM 4,520–5,200) and multidrug/cation efflux pumps (COG0841) pointed to robust environmental sensing and stress tolerance. Notably, arsenate reductases (DMSO/arsenate reductase; CECT 5071) linked to *Shewanella* spp. suggest bioremediation capacity in heavy metal-influenced sediments.

Far-from-algae samples: Microbial communities at sites distant from algae showed a different set of dominant functions. Chemotaxis proteins (COG0840; TPM 6,100–7,200) remained abundant, but additional transport systems were notable, including Na<sup>+</sup>/alanine symporters (COG1115) and spermidine/putrescine transport ATPases (COG3842), reflecting roles in nutrient uptake and amino-acid metabolism. Iron acquisition genes (COG1629) were enriched (TPM 4,199–4,498), consistent with iron limitation in offshore sediments. Signal transduction histidine kinases (COG0642; TPM 5,041–5,463) and multidrug efflux pumps (COG0841; TPM 5,469–7,547) were highly expressed, indicating microbial strategies to cope with variable or oligotrophic conditions. Again, *Shewanella* arsenate reductases (CECT 5071) were detected, supporting widespread roles in heavy-metal detoxification across both habitats.

Overall, these patterns suggest that close-to-algae microbial consortia are functionally tuned to exploit algal exudates and low-oxygen microenvironments, while far-from-algae communities rely more on general nutrient transport and stress response pathways. This functional partitioning underscores the ecological influence of algae on shaping sediment microbiome metabolism.

## 4 Discussion

This study provides the first integrated metagenomic assessment of benthic sediment microbiomes influenced by coral-algal habitats in the northern Red Sea, revealing how geographic context and algal proximity jointly shape microbial taxonomic structure, dominant

species, and functional metabolic strategies. By combining taxonomic and functional profiling, we demonstrate that (i) geographic location imposes the strongest constraint on community composition, (ii) a small number of metabolically versatile taxa (e.g., *Shewanella algae*, *Arenibacter algicola*, *Vibrio algicola*) disproportionately shape local community structure, and (iii) algal proximity establishes distinct functional guilds characterized by enhanced chemotaxis, anaerobic metabolism, and polysaccharide utilization, whereas distant sediments exhibit greater reliance on stress-response and nutrient-transport pathways. Together, these findings illustrate how benthic microbial communities mediate the biological and geochemical consequences of coral-algal interactions.

### 4.1 Taxonomic patterns in context

The dominance of Proteobacteria (Pseudomonadota), Bacteroidota and Cyanobacteria across sediments mirrors patterns repeatedly observed in algal-associated microbiomes and is consistent with the concept of a macroalgal holobiont backbone (Martin et al., 2014; van der Loos et al., 2019). However, the strong geographic dissimilarities observed in this study indicates that baseline physicochemical differences among Alshreah, Saweehal, and Marwan Cave might have exerted a primary structuring effect. Variations in temperature, pH, turbidity, and dissolved oxygen (Table 1) likely regulate redox potential, carbon oxidation processes, and nutrient turnover, creating distinct microbial “starting states” upon which biological interactions, including algal influence, act (Nelson et al., 2013; Barott et al., 2012; Mayali and Azam, 2004). These site-level templates help explain the prominent *Shewanella* dominance at Marwan Cave, where local conditions appear highly favorable for this metabolically flexible lineage. Such cases illustrate how environmental heterogeneity can outweigh or obscure proximity effects—a phenomenon also reported in other reef systems (Silva et al., 2021; Bourne et al., 2016; Rosenberg et al., 2007).

### 4.2 Species-level ecology and implications

Species-level patterns provide mechanistic insight into community assembly. *Shewanella algae* dominated Marwan Cave

and many close-to-algae samples. This taxon's ability to perform facultative anaerobiosis, reduce arsenate and DMSO, and utilize diverse electron acceptors enables it to thrive in redox-dynamic, organic-rich microzones typical of algal interfaces (Lemaire et al., 2020; Roach et al., 2017). Conversely, taxa such as *Arenibacter algicola* and *Zobellia alginiliquifaciens*, enriched at Alshreah and Saweehal, respectively, belong to lineages known for macroalgal-polysaccharide degradation and for close epiphytic associations with macroalgae (Brunet et al., 2021; Martin et al., 2021; Hehemann et al., 2014). The enrichment of *Vibrio algicola* in far-from-algae sediments suggests niche partitioning, with some *Vibrios* exploiting free-living or opportunistic lifestyles where algal-derived labile carbon is low (Geng et al., 2020).

### 4.3 Functional partitioning: metabolism, signaling and stress responses

Functional signatures observed in this study also provide insight into the ecological nature of coral–algal–microbe associations. Sediments close to algal–coral habitats were enriched in chemotaxis receptors, glycerol uptake systems, and anaerobic reductases, traits typical of bacteria that exploit concentrated pulses of labile dissolved organic matter released by macroalgae (Nelson et al., 2013; Stocker, 2012; Singh and Reddy, 2015). These traits support a lifestyle based on rapid resource sensing, biofilm formation, and metabolic flexibility under micro-oxygen gradients created beneath algal canopies (Lian et al., 2021; Kimbrel et al., 2019; Roach et al., 2017; Barott et al., 2012). In this context, the relationship between algae and their associated microbiota is predominantly resource-driven and often mutualistic: algae provide carbon-rich exudates, while bacteria recycle nutrients and detoxify metabolites that can influence the surrounding holobiont. Furthermore, the elevated abundance of anaerobic dehydrogenases and nitrate reductases in algae-proximal samples suggests metabolic tuning to microaerophilic or reducing microzones commonly formed under dense algal mats, consistent with laboratory and field observations showing altered redox conditions and increased microbial energy demand at coral–algal interfaces (Roach et al., 2017; Cárdenas et al., 2018). In contrast, far-from-algae sediments showed higher representation of ABC transporters and spermidine/putrescine transport systems, indicating a shift toward oligotrophic, generalist nutrient acquisition strategies that rely on more recalcitrant and spatially diffuse organic substrates rather than algal exudate inputs. This divergence in functional repertoires reflects a shift from tightly coupled, metabolically interactive consortia near algae toward more generalist, free-living assemblages in background sediments. Collectively, these functional patterns clarify that proximity to algae does not merely reshape taxonomic profiles but establishes distinct metabolic guilds with different ecological roles in coral–algal interaction zones.

Although distant sediments showed strong enrichment of stress-response pathways (e.g., oxidative-stress proteins, universal stress proteins, and multidrug efflux systems), these functions were largely absent in coral–algal–associated microbiomes. This pattern

likely reflects fundamental differences in microhabitat chemistry. Near algal mats, continuous release of dissolved organic carbon, antioxidants, and osmolytes creates chemically buffered microzones that stabilize pH, reduce oxidative stress, and support microbial growth, lowering the selective pressure for broad stress-response systems (Egan et al., 2013; Ramanan et al., 2016). In contrast, sediments far from algae experience greater fluctuations in oxygen, salinity, nutrient concentration, and redox potential, favouring generalist bacteria capable of coping with environmental variability through expanded stress-response repertoires (Hutchins and Fu, 2017; Buchan et al., 2014). Thus, the absence of stress-response genes near algae does not indicate reduced microbial resilience, but rather reflects the formation of a stable, exudate-rich microenvironment in which specialized metabolic traits (chemotaxis, glycerol uptake, polysaccharide degradation) are more advantageous than broad stress-defence mechanisms.

### 4.4 Ecosystem-scale consequences

These taxonomic and functional patterns imply that algal overgrowth can modify sediment microbial processes in ways that reinforce phase shifts on reefs. Enrichment of polysaccharide-degrading taxa and bacteria with chemotactic, biofilm-forming and virulence-linked traits (observed elsewhere when labile carbon increases) can favor persistent algal biofilms and reduce coral recruitment and recovery (Nelson et al., 2013; Barott et al., 2012; Cárdenas et al., 2018). The presence of taxa capable of metal or oxyanion reduction (e.g., *Shewanella* spp.) further suggests that microbial metabolism can mediate local chemical stressors, potentially attenuating or shifting bioavailability of contaminants in ways that affect reef resilience (Lemaire et al., 2020).

### 4.5 Biotechnological and biogeochemical relevance

Algae-proximal sediments are reservoirs of carbohydrate-active taxa and functions (agarases, carrageenases, glycoside hydrolases) with industrial relevance; prior work has shown macroalga-associated microbes as a rich source of novel polysaccharide-degrading enzymes (Hehemann et al., 2014; Gu et al., 2022; Sarwar et al., 2013; Sarwar et al., 1987). At the same time, the strong signal for detoxification-type enzymes in some samples highlights the potential ecological role of sediment bacteria in bioremediation and warrants targeted functional assays to validate enzyme activity *in situ* (Lemaire et al., 2020).

## 5 Conclusions and future directions

This study demonstrates that benthic microbial communities are jointly shaped by geographic environmental context and algal proximity, forming distinct taxonomic and metabolic guilds. Key taxa (e.g., *Shewanella*, *Arenibacter*, *Zobellia*) and functional

signatures (chemotaxis, glycerol transport, anaerobic respiration, metal reduction) reveal mechanistic pathways through which algae shape sediment biogeochemistry. We recommend future work integrating metatranscriptomics, culture-based enzymatic assays, and time-series analyses to identify thresholds and stability of algal-microbiome interactions.

## Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding authors.

## Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

## Author contributions

AmA: Funding acquisition, Conceptualization, Writing – review & editing, Writing – original draft. UJ: Methodology, Writing – original draft, Writing – review & editing. YM: Writing – review & editing, Resources, Writing – original draft. HG: Writing – original draft, Data curation, Writing – review & editing, Methodology. BA: Validation, Writing – review & editing, Writing – original draft, Software. DiA: Writing – original draft, Formal Analysis, Writing – review & editing, Software, Validation. DoA: Resources, Writing – review & editing, Funding acquisition, Formal Analysis, Writing – original draft. AbA: Writing – review & editing, Supervision, Writing – original draft, Project administration. AbdA: Validation, Writing – review & editing, Software, Writing – original draft, Supervision. AsA: Software, Investigation, Writing – original draft, Writing – review & editing, Supervision. FA: Writing – review & editing, Validation, Writing – original draft, Software, Data curation. MA: Writing – review & editing, Writing – original draft, Software, Resources. MG: Software, Writing – review & editing, Writing – original draft, Visualization, Methodology, Resources. RM: Software, Writing – original draft, Conceptualization, Methodology, Project administration, Writing – review & editing, Funding acquisition, Supervision, Formal Analysis.

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## Conflict of interest

The authors declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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