Journal of Soils and Sediments (2025) 25:1737–1748
https://doi.org/10.1007/s11368-025-04024-8

SEDIMENTS, SEC 4 • SEDIMENT-ECOLOGY INTERACTIONS • RESEARCH ARTICLE

The spatial patterns of bacterial communities in suspended particulate matter across the inner Great Barrier Reef

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Received: 16 December 2024 / Accepted: 28 March 2025 / Published online: 7 April 2025

Abstract

Purpose Microbial communities play a significant role in maintaining the health of Great Barrier Reef (GBR) ecosystems, however, the influence of sediment composition and other environmental factors such as temperature and wave regime on microbial communities are largely unknown. Here we show how sediment composition and exposure influences bacterial communities across the inner section of the GBR (Cleveland Bay, Halifax Bay and Dunk Island) between 2016 and 2018.

Materials and methods Sediment traps were installed and routinely deployed (~every 3 months) at eight sites in the inshore GBR and analysed for water chemistry, sediment geochemistry and organic characteristics and associated bacterial communities.

Results and discussion Results showed a significant variation in water turbidity, sediment collection rate and geochemistry across the trap sites. Bacterial communities also significantly varied along the inner GBR, with the shift in relative abundance of Actinobacteria, Acidobacteria, Planctomycete, Verrucomicrobia and Chloroflexi being the main cause of the bacterial community dynamics. The variation in spatial patterns of bacterial communities was highly correlated with water turbidity and the geochemical characteristics of associated sediments (e.g., K, Fe, Mn, Co, Al, Cr, Ca) collected across the marine trap sites.

Conclusion Our findings indicate that sediment composition and collection rate (and linked water turbidity) can change the spatial patterns of bacterial communities by creating environmental gradients along the inner section of the GBR.

Keywords Water quality · Coral reefs · Microbial community

1 Introduction

The Great Barrier Reef (GBR) is the world's largest coral reef ecosystem stretching over 2100 km along the Queensland coast of Australia (Angly et al. 2016). It is among the most biologically diverse and productive ecosystems on Earth (Richards and Day 2018). However, this complex assemblage of coral reefs is under threat due to increasing anthropogenic pressures (Wolff et al. 2018).The GBR is exposed to a combination of local pressures (e.g., nutrient, sediment) from land-based activities (Brodie et al. 2012) and global disturbances such as climate change (Hughes et al. 2017). Riverine runoff introduces a considerable amount of sediment and nutrients to the inshore coastal waters (McCloskey et al. 2021) resulting in a deteriorating effect on water quality and associated ecosystems of the inner GBR (Thompson et al. 2014; Fabricius et al. 2016; Lambert et al. 2021). Declining water quality has been linked to reductions in coral biodiversity (Fabricius and De'ath 2000; Fabricius

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Responsible editor: Rebecca Bartley.

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et al. 2005; DeVantier et al. 2006) and significant alterations in coral reef dynamics (Van Woesik et al. 1999; McCook 2001; Fabricius et al. 2003). Alterations also include microbial communities (Uthicke and McGuire 2007; Witt et al. 2012) that play a crucial role in reef ecosystem productivity and sustainability (Lock et al. 1984; Battin et al. 2003; Ainsworth et al. 2010).

Microorganisms are fundamental drivers of biogeochemical cycling in coral reef ecosystems (Frade et al. 2020). They contribute to carbon (C) and sulfur cycling (Wegley et al. 2007; Raina et al. 2009; Kimes et al. 2010), nutrient fixation and organic remediation (Lema et al. 2012; McDevitt-Irwin et al. 2017) as well as the production of secondary metabolites and antibiotics (Ritchie 2006). Changes in the composition of microbial communities can influence the health of reef ecosystems (McDevitt-Irwin et al. 2017). The functional basis for most reef bacterial symbioses centres on cycling of essential nutrients (e.g., C, N, S, P) in addition to passage of trace metals, vitamin synthesis and provision of other cofactors (Bourne et al. 2016). Bacteria also support the persistence of corals through the production and exchange of secondary metabolites and bioactive compounds (Matthews et al. 2018, 2020). Coral-associated bacteria can regulate the health of corals, especially given the importance of bacterial-algal interactions for nutrient cycling (Cole 1982; Seymour et al. 2017; Matthews et al. 2020). However, bacterial communities have been reported to be highly responsive to changing environmental conditions (Witt et al. 2012). Changes in the compositional and functional diversity of both coral-associated and free-living microbial communities have been correlated with varying degrees of anthropogenic influence, including alterations in water quality (Frade et al. 2020). Bacterial community along the GBR lagoon has particularly shown seasonal and spatial dynamics related to riverine floodwaters and seasonal weather events (Angly et al. 2016). Free-living microbial communities in seawater has been reported to be five-times more responsive to the environment compared to coral associate microbial communities (Glasl et al. 2019). Thus, an understanding of the effect of environmental changes on the composition and dynamics of the bacterial communities in coral reef ecosystems is a significant knowledge gap that needs to be addressed. While the stable members of coral-associated bacterial communities are essential for the health and resilience of the reef, the transient members may only contribute to the coral reef ecosystem function under specific environmental conditions or, conversely, may play detrimental and antagonistic roles within the system (McDevitt-Irwin et al. 2017). Any stress events (e.g., excessive sediment and nutrient, high temperature, acidity) may lead to changes in bacterial communities within coral reef ecosystems by disrupting the functioning members and facilitating an invasion of bacteria that are not typically associated with the habitat (Uthicke and McGuire 2007; McDevitt-Irwin et al. 2017; Frade et al. 2020; Glasl et al. 2020). Despite the significance, the environmental drivers of bacterial community change are poorly resolved along the inner GBR, and it is unclear how the influence of sediment can affect their community composition, diversity, structure and functioning. Thus, this study aims to explore the spatial variations and response of bacterial communities to sediment exposure across the inner GBR. We hypothesised that the spatial patterns of bacteria would change as a response to the environmental gradient of sediment load and composition along the inner section of the GBR.

2 Materials and methods

2.1 Study area

This study was carried out at eight sites across three embayments in the central inshore GBR, north-east Queensland, Australia including: (1) Dunk Island within Rockingham Bay (-17.94° S, 146.15° E); (2) Orpheus, Pelorus and Havannah Islands within Halifax Bay (-18.84° S, 146.54° E); and (3) Middle Reef, Cleveland Bay, Orchard Rocks and Geoffrey Bay within Cleveland Bay (-19.16° S, 146.86° E). These site locations form part of a long-term research project using sediment traps to examine spatial and temporal variability in sediment dynamics and composition in the inshore GBR (Lewis et al. 2020). The site at Dunk Island, during the wet season months (November to April), is regularly influenced by river flood plumes from the Tully River (and occasionally the Herbert River) within the Wet Tropics region. The sites within Cleveland Bay have variable exposure to the prevailing south-easterly winds and are occasionally influenced by flood plumes from the Burdekin, Haughton and Ross Rivers of the Dry Tropics region during the wet season months (November to April). The Halifax Bay sites are located on relatively sheltered reef slopes where turbidity levels tend to be much lower than at Cleveland Bay (Bainbridge et al. 2021). These sites are also occasionally influenced by river flood plumes from the Burdekin River and possibly other local coastal streams such as the Herbert River (Fig. 1 and Fig. S1).

2.2 Marine trap sediment collection

The sediment trap used in this study was the SediSampler® (Integral Aqua Pty Ltd) patented cylindrical trap head (Lewis et al. 2018) with an internal diameter of 52 mm, and 300 mm length, containing 30 mm deep baffles in the upper section (Fig. S2). The trap head is designed to screw onto a

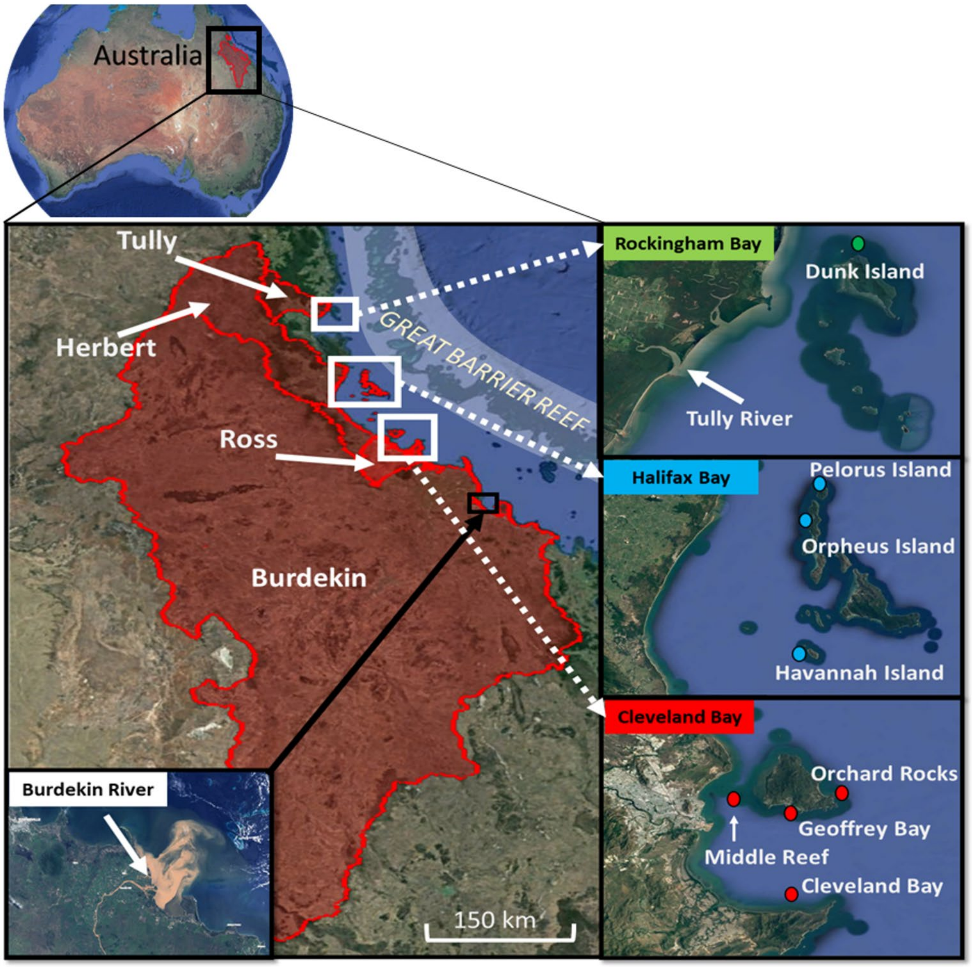

Fig. 1 Sediment trap locations at Cleveland Bay, Halifax Bay and Dunk Island sites across the inner Great Barrier Reef, Queensland, Australia

variety of sample bottles, with a 1 L polypropylene bottle used for this study. The sample bottle added an additional 185 mm to the effective trap length (i.e., aspect ratio ~ 9.4). In addition, the trap heads are entirely coated with antifoul to maintain trap surface conditions, collection efficiencies and to reduce blockages for long (e.g., 3 months) deployment periods. The marine sediment traps were each installed 50 cm above the seafloor at the sites of the inshore central GBR to capture sediment resuspension events and, during the wet season deployments, the influence of suspended sediments delivered in riverine flood plumes. A total of 29 trap sediment samples (Dunk Island site; two samples; Halifax Bay: 11 samples; and Cleveland Bay: 16 samples) were collected for analysis in this study between 2016 and 2018.

2.3 Trap sediment deployment and geochemical and organic matter characterisation

The sediment trap samples were collected ~ 3 monthly (Table S5) throughout the year within a 1 L bottle screwed onto the sediment trap head (Lewis et al. 2018). Upon collection of the sediment traps, the scuba divers unscrewed the ‘trap head’ and then capped the 1 L bottle. The mass retained by the sediment traps in the 1 L bottles was measured by the total suspended solids method (TSS method 2540D; APHA, 2005) in which a well-mixed 30 ml aliquot from the 1 L bottle was taken and, from this 30 ml aliquot, a 1 to 2 ml subsample was pipetted for analysis. The analysis comprised vacuum filtering known volumes of sample (i.e., in this case 1 to 2 ml added to a pre-filled 250 ml container of RO water) onto pre-weighed Whatman GF/C filter papers (nominal pore size 1.2 µm) which were dried overnight in a 103–105 °C oven and reweighed to provide a concentration in g L^{-1}.

Additional 250 ml aliquots of the 1 L sample were taken and kept frozen until further analysis. These 250 ml aliquots were defrosted and centrifuged (5000 rpm for 10 min) with the supernatant water discarded. Subsamples were collected for DNA extraction and the remaining sediment sample was oven dried (60 ˚C, 24 h) for total organic C (TOC) and total nitrogen (TN), inorganic C (IC), stable isotopes (δ^{13}C and δ^{15}N) and elemental analysis (Bahadori et al. 2020).

To measure the total C and stable isotope composition of nitrogen (δ^{15}N), sediment samples were pelletized in tin capsules. For TOC and $\delta^{13}C$ analysis firstly IC was removed by 10% hydrochloric acid (HCl), then the samples were pelletized in silver capsules and weighed prior to analysis by a Sercon Hydra 20–22 Europa EA-GSL isotope-ratio mass spectrometer. Stable isotope ratios are reported in standard delta (δ) notation per mil (‰) as: $\delta_X = [(R_{sample}/R_{standard})-1]\times1000$ where X is ^{13} or ^{15} N and $R={}^{13}C/{}^{12}$ or ^{15} $N/{}^{14}N$, respectively. Standard reference materials were PDB limestone for C and Air was the standard for N (Bahadori et al. 2019). The IC content of samples was calculated as the difference in total C and TOC content of sediments. Chemical elements (e.g., Na, K, Ca, Mg, Cr, Ni, Mn, Co, Al, Fe and P) were analysed in trap sediments, using ICP-OES; Perkin Elmer; Optima 8300, after direct digestion with nitric and perchloric acid following standard procedure (Miller 2019). Particle size distribution was measured using the Mastersizer 3000 (Malvern Panalytical) laser diffraction analyser (Bahadori et al. 2021).

Solid-state ^{13}C cross polarisation magic angle spinning nuclear magnetic resonance (^{13}C CPMAS NMR) spectroscopy was used to determine soil organic C (OC) functional groups. Sediments were pre-treated with hydrofluoric acid (HF) prior to solid-state ^{13}C NMR analysis to remove paramagnetic species (e.g., Fe^{3+} and Mn^{2+}), minimizing their impacts on NMR spectra and concentrating the OM of the whole sample (Bahadori et al. 2019, 2022). The ^{13}C NMR spectra were acquired using a 300 MHz Varian VNMRS spectrometer (Varian Inc., CA) operating at a frequency of 75.4 MHz. Samples were packed in a 7 mm diameter silicon nitride rotor and spun at 5 kHz at the magic angle. The Tangent Cross Polarization (tancpx) sequence within the VnmrJ 3.1 A software package was used to perform the cross polarization. A total of 20,000 transients was collected. A contact time of 1.2 ms, an acquisition time of 20 ms, a recycle delay of 2.5 s and a spectral width of 477 ppm were used in all cases. Spectra were processed using the MestReNova version 11.0 software package (Mestrelab Research S.L.). Lorentzian line broadening functions of 50 Hz were applied to all spectra. ^{13}C chemical shifts were referenced relative to external hexamethylbenzene (HMB; δ_{CH3}, 17.4 ppm). To quantify different OC functional groups, the following chemical shift boundaries were selected for the ^{13}C NMR spectra (Prietzel et al. 2018; Bahadori et al. 2021). The alkyl C and O-alkyl C functional groups were within the chemical shift regions 0–45 ppm and 45–110 ppm, respectively. The chemical shift boundary 110–160 ppm included the aryl C representing aromatic compounds, and the chemical shift region 160–180 ppm represented carboxyl functional group. Representative solid-state ^{13}C NMR spectra for sediments collected at different sites are provided in Fig. S3.

2.4 DNA extraction, high-throughput sequencing, and bioinformatic analysis

The total genomic DNA was extracted from 0.3 to 0.5 g of frozen sediment sample using the MoBio Powersoil DNA isolation kit following the manufacturer`s instruction. A NanoDrop ND-2000 UV–vis spectrophotometer (NanoDrop Technologies, Wilmington, DE, USA) and an agarose gel electrophoresis were used to assess the concentration and quality of extracted DNA, respectively. Primers 515 F/806R (Bates et al. 2011) targeting the V4 region of bacterial 16 S rRNA gene was used for Polymerase Chain Reaction (PCR) analysis. PCR was conducted in a total volume of 30 µL containing 15 µL of Phusion® High-Fidelity PCR Master Mix (NEB, Ipswich, MA, USA), 0.2 mM of forward and reverse primers, and ~ 10 ng DNA template; each PCR run included a negative control. Purified PCR products and sequence library were prepared according to(Du et al. 2020), and the sequencing was performed on an Illumina Miseq sequencing platform (Illumina, San Diego, CA, USA). The obtained raw sequences were quality filtered, assembled, de-multiplexed, and assigned to individual samples using Quantitative Insights Into Microbial Ecology 2 (QIIME 2, version 2021.2) bioinformatic tool. High-throughput search and clustering tool (USEARCH) was used to cluster the sequences into operational taxonomic units (OTUs) at the 100% sequence identity (Edgar 2010, 2013). Representative sequences of OTUs were annotated against the SILVA version 132 reference database (Quast et al. 2012). Ambiguous taxonomic predictions (unassigned) were further checked against the reference sequence database in gen bank. To minimize the variation caused by the sampling sequences, each sample was rarefied by 23,100 sequences. All raw sequences were deposited to the Sequence Read Archive (SRA) with the accession number PRJNA690602.

2.5 Statistical analysis

Mantel correlation and non-metric multidimensional scaling (NMDS) ordination was conducted based on Bray-Curtis distance using vegan package in R version 3.5.3 (R Core Team 2013). Redundancy analysis (RDA) was also conducted using vegan package. The principal component analysis (PCA) was conducted in FactoMineR package in R (Lê et al. 2008). Analysis of Variance (ANOVA) and Spearman's rank correlations were constructed in IBM SPSS software (George and Mallery 2019). The network analysis was performed using Fastspar which is capable of predicting connections of bacteria and identifying bacterial groups that are closely related (Watts et al. 2019). To minimize the influence of rare taxa, only OTUs with more than four observations were kept. The False Discovery

Rate (FDR) was controlled by performing 1000 bootstraps. Only the strong ($r > 0.60$) and robust ($p < 0.001$) correlations were retained. Significant correlations (with 100 bootstraps, $p < 0.01$) between bacterial OTUs and geochemical (Na, K, Mg, Ca, Mn, Al, Co, Cr, Fe, IC, particle size, pH and water temperature) and organic matter (TOC and TN) characteristics of sediment were calculated. The correlation between bacteria and sediment trap site condition including total sediment collected (TSC), average nephelometer turbidity unit (NTU) and trap sediment collection rates (SCR) were also calculated and included in the network analysis. Nodes were coloured according to the sources of groups as mentioned above, e.g., bacteria, sediment trap site, geochemical and organic matter characteristics of collected sediment. The networks were laid out in the Gephi software (Bastian et al. 2009). Metabolic pathway abundance prediction, based on the METACYC database, was performed using PICRUST2 (Douglas, Maffei et al. 2020) applying the default parameters.

3 Results

3.1 Geochemical and organic matter characteristics of sediments across the inner GBR

The mean total sediment collected at the sites in Halifax Bay (8.6 ± 2.1 g) was lower than the mean total sediment collected from the Cleveland Bay (67.5 ± 42.5 g) and Dunk Island (69.0 ± 58.0 g) sites (Fig. 2a). The mean trap sediment collection rates (Fig. 2b) were also lower in the sites from Halifax Bay (3.4 ± 0.9 mg cm^{-2} day^{-1}) compared to

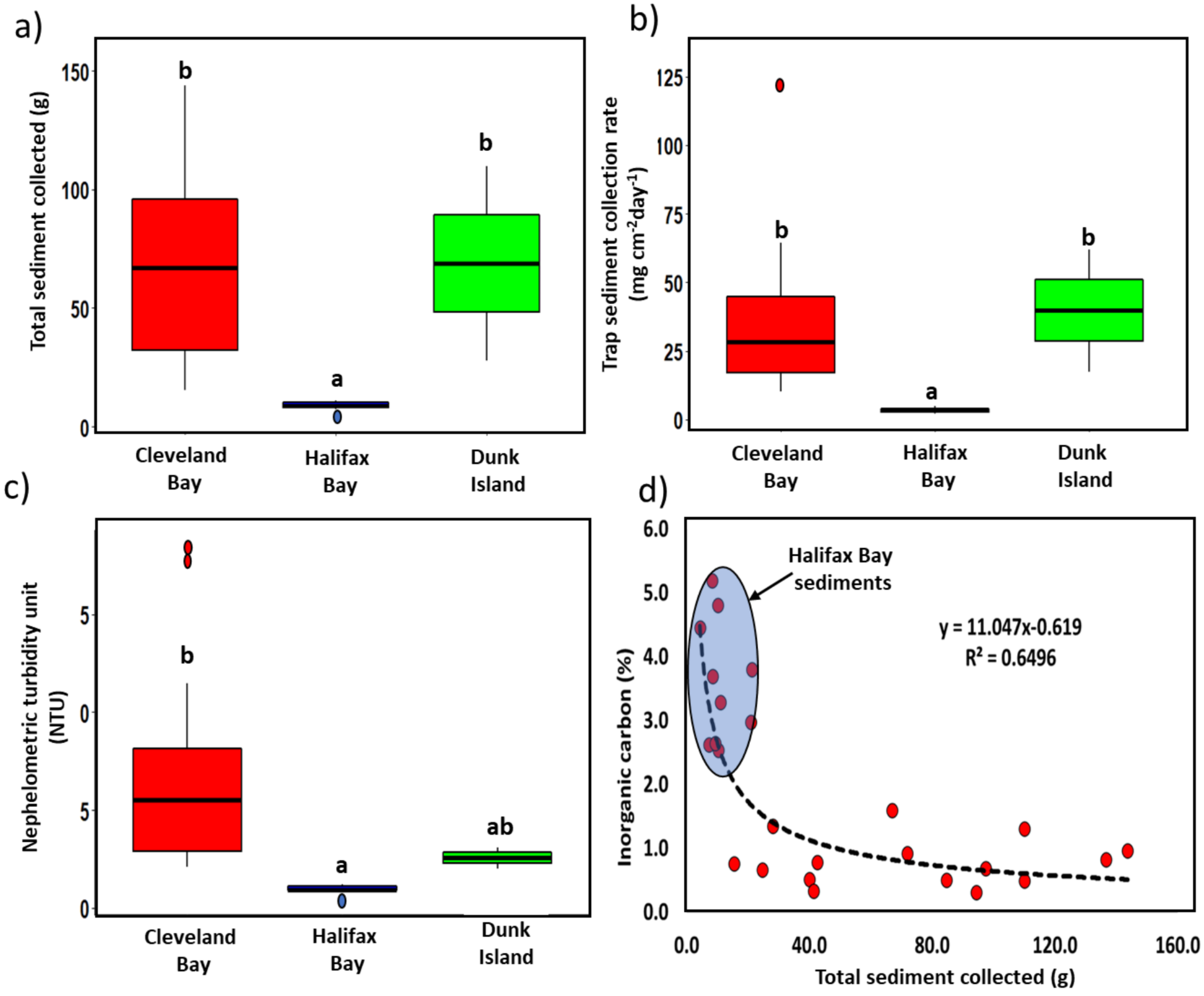

Fig. 2 Comparison of (**a**) total sediment collected, (**b**) trap sediment collection rate, and (**c**) nephelometer turbidity unit across the trap sites (Cleveland Bay, Halifax Bay and Dunk Island); and (**d**) relationship between total sediment collected and inorganic carbon content of sediments. Mean values (STDEV) with the same letter are not significantly different at $p < 0.05$

the Cleveland Bay (36.6±29.1 mg cm^{-2} day^{-1}) and Dunk Island (39.7±31.5 mg cm^{-2} day^{-1}) sites (Table. S1). Likewise, the turbidity logger data showed that mean nephelometer turbidity units (NTU) at the Cleveland Bay sites (6.96±5.02 NTU) were higher but within the 1σ standard deviation compared to the Dunk Island (2.6±0.8 NTU) site and were higher than the Halifax Bay sites (1.0±0.2 NTU) (Fig. 2c). Plotting the total sediment collected against the IC content of sediments across our sites showed that the marine traps with higher sediment amounts generally had lower IC contents (Fig. 2d). The geochemical characteristics (Na, Ca, Mn, Co, Fe and IC) of trap-collected sediments varied along the inner section of the GBR, however, the organic matter characteristics (TOC, TN, TOC: TN ratio, δ13C, δ15N, Carboxyl C, Aryl C, Alkyl C, O-alkyl C) of sediments were consistent across all the trap sites (Table S2). The variation in geochemical and organic matter characteristics of sediments collected along the inner GBR were further analysed through principal component analysis (PCA). Results showed that the sediments collected from Halifax Bay, Dunk Island and Cleveland Bay trap sites could be separated from each other due to the variation in their geochemical characteristics (Fig. 3a). The first principal component (PC1: 55.2%) largely represented the variation in trap sites with the most contributions from Ca, IC, Fe, Co and Mn (Fig. S4a and b). In contrast to geochemical characteristics, sediments collected from our trap sites could not be separated based on their organic matter characteristics (Fig. 3b).

3.2 Bacterial community composition across the inner GBR

Proteobacteria, Bacteroidetes, Actinobacteria, Acidobacteria, Firmicutes and Planctomycetes were the dominant bacterial groups, accounting for ~95% of bacterial relative abundance in trap sediments along the inner GBR (Fig. 4a). The relative abundance of Actinobacteria, Acidobacteria and Planctomycetes were higher in sediments collected from the Cleveland Bay sites compared to the Halifax Bay and Dunk Island sites (Table S3). The non-metric multidimensional scaling analysis (NMDS) also showed that the bacterial community structure in the trap sediments from Cleveland Bay was different to the sediments from the traps deployed in Halifax Bay and Dunk Island (Fig. 4b and Fig. S6). Bacterial diversity (Chao-1 Index) in sediments collected from the Dunk Island trap site (5502±136) was higher than those collected from both Cleveland Bay (3991±501) and Halifax Bay (4321±840) sites.

3.3 Environmental factors driving bacterial community dynamics across the inner GBR

Spearman correlations between bacterial community composition with sediment geochemical characteristics and organic matter characteristics across the sediment trap sites are provided in Fig. 5a and b, respectively. Actinobacteria, Acidobacteria and Planctomycetes were negatively correlated ($P<0.01$) with the Na and Ca and positively correlated with the Mn and Co contents of sediments (Table S4). The relative abundance of Acidobacteria and Planctomycetes

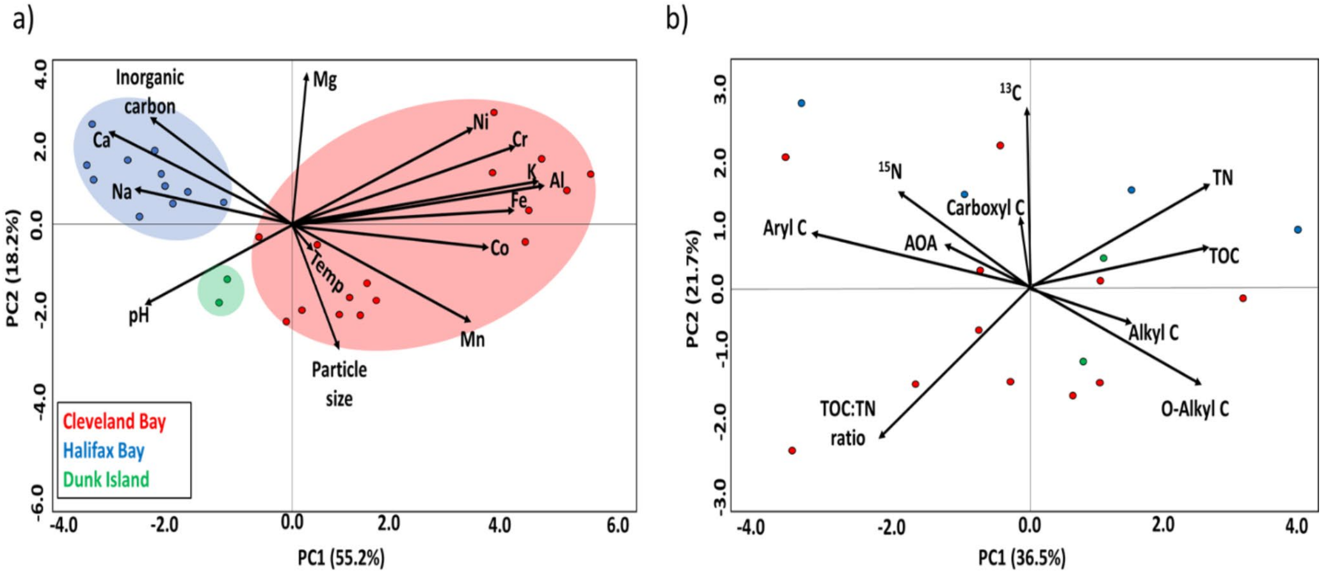

Fig. 3 Principal component analysis of (**a**) geochemical and (**b**) organic characteristics of sediment collected from marine traps at Cleveland Bay, Halifax Bay and Dunk Island sites (TOC: TN ratio = total organic carbon (TOC) to total nitrogen (TN) ratio; Temp = water temperature; AOA = alkyl C to O-alkyl C ratio)

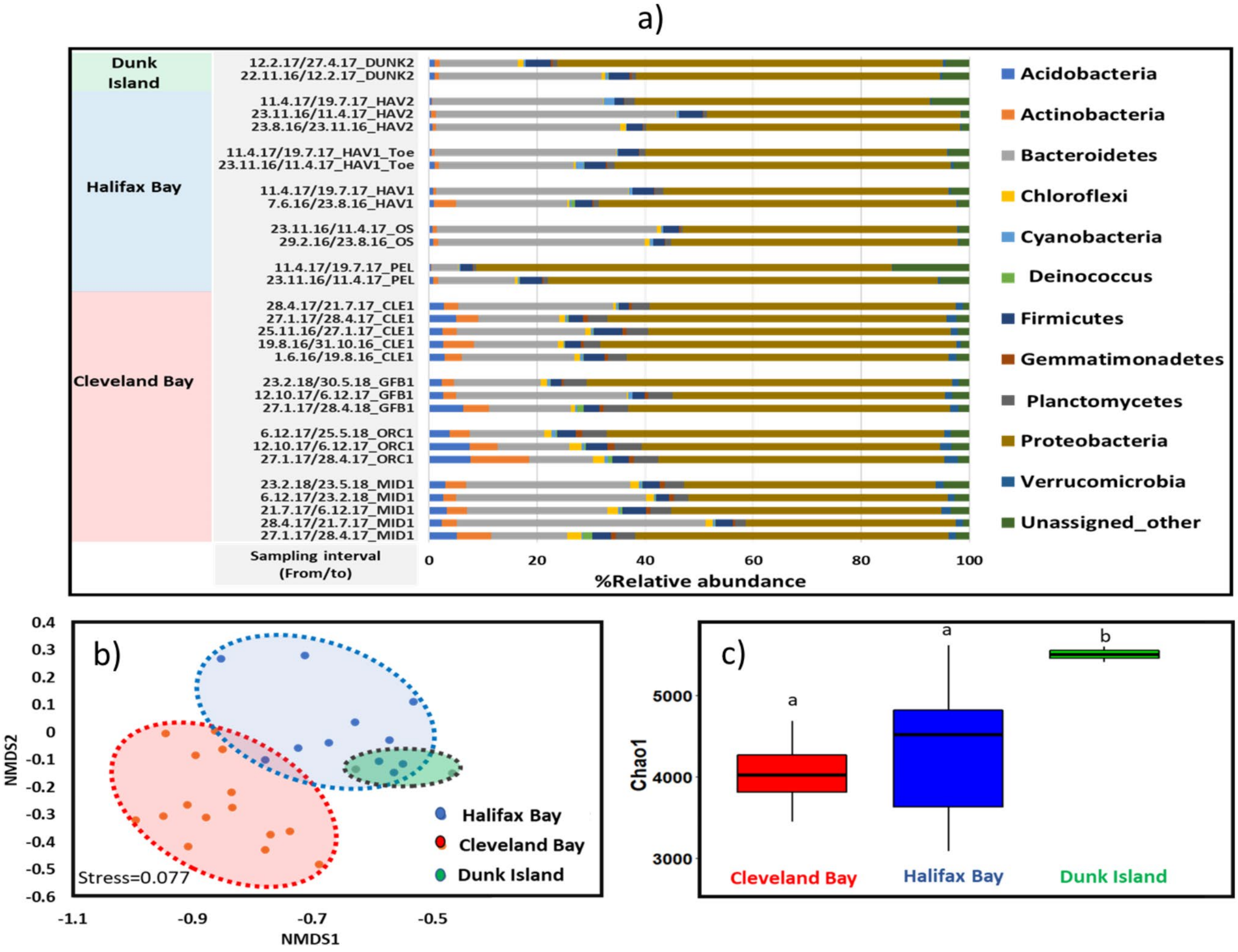

Fig. 4 Variations in the (**a**) bacterial community composition, (**b**) bacterial community structure (NMDS: nonmetric multidimensional scaling), and (**c**) bacterial diversity (Chao1 index) in sediments collected from the Cleveland Bay, Halifax Bay and Dunk Island sites (Mid: Middle Reef; ORC: Orchid Rocks; GFB: Geoffrey Bay; CLE: Cleveland Bay; PEL: Pelorus Island; OS: Orpheus Island; Hav: Havannah Island; DUNK: Dunk Island). Mean values (STDEV) with the same letter are not significantly different at $p < 0.05$

were also significantly ($P < 0.01$) and positively correlated with the Mn, Co, Al and Fe contents of sediments.

In the case of organic matter, the relative abundance of Actinobacteria was negatively correlated ($P < 0.01$) with the TN content of the sediment. These relationships were further analysed through the Mantle correlation analysis that demonstrated the effects of shifts in geochemical and organic matter characteristics of sediment on the overall composition patterns of associated bacterial communities (Fig. 5c and d). The Mantle correlation plot showed that the variation in geochemical characteristics of sediment was correlated with the shift in bacterial community (Fig. 5c). Although the r value was low ($r = 0.30$, $p = 0.002$), but the individual elements exhibit moderate correlation. Network analysis also showed that the variation in geochemical characteristics (e.g., Mn, and Ca contents) of sediments as well as average water nephelometer turbidity unit (NTU) and trap sediment collection rates (SCR) were the most factors in shaping the relative abundance of bacterial groups across the trap sites of the inner GBR (Fig. 6), while bacteria from the phylum Acidobacteria, Bacteroidetes, Proteobacteria and Chloroflexi are closely regulated by Mn and Ca contents. In particular, Mn showed a positive correlation, whereas Ca had a negative correlation with bacterial genera (Table S4). Proteobacteria and Bacteroidetes, often associated with organic matter degradation, respond to Mn-driven redox processes, while Acidobacteria and Chloroflexi are known for their adaptability to oligotrophic conditions, and they may be regulated by Ca-rich carbonate sediments. These relationships suggest that sediment composition and mineral availability shape microbial community structures, potentially influencing nutrient dynamics and reef ecosystem health.

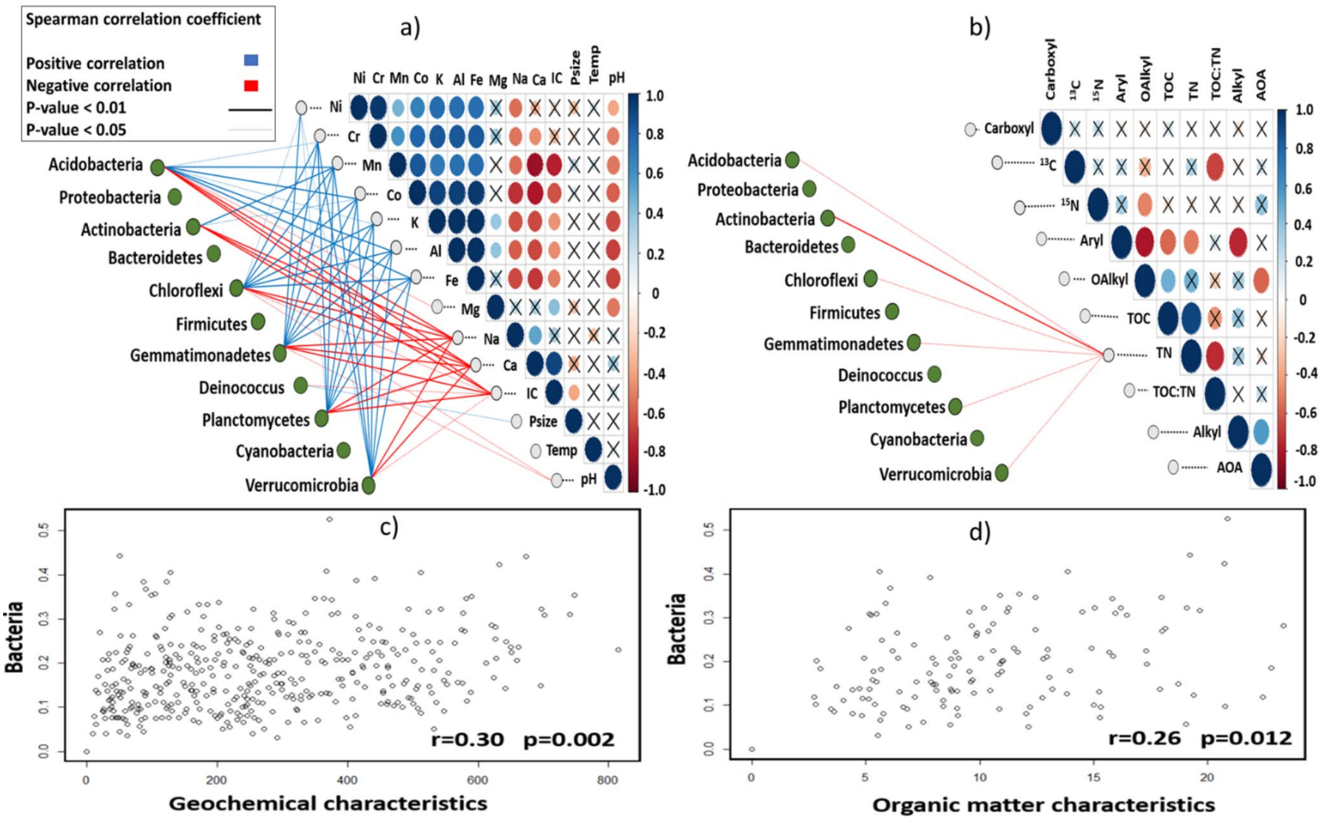

Fig. 5 Spearman correlation (**a** and **b**) and Mantle correlation (c and d) between bacterial community composition with sediment geochemical characteristics (**a** and **c**) and organic matter characteristics (**b** and **d**) across the sediment trap sites (TOC: TN = total organic carbon (TOC) to total nitrogen (TN) ratio; Temp = temperature; Psize = particle size; AOA = alkyl C to O-alkyl C ratio; IC = inorganic carbon). The Mantle analysis shows the overall correlation where the bacterial communities were characterised by the Bray–Curtis dissimilarity, and geochemical and organic matter characteristics of sediment samples were demonstrated via Euclidean distance. The Pearson correlation of the two metrics was performed based on 999 permutations

4 Discussion

Our results showed that the spatial patterns of bacterial communities varied across the inner GBR, and these variations were highly correlated with the water turbidity and geochemical characteristics of sediments across the trap sites. The collected sediments are a mix of terrigenous sediment and biogenic carbonate deposited within the traps over the ~3-monthly deployment periods. This mixed composition is best known as siliciclastic/carbonate systems, which is typical for inshore continental margins and is well established in the GBR (Belperio 1983; Orpin et al. 2004; Browne et al. 2013). We observed a significant spatial variation in the geochemical characteristics and IC content of siliciclastic/carbonate systems along the inner GBR. This spatial variation is due to the regional differences in sediment supply, carbonate production, geographic location of the embayments (e.g., relative exposure, water depth and turbidity) as well as the existing/accumulated sediments in each region (Johns et al. 1994; Ward et al. 1995). These results suggest that riverine and estuarine inputs have a major influence on benthic microbial communities by creating environmental conditions in which particular species may exist and form distinctive communities along the inner section of the GBR. Bacteria are highly responsive indicators of changing environmental conditions(Paerl and Pinckney 1996; Bahadori et al. 2023) as demonstrated in different aquatic environments such as in rivers (Araya et al. 2003), estuaries and marine environments (Dang et al. 2008; Frade et al. 2020). Our results have further indicated that the spatial variation in bacterial community was highly correlated with the geochemical gradient along the inner section of the GBR. Particularly, the shift in low-abundance members of bacterial communities (e.g., Actinobacteria, Acidobacteria, Planctomycete, Verrucomicrobia, Chloroflexi) was the main cause of the variation in community dynamics across the marine trap sites, while their relative abundance was stable in samples collected within the same site (Fig. 4a). It indicates that the lower abundance bacteria have higher spatial heterogeneity and exhibit stronger correlation with environmental factors than the higher abundance bacterial groups (e.g., Proteobacteria and Bacteroidetes). This is consistent

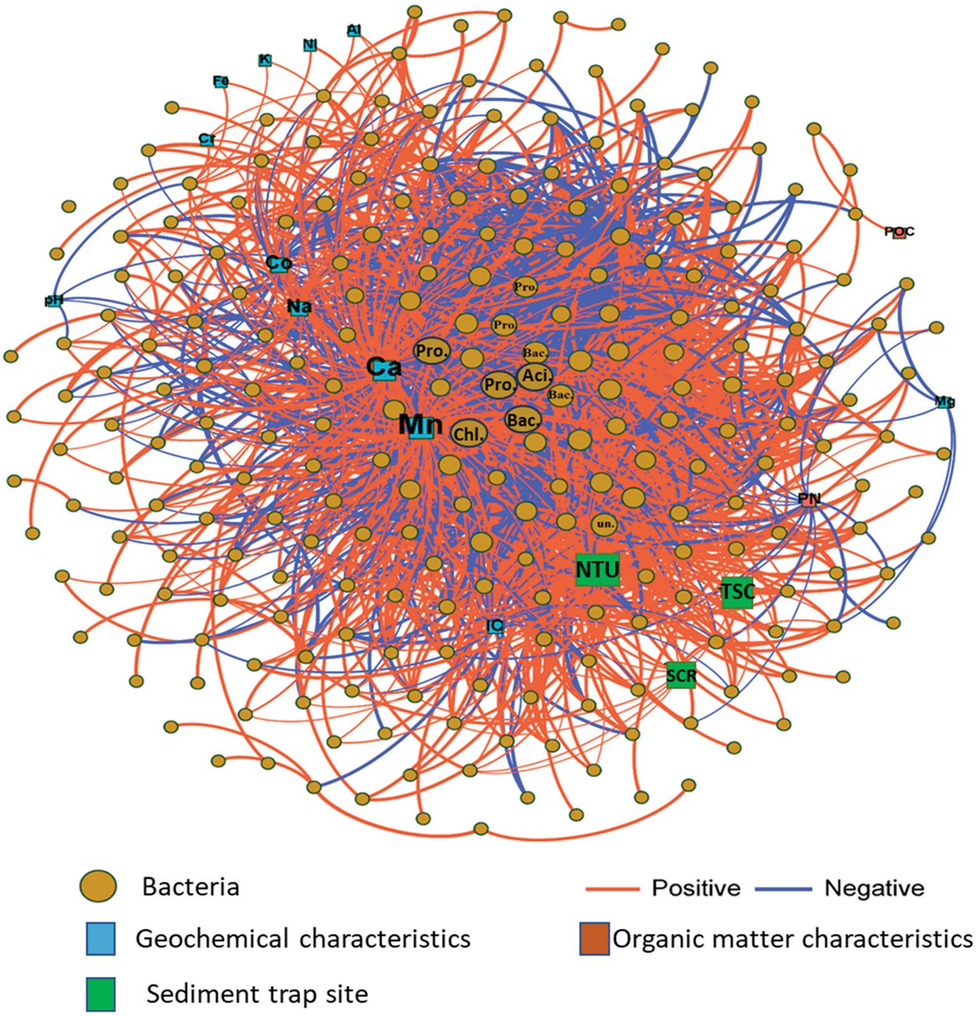

Fig. 6 An overview of network analysis between bacterial OTUs and geochemical and organic matter characteristics of sediment across the inner Great Barrier Reef trap sites. Geochemical characteristics: Na, K, Mg, Ca, Mn, Al, Ni, Co, Cr, Fe, pH, particle size, temperature, and inorganic carbon (IC). Organic matter characteristics: particulate organic carbon (POC) and particulate nitrogen (PN). Marine traps: nephelometer turbidity unit (NTU), total sediment collected (TSC) and trap sediment collection rate (SCR). Orange lines represent significant positive (Pearson correlation, $r > 0.6$, $p < 0.01$) relationships and blue lines denote negative relationships. The size of nodes is proportional to the number of edges connecting each node (e.g., the degree). Abbreviations for the top 10 highest degree bacterial OTUs: Aci., Acidobacteria; Pro., Probacteria; Bac., Bacteroidetes; Chl., Chloroflexi

with the increasing number of studies showing that the low-abundance members of microbial communities are more sensitive to environmental changes than high abundance microbial groups and are thus more geographically restricted (Szabó et al. 2007; Elshahed et al. 2008; Vergin et al. 2013; Troussellier et al. 2017). Spatially restricted bacteria (e.g., endemic) can be particularly abundant in coastal ecosystems where their repeated transitions from local rarity to prevalence is mainly driven by local and short-term environmental fluctuations (e.g., flood plumes) that allows them to thrive and contribute to key ecological and biogeochemical processes (Troussellier et al. 2017). This explains our results showing that the variations of low-abundance groups are more significant in reflecting the bacterial community responses to environmental change which particularly relates to the geochemical characteristics of sediment and water turbidity along the inner section of the GBR (Figs. 5 and 6). We argue that locations with higher water turbidity (e.g., Cleveland Bay) may offer higher nutritive environments containing suspended sediment, dissolved nutrients and debritic particulate organic matter compared with other sites (e.g., Halifax Bay). Such nutritive environments can offer the low-abundance bacteria the opportunity to reach higher growth rates compared to surrounding oligotrophic environments. However, this hypothesis is worth further investigation with higher number of samples and specific focus on the correlation between dissolved nutrients and the low-abundance bacterial groups.

The geochemical heterogeneity along the inner GBR offers bacteria a large range of micro-gradients and environmental niches that allow small bacterial populations to grow in specific micro-environments(Troussellier et al. 2017). Although the ecological role of these low-abundance bacterial groups in coral reef ecosystems is still largely unknown, recent evidence suggests that they may contribute to key processes such as community resilience and stability under local stresses (Alonso-Sáez et al. 2009; Aanderud et al. 2015; Shade and Gilbert 2015). However, a remaining challenge is to explain whether their increasing relative abundance under explicit environmental conditions (e.g., sediment exposure) mitigate or exacerbate the impacts of disturbance on coral reef ecosystems? This is particularly important for the coastal and inner section of the GBR where water quality is frequently influenced by inputs from adjacent river catchments. In such dynamic environments, some bacterial taxa are stable members of the community and likely play more important roles in promoting the health and longevity of ecosystems compared to transient members which are only present under explicit environmental conditions (McDevitt-Irwin et al. 2017). Thus, future research should focus on identifying the stable and transient members of the bacterial communities across the broader GBR. It is also essential to advance our knowledge of their ecological role in coral reef ecosystems and how they respond under local and global stresses. This is particularly important given that climate projections have predicted that global stresses (e.g., rising temperature) will increase the susceptibility of coral reef ecosystems to local stresses (e.g., water quality).

5 Conclusions

This study explored the spatial variations in bacterial communities in sediments along the inner section of the GBR and their response to the environmental gradient created by sediment composition and exposure. Results showed that the spatial patterns of bacterial communities varied across the investigated marine trap sites, and this variation was highly correlated with the water turbidity and geochemical characteristics of sediments. This result advances our current understanding of the effect of sediment exposure on bacterial communities in reef ecosystems and will improve our capacity to understand the effect of local environmental disturbances on coral reefs as a rationale for incorporating bacterial ecology into future studies on coral reef resilience. Further investigations, incorporating more sampling, are required to link how the observed varied dynamics of bacterial communities may relate to their existing coral populations or reef ecosystem health.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11368-025-04024-8.

Acknowledgements We thank Dr Sue Boyd for her help in using Magnetic Resonance Facilities at Griffith University and Dr Yan Gao from the Institute of Agricultural Resources and Environment, Jiangsu Academy of Agricultural Sciences, Nanjng, China for analysing soil DNA sequences. The field sediment traps, and instrument loggers were deployed under permits G17/38148.1 and G16/38774.1 issued by the GBRMPA. We thank Simon Griffiths, Andreas Dietzel, Adam Wilkinson, Cassandra Thompson, Sofia Valero Fortunato, Blanche Danastas, Ian McLeod, Lauren Firby, Eridani Mulder, Jane Waterhouse, Sandra Erdmann, Kai Pacey and Glen Ewels for being part of the dive team who collected the sediment trap samples. The Marine Geophysics Laboratory is thanked for supplying and helping with calibrating the nephelometers.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions

This work was financially supported by the Australian Government's National Environmental Science Program (NESP projects 2.1.5 and 5.8), Griffith University and the Great Barrier Reef Marine Park Authority (GBRMPA) Reef Guardian Research Grant 2019.

Data availability All raw sequences were deposited to the Sequence Read Archive (SRA) with the accession number PRJNA690602.

Declarations

Competing interests The authors declare no competing interests.

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