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First insights into bacterial and microalgal endosymbiont communities of various coral morphotypes from Maldives

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The Maldivian Archipelago is home to valuable coral reefs that have been extensively studied for their ecological diversity. However, the diversity of the microbiome in Maldivian corals remains largely unexplored. In this study, the microbiota compositions (including both algal endosymbionts and bacteria) were investigated for the first time across various coral morphotypes sampled in May 2022 from four Maldivian atolls (Ari, North Malé, South Malé, and Rasdhoo). Coral and gorgonian specimens were collected via scuba diving at reef sites located on both ocean-exposed reefs and lagoon sites, across various depths (0–40 m). Surface seawater samples were also collected near coral assemblages. Metabarcoding analyses were performed, targeting the 16S rRNA gene to assess bacterial composition, and the Internal Transcribed Spacer 2 (ITS2) rRNA region to evaluate microalgal endosymbiont diversity. Generally, the bacterial communities associated with corals exhibited significant diversity, which was primarily influenced by coral morphotype rather than depth or geographic location. These communities were also markedly different when compared to those found in seawater. The three most abundant bacterial taxa in coral samples were Proteobacteria (ranging from 10 to 95%), Bacillota (formerly known as Firmicutes, ranging from 5 to 10%), and Planctomycetota (ranging from <1–30%). Most Symbiodiniaceae belonged to the genera *Cladocopium*-C and *Durusdinium*-D (>90%), while host specificity was observed for variant types. Overall, this study provides first insights into the structure of Maldivian coral microbiota, which could be crucial for monitoring the health of local coral populations and predicting the potential impacts of changing environmental conditions in the region.

Keywords Maldives, Corals, 16S, Microbiota, ITS2, Symbiodiniaceae

The Maldives, with 6,372 km² of reef area, accounts for 58.2% of the coral reefs in South Asia and 3% of the world's total coral reefs. The region heavily relies on the coastal reef economy, including fisheries and tourism, despite experiencing less human pressure compared to other South Asian countries like India or Bangladesh[1]. Coral reefs are key components of the Indian Ocean and are regularly monitored for community composition and ecological status[2,3]. These ecosystems host a wide variety of coral communities, which differ in structure, biodiversity, proximity to the coast, and levels of anthropogenic impact. Hermatypic corals, also known as scleractinian corals, are considered foundational to reef ecosystems, and disturbances affecting their health are of great concern[4]. In particular, sea level rise and global warming pose major threats to Maldivian corals and in recent years, several bleaching-induced mortality events have been recorded, with extensive bleaching occurring in 2016 and localized events from 2017 to 2019, leading to declines in live hard coral cover[2].

The health of coral reefs is closely linked to the complex interactions between corals and their associated microorganisms[5]. The coral holobiont is comprised of the coral animal and its associated microorganisms, including bacteria, archaea, fungi, viruses, and symbiotic dinoflagellates (such as Symbiodiniaceae), that live in and around coral tissues[6]. These microorganisms play a crucial role in maintaining coral health, helping corals with nutrient cycling, disease resistance, and stress responses. Composition of the microbiome is known to be strongly influenced by the physiology and the morphotype of corals[7]. Bacterial symbionts are usually specifically

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associated to three different microhabitats inside corals, such as surface mucous layer, tissue and skeleton, that display specific roles for the host. These microorganisms are non-static colonies, they can evolve over time, and be influenced by abiotic parameters (e.g., season, temperature, geography) and stress (e.g., pollution, chemicals)[8]. In corals, a strong variability in microbial compositions among individuals was observed and related to the age of the colony; their composition was variable from young to adult corals, becoming less diverse in the latter[9]. Recent studies have also emphasized significant shifts in the abundance, biomass, and composition of coral-associated microbiomes in response to environmental stressors, such as rising sea temperatures, ocean acidification, pollution, and other anthropogenic influences[10–12]. These shifts often result in an increase in pathogens or harmful microorganisms, which can negatively impact coral health[13]. Under stressful conditions, the balance of the microbiome can be disturbed, resulting in a decline in beneficial microorganisms that play a key role in coral immunity and nutrient cycling (as reviewed in[6]), while fostering the growth of pathogenic microorganisms, thereby intensifying coral diseases[13].

Good health of hermatypic corals also depend on the products of photosynthesis by symbiotic dinoflagellates (Symbiodiniaceae) residing within the tissues of the coral polyp to meet up to 90% of the coral's energy needs for growth and reproduction[14]. These microalgae represent a diverse group of organisms which can be differentiated by their nuclear ITS2 region and exhibit unique ecological and physiological traits[15]. Specifically, the family Symbiodiniaceae includes seven distinct genera: *Symbiodinium* (formerly known as clade A), *Breviolum* (clade B), *Cladocopium* (clade C), *Durusdinium* (clade D), *Effrenium* (clade E), *Fugacium* (clade F), and *Gerakladium* (clade G)[16]. Each genus is further divided into variants types, with hundreds of distinct lineages that exist, though many have not been formally classified up to the species level[17]. To date, the preferential establishment of these symbionts in certain hosts is not fully understood.

Coral endosymbionts contribute to the host's health and are believed to be closely linked to other components of the coral microbiome. However, under conditions of high environmental stress, this symbiosis can break down, leading to coral bleaching, where corals expel their Symbiodiniaceae symbionts. Notably, several studies have demonstrated that the temperature tolerance of scleractinian reef-building corals is partially determined by the symbiotic algae they host, with the type of Symbiodiniaceae influencing the coral's temperature tolerance, regardless of the host species[18]. For example, Symbiodiniaceae from Clade D, particularly D1, is often associated with more heat-resistant corals[19]. Silverstein et al. (2015)[20] found that *Montastraea cavernosa* exhibited enhanced thermal tolerance and resilience after switching its endosymbionts from the heat-sensitive C3 type to the heat-tolerant D1a type following acute heat stress. This variation in Symbiodiniaceae types is one reason why some corals are more resilient to warming oceans, while others are more vulnerable to coral bleaching during temperature spikes.

Understanding how corals respond to thermal stress, environmental pressures and the effects of bleaching on the physiology and ecology of coral-algal symbiosis, as well as the microbiota, is critical for forecasting the future of coral reefs. However, little is known about the composition and biogeography of the coral-associated microbiome in the Maldives, one of the world's largest and most iconic coral reef systems. This study aims to provide pioneering information on the bacterial and endosymbiont microbiome components in various coral morphotypes collected from different Maldivian atolls, analysed using a molecular metabarcoding approach.

Materials and methods

Study area and sampling activities

Coral fragments were obtained during an annual DISTAV scientific expedition in the Maldives that took place in May 2022, in reefs located in four different Maldivian atolls: Ari, North Malé, South Malé, and Rasdhoo (Fig. 1). A total of 26 samples belonging to the most common species of the area, including different hard coral (*Acropora*, *Pocillopora*, *Porites*, and *Fungia*) and gorgonian (*Annella* and *Ellisella*) taxa were collected. Each coral sample was composed of 3 to 6 fragments (1 cm in size), collected from at least 3 different coral colonies, to ensure the identification of major microbiome components through pooled metabarcoding analysis. Sampling was conducted by scuba divers on specimens with apparent healthy features (i.e., showing no sign of disease and no necrotic tissues) at reef sites located either on the ocean-exposed reefs or in the lagoon reefs (lagoon-facing sides of the atoll rim or patch reefs), at different depths from 3 m (on the reef flat) up to 40 m (see **Table S1a** for details). Coral fragments were collected from each hard coral colony by sterile hammer and chisel, from gorgonians by shears and each fragment was placed into sterile falcon tubes containing ambient seawater. Corals were washed twice with 0.2-µm filtered water to remove transient microorganisms. They were preserved in RNA*later* at 4 °C for a maximum of 10 days, during the cruise, and then stored at −80 °C (in laboratory) for 1 week before DNA extraction. Samples of surface seawater (8 to 10 L) across the five surveyed atolls (same as for corals, plus Baa Atoll) ($n = 9$; Fig. 1), were also collected in proximity to the sampled corals, using an innovative eDNA pump (Smith-Root-inc, Vancouver, USA) equipped with self-preserving filters of 0.45 µm pore diameter, able to preserve nucleic acid at room temperature up to 6 months[21] (**Table S1b**).

All necessary permits to conduct research activities in the Maldives and for sampling and observational field studies have been obtained by the authors from the Ministry of Fisheries and Ocean Resources. The study is compliant with CBD and Nagoya protocols. All samples were collected under permit no. (OTHR)30-D/INDIV/2022/119.

DNA extraction from coral and water samples

Coral fragments were thawed and rinsed with DNA/RNAse free water to remove excess preservative, before being crushed with a sterile ceramic mortar and placed into the appropriate DNA extraction tube. Between each sample, the pestle and mortar were sterilized in an autoclave. Aliquot of 300–350 mg were used to extract DNA with the kit DNeasy PowerSoil Pro (Qiagen), and DNA from filters was extracted using the DNeasy PowerWater

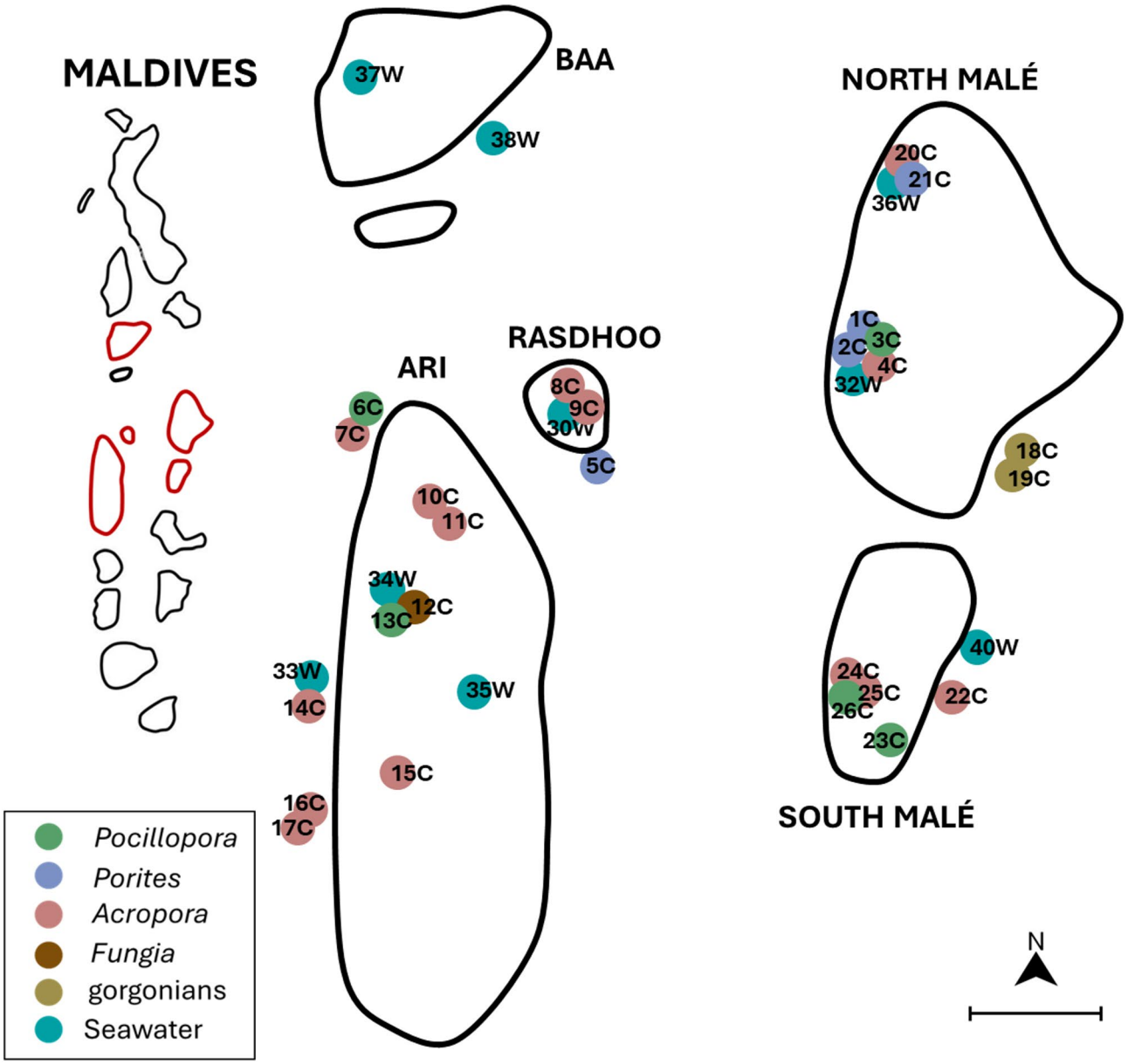

Fig. 1. Overview of sampling sites for corals, gorgonians and seawater in the Maldivian archipelago. Scale bar: 20 km.

kit (Qiagen), according to the manufacturer's instructions. The DNA extracted was quantified fluorimetrically with QuantiFluorTM dsDNA System using a QuantiFluorTM fluorometer (Promega Italia srl, Milano, Italy).

16S rRNA gene amplification and sequencing

16S rRNA gene PCR amplicon libraries were generated from genomic DNA samples (corals and water) using primers amplifying the V4 – V5 variable regions of 16S rRNA gene of bacteria. The libraries were obtained using Illumina 16S Metagenomic Sequencing Library preparation protocol (15044223 Rev. B) and the primers used were 515 F (5'-GTGYCAGCMGCCGCGGTAA-3') and 926R (5'-CCGYCAATTYMTTTRAGTTT-3')[22]. The obtained libraries were sequenced using Illumina MiSeq platform, using MiSeq Reagent Kit v3 and 300 bp paired-end.

ITS2 for Symbiodiniaceae diversity

From coral DNA samples only, libraries were prepared using the Internal Transcribed Spacer 2 (ITS2) rRNA gene. The libraries were obtained using the same protocol as for the 16S rRNA gene, but using the primers SYM_VAR_5.8S2 (GAATTGCAGAACTCCGTGAACC) and SYM_VAR_REV (CGGGTTCWCTTGTYTGACTTCATGC), and modified PCR conditions (98 °C for 2 min; 27 cycles of 10 s at 98 °C, 30 s at 56 °C, 30 s at 72 °C; and 72 °C for 5 min)[23] (Hume et al. 2018). Libraries were sequenced using Illumina MiSeq platform, using MiSeq Reagent Kit

v3 and 300 bp paired-end. For technical reasons (low amount of sample available), sample 10 C and 2 C were not analysed for ITS2 diversity. Moreover, gorgonians (18 C and 19 C) samples were not successfully amplified and consequently they were not sequenced.

Bioinformatic analyses

Preliminary quality control of raw reads was performed using Fastqc[24]. Default parameters were used along all analysis, otherwise indicated. 16S rRNA gene amplicons were imported into Quantitative Insights into Microbial Ecology (QIIME 2) version 2022.8[25]. For 16S rRNA amplicons DADA2 was used to trim the primers and denoise the reads[26]. Afterward, the taxonomy was assigned to the amplicon sequence variants (ASV) using the Silva-138 database[27] (**Table S2a**). For the ITS2 amplicons, the primers were removed with Cutadapt[28] and DADA2 was used to denoise and infer ASV following the ITS workflow (https://benjjneb.github.io/dada2/ITS_workflow.html) (**Table S2b**). The taxonomy was assigned using the GeoSymbio ITS2 database[29]. The main outputs (i.e., ASV table, ASV taxonomy) and the corresponding metadata were analysed separately using R (R Core Team 2013) in RStudio (RStudio Team 2015). From the 16S rRNA gene, ASVs assigned taxonomically to chloroplasts, mitochondria and potential contaminants (i.e., Eukaryota, Propionibacteriaceae, Unclassified domain and phylum) were removed, then the rarefaction curves were visualized using ggplot2. From both the ASVs tables, the singletons were discarded and then the frequencies of the ASVs were normalized by Cumulative Sum Scaling transformation, using MetagenomeSeq package[30]. Alpha- (i.e., Species Richness, Shannon and Pielou indices) and Beta- (PCoA ordination based on Bray-Curtis dissimilarity of presence/absence-transformed data) diversities were assessed with Phyloseq package[31]. Then the data was transformed to relative abundance to plot the compositional barplots with ggplot2 and to identify the core bacterial community using Microbiome package[32]. A threshold of minimum genus prevalence was set to 0.5, meaning that only genera present in at least 50% of the samples were included in the heatmap. Functional prediction of the 20 most abundant bacterial genera for each community (e.g. corals, gorgonians, and water) was performed using tax4fun2[33] with a minimum identity to consider BLAST hit results of 0.97. A heatmap with the 15 most abundant predicted KEGG level 2 pathways plus an additional category (with all other pathways) was generated, values were standardized with z-score. All the SSU rRNA data are available in the NCBI SRA repository (BioProject ID: PRJNA1200062).

Permutational multivariate analysis of variance (PERMANOVA), using adonis2 from the vegan package with 9999 permutations, was used to evaluate the null hypothesis that there were no significant differences between bacterial and microalgal communities in the samples according to their atolls of provenance (as proxy of biogeography), depth (reef flat 0–9 m and deep > 10 m) and types (i.e., *Acropora*, *Fungia*, gorgonians, *Pocillopora*, *Porites*, Seawater).

Results

General sequencing

A total number of 11,267 ASVs was recovered of 16S rRNA sequences, with an average of 315 ASVs in corals and 1,234 ASVs in seawater samples (**Table S3**). Among them, 4,626 ASVs were exclusive of the water samples and 6,142 ASVs of the corals whereas 499 ASVs were shared (**Fig. S1A**). For ITS2, 359 ASVs was recovered (**Table S3**). Rarefaction curves calculated for the total ASVs abundance (**Fig. S1B-C**) reached the plateau, showing that a good sequencing depth was achieved to capture most of the total diversity.

Bacterial composition (16S) in coral morphotypes

A total of 46 different bacterial taxa were identified in the different coral and gorgonian specimens (Fig. 2A). The five most abundant phyla across all samples were the Proteobacteria (20–60%, divided between alpha- and gamma-proteobacteria), followed by Bacillota (formerly known as Firmicutes, 5–10%), and Planctomycetota (0.5–30% across coral morphotypes), Cyanobacteriota (2–17%) and Bacteroidota (0.6–9%, except for 18 C that was higher with 27%). Interestingly, only in *Acropora* corals the phylum Actinomycetota was also abundant (1–13%).

For *Acropora* corals ($n = 14$), *Pseudomonas* (0.8–8%), *Bradyrhizobium* (0.8–11%), *Synechococcus* (0.8–6%), *Curvibacter* (0.8–4.6%), and *Sphingomonas* (0.5–5%) were the most abundant bacterial genera encountered in all the samples (Fig. 2B). For the *Pocillopora* corals ($n = 5$), the bacterial community was different, with *Epulopiscium* (1–9%) and *Synechococcus* (1.2–8%) as the most abundant genera, together with *Romboutsia* (1.5–6%). The *Porites* corals ($n = 4$) showed more variability, with *Endozoicomonas* as the most abundant genera in two samples (7.7% in 5 C and 22% in 21 C), while less observed in the samples 1 C and 2 C (< 1% for both). *Thalassobaculales-Uncult.* (5.4%) and *Pirellulaceae-Pir4_lineage* (3.2%) were the most abundant genera in 1 C, while SAR202_clade (6.6%) and *Pirellulaceae-Pir4_lineage* (4%) in 2 C. For the unique *Fungia* specimen (12 C), bacterial genera were more homogeneously distributed with *Synechococcus* as the most abundant genera (3%).

In the two gorgonians *Annella mollis* (18 C) and *Ellisella* cf. *ceratophita* (19 C), the microbial distribution was different and showed a more homogenous distribution of the bacterial genera. For *A. mollis*, *Rhodobacteraceae-Unclass.*, *Vibrio* and *Fusibacter* were the most abundant genera (1.9–5%), while for *E.* cf. *ceratophita*, *Pirellulaceae-uncult* (8.5%) and the genera *Synechococcus* (8.1%), *Cyanobium* (5.6%) *and Pseudomonas* (4.4%) were the most abundant, followed by *Coxiella*, *Curvibacter* and *Sphingomonas* (3.4–3.9%).

The PERMANOVA analysis showed a significant difference in microbiome composition between coral taxa ($p < 0.05$), but not for geographic location ($p > 0.05$, ns) and depth ($p > 0.05$, ns). The core microbiome, i.e. the stable microbial taxa that are shared among all investigated coral and gorgonian taxa, was quantified and represented as a heatmap (Fig. 2C). Ten bacterial genera were identified with a minimum detection threshold of 0.5, with *Synechococcus (strain CC9902)*, *Pseudomonas*, *Curvibacter* and *Sphingomonas* being the most prevalent bacterial genera across all samples from the Maldives.

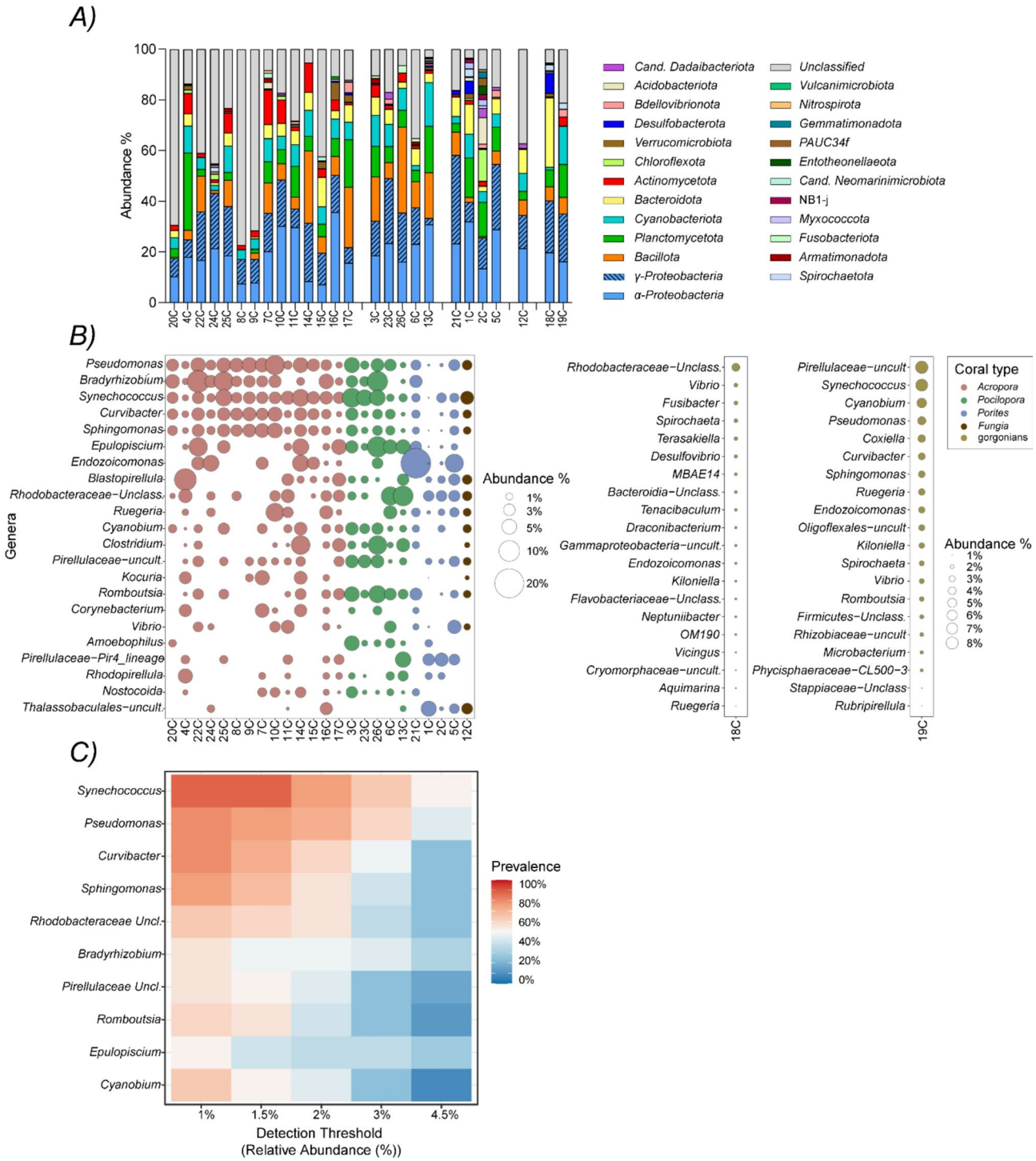

Fig. 2. Bacterial communities structure in the hard coral and gorgonian samples. Identified when possible, at the phylum level (class level for proteobacteria) (**A**), at the genus level (**B**). Data are expressed as a percentage of the total abundance (see Table S1 for sample codes). Core microbiome analysis for all samples of coral displayed as a heatmap analysed at different prevalence (ubiquity) and minimum threshold abundance of 0.5 (**C**).

Bacterial composition in seawater

The bacterial community composition in the surface seawater samples showed a high diversity, and the patterns were generally conserved across the different sites (Fig. 3). In all samples, 5 bacterial phyla represent more than 80% of the total abundance, with Proteobacteria (28–57%; α-Proteobacteria 17–48%, γ-Proteobacteria 8–18%) being the most dominant, followed by Bacteroidota (19–31%), Bacillota (1–4.7%, except for 33 W and 37 W where they reach 18–29%), Planctomycetota (3–9%), and Cyanobacteriota (3–5%) (Fig. 3A).

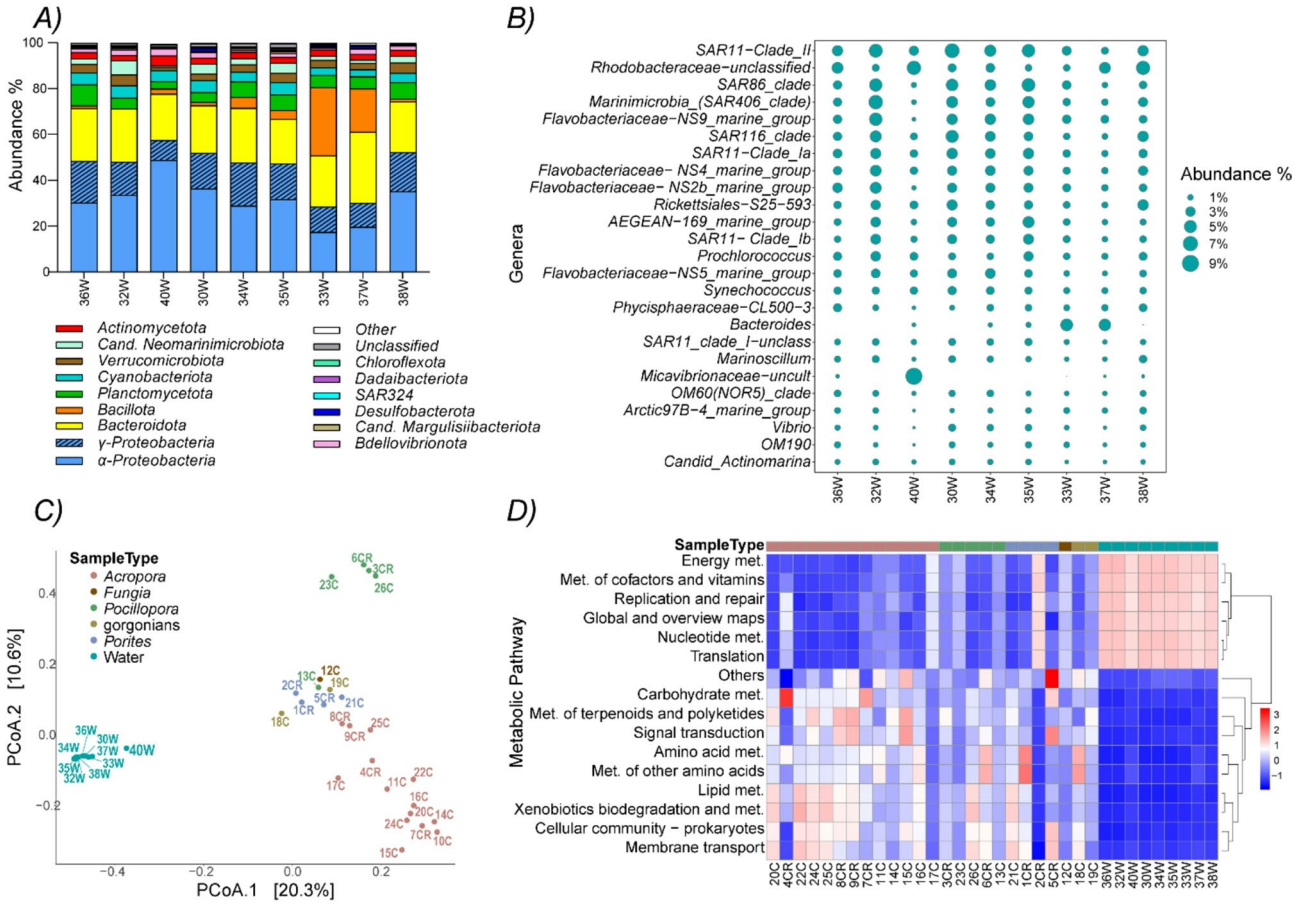

Fig. 3. Bacterial communities structure in seawater samples. Microbial communities at the phylum (**A**) and the genus level (**B**) in surface seawater samples (expressed in % of the total abundance), PCoA plots of the beta-diversity in bacterial community presence-absence, including all samples of coral, gorgonian and seawater (**C**), Heatmap of the predicted bacterial metabolic functional data for coral and seawater samples (**D**). Met. = metabolism.

At the genus level the 24 most abundant taxa represented between 40 and 60% of the total abundance (Fig. 3B). Several bacterial SAR groups were observed among the most dominant bacteria genera in the surface water, with SAR11 (α-Proteobacteria, Pelagibacterales) being the most represented (7–14%, and composed by different clades, with clade I and II as the most abundant). SAR86 (γ-Proteobacteria) was also widespread (0.9–5.6%). Moreover, different bacteria from the Flavobacteriaceae family (from different marine groups) were also very spread among samples (~ 2.5%). The genus *Synechococcus* showed similar abundance among samples (1.2–2.3%).

Principal coordinates analysis (PCoA) and diversity indices

To visualize the results obtained for coral, gorgonian and seawater samples, a principal coordinates analysis (PCoA) plot was generated based on Bray-Curtis beta-diversity with two components. The first two PCoA axes (Fig. 3C) (which accounts for 20.3% and 10.6% of the total variance, respectively) clearly separates corals and seawater samples based on the similarity in their bacterial communities. The predicted functional profiles from 16S showed a clear difference in microbial metabolic pathways between coral and seawater samples (Fig. 3D). As expected, the metabolic pathways in coral microbial communities were more diversified due to interactions with the host.

The species richness index displayed some variations, but the highest difference was observed for the seawater samples that showed higher median scores (860–1844 ASVs), indicating high bacterial community diversity when compared to hard corals (78–2024 ASVs) (**Fig. S2**). *Acropora* and *Pocillopora* corals showed a median value of 134 and 144 ASVs, while the *Porites* corals showed higher variability with median value of 327 ASVs. Similarly, the Shannon index (indicative of the number of bacterial taxa in the community) and the Simpson index (indicative of the evenness of the bacterial community) showed the same pattern. Data for *Fungia* corals and gorgonians (*Annella* and *Ellisella)* were not included as they were represented only by one specimen.

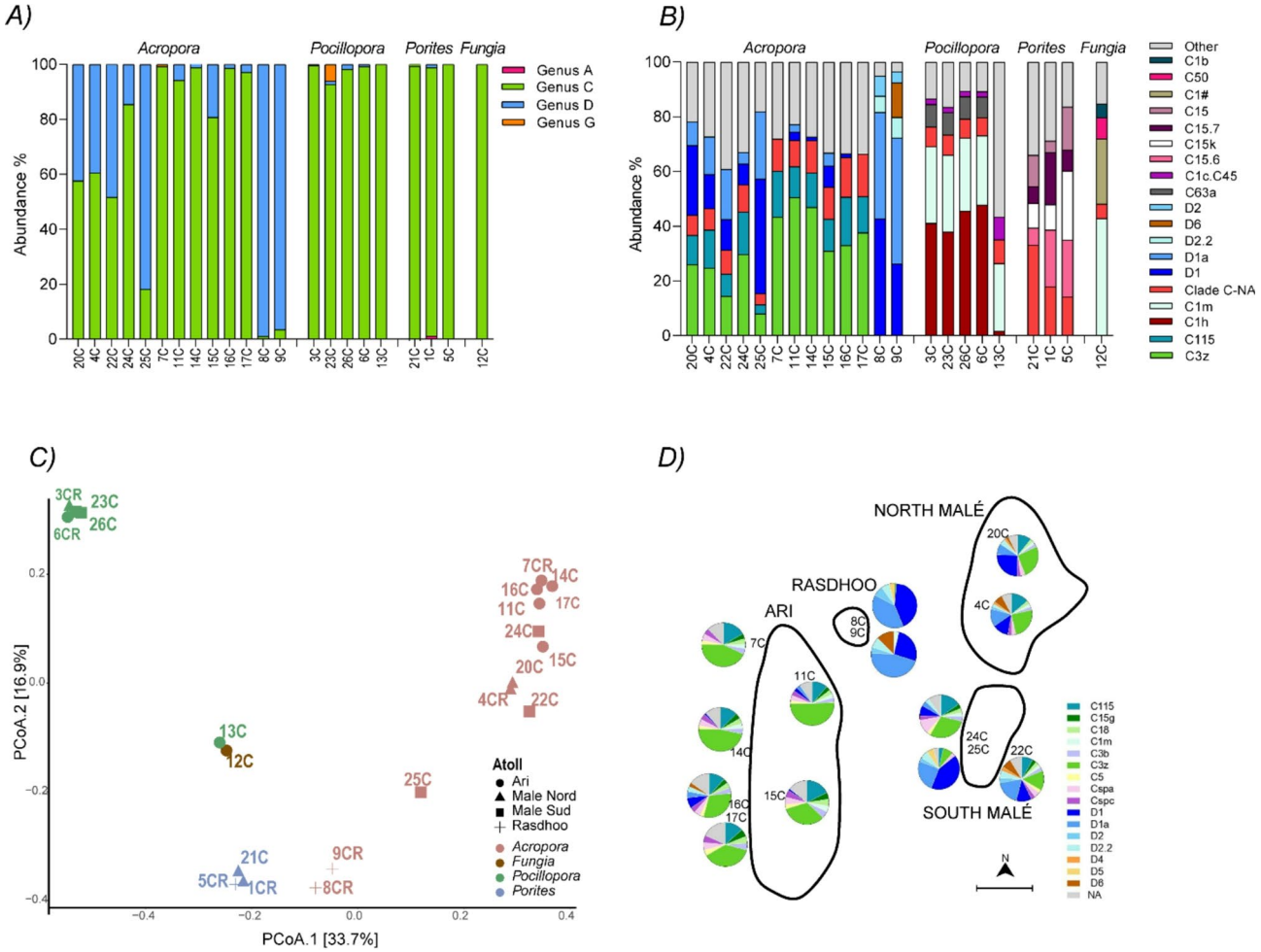

Fig. 4. Distribution of the Symbiodiniaceae found in the different hard coral samples. Genus (previously called clades) (**A**) and variants (the five most abundant for each coral taxa) (**B**), PCoA plots of the beta-diversity in microalgal community composition, including all samples of coral (**C**). *Acropora* microalgal assemblage displayed as pie charts over the Maldivian atolls (**D**). NA = not assigned.

Symbiodiniaceae community across the different coral taxa

The ITS2 region was used to elucidate the Symbiodiniaceae family diversity in the different hard coral taxa. Most of the ITS2 types belong to two genera *Cladocopium* and *Durusdinium* (from the previously described clades C and D, respectively) (Fig. 4A). The genera *Gerakladium* (clade G) and *Symbiodinium* (clade A) were only observed in one sample each (23 C and 1 C, respectively). Interestingly, in *Acropora* corals from Rasdhoo atoll (samples 8 C and 9 C), the genus *Cladocopium* (clade C) was almost absent (< 1%) and the types belonged mainly to *Durusdinium* (clade D). This was not observed in the *Porites* coral (5 C).

In general, for all coral taxa, > 60% of the total abundance of Symbiodiniaceae was represented by only five dominant types (Fig. 4B). Each coral taxa showed a specific dominance of variants. In *Acropora* corals, the variants were dominated by C3z, C115, D1 and D1a, in *Pocillopora* corals by C1 h, C1 m, C63a and C1cC45, while for *Porites* corals by C15.6, C15k, C15.7 and C15. In the *Fungia* corals C1 m, C1#, C50 and C1b were the main variants observed.

Similar to what was found for bacterial communities, the PERMANOVA analysis showed a significant difference in microalgal composition between coral taxa ($p < 0.05$). In addition, when only *Acropora* species were analysed, a significant difference was observed in microalgal composition across the different atolls ($p < 0.05$) (Fig. 4C). Moreover, for *Acropora* samples, microalgal assemblages were reported on a map, highlighting a geographical effect on Symbiodiniaceae clades abundances (Fig. 4D). *Pocillopora* showed a higher richness for ITS2 composition in confront to the other coral taxa, and this pattern was similar for the other alpha-diversity indices (**Fig.S3**).

Discussion

Since 1989, we have been studying Maldivian coral reefs, collecting coral data before, during and after the bleaching and mass mortality event of 1998[2,34]. As part of this long-term monitoring effort, this study is the first to characterize microbial communities (including algae and bacteria) associated with various coral and

gorgonian taxa in the Maldives, aiming to establish a local inventory of coral microbiomes. In fact, changes in coral microbiota, or dysbiosis, significantly affect coral health[35] and by combining microbial profiles with coral reef assessments, we can gain a deeper understanding of Maldivian coral reef dynamics and support preventive or remedial actions against climate change impacts. This approach will also provide valuable insights for designing future monitoring campaigns in the region.

16S rRNA gene sequence analysis revealed that Proteobacteria (including both Gamma- and Alpha-Proteobacteria), were the most abundant bacterial phyla in Maldivian hard corals and gorgonians. These results align with other studies on coral microbiota in tropical regions[9,36]. Among all the corals sampled, coral taxa were found to be the most significant factor influencing microbiome composition, compared to depth and biogeography. Indeed, at the genus level, the composition was more conserved between coral taxa. In *Acropora* and *Pocillopora* corals, a similar bacterial genus composition was found. In *Pocillopora* corals, *Epulopiscium* was the most abundant genus. *Porites* corals showed greater variability, with a notable presence of *Endozoicomonas* in some samples. Gorgonians had a distinct profile, with a more homogeneous distribution and no dominance by a few species, as seen in hard corals. In general, species-specific coral traits likely shaped microbial assemblages, regardless of the coral's geographic distance and location across the different atolls[37]. Notably, bacteria from the genera *Vibrio* and *Pseudoalteromonas* were not abundant, indicating corals in a healthy state rather than experiencing dysbiosis[6]. Accordingly, the high prevalence of *Vibrio* in corals has often been linked to alteration of the coral holobiont and to various coral diseases, while a lower presence is typically part of their natural microbiota[36]. *Endozoicomonas* was consistently found in coral samples and their relative abundance could be correlated with coral health[38], with high abundance found in healthy corals and low abundance in stressed, bleached, or diseased corals[12,39,40]. Based on this knowledge, the presence and temporal changes of these bacterial taxa in the coral microbiome could serve as valuable indicators of coral health and be used as a monitoring tool in our program. For example, it is known that *Pocillopora* has a stable microbiome that often remains unaltered during exposure to environmental stress, while other coral genera, such as *Acropora* and *Porites*, typically exhibit rapid shifts in their bacterial communities, with a decrease in the relative abundance of Endozoicomonadaceae and an increase in Vibrionaceae, Alteromonadaceae, or Rhodobacteraceae under stressful conditions[36].

Interestingly, although scleractinian corals can influence and reflect the pelagic microbial communities found in the overlying waters (e.g., through mucus release linked to filter feeding), microbial profiles from seawater samples differed markedly from those found in corals, even though they shared some common genera (the bias introduced by using different extraction methods for seawater and coral is estimated to be negligible in our study).

The microbial composition of seawater across all atolls was highly uniform, dominated by several bacterial SAR groups (e.g., SAR11 and SAR86) and Flavobacteria, which are among the most abundant uncultivated microorganisms in the ocean[41–43]. Differences in microbial communities found in coral and seawater samples were also evident when comparing predicted microbial functional profiles using 16S rRNA marker gene sequences. Overall, these results suggest that coral hosts actively influence the composition of their associated microbial communities[44].

Endosymbiont clade diversity was also strongly linked to coral taxa, indicating high host specificity. In general, most endosymbionts belonged to two genera: *Cladocopium* and *Durusdinium* (clades C and D, respectively). In particular, *Acropora* corals were dominated by C3, C11, and D1 type groups, *Pocillopora* by C1, *Porites* by C15, and *Fungia* by C1 and C50 types. Similar assemblages were reported in a study from the Chagos Archipelago, 500 km south of the Maldives, where *Acropora* corals showed abundant C3 variants and *Pocillopora* C1 [45]. In *Porites* corals from different Indian Ocean regions, C15 was the dominant variant[46], but distinct profiles were reported for other coral species, likely due to varying biogeographic factors. The present study highlighted a significant effect of geographic location on coral microalgal communities solely for *Acropora*, nonetheless it could be attributed to the difference in specimen numbers between each coral taxa studied. In Ari atoll, the C3z clade was more abundant than in Malé Nord, and the opposite for the clade D1. It was reported that D1, is often associated with more heat-resistant corals[19], and a switch from C3 to D1 was observed after a heat stress in *M. cavernosa*[20]. This could suggest a possible higher heat stress occurring in Malé as compared to Ari atoll at the period of the study. In adult corals, enhanced thermal tolerance may result from a shift in the type of symbionts predominating in their tissues[47]. For example, by investigating the acclimatization potential of *A. millepora*, a common and widespread Indo-Pacific hard coral species, Berkelmans and Madeleine (2006)[48] found that the level of increased tolerance gained by the corals is a direct result of a change from Symbiodiniaceae type C to D (the most thermally resistant type known). Several other studies found a significantly higher proportion of Clade D in corals exhibiting high temperature tolerance and survival during bleaching events[49–51], supporting the role of symbionts in the evolution of tolerance to heat stress. Interestingly, the genus *Durusdinium* (clade D) was mainly found in *Acropora* corals from Rasdhoo Atoll, which could reflect the unique characteristics of this atoll, with large sandbanks potentially more affected by high tidal exchanges that expose corals to aerial desiccation[46]. However, further investigation would be needed to properly address the factors shaping this geographical distribution on the variant types in these Maldivian atolls, as microalgal diversity is known to be multifactorial (e.g. light, heat, pH, nutrients)[15]. Therefore, as for bacteria, understanding and tracking the local composition of dinoflagellate endosymbionts in the coral microbiome could help assess the health of coral reefs, providing a tool for their preservation.

Overall, this study provides an initial insight into the microbiome composition of Maldivian corals, paving the way for future research and monitoring efforts aimed at assessing the impact of human activity and climate change on the health of coral reef communities.

Data availability

All the SSU rRNA data are available in the NCBI SRA repository (BioProject ID: PRJNA1200062).

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Declarations

Competing interests
The authors declare no competing interests.

Ethics approval
No approval of research ethics committees was required to accomplish the goals of this study because experimental work was conducted with an unregulated invertebrate species.

Additional information
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