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Coral polyp and skeletal microbiome in tropical and subtropical reefs in the South China Sea: spatial variation and implications for coral environmental adaptability

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Abstract

The environments of tropical and subtropical coral reef regions (CRR) differ from each other; however, it is not known if these environmental differences influence coral polyp and skeleton microbiome composition. In this study, *Coelastrea palauensis* corals were collected from tropical and subtropical CRR in the South China Sea, and bacterial, archaeal, and fungal communities in polyps and skeletons were analyzed. Results showed that the microbial diversity and composition of *C. palauensis* significantly differed between the polyps and skeletons, and between the tropical and subtropical CRR. Regarding bacteria associated with corals, *C. palauensis* was mainly associated with bacteria closely related to the nitrogen cycle in the subtropical CRR. The relative abundances of Terasakiellaceae and *Chlorobium* in both coral polyps and skeletons in the subtropical CRR were higher than those in the tropical CRR. In the tropical CRR, *C. palauensis* was mainly associated with opportunistic pathogenic bacteria. The relative abundances of *Tenacibaculum* and *Vibrio* in coral polyps and skeletons in the tropical CRR were higher than those in the subtropical CRR. Regarding archaea associated with corals, polyps and skeletons of *C. palauensis* in both tropical and subtropical reef areas were dominated by n_Woesearchaeales, and the relative abundance of n_Woesearchaeales in skeletons is significantly higher than that in polyps. In addition, the relative abundances of n_Woesearchaeales in polyps and skeletons in the subtropical CRR were significantly higher than those in the tropical CRR. Regarding fungi associated with corals, Ascomycota was dominant in polyps and skeletons in the subtropical CRR, while Sordariomycetes, *Periconia*, *Cladosporium*, and *Aspergillus* were dominant in polyps and skeletons in the tropical CRR. Besides, the diversity differences of coral-associated microorganisms were related to environmental factors such as nutrients and temperature that may affect the survival of coral-associated microorganisms. These results implied that corals may adjust the composition of microorganisms, conducive the coral holobiont to better adapting the environment. Our research will be beneficial in understanding the differences and adaptations of coral polyp and skeletal microbiome.

Key words coral microbiome, polyp microbiome, skeleton microbiome, microbial diversity, environmental adaptability

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1 Introduction

Reef-building corals are the main constructors of coral reef ecosystems, and are composed of a large number of porous voluminous calcium carbonate skeletons and polyps (Levy et al., 2021). Coral polyps and skeletons are associated with various microorganisms, including Symbiodiniaceae, bacteria, fungi, archaea, viruses, and protozoa (Bourne et al., 2016). Coral polyps include the mucus and tissue layers. In the mucus layer, the microbial community play an important role in nutrient cycling and prevention of pathogen invasion (Kemp et al., 2015). In the tissue layer, the microbial community is usually stable, and some microorganisms form cell-associated microbial aggregates (Sweet et al., 2011; Work and Aeby, 2014; Bourne et al., 2016). Bacteria play important roles in coral polyps, such as in the nitrogen cycle (Lesser et al., 2004; Lema et al., 2012), carbon cycle (Kimes et al., 2010), sulfur cycle (Raina et al., 2009), and antibiotic secretion (Ritchie, 2006).

The coral polyp microbiome is typically dominated by Proteobacteria (especially Gammaproteobacteria and Alphaproteobacteria), Actinobacteria, Bacteroidetes, Firmicutes and Cyanobacteria (Blackall et al., 2015; Huggett and Apprill, 2019). The coral skeletal microhabitat clearly differs from that of coral polyps (Luo et al., 2021). The coral skeleton is composed of aragonite crystals, and its loose and porous structure provides a good habitat for the survival of microorganisms (Meibom et al., 2008). Skeletal microbes survive in low light and low oxygen content, and the pH of coral skeletons fluctuates significantly due to some microorganisms in the coral perform light deterioration during the day and respiration at night carry out photosynthesis during the day and respiration at night (Shashar and Stambler, 1992; Ricci et al., 2019; Pernice et al., 2020). The difference of microhabitat strongly affects the composition of the skeletal microbial communities (Ainsworth et al., 2010). Microbes in coral skeletons usually exhibit high biodiversity and mainly include Proteobacteria, Bacteroides, Firmicutes, Actinomyces, Phytococca, Acidobacter and Chlorophyta (Li et al., 2014; Williams et al., 2015; Marcelino and Verbruggen, 2016; Yang et al., 2019; Chen et al., 2021; Ricci et al., 2021). These skeletal microbes contribute to material circulation and energy exchanges of microbial communities to hosts, such as the nitrogen and carbon cycles (Sangsawang et al., 2017; Yang et al., 2019). Coral polyps and skeletons have different microbial associations and respond differently to environmental stress, which may influence the microbial communities (Sweet et al., 2011; Luo et al., 2021). In addition, it has been reported that the composition and diversity of bacterial communities in coral skeletons can be driven by biogeographical or local environmental factors, resulting in regional differences (Liu et al., 2022; Yang et al., 2016, 2019, 2020; Ricci et al., 2021). However, few studies have focused on the diversity and composition differences in coral skeletal bacteria in tropical and subtropical coral reef regions (CRR) as well as differences from coral polyps' bacteria.

Similarly, few studies have focused on the differences of archaea and fungi between coral polyps and skeletons. Previous studies have indicated that members of Euryarchaeota and Thaumarchaeota are associated with corals and that some archaea members play key roles in ammonia oxidation, affecting the nitrogen cycle in corals (Francis et al., 2007; Huggett and Apprill, 2019). Most fungi in corals belong to *Ascomycota*, followed by Basidiomycota and Chytridiomycota (Wegley et al., 2007; Raghukumar and Ravindran, 2012). Fungi are generally considered opportunistic pathogens in corals under environmental stress but may also be non-pathogenic invasive microorganisms (Le Campion-Alsumard et al., 1995b; Ainsworth et al., 2017). In addition, some fungi play important roles in coral mineralization (Le Campion-Alsumard et al., 1995b) and antibacterial activity (Xu et al., 2018; Wang et al., 2011). However, the differences between skeletal archaea and fungi of corals in tropical and subtropical CRR as well as the differences in coral polyps are not well studied.

The massive *Coelastrea* corals are stress tolerant, and are the dominant coral populations in Indo-Pacific coral reefs (Darling et al., 2012). *Coelastrea* corals are distributed in coral reefs in different regions of the South China Sea (SCS), with a high abundance in tropical CRR (such as Xisha Islands and Nansha Islands) and subtropical CRR (such as Weizhou Island and Daya Bay) (Liao et al., 2021). In these regions, *Coelastrea palauensis* is the common species of *Coelastrea* genus (Zou, 2001; He and Huang, 2019). The specific skeletal structure and distribution of *Coelastrea* corals affect the composition and function of associated microorganisms in response to environmental fluctuations (Torda et al., 2017). However, the spatial variation of *Coelastrea* skeletal and polyp microorganisms in different climate zones and between coral skeletons and polyps remains unclear. These differences are important for studying the interaction of coral microorganisms and their relationship with environmental stress adaptation.

In this study, we examined *C. palauensis* in tropical and subtropical CRR. Based on the composition and diversity of *C. palauensis* polyp and skeleton bacteria, archaea, and fungi, and environmental parameters of the two CRR, two scientific problems were investigated: (1) the differences in the composition and diversity of *C. palauensis* polyp and skeletal bacteria, archaea, and fungi in tropical and subtropical CRR; and (2) the potential relationship of bacteria, archaea, and fungi in *C. palauensis* skeletons and polyps with coral environmental adaptability. Regarding this, two scientific hypotheses were proposed: (1) there is a difference between the composition and diversity of *C. palauensis* polyp and skeletal bacteria, archaea, and fungi in tropical and subtropical CRR; and

(2) the differences in the composition of bacteria, archaea, and fungi in the polyp and skeletons of *C. palauensis* corals correlate with the coral environments. The composition and diversity of bacteria, archaea and fungi in coral polyp and skeletons from the subtropics and tropics CRR in the SCS were investigated to test our hypotheses in relation to *in situ* aquatic environmental parameters in the study area. Our research will be beneficial in understanding the differences and adaptations of coral polyp and skeletal microbiome.

2 Materials and methods

2.1 *Study area*

The study areas (Fig. 1) in this study spanned two climate zones in the SCS, the Bombay Reef (16°03′N, 112°33′E) in the tropical CRR and Weizhou Island (21°00′N, 109°00′E) in the subtropical CRR. The annual average sea surface temperature (SST) of the Xisha Islands is 27.5℃. The lowest SST was 24.8℃, which occurred between December and February, while the highest average SST was 29.9℃, which occurred between May and September (Zhang et al., 2014). An ecological survey suggested that the average live coral cover (LCC) of the Bombay Reef in the tropical reef area was 11% (Chen et al., 2019).

The annual average SST of Weizhou Island in the subtropical reef area is 24.6℃. Low SST was observed during winter, with an average of 17.5–19.8℃, while high SST was observed during summer, with an average of 29.0–30.3℃ (Wang et al., 2016; Yu et al., 2019). The coral reefs on Weizhou Island have suffered from serious degradation due to destructive human activities, with the average LCC decreasing from about 42% in 1984 to about 10% in 2015 (Yu et al., 2019).

2.2 *Coral sample collection and seawater parameter measurement*

A total of 34 *C. palauensis* nubbins were sampled from the Bombay Reef and Weizhou Island in August 2021. All the coral samples were collected in 5–6 m depths at the outer reef slope both of Bombay Reef and Weizhou Island. To remove attached microorganisms, coral samples were washed with sterile seawater. After quick freezing with liquid nitrogen, the samples were stored at –20℃, and transported to the laboratory for subsequent sample treatment. In the laboratory, surface polyps of each coral sample were obtained by sterile scissor in 2 mL sterile centrifuge tube on sterile console. After the polyp on the coral surface was removed, the coral sample was thoroughly washed using a Waterpik containing sterile seawater to remove the residual tissue of coral polyps. The coral skeleton was then split, and the skeleton sample was cut using sterile forceps, the skeleton piece which does not directly contact the tissue layer was carefully separated. The coral polyp and skeleton fragments were stored 15 mL freezing tubes in a –80℃ freezer.

Environmental parameters were measured including water temperature, salinity, dissolved oxygen (DO), pH, transparency, turbidity, dissolved inorganic nitrogen (DIN), and soluble reactive phosphorus (SRP). Water temperature, salinity, and DO were assessed with a YSI water quality analyzer (YSI Inc., Yellow Springs, OH,

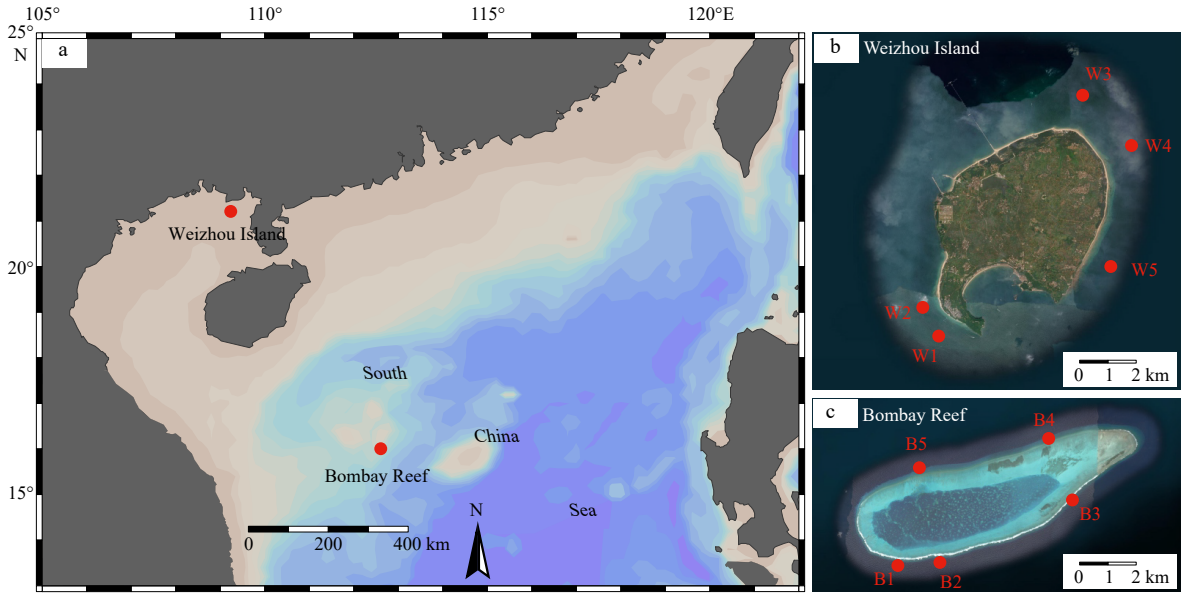

Fig. 1. Location map of coral reef sampling sites in the Bombay Reef and Weizhou Island. *Coelastrea palauensis* nubbins were sampled in B1–B2 from the Bombay Reef and W1–W2 from the Weizhou Island. Environmental parameters were measured and water samples were collected in B1–B5 from the Bombay Reef and W1–W5 from the Weizhou Island.

USA). Seawater samples were collected and immediately filtered (Whatman GF/F; GE Healthcare, Chicago, IL, USA). The pH was measured with separate portable meters (PHB-4). Turbidity was measured by a portable turbidity meter (WGZ-20B, 0–20 NTU). Transparency was measured with a Secchi disc (SD 30). Nitrate and SRP were measured using a continuous flow analyzer (SEAL QuAAtro; SEAL Analytical Shanghai, Shanghai, China). In this study, environmental parameters were measured at five sites in the Bombay Reef or Weizhou Island, and each site was measured once (Fig. 1, Table S1). Since no significant difference in these environmental parameters among five sites on a same island, these parameters on a same island were served as a set of data. The Wilcoxon rank-sum test was used to analyze the differences between the Bombay Reef and Weizhou Island, and the Mann-Whitney test was used to perform post hoc tests. The statistical results of these environmental parameters were expressed using mean ± standard deviation (SD), and the significant level threshold was defined as 0.05 ($p < 0.05$).

2.3 *DNA extraction, PCR and sequencing*

Total DNA was extracted from *C. palauensis* polyp or skeleton samples using the TIANamp Marine Animals DNA Kit (Tiangen Biotech, Beijing, China) according to the manufacturer's instructions. After extraction, 1 μL of DNA was used to determine the concentration and purity using a NanoDrop2000 trace UV spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA). After quality and purity testing, the extracted DNA sample was used as a PCR template. Primers were used to amplify the following regions: V3−V4 region of the 16S rRNA gene in bacteria (338F:5'-ACTCCTACGGAGGCAGCAGCAG-3', 806R: 5'-GGACTACHVGGGTWTCTAAT-3') (Mori et al., 2014, Xu et al., 2016); V4−V5 region of the 16S rRNA gene in archaea (524F10extF:5'-TGYCAGCGCCGCGGTAA-3', Arch958RmodR:5'-YCCGCGGTTGAVTCCAATT-3') (Liu et al., 2016); and Internal Transcribed Spacer 2 (ITS2) region in fungi (ITS3F:5'-GCATCGATGAAGAACGCAGC-3' and ITS4R:5'-TCCTCGCTTATTGATGC-3') (Toju et al., 2012).

Each sample had a unique barcode, and PCR amplification was performed in a 50-μL reaction volume containing approximately 50 ng of DNA, 25 μL of 2X Taq platinum polymerase chain reaction stock solution (Tiangen Biotech, Beijing, China), 200 nmol/L of each primer, and double-distilled H_2O to make up the final volume. Using an ABI GeneAmp system with a 9 700 Thermal Cycler (Applied Biosystems, Waltham, MA, USA), the reaction was allowed to proceed for 5 min at 94℃; 35 cycles were subsequently carried out at 94℃, 51℃, and 72℃ for 30 s each, and, finally, the temperature was maintained at 72℃ for 5 min (Sun et al., 2014). 3 μL PCR product was collected per sample and tested product integrity using 2% agarose gel electrophoresis (115 V, 45 min) to ensure that the amplicon was in the size of 301–340 bp. An AxyPrep DNA gel extraction kit (Axygen Biosciences Inc. Union City, CA, USA) and a QuantiFluor ST fluorescence quantification system (Promega, Madison, WI, USA) were used to purify and quantify the amplicon.

After quality inspection, the amplified samples were subjected to paired-end sequencing on an Illumina MiSeq platform (Majorbio Bio-pharm Technology, Shanghai, China). The raw sequences were deposited in the National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA) database (accession number: fungi: PRJNA923503; bacteria: PRJNA923743; archaea: PRJNA923739).

2.4 *Bioinformatics and statistical analysis*

The original bacterial and archaea data from *C. palauensis* samples were derived from the raw sequences obtained using Illumina MiSeq sequencing. PEAR (v.0.9.8) was used to assemble the paired reads of the bacterial 16S rRNA gene produced by the Illumina MiSeq platform to generate the complete V3−V4 region sequence of the 16S rRNA gene, and archaea 16S rRNA gene produced by the Illumina MiSeq platform to generate the complete V4−V5 region sequence of the 16S rRNA gene, with a maximum allowed mismatch ratio of 0.2 (Zhang et al., 2014). The valid sequences of the samples were then identified based on the sequence primer sequences and barcodes, and the sequence orientation was adjusted (barcode quality control threshold: mismatch number 0; maximum primer mismatch number 2). Non-repetitive sequences were extracted from the optimized sequences using Uparse (version 7.1), while removing single sequences without repeats and chimeras. The SILVA 138.1/16S_Bacteria and SILVA 138.1/16S_Archaea were used to identify and classify the bacteria, archaea, respectively, and clustering them into groups of amplicon sequence variants (ASV) (Callahan et al., 2016; Savary et al., 2021). Based on ASV clustering and rarefied, Mothur (version 1.30.1) was used to calculate α diversity indices, including the Shannon–Wiener, Simpson, Sobs, and Ace indices (Schloss et al. 2011).

The raw fungal ITS2 sequences were screened, and the unqualified sequences were deleted using the Mothur (version 1.30.1) platform (Caporaso et al., 2010; Zhang et al., 2014). According to the next generation sequencing data quality control standards, the "trim.seqs" function was used to remove low-quality reads, including barcode sequences, up-stream primers, homopolymers (>6 bp), and short length sequences (<250 bp) (Schloss et al., 2009). Chimeras were removed from the sequence using UCHIME. NT_v20200327/ITS was used to identify and classify the fungi, and clustering them into groups of ASV (Nilsson et al., 2019). Based on ASV clustering and rarefied, Mothur (version 1.30.1) was used to calculate fungal α diversity indices, including the Shannon-Wiener (H′), Simpson, Sobs, and Ace indices (Schloss et al.,

2011).

The Wilcoxon rank sum test was used to compare the differences in α diversity and microbial composition between the skeletons and polyps of *C. palauensis* in the Bombay Reef and Weizhou Island, and the Mann-Whitney test was used to perform post hoc tests. The Circos (version 0.67-7, http://circos.ca/) was used to analyze the composition of dominant bacteria, archaea, and fungi, and the proportion of dominant microbial members between the skeletons and polyps. Venn diagram analysis at ASV level was conducted using VennDiagram package. Principal coordinates analysis (PCoA) at the ASV level was used to conduct a β-diversity analysis of the coral associated bacteria, archaea, and fungi. They were used to visualize the results of Permutational Multivariate Analysis of Variance (PERMANOVA) generated by the Bray Curtis distance to reveal the microbial community structure of the different groups of coral skeletons and polyps in the Bombay Reef and Weizhou Island. All multi-dimensional statistical analysis was performed using R version 3.1.2 and the Vegan package (Oksanen et al., 2015). In this study, because of Detrended Correspondence Analysis (DCA) < 3, a redundancy analysis (RDA) was performed in Canoco 4.5 software to examine the correlation among environmental factors, sampling areas, and ASV of bacteria, archaea, and fungi. Statistical results of this study were expressed using mean ± SD in this study, and the significance level threshold was defined as 0.05 (p < 0.05). The data of environmental parameters, diversity community bacteria, archaea and fungus from coral polyp and skeleton in tropical and subtropical CRR can be available from the Dryad (https://datadryad.org. DOI: 10.5061/dryad.c59zw3rh8).

3 Results

3.1 *Environmental parameters*

The DIN and SRP in the subtropical CRR were higher than those in the tropical CRR (Table S1, Wilcoxon rank sum test, p = 0.008). In contrast, the SST, salinity, and transparency of the tropical CRR were higher than those of the subtropical CRR (Wilcoxon rank sum test, p = 0.008). No significant differences were found in DO and pH between the subtropical and tropical CRR (Wilcoxon rank sum test, p > 0.05). These data show that the seawater of the subtropical CRR is characterized by a relatively high nutrient content and high turbidity while that of the tropical CRR is characterized by high water temperature, high transparency, and low nutrient content.

3.2 *The bacterial community of coral polyp and skeleton in tropical and subtropical CRR*

After quality filtering, 18 571 ASV were obtained using Illumina MiSeq platform. α-diversity index was measured using the Sobs, Ace, Shannon-Wiener, and Simpson indices (Table S2, Figs 2 and S1). In the tropical CRR, the Shannon-Wiener (Wilcoxon rank sum test, p = 0.185) and Simpson (Wilcoxon rank sum test, p = 0.181) indices of skeletal bacteria in *C. palauensis* were not significant different from those of polyp bacteria. In the subtropical CRR, the Ace and Sob indices of skeletal bacteria in *C. palauensis* were significantly higher than those of polyp bacteria (Wilcoxon rank sum test, Ace, p < 0.001; Sob, p = 0.001). Besides, this study showed that the Shannon-Wiener index of coral polyp bacteria in tropical CRR was significantly higher than that in subtropical CRR (Wilcoxon rank sum test, p = 0.014), while the Simpson diversity index coral polyp bacteria in tropical CRR was significantly lower than that in subtropical CRR (Wilcoxon rank sum test, p < 0.001). The Ace and Sob indices of the coral skeletal bacteria in the subtropical CRR were significantly higher than those indices in the tropical CRR (Wilcoxon rank sum test, Ace index, p = 0.002; Sob, p = 0.003).

Total taxonomic composition of bacteria in the analyzed samples included 52 phyla, 156 classes, 390 orders, 643 families, and 1 273 genera. At the class level, 17 classes of bacteria in *C. palauensis* had an abundance greater than 1% (Table S3). In the tropical CRR, the relative abundance of Bacteroidia in coral polyps was significantly higher than those in the skeletons (Wilcoxon rank sum test, p = 0.047), but the relative abundance of Gammaproteobacteria in coral polyps was significantly lower than those in the skeletons (Wilcoxon rank sum test, p = 0.001). In the subtropical CRR, the relative abundance of Alphaproteobacteria in coral polyps was significantly higher than those in the skeletons (Wilcoxon rank sum test, p = 0.001), but the relative abundance of Gammaproteobacteria in coral polyps was significantly lower than those in the skeletons (Wilcoxon rank sum test, p = 0.001). Besides, the relative abundance of Gammaproteobacteria and Bacteroidia of the coral polyps in the tropical CRR was significantly higher than that in subtropical CRR (Wilcoxon rank sum test, p < 0.001 and p = 0.015, respectively), but significantly lower in the relative abundance of Alphaproteobacteria (p = 0.006). Meanwhile, the coral skeletal bacteria were dominated by Gammaproteobacteria and Alphaproteobacteria in the subtropical and tropical CCRs, but there was no significant difference (Wilcoxon rank sum test, p = 0.423 and p = 0.815, respectively). In the subtropical CRR, higher abundance of Chlorobia was found in the coral skeletons, whereas was barely detected in tropical CCR (<0.1%). The percentage of Anaerolineae of the coral skeletons in the tropical was significantly higher than that in the subtropical (Wilcoxon rank sum test, p = 0.000).

At the bacterial genus level, the composition of associated bacterial communities significantly differed among *C. palauensis* samples in the tropical and subtropical CRR (Table S4, Fig. 3a). For polyp bacteria, high relative abundances of Terasakiellaceae (Wilcoxon rank sum test, p < 0.001), *Blastocatella* (p = 0.002) and *Chlorobium* (p <

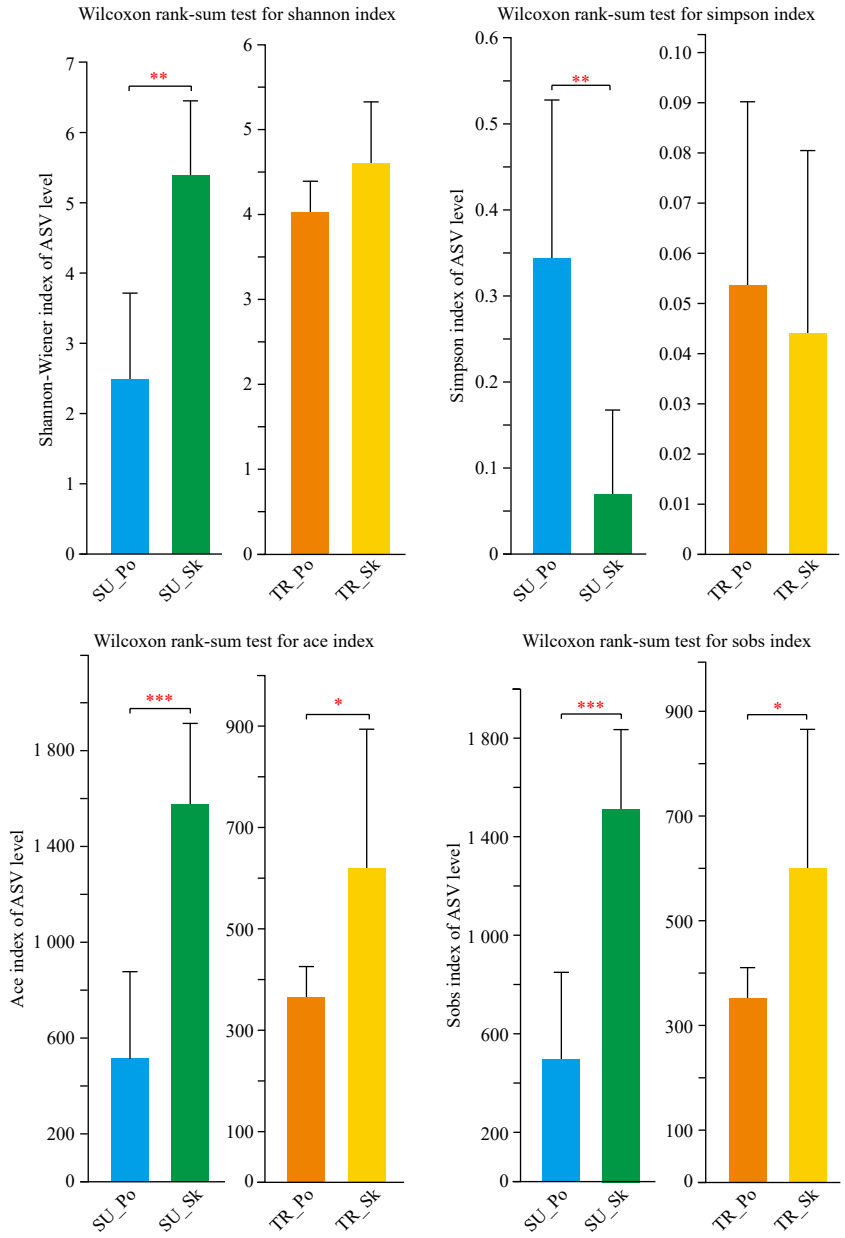

Fig. 2. The Ace, Sobs, Shannon-Wiener, and Simpson diversity indices of associated bacteria based on ASV level in coral polyp and skeleton in the tropical and subtropical coral reef regions (CRR) in the South China Sea (SCS). The "SU_Po" "SU_Sk" "TR_Po" "TR_Sk" represent "coral polyp in subtropical CRR" "coral skeleton in subtropical CRR" "coral polyp in tropical CRR" "coral skeleton in tropical CRR", respectively. The red asterisks "*" "**" and "***" represent "$0.01 < p < 0.05$" "$0.001 < p < 0.01$" and "$p < 0.001$", respectively.

0.001) was detected in the subtropical CRR than in the tropical CRR, as shown in Fig. 4. In contrast, high relative abundances of Rhodobacteraceae ($p < 0.001$), *Pseudoalteromonas* (Wilcoxon rank sum test, $p < 0.001$), and *Vibrio* (Wilcoxon rank sum test, $p < 0.001$) was suggested in the tropical CRR. For skeletal bacteria, high relative abundances of Terasakiellaceae (Wilcoxon rank sum test, $p < 0.001$) and *Chlorobium* ($p = 0.001$) was detected in subtropical CRR. In contrast, the relative abundances of *Cyclobacilluscaeae* (Wilcoxon rank sum test, $p < 0.001$) and A4b (Wilcoxon rank sum test, $p = 0.002$) were low in the subtropical CRR.

Some bacterial taxa differed significantly between polyps and skeletons of *C. palauensis*. For example, in the subtropical CRR, the relative abundances of Terasakiellaceae (Wilcoxon rank sum test, $p < 0.001$) and *Blastocatella* (Wilcoxon rank sum test, $p = 0.004$) in coral polyps were significantly higher than those in skeletons, but those of *Ruegeria* and *Woeseia* (Wilcoxon rank sum test, $p = 0.002$) in skeletons were significantly higher than those in polyps (Wilcoxon rank sum test, $p = 0.024$). In the tropical CRR, the relative abundances of Rhodobacteraceae (Wilcoxon rank sum test, $p = 0.017$), *Pseudoalteromonas* (Wilcoxon rank sum test, $p < 0.001$), *Vibrio* ($p = 0.002$), A4b ($p < 0.001$), and SAR202_clade ($p < 0.001$) differed significantly between polyps and skeletons.

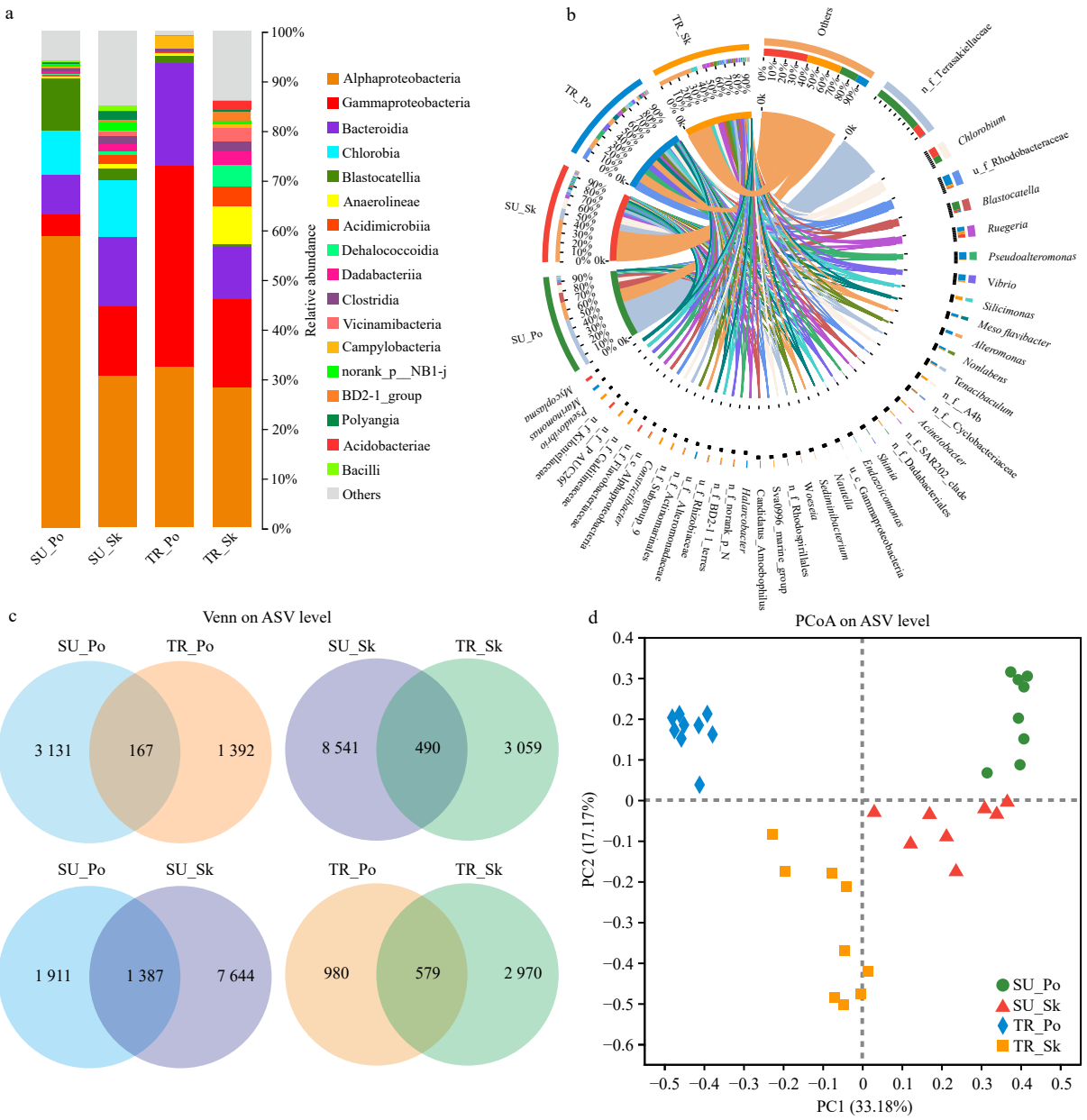

Fig. 3. Relative abundances of coral-associated bacterial communities at class level in polyp and skeletal of *C. palauensis* in the tropical and subtropical CRR in the SCS. a. The relative abundance of coral-associated bacteria at class level. b. The relative abundance of coral-associated bacteria at genus level. c. Venn, Venn analysis was based on ASV level. d. Principal co-ordinates analysis (PCoA). PC1 and PC2 explained 33.17% and 17.17% of total variation, respectively.

Venn diagram analysis revealed common and specific bacterial ASV in different polyps and skeletons of *C. palauensis* (Fig. 3c). The results showed that ASV found in coral skeletons were higher than in coral polyps, and ASV found in the subtropical CRR were higher than in the tropical CRR. PCoA showed that the coral samples of coral polyps in subtropical CRR, coral skeletons in subtropical CRR, coral polyps in tropical CRR, and coral skeleton in tropical CRR were divided into four independent groups (Fig. 3d, PERMANOVA, df = 3, F = 11.09, p = 0.001). PCoA and Venn analyses showed that the associated bacterial communities were different between the skeletons and polyps of *C. palauensis*, as well as between different climate zones. According to the RDA analysis (Fig. S4a), SST, DIN, SRP and transparency were the main factors affecting bacterial ASV of polyps and skeleton. Coral polyp and skeletal bacterial ASV were significantly negatively correlated with DIN and positively correlated with transparency and SST.

3.3 *The archaeal community of coral polyp and skeleton in tropical and subtropical CRR*

After quality filtering, 1 268 effective ASV were obtained using the Illumina MiSeq platform. α-diversity was measured using the Sobs, Ace, Shannon–Wiener, and Simpson indices (Table S5, Figs 5 and S2). The Sobs and

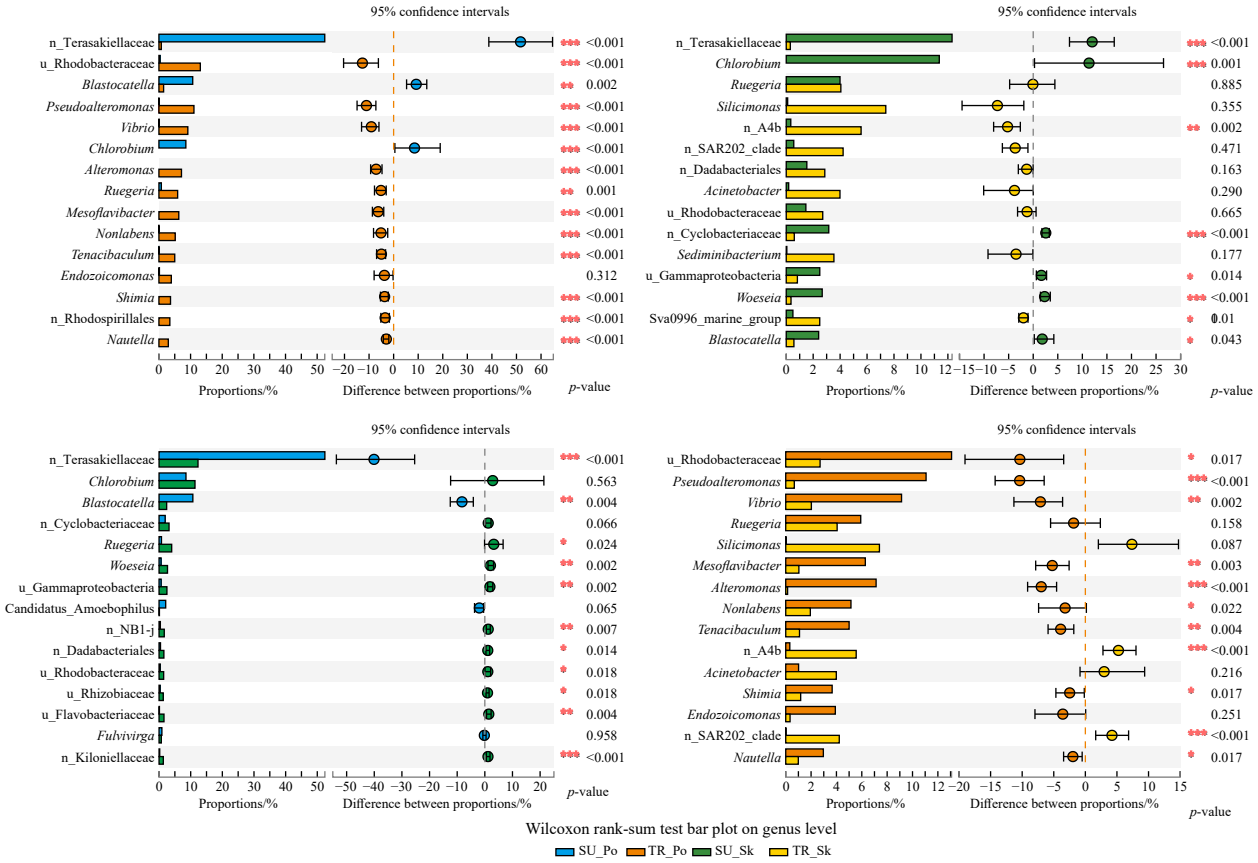

Fig. 4. Wilcoxon rank-sum test bar plot of associated bacterial communities at genus level in coral polyp and skeleton in the tropical and subtropical CRR in the SCS. Some of microbes such as n_Terasakiellaceae, u_Rhodobacteraceae represent norank coral-associated microbial genera of Terasakiellaceae and unclassified coral-associated microbial genera of Rhodobacteraceae, respectively. The red asterisks "*" "**" and "***" represent "$0.01 < p < 0.05$" "$0.001 < p < 0.01$" and "$p < 0.001$", respectively.

Ace indices of *C. palauensis* polyp archaea were significantly higher in the subtropical CRR than in the tropical CRR (Wilcoxon rank sum test, Sobs $p = 0.012$, Ace $p = 0.016$), while the Ace index of skeletal archaea was significantly higher in the tropical CRR than in the subtropical CRR (Wilcoxon rank sum test, $p = 0.046$). Meanwhile, the Shannon and Simpson indices of polyp archaea were significantly higher in the subtropical CRR than in the tropical CRR (Wilcoxon rank sum test, Shannon $p = 0.001$; Simpson $p = 0.002$).

The total taxonomic composition of archaea in the analyzed samples included five phyla, seven classes, eight orders, nine families, and nine genera. At the class level, unclassified_Archaea [(11 ± 4)%–(69 ± 18)%] and Nanoarchaeia [(31 ± 18)%–(89 ± 4)%] were detected (Table S6, Fig. 6a). At the genus level, Woesearchaeales [(64 ± 4)%–(88 ± 4)%] were dominant in the coral polyps in subtropical CRR, coral skeletons in subtropical CRR and coral polyps in tropical CRR groups. In the coral polyps in tropical CRR groups, Woesearchaeales [(31 ± 18)%] were also dominant archaea (Fig. 6a).

Common and unique archaeal ASV (Fig. 6c) were detected in the polyps and skeletons in the tropical and subtropical CRR. In the tropical CRR, the ASV found in coral skeletons were higher than in coral polyps. In the subtropical CRR, the ASV found in coral polyps were higher than in coral skeletons. Besides, in coral polyps, the ASV found in the subtropical CRR were higher than in the tropical CRR. For coral skeletons, the ASV found in the tropical CRR were higher than in the subtropical CRR. PCoA showed that the coral samples of coral polyps in subtropical CRR, coral skeletons in subtropical CRR, coral polyps in tropical CRR, and coral skeletons in tropical CRR were divided into four independent groups (Fig. 6d, PERMANOVA, df = 3, $F = 55.54$, $p = 0.001$). PCoA and Venn diagram analysis showed that the associated archaeal communities were different between tropical and subtropical CRR as well as between polyps and skeletons.

For polyp archaea, the relative abundance of archaea was significantly higher in the subtropical CRR than in tropical CRR (Table S7, Wilcoxon rank sum test, $p < 0.001$), while that of Woesearchaeales showed the opposite trend (Wilcoxon rank sum test, $p < 0.001$), as shown in Fig. 7. For skeletal archaea, the relative abundance of Woesearchaeales was significantly higher in the subtropical CRR than in the tropical CRR (Wilcoxon rank sum test, $p < 0.001$). Moreover, some archaea of *C. palauensis*

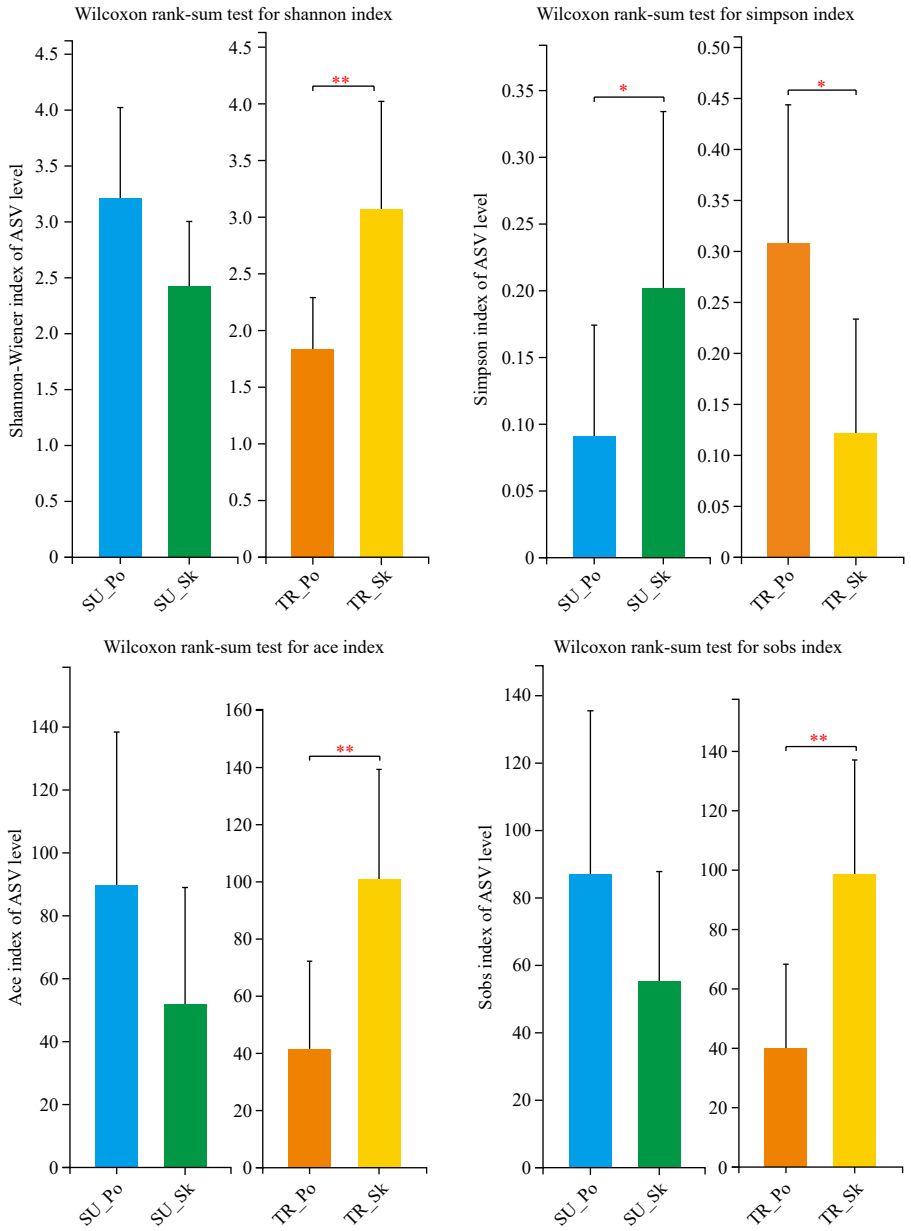

Fig. 5. The Ace, Sobs, Shannon-Wiener, and Simpson diversity indices of coral-associated archaea in coral polyp and skeleton in the tropical and subtropical CRR in the SCS. The red asterisks "*" "**" and "***" represent "$0.01 < p < 0.05$" "$0.001 < p < 0.01$" and "$p < 0.001$", respectively.

differed significantly between the polyps and skeletons. In the subtropical CRR, the relative abundance of Woesearchaeales was significantly higher in the skeletons than in the polyps (Wilcoxon rank sum test, $p < 0.001$). In the tropical CRR, the relative abundance of unclassified_Archaea was significantly higher in the polyps than in the skeletons (Wilcoxon rank sum test, $p < 0.001$), while that of Woesearchaeales was significantly higher than in the skeletons than in the polyps (Wilcoxon rank sum test, $p < 0.001$). According to the RDA analysis (Fig. S4b), SST, DIN, SRP and transparency were the main factors affecting archaeal ASV of polyps and skeleton. Coral polyp and skeletal bacterial ASV were significantly negatively correlated with DIN and positively correlated with transparency and SST.

3.4 *The fungal community of coral polyp and skeleton in tropical and subtropical CRR*

After quality filtering, 857 valid fungal ASV were obtained using an Illumina MiSeq platform. α-diversity was measured using the Sobs, Ace, Shannon-Wiener, and Simpson indices. In the subtropical CRR, the Sobs, Ace, Shannon-Wiener, and Simpson indices of skeletal fungi were significantly higher than those of polyp fungi (Table S8, Wilcoxon rank sum test, Sobs, $p = 0.001$; Ace, $p = 0.008$; Shannon-Wiener, $p = 0.025$; Simpson, $p = 0.01$; Figs 8 and S3). Meanwhile, the Sobs and Ace indices of polyp fungi were significantly higher in the tropical CRR than in the subtropical CRR (Sobs $p = 0.001$, Ace $p = 0.042$).

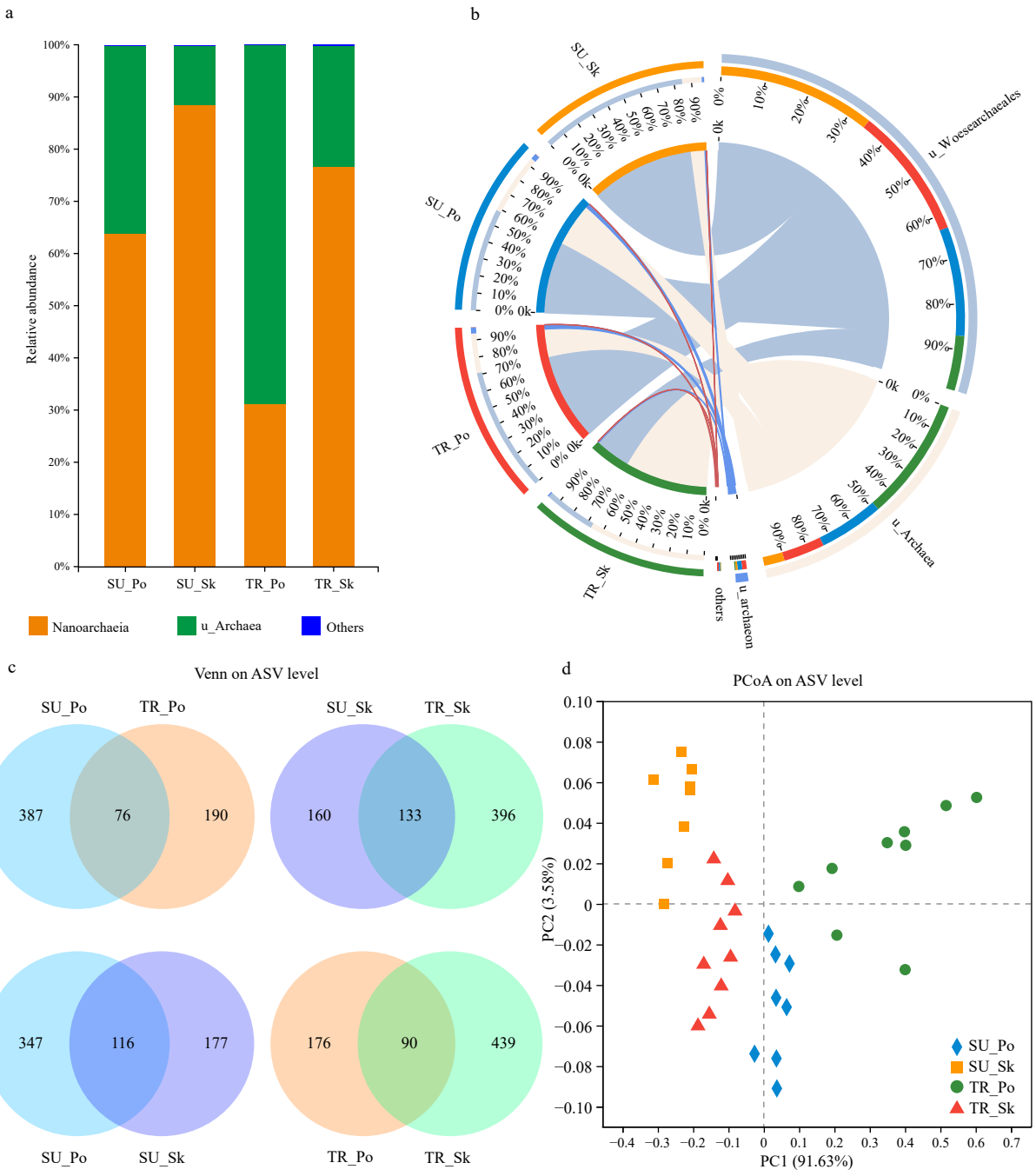

Fig. 6. Relative abundances of associated archaea communities at class level in coral polyp and skeleton in the tropical and subtropical CRR in the SCS. a. The relative abundance of coral-associated bacteria at class level. b. The relative abundance of coral-associated bacteria at genus level. c. Venn, Venn analysis based on ASV level. d. PcoA. PC1 and PC2 explained 91.63% and 3.58% of total variation, respectively.

At the genus level, *Ascomycota* (99%–100%) was dominant in the subtropical CRR, while *Ascomycota* [(41 ± 19)%–(81 ± 7)%] and *Sordariomycetes* [(2 ± 3)%–(32 ± 21)%] were dominant in the tropical CRR (Fig. 9a). Comparison of the sequences of fungi revealed unique ASV in the polyps and skeletons of *C. palauensis* corals in the tropical and subtropical CRR (Fig. 9c). In coral skeletons, the ASV were found higher than in coral polyps. And in the subtropical CRR, the ASV were found higher than in the tropical CRR. PCoA analysis showed that coral samples were divided into four independent groups (Fig. 9d, PERMANOVA, df = 3, F = 13.61, p = 0.001). PCoA and Venn diagram analysis showed that the coral-associated fungal communities were different between coral polyps and skeletons as well as between coral locations.

The fungal composition of *C. palauensis* corals varies regionally in the tropical and subtropical CRR (Table S9 and S10, Fig. 10). In coral polyps, the relative abundance of *Ascomycota* was high in the subtropical CRR (Wilcoxon rank sum test, p < 0.001), while that of Sordariomycetes was significantly higher in the tropical CRR

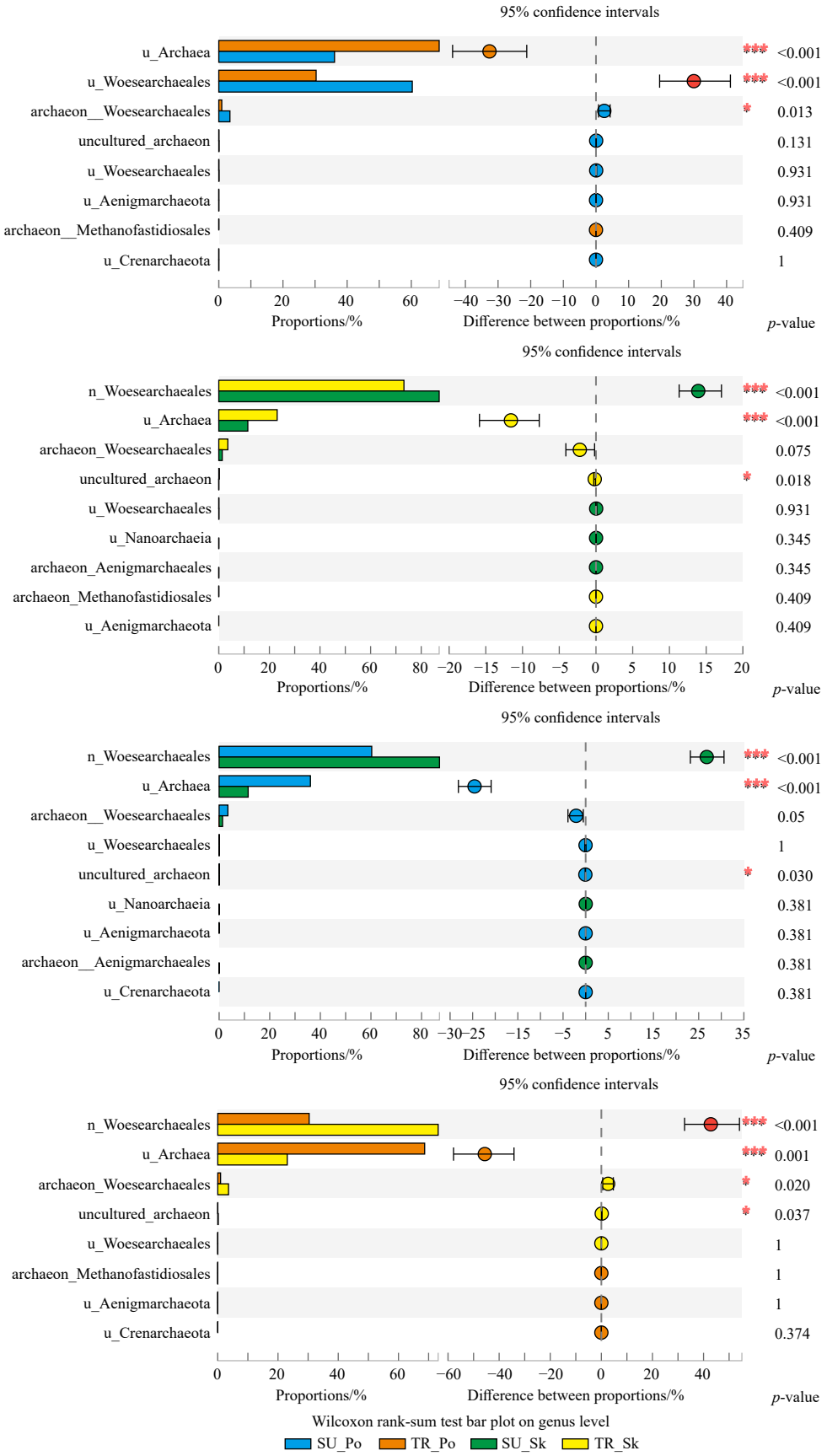

Fig. 7. Wilcoxon rank-sum test bar plot of associated archaea communities at genus level in coral polyp and skeleton in the tropical and subtropical CRR in the SCS. The red asterisks "*" "**" and "***" represent "$0.01 < p < 0.05$" "$0.001 < p < 0.01$" and "$p < 0.001$", respectively.

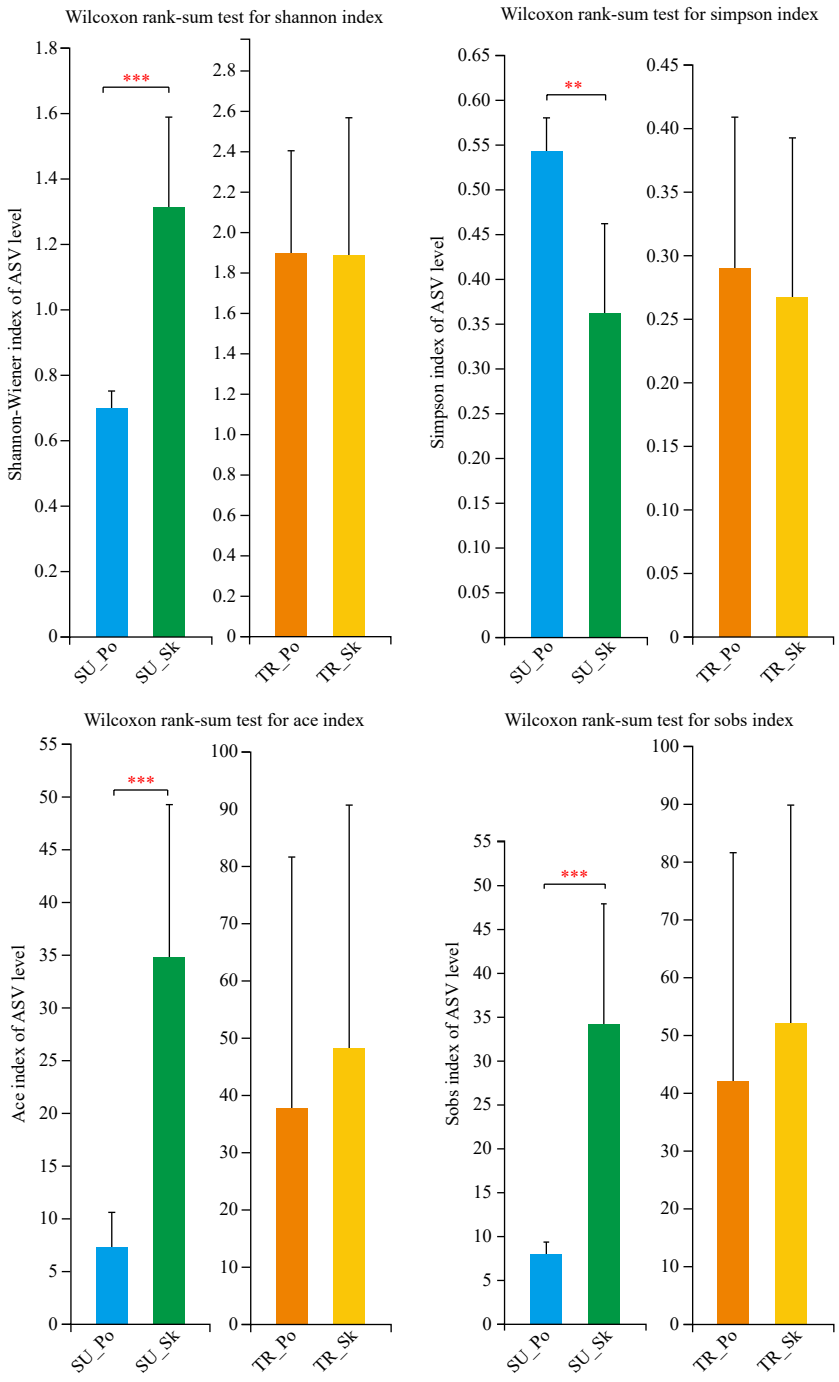

Fig. 8. The Ace, Sobs, Shannon-Wiener, and Simpson diversity indices of associated fungi communities in coral polyp and skeleton in the tropical and subtropical CRR in the SCS. The red asterisks "**" and "***" represent "$0.001 < p < 0.01$" and "$p < 0.001$", respectively.

(Wilcoxon rank sum test, $p = 0.020$). Similarly, in coral skeletons, the relative abundance of *Ascomycota* was significantly higher in the subtropical CRR than in the tropical CRR (Wilcoxon rank sum test, $p < 0.001$), while that of *Sordariomycetes* showed the opposite trend (Wilcoxon rank sum test, $p < 0.001$). According to RDA analysis (Fig. S4c), SST, DIN, SRP and transparency were the main factors affecting fungal ASV of polyps and skeleton. Coral polyp and skeletal bacterial ASV were significantly negatively correlated with DIN and positively correlated with transparency and SST.

4 Discussion

4.1 *Differences and influencing factors in the polyp and skeletal bacterial communities of corals in tropical and subtropical CCRs*

In this study, the community compositions of bacteria in coral polyps and skeletons were significantly different between tropical and subtropical CRR. Environmental stresses such as high temperature (Santos et al., 2014; Bourne et al., 2008), eutrophication (Jessen et al., 2013),

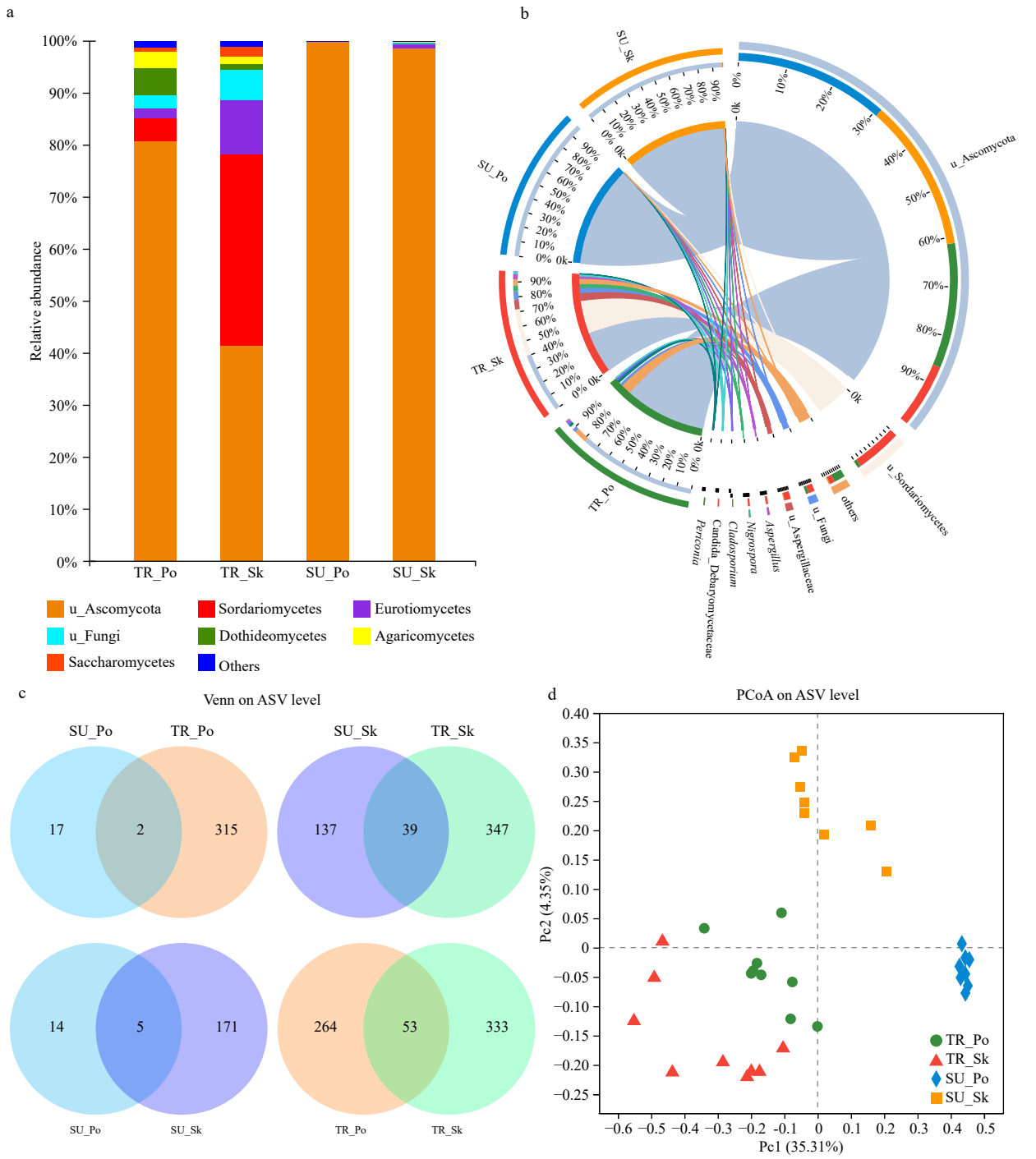

Fig. 9. Relative abundances of associated fungi communities at class level in coral polyp and skeleton in the tropical and subtropical CRR in the SCS. a. The relative abundance of coral-associated bacteria at class level. b. The relative abundance of coral-associated bacteria at genus level. c. Venn, Venn analysis based on ASV level. d. PcoA. PC1 and PC2 explained 35.31% and 4.35% of total variation, respectively.

and water pollution (Ziegler et al., 2016) reduce the ability of the coral host or its microbiome to regulate community composition, which could affect the α-diversity of bacterial community (Zaneveld et al., 2017; McDevitt-Irwin et al., 2017). In this study, coral-associated bacteria may have been influenced by different environmental stresses between tropical and subtropical CRR. High SST and salinity may influence corals in the tropical CRR, while relative high eutrophication and turbidity may influence corals in the subtropical CRR. RDA analyses showed that DIN, SST and transparency were the main environmental influences in coral polyps and skeletal bacteria (Fig. S4a). The different responses of coral polyp and skeletal bacteria to these environmental stresses may be the main reason for the regional differences in Sobs, Ace, Shannon-Wiener, and Simpson indices.

In the subtropical CRR of the SCS, coral polyps and skeletons contain a high relative abundance of bacteria

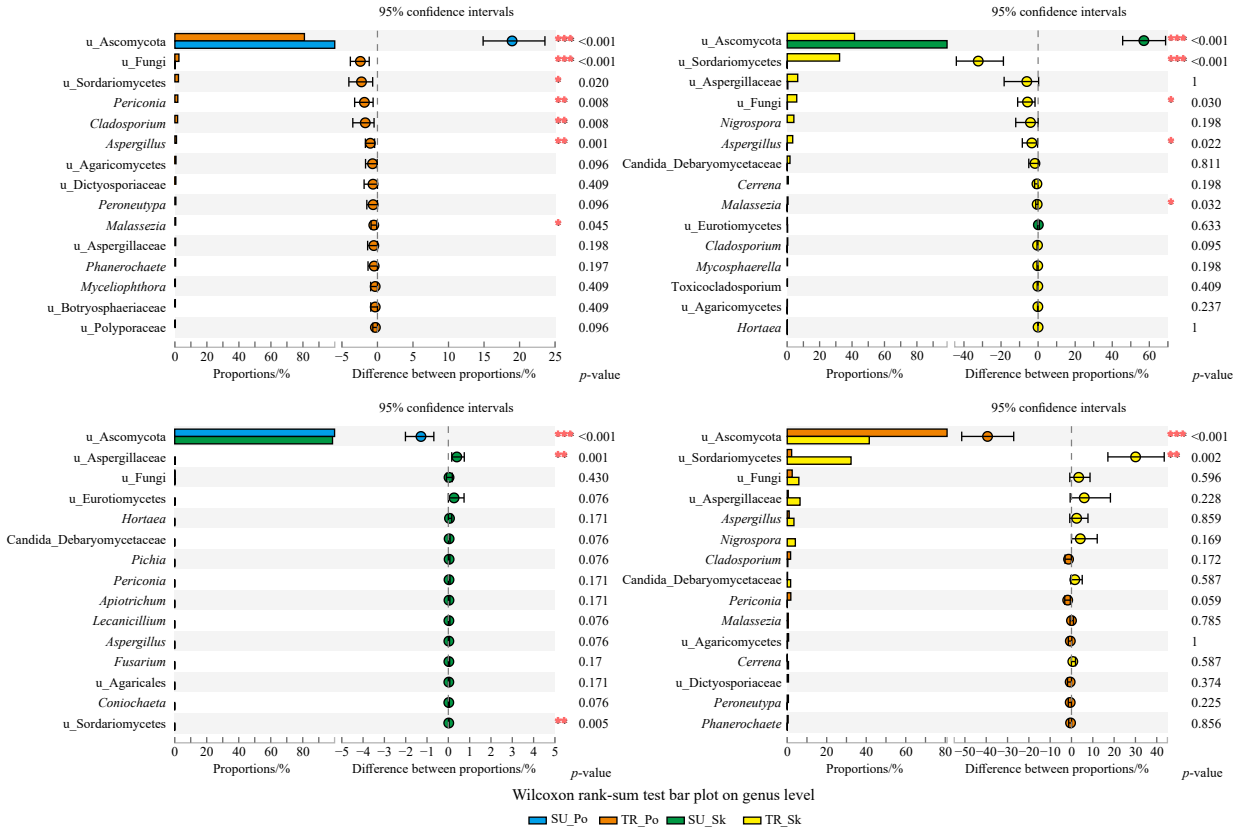

Fig. 10. Wilcoxon rank-sum test bar plot of associated fungi communities at genus level in coral polyp and skeleton in the tropical and subtropical CRR in the SCS.

that are related to the nitrogen cycle and local environment adaptation. A high abundance of Terasakiellaceae was detected in coral polyps in the subtropical CRR, which may contribute to nitrogen cycling of coral holobionts, especially in habitats where nutrients are limited (Weiler et al., 2018; Quintanilla et al., 2022). The Terasakiellaceae were documented to be nitrogen fixed and may be important for the nitrogen metabolism (Tiedje, 1988). It may be a biomarker for organisms involved in the nitrogen cycle (Weiler et al., 2018). The azotobacter *Chlorobium*, which usually survives in hypoxic aquatic environments (Frigaard and Bryant, 2004), was also the dominant bacteria in coral polyps and skeletons in the subtropical CRR. The RDA analysis showed that DIN was the main factor influencing in the subtropical CRR, which may be a factor resulting in high abundance of *Chlorobium* in coral skeletons and polyps. Some members of *Chlorobium* belong to the nitrogen-fixing bacteria, which are related with the nitrogen cycle and may be high abundance in high nutrient environment (Frigaard and Bryant, 2004; Fan et al., 2021). In addition, *Cyclobacilluscaeae* which can assimilate ammonia nitrogen (Fan et al., 2021), Woeseia (Mußmann et al., 2017; Zhang et al., 2020), which is capable of dissimilatory sulfur oxidation and denitrification, and Blastocatalla (Huang et al., 2017), which can remove nitrogen, phosphorus, and organic matter, were also highly abundant in the *C. palauensis* coral in the subtropical CRR in the SCS.

In the tropical CRR, a relatively high relative abundances of opportunistic, pathogenic, and antibacterial bacteria were detected in coral polyps of *C. palauensis*. High SST influences the dynamic balance between invasion and resistance of opportunistic and pathogenic coral bacteria (Qin et al., 2020). In this study, some members of Rhodobacteraceae were dominant in coral polyps, some of which were fast-growing opportunistic bacteria that significantly increased in abundance in stressed corals that found in previous studies (Teeling et al., 2012; Meron et al., 2011; Sharp et al., 2012). In addition, some potential pathogens, namely *Tenacibaculum*, *Nonlabens*, *Mesoflavibacter*, and *Vibrio,* also had relatively high abundances in coral polyps. *Tenacibaculum*, *Nonlabens*, and *Mesoflavibacter* belong to the family Flavobacteriaceae, which is related to coral bleaching (Gignoux-Wolfsohn and Vollmer, 2015). The abundance of pathogenic bacteria will significantly increase when coral holobionts suffer from thermal stress and coral diseases, causing an increase in gene expression related to virulence factors (McDevitt-Irwin et al., 2017; van Oppen and Blackall, 2019). However, high relative abundances of the *Pseudoalteromonas* and *Alteromonas* were also detected in coral polyps. Some members of *Pseudoalteromonas* have antibacterial activity against coral bacteria (Shnit-Orland et al., 2012; Tang et al., 2020), and some members of *Alteromonas* can participate in the coral nitrogen and sulfur cycle (Raina et al., 2009; Ceh et al., 2013). In addition,

20% of the members of coral-associated bacteria *Photobacterium* and *Alteromonas* can secrete antibiotics to resist the invasion of coral pathogens (Ritchie, 2006). Therefore, coral polyps in the tropical CRR may be associated with potential probiotics to resist the negative effects of a high abundance of pathogenic bacteria.

In the coral skeletons in the tropical CRR, a high relative abundance of A4b was detected. The bacteria of A4b belong to the Anaerolineae, which is related to carbohydrate decomposition during anaerobic digestion of organic substances (Ni et al., 2022). Sangsawang et al. (2017) found that coral skeleton bacteria have a high primary productivity and can be transferred to coral polyps. Therefore, coral skeleton bacteria may be important for the survival and recovery of corals.

4.2 *Differences and influencing factors in the polyp and skeletal archaeal communities of corals in tropical and subtropical CRR*

In this study, Nanoarchaeota and unclassified Archaea were the dominate archaea in corals in the tropical and subtropical CRR. Woesearchaeales and unclassified Archaea accounted for approximately 99% of the relative abundance of archaea. Recent research has revealed the potential role of Woesearchaeales in anaerobic biogeochemical cycles of carbon, nitrogen, and sulfur (Liu et al., 2021). Liu et al. (2018) reported that various Woesearchaeales were distributed in different biological communities and were mainly concentrated in anoxic environments. Most Woesearchaeales are anaerobes or facultative anaerobes, and the environmental oxygen content is one of the key factors affecting the Woesearchaeales community (Kühl et al., 2008). In deeper parts of coral skeleton below the endolithic algal layer, oxygen content decreases rapidly, creating a hypoxic or anaerobic environment (Kühl et al., 2008; Ricci et al., 2019) that is conducive to the survival of the Woesearchaeales community. Our study showed that the relative abundance of Woesearchaeales in coral skeletons was significantly higher than that in coral polyps. RDA analysis showed that DIN, SRP, SST and Transparency were the main environmental influences on coral polyp and skeletal archaeal ASV. DIN and SRP were positively correlated, while SST and transparency were negatively correlated. DO was positively correlated with archaeal ASV. The significant difference in Woesearchaeales may be due to the combined effects of DO content, elevated nutrients due to water pollution, and SST.

4.3 *Differences and influencing factors in the polyp and skeletal fungal communities of corals in tropical and subtropical CRR*

The α-diversity of coral-associated fungi showed regional differences. Generally, SST is an important environmental factor that drives the richness and community of fungi in seawater with a positive correlation (Li et al., 2019). A high SST could result in an increase in fungal community diversity in corals (Thurber et al., 2009). Our results showed a high α-diversity of fungal community of coral skeletons and polyps in the tropical CRR with higher SST. Although invasion from the polyps to the skeleton triggers the defense mechanism, fungi with strong drilling capacity can successfully break through coral skeleton structures under the influence of high SST (Golubic et al., 1975, 2005; Bentis et al., 2000). The relatively high abundance of fungi in the tropical CRR causes intense competition in the skeletons, resulting in the survival of some fungi in coral polyps. Besides, high abundances of Sordariomycetes, Periconia, Cladosporium, and Aspergillus were detected in the tropical CRR. A higher SST could be the driving factor for these fungal abundances. Most members of Sordariomycetes are classified as Halosphaeriales and Lulworthiales. Halosphaeriales are adaptable to extremely high temperatures (Zhang et al., 2006). Meanwhile, combined with the RDA, the results showed that SST was the main environmental influencing factor for the fungal communities in coral skeletons and polyps. This could explain why Sordariomycetes were the dominant fungi in coral polyps and skeletons in the tropical CRR, which had relatively high SST.

In this study, *Ascomycota* was the dominant fungus in coral skeletons and polyps in tropical and subtropical CRR. Several studies have reported a relatively high abundance of *Ascomycota* in corals from coral reefs including the SCS (Xu et al., 2018), Bocas del Toro (Wegley et al., 2007), Florida (Bonthond et al., 2018), Ofu Island in USA (Amend et al., 2012), the Great Barrier Reef (Littman et al., 2011), and Hawaii (Thurber et al., 2009). In addition, microscopic observations of coral skeletons suggested that *Ascomycota* are common fungi in healthy coral skeletons (Wegley et al., 2007; Góes-Neto et al., 2020). These *Ascomycota* associate with coral early in life and grow with the carbonate skeleton to maintain their position just under the coral polyps (Le Campion-Alsumard et al., 1995a; Wegley et al., 2007). The abundance of *Ascomycota* is closely related to the organic matter and chemical composition of coral skeletons and polyps (Paulino et al., 2017, 2020). Some *Ascomycota* can degrade organic carbon and sugars, and thereby promoting their growth (Suh et al., 2006). The mucus in coral polyps is mainly composed of glucose, galactose, lipids, and other monosaccharides (Ducklow and Mitchell, 1979; Glasl et al., 2016), whereas the coral skeleton is mainly composed of calcium carbonate, resulting in a higher abundance of *Ascomycota* in the polyps than in the skeletons. Some Ascomycetes can participate in multiple carbon nitrogen coupled cycles, such as carbon fixation, ammonia assimilation, and ammoniation, and bioactive substances can participate in immune regulation and antibacterial activity (Gleason et al., 2017, Wegley et al., 2007). *Ascomycota* is the dominant fungal phylum in the honeycomb corals in the tropical and subtropical CRR, and some of

them have positive effects. It is possible to conduct in-depth research on how to utilize these beneficial fungi to maintain the ecology of coral reefs.

5 Conclusions

In this study, coral-microbial assemblages in coral polyps and skeletons varied at tropical and subtropical reefs in the SCS. In the subtropical CRR of Weizhou Island, the nitrogen-fixing bacterium *Chlorobium* was the dominant bacterium in the polyps and skeletons of *C. palauensis*. The *Woeseia*, which is capable of sulfur oxidation and denitrification, as well as high abundance of *Blastocatella*, which could remove high nitrogen, phosphorus, and organic particulate matter were detected in the *C. palauensis* polyps or skeletons. In addition, the relative abundance of Woesearchaeales was significantly higher than that of corals from the tropical CRR. This may be due to anthropogenic activities impacts such as high nutrients and turbidity. Relatively high abundance of opportunistic, pathogenic and antimicrobial bacteria was detected in *C. palauensis* polyps in the tropical CRR. The potentially pathogenic fungi such as *Periconia*, *Cladosporium*, and *Aspergillus* were significantly higher in polyp and skeleton from the tropical CRR than the subtropical CRR. Suffered from high thermal stress in summer, corals in the tropical CRR may be threatened by potential bacterial or fungal diseases, and are susceptible to coral bleaching under the thermal stress. Therefore, in the subtropical CRR, anthropogenic activities should be reduced, which is conducive to corals' health. In the tropical CRR, it is advised to enhance monitoring for abnormally high temperatures, which will be conducive to early detection the threat of abnormally high thermal to the corals.

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Supplementary information:

Figure S1. The Ace, Sobs, Shannon-Wiener, and Simpson diversity indices of associated bacteria based on ASV level in coral polyp and skeleton between the Bombay Reef and Weizhou Island in the South China Sea (SCS). The “SU_Po” “SU_Sk” “TR_Po” “TR_Sk” represent “coral polyp in subtropical CRR” “coral skeleton in subtropical CRR” “coral polyp in tropical CRR” “coral skeleton in tropical CRR”, respectively. The red asterisks “*” “**” and “***” represent “$0.01 < p < 0.05$” “$0.001 < p < 0.01$” and “$p < 0.001$”, respectively.

Figure S2. The Ace, Sobs, Shannon-Wiener, and Simpson diversity indices of associated archaea based on ASV level in coral polyp and skeleton between the Bombay Reef and Weizhou Island in the SCS.

Figure S3. The Ace, Sobs, Shannon-Wiener, and Simpson diversity indices of associated fungi based on ASV level in coral polyp and skeleton between the Bombay Reef and Weizhou Island in the SCS.

Figure S4. The correlation among environmental factors, sampling areas, and ASV of coral associated bacteria, archaea, and fungi based on redundancy analysis (RDA). a. bacteria-ASV, b. archaea-ASV, c. fungi-ASV.

Table S1. Data of seawater temperature, DIN, SRP, DO, pH, salinity, and transparency in the Bombay Reef and Weizhou Island.

Table S2. Sample information of associated bacteria including number of sequences and diversity indicated by the Shannon-Wiener, Simpson, Ace and Chao indices of Coelastrea palauensis corals in the Bombay Reef and Weizhou Island.

Table S3. The relative abundance of coral-associated bacterial community of Coelastrea palauensis corals on class level in the Bombay Reef and Weizhou Island.

Table S4. The relative abundance of coral-associated bacterial community of Coelastrea palauensis corals on genus level in the Bombay Reef and Weizhou Island.

Table S5. Sample information of associated archaea including number of sequences and diversity indicated by the Shannon-Wiener, Simpson, Ace and Chao indices of Coelastrea palauensis corals in the Bombay Reef and Weizhou Island.

Table S6. The relative abundance of coral-associated archaeal community of Coelastrea palauensis corals on class level in the Bombay Reef and Weizhou Island.

Table S7. The relative abundance of coral-associated archaeal community of Coelastrea palauensis corals on genus level in the Bombay Reef and Weizhou Island.

Table S8. Sample information of associated fungi including number of sequences and diversity indicated by the Shannon-Wiener, Simpson, Ace and Chao indices of Coelastrea palauensis corals in the Bombay Reef and Weizhou Island.

Table S9. The relative abundance of coral-associated fungal community of Coelastrea palauensis corals on class level in the Bombay Reef and Weizhou Island.

Table S10. The relative abundance of coral-associated fungal community of Coelastrea palauensis corals on genus level in the Bombay Reef and Weizhou Island.

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