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Microbiome of juvenile corals in the outer reef slope and lagoon of the South China Sea: insight into coral acclimatization to extreme thermal environments

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Summary

Environmental conditions between the outer reef slope (ORS) and lagoon in tropical atolls are significantly different, but the variations of juvenile coral-microbiomes in the two environments and their relationship with coral thermal acclimatization are poorly understood. We explored this issue based on local water conditions and the microbiome of juvenile corals in the ORS and lagoon in the central South China Sea. Coral-symbiotic Symbiodiniaceae showed significant differences among coral species; *Pocillopora verrucosa* and *Pachyseris rugosa* in the ORS, and *Acropora formosa* in the lagoon were dominated by *Durusdinium*, but other corals were dominated by *Cladocopium*. Although *A. formosa* in the ORS were dominated by *Cladocopium* (C3u), they were dominated by *Durusdinium* (D1/D1a) and *Cladocopium* (C50) in the lagoon. Other coral species were both dominated by *Cladocopium* in the lagoon and ORS. The relative abundance of bacteria in the Deinococcus–Thermus was generally higher in the lagoon corals than in the ORS corals. Our study indicates that *P. verrucosa*, *P. rugosa* and *Porites lutea* may have high thermal tolerance based on the relatively high abundance of heat-tolerant *Durusdinium* and *Thermus scotoductus*. Likewise, *A. formosa* in the lagoon may acclimatize to the thermal environment based on a high relative abundance of heat-tolerant *Durusdinium*.

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Introduction

Coral reefs are the most biodiverse and productive ecosystems in the world, and they play important roles in the diversity and stability of the global ecosystem (Brown, 1997; Hoegh-Guldberg, 1999). However, in recent decades, they are being threatened by global warming, human destructive activities (e.g., anthropogenic eutrophication, overfishing and pollutants) and rapid degradation (e.g., Hoegh-Guldberg *et al*., 2007; Hughes *et al*., 2017a,b). Among these threats, abnormally high sea surface temperatures (SSTs) are the main cause of large-scale coral death and the deterioration of coral reefs worldwide (Douglas, 2003; Hughes *et al*., 2017a). Abnormally, high SSTs may disrupt the coral-Symbiodiniaceae symbiosis, resulting in mass Symbiodiniaceae (formerly named zooxanthellae) discharge and coral bleaching (Baker *et al*., 2008). Since the late 1990s, frequent El Niños have triggered a series of global-scale coral bleaching events (GCBEs) (Hughes *et al*., 2017a, 2018a; Eakin *et al*., 2019). For example, the 1998 thermal bleaching event caused great damage to global coral reefs, resulting in the loss of 16% of the global coral reefs, and bleaching of 87% of the corals in the Great Barrier Reef (GBR), ~95% of the corals in Bahrain and the Maldives and ~85% of the corals in Japan (Wilkinson, 1998; Berkelmans and Oliver, 1999; Loya *et al*., 2001). Record high temperatures during 2015–2017 triggered the third recorded global bleaching event since the first large-scale bleaching in the 1980s, causing severe damage to the survival and health of global coral reefs, such as those in the GBR (Hughes *et al*., 2017a, 2018a) as well as in Western Australia (Gilmour *et al*., 2019), Caribbean (Weiler *et al*., 2019) and Southeast Asia (Guest *et al*., 2016). These thermal bleaching events are severely harmful to the survival and health of coral reefs worldwide and accelerate coral reef degradation.

Interestingly, many corals may survive repeatedly high thermal stress and acclimatize to a changing thermal environment (Rowan, 2004; Ainsworth and Gates, 2016; McClanahan, 2017). Several factors affect the ability of different corals to adjust to climate warming; among these, the physiological regulatory capacity of coral symbionts is a key factor (Suggett *et al*., 2017; van Oppen and Blackall, 2019). Coral holobiont microorganisms may regulate physiological and ecological characteristics (e.g., stress response of coral hosts, Symbiodiniaceae density (SD), Symbiodiniaceae genus/subclade and bacterial composition) to help acclimatize to changing environments (e.g., D'Angelo *et al*., 2015; Boulotte *et al*., 2016). Generally, the microbial community changes dynamically, which includes reorganization when the environment fluctuates (Roche *et al*., 2018; van Oppen and Blackall, 2019). The coral-associated bacterial community has been implicated in a range of functional roles, such as sulfur, carbon and nitrogen cycling; bacterial community composition shifts could affect this cycling under environmental stress as well as coral holobiont resilience and thermal acclimatization (Roche *et al*., 2018). Some evidence indicates the formation of specific bacterial symbiotic associations, demonstrating their potential role in habitat acclimatization (Burt *et al*., 2020), such as deep-water reefs (Röthig *et al*., 2020), volcanic vents (e.g., Fabricius *et al*., 2011; Enochs *et al*., 2015) and warmer back reef pools (Ziegler *et al*., 2017a). Consequently, investigating the composition and diversity of coral-associated microbes may provide a basis to assess the health state and thermal acclimatization potential of corals.

Juvenile corals are good candidates for studying extreme thermal environmental acclimatization (Holbrook *et al*., 2018; Liao *et al*., 2021). Global corals are rapidly degraded due to local and global disturbance, and juvenile coral recruitment is critical to the persistence and resilience of coral reefs (Albright *et al*., 2010). Dominance by juvenile corals is a common response of coral populations to environmental disturbances and an important indicator of the recovery of a coral reef (Fong and Glynn, 1998; Done, 1999; Hughes and Tanner, 2000). The composition of symbiotic Symbiodiniaceae in juvenile corals is more flexible than that of adult corals (Little *et al*., 2004; Abrego *et al*., 2009). Juvenile corals can either obtain these microbial communities from their parents or adjust their microbial composition to improve their acclimatization and survival rate (van Oppen and Blackall, 2019). In degraded or severely disturbed coral reef regions (e.g., abnormally high thermal stress and high suspended matter), some small corals can be successfully settled and grown based on stronger acclimatization, whereas others are more susceptible to elimination due to weak acclimatization (Littman *et al*., 2009; van Oppen and Blackall, 2019). Exploring the symbiotic microorganism composition of juvenile corals could facilitate our understanding of coral acclimatization and resilience to global warming.

The environmental characteristics of the outer reef slopes (ORS) and lagoon in tropical atolls differ significantly (Decarlo *et al*., 2017; Ke *et al*., 2018; Guo *et al*., 2019). Lagoons are the most extreme coral habitats with high metabolic demands driven by frequent exposure to low dissolved oxygen (DO) levels and a recurrently reduced pH across the seasonal and tidal cycles (Manzello *et al*., 2012; Camp *et al*., 2017; Burt *et al*., 2020). In the central and southern South China Sea (SCS), for example, the concentrations of dissolved inorganic nitrogen (DIN) and chlorophyll (Chl) *a* in lagoons are on average ~ 1.2 and 3–6 times higher respectively, than levels in the ORS (Guo *et al*., 2019). The maximum temperature and annual average SST in the lagoon is $> 2.5^{\circ}C$ and $> 1.5^{\circ}C$ higher respectively, than in the ORS, and the temperature range between day and night exceeds 10°C in lagoons in the summer. Living conditions in the lagoon are less favourable for coral growth than those in the ORS, but some macro-ecological surveys found that corals in the lagoon can also survive well and are less susceptible to bleaching under similar thermal stress suggesting improved thermal acclimatization (e.g., Tkachenko and Soong, 2017). However, few studies have focused on the influence of various symbiotic associations of juvenile corals form with Symbiodiniaceae and/or bacteria on thermal acclimatization between lagoons and the ORS in tropical atolls.

The Xisha Islands (i.e., Paracel Islands, 15°40′N–17°10′N, 110°E–113°E), located in the central SCS, belong to tropical coral reef regions (CRRs) with a high reef coral diversity and numerous coral species (Zhao *et al*., 2016, 2017). Previous macro-ecological surveys found that *Pocillopora*, *Porites*, *Acropora* and *Montipora* were the four dominant coral genera in the Xisha Islands (Zhao *et al*., 2016). According to live coral cover (LCC) observations, in the past two decades, corals in these islands have been severely threatened and rapidly degraded. Theoretically, branching corals (e.g., *Pocillopora* and *Acropora* corals) would be less likely to dominate due to mass bleaching under the threat of high thermal stress (Hughes *et al*., 2018b). However, *in situ* observations suggest that branching corals in the Xisha Islands (i.e., *Pocillopora* corals in the ORS and *Acropora* corals on the lagoon patch reefs) remain dominant after the 2015–2017 GCBE.

The main aim of this study was to explore the variations of juvenile coral-microbiomes between the ORS and lagoon and their relationship with coral thermal acclimatization. We tested the hypothesis that the dominant *Pocillopora* corals in the ORS and *Acropora* corals in

lagoon patch reefs can adapt to high thermal stress with global climate warming by associating with higher numbers of Symbiodiniaceae, specifically those with higher photosynthetic efficiency and heat-tolerance, as well as heat-tolerant bacteria. Local water conditions data; the density, composition and diversity of Symbiodiniaceae; and the composition and diversity of bacteria were collected from eight dominant coral species in the ORS and lagoon patch reefs of the Passu Keah in the central SCS. Our findings will help us better understand differences among coral species which aid in their thermal acclimatization and explain the key factor(s) influencing changes in coral community composition in the ORS and lagoon in the central SCS.

Results

Local water environmental conditions

Significant differences were found when examining the water parameters between the lagoon and the ORS. For annual temperature, the SST fluctuation in the lagoon was higher than in the ORS. The monthly SSTs in the summer of 2015 were $28.5 \pm 0.4^{\circ}C$ and $30.6 \pm 0.2^{\circ}C$; in 2019 they were $28.2 \pm 0.5^{\circ}C$ and $30.2 \pm 0.3^{\circ}C$ in the ORS and lagoon respectively (Wilcoxon rank-sum test, $P = 0.013$). Salinity ($34.7 \pm 0.8‰$ vs. $33.5 \pm 1.3‰$, Wilcoxon rank-sum test, $P = 0.024$), nutrients (DIN, 1.47 ± 0.16 μmol L^{-1} vs. 1.23 ± 0.24 μmol L^{-1}; SRP, 0.16 ± 0.04 μmol L^{-1} vs. 0.08 ± 0.02 μmol L^{-1}, Wilcoxon rank-sum test, $P < 0.001$) and turbidity (0.8–1.1 NTU vs. 0.2–0.3 NTU, Wilcoxon rank-sum test, $P < 0.001$) were higher in the lagoon than in the ORS. In contrast, the transparency of the lagoon was noticeably lower than that of the ORS (6 ± 1.5 m vs. 22 ± 2.4 m, Wilcoxon rank-sum test, $P < 0.001$).

Symbiodiniaceae density and genus/subclade

SD was significantly different among coral reef regions and juvenile coral species, and a significant interaction effect was observed between the two factors (Table S2, two-way ANOVA, Regions: $F = 90.28$, $P < 0.001$, Species: $F = 275.07$, $P < 0.001$; Interaction: $F = 23.03$, $P < 0.001$). The average SD in the lagoon and ORS juvenile coral species was $1.77 \pm 0.59 \times 10^6$ cells cm^{-2} (range $1.38 \pm 0.25 \times 10^6$ to $2.50 \pm 0.20 \times 10^6$ cells cm^{-2}; Fig. 1A, Table S2). Detailed information on SDs in the lagoon and ORS juvenile coral species is shown in Table S2. Among these eight species, the SD of *Acropora formosa* was the lowest ($1.09 \pm 0.23 \times 10^6$ cells cm^{-2}) and that of *Favia palauensis* ($2.50 \pm 0.20 \times 10^6$ cells cm^{-2}) was the highest in the ORS; *Pocillopora verrucosa*, *Pachyseris rugosa*, *A. formosa* and *Fungia fungites* had similar ranges of SD, i.e., 1.09 ± 0.23–$1.39 \pm 0.40 \times 10^6$ cells cm^{-2}, which were significantly lower than those of *Porites lutea*, *F. palauensis* and *Favites abdita* (two-way ANOVA, $P = 0.027$).

In total, 5,714,051 high-quality sequences were obtained from 96 juvenile coral and seawater samples (30, 332–86, 157 sequences per sample, Table S3). Based on ITS2 database alignments, 224 Symbiodiniaceae ITS2 subclades were assigned, including *Symbiodinium* (formerly Clade A), *Breviolum* (formerly Clade B), *Cladocopium* (formerly Clade C), *Durusdinium* (formerly Clade D), *Effrenium* (formerly Clade E), *Fugacium* (formerly Clade F), *Gerakladium* (formerly Clade G) and clade H. Based on operational taxonomic unit (OTU) analysis, Symbiodiniaceae ITS2 sequences were clustered into 73 OTUs belonging to five Symbiodiniaceae genera (i.e., 2 OTUs in *Symbiodinium*, 52 OTUs in *Cladocopium*, 13 OTUs in *Durusdinium*, 1 OTUs in *Fugacium*, and 5 OTUs in *Gerakladium*) with 97% similarity. At the genus level, *P. verrucosa*, *P. rugosa* and *A. formosa* in the lagoon patch reefs had a high proportion of *Durusdinium* (94.14%, 68.33% and 45.39% respectively), while *Cladocopium* was dominant in the other five juvenile coral species (> 85%, Table S4). In the ORS, *P. verrucosa* and *P. rugosa* also had a high proportion of *Durusdinium* (94.48% and 91.00% respectively), while *Cladocopium* dominated in the other six coral species (> 85%, Table S4). Additionally, free-living Symbiodiniaceae found in seawater samples included *Symbiodinium*, *Cladocopium* and *Durusdinium*.

At the subclade level, 31 dominant/sub-dominant subclades (≥ 10% and 5%–10% respectively) were detected based on ITS2 database alignments, accounting for more than 90% of the total sequences. Subclade composition was significantly different among the coral species (Kruskal–Wallis test, ORS $P = 0.001$, lagoon $P = 0.001$). For example, the main composition of *P. verrucosa* and *P. rugosa* in the ORS was *Durusdinium* D1/D1a/D2.2/D6, whereas for *P. lutea* (C15/C15x) and *F. fungites* (C27), it was *Cladocopium*. Additionally, the difference in Symbiodiniaceae composition of the same coral species between the ORS and lagoon was coral species-dependent. For example, the Symbiodiniaceae composition of *A. formosa* between the lagoon (D1/D1a/C50/Cspc) and the ORS (C3u/Cspc/C3w) exhibited significant difference (Wilcoxon rank sum test, $P = 0.003$), and the Symbiodiniaceae composition of *F. palauensis* and *Merulina ampliata* differed significantly between the two locations (Wilcoxon rank sum test, $P = 0.045$ and 0.043). In contrast, there were no significant differences (Wilcoxon rank sum test, $P > 0.05$) in the Symbiodiniaceae composition of *P. verrucosa*, *P. rugosa*, *P. lutea*, *F. abdita* and *F. fungites* between sites.

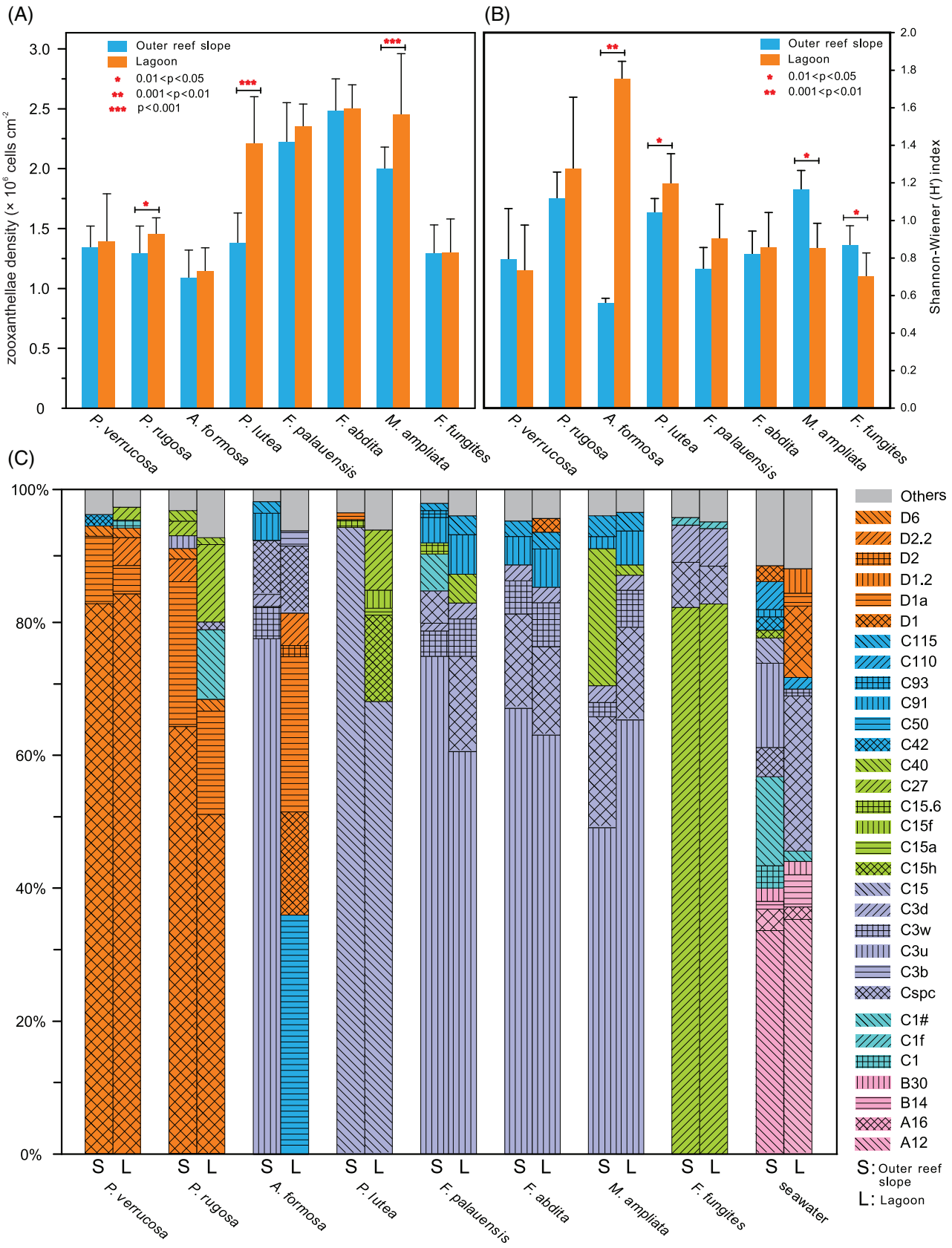

Fig. 1. Density (A), composition (B) and diversity (C) of Symbiodiniaceae in eight coral species in the Passu Keah. [Color figure can be viewed at wileyonlinelibrary.com]

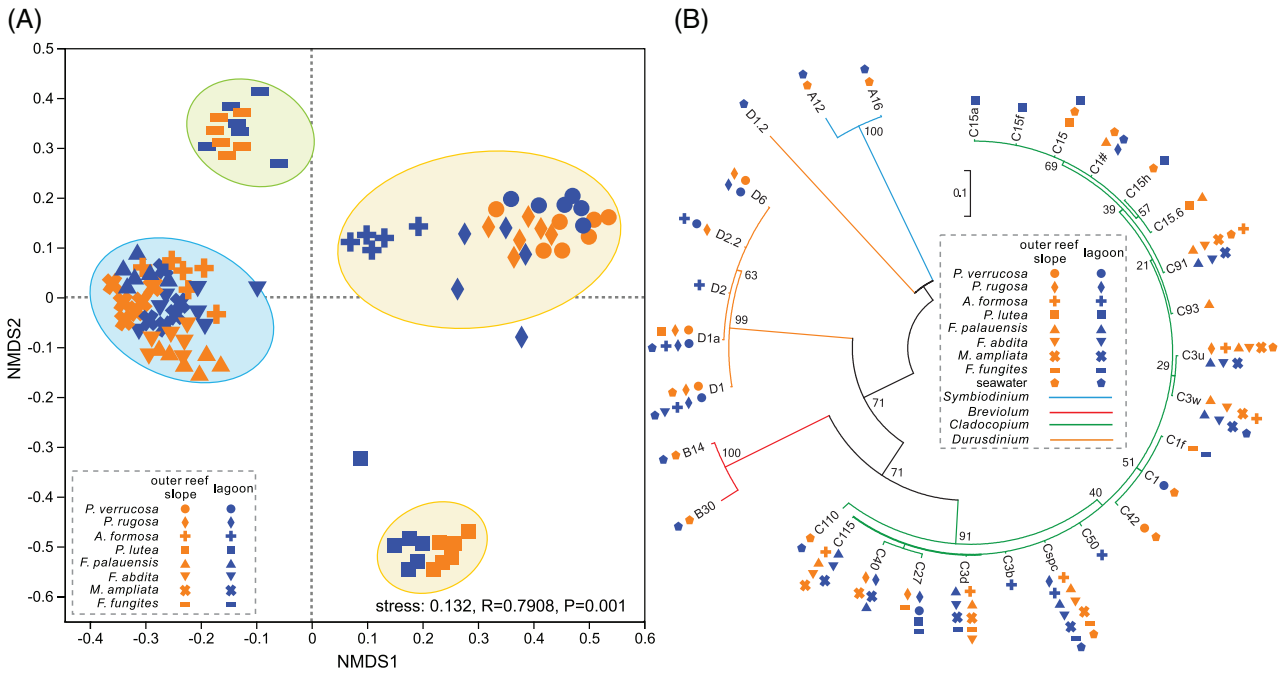

Fig. 2. Nonmetric multidimensional scaling (NMDS) (A) and phylogenetic tree (B) of dominant/sub-dominant Symbiodiniaceae subclades in eight coral species and water samples. NMDS based on operational taxonomic unit level with grouping based on complete linkage cluster analysis of 60% similarity. Each symbol in the phylogenetic tree represents a group with an average subclade relative abundance of ≥ 5%. Phylograms were developed based on ITS2 sequences using maximum likelihood. [Color figure can be viewed at wileyonlinelibrary.com]

The Shannon index of Symbiodiniaceae indicated that water samples had the highest diversity (mean 19.4 in ORS; mean 2.47 in lagoon) and the *P. verrucosa*, *P. rugosa*, *F. palauensis* and *F. abdita* indices did not differ significantly between the ORS and lagoon (Fig. 1B, Wilcoxon rank sum test, $P > 0.05$). The Shannon index of *P. lutea* and *A. formosa* in the lagoon was significantly higher than that of the same corals in the ORS (Wilcoxon rank sum test, $P = 0.041$ and $P = 0.002$). Furthermore, in the lagoon, the Shannon index of *A. formosa* was significantly higher than that of other coral species, whereas it had the lowest value in the ORS (Wilcoxon rank sum test, $P < 0.001$ and $P < 0.001$). The diversity of symbiotic Symbiodiniaceae in *M. ampliata* and *F. fungites* was significantly higher in the ORS (Wilcoxon rank sum test, $P = 0.04$ and $P = 0.003$). non-metric multidimensional scaling (NMDS) revealed a clustering pattern of Symbiodiniaceae in these eight juvenile coral species and seawater in the ORS and lagoon (Fig. 2A). Juvenile corals dominated by symbiotic *Durusdinium* included *P. verrucosa* in the ORS and lagoon, and *P. rugosa* and *A. formosa* in the lagoon. The Symbiodiniaceae composition of *P. lutea* in the ORS and lagoon was similar and clustered into one group; *F. fungites* and *P. lutea* exhibited similar clustering patterns. Other coral-Symbiodiniaceae were clustered into a large group, indicating a similar composition.

A phylogenetic tree of dominant Symbiodiniaceae subclades was established (Fig. 2B). The dominant Symbiodiniaceae subclades associated with conspecific juvenile corals were closely distributed within the phylogenetic tree. For example, D1/D1a/D2.2/D6 associated with *P. verrucosa* due to the close phylogenetic relationships. In *P. lutea*, phylogenetic relationships between C15 and C15x were closer than phylogenetic relationships of C1/C1x/Cspc/C3x. These results indicate that juvenile coral hosts are selectively associated with Symbiodiniaceae-dominant subclades and background types, and possibly show co-evolutionary relationships with the coral holobionts. The phylogenetic relationship between *Durusdinium* D1.2 and *Symbiodinium* (A12 and A16) in seawater was closer than the relationship with *Durusdinium* (D1 and D1a) symbiotic with corals. These results show that corals are symbiotic with *Cladocopium* and *Durusdinium* rather than *Symbiodinium* and *Breviolum* in the central SCS. However, *Symbiodinium* and *Breviolum* are abundant Symbiodiniaceae in the seawater of the tropical SCS.

Coral-associated bacterial assemblages

After quality filtering, the number of recovered bacterial reads from each juvenile coral sample was no less than 31, 132, and these reads were clustered into different

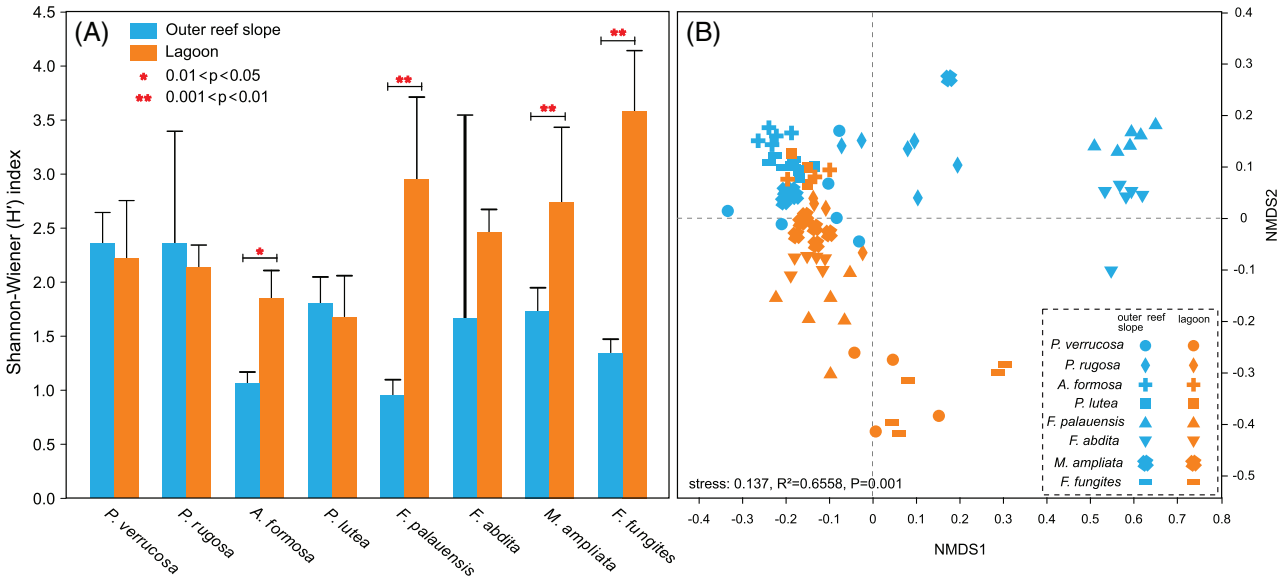

Fig. 3. Diversity (A) and NMDS (B) of associated bacteria in eight coral species in the Passu Keah. NMDS based on operational taxonomic unit level with grouping based on complete linkage cluster analysis of 60% similarity. [Color figure can be viewed at wileyonlinelibrary.com]

OTUs with 97% similarity. The average length of the sequences was 425 bp and the coverage of each sample library exceeded 99%, indicating that these sequencing results represented the true condition of coral-associated bacteria.

The coral-associated bacterial Shannon index showed that bacterial diversity of seawater samples in the lagoon was higher than that of the ORS. For conspecific juvenile coral species, coral-associated bacterial diversity differed between the ORS and lagoon. The bacterial Shannon indices of *A. formosa*, *F. palauensis*, *M. ampliata* and *F. fungites* in the lagoon were significantly higher than the corresponding indices in the ORS (Wilcoxon rank sum test, $P < 0.05$; Fig. 3A). However, the indices of *P. verrucosa*, *P. rugosa*, *P. lutea* and *F. abdita* showed no significant difference between the lagoon and ORS (Wilcoxon rank sum test, $P > 0.05$). For different coral species, significant differences were observed in the number of associated bacterial OTUs (Wilcoxon rank sum test, $P < 0.05$). For example, the average associated bacterial OTUs differed significantly among *P. verrucosa* (496 vs. 350), *P. rugosa* (601 vs. 521), *A. formosa* (184 vs. 360), *P. lutea* (327 vs. 451), *F. palauensis* (211 vs. 566), *F. abdita* (567 vs. 363), *M. ampliata* (322 vs. 390) and *F. fungites* (344 vs. 1032) comparing the ORS and lagoon. Other diversity indices, including H′, Simpson, Ace and Chao 1, are shown in Table S5. Additionally, NMDS showed a clear clustering pattern (Fig. 3B). *A. formosa* and *P. lutea* exhibited a similar bacterial composition between the ORS and lagoon, whereas the bacterial composition of *P. verrucosa*, *P. rugosa*, *F. palauensis*, *F. abdita*, *M. ampliata* and *F. fungites* exhibited significant differences between the two locations.

The seawater and coral-associated bacteria comprised 46 phyla, 109 classes, 317 orders, 606 families and 1429 genera. At the phylum level, Proteobacteria was the most abundant in all juvenile corals and seawater samples (Table S6). Comparing within environmental variability with between-environment differences overall without considering coral species identities, the relative abundance of coral-associated Proteobacteria, Deinococcus-Thermus, Bacteroidetes and Firmicutes showed significant difference (Wilcoxon rank sum test, $P < 0.001$, $P = 0.006$, $P = 0.001$, $P < 0.001$ respectively; Fig. S1). Higher relative abundance of Proteobacteria was observed in the ORS, whereas higher relative abundance of Deinococcus-Thermus, Bacteroidetes and Firmicutes was observed in the lagoon. Considering coral species identities, there was a significant difference in the bacterial composition of conspecific coral species between the two locations. In the ORS, the relative abundance of Proteobacteria in *P. verrucosa*, *P. rugosa*, *F. palauensis*, *M. ampliata* and *F. fungites* was significantly higher than that observed in the same species in the lagoon (Wilcoxon rank sum test, $P < 0.05$; Fig. 4). In contrast, the relative abundance of coral-associated Deinococcus–Thermus in the lagoon was significantly higher than that found in corals in the ORS (Wilcoxon rank sum test, $P < 0.05$); for instance, *P. verrucosa* and *P. rugosa* in the lagoon contained a high proportion of Deinococcus-Thermus (25.61% $\pm$ 31.59% and 27.39% $\pm$ 5.00% respectively).

The relative abundance of Proteobacteria differed significantly among juvenile coral species (Kruskal–Wallis

test, $P < 0.001$), ranging from 66.32% ± 33.88% to 98.29% ± 1.01%. Additionally, the relative abundance of Deinococcus–Thermus in different coral species showed a significant difference between the ORS and lagoon. The relative abundance of Bacteroidetes in *F. palauensis* (6.93% ± 7.89%), *F. fungites* (8.90% ± 3.31%) and *F. abdita* (4.36% ± 7.89%) was relatively high in the lagoon, whereas in other coral species abundance was relatively low (< 5%). Additionally, *P. verrucosa* (5.15% ± 9.57%) and *P. rugosa* (3.11% ± 3.27%) in the ORS and *F. fungites* (4.90% ± 2.79%) in the lagoon were associated with a relatively high abundance of Cyanobacteria.

At the genus level, numerous coral-associated bacteria, such as *Endozoicomonas*, *Thermus*, *Pseudoalteromonas*, *Vibrio* and *Alteromonas*, showed significant differences (Wilcoxon rank sum test, $P = 0.003$, $P = 0.006$, $P < 0.001$, $P < 0.001$, $P < 0.001$ respectively; Fig. S2). *Pseudomonas* predominated in most juvenile coral species except for *F. palauensis* and *F. abdita* in the ORS and *F. fungites* in the lagoon (Table S7). There was a significant difference in the relative abundance of *Pseudomonas* among juvenile coral species (Kruskal–Wallis test, ORS $P < 0.0001$, lagoon $P = 0.0005$). In contrast, the relative abundance of *Pseudomonas* in seawater samples was relatively low in both locations (< 5%). The relative abundance of *Pseudomonas* in *A. formosa* in the ORS was significantly higher than that in the lagoon (95.19% ± 1.59% vs. 78.94% ± 11.85%, Wilcoxon rank sum test, $P = 0.025$), similar to what was observed for *M. ampliata* and *F. fungites* (Wilcoxon rank sum test, $P = 0.045$ and 0.006). In contrast, the relative abundance of *Pseudomonas* in *F. palauensis* and *F. abdita* in the lagoon was significantly higher than that in the ORS (Wilcoxon rank sum test, $P = 0.004$ and 0.004). Regardless of location, the relative abundance of *Endozoicomonas* was significantly different among coral species (Kruskal–Wallis test, $P < 0.05$). *Endozoicomonas* associated with *P. lutea*, *F. palauensis* and *F. abdita* in the ORS was significantly higher than that observed in the same juvenile corals in the lagoon (Wilcoxon rank sum test, $P = 0.049$, 0.004 and 0.004 respectively). Furthermore, the relative abundance of *Thermus* differed significantly among juvenile coral species (Wilcoxon rank sum test, $P < 0.05$) and between the lagoon and ORS in conspecific juvenile corals. For example, for *P. verrucosa* (30.82%), *P. rugosa* (29.34%), *P. lutea* (12.05%), *F. palauensis* (13.87%) and *F. abdita* (11.81%) in the lagoon, *Thermus* exhibited relatively high abundance, which was higher than that in the ORS (Fig. 5).

Analysis of similarity (ANOSIM) was used to assess bacterial community similarities between different colonies of the same juvenile coral species within an environment. ANOSIM showed that the coral-associated microbial community compositions differed significantly between the ORS and lagoon ($R = 0.1504$, $P = 0.001$). Specific to coral species, most of the microbial community compositions differed significantly between these two

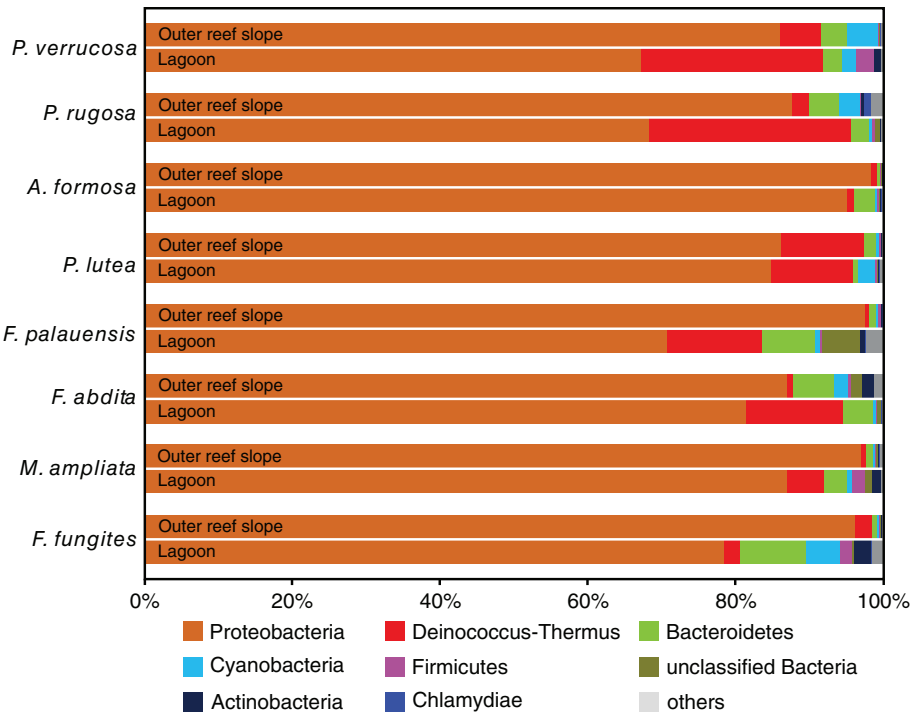

Fig. 4. Coral-associated community relative abundance at the phylum level in coral species and water samples in the outer reef slope and lagoon of the Passu Keah. [Color figure can be viewed at wileyonlinelibrary.com]

locations, i.e., *P. verrucosa* $R = 0.3214$, $P = 0.048$; *P. rugosa* $R = 0.138$, $P = 0.183$; *A. formosa* $R = 0.8462$, $P = 0.014$; *P. lutea* $R = 0.1852$, $P = 0.296$; *F. palauensis* $R = 1$, $P = 0.003$; *F. abdita* $R = 1$, $P = 0.003$; *M. ampliata* $R = 0.3413$, $P = 0.011$; and *F. fungites* $R = 1$, $P = 0.005$. Moreover, NMDS was also used to assess the differences in bacterial communities of the same coral species between the ORS and lagoon at the OTU level. The results showed that most of the coral-associated microbial community compositions differed between the samples collected in the ORS and lagoon (Fig. 3B).

PICRUSt was used to predict the metagenomic functional capacities of different juvenile corals based on coral-associated bacterial 16S rRNA sequencing data. Twenty-three metabolic predictive functional categories were analysed at the KEGG level 2 (Table S8). The average relative abundance of a bacterial metabolic category was closely related to the coral species in both the ORS and lagoon. Amino acid metabolism, biosynthesis of other secondary metabolites, glycan biosynthesis and metabolism, metabolism of terpenoids and polyketides, and nucleotide metabolism differed significantly in the associated bacteria of *P. rugosa*, *A. formosa*, *F. palauensis*, *F. abdita*, *M. ampliata* and *F. fungites* (Wilcoxon rank sum test, $P < 0.05$). In contrast, the metabolic properties of these associated bacteria in *P. verrucosa* and *P. lutea* showed no significant difference (Wilcoxon rank sum test, $P > 0.05$). Additionally, the metabolism of associated bacteria differed significantly in

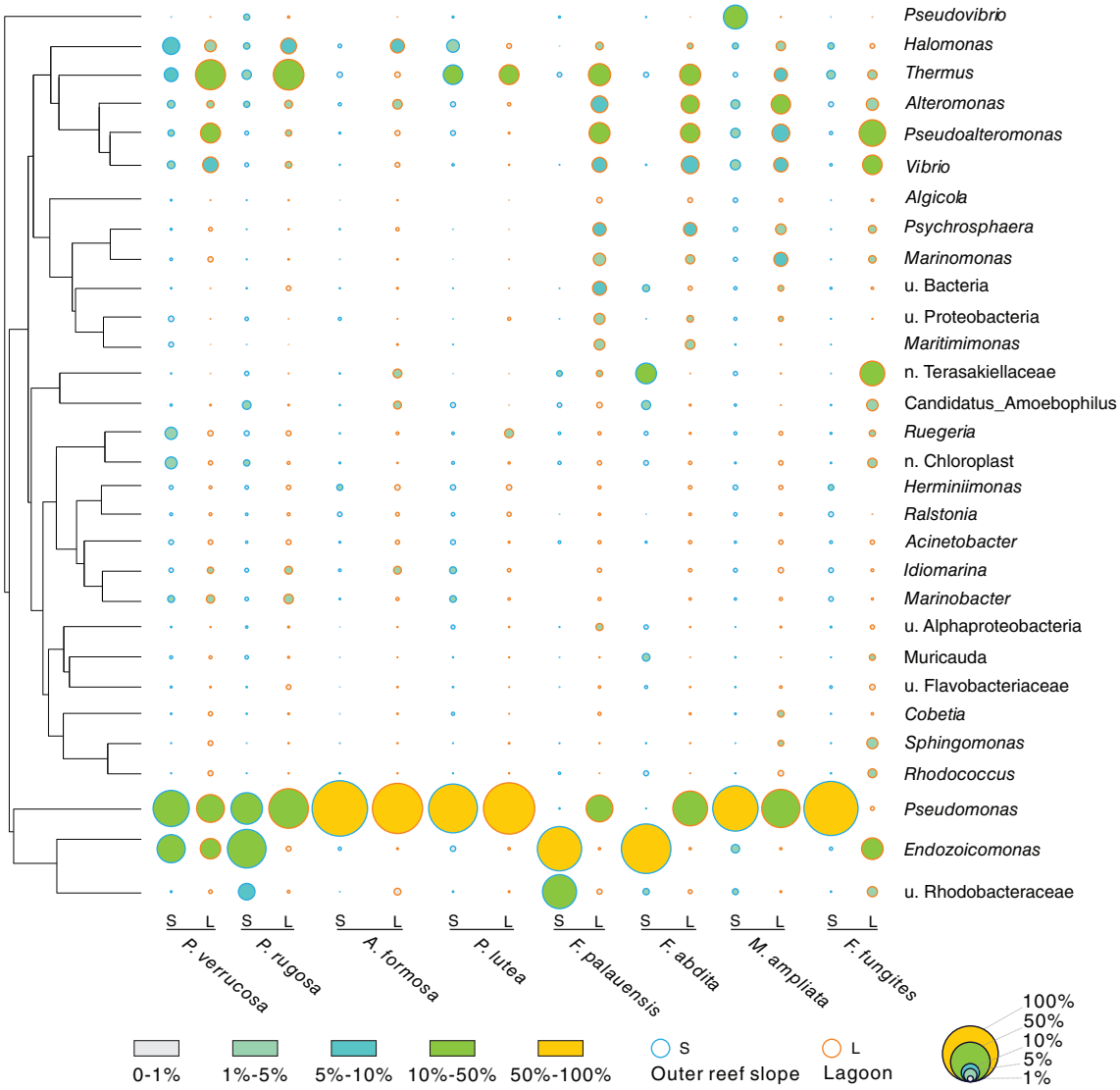

Fig. 5. Coral-associated community relative abundance at the genus level in coral species in the outer reef slope and lagoon of the Passu Keah. [Color figure can be viewed at wileyonlinelibrary.com]

different juvenile corals in the ORS (except for the synthesis of other secondary metabolites). Energy metabolism, enzyme families, lipid metabolism, the metabolism of cofactors and vitamins, metabolism of terpenoids and polyketides, nucleotide metabolism and xenobiotics biodegradation and metabolism differed significantly in the lagoon.

Discussion

In this study, water parameters between the lagoon and ORS were significantly different. SST fluctuations and the monthly summer-SSTs in the lagoon were significantly higher than those in the ORS. Salinity, nutrients and turbidity were also higher in the lagoon than in the ORS, but the transparency of the lagoon was significantly lower than that of the ORS. Significant differences in water environmental conditions between the ORS and lagoon could serve as key factors to shape the microbiome of juvenile corals in the Xisha Islands. Long-term chronic environmental stress will gradually screen out coral species that are more susceptible to disturbances, which will promote the recovery and recruitment of corals that associate with a microbiome with a higher environmental acclimatization potential (Chou *et al*., 2016).

High-abundance of heat-tolerant Symbiodiniaceae may increase acclimatization of juvenile corals to high-temperature environments

Significant differences in density and genera of Symbiodiniaceae among juvenile coral genera/species exist and these differences may be demonstrated by differences in acclimatization among coral species. In the Indo-Pacific, massive corals such as *Porites* and *Favites* are considered to have high thermal tolerance and are less threatened by coral bleaching events due to their relatively high SD (Stimson *et al*., 2002; Harithsa *et al*., 2005; Ulstrup *et al*., 2006; Xu *et al*., 2017). In contrast, branching corals such as *Pocillopora* and *Acropora* usually have very low SD and exhibit sensitivity to thermal stress (Loya *et al*., 2001; Li *et al*., 2008; Wooldridge, 2014). In our study, the SDs of these branching corals ($\sim$1.09–1.34 $\times$ 10^6 cells cm^{-2}) were the lowest among the eight coral species studied. However, during *in situ* investigation, we observed that *Pocillopora* corals in the ORS and *Acropora* corals in the lagoon patch reefs remained the most abundant corals (61.90% and 91.20% respectively). Thus, this ecological phenomenon could not be explained based on SD data alone; the coral-symbiotic Symbiodiniaceae genus/subclade data needed to be considered. Our results showed that *P. verrucosa* in the ORS was associated with heat-tolerant *Durusdinium*. Although *P. verrucosa* exhibits a low SD ($\sim$1.34 $\times$ 10^6 cells cm^{-2}), it may effectively enhance its thermal stress tolerance by associating with heat-tolerant Symbiodiniaceae. In addition, *Pocillopora* corals are fast-growing coral taxa with morphological plasticity and highly flexible symbiotic associations (Veron, 2000; Adjeroud *et al*., 2018; Holbrook *et al*., 2018). The variations in the dominant Symbiodiniaceae showed that *Pocillopora* corals could accommodate their symbiotic algae based on symbiosis 'reorganization' and/or 'transformation' during long-term thermal acclimatization (Hume *et al*., 2015; Silverstein *et al*., 2015). For example, Tkachenko and Soong (2017) found that *Pocillopora* in lagoons of Dongsha atoll had higher heat-tolerance than those found in the ORS. Here, because colony branches of *P. verrucosa* are thick and compact in habitats exposed to strong waves and preferred living in mostly shallow water environments with high transparency and seawater exchange (Veron, 2000), *P. verrucosa* were dominant in the ORS but not in the lagoon, despite both containing a high-abundance of *Durusdinium* in these two locations.

Moreover, *A. formosa* found in the lagoon patch reefs with relatively high SST, salinity and nutrients associated with highly photosynthetically efficient *Cladocopium* C50/Cspc and heat-tolerant *Durusdinium* D1/D1a. In addition to enhancing the heat stress tolerance of *A. formosa*, these symbionts may facilitate rapid growth. *Acropora* is a representative fast-growing genus with high symbiotic flexibility; the fast-growing attribute allows for rapid colonization of specific niches (Darling and Côté, 2018; Hughes *et al*., 2018b). During long-term thermal acclimatization, the offspring of *A. formosa* in the lagoon may exhibit improved thermal tolerance, similar to that of corals effectively harbouring a highly variable microbiome that exhibit lower susceptibility to bleaching than those harbouring a moderately variable microbiome (Ziegler *et al*., 2017b). By contrast, *A. formosa* in the ORS associates with *Cladocopium* (Cspc/C50/C40), similar to that observed in other coral reefs in the Xisha and Nansha Islands (e.g., Chen *et al*., 2019; Qin *et al*., 2019). The low SD and association with heat-sensitive Symbiodiniaceae mostly explain why *A. formosa* corals are rare in the ORS under repeated high thermal stress. Fast-growing coral taxa will occupy the coral community using a fast-growing strategy. Moreover, after repeated coral bleaching events or high thermal acclimatization, those coral species symbiotic with heat-tolerant Symbiodiniaceae can survive and become the dominant corals.

Transmission strategies and flexibility of symbiotic Symbiodiniaceae affect the homeostasis of the coral holobiont, which directly influences coral thermal environment acclimatization (Boulotte *et al*., 2016; Quigley *et al*., 2017). Analysis of sexually reproduced coral larvae

(broadcast spawning and brooding) has suggested that heat-tolerant Symbiodiniaceae can be effectively obtained from the parent colony based on vertical transmission (Boulotte *et al*., 2016; Quigley *et al*., 2017). More recently, corals such as *Montastraea* have been shown to acquire heat-tolerant Symbiodiniaceae after repeated thermal bleaching stress (Pratchett *et al*., 2013; Silverstein *et al*., 2015; Boulotte *et al*., 2016). Hermaphrodites, such as *Pocillopora* corals, may vertically transmit symbiotic Symbiodiniaceae to their gametes; however, they are also highly flexible and can acquire Symbiodiniaceae from the parent colony and/or surrounding water (van Oppen and Blackall, 2019). In the Indo-Pacific, including the SCS, Indonesia and the GBR, but excluding the Red Sea with extremely high SST, *Porites* corals mainly associate with *Cladocopium* C15/C15x (e.g., Gong *et al*., 2018; Chen *et al*., 2019; Robbins *et al*., 2019), showing stability in different coral reefs. This also means that compared with other general corals, *Porites* coral lack flexibility (Putnam *et al*., 2012) and may have suffered from thermal bleaching in the 2015–2017 GCBE. For example, Gust and colleagues (2016) found that 43%–53% of *Porites* corals were bleached after experiencing a high thermal stress in Pulau Satumu, Singapore. Besides, *Porites* are part of slow-growing coral taxa, which may not favour rapid recovery and becoming the dominant coral in the CRR.

High-abundance of heat-tolerant bacteria may also increase acclimatization of juvenile corals to high-temperature environments

Differences among bacteria associated with juvenile corals provide a basis for understanding coral high thermal acclimatization strategies between the ORS and lagoon. In changing environments, some coral species can improve their thermal environmental acclimatization by maintaining a stable core of bacteria (ranging from 30% to 100% presence in all individuals of a coral species), especially by forming associations with heat-tolerant bacteria (Peixoto *et al*., 2017; Ziegler *et al*., 2017b; van Oppen and Blackall, 2019). For instance, Ziegler and colleagues (2017b) found that ~2/3 of the indicator bacteria in thermally highly variable area belonged to the class Alphaproteobacteria; the remaining bacteria belonged to the classes Cytophagia, Deltaproteobacteria, Deinococcus–Thermus, Phycisphaerae and Spirochaetes, which were not (or only rarely) present in corals from thermally moderately variable area that displayed a response to heat stress. Therefore, these indicators of coral-associated bacteria are closely related to the ability of coral symbiosis to acclimatize to different thermal habitats (Ainsworth and Gates, 2016; van Oppen and Blackall, 2019). Heat-tolerant bacteria showed that there were significant differences among coral species. *P. verrucosa*, *P. rugosa*, *P. lutea*, *F. palauensis* and *F. abdita* in the lagoon contained a high-abundance of heat-tolerant bacteria (e.g., *Thermus scotoductus*). These juvenile corals survive in the lagoon with high temperature fluctuations and high salt based on their association with heat-tolerant bacteria.

The level of abundance of symbiotic *T. scotoductus* with *A. formosa* in lagoon patch reefs and the ORS was extremely low, indicating that the heat-tolerance mechanism may differ completely in *A. formosa* when suffering from thermal threats between lagoon patch reefs and ORS. *A. formosa* in lagoon patch reefs is associated with more than 40% heat-tolerant *Durusdinium*, which may effectively enhance thermal stress tolerance (Kennedy *et al*., 2015; Swain *et al*., 2017). In contrast, *A. formosa* of the ORS, with almost no thermotolerant bacteria, is dominantly associated with a heat-sensitive *Cladocopium*. Consequently, these corals are considered highly vulnerable to thermal stress. These variations could well explain the fact that *Acropora* corals are rare in the ORS but are the dominant corals in the lagoon patch reefs. Additionally, the relative abundance of the potential pathogenic bacteria *Vibrio* (e.g., *V. harveyi*, *V. fortis*) and *Ruegeria* (e.g., *R. mobilis*) in *A. formosa* in lagoon patch reefs was low; thus, this coral may not have been threatened by coral diseases. Coral-associated beneficial bacterial groups, including members of the Flavobacteriaceae (Howard *et al*., 2011), *Halomonas* (Todd *et al*., 2010), *Roseobacter*, *Pseudomonas* and Oceanospirillales (Raina *et al*., 2010, 2013), are capable of metabolizing dimethylsulfoniopropionate and consuming its products for their own metabolic processes (Peixoto *et al*., 2017). These findings suggest that *Acropora* juvenile corals survive in lagoon patch reefs by maintaining high heat-tolerant *Durusdinium* or establishing healthy and beneficial bacterial communities after long-term high temperature environmental acclimatization (Peixoto *et al*., 2017; van Oppen and Blackall, 2019).

Functional predictions of the coral-associated microbial community indicated significant differences in juvenile coral species between the ORS and lagoon, which in turn may affect metabolism-related functions (Langille *et al*., 2013; Ziegler *et al*., 2017a). These differences may imply that some juvenile coral species acclimatized in the ORS and lagoon by regulating the bacterial community composition through mucus regulation, resulting in various metabolism-related functions. Likewise, previous studies found that functional predictions were different between corals in thermally highly variable areas and thermal moderately variable areas, following the differences in microbial community composition. This may reflect signatures of bacterial heat tolerance, as implied by the role of altered carbohydrate composition in the

mucus of heat-stressed corals (Lee *et al*., 2016; Ziegler *et al*., 2017a).

Overall, the diversity and flexibility of juvenile coral symbiotic microbial communities are closely related to thermal stress tolerance and environmental adaptability of juvenile corals. A large temperature fluctuation range characterizes the lagoon, and it has suffered from extremely high temperatures. Our data provide new insights into the survival strategy, tolerance and acclimatization of juvenile coral holobiont microorganism in extreme environments. These results could provide important evidence for coral acclimatization and resilience to extreme climatic environments in the SCS.

Experimental procedures

Study site, water parameter measurements and juvenile coral sample collection

Research sites in this study were located in Passu Keah, Xisha Islands (16°01′19″N–16°04′25″N, 111°44′30″E–111°49′47″E, Fig. 6A and B). Passu Keah is ~330 km from Hainan Island and belongs to a tropical atoll with ~26 km^2 reef region. Corals are mainly distributed in the outer reef flats/slopes and lagoon patch reefs. *In situ* surveys of the coral assemblages were conducted at 2–6 m depths in the ORS and lagoon patch reefs in 2019. As shown in Table S1, the absolute dominant coral genus in the ORS was *Pocillopora* (61.90%), followed by *Porites*, *Montipora*, *Favia* and *Favites*. In contrast, in lagoon patch reefs, *Acropora* was the dominant coral genus (91.20%; Table S1).

Seawater temperature and salinity were measured using the SBE 52-MP conductivity, temperature, depth/pressure sensor manufactured by Sea-Bird Scientific. Transparency was measured using a Secchi disc (SD 30). DO was assessed using a portable DO200A meter. Seawater samples were collected, filtered immediately (0.22 μm Whatman GF/F), and DIN and soluble reactive phosphorus were measured using a continuous flow analyser (SEAL QuAAtro). After filtering 2-L seawater through a 0.22 μm membrane, the membrane was stored in liquid nitrogen for total DNA extraction. Coral specimens ($n = 96$) from eight species, including *P. verrucosa*, *P. rugosa*, *A. formosa*, *P. lutea*, *F. palauensis*, *F. abdita*, *M. ampliata* and *F. fungites*, were randomly collected in 3–8 replicates from different colonies (~30 cm^2 each sample) at ~6 m water depth (Table S1). To avoid contamination during sampling, juvenile coral samples were collected using a hammer and chisel from a depth range of ~6 m via scuba diving and immediately placed in sample bags. Each coral sample was divided into two small nubbins, one nubbin (~10 cm^2) was used for SD determination, and the other (~5 cm^2) was used for Symbiodiniaceae and bacterial DNA extraction. All seawater and coral samples collected were preserved in liquid nitrogen and transported to the laboratory immediately.

Symbiodiniaceae density determination

Coral tissue was removed using Waterpik™ (3–5 kgf cm^{-2}) containing seawater (passed through a 0.45 μm filter) until only white coral skeleton remained (1–3 min). The initial coral tissue and Symbiodiniaceae slurry volume was measured in a graduated cylinder and then homogenized and subsampled into four 3-ml aliquots. The aliquots were then centrifuged at 5000 rpm for 5 min. SDs were calculated using replicate haemocytometer counts ($n = 8$) under a light microscope. Coral sample surface area was determined based on the correlation between aluminium foil weight and surface area (Marsh, 1970; Fitt *et al*., 2000; Li *et al*., 2008).

DNA extraction, PCR amplification and Illumina MiSeq sequencing

Genomic DNA was extracted from ~100 mg of coral (including tissue, mucus and skeleton) and seawater samples using a DNeasy® Plant Mini Kit (Qiagen, Hilden, Germany) for Symbiodiniaceae DNA extraction and a FastDNA® SPIN Kit for Soil (MP Biomedicals, Irvine, CA, USA) for bacterial DNA extraction according to the manufacturers' protocol. After the quality and purity examination, the extracted DNA samples were used as PCR templates. The Symbiodiniaceae rDNA ITS2 region was amplified using primers F: 5′-GAATTGCAGAACTCCGTG-3′ and R: 5′-GGGATCCATATGCTTAAGTTCAGCGGGT-3′, with a six-nucleotide barcode unique to each sample (Lajeunesse *et al*., 2003). The V3–V4 region of the 16S rRNA bacterial gene was amplified using the barcoded forward primer 338F: 5′-ACTCCTACGGGAGGCAGCAG-3′ and reverse primer 806R: 5′-GGACTACHVG GGTWTCTAAT-3′ (Mori *et al*., 2013; Xu *et al*., 2016). Reactions were prepared using a TransGen AP221-02 PCR Kit (which contains TransStart FastPfu DNA Polymerase) and run on an ABI GeneAmp® 9700 thermal cycler, as described by Sun and colleagues (2014). PCR was performed with ~10 ng of DNA, 1.6 μl (5 μm) primer, 0.4 μl TransStart Fastplu DNA Polymerase, 0.2 μl BSA, 4 μl 5 × FastPfu Buffer, 2 μl of 2.5 mM dNTPs, and ddH_2O to a total volume of 20 μl. PCR amplification conditions were as follows: 3 min at 95°C; followed by 29 cycles of 95°C for 30 s, 53°C for 30 s and 72°C for 45 s; and a final extension at 72°C for 10 min. Each product from triplicate PCR reactions was pooled, and fragment sizes in the range of 280–300 bp (for Symbiodiniaceae) and 420–460 bp (for bacteria) were purified and quantified using the

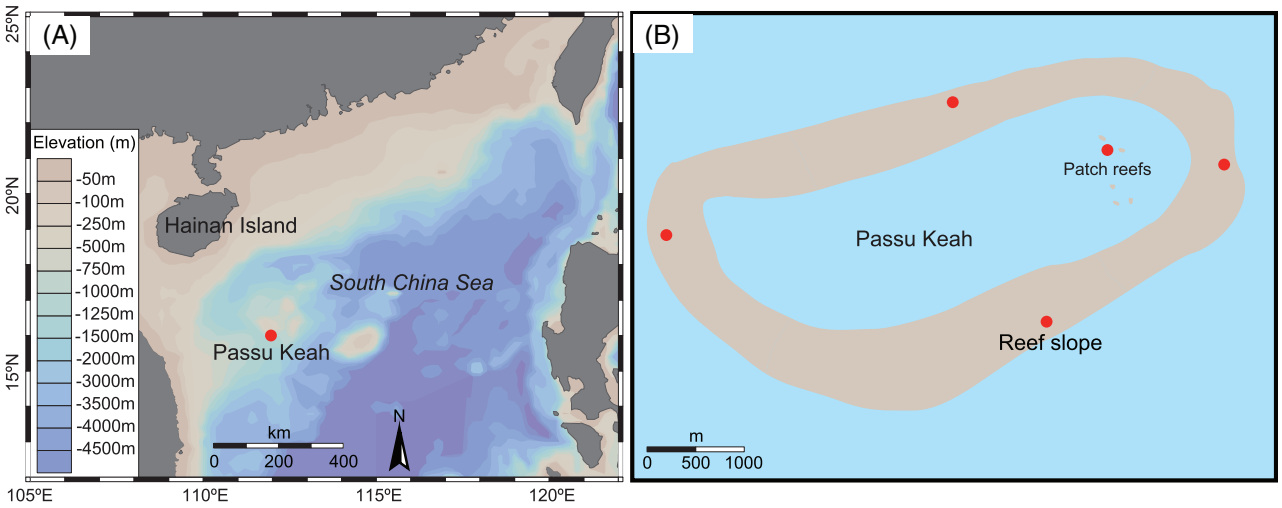

Fig. 6. Location map of coral reef sampling sites in the Passu Keah of Xisha Islands, central South China Sea. [Color figure can be viewed at wileyonlinelibrary.com]

AxyPrep DNA gel extraction kit and QuantiFluor™-ST fluorescence quantitative system. Purified amplicons were pooled in equimolar amounts and pair-end (PE) sequenced (2 × 300) on an Illumina MiSeq platform according to standard protocols (Majorbio Bio-Pharm Technology, Shanghai, China). Raw reads were deposited into the NCBI Sequence Read Archive (SRA) database (Accession Number: PRJNA650279 and PRJNA650300).

Next-generation sequencing data processing and data analysis

In this study, strict quality control and sequence filtration were used to ensure analytical accuracy. Majorbio Bio-Pharm Technology (Shanghai, China) removed adaptors, short reads and low-quality reads. To generate ITS2 sequences, full-length ITS2 rDNA fragments with merging overlapping PE reads were obtained using a paired-end read merger (PEAR) tool (Zhang *et al*., 2014). ITS2 tags were de-multiplexed into all seawater- and coral-symbiotic Symbiodiniaceae samples for identifying unique barcodes in the QIIME platform (Caporaso *et al*., 2010). To cope with the challenge of using the ITS2 gene as a multicopy marker, sequence-based ITS2 analysis and OTU analysis were used to evaluate Symbiodiniaceae diversity and community composition. This methodology provides a comprehensive description of the molecular diversity of Symbiodiniaceae. Furthermore, sequence-based ITS2 analysis can directly assess the associations between corals and Symbiodiniaceae, and OTU-based analysis can be used to estimate Symbiodiniaceae diversity while requiring no formal description of ITS2 Symbiodiniaceae types (Ziegler *et al*., 2017b; Chen *et al*., 2019). After downloading Symbiodiniaceae ITS2 types from a BLAST Symbiodiniaceae-specific database (Supporting Information ITS2 Database.FASTA; Franklin *et al*., 2012; Arif *et al*., 2014; Chen *et al*., 2019), all coral-symbiotic Symbiodiniaceae ITS2 sequences were assigned to the ITS2 types (Altschul *et al*., 1990). Analysis of seawater- and coral-symbiotic Symbiodiniaceae ITS2 sequence data alignment and OTU was according to the method described by Qin and colleagues (2019).

Moreover, dominant/sub-dominant Symbiodiniaceae genera/subclades assemblages (≥ 5%) were analysed after ITS2 sequence data alignment. Alpha- and beta-diversity of coral-symbiotic Symbiodiniaceae assemblages, including OTUs, H′, ACE, Chao 1, Simpson and NMDS were analysed among coral species studied in the ORS and lagoon in the R software environment (R 3.1.2) by Bray-Curtis. A phylogenetic tree was constructed for dominant/sub-dominant Symbiodiniaceae subclades (≥5%), based on the Kimura 2-parameter model with uniform ratios among sites using maximum likelihood in MEGA 6 (Ronquist *et al*., 2012). Raw sequences of coral-associated bacteria obtained from Illumina MiSeq sequencing were optimized using the software platform Trimmomatic (v0.33) to exclude reads with homopolymer inserts > 6 bp and low-quality tail scores (< 20) setting a quality window of 50 bp (Bolger *et al*., 2014). Similarity percentage analysis was performed to examine which OTU contributed most to the dissimilarity among coral samples of the ORS and lagoon. Alpha- and beta- diversities of coral-associated bacterial communities (including OTUs, H′, ACE, Chao 1, Simpson and NMDS). ANOSIM was based on unweighted UniFrac distances, and bacteria predicted gene functions were analysed based on PICRUSt among coral species studied in the ORS and

lagoon. Detailed descriptions of the analytical methods are reported by Qin and colleagues (2020). Significant differences in coral-associated bacterial communities were tested by ANOSIM with 9999 permutation-based Bray–Curtis dissimilarity matrix in R (vegan package; Oksanen *et al*., 2015).

A two-way factorial ANOVA was used to compare coral-symbiotic SDs in geomorphological variations and coral species based on SPSS Statistics 19 (IBM). Levene, Durbin–Watson and Shapiro–Wilk testes were used to assess whether the data met the assumptions of homogeneity, normality and independence respectively. The Student–Newman–Keuls test was used for post hoc multiple comparisons of significant ANOVA results. All data are presented as mean ± standard deviation. The statistical significance level was set at $P < 0.05$ for all analyses. The local water parameters, alpha diversity and microbial genera of coral specimens between the ORS and lagoon were compared using the Wilcoxon rank-sum test. The Kruskal–Wallis test was used to compare specimens among these coral species between the ORS and lagoon. All multidimensional statistical analyses were performed in the R software environment (R 3.1.2) using the vegan package (Oksanen *et al*., 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Fig. S1. Coral-associated community relative abundance at the phylum level of corals between the outer reef slope and lagoon of the Passu Keah.

Fig. S2. Coral-associated community relative abundance at the genus level of corals between the outer reef slope and lagoon of the Passu Keah.

Table S1. The sampling time, sampling depth and coral genera/species identification in the Passu Keah of the Xisha Islands.

Table S2. Coral-symbiotic Symbiodiniaceae densities among corals studied in the Passu Keah.

Table S3. Sample information including number of sequences, number of coral-symbiotic Symbiodiniaceae in different taxonomic levels, number of OTUs and diversity indicated by the Shannon, Simpson, Ace and Chao 1 index.

Table S4. The relative abundance of coral-symbiotic Symbiodiniaceae subclades in coral samples.

Table S5. Sample information including number of sequences, number of coral-associated bacterial community in different taxonomic levels, number of OTUs and diversity indicated by the Shannon, Simpson, Ace and Chao 1 index.

Table S6. The relative abundance of coral-associated bacterial community of coral samples on phylum level.

Table S7. The relative abundance of coral-associated bacterial community of coral samples on genus level.

Table S8. Relative abundance of each predicted functional trait given in KEGG pathways (level 2).