



# Locality Effect of Coral-Associated Bacterial Community in the Kuroshio Current From Taiwan to Japan

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The Kuroshio Current (KC) is one of the fastest water currents in the world, running through the western boundary of the North Pacific Ocean. The KC strongly influences the regional hydroclimate by creating temperature, salinity, and pH gradients from tropical to subtropical and temperate zones, including regions with rich coral reef habitats. Microbial community composition of corals is influenced by various environmental factors, including salinity, pH, and geographical location. However, to date, it is unclear how coral-associated microbial communities would respond to the same water current running through different locations with a time lag. Therefore, we hypothesized that the locations subjected to the KC at higher latitudes experience similar but sequential lag in environmental variability compared to those at lower latitudes, and thus the coral communities of both will respond similarly, but at different times. In this year-long study, we compared the bacterial communities of *Acropora muricata* at Taiwan, Okinawa, and Kochi subjected to the KC. We found that site-specific conditions and site latitude may have stronger effects on bacterial composition and dynamics than a water current. Consequently, we suggest that latitude largely determines the temperature tolerance range of coral microbiota. Additionally, among the dominant coral associated bacteria, *Endozoicomonas* from *A. muricata* and *Stylophora pistillata* forms distinct phylogroups, while *Acinetobacter* is more likely a host generalist.

**Keywords:** Kuroshio Current, coral-associated bacteria, *Endozoicomonas*, *Acinetobacter*, generalist and specialist, *Acropora muricata*

## INTRODUCTION

Coral associated microbes, together with their coral host, form an integrated holobiont, and have diverse interactions with their host and maintain coral holobiont function, such as nutrient acquisition and coral's health (Rosenberg et al., 2007). With respect to the coral-associated microbial community, *Gammaproteobacteria* is dominant (Bourne et al., 2013), and the putative symbiont

*Endozoicomonas*-like group in particular has received notable attention for its potential role in coral fitness (Meyer et al., 2014; Morrow et al., 2015). Based on genomics evidence, *Endozoicomonas* is proposed being beneficial to coral host by modulating coral metabolisms to prevent mitochondrial dysfunction (Ding et al., 2016), and furthermore by participating in coral-associated carbohydrate cycling and protein provision (Neave et al., 2017). The relative abundance of coral microbiome varies depending on different factors, such as temperature (Shiu et al., 2017) and coral species (Neave et al., 2016). Our recent report investigating the same coral species from different locations around Taiwan further demonstrated that the coral-associated microbiome was dominated by different bacterial taxa (Yang et al., 2017), indicating local environmental factors playing an important role affecting microbial composition in corals.

Coral-associated microbial communities were reportedly influenced by environmental factors such as seawater temperature, pH, salinity, and nutrients (Guppy and Bythell, 2006; Klaus et al., 2007; Hong et al., 2009; Littman et al., 2009), all of which are largely affected by ocean currents. In fact, ocean currents transport a massive amount of waters (of distinct properties) and nutrients across a long distance and even different climate zones, resulting in latitudinal gradients of water parameters (Qu et al., 2018). Furthermore, the change in current speed and current structure also contributed to the variation of oceanic nutrient flux (Guo et al., 2012). Along the Western Australian coast, the Leeuwin Current has been proposed to explain the conserved microbial community in corals at geographically distant locations (Ceh et al., 2011). This report thus aroused the curiosity about to what extent the coral microbial communities in different climate zones are affected by the same ocean current that results in differential temperature, pH, and salinity gradients.

The Kuroshio Current (KC) is a strong northward current that runs through the western boundary of the North Pacific Ocean, transporting heat, salt, and water from low to high latitude regions. The KC is warm, low in nutrients, has a small plankton population and a high flow speed (roughly two to four knots). It passes through three climate zones, from tropical (the Philippines and southern Taiwan) to subtropical (northern Taiwan and Okinawa, Japan), and finally to the temperate zone (mainland Japan), resulting in temperatures of 15–29°C (Abbot et al., 2003) and a pH of 7.8–8.5 (Dai, 1991; Chen et al., 1995) at shallow depth above 300 m. The KC is analogous to a high-speed “freeway” that moves marine organisms from low to high latitudes in the western Pacific Ocean. Warming temperatures are associated with a poleward coral expansion (Yamano et al., 2011), and the coral reefs around Taiwan and Japan are therefore implicitly linked by the warm KC water (Fujiwara et al., 2000; Chen and Shashank, 2009).

Given its large latitudinal distance and wide temperature and pH gradients, the KC provides a unique opportunity to investigate the relationship between environmental factors driven by the current and their impacts on coral-associated microbial communities. We hypothesized that the locations subjected to the KC at higher latitudes experience similar but delayed

environmental conditions compared to those at lower latitudes, and thus the coral communities of both respond similarly, but at different times.

To test this hypothesis, simultaneous observation and sampling (of the same coral species) were performed at different locations. Although the locational variations in soft coral-associated microbial composition among six sites subjected to the KC (Woo et al., 2017) were reported, there is still a knowledge gap that can be fulfilled by repetitive sampling for investigating microbial dynamics in corals under the same seasonal conditions. In addition, coral-associated bacteria can be coral species- or colony-specific (Hernandez-Agreda et al., 2018), making it difficult to compare observations obtained from different coral species. Therefore, in this study, we chose *Acropora muricata* (Linné, 1789) as our monitoring coral species to investigate the impacts of KC temperature and pH on coral-associated microbial communities across different climate zones. The sampling was performed bimonthly throughout 1 year in coastal areas of southern Taiwan and Okinawa and Kochi, Japan, which are all subjected to the KC, and their reefs are all dominated by *A. muricata*. *A. muricata*-associated microbiota is reportedly influenced by the environment (Casey et al., 2015). Therefore, we further explored the abundance variation and dynamics of *Endozoicomonas* and other genera in *A. muricata* in different climate zones but subjected to the same water current.

## MATERIALS AND METHODS

### Sample Collection and Measurement of Environmental Parameters

A total of 189 *A. muricata* coral and 21 seawater samples were collected in Kochi (32°46′42.95″N, 132°43′56.06″E), Okinawa (26°41′39.1″N, 127°52′31.8″E), and Taiwan (21°56′58.3″N, 120°45′11.9″E) from August 2011 to September 2012 (Table 1). During the sampling period, a typhoon occurred 1 month earlier than sampling O6, and shortly before O7, T1, and T7. At each site, three branches from three distinct colonies were randomly selected to represent biological replicates ( $n = 9$ ) for the local ecology of *A. muricata*. The coral branches were fixed with 95% ethanol after sampling. Seawater (1 L) was collected and its parameters (including pH, salinity, and temperature) were measured at the time of sampling. Seawater was filtered with a 0.2  $\mu\text{m}$  membrane (0.2  $\mu\text{m}$  pore size; Adventec, Japan) to collect microbial particulate and stored at 4°C until DNA extraction.

### DNA Extraction, Sequencing, and Processing

Coral and seawater samples were sent to the laboratory at Academia Sinica, Taiwan, for DNA extraction within 1 week of collection. Microbial DNA of samples was extracted via the cetyltrimethylammonium bromide (CTAB) method (Wilson, 2001). The hypervariable V1–V2 regions of bacterial 16S rRNA genes were amplified by polymerase chain reaction (PCR) using universal primers 27F (F: forward) and 341R (R: reverse), both

**TABLE 1** | Sampling information and sample identifier of *Acropora muricata* and seawater.

Sampling location	Sample name	Sampling time	Date	Coral sample	Seawater sample
Kochi	K1	1	2011 Aug. 30	K1C1, K1C2, K1C3 ( <i>n</i> = 3)	K1SW <sup>a</sup>
	K2	2	2011 Oct. 30	K2C1, K2C2, K2C3 ( <i>n</i> = 3)	K2SW <sup>a</sup>
	K3	3	2011 Dec. 20	K3C1, K3C2, K3C3 ( <i>n</i> = 3)	K3SW
	K4	4	2012 Feb. 23	K4C1, K4C2, K4C3 ( <i>n</i> = 3)	K4SW
	K5	5	2012 April 27	K5C1, K5C2, K5C3 ( <i>n</i> = 3)	K5SW
	K6	6	2012 July 10	K6C1, K6C2, K6C3 ( <i>n</i> = 3)	K6SW
	K7	7	2012 Sep. 6	K7C1 <sup>a</sup> , K7C2, K7C3 ( <i>n</i> = 2)	K7SW
Okinawa	O1	1	2011 Aug. 28	O1C1, O1C2, O1C3 ( <i>n</i> = 3)	O1SW
	O2	2	2011 Oct. 30	O2C1, O2C2, O2C3 ( <i>n</i> = 3)	O2SW
	O3	3	2011 Dec. 21	O3C1, O3C2, O3C3 ( <i>n</i> = 3)	O3SW
	O4	4	2012 Feb. 24	O4C1, O4C2, O4C3 ( <i>n</i> = 3)	O4SW
	O5	5	2012 April 25	O5C1, O5C2, O5C3 ( <i>n</i> = 3)	O5SW <sup>a</sup>
	O6	6	2012 July 26	O6C1, O6C2, O6C3 ( <i>n</i> = 3)	O6SW
	O7	7	2012 Aug. 30	O7C1, O7C2, O7C3 ( <i>n</i> = 3)	O7SW
Taiwan	T1	1	2011 Sep. 9	T1C1, T1C2, T1C3 ( <i>n</i> = 3)	T1SW
	T2	2	2011 Oct. 21	T2C1, T2C2, T2C3 ( <i>n</i> = 3)	T2SW
	T3	3	2011 Dec. 29	T3C1, T3C2, T3C3 ( <i>n</i> = 3)	T3SW
	T4	4	2012 Feb. 23	T4C1, T4C2, T4C3 ( <i>n</i> = 3)	T4SW
	T5	5	2012 April 24	T5C1, T5C2, T5C3 ( <i>n</i> = 3)	T5SW
	T6	6	2012 July 17	T6C1, T6C2, T6C3 ( <i>n</i> = 3)	T6SW
	T7	7	2012 Sep. 4	T7C1 <sup>a</sup> , T7C2, T7C3 ( <i>n</i> = 2)	T7SW

<sup>a</sup>Not available because of less than 200 reads available for analysis.

of which were tagged with 4-base barcodes at their 5'-end as described previously (Chen et al., 2011). Amplified DNA was quantified by Qubit Fluorometer (Thermo Fisher Scientific, United States) and pooled in equal amounts. Multiplexed sequencing was performed using the Genome Sequencer FLX Titanium System (Roche 454 Life Sciences, Branford, CT, United States) at Mission Biotech (Taipei, Taiwan).

The raw sequencing reads were sorted into different samples according to the barcodes using an in-house script, which also removed the barcode and primer sequences. Reads (1) of lengths shorter than 280 bp or longer than 350 bp, (2) with an average quality score less than 20, (3) with a homopolymer longer than 8 bp, or (4) containing ambiguous bases were quality-filtered using Mothur (Schloss et al., 2009). Chimeric reads predicted by UCHIME (Edgar et al., 2011) implemented in USEARCH (v8.0.1623; reference mode, rdp\_gold database, mindiv of 3) (Edgar, 2010) were also eliminated. Non-chimeric reads (including borderline cases by UCHIME) were retained for further analysis. Reads of coral branches from the same colony were pooled as one sample, resulting in a total of 84 samples. The read processing code is available in **Supplementary Data**.

For operational taxonomic unit (OTU) analysis, quality-filtered and non-chimeric reads were analyzed on a per-sample basis with UPARSE (Edgar, 2013); the chimera removal step was excluded, as it had been performed in previous quality filtering steps. The OTU approach has been shown to have comparable validity of results to the more stringent amplicon sequence variants (i.e., ASV) methods (Glassman and Martiny, 2018). OTUs were generated at a 97% identity threshold. Each OTU

was searched (with global alignment) using USEARCH against the Ribosomal Database Project's database (training set 16 and release 11.5) to find the corresponding taxonomy of the best hit. OTUs with no hit or weak hits (i.e., the average of % identity and % query coverage <93) were excluded. After filtering OTUs of the chloroplast, which occupied a mean ( $\pm$  SD) of 1.35% ( $\pm$  1.65%) in coral and 27.67% ( $\pm$  25.41%) in seawater samples, samples containing  $\geq$  200 reads were used for downstream analysis.

## Statistical Analysis

All the statistical analyses were performed in R software<sup>1</sup> unless stated otherwise. Community data were handled with the R package phyloseq (McMurdie and Holmes, 2013), by which alpha diversity indices were estimated. Non-parametric tests were performed to compare alpha diversities between groups; Kruskal-Wallis test was used for three-group and Wilcoxon test for two-group comparison. Hierarchical clustering with average linkage was performed and visualized using the R package pheatmap (Kolde, 2012). At the genus level, samples were clustered based on the Euclidean distance of a base-10 logarithmic transformation of percent relative abundance, while taxa were based on the Bray-Curtis distance of non-transformed percent relative abundance. During the distance calculation, a pseudo-count of  $1 \times 10^{-8}$  was added to each taxon (Costea et al., 2014), and taxa with unknown taxonomy or <0.1% average relative abundance were classified as "Others." The distance matrix was calculated using the R package vegan (Dixon, 2003). The analysis of similarities

<sup>1</sup><https://www.r-project.org/>

(ANOSIM) was performed to statistically test whether there is a significant difference in community composition between two or more groups.

## OTU Analysis of *Acinetobacter* and *Endozoicomonas*

*Endozoicomonas* and *Acinetobacter* OTUs were originally defined on a per-sample basis and were difficult to pool directly by taxonomy because most species of these two genera are unclassified. Therefore, the cross-sample OTUs were analyzed. After extracting amplicon reads of *Endozoicomonas* and *Acinetobacter* OTUs, reads of each genus were clustered at 97% identity by USEARCH (with `-cluster_smallmem`), and the abundance profiles were constructed according to the sampling source information retained on each read.

Correlation (Pearson) heatmaps were generated in R with the `corrplot` package (Wei and Simko, 2017) using the relative abundance and presence-absence profiles of *Endozoicomonas* and *Acinetobacter* OTUs across all samples. Correlation significance was tested at 95% confidence intervals.

Beta diversity was assessed and visualized using non-metric multidimensional scaling (nMDS) on Primer 6 (PRIMER-E, Lutton, Lvybridge, United Kingdom) and fitted with environmental factors through constrained correspondence analysis (CCA) on the R package `vegan`. The top-20 *Endozoicomonas* and *Acinetobacter* OTUs (in abundance) were used for phylogenetic analysis, using the maximum likelihood method based on the Jukes-Cantor model (Jukes and Cantor, 1969) to obtain the tree. Phylogenetic analyses were conducted in MEGA7 (Kumar et al., 2016).

## Data Availability

All sequence data generated in this study have been deposited in NCBI under the Bioproject accession PRJNA636267.

## RESULTS

### Comparison of Environmental Parameters

Salinity, pH, and temperature were measured from concurrently sampled seawater as environmental parameters. Kochi, Okinawa, and Taiwan were the sampling sites from north to south. The seawater salinity in Kochi exhibited large seasonal variation (showing a statistical variance of 42.2, defined as the average of the squares of difference between the data points and the mean) and remained relatively stable throughout the year in Okinawa (showing a variance of 2.2) and Taiwan (showing a variance of 6.4) (Supplementary Figure S1A). The pH values varied widely during summertime in all three sites, with particularly high fluctuations in Okinawa (from sampling time 6, 7, and 1; Supplementary Figure S1B). A distinct time-lag was observed for temperature; in Taiwan, the temperature began to rise at the third sampling, which was, however, observed in Okinawa and Kochi at the fourth sampling (Supplementary Figure S1C). In general, Okinawa and Taiwan shared similar salinity, pH, and temperature values. Kochi showed large fluctuations in salinity

and pH, and consistently had lower temperatures than the other two sites.

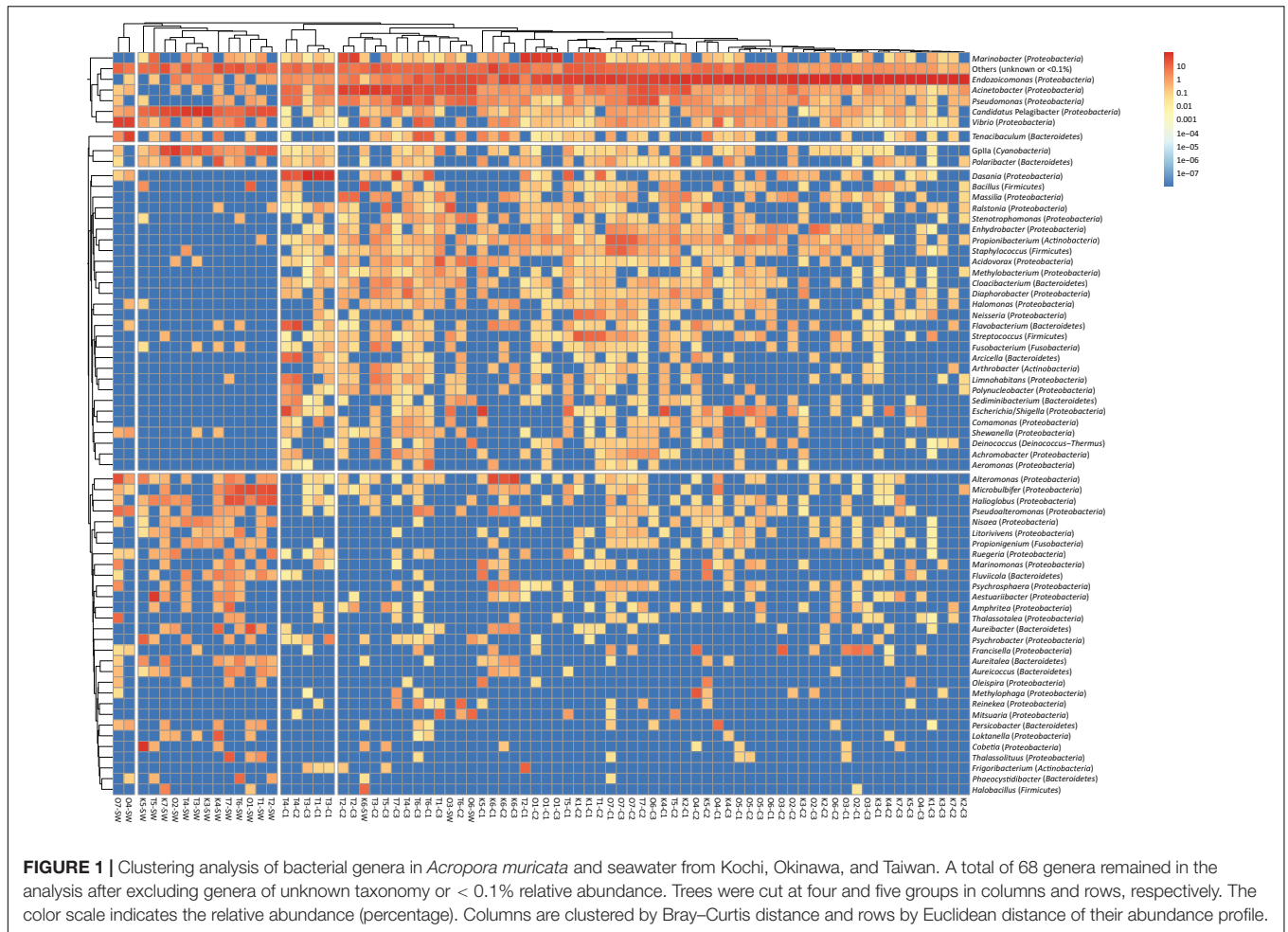
### Bacterial Diversity and Composition

Hierarchical clustering revealed that bacterial composition (at the genus level) was distinct in coral and seawater samples (ANOSIM  $R = 0.41$ ,  $p = 0.01$ ) (Figure 1). The bacterial Shannon diversities in coral were significantly higher in Taiwan than the other two sites ( $p = 0.0012$  by Kruskal-Wallis); seawater samples were also higher in Taiwan but not significant ( $p = 0.84$  by Kruskal-Wallis). Regarding each location, although with only a marginal significance, the bacterial Shannon diversities were higher in seawater than coral samples in Kochi ( $p = 0.17$  by Wilcoxon) and Okinawa ( $p = 0.049$  by Wilcoxon) (Supplementary Figure S2), while higher in coral than seawater samples in Taiwan ( $p = 0.57$  by Wilcoxon) (Supplementary Figure S2), suggesting that bacteria at the low latitude site thrived better in corals than seawater. Results of the Inverse Simpson, richness, and Shannon analyses suggested that the coral bacterial diversities did not show any time-lag trend among the three sampling sites (Supplementary Figure S3). The highest diversity for each site was found during the fifth sampling in Kochi and Taiwan, and the seventh sampling in Okinawa (Supplementary Figure S3).

The nMDS analysis showed that the coral bacterial compositions in Kochi and Okinawa were relatively stable compared to that of Taiwan (Figure 2). High variation in bacterial composition was found in coral samples in Taiwan during autumn and winter (Figure 2A), while in Kochi similar results were identified during spring and summer (Figure 2B). In seawater samples, the bacterial compositions in Taiwan were similar to those in Kochi (ANOSIM  $R = 0.22$ ,  $p = 0.059$ ), but significantly different from those in Okinawa (ANOSIM  $R = 0.26$ ,  $p < 0.01$ ) (Supplementary Figure S4). No significant difference was found between the compositions of Kochi and Okinawa (ANOSIM  $R = 0.04$ ,  $p = 0.33$ ).

Among the 20 most abundant bacterial genera, corals in Taiwan harbored a greater diversity than the other two sites (Figure 3). *Endozoicomonas* was consistently dominant in corals from Kochi and Okinawa but not Taiwan, where it was particularly low in abundance during autumn and winter months (T1–T4 in Figure 3). Inspired by our recent study which reported that *Endozoicomonas acroporae* is an *Acropora*-associated dimethylsulfoniopropionate (DMSP) degrader (Tandon et al., 2020), we further investigated how many of our *Endozoicomonas* amplicons were associated with *E. acroporae*. By analyzing the best BLASTn match, we observed 6.35 and 4.36% relative abundance of *E. acroporae* in Okinawa and Taiwan, respectively, but only 0.3% in Kochi (Supplementary Figure S5).

The CCA results showed that temperature and salinity had larger influences on coral bacterial composition than pH when considering all samples (Supplementary Figure S6A). In the site-specific analysis, salinity and temperature had the largest effect on Kochi (Supplementary Figures S1A,C) and were the main factors contributing to its coral bacterial community composition (Supplementary Figure S6B). In Kochi, the abundance of many genera was negatively correlated with temperature, indicating that they acclimated to the lower water temperature ( $<20^{\circ}\text{C}$ ). In Okinawa, temperature and pH were the major factors



**FIGURE 1 |** Clustering analysis of bacterial genera in *Acropora muricata* and seawater from Kochi, Okinawa, and Taiwan. A total of 68 genera remained in the analysis after excluding genera of unknown taxonomy or < 0.1% relative abundance. Trees were cut at four and five groups in columns and rows, respectively. The color scale indicates the relative abundance (percentage). Columns are clustered by Bray–Curtis distance and rows by Euclidean distance of their abundance profile.

influencing the coral bacterial community (Supplementary Figures S1, S6C). In Taiwan, most genera were positively correlated with temperature, indicating an acclimation to the warmer environment (Supplementary Figure S6D). As a result, temperature, pH, and salinity had site-specific and differential effects, suggesting that ambient conditions have an important role in the coral-associated bacterial composition.

### Endozoicomonas and Acinetobacter

*Endozoicomonas* and *Acinetobacter* were the most dominant genera in corals (Figure 3), so we further analyzed them to resolve their relationships to sampling times from all three sites in greater detail (see section “Materials and Methods”). Both *Endozoicomonas* and *Acinetobacter* abundance (log-transformed) demonstrated higher correlation values within sites than between sites, indicating that the compositional differences were site-specific (Figure 4A; ANOSIM  $R = 0.695$ ,  $p = 0.0001$  for *Endozoicomonas*;  $R = 0.416$ ,  $p = 0.0001$  for *Acinetobacter*), but the correlations diminished in Boolean transformation (i.e., presence and absence) (Figure 4B). Neither *Endozoicomonas* nor *Acinetobacter* demonstrated any time-lag phenomenon in OTU compositions across locations, indicating that the time-lag succession did not apply to dominant

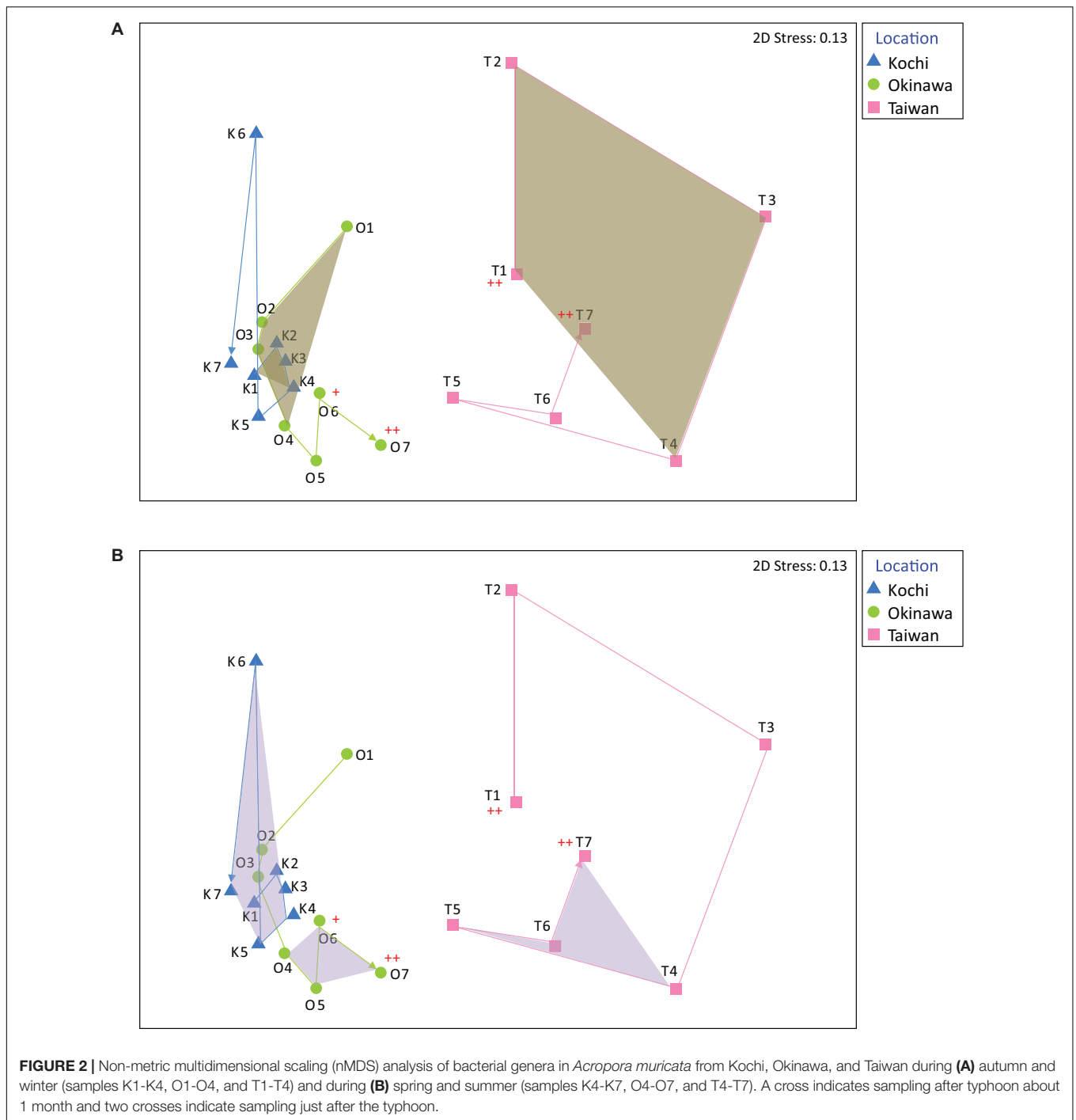
bacteria in corals along the KC. The site-specific CCA analysis revealed that temperature and salinity were the main factors affecting genera composition in both Kochi (Supplementary Figure S7A,D) and Okinawa (Supplementary Figures S7B,E), while temperature and pH were the major factors in Taiwan (Supplementary Figures S7C,F).

Lastly, the 20 most abundant OTUs of *Endozoicomonas* and *Acinetobacter* were phylogenetically analyzed with their counterparts from a different coral species, *Stylophora pistillata*, obtained from our previous study (Yang et al., 2017), to verify the existence of host specificity. Results showed that *Endozoicomonas* from *S. pistillata* and *A. muricata* formed distinct phylogroups (Figure 5A), but *Acinetobacter* OTUs did not (Figure 5B), suggesting that *Endozoicomonas* has a higher host specificity than *Acinetobacter*.

## DISCUSSION

### Influences of Current and Location

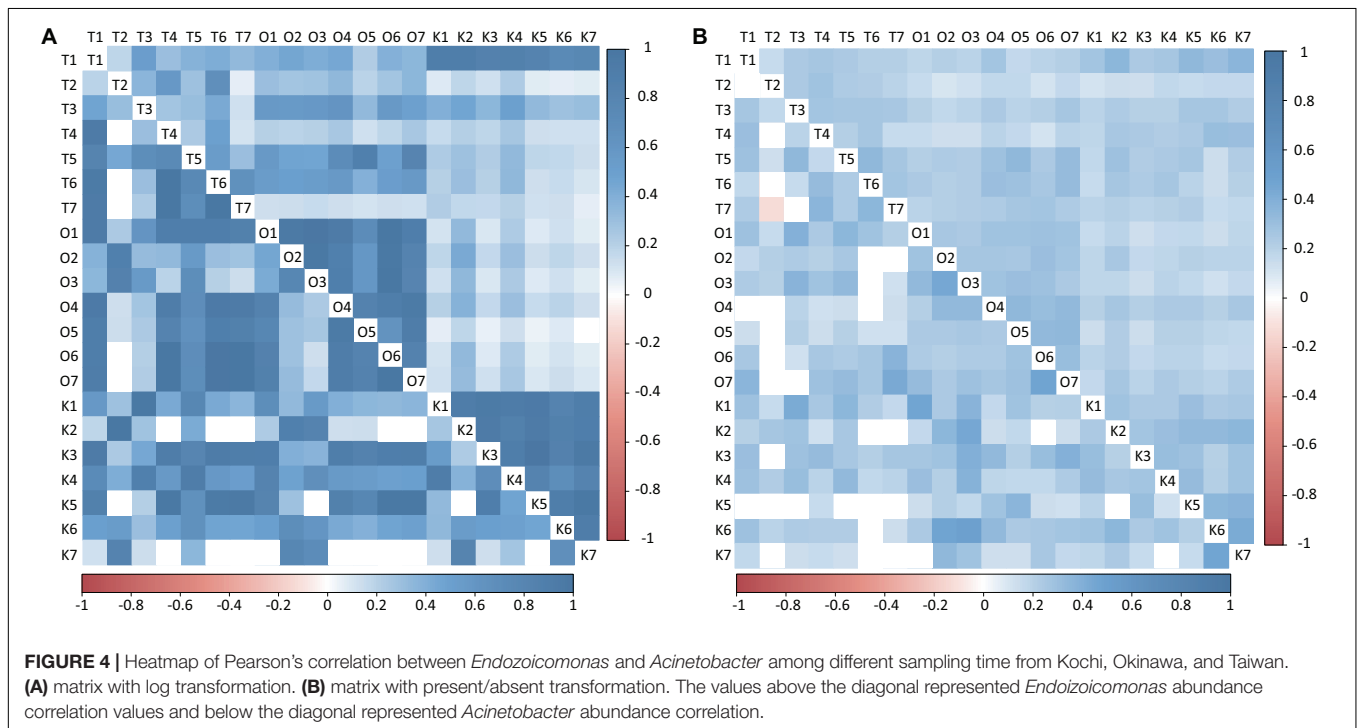
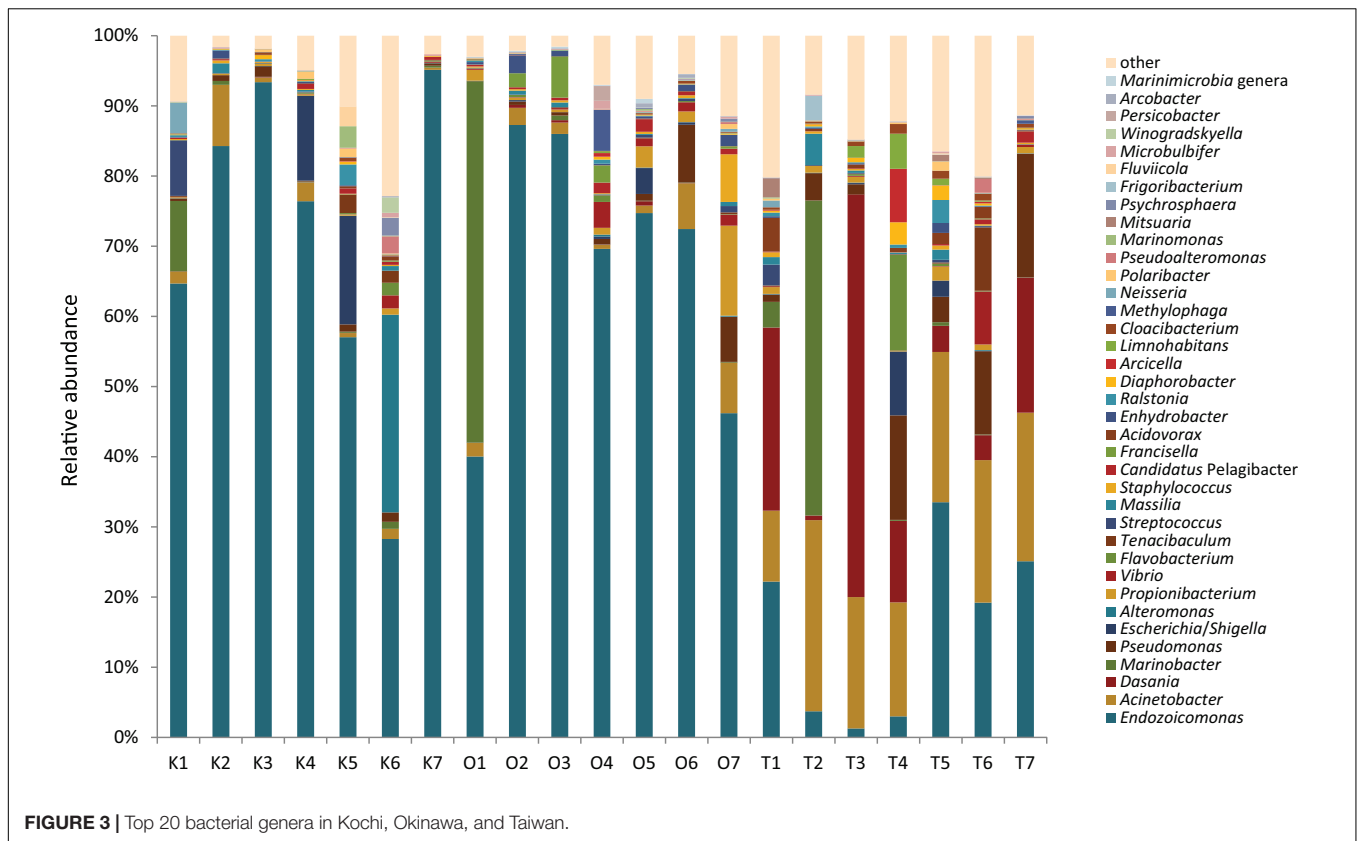
Current is driven by gradients of temperature, pH, and salinity and was expected to result in time-lagged shifts in microbial composition. However, the present study did not find enough



evidence to support the hypothesis that the microbiota of coral and seawater samples can be influenced by water current from low to high latitude. Along the path of the KC, the sampling sites were more or less influenced by its water (Chu, 1974; Andres et al., 2008; Kuroda et al., 2008), but the coral-associated bacterial composition exhibited significant site-specific differences and no obvious sign of time-lag succession. In addition, further comparisons between the two most dominant genera, *Endozoicomonas* and *Acinetobacter*, repeatedly found

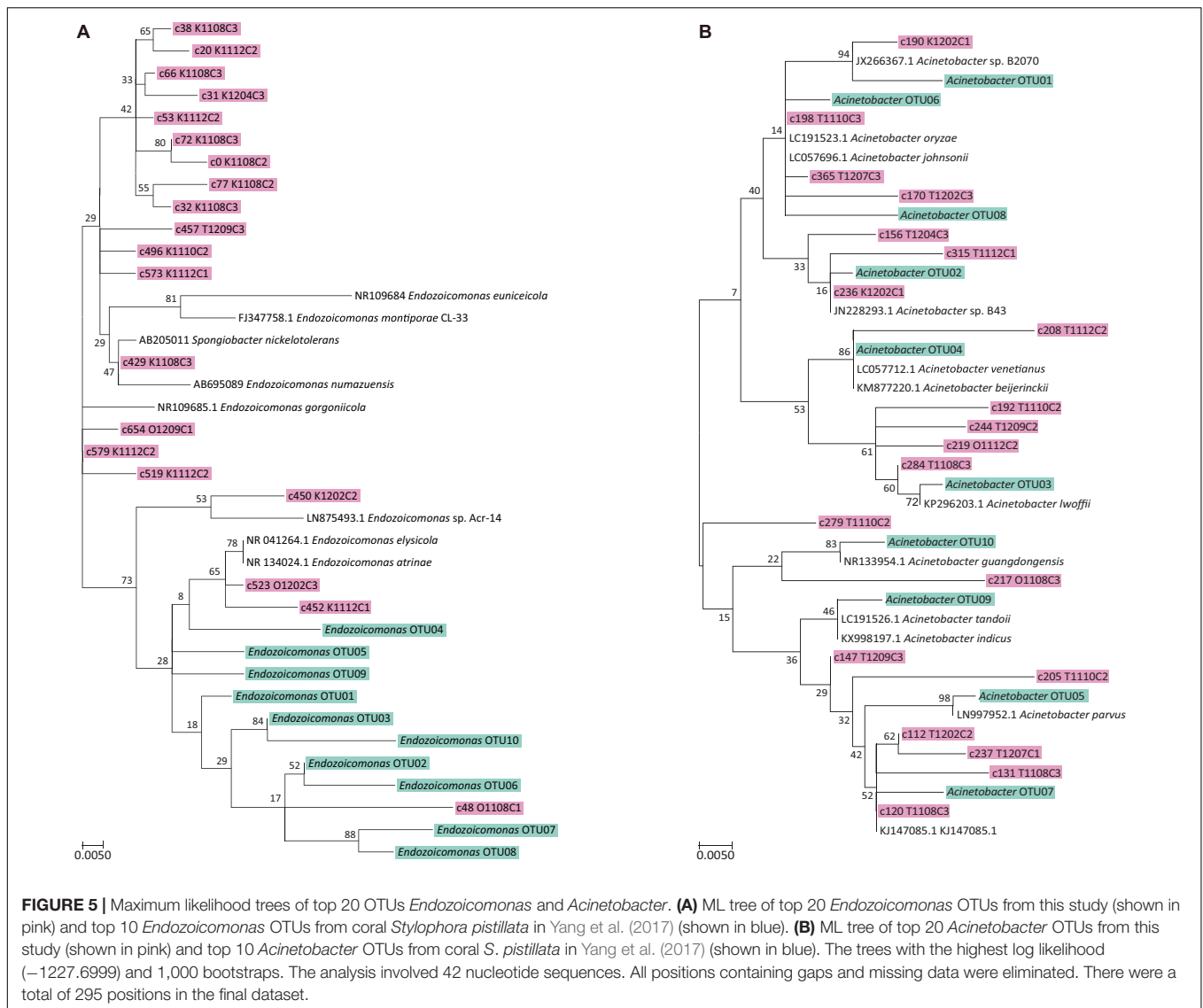
site-specific and season-independent correlations in abundance profiles without time-lag succession. These results collectively suggest that local conditions may have stronger effects on bacterial compositions and dynamics than does the KC.

The coral-associated bacterial community in Taiwan demonstrated higher seasonal variation than those of Okinawa and Kochi, plausibly attributable to the water flow velocity. Advection in currents has been suggested to influence microbial community assemblies (Doblin and Van Sebille, 2016), and



increased water flow velocity has also been shown to modify the bacterial composition in the coral surface mucus and tissue layers (Lee et al., 2016). Compared to Kochi, the sampling

sites in Taiwan and Okinawa had faster current flow because of their physical proximity to the KC mainstream (according to the Ocean Data Bank, Ministry of Science and Technology,



Taiwan)<sup>2</sup>. Moreover, the site in Taiwan is affected not only by the KC but also waters from the South China Sea (Hu et al., 2000), which in combination may impact coral-associated bacterial compositions. Last but not least, extreme hydrodynamics (e.g., typhoons) can cause a shift in the coral ecosystem (White et al., 2017) and phytoplankton composition (Blanco et al., 2008), and lead to disease in corals (Bright et al., 2016) by disrupting local environments for coral holobionts. In Taiwan and Kochi, the first and last sampling (T1 and T7, K1 and K7) were similar in community composition (Figure 2), which was not observed in Okinawa (i.e., O1 and O7 were separated from each other). As O7 sampling was performed shortly after a typhoon, it was very likely that the observed microbial community has been substantially disrupted.

The coral microbiota is also associated with site latitude. Our previous study found that *Stylophora pistillata*-associated

bacterial compositions differed between tropical and subtropical zones (Yang et al., 2017). A one-degree latitudinal difference was proposed to be the distribution boundary for similar bacterial compositions in the same coral (i.e., two corals of the same species separated by more than one degree would have different bacterial compositions) (Woo et al., 2017). Pollock et al. (2018) found that the coral microbiota has lower richness at higher latitudes, corresponding to the lower coral bacterial diversity in Okinawa and Kochi than Taiwan. The coral microbiota in Kochi and Okinawa shared similar compositions, but largely differed from those in Taiwan, suggesting that coral bacterial dynamics correspond with the climate zone. However, the geographic location is still attributable to this observation as they may differentially be influenced by the water currents from the South China Sea.

Several variation patterns associated with seasons in coral microbiota were discovered. Being a middle-latitude site, the coral microbiota in Okinawa highly overlapped with those

<sup>2</sup><http://www.odn.ntu.edu.tw/>



in Kochi (the high-latitude site) during autumn and winter but became closer to those of Taiwan (the low-latitude site) during spring and summer. Also, compared to autumn and winter, the coral microbiota in Kochi largely fluctuated during spring and summer, while those in Taiwan demonstrated the opposite trend. The coral microbiota has been shown to tolerate a temperature range similar to ambient thermal history (Shiu et al., 2017). In this study, the *Acropora*-associated microbial composition in the low-latitude site (i.e., Taiwan) demonstrated a relatively small fluctuation during spring and summer; the counterparts in the high-latitude site (i.e., Kochi) demonstrated a relatively small fluctuation during autumn and winter. Therefore, the latitude largely determines the temperature tolerance range of coral microbiota. Although coral microbiota is slightly fluctuating from time to time, this phenomenon is escalated while the ambient temperature varies beyond the tolerance range.

### Site and Host Specificities of *Endozoicomonas* and *Acinetobacter*

*Endozoicomonas* is a ubiquitous taxon in coral (Neave et al., 2016). Its high abundance has been suggested as an indicator of good coral health (Bourne et al., 2008). However, in the present study performed on healthy *A. muricata*, the abundance of *Endozoicomonas* varied across sampling sites. As our sampling was performed at inshore sites, the impact of terrestrial nutrient influx (e.g., P and N) on coral microbiota cannot be ignored (Vega Thurber et al., 2014).

It has been suggested that ubiquitously dominant taxa may be eurythermic environmental generalists or composed of multiple subtypes selected through different environmental factors (Yung et al., 2015). Although *Endozoicomonas* is common in corals, at low latitude the *A. muricata*-associated microbiota was simultaneously dominated by other genera, such as *Acinetobacter*, *Dasania*, and *Pseudomonas*. *Acinetobacter* was found particularly more in *S. pistillata* around Taiwan than was *Endozoicomonas* (Yang et al., 2017).

Among the *Endozoicomonas* species, *Endozoicomonas* amplicons associated with *E. acroporae* were detected at all three sites, and its abundance in Okinawa and Taiwan increased during the warm seasons (spring and summer). *E. acroporae* is a DMSP degrader (Tandon et al., 2018, 2020), and DMSP and its breakdown products can quickly scavenge hydroxyl radicals and mitigate oxidative stress to protect corals from bleaching (Sunda et al., 2002; Lesser, 2006). However, the coral microbiota in Taiwan was not overwhelmed by *Endozoicomonas*, and the second-most abundant genus, *Acinetobacter*, is proposed to be a DMSP degrader performing a similar protective function for *A. muricata* (Raina et al., 2010). *Acinetobacter* was abundant in different stony corals in various regions, including the tropics (Littman et al., 2009; McKew et al., 2012; Li et al., 2014; Leite et al., 2018), and its role is still elusive as being reportedly beneficial (Shnit-Orland and Kushmaro, 2009) and detrimental (Sweet et al., 2013) to corals. Given the observation that *Acinetobacter* abundance was higher and more stable in low-latitude (Taiwan) than high-latitude (Okinawa and Kochi) sites, the question of

whether *Acinetobacter* could edge *Endozoicomonas* out of the microbial assemblage dominance in *Acropora* warrants further study, especially with the rising seawater temperature in the age of global warming.

## CONCLUSION

This year-long study compared the bacterial communities of *A. muricata* at three sites subjected to the KC at different climate zones (Taiwan, Okinawa, and Kochi), and found an inverse correlation between coral bacterial diversity and site latitude. The bacterial composition in coral has no obvious time-lag succession along with the KC, but a strong correlation with ambient conditions, indicating that environmental parameters are more influential to the indigenous bacterial community. *Endozoicomonas* were substantially detected in temperate and subtropical sites but outnumbered by *Acinetobacter* in tropics, indicating *Acinetobacter* having a lower host specificity and better adaptability to the warmer environment than *Endozoicomonas*.

Manipulation of the coral microbiome was recently proposed as a promising means to improve coral health by strengthening coral resistance and resilience to environmental stress (Damjanovic et al., 2017; Sweet et al., 2017), and *Endozoicomonas* has been proposed as an environmental probiotic for this purpose (Peixoto et al., 2017). According to the site-specific distribution of *Endozoicomonas*, the microbial manipulation in coral would be more effective if we factor in local environmental parameters and host species. Finally, the dominance of *Acinetobacter* in tropical corals suggests its potential role of being another environmental probiotic candidate.

## DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories, <https://www.ncbi.nlm.nih.gov/bioproject/PRJNA636267>.

## AUTHOR CONTRIBUTIONS

S-LT designed the study and edited the draft manuscript. S-HY, C-HT, and KT performed data analysis and manuscript writing. H-PL, P-WC, H-JC, J-HS, H-CL, NI, TM, and HY performed sampling. All authors read and approved the final version of the manuscript.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2020.569107/full#supplementary-material>

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The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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