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Bacterial community dynamics, co-occurrence relationship and assembly processes associated with two *Acropora* corals in nursery transplantation

Wentao Zhu[1, 3], Hongmin Wang[1], Junling Zhang[1], Zhuoran Li[1], Xiangbo Liu[2], Hao Wang[1], Rouwen Chen[1, 3], Xiubao Li[1, 3*]

[1] School of Marine Biology and Fisheries, Hainan University, Haikou 570228, China

[2] School of Ecology, Hainan University, Haikou 570228, China

[3] State Key Laboratory of Marine Resource Utilization in South China Sea, Hainan University, Haikou 570228, China

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Abstract

Coral gardening has become a promising technique for restoring reefs worldwide in the Anthropocene era. The microbiome plays an important role in enhancing adaptive resilience in situ nursery propagation of corals. However, little is known about the response patterns of bacterial community dynamics, co-occurrence networks and assembly processes of different species in coral restoration nurseries over time. Here, we collected two *Acropora* coral samples from transplanted fragments and source colonies at 1-month and 3-month post-transplantation (May and July 2022) in an upwelling-affected fragmented reef. Full-length 16S rRNA gene sequencing revealed that bacterial communities of coral fragments in nurseries exhibited consistent temporal shifts compared to those of the source colonies. High host specificity was observed in the bacterial community and network structure associated with source colonies. In contrast, for the two coral species within nurseries, there were no differences in bacterial diversity, composition and core microbiome. Stochastic assembly processes were identified as the primary drivers of bacterial communities in all May samples, whereas deterministic processes played a more prominent role in July. Seawater properties (e.g., temperature and ammonium concentration) partially explained the compositional changes in the bacterial communities of these coral samples. Our findings suggested that coral nurseries contributed to the homogenization of bacterial communities in different *Acropora* corals, despite the apparent temporal dynamics of bacteria. These results enhance our understanding of the coral microbiome, ecological interactions and assembly principles in different host within *in situ* nurseries.

Key words *in situ* nursery, coral transplantation, bacterial community dynamics, host specificity, similar assemblages, environmental adaptation

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1 Introduction

Coral reefs are one of Earth's most biodiverse and productive ecosystems, providing a wide range of goods and services (Moberg and Folke, 1999; Ramesh et al., 2020). However, coral reefs coverage worldwide is declining precipitously due to both global and local stressors (Hughes et al., 2017). Given the ongoing impacts of climate change and human activities, conventional management is proving to have limited effectiveness for reef recovery (Rinkevich, 2021; Williams et al., 2019). Thus, there is a growing recognition that local active management approaches are needed to assist reef recovery (Rinkevich, 2021). In particular, coral gardening has emerged as an active and innovative management approach that involves transplanting live coral fragments onto suitable underwater nurseries (Abrina and Bennett, 2021). Asexual reproduction through in situ coral nurs-

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*Corresponding author, E-mail: xiubaoli@hainanu.edu.cn

eries has been widely employed as a quick cloning strategy for coral restoration (Ramesh et al., 2020). Overall, coral gardening is a successful, low-technology, and low-cost restoration technique for increasing coral cover and restoring degraded reefs (Strudwick et al., 2022). However, the success of coral fragments in nursery is subject to considerable variability and influenced by multiple factors, including attachment substrate, water quality, coral characteristics, and transplant methods (Smith et al., 2019).

The holobiont is the complex assemblage constituted by the coral host and the associated microorganisms (Deignan and McDougald, 2022; Kanisan et al., 2023). Coral-associated microbial communities play crucial roles in promoting the health and resilience of corals (Bourne et al., 2016; Peixoto et al., 2017), encompassing critical functions such as energy provision, nitrogen fixation, and protection against pathogen (Beatty et al., 2022; Miller et al., 2020). Numerous studies have reported that the composition of coral-associated bacterial community is strongly influenced by both environmental factors and host identity (Damjanovic et al., 2020; Ziegler et al., 2019). For example, bacterial community associated with *Acropora hemprichii* is highly flexible in response to environmental disturbances, whereas *Pocillopora verrucosa* exhibits more stable microbiomes even under changing environmental conditions (Ziegler et al., 2019). Recently, increased research effort has been devoted to comprehensively characterize coral microbial communities in response to climate change and understand their potential to withstand environmental perturbations (Deignan and McDougald, 2022; Webster and Reusch, 2017). Given the critical role of microbial communities in the fitness of their hosts, manipulation of coral probiotic strains has recently been proposed to improve restoration efforts and mitigate the loss of coral reefs (Miller et al., 2020). Consequently, it is imperative to thoroughly investigate the environmental drivers and limitations of microbial flexibility in coral fragments within in situ nurseries to ensure the effectiveness and success of coral propagation procedures (Strudwick et al., 2022).

Gaining a comprehensive understanding of the dynamics in coral microbiome across coral species can greatly aid restoration efforts, as they play pivotal roles in coral plasticity and holobiont adaptation (Aguirre et al., 2022). For instance, recent studies have found potential differences in the flexibility of bacterial associations across environmental gradients, as demonstrated by reciprocal transplantation designs (Strudwick et al., 2022; Ziegler et al., 2019), where coral fragments from pristine sites are transplanted into novel reef environments (Deignan and McDougald, 2022; Ziegler et al., 2019). However, the response of the microbial community associated with transplanted corals to nurseries has often been overlooked, severely limiting the optimization of coral transplantation as a reef restoration effort (Strudwick et al., 2022). Additionally, information on the species coexistence and assembly mechanism of bacterial community within transplanted colonies is limited. Hence, we aimed to address this knowledge gap by studying coral fragments in nurseries over small geographic scales and determining the extent of host type and propagation process in maintaining bacterial assemblages over time. More specifically, our objectives were to address the following questions: (1) Whether bacterial communities associated with *Acropora* corals exhibit high host specificity and temporal dynamics in nursery fragments and source colonies? (2) What are the patterns of interaction network and community assembly in these different bacterial communities? Our findings can serve as a fundamental basis for elucidating the relationships between coral microbiome flexibility and environmental adaptation potential within propagation nurseries.

2 Materials and methods

2.1 *Transplantation experiment and samples collection*

The study site, Fenjiezhou (FJZ) Island, is located in the South China Sea off the east coast of Hainan Island, known for its popularity among recreational divers and tourism development (Zhu et al., 2023a). The northwest area of FJZ Island, specifically at coordinates 18°34′N and 110°11′E, has been significantly impacted by increasing human disturbance, resulting in noticeable degradation of the coral reefs, thus necessitating urgent artificial restoration efforts (Fig. S1). The nursery (patent publish number: ZL202210374323.1) used in this project is a new and cost-effective tool for coral restoration (Liu et al., 2024). Branching corals in the genus *Acropora* have been heavily favored in transplantation experiments due to their high potential of asexual reproduction and reattachment capacity. The project work commenced on April 19, 2022, and was completed on April 24. A total of 52 nurseries were constructed in the degraded area (on the sand and rocky base) immediately adjacent to the reef, and 628 *Acropora hyacinthus* and *Acropora microphthalma* fragments were transplanted (Fig. 1). All *Acropora* fragments in coral nurseries were randomly selected and originally collected from source colonies on the reef. Coral branches were fragmented from a maximum of one quarter of each colony, and cable ties were employed to secure the fragment to the nursery frame (Fig. S2).

Vertical projection photos of each transplanted coral fragment in the nursery were taken using an underwater camera (Olympus-TG4) and a ruler during the surveys, conducted after 1 month (May) and 2 months (June) of transplantation. The survival, mortality and growth rate of transplanted corals were calculated based on these photos (Liu et al., 2024). Specifically, orthographic projection area of the living part of each coral fragment was deter-

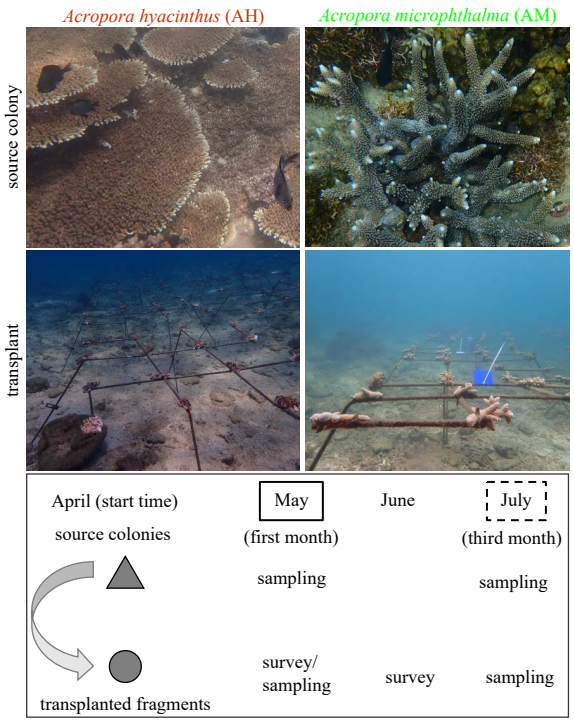

Fig. 1. Experimental design and sampling timeline during the nursery phase. *In situ* coral nursery frame that transplanted coral fragments of *Acropora hyacinthus* and *Acropora microphthalma* were built in the degraded area adjacent to the reef in Fenjiezhou Island. *Acropora* fragments were originally collected from source colonies on the reef (triangle), and then each fragment was based to the nursery frame using a cable tie (circle). For a sampling event (in May and July) during of the experiment, six small partial fragments of each species were obtained from the coral nursery and the six corresponding source colonies of each species were sampled.

mined in these photos with a ruler inside using ImageJ software. The growth rate of each fragment was calculated as difference between the final area and the initial area divided by the transplantation months. Meanwhile, we used the photos to determine the survival based on the absence of living tissue or loss of coral. In addition, in May and July 2022 (1-month and 3-months post-transplantation), six replicate of visually healthy fragments (about 5 cm^2) of the two *Acropora* species were randomly collected from transplants in coral nurseries and source colonies on the reef. Finally, 48 visually healthy coral samples were selected using self-contained underwater breathing apparatus diving (SCUBA) with diagonal pliers, and they were then stored at −20℃ in sterile centrifuge tubes.

In April 2022, a HOBO water temperature logger (UA-002-08) was deployed on a coral nursery in the experimental area. General environmental parameters and dissolved nutrients concentrations within 1 m of the transplant frames and reefs were determined on each sampling day according to methods described in our previous study (Zhu et al., 2023b). Specifically, we used a water quality multiprobe (Eureka Water Probes, USA) to record the seawater temperature, salinity, and dissolved oxygen (DO), then measured turbidity and depth using an AQU Alogger 210 (Aquatec, United Kingdom). Water Samples (100 mL) were filtered (Whatman GF/F, 0.45 μm, United Kingdom) and the inorganic nutrients was analyzed by an automatic nutrient analyzer (Seal AA3, Germany).

2.2 *DNA extraction and full-length 16S rRNA gene sequencing*

For all coral samples, the entire sampled fragment was crushed in liquid nitrogen. DNA was extracted using the DNA extraction kit following the manufacturer's instructions. DNA concentration was measured using a nanodrop 2000 spectrophotometer (bio rad Laboratories Inc., USA). The 16S rRNA full-length gene amplification amplicons were amplified using the primers 27F (5′-AGGRGTTYGATYMTGGCTCAG-3′) and 1492R (5′-RGYTACCTTGTTACGACTT-3′) for bacterial communities. PCR amplifications were performed in triplicate for each sample using the following conditions: an initial denaturation at 95℃ for 30 s, followed by 35 cycles each with 30 s at 95℃, 30 s at 60℃, and 45 s at 72℃, and a final extension of 10 min at 72℃. According to the standard protocol of Majorbio Biopharm Technology Co., Ltd. (Shanghai, China), purified amplicons were used for sequencing on the Pacbio Sequel Ⅱ System (Pacifc Biosciences, USA). The PacBio raw reads were processed and sequences after quality filtering sharing 97% similarity were clustered into Operational Taxonomic Units (OTUs) as previously described (Zhu et al., 2023). The taxonomy of OTUs was assigned against the Silva database (v138) by the Ribosomal Database Project (RDP) classifier.

2.3 *Statistical analysis*

The differences of environmental parameters between different locations from the same season or different seasons from the same location were analyzed by Student's t-test. The independent sample *t*-test was performed on the growth rate of the same season in different species or the same coral in different seasons. Results were expressed as mean ± standard error at a significance level of $p < 0.05$.

In the downstream analysis, OTU normalization was performed by rarefying the sequencing depth of the sample with the fewest sequences. Shannon index was calculated using the "vegan" package in R v4.02 to assess the diversity of bacterial communities. To examine differences in the Shannon index among different groups, analysis of variance (ANOVA) was used after verifying homogeneity of variance and normality assumptions. In addition, canonical analysis of principal coordinates (CPCoA) plots and permutational multivariate analyses of variance (PERMANOVA) utilizing Bray-Curtis dissimilarity matrices were employed to examine differences in coral-associated bacterial community structure across

coral species and sampling types over time. In the study, p-values < 0.05 were considered statistically significant. In addition, members of the coral core microbiomes, present in at least 95% of all coral samples regardless of their relative abundance, were identified (Osman et al., 2020).

Co-occurrence networks were inferred based on the Spearman correlation matrix constructed with correlation coefficients $|r| \geqslant 0.6$ and p-values < 0.01, and OTUs with detectable or low average relative abundance (less than 0.1% in data sets) were removed in the co-occurrence network. The topological characteristics were calculated using the "igraph" package, and the networks were visualized using Gephi software. A neutral community model (NCM) was used to estimate the effects of stochastic processes on bacterial community assembly by fitting the relationship between the frequency of OTUs occurrence and their relative abundance (Sloan et al., 2006). In this model, R^2 indicates the goodness of fit to the NCM. To quantify the relative importance of deterministic and stochastic processes in community assembly, we further calculated the modified stochasticity ratio (MST), with 50% as the threshold between more deterministic (MST < 50%) and more stochastic (MST > 50%) assembly (Ning et al., 2019).

3 Results

3.1 *Water quality, coral samples and sequencing overview*

The results from the HOBO temperature record revealed that the seawater temperature at FJZ Island decreased from June to July 2022, which was attributed to the influence of Qiongdong upwelling (QDU) (Fig. S3). Detailed information about *in situ* water quality variables of the study can be found in Fig. S4. Moreover, the concentrations of ammonium and dissolved oxygen were significantly higher in May compared to July ($p < 0.05$), with values changing from (8.573 ± 0.264) μmol/L to (4.569 ± 0.213) μmol/L and (7.685 ± 0.013) mg/L to (6.78 ± 0.074) mg/L, respectively. Seawater nitrate, phosphate, silicate concentrations, and turbidity showed no significant changes between the two months. Most environmental conditions in the same month had no difference between nursery structure and reef site. Overall, the water quality parameters were more influenced by seasonal dynamics rather than regional properties, as most parameters in the source and transplant areas exhibited similarities.

Transplanted coral survival and growth rate were monitored and analyzed (Fig. S5). In May, 1 month after transplantation, *A. hyacinthus* (AH) fragments exhibited a high survival rate of 99.79% (with only 1 out of 483 fragments showing mortality), while the survival rate of *A. microphthalma* (AM) was slightly lower at 97.9% (with 3 out of 143 fragments showing mortality). However, in June, 2 months after transplantation, the survival rate of AH and AM decreased to 99.38% (with 3 out of 482 fragments showing mortality) and 95% (with 7 out of 140 fragments showing mortality), respectively. After transplantation, both AH and AM showed higher growth rates in June [(2.49 ± 0.26) cm^2/month and (1.04 ± 0.02) cm^2/month] compared to May [(3.70 ± 0.24) cm^2/month and (1.18 ± 0.02) cm^2/month], but the growth rate of AH was significantly higher than that of AM in both months ($p < 0.05$).

Coral sampling was conducted in May and July for bacterial sequencing analysis, including two coral species from nursery fragments and source colonies. Full-length 16S rRNA genes were amplified from coral-associated bacterial communities of 48 samples. A total of 2 331 052 clean reads were obtained for all samples, with an average length of 1 488 bp and ranging from 22 493 to 73 352 reads per sample. After rarefying to 22 493 sequences per sample for downstream analysis, rarefaction curves were approaching saturation (Fig. S6), indicating that most bacterial communities were recovered in the sequencing analysis.

3.2 *Bacterial diversity*

The Shannon diversity of AH from source colonies and transplanted AM samples showed significant variation among collection times ($p < 0.05$), with lower values occurring in July for both groups (Fig. 2). Differences in bacterial diversity between AH and AM were more significant in the source colonies, with Shannon diversity of AH being much higher than that of AM in May, while Shannon diversity was significantly lower in AH compared to AM in July ($p < 0.05$). However, there were no significant changes in Shannon diversity for transplants within each coral species during the experiment ($p > 0.05$), indicating that the bacterial diversity of transplanted AH and AM fragments showed similar patterns in response to the

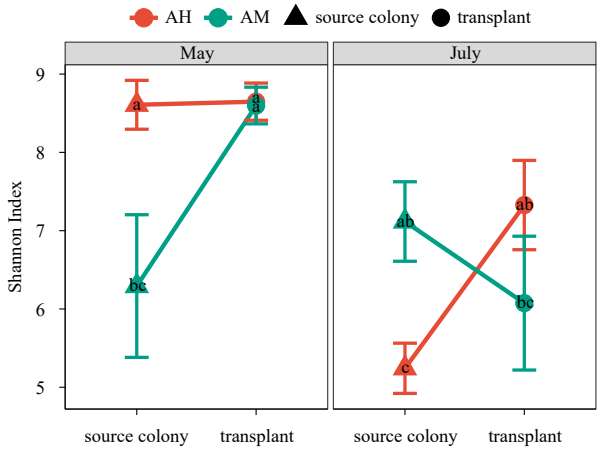

Fig. 2. Diversity of bacterial communities associated with two *Acropora* corals of nursery fragments and source colonies in May and July.

transplantation effect.

3.3 *Coral-associated bacterial community structure and composition*

CPCoA revealed that the whole bacterial communities tended to cluster together based on different months (p = 0.001) rather than coral species or sampling types (Fig. 3a). Furthermore, the sampling types were found to significantly influence the formation of bacterial communities in May between the two coral species, accounting for up to 19.3% of the overall variance in the data (Fig. 3b). There were significant differences in the community composition between the transplants and source colonies of both AH and AM in May ($p < 0.05$). Notably, the species specificity of the bacterial community structure in transplanted coral fragments in May (AH vs AM: $p > 0.05$) was considerably lower compared to the natural condition (AH vs AM: $R^2 = 0.187$, $p < 0.05$). There were no significant changes in the community composition of the transplants compared to the source colonies in both AH and AM in July (Fig. 3c), suggesting that the bacterial communities of transplanted fragments stabilized and resembled those of the source colonies after 3-months transplantation.

The relative abundance of dominant bacterial families including Moraxellaceae, Nocardiaceae, Propionibacteriaceae, and Enterobacteriaceae significantly decreased, while the families Comamonadaceae, Burkholderiaceae, and Xanthobacteraceae exhibited a significant increase from May to July (Fig. 3d). After 1 month of transplantation experiment in May, the abundance of the dominant families in transplanted coral fragments of AH showed no significant changes compared to AM. In July, there was no difference in the abundance of dominant families between transplanted corals and source colonies in both AH and AM. Our results indicated that transplantation promoted compositional homogeneity of the bacterial communities associated with the two coral species, as evidenced by consistent patterns observed in different monthly monitoring periods.

3.4 *Coral core microbiome*

To investigate the potential existence of a core microbiome, we considered all bacterial OTUs present in at

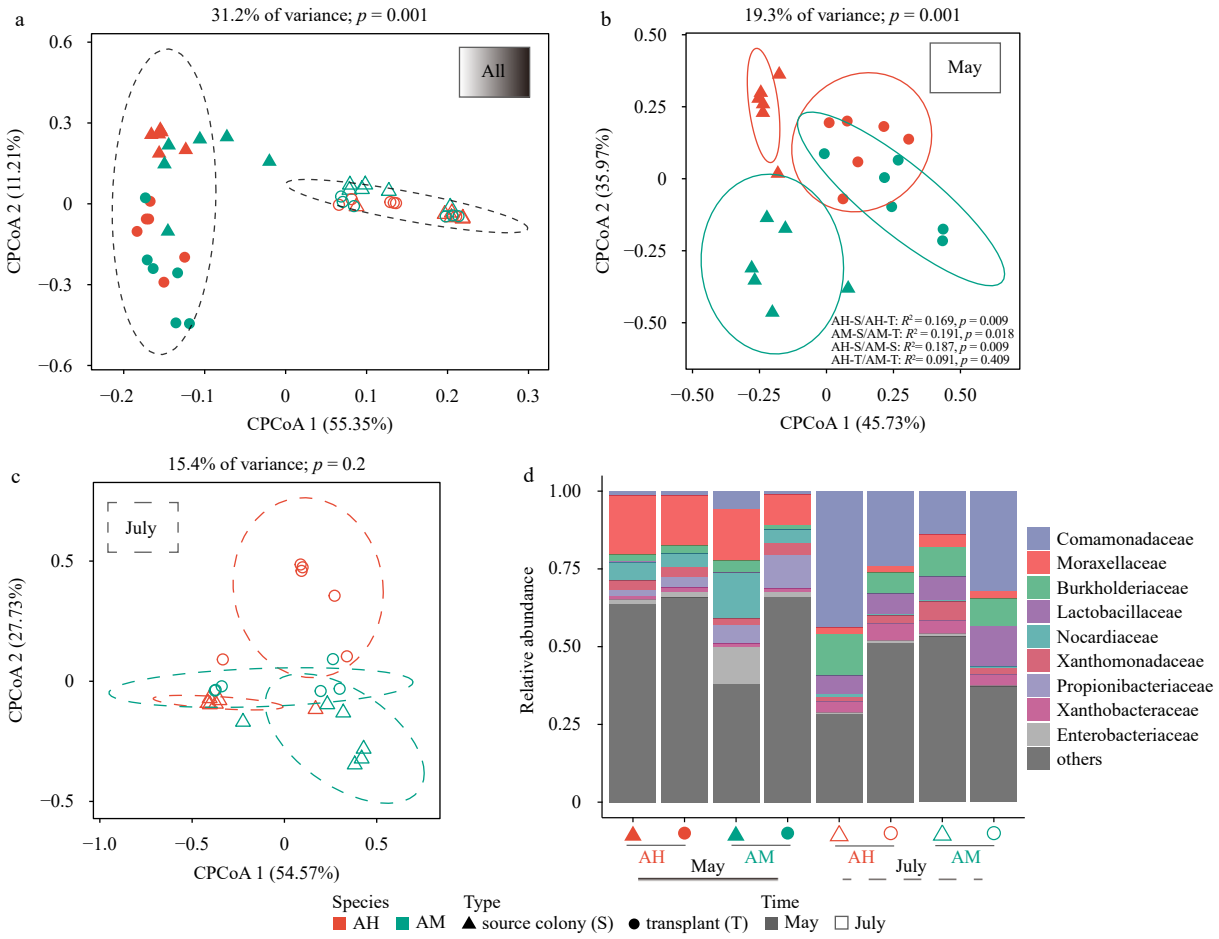

Fig. 3. CPCoA (Bray-Curtis) plot of bacterial associations within coral host habitats of two *Acropora* corals (a). The profiles of bacterial community associated with two *Acropora* corals in May (b) and July (c) between nursery fragments and source colonies. Bacterial community composition (relative abundances) at the family level of nursery fragments and source colonies in May and July (d).

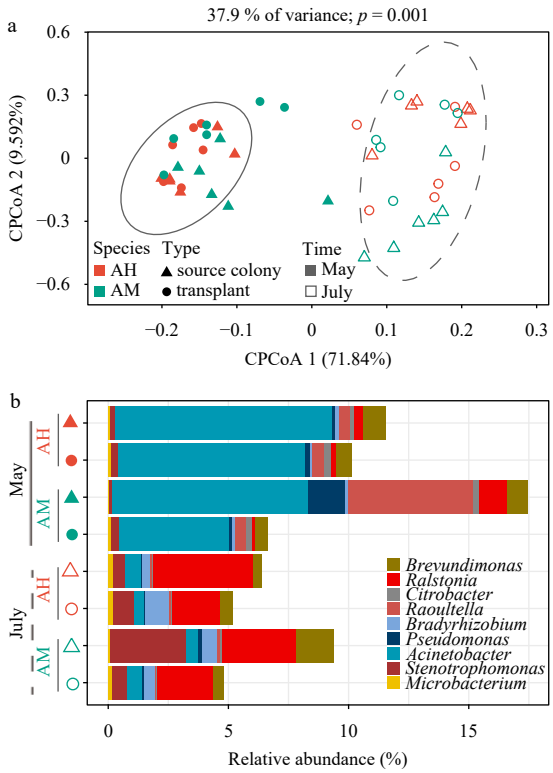

Fig. 4. Community structure (a) and core community at the genus level (b) of coral core microbiome (conserved bacterial OTUs present in >95% of coral samples) for two *Acropora* corals collected from nursery fragments and source colonies in May and July.

least 95% of all samples. We identified 13 consistently present bacterial OTUs as members of the core microbiomes. Interestingly, significant temporal changes in the assemblage structure of the core microbiome were observed, but no differences were observed in terms of species or source (Fig. 4a). Specifically, the relative abundance of *Acinetobacter* sp. (OTU3324 and OTU3420), *Raoultella* sp. (OTU2777, OTU3438, and OTU2780), and *Pseudomonas* (OTU2770) significantly decreased, while the relative abundance of *Ralstonia* (OTU3390 and OTU3438), *Brevundimonas* sp. (OTU3329 and OTU3358), *Stenotrophomonas* (OTU3309, OTU3248), and an OTU belonging to *Bradyrhizobium* sp. (OTU3358) was significantly increased from May to July (Fig. 4b).

3.5 *Bacterial interaction network*

To evaluate the interaction patterns of bacteria associated with corals, we constructed co-occurrence networks by analyzing correlation relationships among different groups (Fig. 5a). The topological properties of these networks were summarized in Fig. 5b to provide a comprehensive description of the intricate interrelationships. Overall, the complexity of all networks, except for AM-S, decreased from May to July, as evidenced by the reduction in the number of edges, nodes, and average degree. Notably, the network structure in AM natural populations displayed a higher connectivity level than AH throughout the experiment. Consistent with the changes in network size (i.e., number of edges and average degree), the robustness of AH-T (0.34) and AM-T (0.33) was comparable in July. However, the robustness of all networks, except for AH-S, decreased from May to July.

3.6 *Bacterial community assembly processes and environmental drivers*

To investigate the contribution of stochastic processes to community assembly, we fitted the bacterial communities to Sloan's neutral model (Fig. 6a). The neutral model best described the composition of samples in May, with R^2 values ranging from 0.135 to 0.535. However, the fit of the bacterial communities from July to the neutral model was poor, with R^2 values less than 0 in all four groups. To further quantify the relative contributions of deterministic and stochastic processes in bacterial community assembly, we employed the MST (Fig. 6b). The results revealed that except for AM-T (with a mean MST of 41.44%) in May, bacterial communities were primarily governed by stochastic processes (with mean MSTs ranging from 55.42% to 70.75%). In contrast, the bacterial community in July exhibited a higher contribution of deterministic processes (with mean MSTs ranging from 11.48% to 36.67%). These findings indicated that the significant assembly processes of bacterial communities differed significantly between May and July.

Further, the redundancy analysis (RDA) (Fig. 6c) was used to explore the main environmental drivers for bacterial composition associated with AH and AM. The overall results of RDA were significant for both bacterial communities of AH ($F = 2.299$, $p = 0.001$) and AM ($F = 1.985$, $p = 0.001$). The selected environmental variables could explain 44.80% and 39.56% of the overall bacterial composition variations, respectively. Temperature and ammonium had significant effects based on the 999 permutations of the Monte Carlo test ($p < 0.01$). The Mantel test (Fig. S7) further confirmed that the temperature and ammonium exhibited the strongest relationships with the bacterial communities of two Acropora corals ($r > 0.4$, $p < 0.001$).

4 Discussion

Understanding the response mechanisms of coral environmental flexibility with a microbial perspective is critical to reveal the adaptive potential to in situ transplantation. The response of coral-associated bacterial communities to restoration nurseries and the underlying factors driving these changes, especially for interactional networks and community assembly mechanisms, are poorly understood. Through a series of analyses, we have provided a detailed characterization to gain insight into how the coral bacterial communities of different species respond to nursery environments over time. To the best of our knowl-

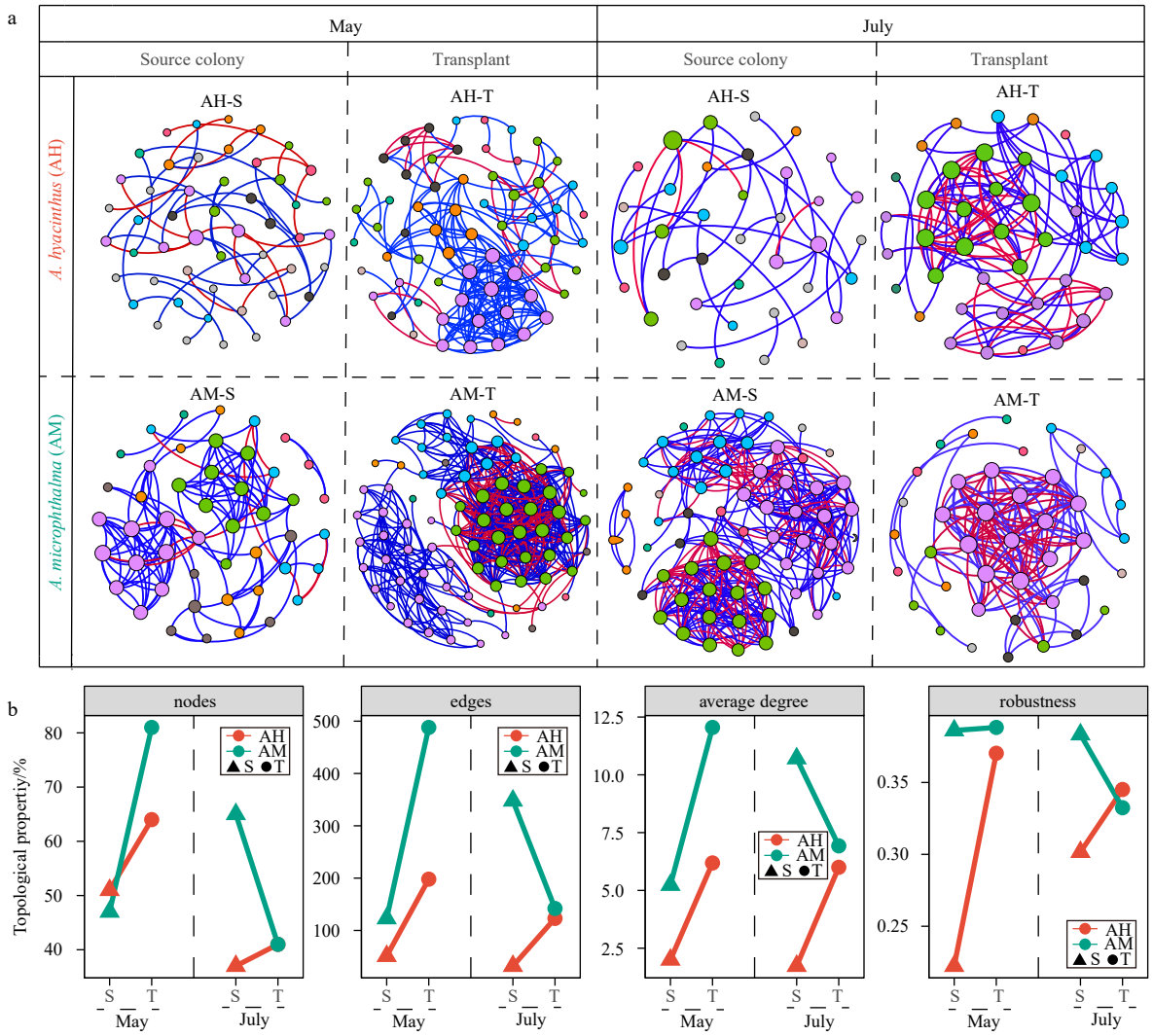

Fig. 5. Co-occurrence networks (a) and topological properties (b) of coral microbiomes for two *Acropora* corals collected from nursery fragments and source colonies in May and July. Node color represents different abundant bacterial OTUs within each network. The size of the nodes indicates the number of connections (degree) for each node. Connection between two nodes represents correlations, positive and negative correlations are shown in blue or red lines, respectively.

edge, this study was the first to explore the dynamic changes of the coral microbiome between nursery transplants and source colonies, especially the ecological drivers of ecological networks and assembly processes. The results of this study significantly enhance our understanding of coral microbiome flexibility of nursery-planting fragments.

4.1 *Short-term assessment of in situ coral transplantation*

Globally, active restoration techniques involving the transplantation of live coral fragments have been developed to facilitate the recovery of damaged reef habitats (Rinkevich, 2005, 2021). In this study, coral fragments from two coral species (AH and AM) were transplanted to the nursery in FJZ, an area influenced by Qiongdong upwelling (QDU) and anthropogenic disturbance (Zhu et al., 2022a). Ammonium concentrations were significantly higher than nutrient thresholds reported for healthy coral reefs (Houk et al., 2022). However, a remarkable survival rate (⩾ 95%) of the transplanted corals was observed in two underwater surveys. The average survivorship was consistent with the previous study in Wuzhizhou island of QDU zone (Xia et al., 2022). One possible explanation for this result was that the open structures utilized in the experiment might have provided crucial support for the transplanted coral fragments, allowing relatively unimpeded water flow (Williams et al., 2019). This could have served as a vital nursery tool for cultivating specific coral species with stress resistance through phenotypic plasticity (Rinkevich, 2021). The results revealed that the growth rate of AH was significantly higher than AM, consistent with previously observed transplantation effects (Ramesh et al., 2020; Xia et al., 2022). Furthermore, both AH and AM exhibited higher growth rates in June than May, suggesting that the upwelling environment might be a poten-

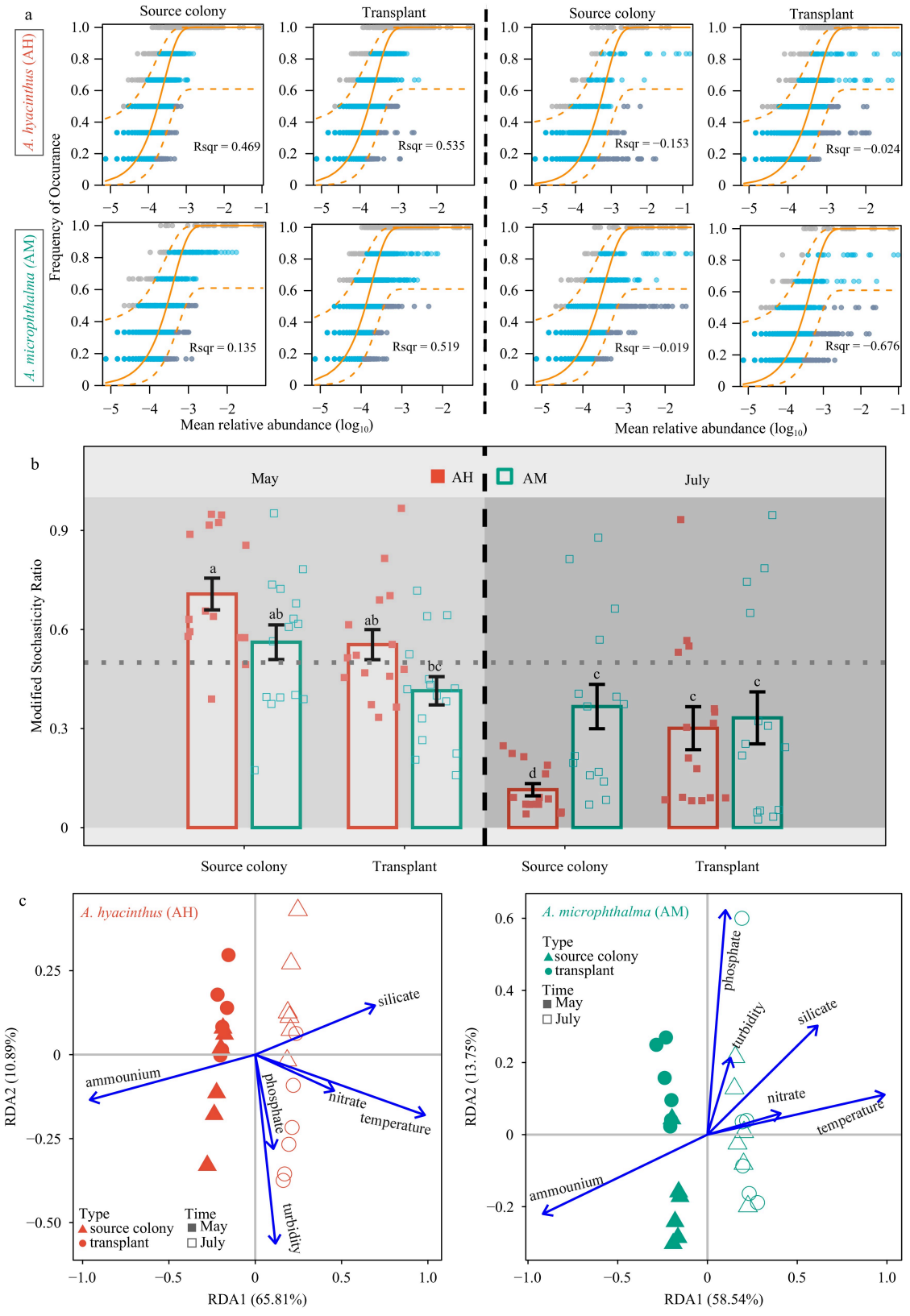

Fig. 6. Fit of the neutral community model (a) and comparison of modified stochasticity ratio (b) showing ecological processes that shape the bacterial community assembly for two *Acropora* corals collected from nursery fragments and source colonies in May and July. The solid orange line is the best fit to the neutral community model, and the dashed orange line indicates 95% confidence intervals around the model prediction. OTUs that occur more or less frequently than predicted by the model are shown in grey and brown, respectively. Rsqr represents the goodness of fit to the model. Different lowercase letters indicate significant differences ($p < 0.05$). Redundancy analysis (RDA) of coral-associated bacterial community dynamics with environmental variables (c).

tial driver of temporal-specific growth rates. This inference was supported by previous studies demonstrating the positive influence of increased nutrient and organic matter availability resulting from terrestrial input and upwelling on coral growth (Randall et al., 2020; Zhu et al., 2023b).

4.2 *Transplanted fragments from nursery have similar bacterial diversity between coral species*

Previous studies have demonstrated that coral morphology and host trait significantly determine the high species-specific diversity of coral-associated bacteria (Morrow et al., 2022; Ricci et al., 2022). Bacterial diversity of AH from source colonies and transplanted AM were lower in July compared to May in this study, which was consistent with the finding that high water temperature during the summer months leads to lower alpha diversity of coral-associated bacteria (Zhu et al., 2023b). The alpha diversity showed no difference in the transplanted fragments between AH and AM over time, while Shannon index of source colonies showed the opposite trend. Despite the species-specificity of the coral microbiome, specific biotic and abiotic factors that vary from nursery frames to the source reef are likely drivers of differences in coral bacterial communities (Strudwick et al., 2022). In particular, the transplanted fragments were affixed to artificial reefs constructed using similar materials and architectural complexity. On the contrary, the source colonies grew on natural coral reefs with distinct benthic assemblages and structural complexities. The geographic location and water quality parameters were similar, but it was necessary to note that the nursery might not have provided identical attachment conditions for corals compared to the surrounding reef environment. These findings supported the concept of local acclimatization through coral gardening over small geographic scales.

4.3 *Temporal dynamics and host specificity of bacterial community structure and core microbiome*

The distinct temporal dynamics of bacterial community structure observed in this study suggested that the coral microbiome was flexible and capable of rapid adaptation to changes, which might facilitate adaptation of the source colonies or transplanted corals to stressful environments (Reshef et al., 2006; Ziegler et al., 2019). Furthermore, bacterial communities of transplanted corals still exhibited significant differences from donor colonies after 1 month of nursery planting in May; whereas by July, they had developed similar bacterial assemblages. Other factors such as benthic assemblage, fragmentation of the natural reef, and nursery frames, might drive bacterial differences (Strudwick et al., 2022). Consistent with our results, microbial communities of *Pocillopora acuta* became similar to those of the local corals at the destination reef within one day and two days post-transplantation (Deignan and McDougald, 2022), while bacterial communities of *A. millepora* fragments changed to more closely resemble source colonies within 30 days of nursery-planting (Strudwick et al., 2022). In comparison with previous studies that revealed a high degree of host specificity from the transplanted fragments (Strudwick et al., 2022; Ziegler et al., 2019), we found similar bacterial community between transplanted AH and AM. These thus highlight that nurseries can contribute to the establishment of similar bacterial communities over time and reduce species-specific differences in bacterial community dynamics compared to the natural reef environment. Moreover, coral can undergo shifts in microbial composition without succumbing to dysbiosis (Deignan and McDougald, 2022). For example, although bacterial families (Moraxellaceae, Comamonadaceae) were more abundant in the affected corals, they can also be isolated from healthy corals (Ziegler et al., 2019). Accordingly, shift in the symbiotic bacterial composition does not exclusively reflect a pathobiome and may contribute to coral holobiont plasticity for withstanding environmental fluctuations (Ziegler et al., 2017, 2019).

The presence of core microbiomes indicates the crucial functional role they play for the host (Zanotti et al., 2020). Significant temporal changes were observed in the core microbiome, but no differences were found based on coral species or transplant treatment. Bacterial groups such as Acinetobacter, Pseudomonas, Bradyrhizobiaceae, Raoultella (Enterobacteriaceae) have commonly been found in coral core microbiomes (Kellogg, 2019). Acinetobacter, a gamma-proteobacteria, has been reported in both healthy and diseased corals, with members of this genus potentially contributing to pathogen defense (Brener-Raffalli et al., 2018; van Bleijswijk et al., 2015). The genus Pseudomonas, known to be part of the coral-associated beneficial core microbiome in the QDU zone, plays an important role in nutrient cycle metabolism and production of anti-microbial compounds (Hernández-Zulueta et al., 2022; Zhu et al., 2023b). *Ralstonia* has been reported as a core microbiome member in both zooxanthellate and azooxanthellate corals, associated with functions like nitrogen fixation, transport, and amino acid metabolism (Ainsworth et al., 2015; Engelen et al., 2018). Despite the genus Stenotrophomonas has a high abundance in the diseased corals from eutrophic waters (Cárdenas et al., 2012; Lee et al., 2012), it also is the dominant genus in the apparently healthy stony and soft corals (Hernández-Zulueta et al., 2022). Bradyrhizobium is widely reported as nitrogen-fixing bacteria in coral holobiont and may assist its hosts by fixing nitrogen (Ceh et al., 2013; Lema et al., 2014). Therefore, the observed changes in the core microbiomes between May and July in our study further suggested the reasonable flexibility of the coral microbiome in response to environmental changes (Aguirre et al., 2022). Taken together, the coral fragments planted in the nursery did not exhibit a distinct reduction in putatively

beneficial core microbiomes compared to the source colonies on the reef (Strudwick et al., 2022), which have been suggested to provide essential functions that allow coral to thrive.

4.4 *Co-occurrence patterns and assembly mechanisms of bacterial communities*

Network analyses can provide a comprehensive understanding of the ecological interactions among microbiome members within the coral holobiont (Leite et al., 2018a; Lima et al., 2020). Our results indicated that the network complexity and robustness decreased from May to July, because sensitive network structures in the QDU season can facilitates rapid coral adaptation to the dynamic upwelling environment (Zhu et al., 2023b). The transplanted coral has higher complexity and stability in addition to the AM network in July compared with the natural population, coral hosts with highly connected microbiomes are potentially more robust to environmental perturbations. Similarly, the coral microbiome from the inner reef zone exposed to stressful temperature fluctuations, potentially confers resilience to environmental disturbances, whereas host-associated microbial network in the outer reef with a more stable environment exhibits tightly connected interactions (Lima et al., 2020).

The network complexity and stability in source colonies of AM were higher than those of AH throughout the two sampling periods. Another study has also observed significant variation in microbial networks across coral species, showing compartmentalization based on coral host identity (Dunphy et al., 2019). These patterns may be attributed to the successive vertical transmission of specific bacterial populations, leading to correlations (Leite et al., 2018b). Interestingly, we found that differences in the bacterial networks of transplanted corals between species were less pronounced in July, aligning with similar bacterial diversity and community between coral species. In the current study, bacterial communities of two coral species in a more homogeneous nursery environment tended to occupy a similar biological niche and interaction (Freilich et al., 2011; Lu et al., 2022). Additionally, it is believed that higher stability of the coral microbiome is associated with a greater complexity of interactions, making them less susceptible to microbial invasion or switching (Leite et al., 2018a; Mallon et al., 2015).

Understanding the assembly mechanisms that shape microbial community is a key topic in ecology (Nemergut et al., 2013; Stegen et al., 2012), but little is known about the assembly processes of coral microbial communities (Price et al., 2021). In this study, the ecological assembly processes of bacterial communities showed significant differences between May and July, while there was a consistent assembly mechanism for different coral species and transplanted corals. Specifically, stochastic process shaped the bacterial community of all corals in May, while deterministic process dominated the assembly process in July. A previous study also suggested that niche-based deterministic selection dominated the bacterial community assembly in corals during the upwelling season, where upwelling interference, sensitive network structures and closer bacterial associations might partly explain this observation (Zhu et al., 2023b). Stochastic processes are hypothesized to play a more critical role in microbial communities associated with corals under environmental stress, such as elevated temperatures and nutrient pollution (Zaneveld et al., 2016, 2017). However, it is wo rth noting that stochastic processes can also been observed in presumably healthy corals (Price et al., 2021; Zhu et al., 2022b). Therefore, both the bacterial communities of source colonies and transplanted *Acropora* corals were responsive to seasonal environmental fluctuations, contributing to the different community assembly processes.

Understanding the link between coral microbiome and environmental changes is essential for underpinning effective management and restoration strategies (Glasl et al., 2017). More importantly, we correlated the bacterial dynamic response of transplanted fragments to the marine environmental parameters in the area where the nursery was located. Among the detected environmental factors, our study revealed that physical variable (e.g., temperature) and nutrient condition (e.g., ammonium) played key roles in the shifts of coral associated bacterial communities. Water quality has been proved to be the important environmental drivers in controlling the coral microbiome (McDevitt-Irwin et al., 2017). For example, seawater temperature and nutrient enrichment can significantly affect the coral-associated bacterial communities from the Hainan Island (Zhu et al., 2023a, 2023b). Corals with environmental flexibility that adjust microbial composition to offset possible negative dysbiosis will be “winners” from climate change (Röthig et al., 2020; Ziegler et al., 2019). In fact, we found all coral samples from transplanted fragments and source colonies were macroscopically healthy, indicating that microbiome flexibility is a key mechanism for coral to tolerate the environmental pressure (Deignan et al., 2023; Voolstra and Ziegler, 2020). Knowledge about the dynamic response of coral microbiome to specific environmental variables is essential for selecting the most appropriate areas and conservation methods.

5 Conclusions

In summary, our study characterized bacterial temporal dynamics of two Acropora coral hosts between transplanted fragments and source colonies including the community composition, co-occurrence pattern and assembly process. We found that seasonal environmental fluctuations significantly influenced the bacterial composition, assembly, and network, indicating that the microbiome of nursery-planting coral fragments showed similar flexibility to that of corals on source reefs under regional environ-

mental scale. The critical bacterial assemblages and assembly mechanisms between the transplants and source colonies became similar over time for corresponding coral species, with transient changes in bacterial diversity and interaction network attributed to the effects of nursery frames. Furthermore, microbial communities associated with coral species of source colonies persisted high host specificity, while transplanted fragments in nursery had similar bacterial diversity, community structure and core microbiome across coral species, indicating that in situ coral nursery caused microbial community homogenization in transplants. Seawater temperature and ammonium concentration played key roles in the compositional shifts of bacterial communities associated with the transplanted fragments and source colonies. Finally, our findings suggested that shifts and homogeneity in bacterial communities of commonly transplanted *Acropora* corals might be adaptations to environmental perturbations and the nursery-planting process during short-term transplantation. Nevertheless, long-term microbial monitoring of transplanted fragments is needed to understand how they help corals adapt to the nursery environment.

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Supplementary information:

Fig. S1. Location of transplantation sites at the Fennjiezhou Island in the South China Sea. The map is sourced from Google Earth.

Fig. S2. Example of attached coral fragments for *Acropora hyacinthus* and *Acropora microphthalma* from in situ nursery frame.

Fig. S3. Temperature changes showing sampling time and occurrence of Qiongdong upwelling in the repaired area during the experimental period.

Fig. S4. Seawater environmental parameters at coral restoration site and reef area in May and July.

Fig. S5. Survival rate and growth rate for transplanted coral fragments of *Acropora hyacinthus* and *Acropora microphthalma* in May and July.

Fig. S6. The rarefaction curves of the Shannon index of various samples.

Fig. S7. Association of the bacterial community (Bray-Curtis distance) of *Acropora hyacinthus* and *Acropora microphthalma* and environmental factors was analyzed by Mantel tests.

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