RESEARCH ARTICLE

Bacterial and eukaryotic community interactions might contribute to shrimp culture pond soil ecosystem at different culture stages

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HIGHLIGHTS

- Positive microbial interaction dominating in sedimentary bacterial and eukaryotic communities.
- Homogeneous selection process governed the assemblage of both bacterial and eukaryotic communities.
- Bacterial and eukaryotic diversities were in the reverse correlations with microbial positive interaction.

GRAPHICAL ABSTRACT

ABSTRACT

Sedimentary bacterial and eukaryotic communities are major components of the aquatic ecosystem. Revealing the linkages between their community structure and interactions is crucial to understand the diversity and functions of aquatic and soil ecosystems. However, how their diversity and assembly contribute to their interactions on time scale is unclear. This study examined sedimentary bacterial and eukaryotic communities in shrimp culture ponds at different culture stages. The most abundant bacteria were Proteobacteria (38.27%), whereas the most abundant eukaryotes were Chytridiomycota (27.48%). Bacterial and eukaryotic diversities were correlated ($P < 0.05$), implying the strong interactions between bacteria and eukaryotes. Results showed that the bacterial and eukaryotic communities became increasingly similar on a local scale along with the shrimp culture. Only the eukaryotic community significantly increased in similarity along with the shrimp culture ($P < 0.05$), suggesting that the sedimentary eukaryotic community structure is sensitive under shrimp culture. Co-occurrence network modeling indicated that positive microbial interactions were dominant. The homogeneous selection was the major driver of community assembly. Bacterial diversity negatively correlated with operational taxonomic units and positive links in networks ($P < 0.05$), whereas eukaryotic diversities positively correlated with positive links in networks ($P < 0.05$). This study broadens our knowledge about sedimentary microbial diversity, community assembly, and interaction patterns on time scale, providing a reference for the sustainable management in aquaculture production.

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ARTICLE INFO

Article history:

Received December 28, 2020

Revised January 25, 2021

Accepted February 7, 2021

Keywords:

Sediment

Shrimp culture

Bacteria

Eukaryotes

Microbial community

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1 Introduction

Sedimentary microbial communities possess diverse functions and contribute to the food webs and biogeochemical cycles (Peoples et al., 2019). As parts of the pedosphere, sedimentary microbes play important roles in the aquatic ecosystem. From the “One health” perspective, safeguarding planetary health in soil biota management is important because of its complex ecologies, interactions, and evolutionary forces (Holmes et al., 2016; Zhu et al., 2019). The sediment system is important in processes involved in the transformation and transport of terrigenous materials into water, including the adsorption of pollutants and nutrients from the surrounding environment and the growth of microbes (Ramalingam and Chandra, 2018). Sediments could more effectively trap additional materials from the water than sandy soil, making the former more sufficient for microbial growth than the latter (Hope et al., 2020). Microbes, which are primary consumers in sediments, are sensitive to environmental gradients; for instance, crude oil contamination can increase the abundance of hydrocarbon-degrading bacteria in marine sediment (Yue et al., 2019). Bacterial community structure is significantly related to the characteristics of nutrients and heavy metals in sediments, and it could be an important indicator of environmental pollution (Zhang et al., 2020). Those muddy sediments involved in farming productivity probably enrich additive nutrient materials from fodders, such as aquaculture pond sediments. As an important part of the aquaculture ecosystem, pond sediment has diverse functions within ecosystems, as evidenced by the presence of more diverse microbes in sediments than in other aquaculture habitats (Hou et al., 2018; Xiong et al., 2018). However, studies about the microbial community in aquaculture ecosystems remain elusive.

Shrimp culture pond ecosystem (SCPE) mainly consists of pond water, sediment, and culture animal intestinal environments. Microorganisms of multiple habitats in aquaculture ecosystems play important roles in animal health, including the development of diseases, such as shrimp hepatopancreatic necrosis syndrome (Huang et al., 2016) and white feces syndrome (Huang et al., 2020). They are also important for water quality and nutrient cycle. Several microorganisms (e.g., *Streptomyces* sp.) in aquaculture ecosystems can accelerate the decomposition of residual feed and feces to purify water quality (Tan et al., 2016; Hou et al., 2017), and others can convert toxic substances (e.g., ammonia, nitrite, and hydrogen sulfide) into low- or non-toxic formations to protect the survival of cultural species (Su et al., 2016; Wei et al., 2020). Nevertheless, aquaculture pond sediments could also harbor opportunistic pathogens that might be harmful to animals and humans (Fan et al., 2019; Zhou et al., 2019). Thus, microbial communities in culture pond sediments are closely related to environmental and human health. However, studies about SCPE sediment microbial communities and their response at different culture stages are still limited.

Microorganisms do not live separately in the natural

environment. Their interactions are ubiquitous, diverse, and critically important for community function, biogeochemical cycles, and organism evolution (Wright et al., 2013; Ma et al., 2020; Shi et al., 2020). Mutualism is a common interaction in microbial systems, giving rise to nutrient exchange and antibiotic resistance conferral (Peoples et al., 2019). In ecological research, correlation network analysis is widely applied to predict positive and negative ecological interactions between various species in ecosystems, and it is applied to understand the organization of microbial communities and interactions between their components (Berry and Widder, 2014).

The present study investigates the diversity, assembly, and interaction of microbial communities, including bacterial and eukaryotic communities in sediments at different culture stages. SCPE sediments are under long-term feed supplement settlement during shrimp culture activities. Therefore, their abundant nutrients could support the survival of diverse and numerous microbes, which might weaken the competitive relationships within the microbes. In this study, we hypothesize that positive microbial interactions are dominant in sedimentary bacterial and eukaryotic communities at different shrimp culture stages; bacterial and eukaryotic communities could differently contribute to the microbial interaction. Statistical correlation analysis based interaction exploration was performed under the level of microbial operational taxonomic units (OTUs), communities, and temporal scales within the SCPE.

2 Materials and methods

2.1 Sample collection

From June to August 2017, 84 sediment samples were collected from four commercial shrimp culture ponds in Zhuhai (113.22° E, 22.37° N), Guangdong Province, China. The ponds were approximately uniform in size (2000 m²) with approximately 0.7 m water depth. Shrimp larvae were introduced into the ponds. The shrimp length was 0.8 cm on average, and the stocking density was 100 000 shrimps for each pond. Sediment samples were collected (Wei et al., 2020) from the 2nd day after the shrimp larvae were introduced into the pond to the 58th day of culture, with an interval of approximately 8 days (designated as Day02, Day13, Day21, Day 31, Day 42, Day51, and Day58). Sample collection was performed in triplicate with a core sampler. Sediments from each pond were placed into sealed sterile plastic bags in a cooler with ice for transport to the laboratory. These samples were homogenized and dried with a freeze dryer (LGJ-50F, Beijing Songyuan Huaxing Technology Development Co., Ltd., Beijing, China). The other sediments were stored at –80°C for DNA extraction.

2.2 DNA extraction and 16S rRNA amplicons sequencing

Genomic DNA was extracted with a Power Soil DNA Isolation

Kit (QIAGEN, Hilden, Germany) in accordance with the manufacturer's protocol. The PCR products were equally combined and paired-end sequenced (2×300) by Illumina MiSeq platform (Illumina, San Diego, CA, USA) from Majorbio Bio-Pharm Technology Co. Ltd. (Shanghai, China). The 338F and 806R (5'-ACTCCTACGGGAGGCAGCAG-3' and 5'-GGACTACHVGGGTWTCTAAT-3') universal primer pair was used to amplify the V3–V4 regions of the bacterial 16S rRNA gene (Khramenkov et al., 2013). The 817F and 1196R (5'-TTAGCATGGAATAATRAATAGGA-3' and 5'-TCTGGACCTGGTGGATTTC-3') universal primer pair was used to amplify the V5–V7 regions of the eukaryotic 18S rRNA gene (Rousk et al., 2010).

2.3 Statistical analysis

2.3.1 Bioinformatics analysis

Both 16S and 18S rRNA gene amplicon paired-end sequences were merged using FLASH (Magoc and Salzberg, 2011), and the merged sequences were processed following the Usearch pipeline (version 11.0.667). In brief, the sequences with ambiguous bases were discarded if the expected error value was higher than 1.0 (Edgar, 2010). Chimeric sequences were removed using the UCHIME algorithm (Edgar et al., 2011). The 16S rRNA gene amplicon sequences were finally rarefied to 23 153, whereas the 18S rRNA gene amplicon sequences were finally rarefied to 23 338. Sequences with a distance-based identity of 97% or greater were grouped into OTUs using the UPARSE-OTU algorithm (Edgar, 2013). The most abundant sequence from each OTU was selected as a representative and then taxonomically assigned against the Silva SSU database 132 using the RDP Classifier algorithm (<http://rdp.cme.msu.edu/>), which enables each identified OTU to have a close relative.

The richness, Shannon, Simpson, Chao1 ACE, and phylogenetic branch length (PD_whole_tree) indices with Bray–Curtis distance of bacterial and eukaryotic communities were calculated separately using picante package (version 1.8.2) in R (Kembel et al., 2010). The correlation between bacterial and eukaryotic communities was also calculated using the Mantel test based on community sample-paired Bray–Curtis distance matrix correlation calculation under Spearman's algorithm in R (Anderson, 2001).

2.3.2 Co-occurrence network analysis

Co-occurrence network analysis was conducted based on statistically robust consideration if the absolute Spearman's correlation coefficient $|\rho|$ was not less than 0.8 and if the P -value was no more than 0.01 (Quintela-Baluja et al., 2019). The P -value generated from multiple correlation analysis was adjusted using Holm's multiple testing, a less conservative correction algorithm to reduce the chances of false-significant results (Eichstaedt et al., 2013; Fu et al., 2014). Network analyses were performed in R and were visualized in Gephi (Version 0.9.2). The microbes and connections that partici-

pated in the network model, regardless if the correlation was positive or negative, were also counted for further analysis.

2.3.3 Microbial community assembly

The assembly of microbial community was calculated using a framework to quantitatively infer community assembly mechanisms through phylogenetic bin-based null model analysis (iCAMP) in iCAMP packages (version 1.2.9) under the default parameters with the argument of bin.size.limit = 24 (Ning et al., 2020). In detail, the bins were divided according to the phylogenetic relationships of observed taxa. The process governing each bin was identified based on the null model analysis of the phylogenetic diversity by calculating the beta net relatedness index (β NRI) on the basis of the phylogenetic mean pairwise distance (Tsirogiannis and Sandel, 2014). Taxonomic β -diversities were measured using the modified Raup–Crick metric. For each bin, the fraction of pairwise comparisons with β NRI < −1.96 was considered as the percentage of homogeneous selection, whereas the fraction of pairwise comparisons with β NRI > +1.96 was considered as the percentage of heterogeneous selection based on the threshold applied previously (Fine and Kembel, 2011; Stegen et al., 2015). The taxonomic diversity metric RC was used to partition the remaining pairwise comparisons with $|\beta$ NRI| ≤ 1.96. The fraction of pairwise comparisons with RC < −0.95 was treated as the percentages of homogenizing dispersal, whereas the fraction of pairwise comparisons with RC > +0.95 was considered as dispersal limitation. The remains with $|\beta$ NRI| ≤ 1.96 and $|RC|$ ≤ 0.95 represent the percentages of drift (Stegen et al., 2013; Stegen et al., 2015).

2.3.4 Correlation and cluster analyses

The significance (P -value) and explained sum of squares (R -squared value) of the fitted curves from linear regression were summarized using R in version 4.0.2 (Revolution Analytics, America) (Zhou et al., 2020). Non-metric multidimensional scaling (NMDS) of each sample and permutational multivariate analysis of variance (PerMANOVA) were conducted using vegan package (version 2.5-6) in R (Anderson, 2001). k -means cluster analysis was also conducted in R (Hartigan and Wong, 1979). The correlation between bacterial and eukaryotic communities was calculated via Bray–Curtis distance-based mantel test analysis (Beals, 1984).

Sequencing data from this study have been submitted to the NCBI Sequence Read Archive under accession number SRP298633.

3 Results

3.1 Taxonomic composition and diversity of bacterial and eukaryotic communities

A total of 2635695 high-quality merged 16S rRNA gene amplicon sequences were obtained, resulting in 2533

bacterial OTUs. The whole stages of the shrimp culture had 2199 bacterial OTUs, accounting for 86.81% of the total OTUs in the shrimp pond sediments (Fig. 1A). The bacterial OTUs could be classified into 46 phyla. Among them, the most abundant phylum was Proteobacteria (38.27%), followed by Bacteroidetes (26.18%), Chloroflexi (8.43%), and Acidobacteria (5.23%) (Fig. 1C).

For eukaryotic communities, 2678443 high-quality sequences were obtained, resulting in 478 OTUs. The whole stages of the shrimp culture had 272 eukaryotic OTUs, accounting for 56.90% of the total OTUs in the shrimp pond sediments (Fig. 1B). The eukaryotic OTUs could be classified into 47 phyla. Among them, the most abundant phylum was Chytridiomycota (27.48%), followed by Eumetazoa (14.43%), Intramacronucleata (13.74%), and Craspedida (3.75%) (Fig. 1D).

The alpha-diversity of bacterial and eukaryotic communities was calculated (Fig. 2). For instance, the richness of shrimp

pond sedimentary bacterial communities ranged from 1523 to 1975. The richness of sedimentary bacteria showed an increased tendency across the shrimp culture, whereas that of eukaryotic communities ranged from 144 to 294. The Shannon indices of the bacterial and eukaryotic communities ranged from 5.74 to 6.38 and from 1.94 to 4.12, respectively. The Simpson indices of the bacterial and eukaryotic communities ranged from 0.98 to 0.99 and from 0.64 to 0.97, respectively. The PD_whole_tree index, which calculates the sum of the total phylogenetic branch length of the samples, ranged from 181.19 to 215.52 and from 14.99 to 23.22 in the bacterial and eukaryotic communities, respectively. The richness, ACE, and PD_whole_tree indices between the bacterial and eukaryotic communities were correlated ($P < 0.05$ by Spearman correlation analysis, Table 1). Similarly, the Bray-Cutis distance between the bacterial and eukaryotic communities was correlated ($P < 0.05$ by Mantel test).

Fig. 1 OTU number and top taxonomic of bacterial and eukaryotic community OTUs. Common and stage-unique OTU numbers in (A) bacteria and (B) eukaryotes at different culture stages. Top phyla annotated from (C) bacterial community and (D) eukaryotic community.

Fig. 2 Alpha-diversity of bacterial and eukaryotic communities at different culture stages. The column bar consists of mean $\pm$ standard deviation (sd).

3.2 Community turnover in bacteria and eukaryotes

We calculated the community turnover among different shrimp culture stages (Bray–Curtis distance-based NMDS analysis, Figs. 3A, 3B). The bacterial and eukaryotic communities differed between any of the seven time points ($P < 0.05$ by PerMANOVA analysis), which could be clustered into two distinct clusters. The first cluster included Day02, Day13, and Day21, whereas the second cluster included Day31, Day42, Day51, and Day58 (k -means analysis, Figs. 3A, 3B). Temporal distance decay analysis based on linear regression also indicated that the sedimentary bacterial and eukaryotic

communities significantly changed over time ($P < 0.05$ by linear regression analysis, Fig. 3C), with a community turnover rate of 0.39% per day in bacteria and 0.56% per day in eukaryotes (Fig. 3C). The community similarity was extracted from each separate culture stage to examine how they varied temporally on a local scale. Results showed that the bacterial and eukaryotic communities became increasingly similar along with the shrimp culture. This variation in the eukaryotic communities was significant ($P < 0.05$, Fig. 3D), whereas that in the bacterial communities was not significant ($P > 0.05$).

3.3 Interaction between bacterial and eukaryotic communities during shrimp culture

The Spearman's correlation coefficient $|\rho| \geq 0.8$ was used to

explore potential strong interaction between microbes through a co-occurrence network analysis. As shown in Fig. 4, 383 bacterial and 55 eukaryotic OTUs were identified in the network, with positive links between bacteria, between

Fig. 3 Variations in sedimentary bacterial and eukaryotic communities at different shrimp culture stages. MNDS analyses of (A) bacterial communities and (B) eukaryotic communities at shrimp different culture stages. (C) Temporal distance decay analysis of bacterial and eukaryotic communities in shrimp culture. (D) Similarity analysis of bacterial and eukaryotic communities in different culture stages and central points. The deviation bar consists of mean±sd.

Table 1 Spearman's correlation between bacterial and eukaryotic diversities

Microbial diversity		Coefficient	P-value
Alpha	Richness	0.316	0.003
	Shannon	0.143	0.193
	Simpson	0.136	0.218
	Chao1	0.204	0.063
	ACE	0.232	0.033
	PD_whole_tree	0.215	0.049
Beta	Bac-Euk	0.740	0.001

"Bac" means bacteria, "Euk" means eukaryotes.

Fig. 4 Network analyses of sedimentary microbial communities. (A) General co-occurrence network of microbial community. (B) Topological information of the microbial community co-occurrence network. Bacterial and eukaryotic OTUs are network nodes, black line means positive correlations, and red line means negative correlations.

bacteria and eukaryotes, and between eukaryotes accounting for 70.60%, 9.23%, and 4.03%, respectively. For negative edges, links between bacteria, between bacteria and eukaryotes, and between eukaryotes accounted for 8.84%, 7.06%, and 0.23%, respectively. When dividing the networks by time points, bacterial and eukaryotic OTUs identified in the network ranged from 213 to 443 and from 111 to 143, respectively. The total positive edges accounted for 93.35%–97.80% and the negative edges accounted for 2.20%–6.65% in the different stage networks (Table 2).

3.4 Sedimentary community assembly mechanism

The microbial ecological process plays an important role in building community structure, dynamics, and interactions. Community assembly was calculated using iCAMP to quantify various ecological processes within the bacterial and eukaryotic communities (Fig. 5). Sedimentary bacterial communities were mainly driven by a homogeneous selection process, with an increased tendency across the shrimp culture (Fig. 5A). Eukaryotic communities were also mainly driven by homogeneous selection in Day02, Day13, Day21, Day31, and Day58 of the shrimp culture, whereas the drift process was dominant in Day42 and Day51.

3.5 Correlation between sedimentary microbial community diversities, assembly processes, and interaction

We conducted a Spearman algorithm to explore the correlations among sedimentary microbial community diversities, assembly processes, and interaction. The bacterial alpha-diversities and eukaryotic beta-diversities were correlated to the network nodes and edges. In detail, bacteria ACE, Chao1, PD_whole_tree, and richness indices were negatively correlated to the OTUs that participated in the networks ($P < 0.05$ by Spearman correlation, Fig. 6). Bacterial richness was also negatively correlated with bacterial OTUs, total positive links, and positive links between bacteria in networks ($P < 0.05$ by Spearman correlation, Fig. 6). Eukaryotic beta-diversities were positively correlated with total positive links, positive links between bacteria, and positive links between bacteria and eukaryotes ($P < 0.05$). Meanwhile, community assembly processes showed no significant correlations with network nodes and edges.

4 Discussion

Understanding the relationships between microbial diversity and ecosystem is important in ecology (Wu et al., 2019). In the

Table 2 Topological information of sedimentary microbial network analyses at different shrimp culture stages.

Network properties		Day02	Day13	Day21	Day31	Day42	Day51	Day58
Nodes	Bac	443	329	323	295	247	213	330
		(18.62%)	(13.91%)	(13.37%)	(11.80%)	(9.87%)	(8.55%)	(13.38%)
	Euk	143	132	116	127	139	111	119
		(35.31%)	(33.33%)	(28.09%)	(31.99%)	(34.66%)	(27.61%)	(30.91%)
	Bac-Bac	1111	585	381	472	267	188	436
		(57.99%)	(44.28%)	(46.24%)	(47.29%)	(33.42%)	(33.75%)	(46.19%)
Edges (Positive)	Bac-Euk	640	562	307	376	324	244	370
		(33.40%)	(42.54%)	(37.26%)	(37.68%)	(40.55%)	(43.81%)	(39.19%)
	Euk-Euk	120	145	85	122	158	88	84
		(6.26%)	(10.98%)	(10.32%)	(12.22%)	(19.77%)	(15.80%)	(8.90%)
	Bac-Bac	25	14	30	9	26	28	21
		(1.30%)	(1.06%)	(3.64%)	(0.90%)	(3.25%)	(5.03%)	(2.22%)
Edges (Negative)	Bac-Euk	20	12	20	12	19	7	27
		(1.04%)	(0.91%)	(2.43%)	(1.20%)	(2.38%)	(1.26%)	(2.86%)
	Euk-Euk	0	3	1	7	5	2	6
		(0%)	(0.23%)	(0.12%)	(0.70%)	(0.63%)	(0.36%)	(0.64%)

“Bac” means bacteria, “Euk” means eukaryotes.

present study, we examined the SCPE sedimentary diversity, assembly mechanism, and interactions within bacterial and eukaryotic communities at different culture stages. Results suggested that positive microbial interactions dominated the sedimentary bacterial and eukaryotic communities; homogeneous selection governed the assembly of bacterial and eukaryotic communities. Bacterial and eukaryotic diversities showed reverse correlations with microbial positive interaction.

Eukaryotes are multicellular organisms with possible considerable amplicon detection bias because of soil DNA extraction (Countway et al., 2005; Caron et al., 2012). Therefore, the read counts of 18S genes are commonly used to estimate the proportions of eukaryotes in amplicon sequencing analyses (Gong and Marchetti, 2019). However, the relative abundance of 18S gene copies in eukaryotes collected from environmental samples can be attributed to variations in the relative abundance of different organisms and in the genomic 18S copy number among those organisms (Zhu et al., 2005; Godhe et al., 2008). The results of flower plot showed that more OTUs occurred at the whole culture stages in the bacteria than in the eukaryotes, implying that the sedimentary bacterial community structure is more stable than the eukaryotic community structure in shrimp culture. This result was verified by the lower bacterial turnover rate than eukaryotic turnover rate from distance decay analysis. Another explanation could be the different sequence depths derived from the bacterial and eukaryotic communities.

The bacterial and eukaryotic communities were becoming

increasingly different from the beginning of the shrimp culture because of the significant change in microbial communities (Fig. 3). The remained sedimentary microbial community might not be optimum for the growth of juvenile shrimp (Zeng et al., 2017). According to aquaculture production experience, when a pond has finished its culture, its sediment needs disinfection and exposure before the next culture. These dramatic environmental disturbances cause the reconstruction of the pond sediment ecosystem, including the microbial communities (Hou et al., 2017). Finally, the pond sediment status was reset for the growth of juvenile shrimp. The bacterial and eukaryotic communities implied that the sedimentary microbial communities can be treated as two distinct culture periods during shrimp culture (Figs. 3A, 3B). Researchers focused on the biogeographical distance change of microbial community on the global or regional scale (Zhang et al., 2012; Saunders et al., 2016; Wu et al., 2019). Reports about the temporal distance change on a local scale are limited. In the present study, the variation in local sedimentary community similarity was different between the bacteria and eukaryotes at different shrimp culture stages (Fig. 3D). The significance in eukaryotic community similarity might result from the growth of the shrimp and from the dissimilarity generated by different culture pond habitat status, which was more sensitive for the living of eukaryotes than bacteria.

Shrimp culture ponds are typical anthropogenic environments consisting of multiple microbial habitats. Additive nutrients are needed for efficient culture and nutrients enrich

Fig. 5 Community assemblage analysis of sedimentary bacterial and eukaryotic communities at different shrimp culture stages. (A) Bacterial community assembly and (B) eukaryotic community assembly at different shrimp culture stages. The column bar consists of mean $\pm$ sd.

in the culture pond sediment, forming a unique environment for the microbial community succession (Hope et al., 2020). Most microbial interactions were positive, which implied that the abundant nutrients weakened the substantial competitive relationship from proportional changes (Mikhailov et al., 2019). Both bacterial and eukaryotic communities in the shrimp pond sediments became increasingly similar along with the shrimp culture (Fig. 3D), suggesting that homogeneous selection is a dominant process (Zhou and Ning, 2017). By contrast, the dispersal limitation process was relative to species sorting, which can strongly mediate species coexistence in continental-scale agricultural soil microbiomes (Jiao et al., 2020). In the present study, the homogeneous selection correlated with the general positive correlation of the microbial interactions because of homogeneous abiotic and biotic environmental conditions facilitated by continuing additive nutrient settlement (Zhou and Ning, 2017). This result coincided with recent findings that bacterial and eukaryotic communities are governed by homogeneous selection in shrimp gut with age (Xiong et al., 2020). However, the correlation between the assembly and positive interactions

were not significant. The microbial interaction might not be highly sensitive to the quantitative change in assembly (Fig. 6). Interestingly, the bacterial alpha-diversities (ACE, Chao1, PD_whole_tree, and richness indices) were negatively correlated with the microbes identified in the networks, implying that the increase in bacterial diversity caused the decrease in microbes identified in network interactions. Eukaryotic Bray-Curtis beta-diversity and bacterial richness indices showed reverse correlations with the positive interactions, suggesting that sedimentary bacterial and eukaryotic diversities could have different responses to the microbial interactions.

5 Conclusion

A strong correlation was found between bacterial and eukaryotic communities in terms of diversity and variation. The bacterial and eukaryotic communities on a local scale were becoming increasingly similar along with the shrimp culture, but only the eukaryotic community showed signifi-

Fig. 6 Spearman correlation between sedimentary microbial network nodes, edges, and community diversities (alpha- and beta-diversities), assembly processes respectively in shrimp culture stages. “Bac” means bacteria, “Euk” means eukaryotes. The Spearman correlation *P*-values are interpreted as star symbol, * means *P* < 0.05, ** means *P* < 0.01.

cance ($P < 0.05$). The positive interactions were dominant in the relationship within microbial communities. Moreover, the sedimentary bacterial and eukaryotic communities were mainly driven by the homogeneous selection process. Bacterial and eukaryotic diversities were found in reverse correlations with positive interactions. These results enhanced the understanding of microbial interactions within the diversity, variation, and community assembly of the sedimentary bacterial and eukaryotic communities. This study could be used as reference for further understanding the microbial interactions in SCPE and for the sustainable management in aquaculture production.

Acknowledgments

This work was financially supported by the China Agriculture Research System (CARS-48); China-ASEAN Maritime Cooperation Fund, China-ASEAN Center for Joint Research and Promo-

tion of Marine Aquaculture Technology; Guangdong MEPP Fund (NO. GDOE (2019) A21); Key Research and Development Projects in Guangdong Province (2020B0202010009); Guangzhou Science Technology and Innovation Commission Project (201510010071); and Guangdong Ocean and Fishery Bureau Project (20164200042090023).

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