Wu, Lianzuan; Yang, Ping; Luo, Liangjuan; [et al.]. «Conversion of mangrove forests to shrimp ponds in southeastern China destabilizes sediment microbial networks». Geoderma, Vol. 421 (September 2022), art. 115907. DOI 10.1016/j.geoderma.2022.115907

Conversion of mangrove forests to shrimp ponds in southeastern China destabilizes sediment microbial networks

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ABSTRACT

Within the ecosystem, mangroves serve diverse functions by acting as a carbon sink, removing nitrogen, providing habitats for marine organisms, and regulating climate. Nowadays, many mangrove forests are being converted to shrimp ponds across the world, and several studies have quantified the effects of this conversion on soil carbon stocks and greenhouse gas emissions. However, its effects on the soil microbial community structure and assembly processes remain unclear. In the present study, high-throughput sequencing and multivariate statistical analyses were used to quantify the characteristics of soil microbial communities in common mangrove types in southeastern China and the adjacent converted shrimp ponds. The relative abundance of *Verrucomicrobia*, *Cyanobacteria*, and *Firmicutes* was significantly increased in the shrimp pond sediment compared with that in the mangrove sediment, whereas the archaea, represented by *Crenarchaeota* and *Euryarchaeota*, exhibited the opposite patterns. Moreover, the sediment microbial communities in the shrimp ponds exhibited more obvious biogeographical distributions than those in the mangrove habitat. Null model analysis revealed that variable selection (via deterministic processes) governed the microbial community assembly in the mangrove sediments, while dispersal limitation (via stochastic processes) shaped the microbial community structure in the shrimp pond sediments. Our findings suggest that converting mangrove forest habitats to shrimp ponds significantly alters the sediment microbial networks, rendering them unstable (by disrupting the network topology parameters such as modularity, total cohesion, and negative cohesion). This may in turn lead to alterations in various ecosystem functions in response to habitat conversion, highlighting the need for better preserving mangroves through appropriate climate change mitigation measures.

Keywords: Mangroves; Shrimp pond; Land use change; Community assembly; Microbial networks

1. Introduction

Mangrove forests are widely distributed along both tropical and subtropical coasts and provide diverse ecosystem services (Nellemann et al., 2009). However, mangroves are under threat due to both natural (e.g., erosion and aggradation) and anthropogenic forces (e.g., agricultural practices, alien species invasion, aquaculture, tourism, and urban development) (Upadhyay et al., 2002; Sahu et al., 2005). Among these, shrimp pond or fishpond construction in the coastal areas of Southeast Asia is a major cause of mangrove deforestation (Valiela et al., 2001; Giri et al., 2011; Richards and Friess, 2015). Since several ecosystem services associated with mangrove forests (e.g., carbon sink function and nitrogen removal) are mediated by the microbes present in these environments, the microbial communities of these forests represent a critical component of ecosystem health (Quan et al., 2015; Ward et al., 2019). Mangroves harbor large microbial populations, which impact nutrient biogeochemical cycling, methane cycling, ammonia oxidation, and sulfate reduction (Bhattacharyya et al., 2015; Liu et al., 2018). Although several studies have reported changes in both sediment carbon storage and carbon gas emission following the conversion of mangrove forests to aquaculture ponds, little is known regarding the dynamics of sediment microbial community structure and assembly processes in these forests following such conversions.

Mangrove forests in the southeastern coastal zone of China have frequently been converted to shrimp ponds. Given the large expanse of these conversions, estimating the potential differences in the biogeography of sediment microbial communities in these regions is a major challenge. The evaluation of distance–decay relationships (DDRs), which can be used to monitor the variations in microbial communities as a function of geographical distance, is the most well-established method for describing the geographical distribution of microorganisms (Anderson et al., 2011; Chu et al., 2020). At the large scales, DDRs affect various ecological processes, including environmental heterogeneity and dispersal history (Vellend, 2010; Nemergut et al., 2013; Stegen et al., 2013; Wu et al., 2017). Moreover, the DDR slope, which reflects the differences in species turnover rates across various locations, may vary according to the habitats and ecosystems (Wang et al., 2017). Furthermore, artificial reclamation and conversion to aquaculture ponds have evidently altered coastal wetland habitats, turning them from intermittently flooded, semi-open mangrove forests to long-term flooded, closed aquaculture ponds. However, only one study has reported that the mangrove sediment microbial turnover is weakly correlated with the spatial scale owing to the homogeneity of the marine environments (Zhang et al., 2019). Therefore, the biogeography of sediment microorganisms in coastal wetlands must be evaluated under different habitat conditions.

There has been a recent paradigm shift in microbial biogeographical studies from originally being focused solely on describing the geographical distribution patterns of microbes to illustrating the mechanisms that drive the assembly of these microbial communities (Jiao et al., 2021). Both deterministic and stochastic processes are crucial for mediating microbial community assembly and its impact on ecological variation (Dumbrell et al., 2010; Ofiteru et al., 2010; Langenheder and Székely, 2011;

Wang et al., 2013). Niche-based deterministic processes, represented by both abiotic and biotic factors, often shape the microbial community assemblage patterns and are closely aligned with the contemporary environmental conditions (Vellend, 2010; Hanson et al., 2012; Liu et al., 2017). Conversely, stochastic processes (e.g., dispersal and ecological drift) strongly affect microbial community patterns (Ramette and Tiedje, 2007; An et al., 2019). Therefore, community assembly is presumed to largely be mediated by both deterministic and stochastic processes. Changing in microbial community assembly under habitat conversion acrosss various ecosystems have been widely attention (Lan et al., 2020; Liu et al., 2021; Yang et al., 2022; Zhang et al., 2022). It is generally believed that habitat conversion results in changes in the process of microbial community assembly, however, a study involving forest ecosystems claimed no changes in community assembly. A plausible explanation for this discrepancy is that the study did not address a specific ecological process. Thus, land use change may directly alter microbial community assembly process through changing in types and intensity of disturbance, the examined systems and environmental factor (Jiang and Patel, 2008; Liu et al., 2021; Zhou et al., 2014). Deterministic processes play prominent roles in driving sediment bacterial community assembly in mangrove habitats (Zhang et al., 2019). However, the conversion of mangrove forests to aquaculture ponds leads to changes in these habitats from an open to a closed system. A closed habitat inevitably restricts microorganism migration, which may affect the stochastic parameters of these systems, as already evidenced in fluid and non-fluid systems (Zhou et al., 2014). Additionally, the conversion of mangrove forests to shrimp ponds may significantly alter the nutrient balance of the associated sediments. As such, nutrient input can enhance compositional stochasticity by promoting the ecological drift and weakening the competition among microorganisms, thereby increasing the importance of stochastic processes in community assembly (Chase and Myers, 2011). Another study on the mesoscale showed that bacterial community variation in the sediments of aquaculture ponds was mainly controlled by total nitrogen, and then pointed out that the community assembly was dominated by stochastic processes (Hou et al., 2021). Thus, we hypothesized that the conversion of mangrove forests to aquaculture ponds will promote the stochastic effects on microbial communities in these habitats.

Interactions among diverse microbial taxa are another important aspect of ecosystem function and can be evaluated using co-occurrence network analysis (Shi et al., 2016; He et al., 2017). Correlation-based network analysis has been extensively used to infer microbial interactions. Specific network properties, such as microbial keystone taxa, modularity, and cohesion, have been used to successfully predict the stability and major functionality of the given networks (Chen et al., 2019; Hernandez et al., 2021). Microbial keystone taxa are the most connected taxa that individually or in concert with other taxa, irrespective of their abundance, exhibit the greatest explanatory power for the observed network structure and function (Berry and Widder, 2014). Modularity reflects biological processes, such as shared ecological functions among taxa within the same module (Dubin et al., 2016), spatial compartmentalization (Cram et al., 2015), and similar habitat preferences (Faust et al., 2012), all of which impact network stability. The strength of interactions among specific microbial taxa can be represented as a cohesion index. Specifically, cohesion is the primary index describing the complexity of any specific microbial network. Additionally, negative cohesion may be the driving force for stabilizing specific network relationships. Environmental stresses, differences in land use, and climate change alter microbial network stability (Hernandez et al., 2021; Yuan et al., 2021). In general, the soil microbial network is considered a critical indicator of soil health and quality. High-density shrimp cultivation reduces water quality and negatively affects the stability of the native microbiota by favoring potential pathogens and introducing antibiotics into these environments (Tomasso, 1994; Zhang et al., 2015). Additionally, microbial populations rapidly respond to environmental changes. For instance, multiple studies have demonstrated alterations in microbial communities in response to increased nutrient loading and antibiotic application during coastal aquaculture and pisciculture (Qin et al., 2020). However, relatively few studies have explored the responses of belowground microbial networks to either increased nutrient loading or antibiotic input during habitat change. Therefore, it is reasonable to assume that habitat conversion affects the keystone taxa and stability of microbial co-occurrence networks. Thus, we hypothesized that the conversion of mangrove forests to shrimp ponds will destabilize the underlying sediment microbial networks.

To this end, the present study aimed to assess the structure, biogeographical patterns, assembly, and co-occurrence networks of microbial communities following the conversion of mangrove forests to shrimp ponds across southeastern China. We hypothesized that this conversion will (1) promote the stochastic processes associated with microbial community assembly and (2) destabilize the microbial networks. Our findings offer important insights into the effects of mangrove forest conversion to shrimp ponds in southeastern China. Our analyses of the structure, assembly, and cooccurrence networks of sediment microbial communities revealed the key drivers of their large-scale biogeographical patterns in the studied region. This knowledge is fundamental to understand the changes in microbial communities in response to land use changes along coasts and can help predict and manage ecosystem functions across different habitats in coastal regions.

2. Materials and methods

2.1. Soil sampling and analyses

Ten adjacent pairs of mangrove forest and aquaculture pond sites (converted from mangrove forests approximately a decade ago) across southeastern China (20.89°N to 24.45°N and 109.62°E to 117.91°E) were selected (Fig. 1). In December 2018, soil was sampled from all paired mangrove forest and shrimp pond sites. At each site, mangrove soil samples were collected from three plots at least 20 m apart. From each plot, three soil cores were collected from the depth of 0–15 cm using a soil sampler, and the three soil samples were pooled. In addition, two surface sediment samples (0–15 cm) were collected from each shrimp ponds. And then a total of three pond were taken at each of the paired sites and were pooled to form a single sediment sample per site.

Standard analytical methods were used to measure the soil water content; pH; electric conductivity; and total carbon, nitrogen, and phosphorous content. The soil water content was measured gravimetrically (Buchmann, 2000), and the sediment pH was determined using a pH meter (FE20, Mettler Toledo, Switzerland) at a soil-to-water ratio of 2:5 (w/v). Electrical conductivity was determined using the DDS-307 EC Meter (Hua Rui Bo Yuan S and T Co., Beijing, China) at a soil-to-water ratio of 3:5 (w/v). The total carbon (TC) and total nitrogen (TN) content was determined using Elementar Vario EL III (Elementar Analysensysteme GmbH, Germany). The total phosphorus (TP) content was measured using an inductively coupled plasma-atomic emission spectrometer (ICP-AES, iCAP6300, Thermo Jarrell

Ash Co., USA). Subsequently, these values were used to calculate the TC-to-TN (C:N) and TN-to-TP (N:P) ratios, as previously described (Zheng et al., 2020).

2.2 DNA extraction, polymerase chain reaction (PCR), and high-throughput sequencing

Soil microbial communities were analyzed using high-throughput sequencing. From each soil sample, genomic DNA was extracted using the FastDNA Spin Kit (BIO101 systems, MP Biomedicals, Solon, OH, USA), and the microbial communities were profiled using PCR analysis of the V5-V7 hypervariable region in the 16S rRNA gene. PCR was performed using the primer pair 515F (5′-GTGCCAGCMGCCGCGGTAA-3′) and 806R (5′-GGACTACHVGGGTWTCTAAT-3′). Triplicate PCR products from each sample were pooled in equal quantities and purified using the GeneJET Gel Extraction Kit according to the manufacturer’s instructions, and the sequencing libraries were constructed using the Illumina NEBNext Ultra DNA Library Prep Kit (New England Biolabs, USA). The Agilent Bioanalyzer 2100 system was used to evaluate the library quality (Agilent Technologies, Palo Alto, CA, USA). Subsequently, the library was sequenced using the paired-end method on the Illumina MiSeq platform (Illumina Inc., San Diego, CA, USA).

2.3 Taxonomy and operational taxonomic unit (OTU) classification

FLASH (Fast Length Adjustment of Short Reads) was used to assemble the sequenced paired-end reads (Magoč and Salzberg, 2011), and the raw data were processed and analyzed using QIIME2, which removed any chimeric and low-quality sequences (Schloss et al., 2009). Sequences with the following characteristics were removed: (1) sequence length < 150 or > 300 bp; (2) average sequence quality < 30 (3) number of ambiguous bases > 0; and (4) homopolymer length > 6 bp (Liu et al., 2015). The high-quality sequences were then clustered into OTUs based on 97% sequence similarity. OTUs with fewer than two sequences were removed, and the representative sequences for each OTU were identified and blasted against the Ribosomal Database Project 16S rRNA gene training set (version 9, http://rdp.cme.msu.edu) (Maidak et al., 2001). Furthermore, we ensured the comparability between samples by randomly subsampling the OTU table to confirm an equal number of sequences per sample (30,907) based on QIIME2. Eventually, to get comparability between samples, the OTU table was randomly subsampled to confirm an equal number of sequences per sample (30907) based on QIIME. PICRUSt (Langille et al., 2013) was used to predict the metabolic functions of bacterial communities by comparing the existing 16S rRNA gene sequencing data with the microbial reference genome database containing known metabolic functions. In the study, the 16S rRNA gene sequencing data were aligned to KEGG (Kyoto Encyclopedia of Genes and Genomes) functional databases, which could significantly identify biological metabolic pathway.

2.4 Statistical analyses

The Chao index (Chao et al., 2005) was used to determine the distance between two samples. To determine the β-diversity of each sampled microbial community, the distances between samples were calculated using OTU tables resampled with the minimum number of sequences from each sample (30,907). This information was then used to compare the microbial community assembly processes among different regions. Principle coordinate analysis was used to explore the differences in microbial communities between the two habitats studied base on anoism function in vegan package. Significant differences in community composition between any two samples were evaluated using the analysis of similarities (ANOSIM). DDRs were determined as the slopes of the linear regression lines based on the association between geographic distance and community similarity (1 − dissimilarity of the Chao index).

The relative importance of environmental heterogeneity and spatial variables in community assembly was established using variation partitioning analysis (VPA), which separates community variation into the environmental and spatial effects, with the vpa function in the R package vegan. Spatial variables were evaluated using the principal coordinate analysis of neighbor matrices (PCNM) (Dray et al., 2006) based on the longitude and latitude of each sampling station (Peres-Neto, et al., 2006). PCNM was performed using the pcnm function in the R package vegan. Redundancy analysis (RDA) or canonical correspondence analysis (CCA) was used to investigate the associations between bacterial communities and environmental/spatial factors based on the highest gradient lengths of detrended correspondence analysis (DCA). The highest gradient length was <3 for the mangrove forest sediment microbial communities, indicating that RDA was suitable for the evaluation. In addition, the highest gradient length was >4 for the shrimp pond sediment microbial communities, indicating that CCA was suitable for the evaluation of taxa in this habitat. Before RDA or CCA, the environmental variables and PCNMs with high variance inflation factors (VIF > 20) were removed to avoid collinearity. Furthermore, the forward and backward selection was performed to identify the significant explanatory variables ($P < 0.05$) for further analyses (Blanchet et al., 2008). VPA was used to analyze the effects of environmental and spatial variables on community variations (Peres-Neto, et al., 2006). Pure environmental variation without a spatial component represents the effects of environment filtering, while pure spatial variation without an environmental component represents the effects of dispersal limitation.

Null model analysis was performed using the pattern described by Stegen et al. (2013) to sort the ecological processes as the underlying drivers of variable selection, dispersal limitation, homogeneous dispersal, and drift. To evaluate the processes shaping bacterial community assembly, we calculated the standardized effect size of the mean nearest taxon distance (NTI) (Webb et al. 2002) using the function 'SES.MNTD'based on the null model 'taxa.labels' in the 'picante' package in R (Kembel et al. 2010). Sloan's community model (Sloan et al., 2010) was used to assess the potential importance of neutral processes in both the mangrove forest and shrimp pond sediment microbial communities, which is related to the occurrence frequency of specific OTUs within each community and their regional relative abundance across the metacommunity. This neutral model reflects the applicability of the neutral theory of community assembly, adjusted for large microbial populations. The coefficient of determination (R^2) was used to demonstrate the goodness-of-fit to the neutral model. The Nm parameter (where N represents the metacommunity size and m denotes the immigration rate) was used to determine the relationship between the occurrence frequency and regional relative abundance of OTUs.

The difference in microbial organization patterns from random patterns was assessed by null model using R package “EcoSimR”. Co-occurrence networks were used to estimate species coexistence across different habitats. OTUs with a relative abundance of <0.01% were removed to reduce the interference of rare OTUs within these datasets. A Spearman’s correlation coefficient of (ρ) >0.6 and a false discovery rate-corrected P of <0.05 were used to construct the network base on "Hsmic" package. Each node represented a single OTU, and each edge represented a strong and significant correlation between two nodes. The network topology was illustrated using the R package igraph (Csardi and Nepusz, 2006). The networks were visualized using the interactive Gephi platform (Bastian et al., 2009).

3. Results

3.1 Geochemistry of soil samples

The soil samples from the shrimp ponds and mangrove forests significantly differed in terms of the C/N ratio and the TC, TN, and TP. The soil pH in both habitats approached neutrality, exhibiting slight alkalinity or acidity (5.86–7.79). of the shrimp pond sediment were significantly higher than that those of mangrove forest sediment. The contents of TC, TN, and TP increased from 9.54±3.69, 0.99±0.40 and 0.45±0.19 to 11.96±3.35, 1.36±0.47 and 0.77±0.32 with the conversion of mangrove forest sediment to shrimp pond sediment, respectively. In contrast, the mangrove forest sediment samples (9.88±1.52) showed a higher C/N ratio than the shrimp pond sediment samples (8.47±1.25). Meanwhile, there were no significant differences in pH, soil water content, and electrical conductivity between the two habitats (Table 1).

3.2 Diversity of sediment microbial communities

Our analysis generated 756,327 high-quality sequences, which were clustered into 61,605 OTUs at 97% sequence similarity. After subsampling 618,140 sequences per sample, 56,448 sequences (30,907 OTUs) were retained. The Good's coverage index was 88.6–95.7% per sample, suggesting the adequate coverage of microbial richness at the global scale. In the mangrove sediment samples, the Chao1 estimate (8565.5 ± 2387.2) revealed 4502.8 ± 1027.2 OTUs and the ACE diversity indices (species richness, 9289.5 ± 2711.6), which were higher than those in the shrimp pond sediment samples, revealed respectively 6701.6 ± 2559.7, 3299.5 ± 1068.8, and 7069.3 ± 2737.9 OTUs. Based on the estimated species accumulation curves, extrapolated species richness indices (Chao1 and ACE), and Good's coverage index, most of the sediment taxa in both habitats were recovered in our samples.

Furthermore, various methods were applied to compare the microbial community structure between the two habitats. Principle coordinate analysis (PCoA) showed a striking separation (Adonis: $P < 0.001$) of communities between the two habitats (Fig. 2). There were respectively 10,908 and 10,322 unique microbial species in the mangrove forest and shrimp pond sediment samples, with approximately 8,888 shared species were (Fig. S1). *Crenarchaeota* was the most abundant phylum in the mangrove forest sediment, while the *Proteobacteria* was the most abundant phylum in the shrimp pond sediment (Fig. 3). *Proteobacteria*, *Verrucomicrobia*, *Bacteroidetes*, *Gemmatimonadetes*, *Cyanobacteria*, and *Firmicutes* were more abundant in the shrimp pond samples than in the mangrove forest sediment samples. However, the abundance of *Crenarchaeota* and *Euryarchaeota* showed the opposite trend, being higher in the mangrove forest sediments than in the shrimp pond sediments (Fig. S2).

Next, we explored the effects of sediment properties in the mangrove forests and shrimp ponds on the abundance of each microbial phylum. In the mangrove forests, the C:N ratio was the primary positive predictor of variations in the abundance of *Proteobacteria*, *Firmicutes*, and *Bacteroidetes*, while the TN content was the primary negative predictor of variations in the abundance of *Euryarchaeota*. In contrast, in the shrimp ponds, electrical conductivity was the primary positive predictor of variations in the community composition of *Proteobacteria*, *Verrucomicrobia*, and *Gemmatimonadetes*. Meanwhile, in the shrimp ponds, electrical conductivity was a negative predictor of variations in the abundance of *Crenarchaeota*, while the TP content was a positive predictor of variations in the abundance of *Cyanobacteria* (Fig. 4).

3.3 DDRs of the microbial communities

The DDRs of bacterial communities in the mangrove forests and shrimp ponds (water-saturated) across southeastern China (spanning a geographic distance of 940 km) were analyzed using the R package basicTrendline. Although the DDR patterns were significant ($P < 0.05$), the fitness was relatively poor ($R^2 < 0.1$), indicating weak interactions between community similarity and geographic distance in the adjacent paired habitats. The slope of the mangrove samples (-0.018 for microbial communities) was flatter than that of the shrimp pond samples (-0.052 for microbial communities), which coincides with the finding that the shrimp pond sediment samples exhibited a higher β-diversity turnover of the microbial communities than the mangrove sediment samples (Fig. 5).

3.4 Assembly processes and network stabilization of sediment microbiomes

Null model analysis revealed a negligible degree of dispersal limitation, confirming its minor role in the assembly of microbial communities at large distances. Moreover, the microbial assembly index, represented by the average value of the β-nearest taxon index (β-NTI), was between -2 and 2, being governed by stochastic effects in the shrimp pond sediment microbial communities. In contrast, the β-NTI values for the mangrove forest sediments exceeded 2, indicating that these communities were largely shaped by deterministic processes. Pairwise calculations revealed that both deterministic (47–64%; β-NTI > 2 or β-NTI < -2) and stochastic (36–43%; -2 < β-NTI < 2) processes contributed to the variability of microbial assemblages in these samples. Next, the RC bray value was used to subdivide the effects of various ecological processes on community assembly. The relative contributions of variable selection, homogeneous selection, and dispersal limitation on the assembly of microbial communities were 60%, 4.4%, and 35.6%, respectively, in the mangrove forests and 35.6%, 11.1%, and 53.3%, respectively, in the shrimp ponds (Fig. 6). Additionally, these microbial communities were evaluated for their fit to the neutral community model. The mangrove forest communities exhibited greater degree of fit to this model than the shrimp pond communities. Moreover, the migration rates tended to be higher in the mangrove forest sediments than in the shrimp pond samples, suggesting that the mangrove forest microbial communities were less limited by dispersal than the shrimp pond communities (Fig. 7). In C-score analysis, describes as checkerboard score, both shrimp ponds (C-score = 3.2308 and $P < 0.001$) and mangrove forests (C-score = 2.1267, $P < 0.001$) exhibited non-random co-occurrence patterns and segregated distributions. However, the strength of species segregation varied between the two habitats. The SES value, calculated as the difference between the mean of the stimulated and observed indices divided by their standard deviations, for the shrimp pond sediment microbial networks (SES = 7.121) was higher than that for the mangrove forest sediment microbial networks (SES = 4.817), suggesting that the degree of species segregation in was higher in the shrimp ponds than in the mangrove forests.

Considering these findings, we proceeded to construct a co-occurrence network for both habitats based on their correlations. The topology networks of both habitats were well consistent with the power law distribution. The numbers of total nodes and edges were respectively 358 and 1,013 for the mangrove forest sediment microbial community networks and respectively 318 and 3,138 for the shrimp pond sediment microbial community (Fig. 8). The modularity value of networks was 0.667 for the mangrove forests and 0.491 for the shrimp ponds, and they were divided into respectively 36 and 10 modules. Additionally, based on other network topological parameters, such as total and negative cohesion, the cohesion index of the mangrove forest microbial networks was greater than that of the shrimp pond microbial networks (Fig. 9). Overall, the mangrove forest sediment OTUs were consistently more stable than the shrimp pond sediment OTUs. This finding was confirmed by the higher values of network topological parameters for the mangrove forest sediment OTUs. Moreover, core species identification revealed that the mangrove forest sediments harbored more module hub species than the shrimp pond sediments (Fig. S3). These results indicated that the co-occurrence networks of different species were more stable in the mangrove sediment microbial communities than in the shrimp pond sediment microbial communities. As such, there were markedly fewer positive links in the mangrove forest sediment networks (882, represented by negative correlations) than in the shrimp pond sediment networks (2,084). Further evaluation of the nodes for each taxon revealed that the network nodes in the mangrove forest sediments were dominated by *Crenarchaeota*, while those in the shrimp pond samples were dominated by *Proteobacteria*. These findings indicate that the most abundant species also produced the greatest impact on the interactions within each community. The analysis of key taxa using the top three average weighting degree ranks demonstrated that the mangrove forest sediment networks were dominated by *Desulfurococcales* and *Cuniculiplasma*, while the shrimp pond networks were dominated by *Chloracidobacterium*, *Wolinella*, and *Gemmatirosa* (Fig. 8).

3.5 The distribution of predicted metabolic functions between two habitat.

In general, PICRUSt obtained 6909 predicted metagenomes based on 16S rRNA gene amplicon data sets, which clustered into 41 and 328 functional pathways at levels 2 and 3 using KEGG pathway metadata. When the predicted functions between the mangrove and shrimp ponds sediment were compared at levels 2 and 3 KEGG pathway, significant differences were observed. At levels 2, energy metabolisms were significantly more abundant than in shrimp ponds, while amino acid metabolism were shown contrast lower than shrimp ponds. Specific to levels 3 revealed significant over-representation of carbohydrate metabolism, nitrogen metabolism and sulfur metabolism in shrimp pond habitat, while lower-representation of carbon fixation in photosynthetic organisms (Fig. 10).

4. Discussion

Habitat transformation evidently affects microbial community composition, community assembly, and network relationships, and each of these characteristics has been extensively studied in various habitats (Jiao et al., 2021; Zou et al., 2020; Sun et al., 2020; Cheng et al., 2021). Here, we examined microbial community structure, co-occurrence, and assembly in adjacent paired habitats across southeastern China. Our evaluations revealed that the microbial community structure and abundance were significantly altered with land use change. Moreover, following the conversion of mangrove forests to aquaculture ponds, the microorganisms in these environments exhibited increased sensitivity to dispersal limitation. Furthermore, this habitat conversion altered the key taxa in the microbial networks, thereby markedly affecting their stability.

4.1 Changes in community structure following habitat conversion

In coastal wetlands, land use and land cover changes produce a significant impact on the physical, chemical, and biological properties of the sediments in these regions (Yang et al., 2016; Yang et al., 2019). Zou et al. (2020) evaluated sediment samples from five different land use types across coastal wetlands and found that distinct land use patterns significantly affected soil physicochemical properties and microbial community structure. In various coastal wetlands, artificial reclamation for shrimp ponds has significantly altered habitat conditions for the native fauna (Zhang et al., 2020). Moreover, the associated practices, such as bait feeding and drainage, may result in significant changes in soil microbial communities across southeastern China (Shen et al., 2020). Our results showed that the conversion of mangrove forests to shrimp ponds increased the TC, TN, and TP content of the sediment samples from southeastern China. Such differences in soil nutrient content across various land use types are determined by the balance between the ecosystem input and output (Li, 2002), particularly following the conversion from mangrove forests to shrimp ponds.

Intensive shrimp farming is controversial because of the associated increase in nutrient input and output, which results in nutrient enrichment and organic fortification of the surrounding water and sediment due to the discharged waste and fecal matter (Boyd et al., 2010; Thunjai et al., 2015). Therefore, the observed variations in the microbial community may be attributed to changes in the physicochemical properties of the sediments in these areas. The relative abundance of *Firmicutes*, *Cyanobacteria*, *Proteobacteria*, and *Verrucomicrobia* was significantly higher in the shrimp ponds than in the mangrove forests. Amongst these, the increase in the abundance of *Cyanobacteria* may be explained by the accumulation of excessive P in these ponds. *Cyanobacteria* serve as an important contributor to water eutrophication (O'Neil et al., 2012), suggesting that high-density farming practices and excessive feeding can greatly impede their breeding system. Moreover, *Firmicutes* and *Proteobacteria* include many primary and secondary fermenters, which are involved in the metabolism of various carbon sources (Finn et al., 2020). Following the conversion of mangrove forests to shrimp ponds, these microbes may be used as markers for the accumulation of sediment waste and increase in animal residues.

4.2 Alterations in microbial biogeographic patterns and community assembly in response to habitat change

In the present study, the microbiota in both mangrove forests and shrimp ponds showed weak DDRs (fitness $R^2 < 0.1$). The fitness values of these relationships in the studied habitats were significantly lower than those established in natural terrestrial ecosystems (Griffiths et al., 2011; Jiao et al., 2016; Wang et al., 2017). This result indicates that the spatial variability of soil microbial communities is less pronounced in coastal mangrove wetland ecosystems. Meanwhile, the low variability of microbial communities in the artificial cultivation pond ecosystems was consistent with the patterns observed in human-managed agroecosystems (Jiao et al., 2021). The slope of the distance–decay equation was used to reveal changes in community similarity. This analysis revealed that the shrimp pond sediment communities showed a greater degree of inter-correlation than the mangrove forest sediment communities. Furthermore, neutral community modeling revealed that microorganisms in the shrimp pond sediment communities demonstrated a stronger diffusion restriction than their mangrove forest sediment counterparts (Fig. 7). Additionally, the microbial groups in the mangrove forest sediments demonstrated wider niche breadths (Fig. S4) than those in the shrimp pond sediments, as assessed via community-level habitat niche breadth analysis. This finding is consistent with previous reports that habitat generalists with wide niche breadths are less influenced by environmental factors (Pandit et al., 2009; Wu et al., 2017; Jiao et al., 2021). The larger NTI value calculated with the null model also suggested that the microbial system in the shrimp ponds (3.23±0.76) was more concentrated than that in the mangrove forests (1.02±0.25). Moreover, the NTI value indicated that the habitat filtration effect was stronger following conversion from mangrove forest to shrimp pond. This finding may be explained by the fact that the mangrove forest ecosystem is unique, since it spans the land and sea buffer zone. Continuous ocean currents generate a relatively homogenous microbial community across the mangrove forest sediments due perhaps to low dispersal limitation. However, since the artificial cultivation of shrimp pond sediments occurs within a relatively closed system, the dispersal limitation is more obvious in these habitats. Given this dispersal limitation, coupled with other continuous artificial management practices, such as aeration, bait feeding, and drainage, the microorganisms in these habitats are more affected by spatial factors, resulting in increased microbial turnover rate.

We further investigated the contribution of environmental factors and spatial heterogeneity to soil community variability using null model analysis and VPA. In the mangrove forest samples from southeastern China, deterministic processes were more important than stochastic ones, which is consistent with the patterns reported in sediment samples from mangroves in other regions (Zhang et al., 2019; Zhang et al., 2021a). These results indicate that local environmental conditions may be more important factor in driving bacterial and archaea community assembly at the regional scale. While, the opposite trend appears in that the community assembly of archaea is dominated by stochastic in mangrove forest samples from Fujian province (Chen and Wen, 2021). One reason may be that fairly homogenous with few environmental differences hardly drive niche differentiation at the local scale (Chase, 2014; Wilson, 2011). Thus, on broader scales with greater environmental heterogeneity, it appears that stochastic processes have relatively less impact on community assembly, and then determinism instead dominates (Caruso et al., 2011; Lan et al., 2020; Shi et al., 2018). In addition, other studies shown that fungal community assembly, however, is dominated by stochastic process in mangrove sediment at similar scales (Zhang et al., 2021b). This may be attributed by the sizes of bacterial cells are generally smaller than fungal spores, then makes it easier for bacteria to migrate via ocean currents and air (Barberan et al., 2015; Wang et al., 2020). Which in turn results in fungal community assembly primarily affected by dispersal limitation. However, the primary driving forces for microbial community assembly in the artificial shrimp ponds were stochastic. which is consistent with the bacterial assembly reported in shrimp cultural pond sediment samples across China (Hou et al., 2021). The physical characteristics of a given ecosystem strongly affect microbial assembly (Chase and Myers, 2011). The stochastic effects of microbial community assembly are closely linked to system fluidity, which may explain the increase in stochastic impacts in the shrimp pond samples, as the land use change moved the microorganisms from an open to a closed system with dispersal limitation. Nutrient input (e.g., TC) following conversion from mangrove forest to shrimp pond may also contribute to increased compositional stochasticity by enhancing ecological drift and reducing environmental selection through increased resource availability (Zhou et al., 2014). The VPA results showed that both selective and neutral processes governed microbial assemblages in the shrimp pond and mangrove forest sediments across southeastern China (Fig. S5). The community composition within the shrimp pond sediments was mainly shaped by the environment, while that in the mangrove forest sediments was mostly driven by spatial heterogeneity (Fig. S5). However, >80% of the community variation remained unexplained considering only spatial heterogeneity and the environment, and numerous factors may account for this result. First, several environmental variables, including available sulfur, soil organic carbon content, soil sand content, and NO^2-N, which are all known to affect community variability, were not measured. Second, other studies have shown that species interactions may significantly affect community assembly (Lima-Mendez et al., 2015; Wei et al., 2016), which could not be evaluated using VPA. Therefore, further studies addressing the effects of such environmental factors on microbial assembly in coastal wetland are warranted.

4.3 Effects of habitat conversion on microbial stability and ecosystem functions

A previous study has demonstrated that land use changes may significantly affect the network relationships among microorganisms in a given ecosystem (Cheng et al., 2021; Wang et al., 2021a). This phenomenon was also observed in the present study. As such, the microbial networks in reclaimed shrimp ponds exhibited fewer nodes and more edges than those in the mangrove forests. Another remarkable characteristic of the mangrove forest sediment networks was their higher negative cohesion and total cohesion than that of the shrimp pond sediment networks. This cohesion may play significant roles in the stabilization and co-oscillation of the underlying communities by restraining cooperative interactions, which would enhance the stability of these networks (Coyte et al., 2015; De et al., 2018; Lin et al., 2019). Based on these characteristics, shrimp pond sediment microbial networks may respond more rapidly to environmental changes, and such environmental adaptations may be realized through the weakening of microbial networks via attenuated negative cohesion and total cohesion and reduced total number of modules in these networks, which would render them unstable. This conclusion is consistent with previous reports that disturbances in the natural ecosystem result in the formation of less connected co-occurrence networks within the microbial communities (Xue et al., 2020). A reasonable explanation for our results is that the reclamation of shrimp ponds is similar to other artificial disturbances. Moreover, the release of bait and surplus of animal residues lead to the deposition of large amounts of organic matter, which may stimulate positive interactions between the taxa within the shrimp pond sediment networks. Such positive interactions may destabilize the microbial communities by creating positive feedback loops among taxa, thus supporting the fitness of each taxon (Coyte et al., 2015). However, this may increase the vulnerability of the network to the external influences because of reduced negative cohesion and number of network modules. Furthermore, habitat conversion reshaped the distinct key taxa within the microbial networks, marked by changes in the complex interactions within these co-occurrence networks. The key taxa in the mangrove forest samples were *Desulfurococcales* and *Cuniculiplasma*, which were changed to *Chloracidobacterium*, *Wolinella*, and *Gemmatirosa* in the shrimp pond samples. *Desulfurococcales* functions as a key carbon-fixing taxon, since it uses the dicarboxylate/4-hydroxybutyrate cycle to fix carbon. Moreover, its relative abundance is thought to be closely related to the function of mangroves as a major carbon sink (Liu et al., 2020). *Cuniculiplasma* plays important roles in sulfur oxidation (Mura et al., 2020), and its elevated abundance in the shrimp ponds may be explained by the discharge of sulfuric wastewater associated with shrimp production. *Chloracidobacterium*, a green sulfur bacterium, utilizes molecular hydrogen from hydrogen sulfide as an electron transmitter in photosynthesis under high-sulfur conditions (Greening and Lithgow, 2020). Furthermore, *Wolinella*, which is also an important sulfur cycle taxon, utilizes copper-containing octaheme cytochrome sulfite reductase MccA to prevent sulfite uncoupling toxicity (Benjamin et al., 2020; Jakob and Sascha, 2020). Thus, the abundance of *Wolinella* in the shrimp ponds is consistent with the large increase in sulfur content associated with artificial cultivation ponds. *Gemmatirosa*, which is involved in phenanthrene degradation (Dou et al., 2021), was also placed at the core of the shrimp pond sediment networks, implying that the shrimp pond samples might be severely polluted. Such shifts in key taxa between the mangrove forest and shrimp pond samples suggest a major transition in the primary ecological functions of these habitats following land use change. The most obvious change was the switch from carbon fixation to sulfur metabolism. This observation is consistent with the results of a similar study on shrimp pond sediment microbial communities in the Sishili Bay (Wang et al., 2021b), since excessive sulfur is accumulated during the farming of these shrimp (Choi et al., 2020). PICRUSt-based function prediction also confirms the changes in ecological function, compared with mangrove sediment, sulfur metabolism played a more important role in shrimp ponds. Furthermore, the enrichment in the function of energy metabolism involved nitrogen metabolism and carbohydrate metabolism is an effective indicator of the increase in nutrient input after the habitat change. The accumulated nutrients are easily removed in the shrimp environment due to the rapid response of microbial functions to the environment.

5. Conclusions and final remarks

The conversion of mangrove forests to shrimp ponds altered the sediment microbial community composition, assembly, and networks. This land use change restricted the movement of microorganisms by creating a closed system, thus increasing community turnover. Moreover, following this conversion, the microbial diversity decreased and the major driving mechanisms shaping microbial community assembly shifted from deterministic processes in mangrove forests to stochastic processes in shrimp ponds. Furthermore, microbial networks in the shrimp pond sediments were destabilized, while those in mangrove forest sediment were stable. The results of the null model suggest that microbial community assembly may shift from stochastic to deterministic after ten years of habitat transition.. We did not clarify the response of transition years to community assembly and microbial network. Thus, we should consider the effects of transition time on microbial community assembly and microbial networks in future studies. Meanwhile, more environmental factors should be taken into account in future research so that evaluating the driving factors on microbial network and community assembly during the dynamic process of habitat transition.

Acknowledgments

This work was supported by the National Natural Science Foundation of China (No. 41671088, 41801070). JP acknowledges financial support from the Spanish Government grant PID2019-110521GB-I00 and the Fundación Ramón Areces project ELEMENTAL-CLIMATE.

Appendix A. Supplementary data

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