Wetlands (2021) 41: 114
https://doi.org/10.1007/s13157-021-01489-4

WETLAND ANIMALS

Changes of Community Structure and Functional Feeding Groups of Benthic Macrofauna After Mangrove Afforestation in a Subtropical Intertidal Zone, China

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Received: 7 January 2021 / Accepted: 23 August 2021 / Published online: 16 November 2021

Abstract
Afforestation is a primary response to the loss and degradation of mangroves worldwide. The successful restoration of mangrove ecosystems is in part indicated by the rebuilding of macrobenthic community. However, the community dynamic of benthic macrofauna after mangrove afforestation was poorly known. Here, three quarterly surveys (2006–2007, 2014–2015, 2019–2020) of the benthic macrofauna and sediment grain size were conducted in a mix-planted mangrove stand (*Kandelia obovata* + *Sonneratia apetala*) in Xiamen Tong'an Bay, China. Our results showed that the community structure of benthic macrofauna differed significantly after mangrove afforestation. These differences were accompanied by the declines in the species number, abundance, biomass, and diversity (*H'*), as well as the fining of sediments. We also found that the epifauna and infauna exhibited different adaptabilities to mangrove vegetation. Additionally, shifts in the composition of the functional feeding groups were observed, indicating the modification of trophic structure after mangrove afforestation. We recommend that future mangrove afforestation programs call for a guide to coordinate habitats for different taxa.

Keywords Benthic macrofauna · Functional feeding groups · Epifauna and infauna · Mangrove afforestation · Subtropical intertidal zone

Introduction

Mangroves are essential ecosystem in tropical and subtropical coastal intertidal regions, offering an array of services such as protection of shorelines, sediment trapping, nutrient processing, and socioeconomic goods (Ewel et al. 1998; Alongi 2008; Nagelkerken et al. 2008; Walters et al. 2008). Mangroves, however, are negatively impacted by urbanization, pollution, and over-exploitation (Field 1999; Alongi 2002; Duke et al. 2007). Consequently, approximately one-third of mangroves have been degraded over the last decades (Alongi 2002; Bosire et al. 2008). In response, mangrove afforestation programs have been launched worldwide as a way to restore degraded mangrove forests and expand mangrove areas (Lewis 2005; Leung and Cheung 2017). A representative project of wetland restoration is the "South Mangroves and North Tamarisk" in the 13th five-year plan (2016–2020) which is the central government blueprint for China's long-term social and economic policies (Tang et al. 2018).

Previously, the primary objective of mangrove restoration was afforestation (Ellison 2000). Lewis (1984) discussed for the first time that restoration of mangroves should emphasize ecological values, animal habitats, and detrital food sources for coastal food webs. It is widely known that the three-dimensional structure created by mangroves provides shelter from predators, food, and protection from desiccation for a variety of animal species

This article belongs to the Topical Collection: Wetland Animals.

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(Nagelkerken et al. 2008; Kon et al. 2010). Mangrove associated fauna thus can be a useful indicator for judging the success of mangrove restoration (Bosire et al. 2008).

Benthic macrofauna are of great importance in maintaining the structure and function of mangrove ecosystem (Cannicci et al. 2008; Lee 2008). Benthic macrofauna serve as necessary links between the primary detritus at the base of coastal food webs and the consumers at higher trophic levels (Kristensen et al. 2008; Lee 2008), and improve aeration and reduce harmful components in the surrounding sediment through their burrowing and feeding activities (Nagelkerken et al. 2008). Therefore, changes in the macrobenthic community structure would influence local biodiversity and ecosystem functions (Kristensen et al. 2008; Nagelkerken et al. 2008).

Although mangrove afforestation can successfully re-establish the plant community, the effectiveness of restoring the macrobenthic community remains controversial. The establishment of macrobenthic communities is a complex and time-consuming process, and depends on the physical structure of mangrove and local environmental conditions (Kon et al. 2010; Pagliosa et al. 2016; Leung and Cheung 2017). Research has shown that mangrove planting can change sediment properties and habitat complexity, which in turn influence the macrobenthic community (Evin and Talley 2002). Several studies have demonstrated that the macrobenthic community changes with stand age of mangroves in terms of species richness and composition (Morrisey et al. 2003; Chen et al. 2007; Li et al. 2017), functional feeding groups (FFGs) (Feng et al. 2014; Chen et al. 2018b; Feng et al. 2018), and ecological exergy (Chen et al. 2018a). However, previous studies use space-for-time substitution as an alternative approach to evaluate the long-term effects of mangrove plantation or mangrove succession on macrobenthic community. Continuous observation of an identical mangrove stand would help to reduce errors of spatial autocorrelation generated by space-for-time substitution and to better understand the dynamics of macrobenthic community in the mangrove afforestation process, and to our knowledge, such empirical studies are still lacking.

In this study, we explore how sediment properties and macrobenthic community structure change after the mangrove afforestation during three survey periods (2006–2007, 2014–2015, 2019–2020). Generally, benthic macrofauna can be categorized into epifauna (the animals living on the surface of the sediments) and infuana (the animals living in the sediments). Given the distinct characteristics among benthic macrofauna. we therefore assume that the epifauna and infauna have different responses to mangrove vegetation and fauna belonging to different functional feeding groups also respond differently.

2. Materials and Methods

2.1 Study Area

Tong'an Bay is a subtropical semi-enclosed bay located to the northeast of Xiamen Island, China. The mean annual temperature is 20.9 °C, and the mean annual precipitation is 1200 mm. The tidal type is semidiurnal, with a mean tidal range of 4.0 m. In order to establish a mangrove-themed ecotourism area (i.e. Xiatanwei Wetland Park), an initiative proposed by Xiamen municipal government, a ca. 4.5 ha mangrove stand was planted in the intertidal zone of the head of the bay in 2005 (Fig. 1). This stand is mixed with two mangrove species, one is the native species *Kandelia obovata*, and the other is the exotic species *Sonneratia apetala*.

2.2 Field Sampling and Sample Processing

The sampling of benthic macrofauna and sediment grain size was conducted over three survey periods (2006–2007; 2014–2015; 2019–2020), represented different mangrove ages (1-year, 9-year and 14-year). In each sampling period, benthic macrofauna were collected from ten random 25 cm×25 cm quadrats at a depth of 30 cm during the low tide in the spring tide of each season (i.e., January, April, July and October). First, all benthic macrofauna from the sediment surface of each quadrat were collected, and then the sediments within the designated volume were excavated with a shovel. The excavated sediments were washed through a 0.5 mm mesh sieve, and the residues were transferred to sample containers with 5 % formalin buffer *in situ* for further identification (Chen et al. 2017). Three extra sediment samples from surface to 10 cm depth were randomly collected in spring of each survey period for grain size analysis. In the laboratory, benthic macrofauna were identified to the lowest possible taxon, enumerated under a dissecting microscope, and weighted using an electronic balance after blotting surface water off with clean absorbing paper. Then, benthic macrofauna were categorized as epifauna and infauna based on their position relative to the sediment. The sediment grain size was measured using a Mastersizer 2000 particle size analyzer and then was classified into four fractions: gravel (grain diameter > 2 mm), sand (63 μm − 2 mm), silt (4–63 μm), and clay (< 4 μm).

2.3 Classification of Functional Feeding Groups

The species identified were assigned to six functional feeding groups based on their feeding modes (Macdonald et al. 2010; Jumars et al. 2015): (1) phytophages (PH), which feed

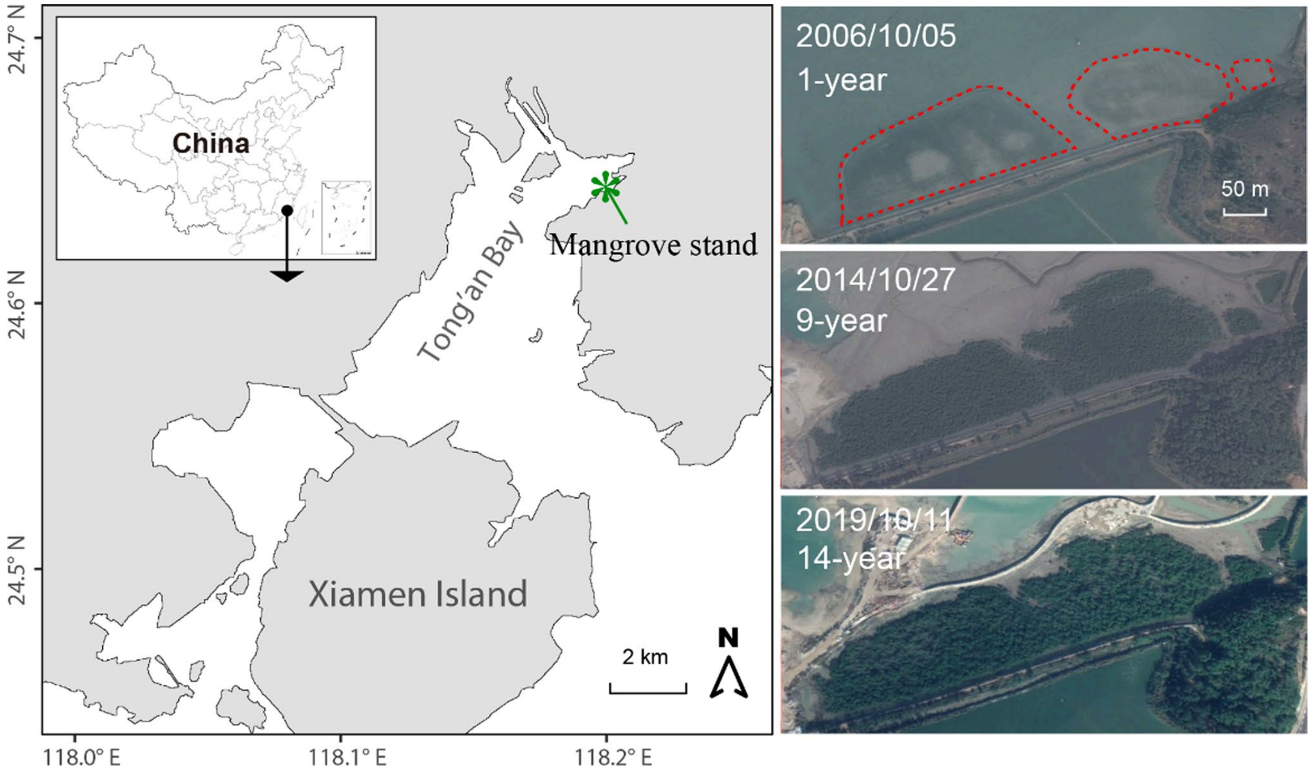

Fig. 1 Location and satellite images of the mangrove stand in Xiamen Tong'an Bay, China. The satellite images on the right were taken in 2006, 2014, and 2019, showing the canopy of mangroves (red dashed areas) of 1-year, 9-year, and 14-year

primarily on living plant tissue and medium to large algae; (2) planktophages (PL), which filter plankton and suspended particles from water column; (3) carnivores (CA), which prey on other animal; (4) surface deposit feeders (SD), which feed on detritus from the sediment surface; (5) subsurface deposit feeders (SSD), which feed on detritus located beneath the sediment-water interface; and (6) omnivores (OM), which can use different types of food sources.

2.4 Statistical Analyses

The species number, abundance, biomass, and Shannon index (H', $\log_2$ based) of epifauna, infauna, and benthic macrofauna (epifauna and infauna) were calculated for each quadrat. The proportions of the species number, abundance, and biomass of FFGs in each quadrat were summarized. One-way ANOVA was used to test whether the mean values of the community parameters (i.e., species number, abundance, biomass, and H') and the proportions of FFGs (in terms of species number, abundance, and biomass) exhibited significant differences among the stand age groups (i.e., 1-year, 9-year, and 14-year) and season groups (i.e., spring, summer, autumn, and winter). Prior to the ANOVA test, Levene's test was performed to assess the homogeneity of variance. If the homogeneity of variance is violated, an adjusted p value from Welch's ANOVA is adopted. Only when the equality of mean values is rejected ($P < 0.05$), a pairwise comparison of mean values is implemented by Tukey's HSD test (Tamhane's T2 test for unhomogeneous variables). The above univariate analyses were performed in SPSS 22.0.

The abundance data of benthic macrofauna from each quadrat were pooled to form the benthic macrofaunal composition in each sampling time (stand age plus season) for multivariate analyses. The similarity of benthic macrofaunal communities among each sampling time was determined using the Bray-Curtis coefficient based on the square-root transformed abundance data. The CLUSTER and nMDS analyses based on the Bray-Curtis similarity were used to explore the temporal variations in benthic macrofaunal community structure, and the significant temporal groups were detected using the SIMPROF procedure (1000 permutations, 5 % significance level). The SIMPER analysis was then implemented to examine the contribution of each species to the dissimilarity between the temporal groups (70 % cut-off). The above multivariate analyses were run in PRIMER 7.0.

3. Results

3.1 Sediment Grain Size

The content of sand in the sediment declined from 35.9 % (1-year) to 0.2 % (14-year); in contrast, the content of silt and clay increased over time, from 48.1 % and 16.0–70.2 % and 29.6 %. No gravel was detected in all sediment samples (Fig. 2).

3.2 Epifauna and Infauna

A total of 77 benthic macrofauna species, including 39 epifauna species (50.6 %) and 38 infauna species (49.4 %), were recorded during the three sampling periods in the mangrove stand in Xiamen Tong'an Bay (Table S1). The species number of benthic macrofauna decreased over time, 53 species (23 epifauna species and 30 infauna species) in the 1-year mangrove stand, 47 species (24 epifauna species and 23 infauna species) in the 9-year mangrove stand, and 25 species (16 epifauna species and 9 infauna species) in the 14-year mangrove stand.

Results of one-way ANOVA showed that the mean values of species number, abundance, biomass, and Shannon index (*H'*) represented by epifauna, infauna, and benthic macrofauna were significantly different among the stand age groups (Table S2). Figure 3 summarized the temporal variations in the species number, abundance, biomass, and *H'* represented by epifauna, infauna, and benthic macrofauna (i.e., total). The mean values of species number, abundance, biomass, and *H'* of epifauna in the first sampling period (1-year) were significantly higher than those in the last two sampling periods (9-year and 14-year), and the mean values of species number and abundance of epifauna in the second sampling period (9-year) were significantly higher than those in the last sampling period (14-year). The mean values of species number, abundance, and *H'* of infauna in the first two sampling periods (1-year and 9-year) were significantly higher than those in the last sampling period (14-year), while the mean value of the biomass of infauna was highest in the second sampling period (9-year). In total, the mean values of species number and abundance of benthic macrofauna decreased significantly over time; the mean value of biomass of benthic macrofauna in the first sampling period (1-year) was significantly higher than that in the last two sampling periods (9-year and 14-year); and the mean values of *H'* of benthic macrofauna in the first two sampling periods (1-year and 9-year) were significantly higher than that in the last sampling period (14-year).

For epifauna, there were no significant differences in the mean values of species number, abundance, biomass, and *H'* among the season groups; for infauna, the mean values of species number, abundance, and biomass exhibited significant differences among the season groups, in general, showing peaks in spring; while no significant differences were identified for the mean values of *H'* regardless of the living position of the fauna (Table S2).

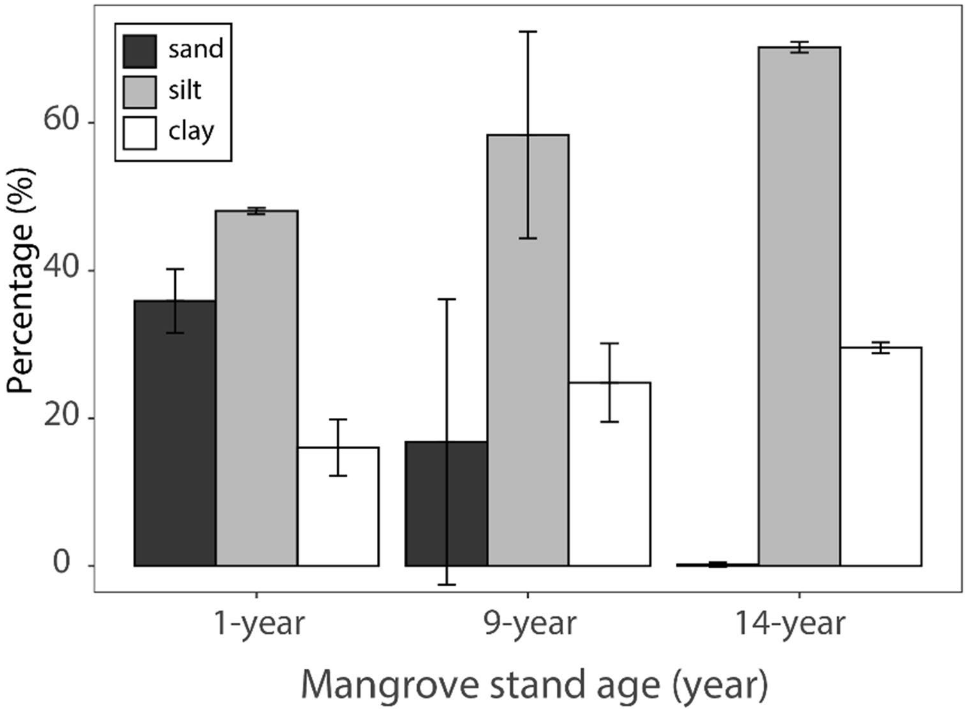

Fig. 2 Temporal variations in the percentages (mean ± SD) of the sediment grain size fractions in the mangrove stand in Xiamen Tong'an Bay

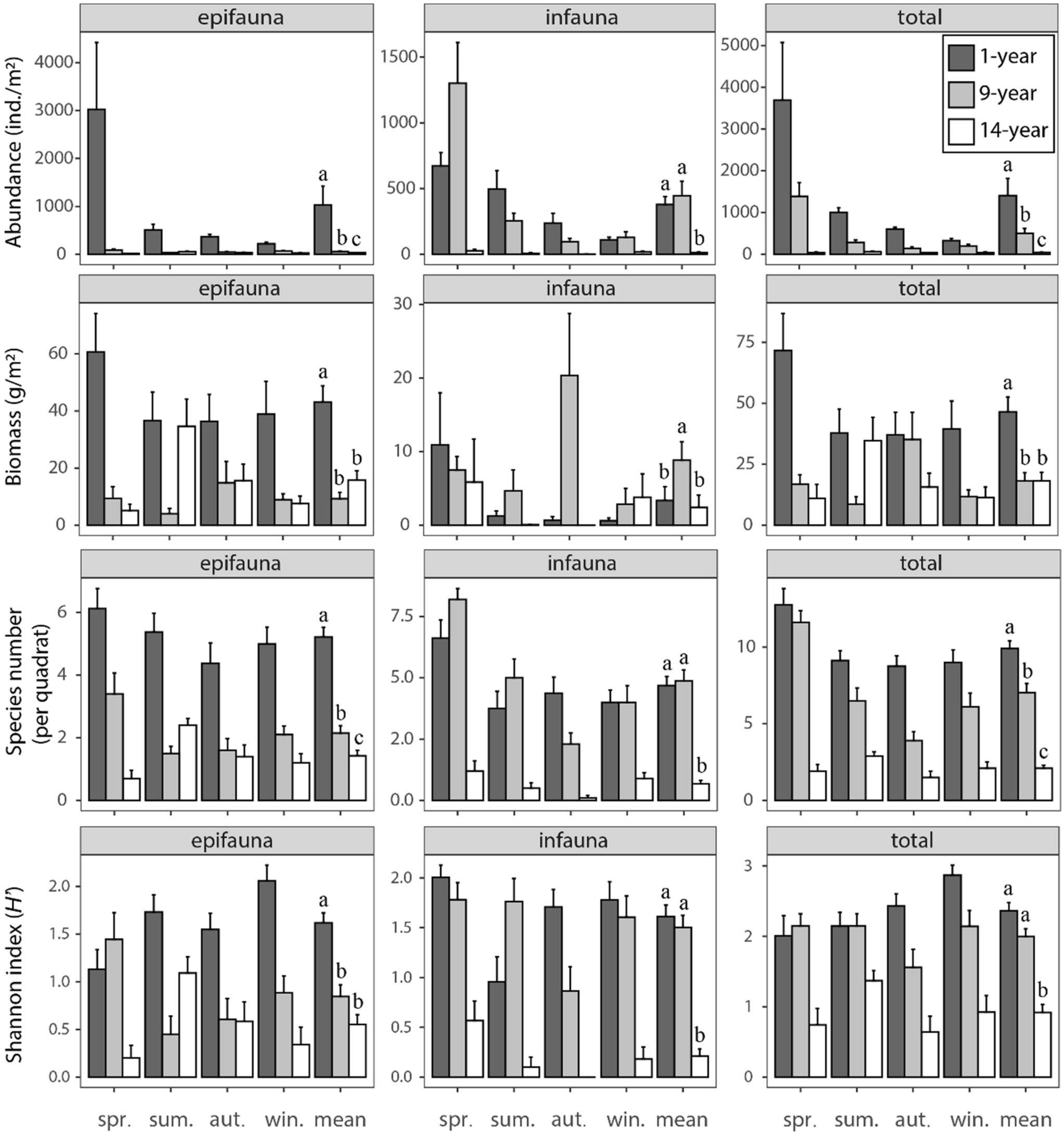

Fig. 3 Temporal variations in the species number, abundance, biomass, and Shannon index (*H'*) of macrobenthic community in the mangrove stand in Xiamen Tong'an Bay. Error bars represent the standard errors. Different lowercase letters indicate significant differences between stand age groups. spr., sum., aut., and win. represent spring, summer, autumn, and winter, respectively

3.3 Functional Feeding Groups

Among the 77 species, 15 species were assigned to PH, 15 species PL, 15 species CA, 11 species SD, 12 species SSD, and 9 species OM based on their feeding modes (Table S1). The results of one-way ANOVA showed that most FFGs varied significantly among the stand age groups in terms of the proportion of species number, abundance, and biomass, except the species number of SD and OM and the abundance and biomass of CA (Table S3). Figure 4 summarized the temporal variations in the proportions of species number, abundance, and biomass represented by FFGs. The

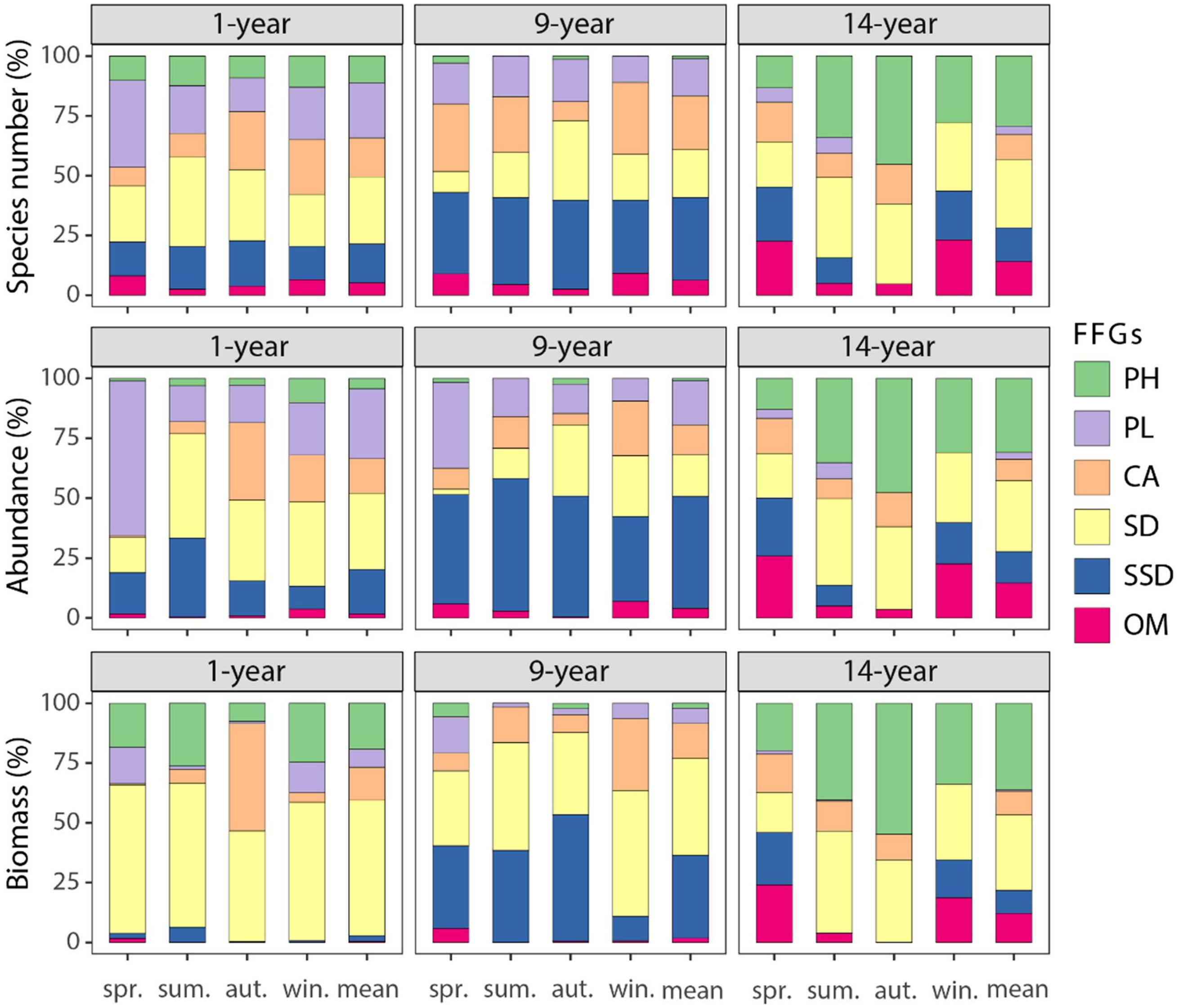

Fig. 4 Temporal variations in the proportions of different functional feeding groups (FFGs) in the mangrove stand in Xiamen Tong'an Bay. spr., sum., aut., and win. represent spring, summer, autumn, and winter, respectively. PH, PL, CA, SD, SSD, and OM represent phytophages, planktophages, carnivores, surface deposit feeders, subsurface deposit feeder and omnivores, respectively

proportions of the species number, abundance, and biomass represented by PH in the second sampling period (9-year) were significantly lower than those in the other two sampling periods (1-year and 14-year, $P < 0.001$, when multiple P-values are involved, select the maximum, hereinafter) and reached maximum in the last sampling period (14-year). The proportions of species number represented by PL deceased significantly over time ($P < 0.05$), and the proportions of abundance and biomass represented by PL in the last sampling period (14-year) were significantly lower than those in the first two sampling periods (1-year and 9-year, $P < 0.001$). The proportion of species number represented by CA in the last sampling period (14-year) was significantly lower than that in the first two sampling periods (1-year and 9-year, $P \leq 0.007$). The proportion of abundance represented by SD in the second sampling period (9-year) was lower than that in the other two sampling periods (1-year and 14-year) but exhibited significant differences only between 1-year and 9-year ($P = 0.015$); the proportion of biomass represented by SD decreased over time but exhibited significant differences only between 1-year and 14-year ($P = 0.001$). The proportions of species number, abundance, and biomass represented by SSD in the second sampling period (9-year) were significantly higher than those in the other two sampling periods (1-year and 14-year, $P \leq 0.003$) and reached minimum in the last sampling period (14-year) except the proportion of the biomass, which the minimum occurred in the first sampling period (1-year). The proportions of the species number, abundance, and biomass represented by OM increased over time but exhibited significant differences only between the first (1-year) and last (14-year) sampling periods in terms of the proportions of the abundance (P = 0.023) and biomass (P = 0.018).

Significant seasonal changes were observed in the proportions of species number represented by OM, abundance represented by PL, SD, and OM, and biomass represented by PL (Table S3). The proportions of abundance and biomass represented by PL in spring were significantly higher than those in the remaining seasons (P ≤ 0.040). The proportion of abundance represented by SD in spring was lower than that in the remaining seasons but exhibited significant differences only between spring and summer (P = 0.028) and between spring and winter (P = 0.038). The proportion of species number represented by OM in spring was significantly higher than that in autumn (P = 0.026), whereas no significant differences were detected for the proportion of abundance by pairwise comparisons.

3.4 Community Structure

At the 30 % similarity level, three groups with significant differences (SIMPROF test, P < 0.05), which were consistent with the stand age groups, can be obtained through CLUSTER analysis (Fig. S1). More importantly, the nMDS ordination plot, overlaying the minimum spanning tree, indicated the gradual changes of macrobenthic community over time (Fig. 5).

The SIMPER analysis identified 30 species as most contributing to the intergroup dissimilarities (Table 1). Among the 30 species, the mean abundance of most epifauna (9/14) declined dramatically during the first two sampling periods (1-year and 9-year) and then remained stable or declined imperceptibly during the last two sampling periods (9-year and 14-year), while the mean abundance of two epi- crustaceans, i.e., *Sesarma dehaani* and *S. plicata*, with PH feeding mode increased slightly during the last two sampling periods (9-year and 14-year); the mean abundance of most infauna (9/16) increased during the first two sampling periods (1-year and 9-year) and then declined during the last two sampling periods (9-year and 14-year), however, the mean abundance of several infauna, e.g., oligochaetes *Limnodriloides* sp. and polychaetes *Paraprionospio cristata*, declined over time. The top five contributive species to the dissimilarities of macrofaunal communities between the first (1-year) and second (9-year) sampling periods and between the first (1-year) and last (14-year) sampling periods could be both epifauna and infauna, whereas the top five contributive species to the dissimilarity between the second (9-year) and last (14-year) sampling periods were infauna only. In addition, the feeding modes of the top five contributive species were among PL, SD, and SSD.

4. Discussion

There is increased evidence that macrobenthic communities change with the stand age of mangrove or the stages of mangrove succession. For instance, Morrisey et al. (2003) found that the faunal taxa number in the younger stands (3–12 years) were generally higher than that in the older stands (> 60 years). Chen et al. (2007) also demonstrated that the younger stands (4-year and 7-year) had more benthic

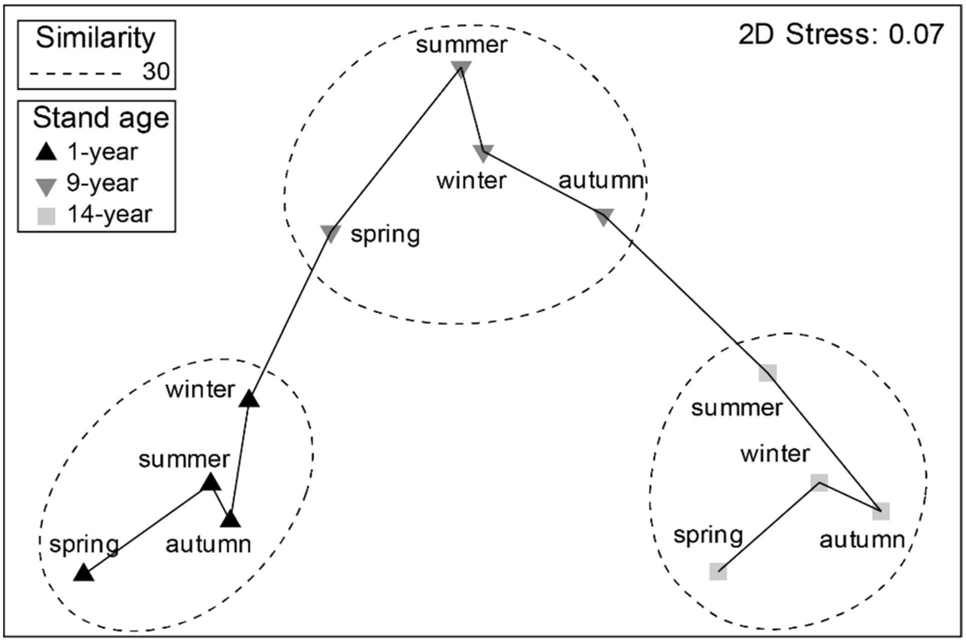

Fig. 5 nMDS ordination plot of macrobenthic communities based on the Bray-Curtis similarity of square-root transformed abundance data in the mangrove stand in Xiamen Tong'an Bay. Dashed circles represent the temporal groups exhibiting significant differences (SIMPROF, P < 0.05) and grouping at the similarity of 30 % (CLUSTER) simultaneously. The black line represents the minimum spanning tree

Table 1 The abundance and contribution rates of species to the dissimilarity of macrofaunal communities between the temporal groups (cut-off applied at 70 %)

Species	Functional feeding groups (FFGs)	Abundance (ind./m^2)			Contribution rate (%)		
		1-year	9-year	14-year	1-year vs. 9-year	1-year vs. 14 -year	9-year vs. 14 -year
Epifauna							
Gastropods							
Assiminea brevicula	SD	128.5	0.8	0.0	**6.3**	**7.9**	
Cerithidea cingulata	PH	10.5	0.0	0.0	2.2	2.6	
Littoraia melanostoma	PH	6.0	0.0	0.0	1.6	2.0	
Crustaceans							
Alpheus sp.	CA	1.0	4.8	1.2			2.6
Chasmagnathus convexus	SD	0.0	5.2	2.8			2.6
Corophium sp.	PL	663.5	0.8	0.0	**7.0**	**7.9**	
Exopalaemon orientalis	CA	46.5	4.8	0.4	3.2	4.4	
Ilyoplax tansuiensis	SD	49.0	10.8	4.0	3.2	3.2	3.2
Macrophthalmus definitus	SD	62.0	4.8	4.4	4.4	**4.8**	2.2
Metapenaeus ensis	CA	11.5	2.4	0.8	1.5	1.8	
Metaplax longipes	SD	0.5	5.6	0.0			2.4
Sesarma dehaani	PH	0.0	0.4	10.4		2.5	4.1
Sesarma plicata	PH	0.0	0.0	4.0			2.2
Uca arcuata	SD	16.0	1.6	0.8	2.0	2.5	
Infauna							
Nemertean							
Cerebratulina sp.	CA	6.5	12.4	0.0		1.9	3.9
Oligochaetes							
Limnodriloides sp.	SSD	41.5	2.0	0.0	2.9	4.0	
Polychaetes							
Capitella capitata	SSD	0.5	8.4	1.6	1.6		2.8
Ceratonereis tripartita	OM	10.0	0.0	0.0	1.7	2.0	
Chaetozone setosa	SSD	1.5	208.4	1.2	**6.3**		**11.9**
Eteone delta	CA	13.0	0.0	0.0	2.5	3.0	
Glycera chirori	CA	3.0	3.2	0.0			2.1
Mediomastus chinensis	SSD	134.0	0.0	1.2	**6.5**	**7.2**	
Neanthes glandicinta	OM	0	19.6	6.0	1.8	1.9	3.1
Nephtys oligobranchia	SSD	6.0	24.8	0.8	1.8		**5.2**
Notomastus latericeus	SSD	3.0	12.4	0.0			4.3
Paraprionospio cristata	PL	103.5	89.6	0.8	**6.4**	**7.3**	**4.4**
Prionpspio japonica	PL	1.0	17.6	0.0	2.4		**5.7**
Scoloplos rubra	SSD	2.0	10.4	0.4			3.2
Spio martinensis	PL	7.0	0.8	0.0	1.5	2.2	
Sipuncula							
Phascolosoma arcuatum	SSD	0.0	21.2	1.2	3.0		**5.5**
Dissimilarity (%)					79.5	90.0	80.8

The contribution rates of the top five contributing species are in bold. PH, PL, CA, SD, SSD, and OM represent phytophages, planktophages, carnivores, surface deposit feeders, subsurface deposit feeder and omnivores, respectively

macrofauna species than older ones (19-year and 43-year), and the dominant species between the younger and older stands were different. Chen et al. (2018b) noted that as mangrove succession progressed, the proportion of omnivores in benthic macrofaunal communities significantly increased, whereas the proportion of detritivores significantly decreased. Consistent with these findings, our results suggested that the community structure of benthic macrofauna differed significantly with the stand age of the mangrove in Xiamen Tong'an Bay. Such differences were accompanied by the declines in species number, abundance, biomass, and diversity (*H'*) and associated with the changes in sediment grain size over time. Furthermore, we also found that epifauna and infauna exhibited different adaptabilities to mangrove vegetation, and the trophic structure was changed.

Compared with the 1-year mangrove stand, the species number, abundance, biomass, and diversity (*H'*) of epifauna in the 9-year mangrove stand declined significantly, while those of infauna remained steady except for biomass (Fig. 3). Albeit mangrove leaf litter provide a certain amount of organic matter, high concentration of tannins in leaves hinder the direct utility for consumers (Li et al. 2017). Benthic macrofauna usually prefer the relatively nutrient-rich food sources, such as benthic microalgae, rather than fresh mangrove leaves (Nagelkerken et al. 2008; Giarrizzo et al. 2011; Feng et al. 2018). The physical structure of mangrove, such as the canopy cover and root density, would change with the growth of mangrove (Bosire et al. 2008). Satellite images clearly indicate that the canopy cover of mangrove stand increases over time in Xiamen Tong'an Bay (Fig. 1). Mangrove vegetation reduces the availability of light, thus affecting the growth of microalgae (Whitcraft and Levin 2007; Kon et al. 2010). Hence, the decline of the proportions of PH and SD may be attributed to the modification of microalgae by mangrove (Fig. 4). For example, the abundances of phytophagous *Cerithidea cingulate* and surface deposit feeder *Macrophthalmus definitus* decreased dramatically in the second sampling period (Table 1). Meanwhile, the fauna with these two feeding modes are usually epifauna (Table S1), and this accounts for the significant drops of epifauna.

Although the community parameters of infauna did not change during the first two sampling periods, the species composition was different. For instance, the tube dwelling polychaete *Chaetozone setosa* increased from 1.5 ind./m^2 to 208.4 ind./m^2, while the free-living polychaete *Mediomastus chinensis* declined from 134.0 ind./m^2 to 0.0 ind./m^2 (Table 1). Leung (2015) found that root biomass was the most important factor in determining the infaunal community. The increased complexity of roots establishes blocks in the sediment, making it difficult for the free-living infauna to create burrows (Leung 2015; Li et al. 2017). Additionally, by reducing water flow, the root system traps fine and organic-rich particles transported by tides or produced from mangrove litter per se (Bird 1971). In the present study, the finer sediments were observed in the late periods (Fig. 2). However, reduced water flow would depress the feeding rate and abundance of suspension feeders (Peterson et al. 1984; Lana and Guiss 1991). Therefore, the proportions of PL decreased significantly in the mangrove afforestation process (Fig. 4).

As mangrove restoration enhances organic matter accumulation in sediments (Morrisey et al. 2003; Khayat et al. 2019), we hypothesized that the sediments contained more organic matter in the late periods (especially in the last period), though that was not included in the present study. Generally, high organic matter indicates abundant food resources, facilitating the growth and reproduction of benthic macrofauna. However, excessive organic matter might lead to selectively eliminate species (e.g. infauna) due to oxygen depletion and generation of toxic by-products (e.g., ammonia and sulfide) associated with the decomposition process (Ryu et al. 2011; Li et al. 2017). Therefore, the sharp decline in the community parameters of infauna in the last sampling period might be related to the excessive organic matter in the sediments.

The composition of crabs and gastropods are considered to be more intensively influenced by the habitat changes associated with mangrove vegetation (Chen et al. 2007). Grapsid crabs (especially sesarmid species) dominated over ocypodid crabs in the mature mangrove stands, whereas *Uca* species and other ocypodids were more abundant than grapsids in the younger or degraded mangrove stands (Macintosh et al. 2002; Chen et al. 2007; Li et al. 2017). Our results suggested that ocypodids *Ilyoplax tansuiensis*, *M. definitus*, and *Uca arcuata* were more abundant in the first sampling period, and grapsids *S. dehaani* and *S. plicata* were absent in the initial phase but emerged later (Table 1). Most ocypodid crabs are surface deposit feeders and sesarmid crabs are capable of consuming mangrove leaf litter (Ravichandran et al. 2006; Chen and Ye 2008; Koo et al. 2019). Thus, this may explain why the proportions of PH increased in the last sampling period (Fig. 4).

Mangrove vegetation could provide moist environments for gastropods and protect them from being washed away (Li et al. 2017). Nevertheless, a low light environment would inhibit the growth of microalgae that gastropods favor (Feng et al. 2018). A field experiment demonstrated that the abundance of gastropods dropped by 83 % after removing most of the mangrove pneumatophores and the attached epiphytic algae (Skilleter and Warren 2000). Therefore, the three gastropods, i.e., *Assiminea brevicula*, *C. cingulate*, and *Littoraia melanostoma*, contributing to the community dissimilarities among the sampling periods may be ascribe to the shifts in food resources (Table 1). Conversely, the results from Macintosh et al. (2002) and Li et al. (2017) described that gastropods (i.e., ellobiids and neritids) were more abundant in the mature stands compared to the younger stands. The abundance of arboreal gastropods such as *C. cingulata* and *L. melanostoma* may be underestimated because these fauna are usually found attached to the trunk, branches or leaves of mangrove plants (Puryono and Suryanti 2019), due to the sampling methods used in the present study.

Although infauna and certain FFGs showed the seasonal characteristics, which might be attributed to the influence of recruitment, the seasonality in macrobenthic community structure in the present study was inconspicuous

(Fig. 5; Fig. S1). For tropical and subtropical communities, more stable climate might minimize the seasonal variations. However, the seasonality is not the focus of this study and would not be discussed further.

Evolving to the mature state for mangroves may take about ten to twenty years, depending on the species considered (Chen et al. 2007; Pagliosa et al. 2016). From our observations the recovery of macrobenthic communities seems difficult and with many challenges, though a lush mangrove stand has been achieved. However, the restoration of macrobenthic communities is a complex and time-consuming process and also depends on the planting strategies and local environments (Ellison 2000; Lewis 2005). Therefore, it would be intriguing to continue exploring the development of macrobenthic community in the next decade.

5. Conclusions

Knowledge on the dynamics of macrobenthic communities in the mangrove afforestation process is conducive to a better understanding of the mangrove restoration at the ecosystem level. Our results showed that the structure of macrobenthic community differed significantly with the stand age of mangrove vegetation. Over time, finer sediments and lower species number, abundance, biomass, and diversity (*H'*) of benthic macrofauna were observed. In addition, the variations in the adaptabilities of epifauna and infauna and the compositions of FFGs may be related to the modification of vegetation characteristics, such as the canopy cover and root density, in afforestation process, though these were not included in the present study. These findings would provide a scientific reference for the scheme of mangrove restoration and further reach ecosystem restoration goals.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s13157-021-01489-4.

Acknowledgements We sincerely appreciate the support of the Third Institute of Oceanography, Ministry of Natural Resources, in the analysis of sediment environmental data. We would like to thank Lulu Yan, Wenjun Li, Guoqiang Li, Jiali Zeng, Wenjuan Tan, Deyuan Yang and Binwen Chen for their support in sample collection. We are also grateful to Jingxiang Lin for his constructive comments as well as the reviewers for their helpful comments on the manuscript. All the members involved in this project are to be acknowledged here.

Authors' Contributions Lizhe Cai conceived of the study and obtained funding. Lizhe Cai, Xiping Zhou, Sujing Fu, Xinwei Chen, Yiyong Rao, Wenqing Chen, and Bin Zheng were responsible for field and laboratory work. Lizhe Cai conducted the identification of benthic macrofauna and created many of the manuscript elements. Yiyong Rao led the data analysis and writing effort, with significant contributions to these by all authors.

Funding This work was funded by the National Key Research and Development Program of China [2017YFC0506101].

Data Availability Not applicable.

Code Availability Not applicable.

Declarations

Ethics Approval Not applicable.

Consent to Participate Not applicable.

Consent for Publication The authors consent to this manuscript's publication.

Conflicts of Interest/Competing Interests The authors declared that they have no conflicts of interest to this work.

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