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Original research article

Habitat heterogeneity affects ecological functions of macrobenthic communities in a mangrove: Implication for the impact of restoration and afforestation



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ABSTRACT

Mangroves have been dwindling rapidly in the last few decades due to human activities, and thus restoration is commonly conducted to recover the ecological functions of degraded mangroves. However, afforestation (i.e. mangrove plantation in mudflats) can lead to habitat conversion and hence modify the ecosystem functions by increasing habitat heterogeneity. Mudflats are scarce in mangroves, but provide vital ecological functions by the macrobenthos. As such, the present study investigated how habitat heterogeneity affects the ecological functions of macrobenthic communities in a mangrove by analysing functional diversity, functional redundancy and biological trait patterns. Samples were collected from different habitats with increasing order of habitat heterogeneity (mudflat < seedling < *Kandelia* < *Kandelia* with algal mats < pneumatophore). Results showed that functional redundancy was generally high in the mangrove, indicating that most of the species performed similar functions. Functional diversity, however, generally decreased with increasing habitat heterogeneity primarily due to the dense root structure. Different habitats had different trait patterns where smaller body size, fewer carnivores and more direct developers were observed when habitat heterogeneity increased. Overall, moderate increase in habitat heterogeneity enhanced the functional diversity of macrobenthic communities, but negative effect was incurred when the habitat heterogeneity was too high. For the sake of conservation and management of mangroves, restoration should consider plant density and plant species to minimize the impact of dense root structures on macrobenthos. Given the lower functional redundancy and distinct trait pattern in the mudflat, afforestation is not recommended so that the integrity of the ecological functions of mangroves can be maintained.

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1. Introduction

Mangroves are biologically productive ecosystems and offer numerous ecological functions (Ewel et al., 1998); however, they have been menaced by urbanization, pollution and over-exploitation over the last few decades (Alongi, 2002). In this regard, mangrove plantation has been conducted worldwide as the primary measure to restore the degraded mangroves or even expand the mangrove area (Field, 1999; Erftemeijer and Lewis, 2000; Lewis, 2005). Ecologically, restoration is conducive to recovering the ecological functions of degraded mangroves, but afforestation (i.e. mangrove plantation in mudflats or areas where no mangrove plants were previously found) for shoreline protection or commercial purposes is

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controversial because it changes habitat heterogeneity (i.e. the abundance of individual structural components in the habitat, McCoy and Bell, 1991) and hence modifies the ecological functions of mudflats (Erfemeijer and Lewis, 2000; Ren et al., 2009). Mudflats are relatively scarce in mangroves, yet host high diversity and biomass of macrobenthos which provide crucial ecological functions, such as energy flow and nutrient recycling (Snelgrove, 1998; Lee, 2008). While habitat heterogeneity was shown to be the determinant of macrobenthic communities (Levin and Talley, 2002; Leung and Tam, 2013; Leung, 2015), whether it could lead to an ensuing change of their ecological functions in mangroves remains largely unknown.

To date, studying ecosystem functions becomes indispensable, and even compulsory in some legislative agreements (United Nations, 1992; EC, 2008), for the sake of conservation and management (Bremner, 2008; Frid et al., 2008). Traditionally, the ecological functions of macrobenthic communities are assessed by species composition and abundance, trait analysis (e.g. feeding guild and size distribution) or integrated indices (Borja et al., 2000; Fano et al., 2003; Mouillot et al., 2006; Reizopoulou and Nicolaidou, 2007). Despite their usefulness, these approaches can only confer limited applicability and information on ecosystem functions in view of small number of traits selected and difficulty in making spatial comparisons (Reizopoulou et al., 1996; Mouillot et al., 2006; Elliott and Quintino, 2007). Therefore, functional diversity which represents the diversity of functional traits (or functional niches) in a community is introduced to evaluate ecosystem functions (Petchey and Gaston, 2002, 2006; Cadotte et al., 2011). Since different species in a community can perform similar or even same functions (i.e. overlapping of functional niches), the loss or replacement of species does not necessarily change the ecosystem functions (Petchey and Gaston, 2002, 2006; Rosenfeld, 2002). As such, functional redundancy is commonly measured to describe the stability of ecosystem functions to species loss (Walker, 1995).

While functional diversity and functional redundancy are the key indicators for conservation and management, they cannot provide a mechanistic understanding of which ecological functions are affected by disturbance or environmental stress. In recent years, therefore, biological trait analysis has been increasingly used to examine the ecological functions of macrobenthic communities (e.g. van der Linden et al., 2012 and Veríssimo et al., 2012). Biological trait analysis takes numerous biological traits into consideration (e.g. life-history, morphology and behaviour), which are associated with ecological functions (Bremner, 2008; Frid et al., 2008; Fleddum et al., 2011; Veríssimo et al., 2012). Since organisms from different phylogenies can evolve similar adaptations and hence ecological functions in response to environmental changes (Naeem, 2002), biological trait analysis allows comparisons of ecological functions between communities irrespective of taxonomic groups and geographical locations (Mouillot et al., 2006), making it promising for evaluation of management measures (Bremner, 2008; Frid et al., 2008).

The present study aimed to elucidate how habitat heterogeneity affects the ecological functions of macrobenthic communities in mangroves. To preclude the impact of anthropogenic activities, a pristine mangrove was chosen as the model site. The biological traits of macrobenthos were studied so that the functional diversity and functional redundancy of the macrobenthic communities were measured. Additionally, the correlation between the trait pattern and environmental variables was examined using multivariate analyses. To the best of my knowledge, this is the first study to assess the ecological functions of macrobenthic communities in mangroves using biological trait analysis. The findings offer a mechanistic understanding of how habitat heterogeneity affects the ecological functions of macrobenthic communities, and thus provide insights for the policy makers into how to conserve, restore and manage mangrove ecosystems in a more sustainable way.

2. Materials and methods

2.1. Collection of macrobenthos and sediment samples

The mangrove in Tai O (22°15'N, 115°51'E), Hong Kong, was selected as the study site. Samples were collected in five sampling areas, where five habitats with increasing order of habitat heterogeneity were found (mudflat < seedling < *Kandelia* < *Kandelia* with algal mats < pneumatophore). The mudflat was an unvegetated area. The seedling area had ca. 280 seedlings of *Kandelia obovata* (about 0.7 m tall), a dominant true mangrove species, in a 5 × 5 m quadrat. The *Kandelia* area had ca. 15 mature individuals of *K. obovata* (about 1.7 m tall) in a 5 × 5 m quadrat. The algal mat area had a similar density of mature *K. obovata* as the *Kandelia* area, but the sediment surface was covered by algal mats. The pneumatophore area had ca. 30 pneumatophores in a 20 × 20 cm quadrat, which were spread from the nearby mature true mangrove *Avicennia marina* (about 2 m tall). The vegetation characteristics in each habitat were similar among the five sampling areas. Macrobenthos and sediment samples were collected using a core sampler (diameter: 8 cm; depth: 20 cm) at each sampling point ($n = 3$ for macrobenthos and sediment, respectively) (Fig. 1). The macrobenthic (abundance and diversity indices) and environmental data (salinity, particle size, redox potential, water content, total organic matter (TOM), weight of debris, biomass of roots and biomass of macroalgae) were shown in Leung (2015).

2.2. Biological trait analysis

A total of seven biological traits, subdivided into 36 trait categories, were selected for biological trait analysis (Table 1). These traits generally represent the ecological functions of macrobenthic communities (e.g. nutrients dynamics, energy flow, biogeochemical cycles and potential recovery patterns) (Fleddum et al., 2011). The biological trait data of each species were

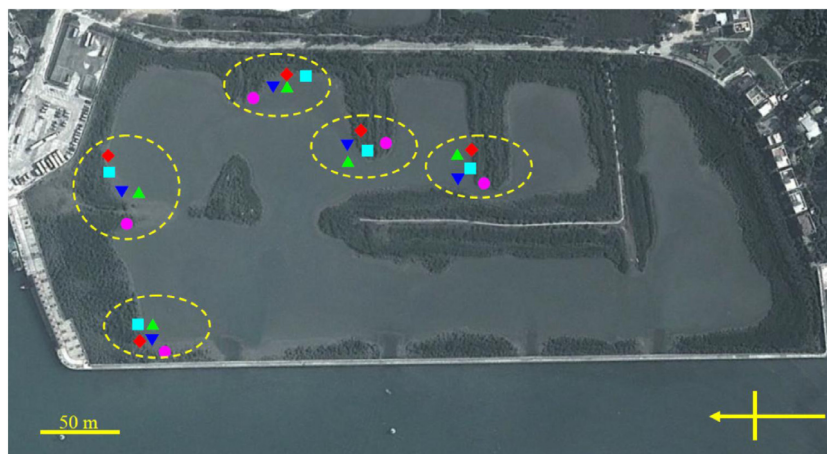


Fig. 1. Locations of the five sampling areas, indicated by the dotted circles, in Tai O mangrove (Retrieved from Google Earth). Each sampling area had five different habitats as the sampling points (▲ Mud: Mudflat; ▼ Seed: Seedling area; ● Ko: *Kandelia* area; ■ Ko + mat: *Kandelia* area with algal mats; ◆ Pneu: Pneumatophore area).

Table 1

The biological traits and trait categories chosen in the present study.

Biological trait	Trait category
Maximum adult size	<5 mm 5 mm–1 cm 1–3 cm 3–6 cm 6–10 cm > 10 cm
Larval development	Planktotrophic Lecitotrophic Direct development
Mobility	None Low Medium High
Body form	Cylindrical Dorsally flattened Laterally flattened Ball-shaped Long thin Irregular
Attachment	None Temporary Permanent
Adult habitat	Sessile Tube (permanent) Tube (semi-permanent) Burrower Surface crawler/swimmer
Feeding mode	Suspension/filter feeder Scraper/grazer Surface deposit feeder Subsurface deposit feeder Dissolved matter/symbiotic Detritivore Scavenger Carnivore Parasite/commensal

gathered from various published sources, including theses, books, scientific papers and online databases (e.g. MarLIN BIOTIC: www.marlin.ac.uk/biotic and Marine Species Identification Portal: www.species-identification.org). Fuzzy coding approach was used to score each trait category, ranging from '0' to '3', according to the affinity of the species to it ('0' indicates no affinity while '3' indicates high affinity). Since species can display various behaviours or characteristics, they can score more than one categories in a particular biological trait. For example, a species can score '2' in two categories of feeding mode if it can show these feeding modes with equal affinity. If there is no currently available information on a particular biological trait, '0' was given to all of its categories. At each sampling point, the score in each trait category of a species (taxa by traits) was multiplied by its abundance (taxa by habitats) and then summed over all species to represent the ecological functions (traits by habitats) (van der Linden et al., 2012).

2.3. Data treatment and statistical analyses

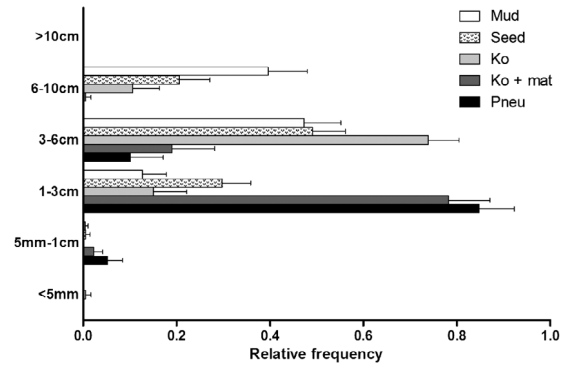
Rao's quadratic entropy index was calculated for each biological trait using a purpose-made Excel macro (Lepš et al., 2006). Functional diversity (FD) was calculated by averaging all these individual indices, while functional redundancy (FD/ H') was calculated as a ratio of FD to Shannon–Weaver index (H') (van der Linden et al., 2012). Nested permutational multivariate analysis of variance (PERMANOVA) with "habitat" (fixed factor) nested within "sampling area" (random factor) was applied to test the effects of habitat heterogeneity on FD and FD/ H' . Since the effect of nesting factor was insignificant, all samples from each habitat were pooled for analysis. Linear regression analysis was applied to examine the relationship between FD and species richness. Pearson correlation analysis was applied to correlate FD and FD/ H' with the environmental variables. For multivariate analyses, the score in each trait category was square-root transformed. Fuzzy correspondence analysis (FCA) was employed to depict the trait pattern among habitats and to estimate the contribution of each biological trait and its categories to the trait pattern. One-way analysis of similarities (ANOSIM) was used to test the spatial difference in the trait pattern using Bray–Curtis similarity. A stepwise distance-based linear model (DistLM) using AIC selection criterion was applied to identify the predictor variables (i.e. environmental data) which significantly explain the variation in the trait pattern. Distance-based redundancy analysis (dbRDA) was applied to provide a visual representation of the trait pattern fitted to the significant predictor variables. PERMANOVA, ANOSIM, DistLM and dbRDA were performed by software PRIMER 6 with PERMANOVA+ add-on. Linear regression analysis and Pearson correlation analysis were performed by software SPSS 20.0 for Windows. FCA was conducted using software R 3.2.1 with package ade4 version 1.7-2.

3. Results

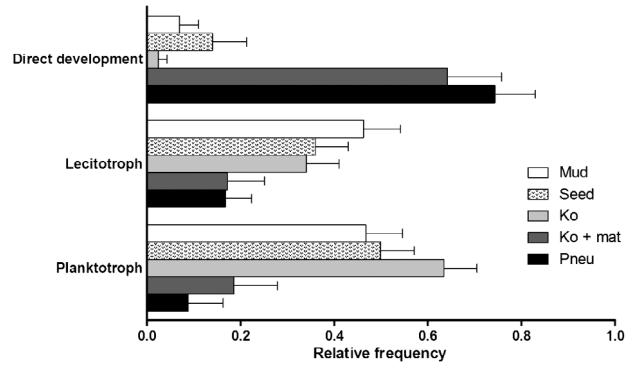
The relative frequency of each category of biological traits is shown in Fig. 2. The maximum adult size of macrobenthos generally decreased with increasing habitat heterogeneity so that '3–10 cm' was dominant in the mudflat and seedling area, while '1–3 cm' in the algal mat and pneumatophore areas (Fig. 2(a)). Lecitotrophic and planktotrophic larvae had similar relative frequency in the mudflat and seedling area, while planktotrophic larvae were more dominant than lecitotrophic larvae in the *Kandelia* area (Fig. 2(b)). Direct development was preponderant in the algal mat and pneumatophore areas. Although most of the macrobenthos had low mobility in all habitats, more highly mobile macrobenthos were found when habitat heterogeneity decreased (Fig. 2(c)). Most of the macrobenthos appeared cylindrical and long thin, and did not attach to the substratum (Fig. 2(d) and (e)), regardless of habitats. Dorsally-flattened body was more common in the mudflat and seedling area than the algal mat and pneumatophore areas. Burrowers were dominant in all habitats, but their relative frequency decreased in the algal mat and pneumatophore areas (Fig. 2(f)). Surface crawlers were frequently found in the mudflat, algal mat and pneumatophore areas. Subsurface deposit feeding was the most prevalent feeding mode, especially in the seedling and *Kandelia* areas (Fig. 2(g)), whereas surface deposit feeding was more prevalent in the algal mat and pneumatophore areas than the mudflat and seedling area. Carnivores were more abundant in the mudflat than other habitats.

Functional diversity, ranging from 0.41 to 0.28, generally decreased with increasing habitat heterogeneity (Table 2). The mudflat and seedling area had higher FD than other habitats, whereas the pneumatophore area had the lowest FD. Lower functional redundancy, indicated by the higher FD/ H' , was found in the mudflat than other habitats. No significant difference in FD/ H' was found among the seedling, *Kandelia*, algal mat and pneumatophore areas. All environmental variables, except salinity and biomass of macroalgae, were negatively correlated with FD, while TOM, redox potential, weight of debris and biomass of root were negatively correlated with FD/ H' (Table 3). Functional diversity was positively correlated with both number of species (Fig. 3(a)) and Margalef's species richness (Fig. 3(b)). The slope was much lower than 1 (0.35 for number of species and 0.26 for Margalef's species richness), meaning that functional redundancy of the macrobenthic community was high.

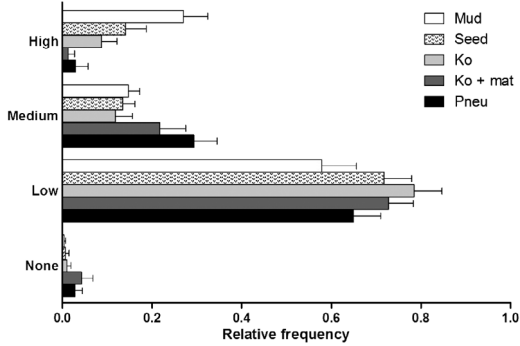
The trait pattern among different habitats is depicted by the FCA plot where Axis 1 and Axis 2 explained 81.3% and 12.2% to the projected inertia, respectively (Fig. 4). The traits 'Maximum adult size' (44.27%), 'Larval development' (41.65%) and 'Feeding mode' (5.25%) were the three major contributors to Axis 1, while 'Maximum adult size' (31.18%), 'Mobility' (22.33%) and 'Feeding mode' (16.80%) to Axis 2 (Table 4). The trait categories '1–3 cm' (27.14%), 'Direct development' (26.75%) and '3–6 cm' (13.97%) contributed most to Axis 1, whereas '6–10 cm' (20.01%), 'Low mobility' (12.87%) and 'Subsurface deposit feeder' (11.55%) to Axis 2. From the plot, it is obvious that different habitats had different trait patterns (ANOSIM: Global



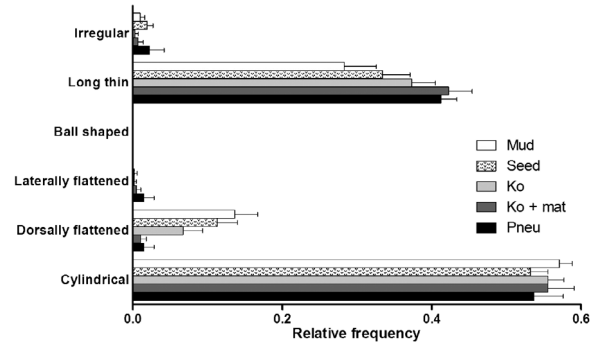
(a) Maximum adult size.



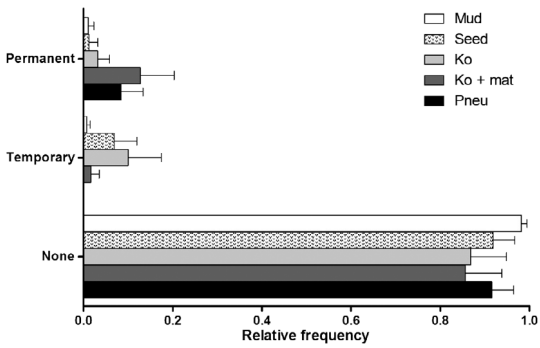
(b) Larval development.



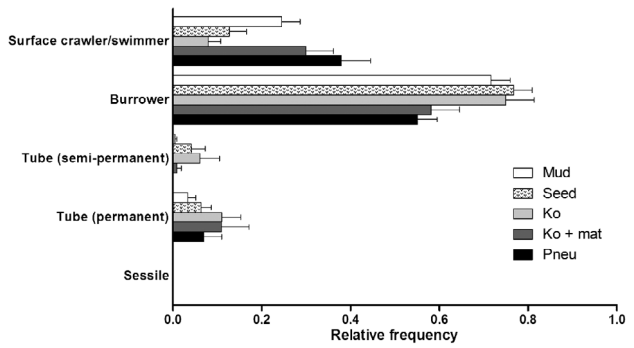
(c) Mobility.



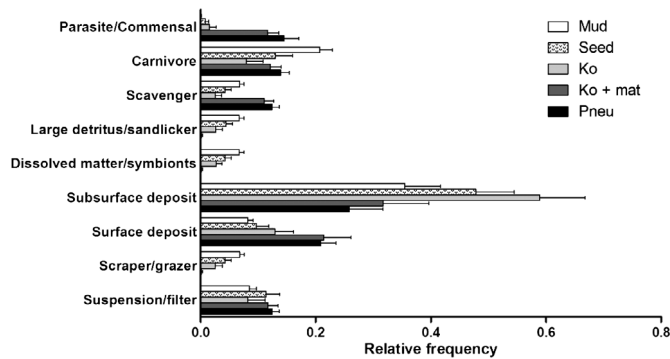
(d) Body form



(e) Attachment.



(f) Adult habitat.



(g) Feeding mode.

Fig. 2. Relative frequency of each trait category in (a) maximum adult size, (b) larval development, (c) mobility, (d) body form, (e) attachment, (f) adult habitat and (g) feeding mode in different habitats (mean + S.D., $n = 15$).

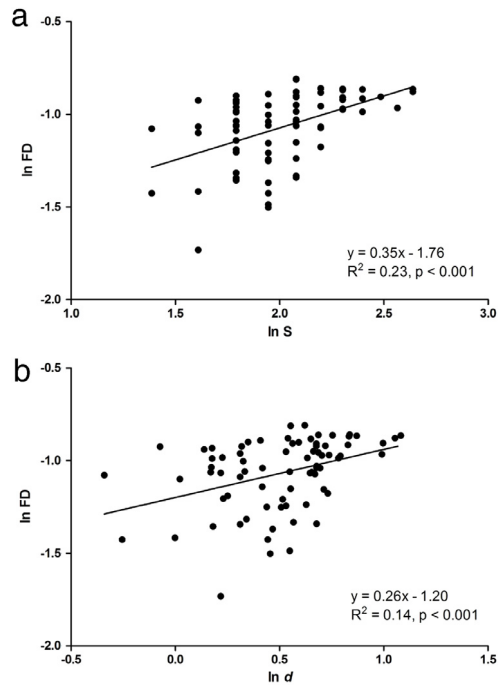


Fig. 3. Linear regression analysis showing the change in ln FD (functional diversity) against (a) ln S (number of species) and (b) ln d (Margalef's species richness).

Table 2

Functional diversity and functional redundancy of macrobenthic communities in different habitats (mean \pm S.D., $n = 15$). The same superscript letter within each variable indicates no significant difference according to PERMANOVA ($p > 0.05$).

	Mud	Seed	Ko	Ko + mat	Pneu
Functional diversity, FD	0.39 \pm 0.02 ^a	0.41 \pm 0.03 ^a	0.34 \pm 0.05 ^b	0.33 \pm 0.06 ^{bc}	0.28 \pm 0.05 ^c
Functional redundancy, FD/H'	0.30 \pm 0.04 ^a	0.24 \pm 0.02 ^b	0.25 \pm 0.03 ^b	0.25 \pm 0.03 ^b	0.23 \pm 0.02 ^b

Table 3

Pearson correlation analysis correlating functional diversity (FD) and functional redundancy (FD/H') with different environmental variables ($n = 75$).

	FD	FD/H'
Lateral root	-0.616 ^{***}	-0.403 ^{***}
Root hair	-0.627 ^{***}	-0.453 ^{***}
Total root	-0.609 ^{***}	-0.433 ^{***}
Macroalgae	-0.197	-0.118
Debris	-0.458 ^{***}	-0.431 ^{***}
Particle size (Φ value)	-0.514 ^{***}	-0.221
Redox potential	-0.557 ^{***}	-0.325 ^{**}
TOM	-0.486 ^{***}	-0.366 ^{**}
Water content	-0.304 ^{**}	0.109
Salinity	-0.210	-0.166

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

$R = 0.851$, $p < 0.001$; Table 5), while the trait pattern changed gradually with increasing habitat heterogeneity. According to DistLM, redox potential, biomass of macroalgae, biomass of root, weight of debris and TOM were the significant predictor variables, explaining 41.3%, 11.3%, 10.2%, 2.2% and 1.3% to the total variation in the trait pattern, respectively. From the dbRDA bi-plot (Fig. 5), the higher biomass of macroalgae and root in the algal mat and pneumatophore areas resulted in different trait patterns from other habitats, whereas the lower TOM and redox potential in the mudflat and seedling area led to different trait patterns from other habitats.

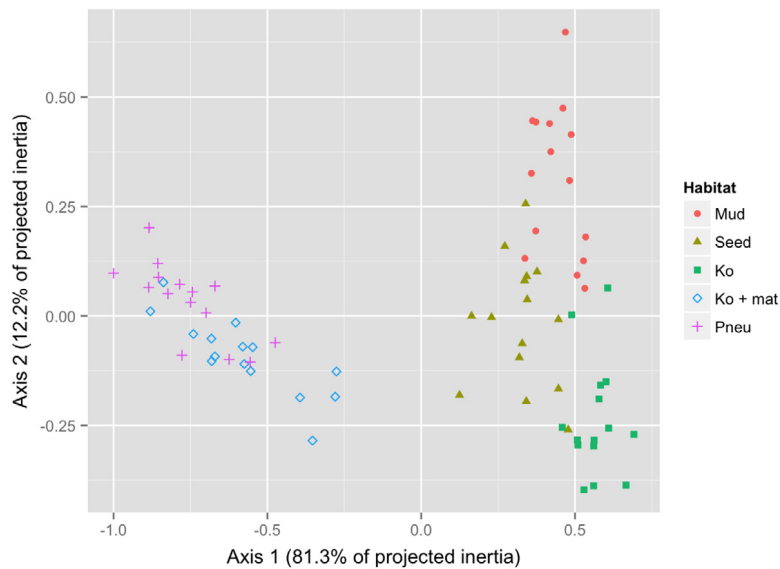


Fig. 4. A FCA plot showing the trait pattern among different habitats.

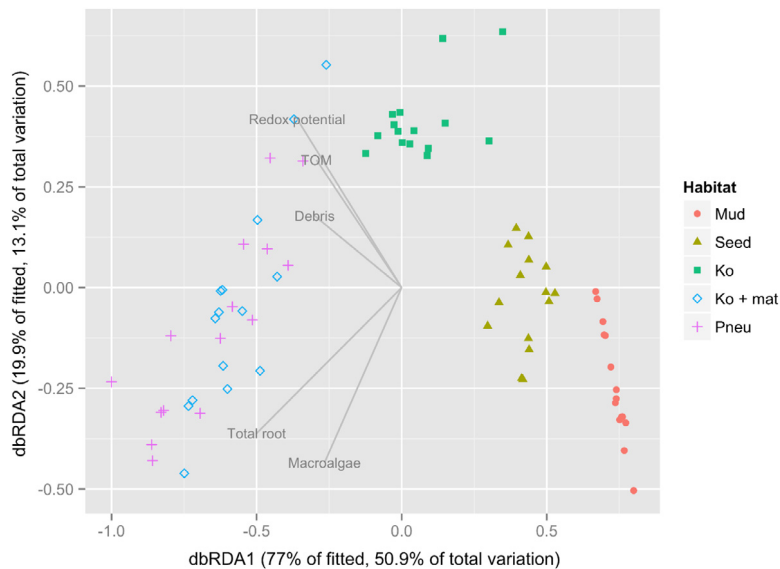


Fig. 5. A dbRDA plot showing the significant predictor variables fitted to the trait pattern using DistLM.

4. Discussion

Habitat heterogeneity, even on a small spatial scale, was shown to influence species diversity and their ecological functions in marine ecosystems (Thrush et al., 2006; Hewitt et al., 2008). The present study, using biological trait analysis, revealed similar results in mangrove ecosystems. Environmental filtering concept can be applied to explain the effects of habitat heterogeneity on the trait pattern because species have to evolve suitable traits in order to survive in a particular habitat. Under the influence of environmental filters (e.g. habitat heterogeneity and sediment properties), species are sorted along the environmental gradients and only those possessing particular traits can pass through the filters and survive (Petchey et al., 2007; Mayfield et al., 2009). In the present study, the effects of environmental filters were mirrored by the low evenness in each trait (i.e. dominance of few categories in each trait). Based on FCA, ‘Maximum adult size’, ‘Larval development’ and ‘Feeding mode’ were the major traits governed by habitat heterogeneity. The maximum adult size decreased with increasing habitat heterogeneity, probably due to the dense root structure that inhibits borrowing and feeding activities of the large-sized species (Posey, 1987), *Neanthes glandicincta*. Instead, the dense root structure could provide shelters for the small-sized species from predator attack (Orth et al., 1984; Capehart and Hackney, 1989), explaining the dominance of small-sized species, such as *Typosyllis* sp, in the algal mat and pneumatophore areas. Robson et al. (2005)

Table 4

Loading and contribution (%) of each trait category to Axis 1 and Axis 2 of the FCA plot. The bold numbers indicate the contribution of a particular trait to Axis 1 or Axis 2.

Biological trait	Trait category	Loading		Contribution (%)	
		Axis 1	Axis 2	Axis 1	Axis 2
Maximum adult size	<5 mm	0.001	−0.001	0.00	0.00
	5 mm–1 cm	−0.018	0.003	0.09	0.02
	1–3 cm	−0.314	−0.041	27.14	2.65
	3–6 cm	0.226	−0.073	13.97	8.51
	6–10 cm	0.106	0.112	3.07	20.01
	>10 cm	0	0	0	0
				4.27	31.18
Larval development	Planktotrophic	0.209	−0.058	11.95	5.42
	Lecitotrophic	0.104	0.071	2.94	8.01
	Direct development	−0.312	−0.013	26.75	0.25
				41.65	13.68
Mobility	None	−0.012	−0.005	0.04	0.03
	Low	0.012	−0.090	0.04	12.87
	Medium	−0.066	0.020	1.18	0.66
	High	0.065	0.074	1.17	8.76
				2.43	22.33
Body form	Cylindrical	0.006	0.007	0.01	0.07
	Dorsally flattened	0.041	0.030	0.47	1.45
	Laterally flattened	−0.005	0.001	0.01	0.00
	Ball-shaped	0	0	0	0
	Long thin	−0.039	−0.041	0.42	2.68
	Irregular	−0.003	0.004	0.00	0.02
				0.91	4.23
Attachment	None	0.011	0.042	0.03	2.87
	Temporary	0.025	−0.028	0.18	1.26
	Permanent	−0.037	−0.014	0.37	0.32
				0.58	4.45
Adult habitat	Sessile	0	0	0	0
	Tube (permanent)	−0.004	−0.025	0.01	1.02
	Tube (semi-permanent)	0.016	−0.017	0.07	0.47
	Burrower	0.088	−0.016	2.13	0.40
	Surface crawler/swimmer	−0.099	0.058	2.71	5.43
				4.91	7.32
Feeding mode	Suspension/filter feeder	−0.016	0.000	0.07	0.00
	Scraper/grazer	0.021	0.017	0.12	0.44
	Surface deposit feeder	−0.050	−0.016	0.68	0.42
	Subsurface deposit feeder	0.101	−0.085	2.79	11.55
	Dissolved matter/symbiotic	0.021	0.016	0.12	0.40
	Detritivore	0.021	0.016	0.12	0.41
	Scavenger	−0.037	0.013	0.37	0.26
	Carnivore	0.000	0.045	0.00	3.27
	Parasite/commensal	−0.060	−0.006	0.99	0.05
					5.25

Table 5

Pairwise tests of one-way ANOSIM comparing the trait patterns between two habitats.

Habitats	R statistic
Mud vs. Seed	0.736*
Mud vs. Ko	0.988*
Mud vs. Ko + mat	1*
Mud vs. Pneu	0.988*
Seed vs. Ko	0.896*
Seed vs. Ko + mat	0.998*
Seed vs. Pneu	0.963*
Ko vs. Ko + mat	0.988*
Ko vs. Pneu	0.982*
Ko + mat vs. Pneu	0.113

* $p < 0.05$.

also proposed that body-size distribution is primarily driven by physical structures since macrobenthos can perceive and utilize the habitat according to their own body size. Ecologically, body size reflects disturbance, movement of organic matter and biological interactions in a community (De Roos et al., 2003; Verissimo et al., 2012). The dominance of small-sized species indicates that the dense root structure in the algal mat and pneumatophore areas could pose disturbance and lead to higher

turnover of organic matter in the macrobenthic community (Mouillot et al., 2006; Veríssimo et al., 2012). Larval development mechanism is associated with dispersal and recovery patterns of macrobenthic communities (Jablonski, 1986; Boström et al., 2010). In general, planktotrophic larvae have longer planktonic stage and hence higher dispersal capability than lecithotrophic larvae and direct developers. The higher relative frequency of direct development in the algal mat and pneumatophore areas than other habitats suggests that larval dispersal and recruitment are hindered by the biogenic structures. Previous studies showed that algal mats can inhibit larval settlement (Ólafsson, 1988; Bolam et al., 2000), but can enhance the colonization of opportunistic species by providing more organic matter (Norkko and Bonsdorff, 1996; Thiel and Watling, 1998). Similarly, pneumatophores are space-occupying structures which could encumber larval dispersal and settlement. As a result, small-sized, opportunistic species with direct larval development, such as *Limnodrilus* sp. and *Typosyllis* sp., dominated the algal mat and pneumatophore areas. Feeding mode is one of the most important traits as it is pertinent to energy flow and nutrient recycling. Since the sediment was silty and detritus was ubiquitous in the mangrove, surface and subsurface deposit feeding were the most dominant feeding modes, meaning that removal and recycling of nutrients, especially organic matter, as well as secondary production are prevalent (Karlson et al., 2010). Carnivores were more abundant in the mudflat than other habitats due to the dominance of errant predator *N. glandicincta*, suggesting that more nutrients in the deposit feeders could be transferred to the mobile pool (Ngai and Srivastava, 2006). On the other hand, *N. glandicincta* is an important prey for some fish and bird species, implying that the dense root structure could hinder energy flow to the higher trophic levels. The more diverse feeding modes in the mudflat and seedling area than other habitats were beneficial to energy flow and nutrient recycling (Pacheco et al., 2011).

Functional diversity has been increasingly used to understand the ecological functions of a community following disturbance or management measures (Micheli and Halpern, 2005; Petchey and Gaston, 2006; Cadotte et al., 2011; van der Linden et al., 2012). In general, higher functional diversity indicates better performance, higher productivity and higher utilization of resources of a community in view of higher niche complementarity (Petchey, 2003). To date, studies on how habitat heterogeneity affects functional diversity are scant and focus only on seagrass habitats. For example, Dolbeth et al. (2013) showed that functional diversity and resilience are enhanced following restoration of seagrass bed in view of higher habitat heterogeneity; Wong and Dowd (2015) found that the presence of seagrass enhances functional diversity to a certain extent, depending on the site characteristics. The present study, however, revealed an opposite trend where functional diversity decreased with increasing habitat heterogeneity. This substantiates that the biogenic structures in mangroves, especially the dense root structure, could act as environmental filters and lead to trait convergence (i.e. reduction in functional niches) (Mason et al., 2005; Villéger et al., 2008). The lower functional diversity in the algal mat and pneumatophore areas could be due to the dominance of direct developers, meaning that these communities rely on local retention rather than dispersal of species from other areas (Boström et al., 2010). In contrast, the higher larval dispersal capability in the mudflat and seedling area indicates higher chance to genetic variation, resulting in higher functional diversity. The higher functional diversity in the mudflat and seedling area indicates more efficient use of resources and higher productivity as the species have different resource requirements (i.e. niche complementarity) (Petchey, 2003; Petchey and Gaston, 2006). The degree of overlapping of functional niches among species can be reflected by functional redundancy (Rosenfeld, 2002). The lower functional redundancy in the mudflat indicates less overlapping of functional niches among species, and thus the ecological functions were more susceptible to species loss than other habitats. Nevertheless, functional diversity increased only slightly with species richness, meaning that functional redundancy in this mangrove was high (Micheli and Halpern, 2005). In other words, there were many functionally similar species in this mangrove and thus the ecosystem functions are robust to the change in species richness. This observation is underpinned by the notion that macrobenthic communities in estuarine ecosystems have intrinsically high resilience to environmental changes because the macrobenthos have been adapted to the naturally high degree of variability (Elliott and Quintino, 2007; Elliott and Whitfield, 2011; Dimitriadis et al., 2012). In this study, the habitats with increasing habitat heterogeneity can be regarded as ecological succession. Previous studies showed that taxonomic diversity generally increases from the early to middle successional stages due to addition of species, but remains similar from the middle to late stages as the use of habitat becomes more specialized (Dean and Connell, 1987; Chen et al., 2015). The present findings using functional diversity also demonstrated this pattern. Overall, the both high functional diversity and functional redundancy in the seedling area suggest that moderate increase in habitat heterogeneity is beneficial to maximize ecological functions and resilience of macrobenthic communities.

Sediment properties were shown to affect trait patterns and functional diversity. For instance, Oug et al. (2012) found that carnivorous feeding is more prevalent in the coarser sediment while surface deposit feeding is positively associated with redox potential; Sivadas et al. (2013) found that filter feeding and deposit feeding prevail when the organic matter in sediment increases. In the present study, the trait pattern was mainly governed by redox potential, while functional diversity was negatively correlated with redox potential, TOM and particle size. The underlying mechanism to explain these results remains enigmatic, but it is noteworthy that these sediment properties are highly correlated with the root biomass (Pearson correlation coefficient: Total root vs. redox potential = 0.729; Total root vs. TOM = 0.662; Total root vs. particle size = 0.607) which can directly alter these properties (Leung, 2015). For instance, the dense root structure can oxygenate the sediment, resulting in higher redox potential. Therefore, I propose that the distribution of macrobenthos and hence their ecological functions were primarily governed by habitat heterogeneity, while the sediment properties only played a secondary role. This proposition is underpinned by a previous study where the biological traits of macrobenthic assemblages are relatively independent of environmental quality (Marchini et al., 2008).

Although taxonomic diversity is inherently associated with functional diversity (Naeem and Wright, 2003), it should not be used as a surrogate for functional diversity because their relationship is affected by functional redundancy and likely varies across habitats. In the present study, functional diversity increased only slightly with species richness, meaning that taxonomic diversity is a weak predictor of ecosystem functions. Similar findings have been demonstrated in previous studies. For instance, Munari (2013) found that the trait composition of macrobenthic communities in a sandy beach has a higher stability than the taxonomic composition to environmental changes; Törnroos et al. (2014) showed that the functional richness in a marine ecosystem can be maintained despite the reduction in species richness; Wong and Dowd (2015) revealed that taxonomic diversity of macrobenthos depends on the presence and abundance of seagrass, while functional diversity shows less dependence. As such, functional diversity rather than solely taxonomic diversity should be incorporated for conservation and management purposes as maintaining species richness does not necessarily maintain ecological functions (Reiss et al., 2009; Cadotte et al., 2011), especially in estuarine ecosystems where the biodiversity is inherently low (Elliott and Quintino, 2007). Nevertheless, the interpretation of ecosystem functions could still be misleading only using univariate parameters, such as functional diversity and functional redundancy. For example, the trait patterns between two *Kandelia* areas (Ko vs. Ko + mat) were different despite the similar values of functional diversity and functional redundancy. This highlights the advantage and importance of using biological trait analysis to decipher the changes in ecosystem functions due to environmental variables.

5. Conclusions

Mangroves in the world have been diminishing fast in the last few decades. Undoubtedly, restoration favours the recovery of ecological functions of degraded mangroves, but whether afforestation should be conducted remains dubious. By studying the biological traits of macrobenthos, the present study unravelled that functional diversity of macrobenthic communities decreased with increasing habitat heterogeneity primarily due to the root biomass which acts as the environmental filter. The biological traits, such as maximum body size, larval development and feeding mode, also indicated the disturbance and negative impacts of the root structure. Given the functional diversity and trait pattern, therefore, restoration of degraded mangroves should consider plant density and plant species to prevent aggregation of root structures. Mudflats are precious in mangroves, yet provide not only unique ecosystem functions but also feeding grounds for migratory birds. The lower functional redundancy and distinct trait pattern in the mudflat imply that its ecological functions are susceptible to afforestation. Considering the conservation and management of mangroves as a whole, afforestation is not recommended whereas restoration should be done only when the mangroves can no longer self-correct and the causes of mangrove loss have been identified (Lewis, 2005).

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