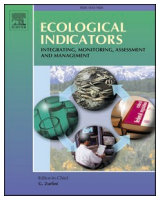
Ecological Indicators 181 (2025) 114479

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Taxonomic and functional diversity reveal contrasting crab community dynamics under artificial and natural pond to mangrove restoration

Xiaoyan Lu [a,b], Xuan Gu [a], Lin Zhang [a], Wenqing Wang [a], Jianxiang Feng [b], Mao Wang [a,*]

[a] Key Laboratory of the Coastal and Wetland Ecosystems (Xiamen University) Ministry of Education, Xiamen University, Xiamen, PR China
[b] School of Marine Sciences, Guangdong Provincial Key Laboratory of Marine Resources and Coastal Engineering, Sun Yat-Sen University, Zhuhai 519082, PR China

ARTICLE INFO

Keywords:
Taxonomic diversity
Functional diversity
Mangrove crabs
Pond-to-mangrove restoration
Artificial restoration
Natural restoration
Dongzhaigang Bay

ABSTRACT

Mangrove restoration is critical for the resilience of coastal ecosystems, yet there remains insufficient research on the ecological effects of artificial versus natural restoration, especially regarding their impacts on faunal communities and ecosystem functions. This study used a space-for-time substitution approach to investigate the taxonomic and functional diversity of crab communities along a 27-year pond-to-mangrove restoration chronosequence in Dongzhaigang Bay, southern China. We analyzed temporal changes in community composition and functional traits under artificial and natural restoration approaches, compared alpha diversity and the components of beta diversity across sites, and explored the influence of environmental variables on variations in crab community structure. A total of 3,700 crabs representing 24 species were recorded. Artificial restoration sites exhibited rapid early colonization, with species richness reaching 1.5 times that of natural restoration sites by year 4. However, by year 27, both artificial and natural restoration sites showed no significant differences in crab taxonomic and functional diversity compared to natural mangroves. The results indicate that species composition in both restoration types underwent a typical successional process, beginning with dominance by filter-feeding Ocypodidae crabs in the early stages and gradually shifting to dominance by herbivorous and omnivorous crabs of the Grapsoidea family in later stages. Nevertheless, the proportion of functional groups in naturally restored sites was closer to that of natural mangroves. Soil pH and salinity were identified as the primary environmental drivers shaping both taxonomic and functional community patterns. Based on these findings, we emphasize the importance of incorporating functional traits and successional dynamics alongside taxonomic metrics to more accurately assess the ecological recovery of mangrove restoration efforts.

1. Introduction

Mangrove ecosystems rank among the most productive and ecologically significant coastal habitats, providing critical services such as shoreline stabilization, carbon sequestration, and critical habitats for diverse fauna (Alongi, 2002; Friess et al., 2019). However, over the past century, large-scale land-use changes, particularly the conversion of mangroves into aquaculture ponds, have resulted in the degradation of more than 35 % of global mangrove forests (Valiela et al., 2001; Giri et al., 2015). In Southeast Asia, which serves as the epicenter of global shrimp aquaculture, mangrove loss has been especially severe due to short-sighted economic incentives combined with weak environmental regulations (Richards and Friess, 2016; Jayanthi et al., 2018). Between 1960 and 1990, Indonesia lost over 269,000 ha of mangroves due to aquaculture development (Primavera, 2000), with similar losses reported in Ecuador and China (Lacerda et al., 2007; Herbeck et al., 2020). Many of these ponds are frequently abandoned after only a few years as a consequence of declining yields, soil acidification, or disease outbreaks, thus resulting in a cyclical process of degradation (Stevenson, 1997; Aslan et al., 2021).

The degradation of mangroves and the increasing recognition of their ecological value have led to the initiation of numerous restoration projects (Lovelock et al., 2022). Historically, restoration efforts have centered on afforestation, particularly in intertidal zones, with Southeast Asian programs beginning in the early 1990 s (Gerona-Daga and Salmo, 2022). The predominant approach has been direct planting of mangrove seedlings (Mariano et al., 2022). However, this method faces limitations, including low survival rates, high costs, and reduced habitat heterogeneity (Wodehouse and Rayment, 2019). Intertidal flats are ecologically sensitive zones characterized by unique functional traits,

* Corresponding author.
E-mail address: wangmao@xmu.edu.cn (M. Wang).

https://doi.org/10.1016/j.ecolind.2025.114479
Received 11 June 2025; Received in revised form 9 November 2025; Accepted 21 November 2025
Available online 27 November 2025
1470-160X/© 2025 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC license (http://creativecommons.org/licenses/by-nc/4.0/).

low functional redundancy, and importance for species such as migratory waterbirds (Ma et al., 2010). Afforestation in these areas may compromise ecosystem functions by simplifying habitat structure (Leung et al., 2015a). In contrast, restoring abandoned aquaculture ponds, particularly those situated in mid-to-upper intertidal zones, has been proposed as an alternative that is more ecologically viable and cost-effective (Duncan et al., 2016; Wang et al., 2021). In many cases, natural regeneration in these abandoned ponds occurs when mangrove propagules are dispersed into the ponds, but successful recovery often depends on some level of hydrological reconnection, such as channel opening or partial dike removal, to facilitate water and propagule exchange (Nitto et al., 2013; Wang et al., 2021). Through this combination of natural dispersal and minimal hydrological intervention, pond-to-mangrove restoration has demonstrated feasibility, and the resulting ecosystems tend to exhibit biodiversity and ecological processes comparable to those in undisturbed mangrove forests (Ellison, 2000; Kitchingman et al., 2022).

Despite the growing recognition of pond-to-mangrove restoration, research and practice remain disproportionately focused on vegetation recovery, while faunal biodiversity and functional processes receive comparatively limited attention (Lovelock et al., 2022; Dinitto et al., 2013). As a result, little is known about how different restoration strategies, particularly artificial versus natural approaches, affect animal community structure and ecosystem functioning. For instance, artificial restoration methods such as pond filling and seedling planting may accelerate vegetation recovery in degraded areas; however, they may also reduce habitat heterogeneity and exclude functionally specialized species (Zhang et al., 2022). Conversely, natural restoration is more likely to preserve ecological processes but tends to proceed more slowly and unpredictably depending on local environmental conditions. Nevertheless, comparative ecological evaluations of these approaches remain limited, and the few existing studies often suffer from short monitoring durations, the absence of faunal indicators, and a lack of functional ecological perspectives.

To overcome the limitations of short-term monitoring, this study adopted a space-for-time substitution approach, which infers temporal ecological changes by comparing spatially distinct sites that represent different restoration ages. This method is commonly used in restoration ecology when long-term datasets are not available, as it allows the assessment of successional processes and community development across a chronosequence. It assumes that selected sites differ mainly in time since restoration, and that other environmental variables are either similar or accounted for in the analysis. While this approach cannot fully control for all spatial variation, it provides a practical and informative framework for evaluating long-term ecological outcomes, particularly for organisms like crabs that respond to both habitat age and structural complexity. Crabs are effective indicators for evaluating mangrove restoration due to their central ecological roles in bioturbation, detritus processing, and trophic transfer (Kristensen, 2008; Gao and Lee, 2022). Their burrowing and feeding activities modify sediment properties and nutrient cycles, and their community structure can reflect restoration stage and habitat complexity (Wang et al., 2010; Rinehart et al., 2024). Crab assemblages also show consistent responses to forest age and management history, which are largely shaped by differences in feeding habits, morphology, and ecological roles. For example, Ocypodid crabs, as deposit feeders adapted to open and unstable substrates, tend to dominate early-successional sites, whereas Sesarmid crabs, through their burrowing and leaf-feeding activities that enhance nutrient cycling and sediment stabilization, prevail in mature mangroves (Ashton et al., 2003; Ashton and Macintosh, 2024). However, few studies have assessed crab biodiversity responses across both artificial and natural restoration trajectories or across multi-decadal timescales. Given their species-specific and ecological relevance, crabs offer a robust means of functionally evaluating restoration progress through community composition monitoring, thereby providing a valuable complement to traditional vegetation-based assessment approaches.

Although pond-to-mangrove restoration is gaining traction in Southeast Asia (Matsui et al., 2010), empirical research remains limited compared to studies on intertidal afforestation (Dinitto et al., 2013). Many artificial restoration projects focus on planting a limited number of mangrove species, which may lead to habitat homogenization, reduced functional diversity, and lower ecological resilience (Lovelock et al., 2022). Considering the urgent demand for effective restoration under accelerating climate change, assisted planting that incorporates a broader range of mangrove species may offer a more ecologically sound and sustainable pathway. Furthermore, critical ecological processes, such as detrital processing efficiency, nutrient cycling, and trophic network complexity, are essential indicators of ecosystem health and functionality (Kelly and Harwell, 1990). However, these factors are often overlooked in conventional restoration assessments. Furthermore, there remains no clear consensus on whether active interventions, such as pond infilling or seedling planting, are necessary to achieve successful restoration outcomes.

This study used a space-for-time substitution approach to examine the ecological outcomes of artificial and natural pond-to-mangrove restoration strategies at three time points (1995, 2014, and 2018) in Dongzhaigang Bay, Hainan Province, China. Focusing on crab communities, we address three key questions: (1) How do artificial and natural restoration strategies affect the temporal dynamics of crab taxonomic and functional diversity? (2) To what extent do crab communities under different restoration strategies converge toward natural mangrove conditions in terms of species composition, functional structure, and beta diversity over time? (3) Which environmental factors drive the spatial variation in crab community composition and functional traits throughout the mangrove restoration process? By integrating taxonomic and functional perspectives, this study provides scientific references for biodiversity-based ecological restoration and the assessment of long-term ecosystem function.

2. Materials and methods

2.1. Study sites

This study was conducted in the Dongzhaigang National Nature Reserve (19°54′-20°02′N, 110°31′-110°37′E) on the northeastern coast of Hainan Island, China. As one of the earliest and most representative mangrove ecosystems, the reserve supports 25 mangrove species, including nine introduced taxa, and holds the highest mangrove species richness in China (Xiong et al., 2021). The dominant species include *Avicennia marina*, *Bruguiera sexangula*, *Ceriops tagal*, *Rhizophora stylosa*, and *Sonneratia apetala*. Large areas of natural mangroves were converted into aquaculture ponds during the last century. Many of these ponds were subsequently abandoned or restored due to declining productivity and growing environmental concerns. Since the mid-1990 s, mangrove restoration in abandoned ponds has been carried out using both natural and artificial approaches. In 2014, following the implementation of a government subsidy policy (as land is state-owned in China) to encourage pond farmers to relinquish their usage rights, most remaining ponds were incorporated into the reserve, and ecological restoration using both approaches was subsequently initiated. In 2018, a further set of abandoned aquaculture ponds underwent pond-to-mangrove restoration using similar natural and artificial methods. This background positions Dongzhaigang as an ideal case study for assessing the long-term effectiveness of mangrove restoration efforts.

To assess the effects of restoration strategy and restoration time on crab community diversity, we used a space-for-time substitution approach to select three representative pond-to-mangrove chronosequences, corresponding to restoration durations of 27 years (DX), 8 years (WL), and 4 years (BD), respectively (Fig. 1A). Each chronosequence includes three habitat types: artificially restored mangroves (AR), naturally restored mangroves (NR), and undisturbed natural mangroves (NM). Artificial restoration was implemented through

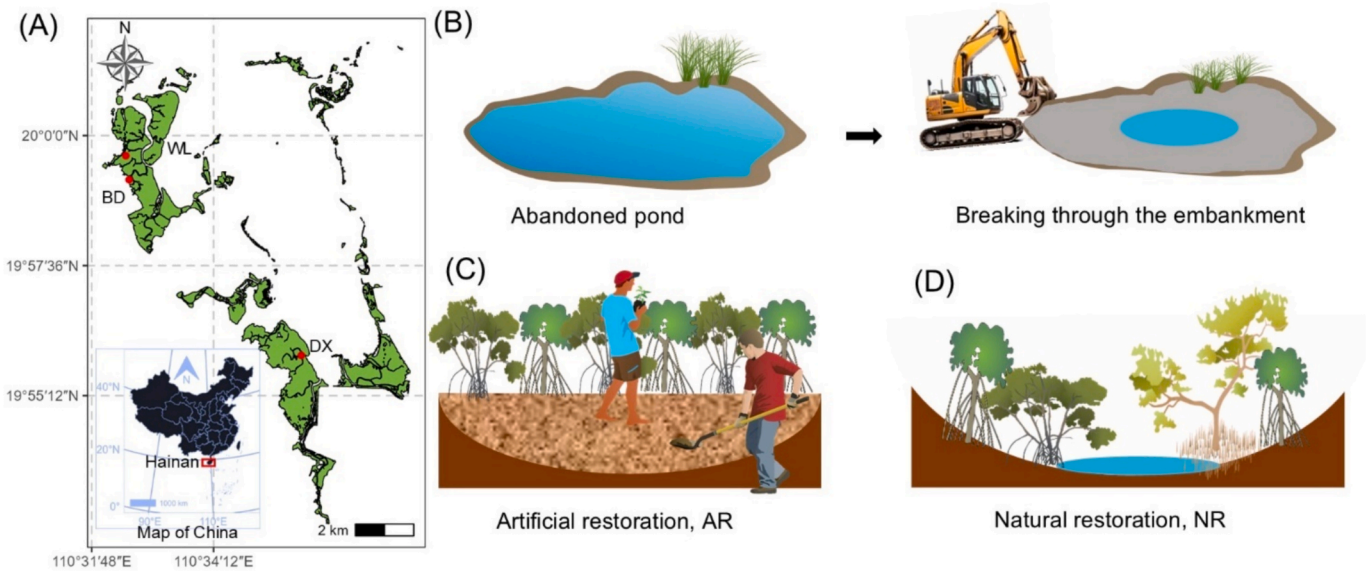


Fig. 1. Distribution of sampling sites and schematic diagrams of restoration methods. (A) Sampling sites in Dongzhaigang National Nature Reserve, Hainan, China, based on a space-for-time substitution with three chronosequences: 27 years (DX), 8 years (WL), and 4 years (BD). Each includes artificial restoration (AR), natural restoration (NR), and natural mangroves (NM). (B) Schematic diagram of breaching the embankment to restore hydrological conditions. (C) Schematic diagram of the artificial restoration method, including hydrological restoration, land reclamation, and planting. (D) Schematic diagram of the natural restoration method, including hydrological restoration only.

sediment infilling and planting of *Bruguiera sexangula*, *Rhizophora stylosa*, and *Sonneratia apetala* following dike removal (Fig. 1B, Fig. 1C). Natural restoration involved dike removal only, with no active planting (Fig. 1B, Fig. 1D). Natural mangroves were used as reference sites. For each restoration type within each chronosequence, five sampling sites were established based on historical land use records, satellite imagery, and field verification to ensure comparable tidal and sediment conditions.

2.2. Field sampling

At each site, three 10 m × 10 m plots were randomly established along the intertidal gradient. Within each plot, we recorded mangrove species composition, tree height, and stem density. To characterize abiotic conditions, relative surface elevation (referenced to the Yellow Sea Datum) was measured using a real-time kinematic global navigation satellite system (iRTK10, HiTarget Corporation, China). Sediment samples were collected from three subplots per plot, pooled, and analyzed for total organic carbon (TOC), total nitrogen (TN), salinity (‰), pH, and soil median particle size (D50, representing the particle size at which 50 % of the sample is finer by weight) to assess sediment properties. During seasonal crab sampling campaigns, key aquatic parameters including dissolved oxygen (mg/L) and salinity (‰) were measured in situ on peak spring tide days using a Professional Plus (Pro Plus) Multiparameter Instrument (YSI, Ohio, USA). To ensure data accuracy, three random points were selected within each quadrat, with each parameter measured in triplicate.

2.3. Crab surveys

Crab communities were sampled during both the summer (July 2022) and winter (January 2023) seasons using a combination of non-destructive camera photography (Gu et al., 2022) and passive capture methods. At each site, three 50 cm × 50 cm plots were established for camera monitoring, with a Canon M100 digital camera (24.2 MP) mounted vertically on a PVC frame positioned above the quadrat (Fig. S1). The cameras were set to program auto-exposure mode to adapt to varying light conditions, with no manual adjustments made to ISO or shutter speed. All photographic sampling was conducted during daylight hours under sufficient natural light to ensure image clarity. A focal length of 15 mm was used, providing an optimal field of view that fully covered the quadrat and maximized species detectability. Cameras were activated during low tide and programmed to capture images at 5-second intervals for 10 min, following a 15-minute acclimation period. The 15-minute acclimation period was chosen based on previous studies and our field observations indicating that most crabs resume normal activity approximately 15 min after deployment of sampling devices (Gu et al., 2022). This approach effectively recorded surface-active and burrow-emergent crab species. A comprehensive inventory of crab species, including their abundance, sampling methods, and distribution across restoration stages, is provided in Supplementary Table S1.

As camera photography was limited to low-tide periods and may not fully capture the activity of swimming crabs, passive capture surveys using unbaited centipede nets (10 m length, 1 cm mesh) were also conducted. To standardize sampling effort and maximize capture efficiency, three nets were deployed perpendicular to the tidal flow within each site to capture crabs active during high tide. Each net was securely fixed by inserting PVC pipes into the substrate and tying both ends of the net to these pipes to ensure stability. Nets were deployed at the same locations and during comparable tidal stages across different sampling seasons, and were retrieved 24 h after deployment to maintain sampling consistency. Captured crabs were fixed immediately in the field using 4 % buffered formalin, rinsed with water, and transferred to 75 % ethanol within three days. All specimens were identified to species level following Shih et al. (2010) and the World Register of Marine Species (https://www.marinespecies.org).

2.4. Statistical analyses

To facilitate comparative analysis of crab population dynamics across sites, we consolidated camera monitoring and centipede netting data collected during different hydrological periods (summer: July 2022; winter: January 2023) into a unified dataset. Rarefaction analysis was employed to standardize sampling effort and compare species richness across restoration methods (Oksanen et al., 2018).

Taxonomic alpha diversity was quantified using *Shannon-Wiener*

diversity, *Simpson* diversity, and *Pielou* evenness, while functional alpha diversity was assessed with functional richness (FRic), functional dispersion (FDis), and functional evenness (FEve). To further evaluate the degree of trait redundancy within communities, we calculated the functional redundancy index (FRI). This index provides a relative estimate of the extent to which species share overlapping functional roles within the community. Prior to statistical analysis, assumptions of normality and homogeneity of variances were tested. Differences among restoration methods were analyzed using one-way ANOVA, followed by Least Significant Difference (LSD) post-hoc tests ($p < 0.05$).

To evaluate temporal variation in crab functional groups during pond-to-mangrove restoration, we computed Gower distances from the species-trait matrix and applied the "ward.D2" clustering method. We selected Gower distance because it can handle mixed data types, including continuous and categorical traits, without requiring variable transformation, thus accurately reflecting ecological differences among traits. The optimal number of clusters was initially determined based on silhouette width, and final groupings were refined to ensure ecological interpretability. Functional groups were characterized based on three trait dimensions: diet (filter-feeding, omnivorous, carnivorous), locomotion (swimming, crawling, climbing), and habitat type (burrowing, semi-arboreal). The relative abundance of each functional group across restoration stages was visualized using stacked bar plots. A summary of trait assignments for each species is presented in Table S2.

The temporal responses of community structure to restoration strategies were examined using non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity. Analysis of Similarities (ANOSIM) was used to test for significant differences in crab community species composition among different pond retreat modes. Both NMDS and ANOSIM analyses were performed using the Vegan package (Oksanen et al., 2024).

To quantify taxonomic beta diversity, we used a Bray-Curtis-based decomposition method (Dray et al., 2024) that partitions total beta diversity into two components: richness difference (nestedness; RichDiff) and species replacement (turnover; Repl) (Legendre, 2014). Abundance-based beta diversity metrics were calculated using the beta.pair.abund function in the betapart R package (Baselga and Orme, 2012). Differences among restoration methods were tested for significance using Welch's ANOVA and Games–Howell post-hoc tests ($p < 0.05$). In parallel, functional beta diversity was assessed by calculating Gower distances among species traits, followed by principal coordinates analysis (PCoA) to construct a reduced trait space. Functional dissimilarities were then partitioned into turnover and nestedness components using the functional.beta.pair and functional.beta.multi functions in betapart.

We performed a Permutational Multivariate Analysis of Variance (PERMANOVA) using the "adonis2" function in the vegan package (Oksanen et al., 2024) to evaluate the effects of restoration method, restoration time, and their interaction on crab taxonomic and functional diversity. Bray-Curtis dissimilarity was calculated for species abundance, and Gower distance was used for functional trait data. In addition to multivariate approaches (PERMANOVA) and functional redundancy (FRI), we calculated Rao's quadratic entropy (Rao's Q) as an abundance-weighted index of functional diversity for each sample. Rao's Q values were subsequently analyzed using two-way ANOVA to test for differences among restoration methods and years.

Constrained distance-based redundancy analysis (dbRDA) was used to identify key environmental drivers influencing the distribution of crab community composition and functional structure. Model selection was performed using the "ordistep" function in the vegan R package (Oksanen et al., 2024), with variable significance assessed through 1,000 permutations. To address multicollinearity, Variance Inflation Factors (VIF) were calculated, and variables with VIF greater than 5 were removed. All data analyses and visualizations were conducted in R version 4.3.1 (R Core Team, 2023).

3. Result

3.1. Crab taxonomic and functional diversity respond to restoration time and method

A total of 3,700 crabs, belonging to 8 families and 24 species, were recorded. Rarefaction analysis showed that after 4 years of pond-to-mangrove restoration, the estimated species pool matched observed richness ((Table S1, Fig. 2). After 8 years, AR, NR, and NM sites harbored 22, 18, and 13 species, accounting for 86 %, 94 %, and 100 % of observed values, respectively. After 27 years, the AR site's estimated pool dropped to 12 species (92 %), while NR and NM matched observations (Table S3, Fig. 2). These findings confirm the feasibility of using camera photography for crab diversity studies in mangrove ecosystems.

The taxonomic and functional diversity of crabs under different mangrove restoration approaches is presented in Fig. 3. By the 4 year of restoration, significant differences in taxonomic alpha diversity were observed among restoration methods, with the AR exhibiting significantly higher diversity than NR ($p < 0.05$), whereas both AR and NR showed significantly lower taxonomic alpha diversity compared to NM ($p < 0.05$). Similarly, functional richness (FRic) and functional dispersion (FDis) in AR and NR were significantly lower than those in NM ($p < 0.05$), while no significant difference was detected between AR and NR. By the 8 years, NM's FRic remained significantly higher than that of NR ($p < 0.05$), and its FDis was also significantly higher than that of AR ($p < 0.05$). By the 27 years, no significant differences in FRic, FDis, or functional evenness (FEve) were found among the AR, NR, and NM sites. Additionally, taxonomic diversity did not differ significantly among AR, NR, and NM at either the 8 or 27 years. Functional redundancy values were high across all sites (>0.93, Table S4), indicating significant functional overlap among species.

3.2. Temporal shifts in species composition and functional groups of mangrove crabs

The relative frequency results of mangrove crabs (Fig. S2) revealed distinct temporal patterns of species occurrence across restoration methods. In the artificially restored sites, *Cleistostoma dilatatum* and *Macrophthalmus definitus*, both belonging to the family of Ocypodidae, appeared only after 4 years of restoration. *Sarmatium germaini*, *Paraleptuca splendida*, and *Thalamita crenata* appeared only after 8 years of restoration, while *Parasesarma continentale* and *Parasesarma eumolpe*, both from the Sesarmidae family, showed the highest frequency after 27 years of restoration. Similarly, naturally restored sites showed the presence of *Macrophthalmus definitus* after 4 years, with additional species appearing at later stages, and some species like *Varuna litterata* and *Myomenippe hardwickii* appeared only after 27 years of recovery.

Based on the clustering results using Gower distance and silhouette width analysis, crabs were grouped into three functional categories according to feeding strategy, mobility, and habitat preference (Fig. 4A). These groups were defined based on ecological roles as follows: Group A consisted of primarily herbivorous-omnivorous crabs belonging to the families Grapsidae, Sesarmidae, and Varunidae; Group B included crabs from the Ocypodoidae family, which primarily filter-feed on the sediment surface; and Group C comprised swimming predators mainly from the Portunidae family.

The composition and relative abundance of these functional groups varied among restoration sites (Fig. 4B). After 4 years of restoration, Group B dominated in both AR and NR sites. By 8 years, the proportion of Group A increased in both AR and NR compared to the 4-year stage, with AR exhibiting a higher proportion of Group A than NR. At 27 years post-restoration, the functional group composition in AR, NR, and the NM reference site followed the same pattern: A > B > C. However, the proportions of functional groups in NR were more similar to those in NM, suggesting greater functional convergence in naturally restored sites over time.

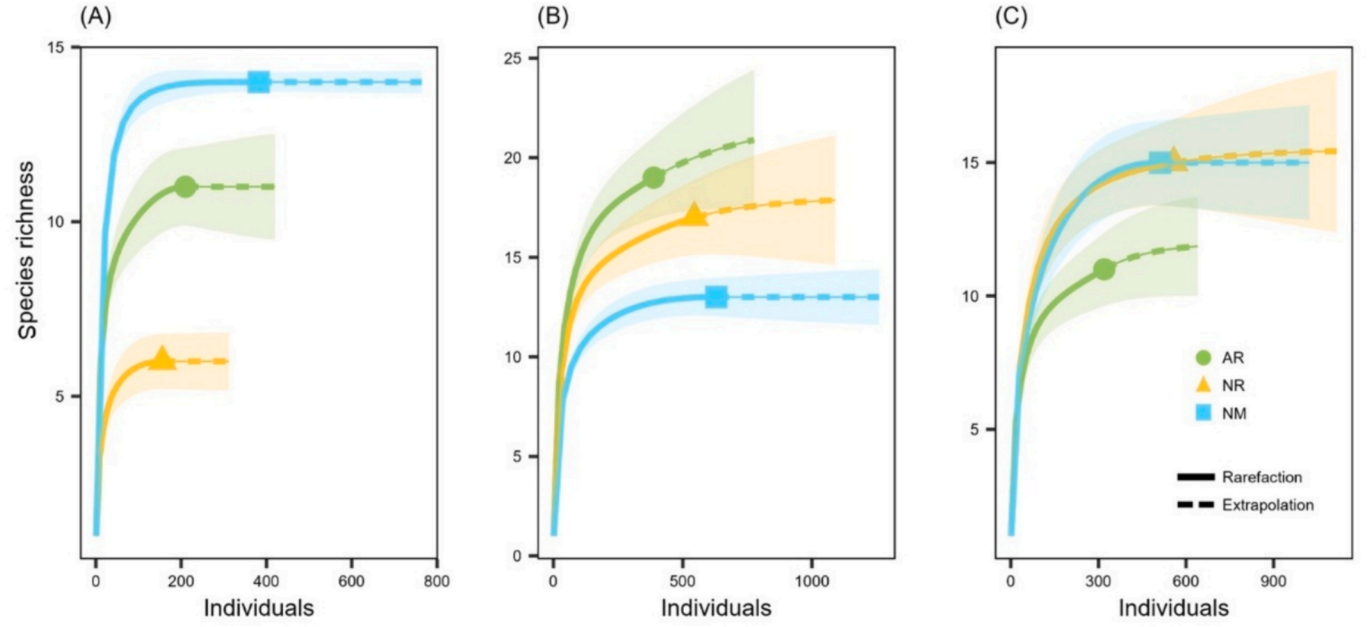


Fig. 2. Species richness of crabs under different pond-to-mangrove restoration methods, calculated from sample-based rarefaction curves and scaled to show the number of individuals on the x-axis. The shadow represents the 95% confidence interval (CI). (A) 4-year post-restoration; (B) 8-year post-restoration; (C) 27-year post-restoration. (AR: Artificial restoration; NR: Natural restoration; NM: Natural mangroves).

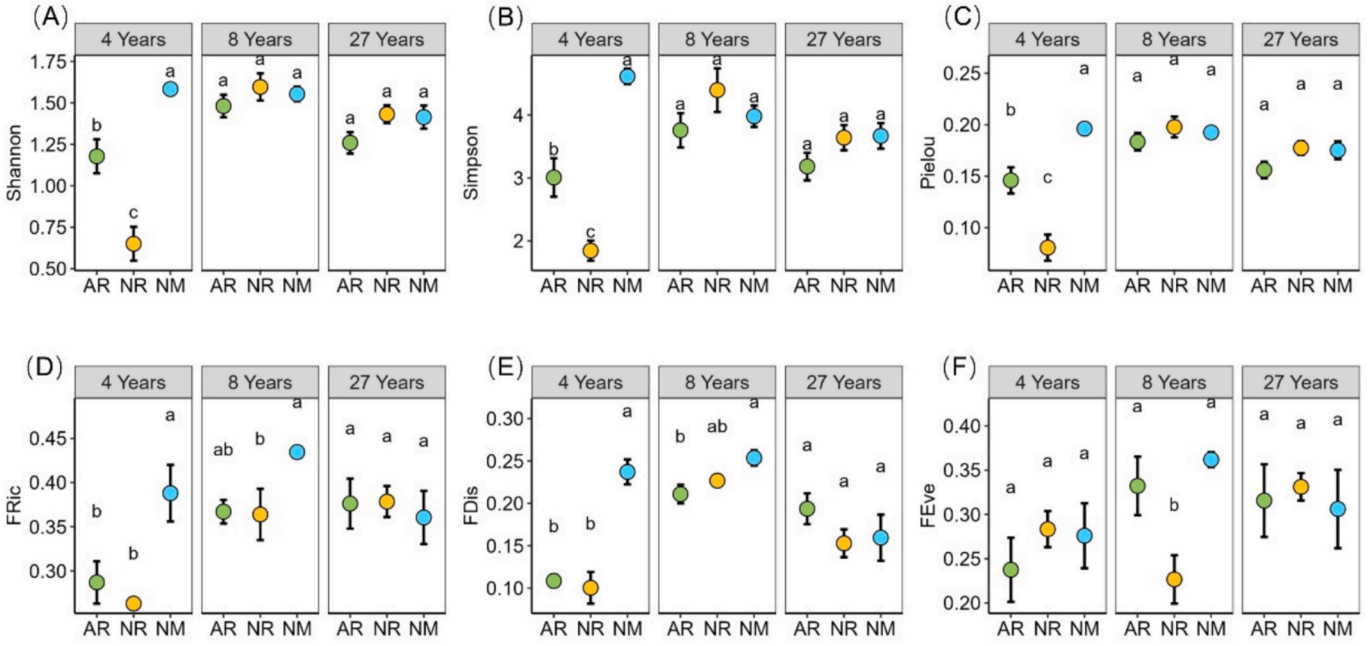


Fig. 3. Comparative analysis of crab alpha diversity indices across pond-to-mangrove restoration approaches:Taxonomic diversity indices: (A) Shannon-Wiener diversity; (B) Simpson diversity; (C) Pielou evenness; Functional diversity indices: (D) Functional richness (FRic); (E) Functional dispersion (FDis); (F) Functional evenness (FEve). (AR: Artificial restoration; NR: Natural restoration; NM: Natural mangroves).

3.3. Temporal convergence and beta diversity dynamics across restoration methods

Analysis of similarities (ANOSIM) revealed significant differentiation in community structure among AR, NR, and NM sites throughout the restoration timeline ($p < 0.05$). Non-metric multidimensional scaling (NMDS) illustrated clear separation of AR communities from NR and NM at early stages, with NR communities gradually converging toward NM over time (Fig. 5). The gradual decrease in R values quantitatively reflects a temporal reduction in community dissimilarity across restoration methods.

The composition of beta diversity (Fig. 6) showed that, throughout the pond-to-mangrove restoration process, the total beta diversity in AR sites was consistently higher than that in NR and NM sites. Moreover, as restoration progressed, the total beta diversity in both AR and NR sites exhibited a declining trend. Additionally, beta diversity at all sites was primarily driven by species turnover, while nestedness components remained relatively low (Fig. 6). Notably, although taxonomic beta diversity was higher in AR sites, functional beta diversity did not show a corresponding increase, suggesting that the elevated taxonomic

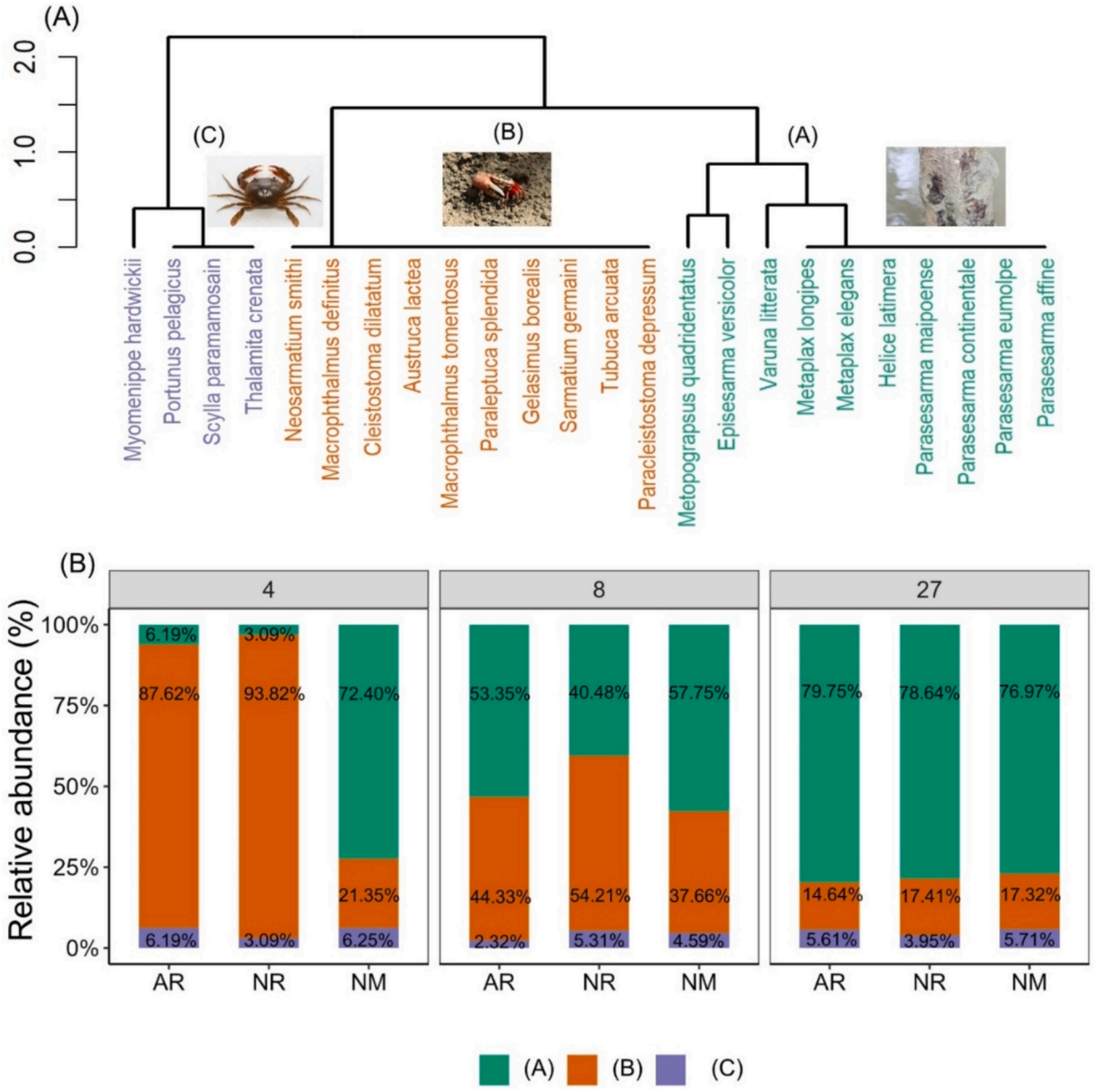


Fig. 4. Functional group classification and spatial distribution of mangrove crabs. (A) Functional groups of mangrove crabs defined by clustering based on Gower distance of the species-trait matrix; (B) Relative abundance of functional groups across different sites.

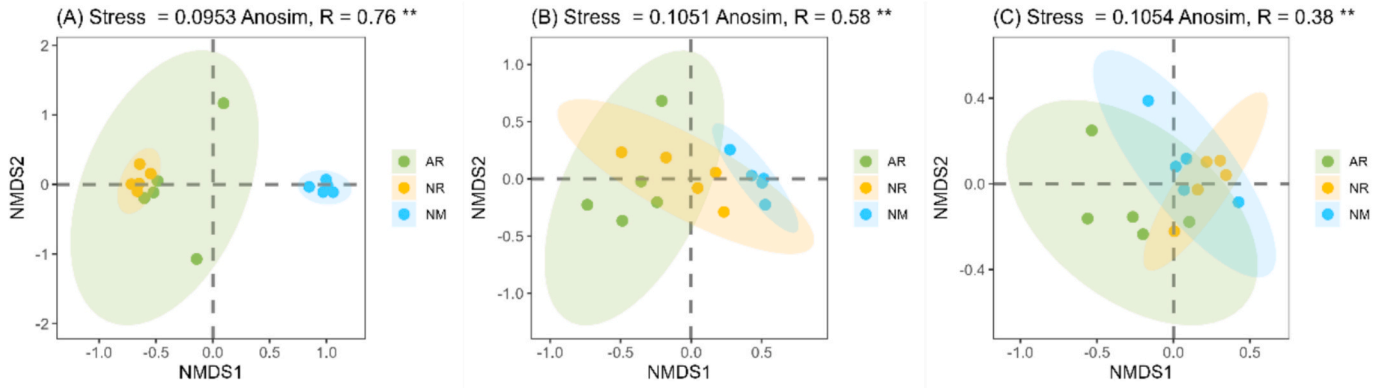


Fig. 5. Non-metric multidimensional scaling (NMDS) ordination of crab community structure across mangrove restoration chronosequences. (A) 4-year post-restoration; (B) 8-year post-restoration; (C) 27-year post-restoration. (AR: Artificial restoration; NR: Natural restoration; NM: Natural mangroves).

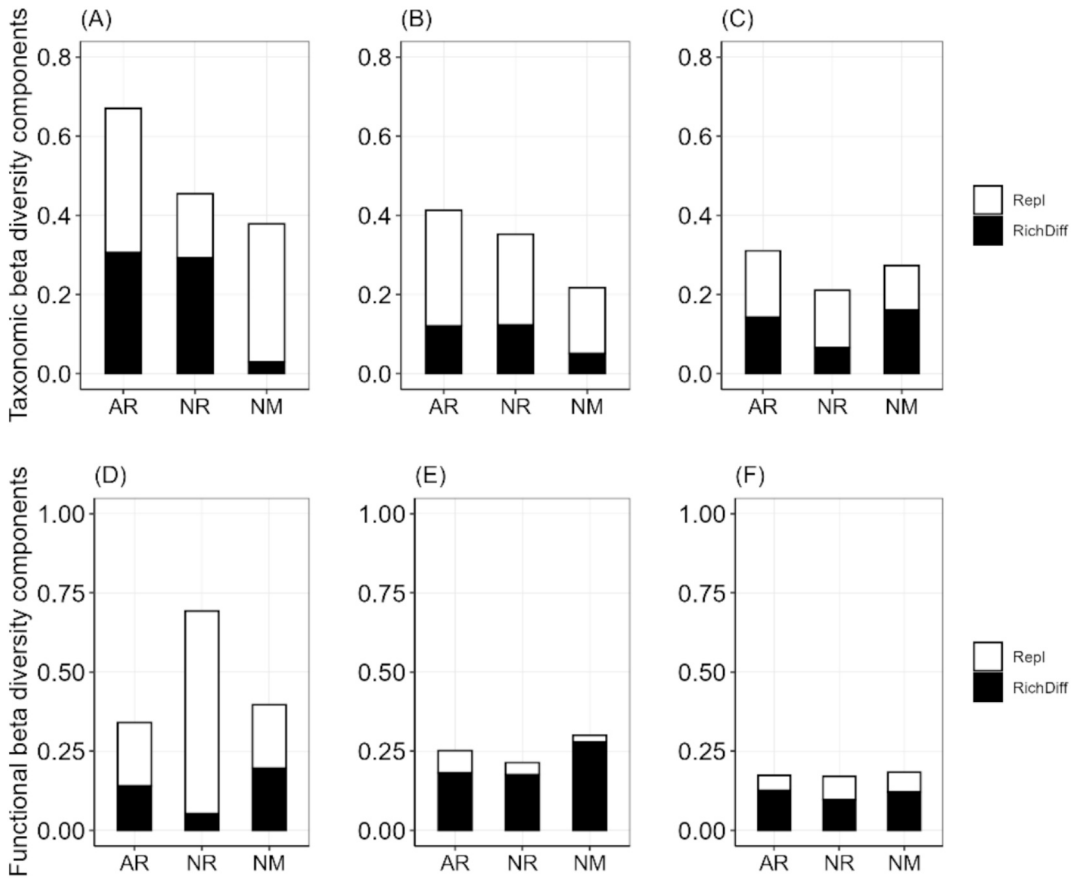


Fig. 6. Stacked bar charts of crab community beta diversity under different pond-to-mangrove restoration methods, partitioned into richness difference (nestedness; RichDiff) and species replacement (turnover; Repl). Taxonomic beta diversity: (A) 4-year post-restoration; (B) 8-year post-restoration; (C) 27-year post-restoration. Functional beta diversity: (D) 4-year post-restoration; (E) 8-year post-restoration; (F) 27-year post-restoration. (AR: Artificial restoration; NR: Natural restoration; NM: Natural mangroves).

dissimilarity in AR sites may largely reflect stochastic turnover rather than functional complementarity (Fig. 6). The results of Welch's analysis of variance and Games-Howell post-hoc tests (Table S5; Table S6) indicated that at 4 years after pond-to-mangrove restoration, the total beta diversity in AR was significantly higher than that in NR and NM sites (both $p < 0.05$). At 8 years post-restoration, there was no significant difference in total beta diversity between AR and NR ($p = 0.418$), while both differed significantly from the NM ($p < 0.05$). At 27 years post-restoration, post-hoc tests showed that the total beta diversity in AR sites remained significantly higher than that in NR ($p < 0.05$).

3.4. Drivers of taxonomic and functional structure across restoration gradients

The PERMANOVA results (Table 1) indicated that restoration method, time and their interaction had significant effects on the taxonomic diversity of crab communities ($p < 0.05$), collectively explaining approximately 70 % of the variation in community structure. Among these variables, restoration time had the greatest explanatory power, highlighting a strong successional trend in community composition. In contrast, at the level of functional diversity, the model explained only 25 % of the variation and was not statistically significant ($p = 0.102$), suggesting that although species turnover occurred during the restoration process, the functional composition of crab communities remained relatively stable. This stability may be attributed to a high degree of functional redundancy. Further two-way ANOVA indicated that Rao's quadratic entropy (Rao's Q) did not differ significantly among restoration methods, restoration years, or their interaction ($p > 0.05$), consistent with the PERMANOVA results.

Table 1
Summary of PERMANOVA results for taxonomic and functional diversity of crab communities under different restoration methods and years. Results represent separate one-factor PERMANOVA models for each factor.

Diversity Type	Variable	R^2 (%)	F-value	P-value
Species Diversity	Method	13.56	3.2942	0.005*
	Year	36.41	12.026	0.001*
	Method × Year	69.61	10.306	0.001*
Functional Diversity	Method	5.27	1.1689	0.322
	Year	8.14	1.8602	0.103
	Method × Year	25.03	1.5022	0.083

The results of distance-based redundancy analysis (dbRDA) revealed that crab community composition was significantly influenced by environmental factors, collectively explaining 79.55 % of the total variation (Fig. 7A). Among these, soil pH (ANOVA, $p = 0.001$) and soil salinity (ANOVA, $p = 0.010$) were negatively associated with community structure, whereas elevation (ANOVA, $p = 0.017$) and sediment median grain size (D_{50}; ANOVA, $p = 0.014$) exhibited positive relationships along the primary RDA axis. Soil total nitrogen and dissolved oxygen showed no significant effects. All environmental variables included in the models exhibited low collinearity (Table S8). Similarly, for functional trait composition, the dbRDA model explained 26.99 % of the total variation, with the first and second constrained axes explaining 19.01 % and 7.98 % of the variation, respectively (Fig. 7B). Soil pH (ANOVA, $p = 0.001$) was positively associated with the first axis, while soil salinity (ANOVA, $p = 0.001$) showed a strong negative association.

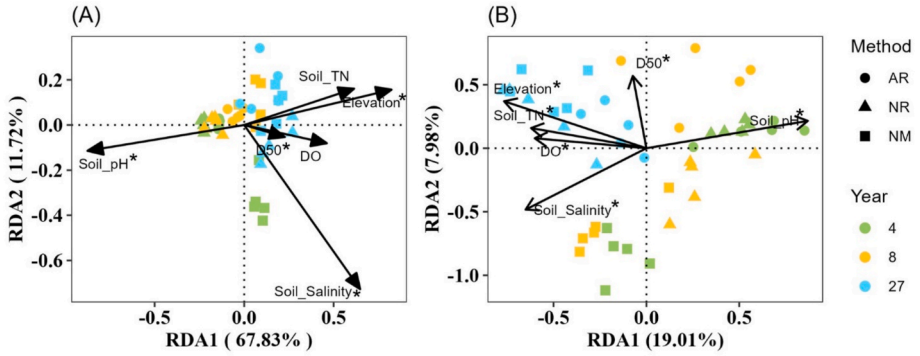


Fig. 7. Distance-based redundancy analysis (dbRDA) of crab communities. (A) Taxonomic community structure; (B) Functional community structure. (AR: Artificial restoration; NR: Natural restoration; NM: Natural mangroves). D50, soil median grain size (the particle size at which 50 % of the sample is finer by weight); DO, dissolved oxygen; * indicates $p < 0.05$.

Elevation (ANOVA, $p = 0.003$), soil total nitrogen (ANOVA, $p = 0.036$), dissolved oxygen (ANOVA, $p = 0.031$), and D_{50} (ANOVA, $p = 0.007$) were all positively correlated with functional trait composition. These patterns suggest that both physicochemical and geomorphic gradients jointly structured taxonomic and functional organization across restoration stages and habitats.

4. Discussion

4.1. Effects of restoration time and method on crab community taxonomic and functional composition

Our results indicate that both artificial and natural restoration pathways enhance the taxonomic and functional diversity of mangrove crab communities, although they follow distinct successional trajectories. In artificial restoration, rapid increases in diversity are primarily driven by interventions such as mangrove planting and substrate modification. These measures create transitional microhabitats that provide shelter for generalist species such as Ocypodid crabs (Ashton and Macintosh, 2024). The resulting habitat heterogeneity promotes temporary species coexistence and increases community complexity through niche partitioning (Stein et al., 2014). In contrast, natural restoration relies on tidal hydrology and propagule dispersal, leading to slower structural development and initially lower crab diversity. Over time, however, differences in taxonomic diversity between artificial and natural restoration diminish, with 27-year-old natural sites reaching levels comparable to those of artificial sites. This trend aligns with the *meta*-analysis by Crouzeilles et al. (2017), suggesting that different restoration strategies may ultimately yield similar long-term ecological outcomes.

Regarding functional diversity, both early artificial and natural restoration sites exhibited lower functional richness and dispersion compared to natural mangroves, reflecting simplified trait composition (MacArthur and Levins, 1967; Díaz et al., 2006). A mid-term decline in functional evenness observed in natural restoration may result from resource monopolization. For instance, the dominance of burrowing fiddler crabs can significantly alter sediment structure and oxygen availability, reducing space for other functional groups and delaying the recovery of ecological functions (Mokhtari et al., 2016; Liu et al., 2019). Along the restoration trajectory, enhanced habitat complexity and niche differentiation promote the reintegration of diverse functional groups, resulting in a gradual convergence of functional diversity and associated ecosystem processes (Loreau et al., 2001; Loke and Chisholm, 2022). Across all mangrove sites, functional redundancy of crabs remained high, indicating that multiple crab species perform overlapping ecological roles. Importantly, our observations are based on a non-invasive photographic survey rather than traditional quadrat excavation, minimizing disturbance and providing a more objective measure of crab diversity. This local pattern contrasts with global mangrove invertebrate communities, which often exhibit extremely low redundancy (Cannicci et al., 2021). These findings suggest that while high local redundancy can buffer short-term functional loss, it does not guarantee long-term ecosystem resilience.

Functional diversity in artificially restored sites showed weak correlations with taxonomic diversity, indicating that increased species richness has not yet translated into functional recovery. This likely reflects the structural uniformity and limited species composition of artificial plantations (Lamb, 2005; Holl and Aide, 2011) and highlights that taxonomic similarity alone does not ensure functional equivalence or ecosystem resilience (Mouillot et al., 2013; Pool et al., 2016). In natural restoration areas, functional richness (FRic), functional differentiation (FDis), and RaoQ were all significantly positively correlated with taxonomic diversity, indicating that the gradual recovery of species composition actively promotes functional recovery (Fig. 8). In natural mangroves, FRic showed weak correlation with taxonomic diversity, whereas FDis and RaoQ remained significantly linked (Fig. 8), suggesting that overall functional richness has approached saturation and that functional patterns are primarily maintained by key trait-bearing species.

Community composition shifts markedly during restoration. In the early stages, communities are dominated by burrowing Ocypodidae species, typically associated with sparsely vegetated mudflats or young mangrove plantations (Li et al., 2015). Over time, these species are gradually replaced by arboreal Sesarmidae crabs that prefer structurally complex, mature mangrove forests (Chen and Ye, 2011; Ashton and Macintosh, 2024). This shift reflects not only successional age but also the influence of vegetation type in providing habitat and food resources, as different crab species exhibit distinct feeding preferences and microhabitat selection based on leaf litter availability, sediment characteristics, and canopy cover (Kristensen, 2008; Alongi, 2008; Bui and Lee, 2014). Functionally, the proportion of filter-feeding taxa declines, while omnivorous guilds gradually dominate, with species such as *Parasesarma eumolpe* playing key roles in litter decomposition, bioturbation, and nutrient cycling (Lu et al., 2024). Trait distributions and relative abundances in naturally regenerated sites more closely resemble those of reference mangroves, highlighting the importance of passive ecological processes, including hydrological restoration and natural propagule dispersal, in reestablishing functional integrity (Chazdon, 2009; Ram et al., 2025). These patterns are consistent with tropical forest restoration studies, which show that passive regeneration better replicates the structural and functional characteristics of reference sites over the long term (Holl and Aide, 2011; Crouzeilles et al., 2017). Nevertheless, due to limited niche overlap and weak statistical support, long-term monitoring remains necessary to determine whether natural regeneration ultimately achieves functional convergence with reference conditions.

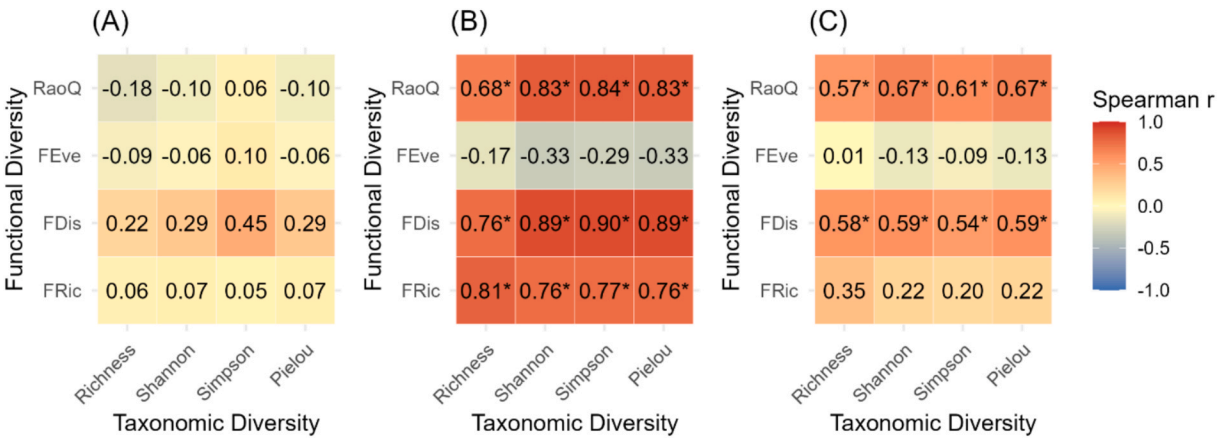


Fig. 8. Correlation coefficients (r) and p-values between functional and taxonomic diversity indices. (A) Artificial restoration; (B) Natural restoration; (C) Natural mangroves. Significant correlations ($p < 0.05$) are indicated with an asterisk (*).Functional diversity indices: FRic, functional richness; FDis, functional dispersion; FEve, functional evenness; RaoQ, Rao's quadratic entropy. Taxonomic diversity indices: Richness, species richness; Shannon, Shannon diversity; Simpson, Simpson diversity; Pielou, Pielou's evenness.

4.2. Community succession and beta diversity during mangrove restoration

Our results reveal distinct successional trajectories of crab communities under artificial and natural restoration pathways, highlighting the importance of tree architecture and composition in shaping these trajectories. In naturally regenerated sites, arboreal Sesarmidae crabs gradually increased, reflecting their preference for structurally complex mangroves with multi-layered canopies and diverse root types (Chen and Ye, 2011; Leung, 2015b). Such structural heterogeneity not only provides refuge and foraging opportunities but also directly influences burrow density and morphology, thereby affecting species occurrence and abundance (Wang et al., 2014; Rahim et al., 2023).

Artificial restoration sites, despite 27 years of development, remained compositionally distinct from natural restoration and reference mangroves. Elevated taxonomic beta diversity in artificially restored sites likely reflects habitat heterogeneity introduced by planting and substrate modification, but this did not translate into functional beta diversity, suggesting stochastic species turnover rather than functionally complementary assembly (O'Brien et al., 2022). Furthermore, non-native tree species commonly used in artificial restoration plots introduce additional variability in microhabitat structure, potentially influencing both successional trajectories and community functional recovery (Lu et al., 2014; Peng et al., 2024).

Temporal patterns of beta diversity showed that species turnover consistently contributed more than nestedness, indicating that shifts in composition primarily arise from species replacement rather than differences in richness (Baselga, 2010). This finding aligns with patterns observed in neotropical mangroves, where crab diversity influences tree establishment and forest structure, which in turn shape subsequent crab communities (Ferreira et al., 2015; Ferreira et al., 2019). Together, these results indicate that tree structure, species composition, and habitat complexity are likely important factors associated with crab community dynamics and beta diversity, in addition to soil and sediment characteristics.

4.3. Environmental drivers of crab communities during mangrove restoration

Our study demonstrates that during mangrove restoration, environmental filtering influences the taxonomic and functional composition of crab communities, although their responses to restoration time and method differ. Taxonomic diversity increased markedly throughout restoration, reflecting strong successional trajectories driven by restoration interventions and natural recolonization processes (Chazdon, 2009; Crouzeilles et al., 2017). In contrast, functional diversity remained relatively stable, suggesting that multiple crab species share overlapping ecological roles that buffer community function against shifts in species composition (Walker, 1992; Rosenfeld, 2002; Cadotte et al., 2011).

This functional stability likely reflects high functional redundancy, allowing communities to maintain key ecosystem functions even amid species turnover (Mouillot et al., 2013). Methodological factors may also contribute to this pattern, as the limited number of functional traits considered, combined with the use of Gower distance and Ward clustering, could group species with similar low-information traits and reduce the sensitivity of functional metrics (Villéger et al., 2008). Moreover, the relatively low explanatory power of dbRDA for functional composition (26.99 %) suggests that unmeasured environmental variables or subtle biotic interactions may play important roles in structuring functional traits (Legendre, 2014).

Key environmental drivers included soil pH, salinity, sediment texture, and elevation, highlighting the importance of physicochemical conditions in shaping both species composition and functional structure. Our results showed that soil pH and salinity were negatively associated with overall community structure, suggesting that more acidic or saline conditions may limit the abundance of certain crab groups, particularly juveniles and species with low salinity tolerance (Simith et al., 2012; Ngo-Massou et al., 2014). In contrast, elevation was positively associated with community structure, likely reflecting its influence on microhabitat suitability and tidal inundation patterns (Alongi, 2014; Leignel et al., 2024). Sediment grain composition may affect burrowing capacity, resource availability, and refuge opportunities, favoring certain burrowing species over others (Pan et al., 2021). Regarding functional composition, dbRDA results indicated that soil pH was positively correlated, whereas salinity was negatively correlated with trait distribution, suggesting that environmental filtering favors species adapted to neutral pH and lower salinity conditions.

Nevertheless, a limitation of the space-for-time substitution approach is that it cannot fully control for differences in vegetation structure among sites. Tree architecture has a profound influence on sediment stability, root complexity, and the availability of microhabitats, which together determine crab distribution and burrowing behavior (Friess et al., 2012; Wang et al., 2014; Rahim et al., 2023). The density and type of pneumatophores and prop roots create vertical and horizontal habitat gradients that mediate resource partitioning among crab guilds. Previous studies in neotropical mangroves have also shown that vegetation composition and root complexity are primary

determinants of crab community assembly and functional diversity (Ferreira et al., 2019). Therefore, the relatively low explanatory power of dbRDA may reflect the exclusion of key biotic and structural variables, particularly vertical and horizontal habitat complexity, which likely shape functional traits beyond the abiotic parameters measured in this study.

4.4. Management implications for mangrove restoration

Given the crucial role of crabs in nutrient cycling and sediment bioturbation through detritus processing, burrow aeration, and carbon retention (Kristensen and Alongi, 2006; Guimond et al., 2020; Arnaud et al., 2022; Yang et al., 2025), changes in their diversity serve as sensitive indicators of functional recovery. Our findings emphasize that tree architecture, habitat heterogeneity, and species composition are critical determinants in mangrove restoration planning (Chazdon, 2009; Stewart et al., 2022). Natural regeneration, through gradual colonization and environmental filtering, can promote both taxonomic and functional convergence toward reference conditions, particularly in sites characterized by multi-species and structurally complex vegetation (Ferreira et al., 2015). In contrast, artificial planting may facilitate rapid canopy establishment and shoreline stabilization, yet long-term success may be constrained when restoration relies on monocultures or non-native species that fail to support diverse faunal assemblages (Ferreira et al., 2023).

To enhance restoration effectiveness, interventions should prioritize the establishment of diverse native tree assemblages adapted to local environmental conditions, thereby increasing habitat heterogeneity, functional redundancy, and resilience under climate change (Rahim et al., 2023). Long-term monitoring programs should incorporate assessments of root architecture, canopy structure, and crab functional traits alongside physicochemical parameters to better predict community responses and functional outcomes (Leung, 2015a; Stewart et al., 2022). Integrating both active and passive restoration strategies within an adaptive management framework, supported by continuous monitoring and clearly defined ecological goals, will help balance short-term restoration needs with long-term ecosystem sustainability (Primavera et al., 2011; Bhargava and Friess, 2022).

5. Conclusion

This study demonstrates that taxonomic and functional diversity of mangrove crabs significantly respond to restoration time and method. Artificial restoration leads to an initial increase in taxonomic diversity and functional richness, but over time, naturally restored communities gradually converge with natural mangrove sites. Species composition undergoes succession from early dominance by filter feeders of the Ocypodidae family to later prevalence of herbivorous-omnivorous crab species, reflecting community successional trajectories. Functional diversity remains relatively stable, indicating high functional redundancy despite frequent species turnover. Artificial restoration sites exhibit higher beta diversity, while natural restoration sites more closely resemble reference conditions. Soil pH, salinity, and sediment particle size are key environmental drivers shaping community structure. The findings emphasize that mangrove restoration should move beyond vegetation recovery alone and prioritize the functional reconstruction and maintenance of faunal communities. By managing soil and sediment physicochemical properties, restoration efforts can promote functional diversity, thereby enhancing ecosystem stability, resilience, and the long-term success and sustainability of ecological restoration.

CRediT authorship contribution statement

Xiaoyan Lu: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Xuan Gu:** Writing – review & editing, Methodology, Investigation, Data curation. **Lin Zhang:** Writing – review & editing, Methodology, Formal analysis. **Wenqing Wang:** Writing – review & editing, Conceptualization. **Jianxiang Feng:** Writing – review & editing, Conceptualization. **Mao Wang:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Mao Wang reports financial support was provided by National Natural Science Foundation of China. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

The authors acknowledge the financial support from the National Natural Science Foundation of China (No. 42076161).

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.114479.

Data availability

Data will be made available on request.

References

Alongi, D.M., 2002. Present state and future of the world's mangrove forests. Environ. Conserv. 29, 331–349.
Alongi, D.M., 2008. Mangrove forests: Resilience, protection from tsunamis, and responses to global climate change. Estuar. Coast. Shelf. s. 76 (1), 1–13.
Alongi, D.M., 2014. Carbon cycling and storage in mangrove forests. Annu. Rev. Mar. Sci. 6, 195–219.
Arnaud, M., Baird, A.J., Morris, P.J., Taylor, A., Dang, T.H., Tran Hong, H., Dinh Quang, T., Nguyen, T.T., Polsenaere, P., 2022. The effect of crab burrows on soil-water dynamics in mangroves. Hydrol. Process. 36 (3), e14522.
Aslan, A., Rahman, A.F., Robeson, S.M., Ilman, M., 2021. Land-use dynamics associated with mangrove deforestation for aquaculture and the subsequent abandonment of ponds. Sci. Total Environ. 791, 148320.
Ashton, E.C., Hogarth, P., Macintosh, D., 2003. A comparison of brachyuran crab community structure at four mangrove locations under different management systems along the Melaka Straits-Andaman Sea Coast of Malaysia and Thailand. Estuaries 26, 1461–1471.
Ashton, E.C., Macintosh, D.J., 2024. Mangrove rehabilitation and Brachyuran crab biodiversity in Ranong. Thailand. Divers. 16 (2), 92.
Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Glob. Ecol. Biogeogr. 19 (1), 134–143.
Baselga, A., Orme, C.D.L., 2012. betapart: an R package for the study of beta diversity. Methods Ecol. Evol. 3, 808–812.
Bhargava, R., Friess, D., 2022. Previous shoreline dynamics determine future susceptibility to cyclone impact in the Sundarban mangrove forest. Front. Mar. Sci. 9, 814577.
Bui, T.H.H., Lee, S.Y., 2014. Does 'you are what you eat' apply to mangrove grapsid crabs? PLoS One 9, e89074.
Cadotte, M.W., Carscadden, K., Mirotchnick, N., 2011. Beyond species: Functional diversity and the maintenance of ecological processes and services. J. Appl. Ecol. 48 (5), 1079–1087.
Cannicci, S., Lee, S.Y., Bravo, H., Cantera-Kintz, J.R., Dahdouh-Guebas, F., Fratini, S., Fusi, M., Jimenez, P.J., Nordhaus, I., Porri, F., Diele, K., 2021. A functional analysis reveals extremely low redundancy in global mangrove invertebrate fauna. PNAS 118, e2016913118.
Chazdon, R.L., 2009. Beyond deforestation: Restoring forests and ecosystem services on degraded lands. Science 320 (5882), 1458–1460.
Chen, G.C., Ye, Y., 2011. Restoration of *Aegiceras corniculatum* mangroves in Jiulongjiang Estuary changed macro-benthic faunal community. Ecol. Eng. 37 (2), 224–228.
Crouzeilles, R., Ferreira, M.S., Chazdon, R.L., Lindenmayer, D.B., Sansevero, J.B.B., Monteiro, L., Iribarrem, A., Latawiec, A.E., Strassburg, B.B.N., 2017. Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. Sci. Adv. 3, e1701345.
Dinitto, D., Erftemeijer, P.L.A., van Beek, J.K.L., Dahdouh-Guebas, F., Higazi, L., Quisthoudt, K., Jayatissa, L.P., Koedam, N., 2013. Modelling drivers of mangrove

propagule dispersal and restoration of abandoned shrimp farms. Biogeosciences 10, 5095–5113.
Dray S, Bauman D, Blanchet G, Borcard D, Clappe S, Guénard G, Jombart T, Larocque G, Legendre P, Madi N, Wagner HH, 2024. adespatial: Multivariate multiscale spatial analysis (R package version 0.3-24). https://CRAN.R-project.org/package=adespatial.
Duncan, C., Primavera, J., Pettorelli, N., Thompson, J., Loma, R., Koldewey, H., 2016. Rehabilitating mangrove ecosystem services: a case study on the relative benefits of abandoned pond reversion from Panay Island. Philippines. Mar. Pollut. Bull. 109, 772–782.
Díaz, S., Fargione, J., Chapin III, F.S., Tilman, D., 2006. Biodiversity loss threatens human well-being. PLoS Biol. 4, e277.
Ellison, A.M., 2000. Mangrove restoration: do we know enough? Restor. Ecol. 8, 219–229.
Ferreira, A.C., Ganade, G., Attayde, J.L., 2015. Restoration versus natural regeneration in a neotropical mangrove: Effects on plant biomass and crab communities. Ocean Coast. Manag. 110, 38–45.
Ferreira, A.C., Bezerra, L.E.A., Mathews-Cascon, H., 2019. Aboveground stock in a restored Neotropical mangrove: Influence of management and brachyuran crab assemblage. Wetl. Ecol. Manag. 27, 223–242.
Ferreira, A.C., Lacerda, L.D., Rodrigues, J.V.M., Bezerra, L.E.A., 2023. New contributions to mangrove rehabilitation/restoration protocols and practices. Wetl. Ecol. Manag. 31, 89–114.
Friess, D.A., Krauss, K.W., Horstman, E.M., Balke, T., Bouma, T.J., Galli, D., Webb, E.L., 2012. Are all intertidal wetlands naturally created equal? Bottlenecks, thresholds and knowledge gaps to mangrove and saltmarsh ecosystems. Biol. Rev. Camb. Philos. Soc. 87 (2), 346–366.
Friess, D.A., Rogers, K., Lovelock, C.E., Krauss, K.W., Hamilton, S.E., Lee, S.Y., Lucas, R., Primavera, J., Rajkaran, A., Shi, S., 2019. The state of the world's mangrove forests: past, present, and future. Annu. Rev. Env. Resour. 44, 89–115.
Gao, X.Q., Lee, S.Y., 2022. Feeding strategies of mangrove leaf-eating crabs for meeting their nitrogen needs on a low-nutrient diet. Front. Mar. Sci. 9, 872272.
Gerona-Daga, M.E., Salmo, S.G., 2022. A systematic review of mangrove restoration studies in Southeast Asia: challenges and opportunities for the United Nation's Decade on Ecosystem Restoration. Front. Mar. Sci. 9, 987737.
Giri, C., Long, J., Abbas, S., Murali, R., Qamer, F., Pengra, B., Thau, D., 2015. Distribution and dynamics of mangrove forests of South Asia. J. Environ. Manage. 148, 101–111.
Gu, X., Chen, G.G., Wang, W.Q., Wang, M., 2022. Feasibility study on the application of camera trapping method in the study of benthic crab community ecology in the intertidal zone. Acta Ecol. Sin. 42, 2974–2983.
Guimond, J.A., Seyfferth, A.L., Moffett, K.B., Michael, H.A., 2020. A physical-biogeochemical mechanism for negative feedback between marsh crabs and carbon storage. Environ. Res. Lett. 15 (3), 034024.
Herbeck, L., Krumme, U., Andersen, T., Jennerjahn, T.C., 2020. Decadal trends in mangrove and pond aquaculture cover on Hainan (China) since 1966: mangrove loss, fragmentation and associated biogeochemical changes. Estuar. Coast. Shelf s. 233, 106531.
Holl, K.D., Aide, T.M., 2011. When and where to actively restore ecosystems? Forest Ecol Manag 261 (10), 1558–1563.
Jayanthi, M., Thirumurthy, S., Muralidhar, M., Ravichandran, P., 2018. Impact of shrimp aquaculture development on important ecosystems in India. Glob. Environ. Chang. 52, 10–21.
Kelly, J., Harwell, M., 1990. Indicators of ecosystem recovery. Environ. Manag. 14, 527–545.
Kristensen, E., Alongi, D.M., 2006. Control by fiddler crabs (*Uca vocans*) and plant roots (*Avicennia marina*) on carbon, iron, and sulfur biogeochemistry in mangrove sediment. Limnol. Oceanogr. 51 (4), 1557–1571.
Kristensen, E., 2008. Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. J. Sea Res. 59, 30–43.
Kitchingman, M.E., Sievers, M., Lopez-Marcano, S., Connolly, R.M., 2022. Fish use of restored mangroves matches that in natural mangroves regardless of forest age. Restor. Ecol. 31, e13806.
Lacerda, L.D., Menezes, M.O.T., Molisani, M.M., 2007. Changes in mangrove extension at the Pacoti River estuary, CE, NE Brazil due to regional environmental changes between 1958 and 2004. Biota Neotrop. 7, 67–72.
Legendre, P., 2014. Interpreting the replacement and richness difference components of beta diversity. Glob. Ecol. Biogeogr. 23, 1324–1334.
Leignel, V., Guermazi, W., Letertre, Y., Annabi-Trabelsi, N., 2024. Grapsidae Family (Decapoda, Brachyura), Semi-Terrestrial Crabs, in Ecotoxicology: State of Knowledge and New Molecular Biomarker Dataset to develop Investigations. Examines Mar. Biol. Oceanogr. 7, 659.
Leung, J.Y.S., 2015a. Habitat heterogeneity affects ecological functions of microbenthic communities in a mangrove: Implication for the impact of restoration and afforestation. Glob. Ecol. Conserv. 4, 423–433.
Leung, J.Y.S., 2015b. Habitat heterogeneity determining the macrobenthic infaunal community in a mangrove swamp in South China: Implication for plantation and plant invasion. J. Coast. Res. 31, 624–633.
Li, W., Cui, L., Zhang, M., Wang, Y., Zhang, Y., Lei, Y., Zhao, X., 2015. Effect of mangrove restoration on crab burrow density in Luoyangjiang Estuary. China. for. Ecosyst. 2, 21.
Liu, Y., Reible, D., Hussain, F., Fang, H., 2019. Role of bioroughness, bioirrigation, and turbulence on oxygen dynamics at the sediment-water interface. Water Resour. Res. 55 (10), 7927–8269.
Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294, 804–808.
Loke, L.H.L., Chisholm, R.A., 2022. Measuring habitat complexity and spatial heterogeneity in ecology. Ecol. Lett. 25 (10), 2269–2288.
Lovelock, C.E., Barbier, E., Duarte, C.M., 2022. Tackling the mangrove restoration challenge. PLoS Biol. 20, e3001836.
Lu, W., Yang, S., Chen, L., Wang, W., Du, X., Wang, C., Ma, Y., Lin, G., Lin, G., 2014. Changes in carbon pool and stand structure of a native subtropical mangrove forest after inter-planting with exotic species *Sonneratia apetala*. PLoS One 9 (3), e91238.
Lu, X.Y., Gu, X., Zhang, L., Zhang, J.H., Wang, W.Q., Wang, M., 2024. Tidal zone effects on the diet composition of leaf-eating crabs in natural mangrove communities: a stable isotope analysis. Front. Mar. Sci. 11, 1351183.
Ma, Z., Cai, Y., Li, B., Chen, J., 2010. Managing Wetland Habitats for Waterbirds: an International Perspective. Wetlands 30, 15–27.
MacArthur, R., Levins, R., 1967. The limiting similarity, convergence, and divergence of coexisting species. Am. Nat. 101, 377–385.
Mariano, H., Aguilos, M., Dagoc, F.L., Sumalinab, B., Amparado, R., 2022. Abandoned Fishpond Reversal to Mangrove Forest: will the Carbon Storage potential Match the Natural stand 30 Years after Reforestation? Forests 13, 1–19.
Matsui, N., Suekuni, J., Nogami, M., Havanond, S., Salikul, P., 2010. Mangrove rehabilitation dynamics and soil organic carbon changes as a result of full hydraulic restoration and re-grading of a previously intensively managed shrimp pond. Wetl. Ecol. Manag. 18, 233–242.
Mokhtari, M., Abd Ghaffar, M., Usup, G., Che Cob, Z., 2016. Effects of fiddler crab burrows on sediment properties in the mangrove mudflats of Sungai Sepang. Malaysia. Biol. 5 (1), 7.
Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. Trends Ecol. Evol. 28 (3), 167–177.
Ngo-Massou, V.M., Essomè-Koum, G.L., Kotte, M.E., Din, N., 2014. Biology and distribution of mangrove crabs in the Wouri River Estuary, Douala. Cameroon. J. Water Resour. Prot. 6, 236–248.
Nitto, D., Erftemeijer, P., Beek, J., Dahdouh-Guebas, F., 2013. Modelling drivers of mangrove propagule dispersal and restoration of abandoned shrimp farms. Biogeosciences 10, 5095–5113.
O'Brien, S.A., Dehling, D.M., Tylianakis, J.M., 2022. The recovery of functional diversity with restoration. Ecology 103 (3), e3618.
Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., 2018. vegan: Community ecology package (R package version 2.5-7). https://CRAN.R-project.org/package=vegan.
Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., Weedon, J., 2024. vegan: Community ecology package (R package version 2.6-8). https://CRAN.R-project.org/package=vegan.
Pan, S.-H., Ho, C.-W., Lin, C.-W., Huang, S.-C., Lin, H.-J., 2021. Differential response of macrobenthic abundance and community composition to mangrove vegetation. For 12 (10), 1403.
Peng, Y., Hu, B., Zhu, Y., Yin, Z., Fu, B., Yang, H., He, Z., Khim, J.S., 2024. Functional traits of macrobenthos substantially indicated habitat change from the invasive saltmarsh to introduced mangrove. Sci. Total Environ. 954, 176536.
Pool, T.K., Cucherousset, J., Boulêtreau, S., Villéger, S., Strecker, A.L., Grenouillet, G., 2016. Increased taxonomic and functional similarity does not increase the trophic similarity of communities. Glob. Ecol. Biogeogr. 25 (1), 46–54.
Primavera, J.H., 2000. Development and conservation of Philippine mangroves: institutional issues. Ecol. Econ. 35, 91–106.
Primavera, J.H., Rollon, R.N., Samson, M.S., 2011. The Pressing challenges of Mangrove Rehabilitation. Treatise on Estuarine and Coastal Science 217–244.
R Core Team. (2023). R: A language and environment for statistical computing (Version 4.3.1). R Foundation for Statistical Computing. https://www.R-project.org/.
Rahim, N.H.A., Yahya, K., Shuib, S., 2023. Spatiotemporal effect reveal the abundance of the crab *Paracleistostoma depressum* negatively correlated with pneumatophore density in a tropical mangrove. Reg. Stud. Mar. Sci. 60, 102834.
Ram, M., Sheaves, M., Waltham, N.J., 2025. Mangrove restoration reinstates similar macrobenthos communities to natural mangroves in Guyana, South America. ICES J. Mar. Sci. 82 (2), fsae172.
Richards, D.R., Friess, D.A., 2016. Rates and Drivers of Mangrove deforestation in Southeast Asia, 2000-2012. PNAS 113, 344–349.
Rinehart, S., Dybiec, J., Walker, J., Simpson, L., Cherry, J., 2024. Effects of burrowing crabs on coastal sediments and their functions: a systematic meta-analysis. Ecosphere 15, e4927.
Rosenfeld, J.S., 2002. Functional redundancy in ecology and conservation. Oikos 98 (1), 156–162.
Shih, H.T., Ng, P.K.L., Fang, S.H., Chan, B.K.K., Wong, K.J.H., 2010. Diversity and distribution of fiddler crabs (Brachyura: Ocypodidae: *Uca*) from China, with new records from Hainan Island in the South China Sea. Zootaxa 2640, 1–19.
Stein, A., Gerstner, K., Kreft, H., 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecol. Lett. 17, 866–880.
Stevenson, N.J., 1997. Disused shrimp ponds: Options for redevelopment of mangroves. Coast. Manage. 25, 425–435.
Stewart, H.A., Janiak, D.S., Wright, J.L., Hunt, D.A.G.A., Carmona Cortes, A., Powell, K. T., Chapman, L.J., Altieri, A.H., 2022. Epibiont community composition of red

mangroves *Rhizophora mangle* are contingent on root characteristics. Mar. Ecol. Prog. Ser. 686, 15–35.
Valiela, I., Bowen, J.L., York, J.K., 2001. Mangrove forests: one of the World's threatened major tropical environments. Bioscience 51, 807–815.
Villéger, S., Mason, N.W., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89 (8), 2290–2301.
Walker, B.H., 1992. Biodiversity and ecological redundancy. Conserv. Biol. 6 (1), 18–23.
Wang, G., Yu, C., Singh, M., Guan, D.S., Xiong, Y.M., Zheng, R.Z., Xiao, R.B., 2021. Community structure and ecosystem carbon stock dynamics along a chronosequence of mangrove plantations in China. Plant and Soil 464, 605–620.
Wang, J., Zhang, X., Jiang, L., Bertness, M., Fang, C., Chen, J., Hara, T., Li, B., 2010. Bioturbation of burrowing crabs promotes sediment turnover and carbon and nitrogen movements in an estuarine salt marsh. Ecosystems 13, 586–599.
Wang, M., Gao, X., Wang, W., 2014. Differences in burrow morphology of crabs between Spartina alterniflora marsh and mangrove habitats. Ecol. Eng. 69, 213–219.
Wodehouse, D., Rayment, M., 2019. Mangrove area and propagule number planting targets produce sub-optimal rehabilitation and afforestation outcomes. Estuar. Coast. Shelf s. 222, 91–102.
Xiong, Y., Jiang, Z., Xin, K., Liao, B., Chen, Y., Li, M., Guo, H., Xu, Y., Zhai, X., Zhang, C., 2021. Factors influencing mangrove forest recruitment in rehabilitated aquaculture ponds. Ecol. Eng. 168, 106272.
Yang, Y., Liang, Q., Peng, Y., Paterson, D.M., 2025. Differential mediation of biogeochemical processes through bioturbation by fiddler and sesarmid mangrove crabs. Mar. Pollut. Bull. 211, 117431.
Zhang, Y.M., Zhang, L., Kang, Y.Y., Li, Y., Chen, Z., Li, R., Tian, C., Wang, W.Q., Wang, M., 2022. Biotic homogenization increases with human intervention: implications for mangrove wetland restoration. Ecography 4, e05835.