ICES Journal of Marine Science, 2024, Vol. 82, Issue 2, fsae172
https://doi.org/10.1093/icesjms/fsae172
Received: 31 August 2024; **revised:** 19 November 2024; **accepted:** 20 November 2024
Original Article

Mangrove restoration reinstates similar macrobenthos communities to natural mangroves in Guyana, South America

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Abstract

Mangrove restoration projects have become increasingly widespread to compensate for mangrove loss. Despite considerable investment in this restoration activity, post-restoration monitoring is often limited to vegetation recovery with no inclusion of faunal groups, such as macrobenthos communities, even though these groups are excellent bioindicators. Here, we used a space-for-time approach to examine whether restored mangrove macrobenthos communities are equivalent to natural mangroves of the same age (5–11 years after colonization). We focused our analyses on sediment samples collected from the lower, middle, and upper intertidal zones of restored and natural mangroves in the dry and wet seasons, along Guyana's coastline, South America. We observed an overall higher macrobenthos abundance in the natural mangroves compared to restored mangrove areas, which contrasted with higher species richness in the restored mangroves compared to natural mangroves. Nonmetric multidimensional scaling, analysis of similarities, and similarity percentage analysis revealed that macrobenthos species composition was not significantly different among the restored and natural mangrove habitats, ages, and seasons ($P > .05$). This suggests that the macrobenthos composition in restored mangrove areas quickly converges, after restoration activities, with communities observed in natural mangroves. Our findings indicate that, at least for biodiversity outcomes, macroinvertebrate communities occupying sediments in restored mangroves resemble natural areas rapidly post-restoration efforts.

Keywords: restoration; coastal habitat; mangroves; biodiversity; Guyana

Introduction

Human activities have altered and degraded mangrove ecosystems globally, resulting in extensive declines and loss of the multiple services and functions that they are commonly known to support (Akram et al. 2023, Rummell et al. 2023). To combat this, mangrove restoration efforts have increased to reinstate critical ecosystem service and functions that are similar to those provided by healthy or intact mangrove ecosystems (Ferreira et al. 2015, Worthington and Spalding 2018, Djamaluddin et al. 2023). As global restoration initiatives increase in the United Nations Decade on Ecosystem Restoration (Waltham et al. 2020), it is essential that monitoring data indicating that the sites are moving in a trajectory toward the targets and goals of the restoration exists (Gann et al. 2019, Young and Schwartz 2019).

Long-term monitoring of mangrove restoration initiatives can help to identify successful and replicable practices and to understand how restoration efforts enhance ecological structure and function (Ellison 2000, Lindenmayer 2020). Most mangrove restoration initiatives, however, are limited to monitoring forest survival or structure (Wortley et al. 2013), and fail to recognize responses associated with faunal groups, ecological functions, or ecosystem services (Catterall 2018). Monitoring restoration success should include ecosystem functions since forest structure alone does not provide compelling evidence that the restored forest provides similar functions and services as it did before degradation (McKee and Faulkner 2000, Bosire et al. 2008). The absence of ecosystem service recovery in monitoring projects can be detrimental to the success of some initiatives because the vegetation responds slowly to restoration, making it difficult to maintain social interest and economic investment without other indicators of early restoration success (Wortley et al. 2013, Shoo et al. 2016).

Despite the compelling evidence that fauna plays complex and critical roles in ecosystem functionality (e.g. seed dispersal, pollination, nutrient cycling, and soil formation), these roles are often overlooked in restoration goal setting, monitoring, and assessments of success (Cross et al. 2020, Sheaves et al. 2021). Faunal communities can respond rapidly to impacts of disturbance or recovery following management intervention, making these taxa an excellent indicator for monitoring biodiversity and ecosystem health (Feary et al. 2007, Siddig et al. 2016). Restoration projects that incorporate faunal recovery monitoring have reported positive outcomes, such as increased biodiversity, ecological functions (e.g. pollination, seed dispersal, herbivory, and predation), ecosystem services (e.g. carbon storage, nutrient cycling, and fisheries catches) (Hagger et al. 2017, Gilby et al. 2018). As vegetation regenerates, ecological restoration efforts frequently anticipate that fauna diversity and abundance should closely mimic predisturbance levels—though this is seldom the case (Palmer et al. 2016). For example, large-scale mangrove restoration projects in Asia, Thailand, and India have re-established mangrove vegetation in several degraded areas. However, the diversity and abundance of associated faunal communities, such as crustaceans and fish, have not returned to similar levels as pre-disturbance (Gerona-Daga and Salmo 2022, Ashton and Macintosh 2024). Restoration practitioners and regulators must consider the value and role of fauna in ecosystem recovery to achieve the goal of full ecosystem recovery (Cross et al. 2019).

Benthic macrofauna plays a pivotal role in maintaining the structure and function of mangrove ecosystems (Cannicci et al. 2008, Lee 2008, Miri et al. 2023). These taxons serve as a key linkage between the primary detritus at the base of coastal food webs, help in the decomposition of organic matter and nutrient cycling through foodweb linkages, enhance sediment porosity, and create pathways for oxygen, nutrients, and water to pass into the sediment (Kristensen et al. 2008, Schratzberger and Ingels 2018). Considering that changes in the macrobenthic community structure can influence local biodiversity and ecosystem functions, these taxa present an ideal indicator for assessing mangrove restoration outcomes (Li et al. 2017, Wang et al. 2021).

While previous studies have assessed the macrofauna species composition and biomass in restored mangroves (Macintosh et al. 2002, Chen et al. 2007, Gorman and Turra 2016), only a few (e.g. Ashton et al. 2003, Ferreira et al. 2015) have compared faunal associations between restored and natural mangroves, while no study has attempted to use natural mangroves of the same age in the comparison in different intertidal zones. Such evidence is needed to examine the success of restoration efforts and convergence of macrobenthos communities in restored and natural mangroves of the same age. Here, we use a space-for-time (SFT) design to investigate the spatial and temporal variation of macrobenthos communities in different intertidal zones of restored and natural mangroves of different ages (5–11 years) in Guyana, South America. We hypothesize that the macrofauna community occupying sediments in natural mangrove forests is analogous to restored mangrove forest areas, particularly as the mangrove trees mature. Monitoring the spatiotemporal variation in macrobenthos composition in restored mangroves can determine if restoration efforts are successful and how long it might take for convergence in the fauna assemblage in restored and natural mangrove areas.

Materials and methods

Study area

Our study was conducted along Guyana's coast, situated on the northern coast of South America, with a geographic area of 214 970 km^2, a 430 km coastline on the northeast, and a continental extent of ∼724 km (Government of Guyana 2012). Guyana's Low Coastal Plain is flat and below 0.5–1 m sea level at mean high tide (Government of Guyana 2012). The Low Coastal Plain occupies <10% of Guyana's land mass but is the most populated natural region, hosting 90% of the general population ($n = 786\,559$) (World Bank Open Data 2020). The Low Coastal Plain supports numerous recreational and commercial activities, government organizations, employment centers, urban centers, infrastructures, and agricultural lands (Government of Guyana 2012).

Guyana mangrove restoration project

The Guyana Mangrove Restoration Project commenced in 2010 by the Guyana Government with financial support from the European Union to conserve, restore, and protect Guyana's mangroves from rising sea levels and flooding (Landell Mills Limited 2013). The National Agricultural Research & Extension Insitute executed the project from 2010 to 2013 and incorporated mangrove restoration into its mandate in 2014 after the project concluded (Landell Mills Limited 2013). The GRMP project has enabled over 500 000 mangrove *Avicenna germinans* seedlings to be planted across 19 locations spanning 8 km of Guyana's coast—17 locations were replanted between 2010 and 2013 under the European Union funding scheme (NAREI 2015). Other mangrove species, such as *Laguncularia racemosa* and *Rhizophora mangle*, have also colonized the restored mangrove forests (Ram et al. 2024). The project has also generated several cobenefits, such as supporting coastal fisheries, protecting coastlines, and supporting biodiversity, that positively impact biodiversity, climate change, local economies, and community resilience (Ram et al. 2021, 2024).

Study design

We used the SFT substitution approach to examine the macrobenthos in the sediment of restored and natural mangrove sites with different ages. This approach is widely used to study wildlife responses along altitude, precipitation, temperature, and land-cover gradients to examine how they have responded over time after restoration intervention (Kratz et al. 2003, De Palma et al. 2018, Zografou et al. 2020). This approach has been applied in restoration ecology studies elsewhere, where it has been useful for designing and funding effective restoration programs in coastal areas (Salmo et al. 2014, 2017). Here, natural mangroves are forests that have naturally colonized mudflats or recolonized disturbed areas, while restored sites are monocultures of black mangroves (*Avicennia germinans*) planted between 2010 and 2018 in Guyana. Restored mangrove sample plots were classified into five different forest ages: 5, 6, 9, 10, and 11 years old. Natural mangrove sites were determined after extensive consultation with local communities from three administrative regions (Regions 2, 4, and 5) in Guyana to accurately select sites of the same ages (5, 6, 9, 10, and 11 years ago) as the restored mangrove areas (Fig. 1).

Forest structure

Permanent circular plots (radius = 10 m) were established 25 m apart via stratified sampling at the mangrove upper, middle, and lower intertidal zones ($N = 3$ per site). One plot occurred in the upper intertidal zone (the area closest to the land and furthest from the shoreline), one plot in the middle intertidal zone (lies between the upper and lower intertidal zones, experiencing moderate tidal inundation during regular high tides), and one in the lower intertidal zone (the area closest to the shoreline, flooded during most tidal cycles, including neap tides). For each plot, tree species, diameter at breast height

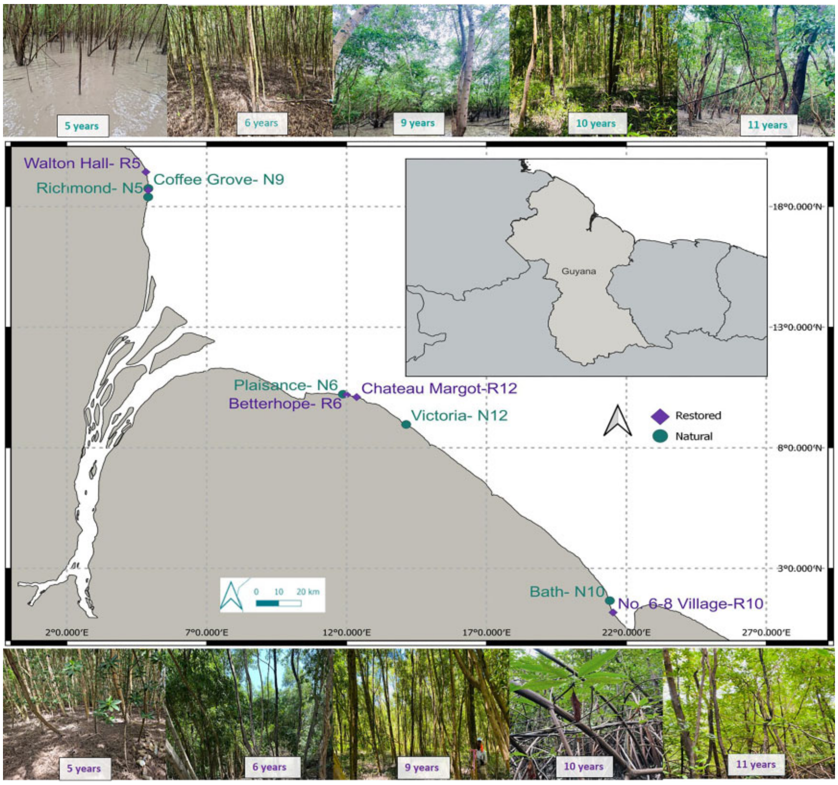

Figure 1. Study locations (circles are natural stands of mangroves where new mangroves grow from adjacent seeds and propagules of parent forests. Diamonds are the location of restored mangrove areas that have been actively replanted under the Guyana Mangrove Restoration Project—GMRP). The supporting photos provide insight into the forest for the different ages since restoration commenced, or similarly, natural forest stands with similar ages.

(DBH; at 1.37 m height, or above the highest prop root for *Rhizophora* spp.) and height (>1.37 m) were measured using a Richter 10 m Fiberglass Diameter Tape and Nikon Forestry Pro II Laser Rangefinder in 10-m radius circular plots. These data were then used to calculate forest structure parameters such as tree density (trees/ha), basal area, relative dominance, relative frequency, and importance value index.

Macrobenthos sampling

Macrobenthos sampling was completed in the wet and dry seasons from January to August 2023. At each site, three 1 × 1 m quadrats were established in the intertidal zones established for the tree plots. One quadrat was established in the upper, middle, and lower intertidal zones. In the 1 × 1 m plots, a total of 30 random points were sampled across three intertidal zones, with 10 points per zone. The sediment samples were transported to the University of Guyana Biology Laboratory, where samples were rinsed with fresh water and sieved (0.5 mm) to separate macrobenthos from the sediments. The macrobenthos samples were placed inside labeled bags containing a 4% alcohol solution for preservation. Macrobenthos were identified to the species level using a dichotomous key, and their species name was confirmed using the World Register of Marine Species database (http://www.marinespecies.org). After identification, the samples were rinsed with distilled water, preserved in 70% alcohol, and stored in the Center for the Study of Biological Diversity collection for future surveys.

Mangrove forest environmental variables

The surface (∼20 cm below the water surface) water temperature (°C), electrical conductivity (EC; µS/cm), and pH were measured to one decimal place using an 86 031 AZ Waterproof IP 67 Combo Water Quality. Dissolved oxygen was measured using an Extech DO600 Waterproof ExStik II Dissolved Oxygen Meter. All measurements were recorded during daylight during the high tide to standardize the method across all mangrove areas.

Statistical analysis

We computed the abundance and sum of macrobenthos orders, families, genera, and species to evaluate the species abundance between mangrove habitats, ages, and seasons. A Wilcoxon test using the function wilcox.test was run in R Studio to compare the abundance between restored and natural mangroves. A Kruskal–Wallis was used to examine the individual effects of habitat and age and their interactions on tree height and diameter. A Kruskal–Wallis test was used to compare the model of differences in the macrobenthos species richness and abundance in the lower, middle, and upper intertidal zones. A non-parametric permutational multivariate analysis of variance (PERMANOVA) was used to assess differences in macrobenthos community structure between mangrove habitats, ages, and seasons. Habitats, ages, and seasons were used as fixed factors for the "adonis2" function in the Vegan package (Oksanen et al. 2022).

The Bray–Curtis dissimilarity index based on the square root transformation data was used to estimate the macrobenthos compositional differences between mangrove habitats, ages, and seasons. We also applied a presence/absence transformation to reduce the effect of abundance in the community data, though there were little differences in the non-metric ordinations between transformations, so we continued analysis with the Bray–Curtis matrix. Both transformations were calculated in RStudio using the "vegedist" function in the Vegan package (Oksanen et al. 2022).

Similarity percentage analysis (SIMPER) analysis based on the decomposition of the Bray–Curtis dissimilarity index was carried out to determine the average percent dissimilarity in macrobenthos community composition between mangrove habitats, ages, and seasons. The SIMPER analysis was done in RStudio using the "simper" function in the Vegan package (Oksanen et al. 2022).

Non-metric multidimensional scaling (nMDS) based on the square root transformation data was used to assess variation in macrobenthos composition and identify the taxa that characterized this variation among mangrove habitats, ages, and seasons (wet and dry). The square root transformation was used to stabilize variance in data that exhibits heteroscedasticity and reduce the variability. All ordinations were done with up to 10 dimensions, and individual scree plots of stress and dimensions were used to reduce and select the most appropriate number of dimensions for further interpretation. This was performed in RStudio using the "NMDS" function in the package Vegan (Oksanen et al. 2022).

A general linear mixed model (GLMM) with Poisson regression to compare the factors impacting the macrobenthos species richness and abundance among mangrove habitats, age, and seasons. Macrobenthos species richness and abundance were used as the response variable, while the "Habitat," "Age," and "Season" were used as the predictors, and sites, period, and intertidal zones were the random variables. Different variable transformations, distributions, and links were tested. Selection criteria for the GLMM included conditional AIC, log-likelihood scores, overdispersion ratios, and a customized iterative approach. The model was built using the "glmmTMB" package in RStudio .

Redundancy analysis (RDA) was used to explore the relationship between macrobenthos species, composition, and environmental variables in different mangrove habitats, ages, and seasons. The environmental variables were scaled using the Hellinger method and transformed to Euclidean distances using the vegan package in RStudio (Oksanen et al. 2022). The selection criteria of the tested RDA models included their significance, the variance inflation factors of the explicative variables, and the proportion of inertia explained by each model. Significances of models, axes, and terms were tested using ANOVAs based on 999 permutations of residuals.

Results

Mangrove forest structure

The mangrove forest structure was similar between the restored and natural areas with three mangrove species: *A. germinans*, *L. racemosa*, and *R. mangle* (Table S2). *Avicennia germinans* was the most dominant species in all areas, except the 5-year-old restored areas where *Laguncularia racemose* was dominant (Table S2). *Avicennia germinans* and *L. racemosa* were 84.2% and 11.6% more abundant in the restored mangroves than in the natural areas. However, natural mangroves were characterized by a 52.1% higher abundance of *R. mangle* than restored mangroves. The restored stands were more abundant than the natural stands, but there were no significant differences ($P > .05$) between the age and abundance of restored and natural mangroves. Both the 6-year-old restored and 6-year-old natural areas had the highest mangrove abundance (Table S2). The average height of the mangroves in natural areas (12.52 ± 0.65 m) was greater than the restored stands (11.0 ± 0.78 m). There was a significant difference ($P < .01$) between tree age and height, but no significant difference ($P > .05$) between the height of restored and natural mangroves. The average DBH in the natural mangrove areas (15.50 ± 1.80 cm) was greater than in the restored areas (12.90 ± 1.27 cm). There was a significant difference ($P < .01$) between tree age and diameter and between the diameter of restored and natural mangroves ($P < .01$).

Overall macrobenthos composition

We recorded a total of 1327 macrobenthos individuals, representing 20 species, 10 orders, and 15 families (Table S1). Malacostraca (45%) was the most abundant class, followed by Gastropoda (30%), Bivalvia (15%), and Polychaeta (10%). There was no clear trajectory or consistent patterns between macrobenthos abundance and the mangrove habitats, ages, and seasons. However, the natural mangroves had an overall higher macrobenthos abundance compared to the restored mangroves, but this was not significant ($P > .05$). The 11-year-old natural mangroves (36.1%), 6-year-old natural mangroves (10.1%), and 6-year-old restored mangroves (8.5%) had the overall highest macrobenthos abundance. In the restored mangroves, the 6-year-old (23.7%), 10-year-old (21.6%), and 5-year-old (21.4%) areas had the highest macrobenthos abundance, while the 11-year-old (56.3%), 6-year-old (15.8%), and 9-year-old (10.1%) natural areas had the highest macrobenthos abundance. *Minuca rapax* (27.6%), *Balanus glandula* (22.5%), *Neritina virginea* (15.6%), *Melampus coffea* (10.3%), and *Ucides cordatus* (7.2%) were the five most abundant species across all areas, representing ∼83% of the total samples collected from restored and natural mangrove areas (Table S1). *Alitta succinea*, *Callinectes ornatus*, *Goniopsis cruentata*, *Austromacoma constricta*, *Cardisoma guanhumi*, *Heleobia australis*, *Nucula semiornata*, *Littorina* sp., *Erodona mactroides*, and *Callinectes bocourti* were the least abundant species representing <1% each. In the restored areas, *M. rapax* (35.0%), *N. virginea* (23.3%), and *M. coffea* (12.5%) were the most abundant species. In contrast, *B. glandula* (35.2%), *M. rapax* (23.6%), and *N. virginea* (7.2%) were the most abundant species in the natural mangrove areas.

The restored mangrove areas ($S = 18$) had higher species richness than the natural mangroves ($S = 16$) (Table S1). The 5-year-old restored mangroves had the highest species richness ($S = 10$), while the 6-year-old areas had the lowest ($S = 5$) (Table S1). The 11-year-old natural mangroves had the highest species richness ($S = 11$), while 5-year-old and 10-year-old mangroves had the lowest ($S = 4$) (Table S1).

The natural mangroves had higher macrobenthos abundance in all three intertidal zones than the restored mangroves, but the species richness was equivalent in all zones between restored and natural mangroves. Overall, the macrobenthos species richness and abundance in our study were highest in the lower and upper intertidal zones, respectively.

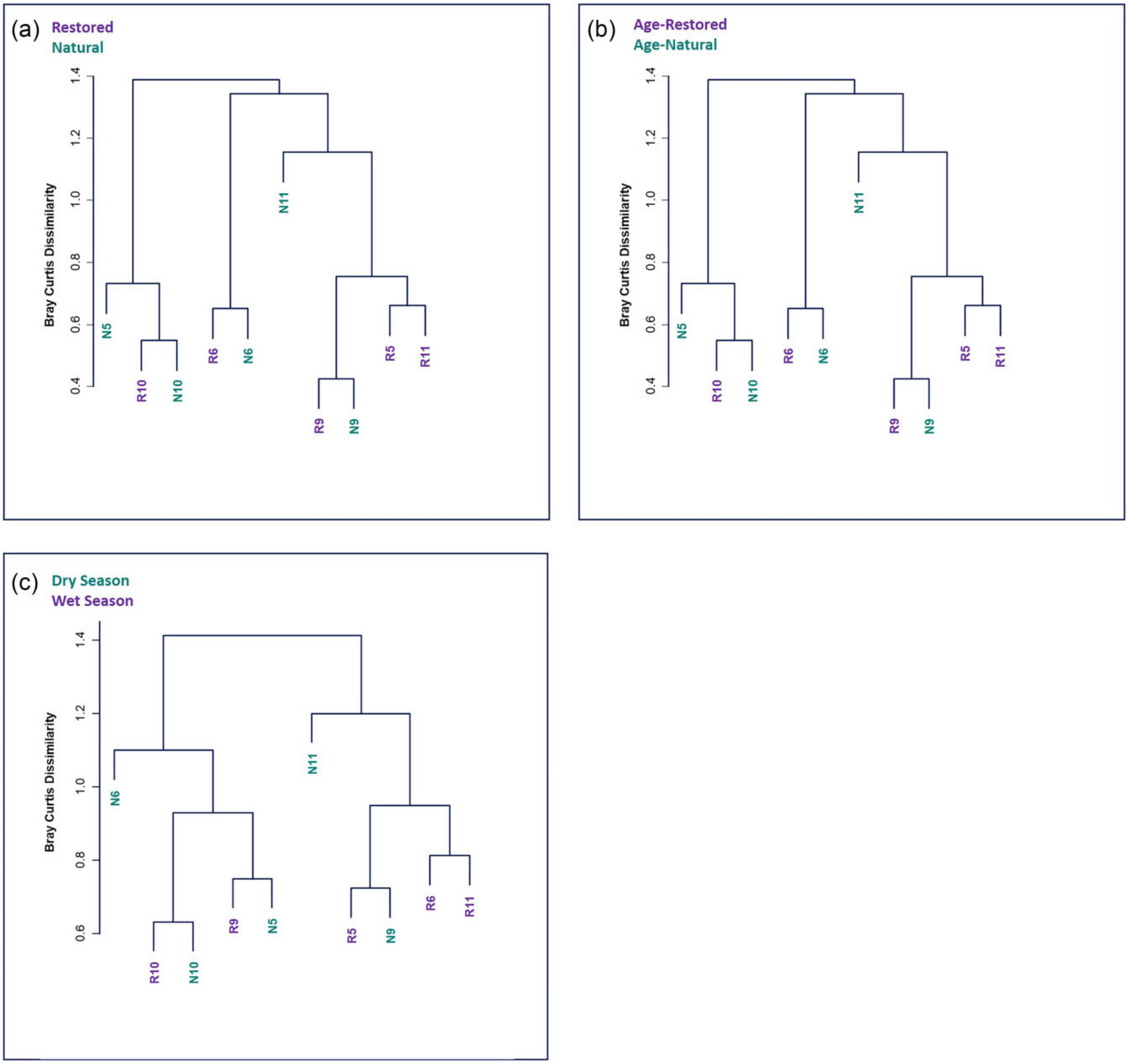

Figure 2. Cluster dendrogram of site dissimilarity of macrobenthos species composition in different mangrove (a) habitats, (b) ages, and (c) seasons. Percentages in axes labels refer to the explained proportion of constrained variance. Where R5 (5 years old), R6 (6 years old), R9 (9 years old), R10 (10 years old), and R11 (11 years old) restored mangroves and N5 (5 years old), N6 (6 years old), N9 (9 years old), N10 (10 years old), and N11 (11 years old).

Spatial and temporal variation in mangrove macrobenthos communities

The natural mangrove areas had a higher dissimilarity in macrobenthos species composition than the restored mangrove areas (Fig. 2). The 6-year-old restored mangrove areas had the highest dissimilarity, while the 11-year-old had the highest dissimilarity for the natural areas (Fig. 2). The 11-year-old restored area had the lowest dissimilarity, while the 9-year-old natural area had the lowest dissimilarity (Fig. 2). The 6-year-old restored and 6-year-old natural areas, 10-year-old restored and 5-year-old natural, 11-year-old restored and 9-year-old natural areas, and 5-year-old restored and 9-year-old natural areas were similar (Fig. 2). There was a lower dissimilarity in macrobenthos species composition between dry and wet seasons, including the 10-year-old restored and 10-year-old natural areas, the 9-year-old restored and 5-year-old natural areas, and the 5-year-old restored and 9-year-old natural areas (Fig. 2).

Mangrove macrobenthos community composition

nMDS ordination of the spatial variation in the macrobenthos composition clustered the 10 sampling areas into different groups with obvious spatial differences. The stress value for mangrove habitats (0.13), age (0.13), and seasons (0.15) suggest a good level of representation or ordination and a low probability of drawing false inferences (Clarke 1993, Defeo and Lercari 2004, Dexter et al. 2018) (Fig. 3). The nMDS plots of macrobenthos composition highlight a clear separation of areas in different mangrove habitats and ages, but a closer association between seasons (Fig. 3).

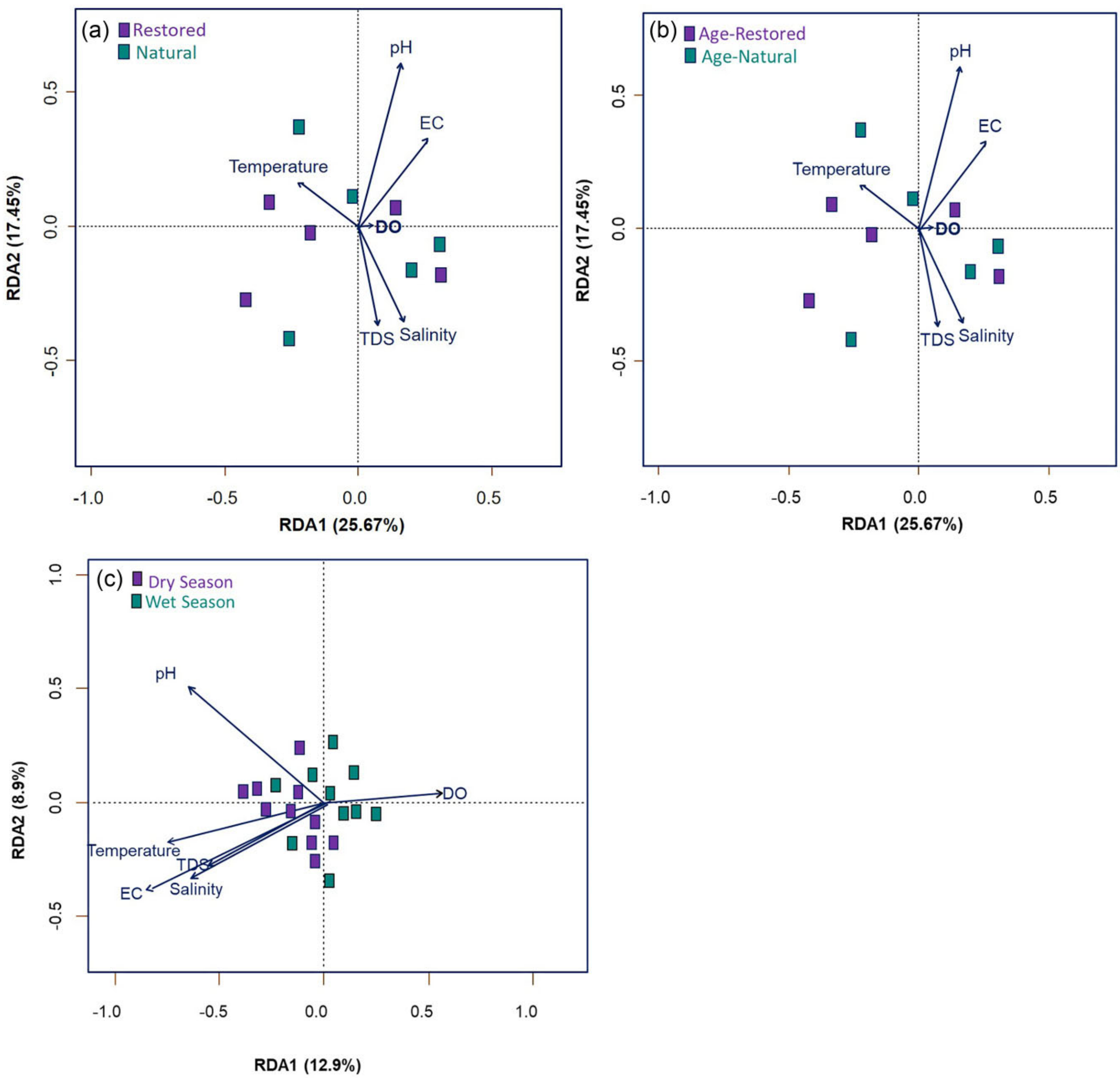

Figure 3. nMDS analysis of macrobenthos species composition in different mangrove (a) habitats, (b) ages, and (c) seasons. Crosses are restored sites, while triangles are natural mangrove sites.

The SIMPER analysis indicated that the four macrobenthos species explaining most of the dissimilarity (41.6%) among different mangrove habitats and ages were *N. virginea*, *B. glandulam*, *M. coffea*, and *M. rapax* (Table 1). In addition, *N. virginea*, *M. coffea*, *M. rapax*, *U. cordatus*, and *Uca maracoani* contributed the most to the average similarity of the restored mangroves (Table 1). In contrast, *B. glandulam*, *M. rapax*, *N. virginea*, *M. coffea*, and *U. cordatus* contributed the most to the average similarity in the natural mangroves (Table 1).

The SIMPER analysis also suggested that four macrobenthos species that explained most of the average dissimilarity (43.7%) between the wet and dry seasons (*N. virginea*, *Minuca rapa*, *B. glandulam*, and *M. coffea)* (Table 2). *Minuca rapax*, *N. virginea*, *M. coffea*, *U. cordatus*, and *Uca maracoani* contributed the most to the average similarity of the dry season (Table 2). In contrast, *B. glandulam*, *M. rapax*, *N. virginea*, *M. coffea*, and *U. cordatus* contributed the most to the average similarity in the wet season (Table 2).

Mangrove macrobenthos response to environmental variables

The RDA with all the explanatory variables for mangrove habitats explained 28.6% of variations (constrained), while 13.1% were unexplained (unconstrained). The environmental variables explained 43% (RDA1 = 25.6%, RDA2 = 17.4%) of the variations in the macrobenthos community between mangrove habitats (Fig. 4). The RDA with all the explanatory variables for ages explained 28.6% of the variation (constrained), while 13.1% was unexplained (unconstrained). The environmental variables explained 43% (RDA1 = 25.6%,

Table 1. SIMPER analysis (analysis of similarities) in groups outlined by ANOSIM, showing the organisms that most contributed to the observed differences among groups between restored and natural mangrove habitats

Species	Average	Ratio	Average		Cummulative sum	*P*-value
			Restored	Natural		
Neritina virginea	0.10	1.64	22.40	19.20	19.50	.07
Balanus glandula	0.10	0.48	0.00	60.20	38.70	.49
Melampus coffea	0.10	0.70	12.00	15.60	56.80	.72
Minuca rapax	0.09	1.15	33.40	40.40	0.74	.87
Uca maracoani	0.04	1.05	7.20	7.60	0.82	.75
Capitella sp.	0.03	0.60	1.40	4.80	0.88	.25
Ucides cordatus	0.01	1.20	9.00	10.40	0.89	.66
Callinectes bocourti	0.01	0.52	1.60	0.80	0.91	.69
Littorina sp.	0.01	0.93	1.40	0.60	0.93	.46
Erodona mactroides	0.01	1.03	1.40	0.80	0.94	.90
Littoraria angulifera	0.01	0.62	0.20	1.20	0.95	.21
Callinectes sapidus	0.06	0.71	0.80	2.00	0.96	.70
Heleobia australis	0.00	0.57	0.80	0.80	0.97	.72
Nucula semiornata	0.00	0.77	0.00	1.60	0.98	.36
Austromacoma constricta	0.00	0.46	1.00	0.00	0.99	.75
Cardisoma guanhumi	0.00	0.60	0.40	0.68	0.99	.57
Goniopsis cruentata	0.00	0.45	0.60	0.00	1.00	.69
Callinectes ornatus	0.00	0.45	0.40	0.00	1.00	.69

Table 2. SIMPER analysis (analysis of similarities) in groups outlined by ANOSIM, showing the organisms that most contributed to the observed differences among groups between dry and wet seasons

Species	Average	Ratio	Average		Cummulative sum	*P*-value
			Dry season	Wet season		
Neritina virginea	12.1	1.13	11.2	9.6	19.7	.31
Minuca rapax	12.1	1.14	16.7	20.2	39.4	.74
Balanus glandula	9.8	0.47	0	30.1	55.6	.26
Melampus coffea	9.7	0.57	6	7.8	71.7	.59
Uca maracoani	4.7	0.07	3.6	3.8	79.5	.62
Capitella sp.	2.8	0.37	0.3	2.4	84.2	.28
Ucides cordatus	1.6	0.87	4.5	5.2	86.9	.36
Aratus pisonii	1.3	0.64	0.8	2	89.1	.82
Littorina sp.	1	0.59	0.7	0.3	90.8	.73
Littoraria angulifera	0.8	0.41	0.1	0.6	92.1	.17
Callinectes bocourti	0.7	0.35	0.8	0.4	93.4	.83
Erodona mactroides	0.6	0.63	0.5	0.4	94.6	.18
Nucula semiornata	0.6	0.46	0	0.8	95.6	.12
Callinectes sapidus	0.5	0.52	0.4	1	96.7	.83
Heleobia australis	0.4	0.35	0.4	0.4	97.6	.73
Austromacoma constricta	0.4	0.31	0.5	0	98.4	.81
Cardisoma guanhumi	0.3	0.39	0.2	0.3	98.9	.75
Goniopsis cruentata	0.3	0.3	0.3	0	99.4	.78
Alitta succinea	0.2	0.32	0	0.2	99.7	.19
Callinectes ornatus	0.1	31	0.002	0	100	.3

RDA2 = 17.4%) of the variations in the macrobenthos community between different mangrove ages (Fig. 4). The RDA with all the explanatory variables for seasonality explained 15.5% of variations (constrained), while 29.9% were unexplained (unconstrained). The environmental variables explained 21.8% (RDA1 = 12.9%, RDA2 = 8.9%) of the variations in the macroinvertebrate community between wet and dry seasons (Fig. 4).

The pH and EC had the strongest positive loading, while temperature had a negative loading in both RDA axes in the mangrove habitats and ages (Fig. 4). DO had the strongest positive loadings, while EC, pH, and TDS had the strongest negative loadings for both RDA axes across seasons (Fig. 4).

Macrobenthos species richness and abundance models

The GLMM found no significant difference between mangrove habitats, age, and seasons ($P > .05$) on macrobenthos species richness (Table 3). The GLMM also revealed that for each additional restoration year, the expected macrobenthos species richness decreased by ~1% for age and habitat and 2% between seasons (Table 3).

The GLMM revealed that mangrove habitat, age, and seasons had a significant effect on macrobenthos abundance ($P < .05$) (Table 3). According to this model, habitat and season had the greatest influence on the abundance of macrobenthos species (Table 3). The GLMM also revealed that for each additional restoration year, the expected macrobenthos abun-

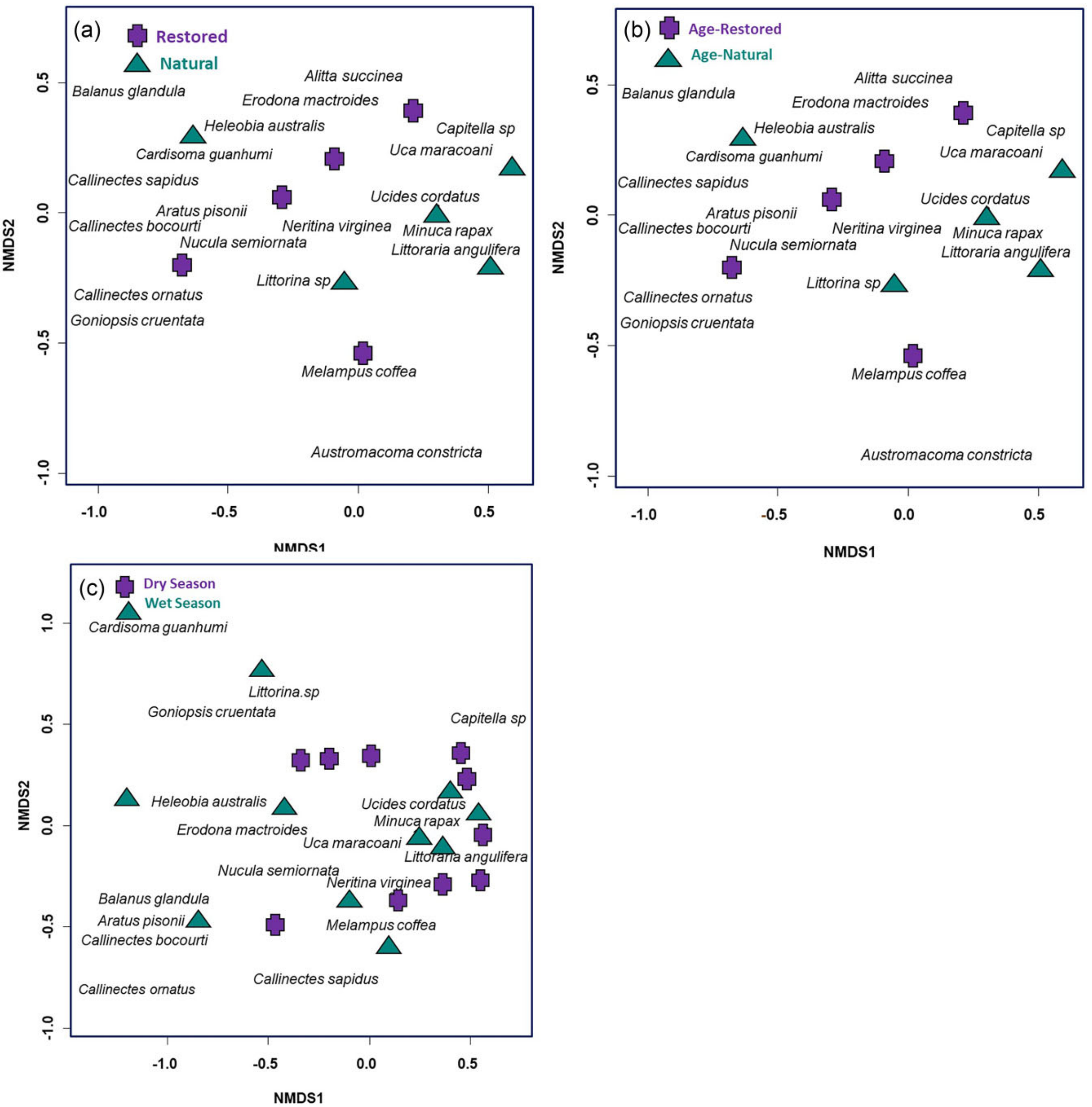

Figure 4. RDA Biplot of macrobenthos species and their associations with the environmental variables in different mangrove habitats, ages, and seasons. Percentages in axes labels refer to the explained proportion of constrained variance.

dance increased by ~3% for age and habitat and 2% between seasons (Table 3).

Seasonal variation of mangrove macrobenthos community

The wet season was characterized by higher species richness ($S = 16$) compared to the dry season ($S = 14$), which was different from species abundance, where it was lower in the wet season ($n = 548$) compared to the dry season ($n = 777$). PERMANOVA tests found no significant difference ($P > .05$) in macrobenthos abundance between mangrove habitats and seasons. Eleven macrobenthos species (*Aratus pisonii*, *B. glandula*, *Callinectes sapidus*, *Capitella* sp., *E. mactroides*, *Littorina* sp., *M. coffea*, *M. rapax*, *N. virginea*, *Uca maracoani*, and *U. cordatus*) were present in both wet and dry seasons. *Goniopsis cruentata*, *Littoraria angulifera*, and *N. semiornata* were only collected during the dry season, while *A. constricta*, *C. bocourti*, *C. ornatus*, *C. guanhumi*, and *H. australis* were found exclusively in the wet season.

Discussion

Mangrove restoration projects have been implemented as a means of compensating for their loss in many places (Worthington and Spalding 2018, Ellison et al. 2020, Waltham et al. 2020). Despite the proliferation of mangrove restoration projects, long-term monitoring of these project's success remains a major shortcoming (Palmer et al. 2016, Catterall

Table 3. GLMM summary table of the fitted models of macrobenthos species richness and abundance across different mangrove habitats, ages, and seasons in Guyana.

Factor	Estimate	Std. error	*P*-value
Species richness			
Habitat	0.310	0.440	.48
Age	0.330	0.530	.58
Season	0.210	0.200	.30
Abundance			
Habitat	0.106	0.124	.003***
Age	0.106	0.124	.003**
Season	0.360	0.055	.0005***

The statistical significance for each covariate (i.e. fixed effects) is included in the final formulation based on the Wald test. Std. Error: Standard error for coefficient.

2018). Where monitoring exists, it is often limited to vegetation recovery, with no annexation of faunal data, even though these taxa are commonly used bioindicators in mangrove ecosystems (Feary et al. 2007, Bosire et al. 2008, Siddig et al. 2016). One such understudied faunal group in mangrove restoration projects is macrobenthos, which plays a major role in mangrove ecosystem functioning and health in coastal ecosystems (Al-Khayat et al. 2019, Ram et al. 2021, Khatun et al. 2023). While previous studies have focused on fish and carbon stocks in restoration projects (Ram et al. 2021, Carnell et al. 2022, Kitchingman et al. 2023), this study explored the macrobenthic community composition and used them as a useful indicator of mangrove restoration recovery.

Although restored mangroves may initially have lower macrobenthos abundance than natural mangroves, they can attain similar composition over time (Salmo et al. 2017, Al-Khayat et al. 2019). In this study, we found lower macrobenthos abundance in the restored mangrove than in natural mangroves, which may be linked to higher organic matter enrichment in natural mangrove stands (Bosire et al. 2004, Bouillon et al. 2004, Lee 2008). However, restored mangroves had a negligibly higher species richness than natural mangroves, a finding similar to Zvonareva et al. (2015), where those authors recorded a higher species richness in the restored mangrove due to mangrove species composition than in natural mangroves in central Vietnam. We found no significant differences in the macrobenthos community composition between the restored and natural mangroves, indicating that restored mangrove macrobenthic communities support a similar assemblage of species compared to natural areas, thereby representing a convergence rapidly after restoration efforts. The similarity may be attributed to more conducive habitat conditions in restored areas, including favorable sediment composition, water quality, and vegetation density. Al-Khayat et al. (2019) reported an analogous species composition between natural and restored mangrove areas, but only after nearly three decades of compensatory planting along the Arabian Gulf—in our study the species convergence was much sooner, in just a few years. Our findings suggest that mangrove restoration can have rapid and beneficial outcomes for the macrobenthos, which is different to other places.

It is widely known that the development stage of mangrove forests plays a crucial role in shaping macrobenthos structure and composition (Macintosh et al. 2002, An et al. 2007, Li et al. 2017). The open canopy of younger mangrove stands (0–5 years) has higher availability of microphytobenthos, an essential food source supporting a more diverse macrobenthic community (Wang et al. 2021). Here, the younger restored mangrove areas with a partially open canopy also supported the highest species diversity compared to the older restored areas. Intermediate forest stands (5–11 years), usually have higher macrobenthos abundance and diversity than mature mangroves (Ashton et al. 2003, Salmo et al. 2017), since this forest stage provides a heterogeneous environment that attracts species from open and forested areas, leading to increases in types of food resources such as feces for the macrobenthic fauna (Chen et al. 2007). Diverse food types, mangrove species composition, and local environmental settings, such as the presence of a freshwater channel, may account for the higher macrobenthos abundance in the oldest natural mangrove site examined here. As planted mangroves mature, the trees modify the sediment environment, which can favor colonization by specifically mangrove-associated species (Salmo et al. 2017). Unfortunately, the forest ages examined here are intermediate and do not contain immature (<5 years) or mature (>15 years) stands for comparison. Salmo et al. (2017) and Macintosh et al. (2002) observed significant changes in mollusk assemblages corresponding with the development stages of mangroves, suggesting that as mangrove forests mature, they support a more diverse and complex community of mollusk species. However, we did not observe a significant shift in the macrobenthos' composition with increasing forest age, implying rapid recovery in the community following restoration, which generally remained stable with increasing age of the restored mangrove stands.

Many studies that have examined the distribution of macrofauna in tidal flats have found that the highest abundance and species diversity exist in the middle intertidal zone and lower intertidal zone (Zvonareva et al. 2015, Sheaves et al. 2016). In contrast, the macrobenthos species richness and abundance in our study were highest in the lower and upper intertidal zones, respectively (Fig. 5). Even though the lower intertidal zones have higher predation rates (from feeding fish and crustaceans) than the other zones (Silva et al. 2010, Storero et al. 2020), it supported the highest macrobenthos abundance since it is submerged most of the time (Fig. 5), providing a more stable environment with less exposure to temperature extremes that are common in the upper and middle internal zones (Zvonareva et al. 2015, Zhang et al. 2023). The higher species richness in the upper intertidal zone was unexpected and could be driven by the diverse Brachyura observed in this zone. Our findings are similar to Zvonareva et al. (2020), where those authors reported the macrobenthos in restored and natural mangroves of Khanh Hoa Province in Vietnam were distributed in different intertidal zones and lower intertidal zones were most abundant.

Seasonal variations in macrobenthos abundance and composition within mangrove ecosystems are common in tropical and subtropical regions (Samidurai et al. 2012, Bhowmik and Mandal 2021, Pan et al. 2021). Fluctuations in species richness and abundance between seasons possibly mirror shifts in the reproductive behaviors of macrobenthos and variations in food availability within the estuarine environment (Morais et al. 2019, Zhou et al. 2019). Some tropical estuaries have the lowest macrobenthic abundances in the dry season due to environmental stress and hypersaline conditions during this period (Teske and Wooldridge 2003, Currie and Small 2005, Lamptey and Armah 2008). We also recorded lower macrobenthos species richness and abundance in the dry season,

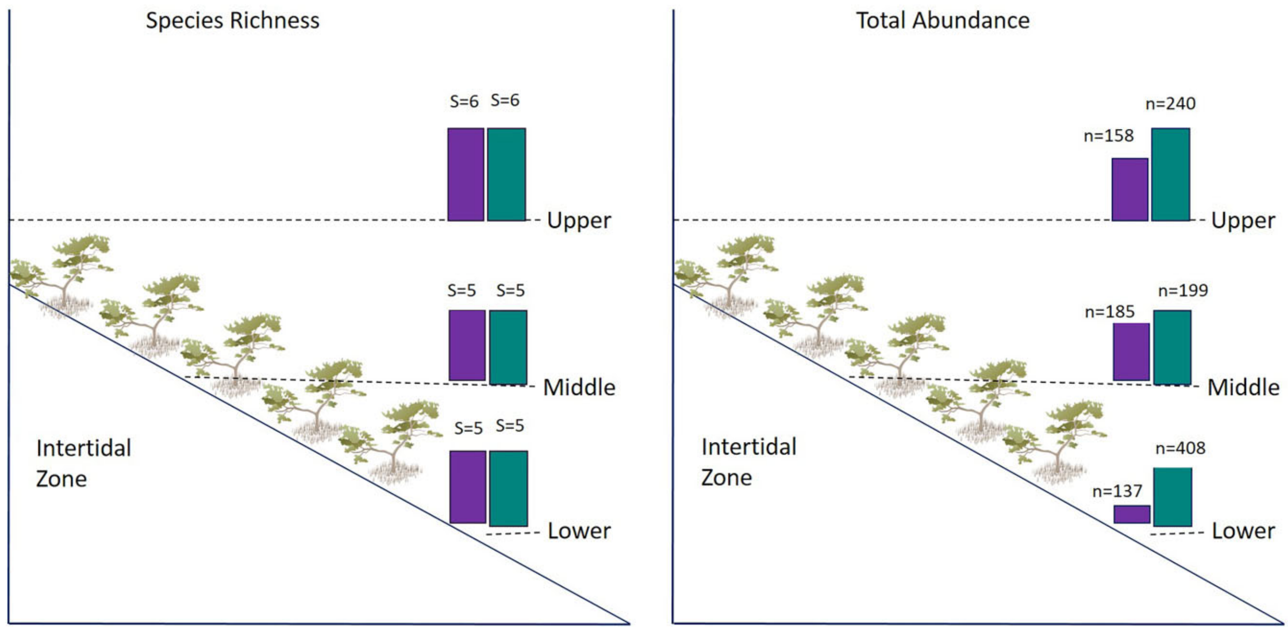

Figure 5. Distribution of macrobenthos species richness and abundance in different intertidal zones. The upper tidal zone is the mangrove zone with the shortest tidal inundation period closest to land, the middle tidal zone is in the middle zone of the mangroves between land and sea, and the lower intertidal zone is the mangrove zone with the longest inundation period and to closest to the ocean.

which is in line with previous studies (e.g. Barletta et al. 2003, Aheto et al. 2014, Wu et al. 2018). Higher species richness and abundance in the wet season can be attributed to favorable habitats and interconnectivity between freshwater and water areas since the rains facilitate the migration of different macrobenthos species to mangrove habitats. Studies conducted in tropical estuaries in humid regions observed that macrobenthos species migrated toward adjacent coastal areas in search of stable saline conditions (Barletta et al. 2003, Dantas et al. 2010).

Changes in the macrobenthos composition are linked to changes in the mangrove forest's physical structure, understory's composition, and maturity (Duke 2001, Peng et al. 2009, Azman et al. 2021). To this end, older mangroves may provide more diverse and complex microhabitats for macrobenthos species, thereby increasing the overall diversity of the community (Gorman and Turra 2016, Checon et al. 2023). They may also accumulate more organic matter and nutrients, enhancing their primary productivity, species richness, and abundance of macrobenthos (Ashton et al. 2003, Kristensen et al. 2008). As mangroves mature, they may also increase the connectivity among different mangrove patches, leading to the immigration of new species and the establishment of more diverse communities (Sheaves 2005, Friess et al. 2012, 2021). However, the magnitude of these changes may vary depending on various factors, including the location, species composition of the macrobenthos community, and the ecological interactions among different species (Chen et al. 2023). Therefore, resources are needed to implement a long-term monitoring program to track changes in the macrobenthos composition with forest maturity and to test whether these predictions are true in mangrove restoration projects across different countries.

The main goal of mangrove restoration projects is the return of natural assemblage structure and function of degraded mangroves (Bosire et al. 2008, Gorman and Turra 2016, Zimmer et al. 2022). Our study provides evidence of early and potentially beneficial changes in macrofaunal communities attributed to mangrove restoration efforts. The macrobenthic communities of restored mangrove areas examined here converge to those typical of natural mangrove forests. Our findings indicate that mangrove restoration represents a realistic management option to restore degraded mangrove habitats' diversity and functional role. This case study of Guyana is an example of a country facing many stressors (e.g. mounting pressure from coastal development expansion, nutrient pollution, terrestrial runoff, and marine litter) that can overwhelm natural recovery via recruitment, resulting in progressive loss of mangrove habitats and associated ecosystem services. Our results suggest that mangrove restoration can restore some of the functional role of mangrove forests, which may assist in building resilience associated fauna in previously degraded areas. However, the success of such restoration initiatives depends on efforts focused on removing or minimizing the effect of the main driving stressors—such as coastal development, erosion, and pollution.

Acknowledgments

We thank the National Agriculture Research & Extension Institute—Mangrove Restoration and Management Department for their valuable technical support. We also thank Rovindra Lakenarine and Jimmy Itwaru for their contributions to the fieldwork, Sarah Alli for her assistance with our lab work and data entry, and Devya Hemraj-Naraine for creating the map.

Author contributions

M.R. conceived the study, conducted and coordinated sample collection, laboratory work, and data analysis, and wrote the original manuscript draft; N.W. and M.S. edited, revised, and refined the manuscript.

Supplementary material

Supplementary data are available at *ICES Journal of Marine Science* online.
Conflict of interest: None declared.

Funding

This study was supported by funding from the WWF Education for Nature Russell E. Train Fellowship (WWF-EFN) (EF10998) and a grant from the Marine Conservation Action Fund of the New England Aquarium.

Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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Handling Editor: Howard Browman