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RESEARCH ARTICLE

Restoring mangrove biodiversity: can restored mangroves support fish assemblages comparable to natural mangroves over time?

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Despite the recent global increase in mangrove restoration efforts, our understanding of the outcomes and recovery of biodiversity and re-establishing functionality, such as productive fish habitat, is limited due to the lack of long-term monitoring. Here, we used a space-for-time approach to investigate whether restored mangroves attain similar fish communities to natural mangroves of the same age (5–11 years old). Fish in restored and natural mangrove forests along the Guyana coastline, South America, were sampled using trammel nets to collect data and compare the abundance, species richness, and biomass. This study found no notable differences in fish assemblages between restored and natural mangroves of the same ages. Nonmetric multidimensional scaling (NMDS), analysis of similarities (ANOSIM), and similarity percentage analysis (SIMPER) revealed a high overlap in fish species composition between the restored and natural mangrove habitats, age, seasons, and diel cycle. There was no clear trajectory between fish abundance, species richness, biomass, and the age of the restored and natural mangrove habitats, which indciates that fish quickly colonized the restored mangrove habitats. Our study provides evidence of the success of mangrove restoration projects in yielding positive ecological benefits as fish habitat. This information is useful for restoration practitioners when setting goals and timelines for fish habitat recovery after mangrove restoration.

Key words: **coastal wetlands, estuary, fish habitat, fish recruitment, habitat restoration**

Implications for Practice

- Restored mangroves can support fish assemblages similar to natural mangroves, providing strong evidence that restoration projects effectively reestablish ecosystem functions.
- The results highlight the potential for restored mangroves to support coastal fisheries by providing habitats similar to those of natural mangroves.
- Policymakers, conservation organizations, and funding agencies should support mangrove restoration initiatives since they are effective in supporting similar ecosystem functions as natural mangroves.

Introduction

Rapid mangrove loss, fragmentation, and degradation have led to a proliferation in conservation and restoration efforts globally (Worthington & Spalding 2018; Su et al. 2021; Chen et al. 2023). These project efforts range from large-scale programs covering tens of square kilometers to small, community-driven, efforts that are a few tens of square meters (Wickramasinghe 2017; Worthington & Spalding 2018; Rossi 2023). Regardless of the restoration project size, the primary goals remain the same, and that is to reverse habitat loss and reinstate important ecosystem services derived from healthy mangrove ecosystems (Worthington & Spalding 2018; Bayraktarov et al. 2020; Su et al. 2021).

Global mangrove restoration initiatives have rapidly increased in response to several major international commitments and pledges. The United Nations Decade on Ecosystem Restoration (2021–2030) implemented a global campaign to halt this destruction and accelerate global restoration efforts to tackle climate change, enhance food security, provide clean water, and protect biodiversity on the planet (Waltham et al. 2020). The Bonn Challenge was launched in 2011 which set a restoration target of 350 million hectares of the world's degraded and deforested lands by 2030 (Verdone & Seidl 2017).

Author contributions: MR designed the study, collected the field data, analyzed the data, and wrote the manuscript; NJW, MS reviewed and edited the manuscript.

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The Global Mangrove Alliance has also set a goal to restore half (4092 km^2) of the total restorable mangroves (8183 km^2) by 2030 (Leal & Spalding 2022). Despite the proliferation of restoration projects, access to long-term monitoring is absent from most of these projects, which is necessary to evaluate the success and outcomes of the investment (Ellison 2000; Biswas et al. 2009; Ram et al. 2024).

Long-term monitoring is central in assessing whether restoration efforts enhance the mangrove's ecological structure and function (Lindenmayer 2020; Gatt et al. 2022; Ram et al. 2024). Unfortunately, monitoring activities are only short-term and are rarely undertaken at all to document the success or failure of restoration programs (Ellison 2000; Sheaves et al. 2021; Ram et al. 2024). When monitoring occurs, it usually focuses on the survival and recovery of the restored species or physical environment (e.g., pH and temperature), and overlooks broader questions relating to faunal community responses (Zhang et al. 2018; Cadier et al. 2020). Animal communities are dynamic and respond rapidly to disturbance or recovery from management intervention (Rummell et al. 2023), making them suitable indicators for monitoring biodiversity and ecosystem health (Feary et al. 2007; Gibb & Cunningham 2013; Siddig et al. 2016). Only a few studies have used faunal composition to evaluate mangrove restoration outcomes/success (Ferreira et al. 2015; Ram et al. 2021; Kitchingman et al. 2023; Rummell et al. 2023; Ashton & Macintosh 2024). Utilizing animal responses to restoration in this way could improve our understanding of how restored habitats are functioning, which would further inform future restoration efforts and provide a means to quantify key ecosystem services for the funding provided by government or industry organizations (Hutchison & Spalding 2014; Kollmann et al. 2016; Huxham et al. 2017).

Mangrove fish communities are influenced by biophysical factors, including vegetation complexity, sediment characteristics, hydrological connectivity, and water quality (Bradley et al. 2024; Crona & Rönnbäck 2007; Liu & Ma 2024). Restored mangroves often differ from natural mangroves during the early stages of recovery and succession (Proffitt & Devlin 2005). These differences raise important questions about whether restored mangroves could replicate the ecological functions of natural mangroves, in particular their ability to support fish assemblages. Restoration practitioners, resource managers, and proponents of mangrove rehabilitation programs propose that restoring mangroves can enhance fish communities, food supplies, and income for coastal communities (Das 2017; Salmo et al. 2017; Jänes et al. 2020). There are debates about the effectiveness of mangrove monoculture restoration in reinstating biodiversity or whether natural rehabilitation is a better alternative (Struebig et al. 2022; Djamaluddin et al. 2023). While some studies suggest that restored mangrove monocultures can rapidly attract fish communities (Schulz et al. 2020; Ram et al. 2021; Kitchingman et al. 2023), others highlight disparities in community composition and trophic dynamics between restored and natural habitats (Adite et al. 2013; Loch et al. 2020). These variations highlight the need for comparative assessments of fish assemblages in restored and natural mangroves of similar age and environmental conditions to determine the ecological equivalence of these habitats.

Habitat provision for fish is a crucial ecosystem service provided by mangroves, however, evaluations on whether the same level of services are provided in restored mangroves, by comparison, are limited (Peralta-Milan & Salmo 2013; Peters et al. 2015; Huxham et al. 2017; Ram et al. 2021; Kitchingman et al. 2023). Most studies have broadly compared fish assemblages between restored and natural mangroves (Salmo et al. 2017; Ram et al. 2021) without considering the age of the restored mangrove. Here, we use a space-for-time design to evaluate fish assemblage of restored mangrove habitats of different ages (5–11 years) relative to natural mangrove areas in Guyana, South America. This study aims to examine the fish assemblage structure in Guyana's restored and natural mangrove habitats by analyzing the interacting effects of seasonality and diel cycles on the fish assemblages. We hypothesize that fish assemblage changes as restored mangroves mature in age post-restoration and will more closely resemble fish assemblage in natural habitats. Examining fish assemblages in restored mangroves in this way provides valuable information on the value and success of mangrove restoration, thereby helping to guide future mangrove restoration investment planned along the Guyana coastline.

Methods

Study Site

The study was conducted along Guyana's coast, which forms part of the North Brazil Shelf Large Marine Ecosystem (NBS LME), stretching from the Orinoco Delta near Trinidad and Tobago to the Mearim Delta near São Luis, Brazil (Hempel & Sherman 2003; Isaac & Ferrari 2017). The NBS LME has approximately one million square kilometers of mangroves, coastal habitats, and open seas (Hempel & Sherman 2003). The area is heavily influenced by runoff from several major rivers (Amazon and Orinoco), which deliver large quantities of sediments and nutrients to downstream coastal areas (Isaac & Ferrari 2017). Due to the major sediment and nutrient input, the NBS LME is a highly productive and valuable region with a USD 610 million fishery that maintains national and regional economies (FAO 2014).

Guyana's coastal regions are covered with mangrove forests that protect it from erosion and flooding, they provide habitat for diverse marine life and sequester carbon (Government of Guyana 2012). The country's coastal mangrove fringe is primarily dominated by *Avicennia germinans* (black mangroves), *Rhizophora mangle* (red mangroves), and *Laguncularia racemosa* (white mangroves) (Toorman et al. 2018; Winterwerp et al. 2020; Ram et al. 2021).

Guyana's Mangrove Restoration Project

Guyana's mangrove belt was once 200 m wide though has since significantly reduced owing to natural and anthropogenic factors along the coastline (NAREI 2015). In 1983, mangrove forest cover was estimated at 150,000 ha, but it decreased to only 81,000 ha by 1992, with a further decline to 22,000 ha by 2011 (NAREI 2015). This widespread mangrove loss has been due to the natural erosion process, mangrove harvesting, excess siltation, and coastal pollution (NAREI 2015). Recognizing the values of mangroves, threats, and increased risk to the low-lying coastline by sea level rise prompted the Government of Guyana (GOG) to conserve, restore, and protect the country's remaining mangrove habitat (NAREI 2015). This led to the Guyana Mangrove Restoration Project (GMRP) implementation in 2010 which was designed to increase the forest cover and protect Guyana's coast against future climate change threats. The GRMP project has resulted in planting over 500,000 mangrove *Avicenna germinans* seedlings at 19 locations spanning 8 km of Guyana's coast (NAREI 2015).

In this study, 10 locations were selected via a stratified random approach, made up of five natural and five restored mangrove forests of different sizes (Fig. 1). Natural mangrove forests consist of black mangroves (*Avicennia germinans*), white mangroves (*Laguncularia racemose*), and red mangroves (*Rhizophora mangle*), while restored habitats typically exist as monocultures of black mangroves (*Avicennia germinans*) planted between 2010 and 2018. The natural mangrove forests regenerated after coastal erosion and mudflat stabilization, which created a suitable substrate for mangrove colonization. The restored mangrove areas ranged between 284 and 450 m in length. Restored mangrove habitats were classified into five different stand ages: 5, 6, 9, 10, and 11 years old. Natural mangrove habitat were selected after consultation with local communities from three administrative regions (Regions 2, 4, and 5) in Guyana to select habitats of the same ages (5, 6, 9, 10, and 11 years old) as the restored mangroves. These habitats were further verified using satellite imagery techniques, such as Multi-Temporal Analysis and the Normalized Difference Vegetation Index (NDVI) to compare satellite images and assess mangrove change 5, 6, 9, 10, and 11 years ago.

Study Design

We created a space-for-time approach (SFT) to examine fish assemblage response to changes in differently aged restored and natural mangrove habitats over time of mangrove vegetation and habitat trajectories. The SFT approach extrapolates temporal trends across a range of stand ages, generating trajectory patterns depicting the restored ecosystem's temporal evolution (Buyantuyev et al. 2012; Salmo et al. 2013).

Vegetation Survey

Permanent circular plots (radius = 10 m) were established 25 m apart via stratified sampling with varying distances from the shoreline ($N = 3$ per habitat). In each plot, tree species, diameter at breast height (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. All trees >5 cm DBH were measured in 10-m radius circular plots.

Environmental Variables

The water temperature (°C), electrical conductivity (EC, μS/cm), total dissolved solvents (TDS, ppm) and pH were measured using an 86031 AZ Waterproof IP 67 Combo Water Quality. Dissolved oxygen (mg/L) was measured using an Extech DO600 Waterproof ExStik II Dissolved Oxygen Meter. Salinity was measured using a Ciztada salinity tester. All measurements were taken during the day and night in the upper water column (20 cm below the water surface).

Fish Sampling

Fish sampling was done during the day and night, representing the diel cycle, and in the wet (December–January 2023) and dry seasons (August–September 2023). Two trammel nets of four different dimensions: (1) 0.3 m × 0.02 m × 50 m; (2) 0.3 m × 0.06 m × 50 m, (3) 0.3 m × 0.08 m × 50 m; and (4) 0.3 m × 0.11 m × 50 m were set in the middle of the mangroves (~5 m from the forest ocean edge), deployed before the high tide, and retrieved after 6 hours of soaking in the day and then the night. All fish caught were counted, with the total length, standard length, and total weight measured. Each fish caught was identified to the lowest possible taxonomic level using the appropriate identification keys and guides (Taphorn et al. 2022). Most fish specimens were released alive, while sub-samples were preserved with 10% formalin and stored in 70% ethanol for later identification as required.

Data Analysis

To evaluate the species composition and compare differences between mangrove habitat, age, seasons, and diel cycle we computed abundance and the sum of fish orders, families, genera, and species. A two-way analysis of similarity (ANOSIM) based on the square transformation of the abundance data was used to test whether there were significant differences in fish assemblages between mangrove habitat, age, seasons, and diel cycle. This test was performed using in RStudio the "adonis2" function in the Vegan package (Oksanen et al. 2022). A non-parametric permutational multivariate analysis of variance (PERMANOVA) was used to assess differences in fish assemblage structure between mangrove habitat, age, seasons, and diel cycle. The test was performed in RStudio using the "anosim2" function in the Vegan package (Oksanen et al. 2022). Pearson correlations exceeding $R > 0.7$ between the ordination and taxa were used to fit vectors on the NMDS plot. The Bray–Curtis dissimilarity index based on the square transformation of the abundance data was employed to estimate the fish compositional differences among mangrove habitat, age, seasons, and diel cycle. The Bray–Curtis dissimilarity index was 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 fish community composition between mangrove habitat, age, seasons, and diel cycle.

We used non-metric multidimensional scaling (NMDS) based on the square transformation of the abundance data to assess variation in fish assemblage composition and identify the taxa that characterize this variation among mangrove habitat, age, seasons, and diel cycle. All ordinations were completed 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. These analyses were performed in RStudio using the "NMDS" function in the package Vegan (Oksanen et al. 2022).

We employed a General Linear Mixed Model (GLMM) with Poisson regression to compare the factors impacting the fish species richness and abundance among mangrove habitat, age, seasons, and diel cycle. Fish species richness and abundance were used as the response variable, while the "Habitat," "Age," "Season," "Diel Cycle," "DBH," and "Canopy" were all used as predictors. Different variable transformations, distributions, and links were tested. Selection criteria for the GLMM included conditional AIC, log-likelihood scores, and overdispersion ratios. The model was built using the "glmmTMB" package in RStudio (Knudson et al. 2018).

We utilize Redundancy Analysis (RDA) to explore the relationship between fish species, composition, and environmental variables (electrical conductivity, dissolved oxygen, pH, salinity, temperature, and total dissolved solvents) in different mangrove habitats, ages, seasons, and diel cycle. 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 (VIF) 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

A total of 559 fish, representing 14 families and 18 species were recorded in this study (Table 1). There were no significant differences in fish abundance between the restored and natural mangrove habitats, and age (Fig. 2). The 6-year-old (40%), 5-year-old (26%), and 11-year-old (19.5%) restored habitats had the highest abundance, while the 6-year-old (50.1%), 11-year-old (16.1%) and 5-year-old (11.7%) natural habitats had the highest fish abundance. However, there were no clear trends between fish abundance and the ages of the restored and natural mangrove habitats.

Sciades couma (57.7%), *Anableps anableps* (23.6%), *Sciades herzbergii* (8.1%), *Amphiarius rugispinis* (2.8%), and *Colomesus psittacus* (1.6%) were the five most abundant species across all habitats, and together, represented ~94% of the total catch in restored and natural mangrove habitats (Fig. 2). *Aspredinichthys tibicen*, *Batraichoides surinamensis*, *Cynoscion jamaicensis*, *Guavina guavina*, *Hypophthalmus marginatus*, *Plagioscion squamussisimus*, and *Stellifer microps* were the least abundant species representing <1% each. In the restored habitats, *Sciades couma* (50.8%), *Anableps anableps* (32.2%), and *Sciades herzbergii* (5.3%) were the most abundant species. In contrast, *Sciades couma* (70%), *Sciades herzbergii* (12.6%), and *Anableps anableps* (8.7%) were the most abundant species in the natural habitats.

Spatial and Temporal Variation in Mangrove Fish Assemblages

ANOSIM revealed that the fish composition was not significantly different among the clustering habitats ($R = 0.14$, $p = 0.12$), age ($R = 0.25$, $p = 0.16$), seasons ($R = 0.04$, $p = 0.22$), and diel cycle ($R = -0.61, p = 0.83$), indicating that the observed differences in fish composition are random (Fig. 2). These results indicate a very slight separation in fish composition among different habitats, mangrove ages, and diel cycles and no separation between the seasons (Fig. 2).

The restored mangrove habitats had a higher dissimilarity in fish species composition compared to the natural mangrove habitat with clustering among sites similar habitat type (Fig. 3). The fish species composition was similar in the same habitats of equivalent age (Fig. 3). The fish species composition was similar between seasons and diel cycle (Fig. 3). The 5-year-old, and 10-year-old restored habitats, and the 5-year-old and 9-year-old natural habitats had the greatest dissimilarity in fish species composition between habitat, age, and seasons (Fig. 3).

Mangrove Fish Assemblage Composition

NMDS ordination of the spatial variation in fish assemblages clustered the 10 sampling habitats into different groups with obvious spatial differences. Meanwhile, the stress level for habitats (0.16), age (0.16), seasons (0.17), and diel cycle (0.17) suggest a very good level of representation or ordination and a low probability of drawing false inferences (Fig. 4). The NMDS revealed that the habitats did not segregate clearly between habitats, age, season, and diel cycle.

The SIMPER analysis indicated that the two species that explained most of the average dissimilarity between the mangrove habitats, age, seasons, and diel cycle were *Sciades couma* and *Anableps anableps* (Tables S1–S4). *Sciades couma*, *Anableps anableps*, *Sciades herzbergii*, *Amphiarius rugispinis*, and *Aspredo aspredo* contributed the most to the average similarity in different mangrove habitats, ages, seasons, and diel cycles (Tables S1–S4).

Mangrove Fish Response to Environmental Variables

The RDA with all the explanatory variables for restored and natural mangrove habitats explained 13.0% of the variation in the data (constrained), while 6.1% of the variation remained unexplained (unconstrained). The first two RDA axes explain 41.1% of the total variation in the dataset, with RDA1 accounting for 26.3% and RDA2 for 14.8% (Fig. 5). Natural habitats exhibited greater dispersion, suggesting higher variability in water quality conditions, whereas restored habitats cluster more

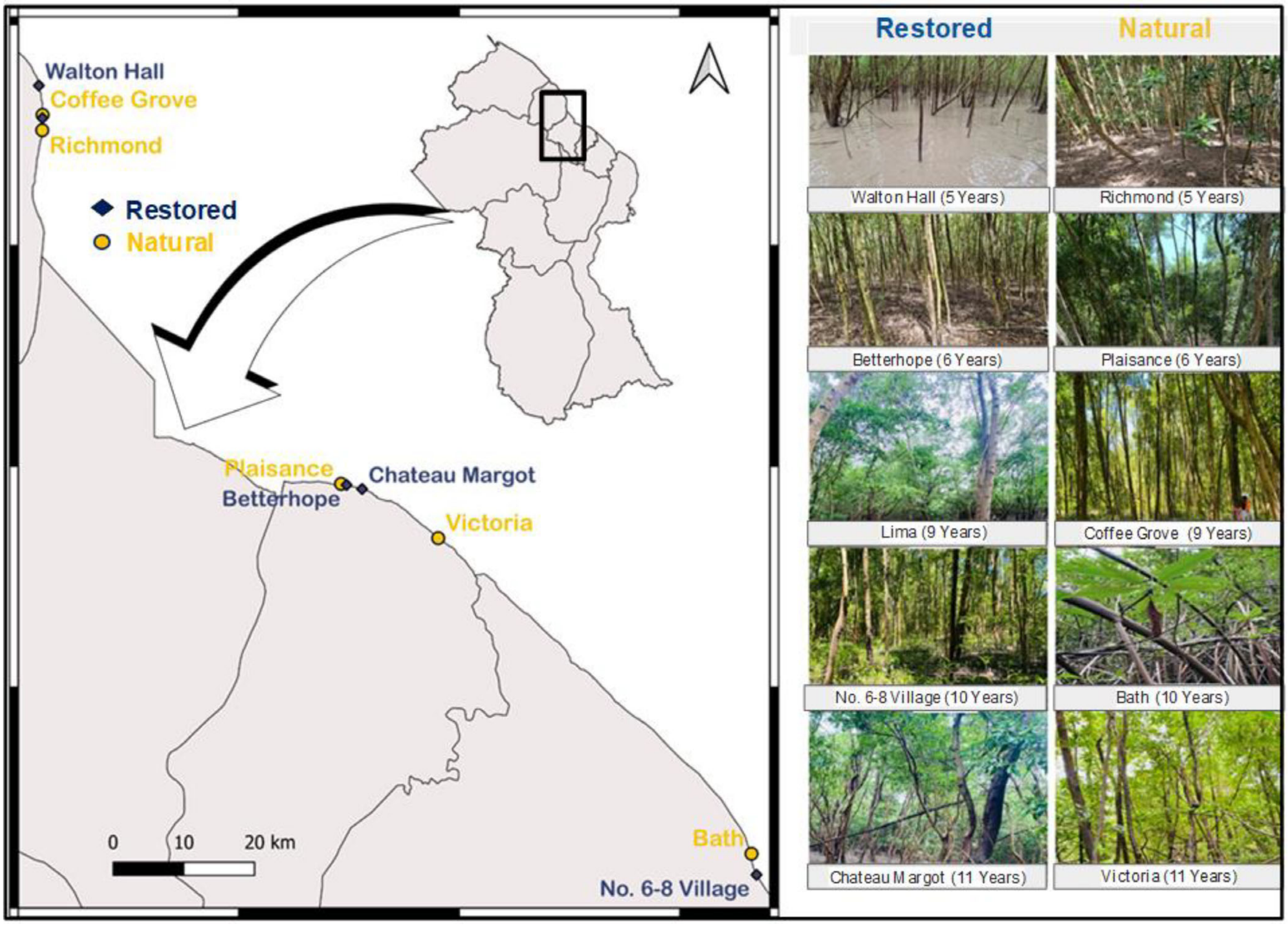

Figure 1. Study locations (Yellow circles are natural stands of mangroves where new mangroves grow from the seeds and propagules of parent trees). Blue diamonds are restored mangrove areas replanted by the Guyana Mangrove Restoration Project and the National Agricultural Research & Extension Institute.

tightly, indicating more homogenous conditions (Fig. 5). The RDA with all the explanatory variables for different mangrove ages explained 13.0% of variations in the data (constrained), while 6.1% remained unexplained (unconstrained). The first two RDA axes explain 41.1% of the total variation in the dataset, with RDA1 accounting for 26.3% and RDA2 for 14.8% (Fig. 5). Age-natural habitats are more dispersed, suggesting greater variability in water quality conditions, whereas age-restored habitats cluster more closely, indicating relatively homogenous conditions (Fig. 5).

The RDA with all the explanatory variables for seasonality explained 9.8% of the variation in the data (constrained), while 22.5% remained unexplained (unconstrained). The first two RDA axes explain 22.2% of the total variation in the dataset, with RDA1 accounting for 13.6% and RDA2 for 8.6% (Fig. 5). The distribution of samples suggests distinct seasonal patterns in water quality. DO was positively associated with the dry season, indicating, that salinity, EC, TDS, and temperature are more closely associated with the wet season (Fig. 5). The RDA with all the explanatory variables for the diel cycle explained 10.6% of the variation in data (constrained), while 22.8% remained unexplained (unconstrained). The first two RDA axes explained 22.8% of the total variation in the dataset, with RDA1 accounting for 12.2% and RDA2 for 10.6% (Fig. 5). DO, TDS, and salinity were positively correlated with night samples. In contrast, day samples are associated with higher temperatures and pH (Fig. 5).

Mangrove Fish Species Richness and Abundance Models

Fish species richness was not significantly affected by mangrove habitats (Est = −0.07), age (Est = −0.07), seasons (Est = −0.008), diel cycle (Est = −0.002), DBH (Est = −0.311), and canopy (Est = −0.24) (Table 2). Similarly, fish species abundance was not significantly affected by mangrove habitats (Est = −0.01), age (Est = −0.01), seasons (Est = −0.001), diel cycle (Est = −0.004), DBH (Est = 0.300), and canopy (Est = −0.01) (Table 2).

Seasonality

The wet season was characterized by a marginally higher species richness ($n = 14$) than the dry season ($n = 13$), but there was a lower total abundance in the wet season ($n = 193$)

Table 1. Fish composition across different mangrove habitats, age, seasons, and diel cycle. R5 (5 years old), R6 (6 years old), R9 (9 years old), R10 (10 years old) & 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). Habitat type codes indicate that all species listed were recorded in that habitat.

							Season		*Diel cycle*	
Habitat type	*Order*	*Family*	*Species*	*Functional group*	*Abundance*	*Biomass (g)*	*Dry*	*Wet*	*Day*	*Night*
◆ R5	Cyprinodontiformes	Anablepidae	*Anableps anableps*	Omnivore	45	6807	43	2	25	20
	Siluriformes	Ariidae	*Amphiarius rugispinis*	Carnivore	8	1372	4	4	6	2
	Batrachoidiformes	Batrachoididae	*Batraichoides surinamensis*	Carnivore	1	158	0	1	0	1
	Tetraodontiformes	Tetraodontidae	*Colomesus psittacus*	Omnivore	1	23	1	0	0	1
	Siluriformes	Loricariidae	*Hypostomus plecostomus*	Herbivore	2	215	0	2	2	0
	Mugiliformes	Mugilidae	*Mugil curema*	Planktivore	2	848	0	2	2	0
	Clupeiformes	Pristigasteridae	*Odontognatus mucronatus*	Carnivore	1	65	0	1	0	1
	Siluriformes	Auchenipteridae	*Pseudauchenipterus nodosus*	Carnivore	6	1106	2	4	0	6
	Siluriformes	Ariidae	*Sciades couma*	Carnivore	22	4244	22	0	7	15
	Siluriformes	Ariidae	*Sciades herzbergii*	Carnivore	7	66,665	7	0	1	6
◆ R6	Cyprinodontiformes	Anablepidae	*Anableps anableps*	Omnivore	27	273	25	2	26	1
	Tetraodontiformes	Tetraodontidae	*Colomesus psittacus*	Omnivore	5	70	0	5	5	0
	Siluriformes	Ariidae	*Sciades couma*	Omnivore	84	11,882	70	14	44	40
◆ R9	Cyprinodontiformes	Anablepidae	*Anableps anableps*	Carnivore	11	1522	5	6	9	2
	Gobiiformes	Eleotridae	*Guavina guavina*	Omnivore	1	100	0	1	0	1
	Siluriformes	Pimelodidae	*Hypophthalmus marginatus*	Omnivore	1	80	0	1	0	1
	Siluriformes	Ariidae	*Sciades couma*	Detritivore	22	2726	16	6	6	16
	Siluriformes	Ariidae	*Sciades herzbergii*	Carnivore	5	870	5	0	0	5
◆ R10	Cyprinodontiformes	Anablepidae	*Anableps anableps*	Onmivore	5	989	3	2	1	4
	Siluriformes	Ariidae	*Amphiarius rugispinis*	Carnivore	2	500	2	0	0	2
	Siluriformes	Aspredinidae	*Aspredo aspredo*	Detritivore	5	290	1	4	2	3
	Acanthuriformes	Sciaenidae	*Cynoscion jamaicensis*	Carnivore	1	20	1	0	1	0
	Mugiliformes	Mugilidae	*Mugil cephalus*	Planktivore	2	150	2	0	2	0
	Acanthuriformes	Sciaenidae	*Plagioscion squamussisimus*	Carnivore	1	136	1	0	0	1
	Siluriformes	Ariidae	*Sciades couma*	Carnivore	10	4290	4	6	7	3
	Siluriformes	Ariidae	*Sciades herzbergii*	Carnivore	6	2310	5	1	2	4
	Acanthuriformes	Sciaenidae	*Centropomus ensiferus*	Carnivore	1	210	1	0	0	1
	Acanthuriformes	Sciaenidae	*Stellifer microps*	Carnivore	1	145	1	0	1	0
◆ R11	Cyprinodontiformes	Anablepidae	*Anableps anableps*	Omnivore	43	4582	1	42	41	2
	Siluriformes	Ariidae	*Sciades couma*	Carnivore	25	8717	25	0	18	7
	Siluriformes	Ariidae	*Sciades herzbergii*	Carnivore	1	1814	0	1	1	0
● N5	Cyprinodontiformes	Anablepidae	*Anableps anableps*	Omnivore	3	132	0	3	0	3
	Siluriformes	Aspredinidae	*Aspredo aspredo*	Carnivore	1	110	0	1	0	1
	Siluriformes	Loricariidae	*Hypostomus plecostomus*	Herbivore	1	164	1	0	1	0
	Siluriformes	Ariidae	*Sciades couma*	Carnivore	17	2760	11	6	6	11
	Siluriformes	Ariidae	*Sciades herzbergii*	Carnivore	2	425	0	2	2	0
● N6	Cyprinodontiformes	Anablepidae	*Anableps anableps*	Omnivore	8	456	0	8	0	8
	Siluriformes	Ariidae	*Amphiarius rugispinis*	Carnivore	6	625	0	6	0	6
	Siluriformes	Ariidae	*Sciades couma*	Carnivore	77	10,226	66	11	11	66
	Siluriformes	Ariidae	*Sciades herzbergii*	Carnivore	7	1650	7	0	0	7
● N9	Siluriformes	Ariidae	*Amphiarius rugispinis*	Carnivore	6	750	0	6	6	0
	Cyprinodontiformes	Ariidae	*Anableps anableps*	Omnivore	2	240	0	2	2	0

Table 1. Continued

Habitat type	Order	Family	Species	Functional group	Abundance	Biomass (g)	Season		Diel cycle	
							Dry	Wet	Day	Night
	Tetraodontiformes	Tetraodontidae	*Colomesus psittacus*	Omnivore	2	17	2	0	0	2
	Siluriformes	Ariidae	*Sciades couma*	Carnivore	13	1940	10	3	6	7
	Siluriformes	Ariidae	*Sciades herzbergii*	Carnivore	4	735	0	4	1	3
● N10	Cyprinodontiformes	Anablepidae	*Anableps anableps*	Omnivore	5	465	1	4	1	4
	Siluriformes	Ariidae	*Sciades couma*	Carnivore	11	3010	6	5	11	0
	Siluriformes	Ariidae	*Sciades herzbergii*	Carnivore	2	1620	1	1	2	0
	Clupeiformes	Pristigasteridae	*Odontognatus mucronatus*	Carnivore	3	185	3	0	0	3
● N11	Tetraodontiformes	Tetraodontidae	*Colomesus psittacus*	Omnivore	1	27	0	1	1	0
	Siluriformes	Loricariidae	*Hypostomus plecostomus*	Herbivore	2	540	0	2	1	1
	Siluriformes	Ariidae	*Sciades couma*	Carnivore	19	6295	7	12	11	8
	Siluriformes	Ariidae	*Sciades herzbergii*	Carnivore	11	4809	2	9	8	3
	Perciformes	Centropomidae	*Centropomus ensiferus*	Omnivore	2	345	2	0	2	0

compared to the dry season ($n = 366$). The PERMANOVA test revealed that there was no significant difference between fish abundance and restored mangroves in the dry and wet seasons. Ten species (*Amphiarus rugispinis*, *Aspredo aspredo*, *Anableps anableps*, *Colomesus psittacus*, *Hypostomus Plecostomus*, *Odontognatus mucronatus*, *Plagioscion squamussisimus*, *Sciades couma*, *Sciades herzbergii*, and *Pseudauchenipterus nodosus*) were captured in both wet and dry seasons. *Centropomus ensiferus*, *Cynoscion jamaicensis*, *Mugil cephalus*, and *Stellifer microps* were only captured during the dry season, while *Batrichoides surinamensis*, *Guavina guavina*, *Hypophthalmus marginatus*, and *Mugil curema* were captured exclusively in the wet season.

Diel Cycle

Species richness was marginally higher at night ($n = 14$) compared to during the day ($n = 12$). Abundance was slightly higher at night ($n = 281$) compared to during the day ($n = 278$). The PERMANOVA test indicates that there was no significant difference between the fish abundance day and night. Twelve species (*Amphiarus rugispinis*, *Aspredo aspredo*, *Anableps anableps*, *Colomesus psittacus*, *Hypostomus Plecostomus*, *Odontognatus mucronatus*, *Plagioscion squamussisimus*, *Sciades couma*, *Sciades herzbergii*, and *Pseudauchenipterus nodosus*) were captured during both the day and night. *Cynoscion jamaicensis*, *Mugil cephalus*, *Mugil curema*, and *Stellifer microps* were only captured during the day, while *Guavina guavina*, *Hypophthalmus marginatus*, *Odontognatus mucronatus*, *Plagioscion squamussisimus and Pseudauchenipterus nodosus* were found exclusively during the night.

Mangrove Vegetation

The vegetation structure was similar between the restored and natural mangroves. Three mangrove species (*Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*) were recorded at the restored and natural mangrove habitats. *Avicennia germinans* was the most dominant species overall, except the 5-year-old restored mangroves where *Laguncularia racemose* was more dominant. *Avicennia germinans* and *Laguncularia racemosa* were 84.2% and 11.6% denser in the restored mangroves than in the natural stands. However, natural mangroves were characterized by a 52.1% higher density of *Rhizophora mangle* compared to restored mangroves. The restored stands ($n = 894$) were 50.1% denser than the natural stands ($n = 446$). The 6-year-old restored and 6-year-old natural habitats had the highest mangrove density. The average height of the mangroves in natural habitats (12.52 ± 0.65 m) was marginally greater than the restored habitats (11.0 ± 0.78 m). There was a significant difference ($p < 0.01$) between tree age and height, but no significant difference between the height of restored and natural mangroves. The average DBH in the natural mangrove habitats (15.50 ± 1.80 cm) was greater than in the restored habitats (12.90 ± 1.27 cm). There was a significant difference ($p < 0.01$) between tree age and diameter, and

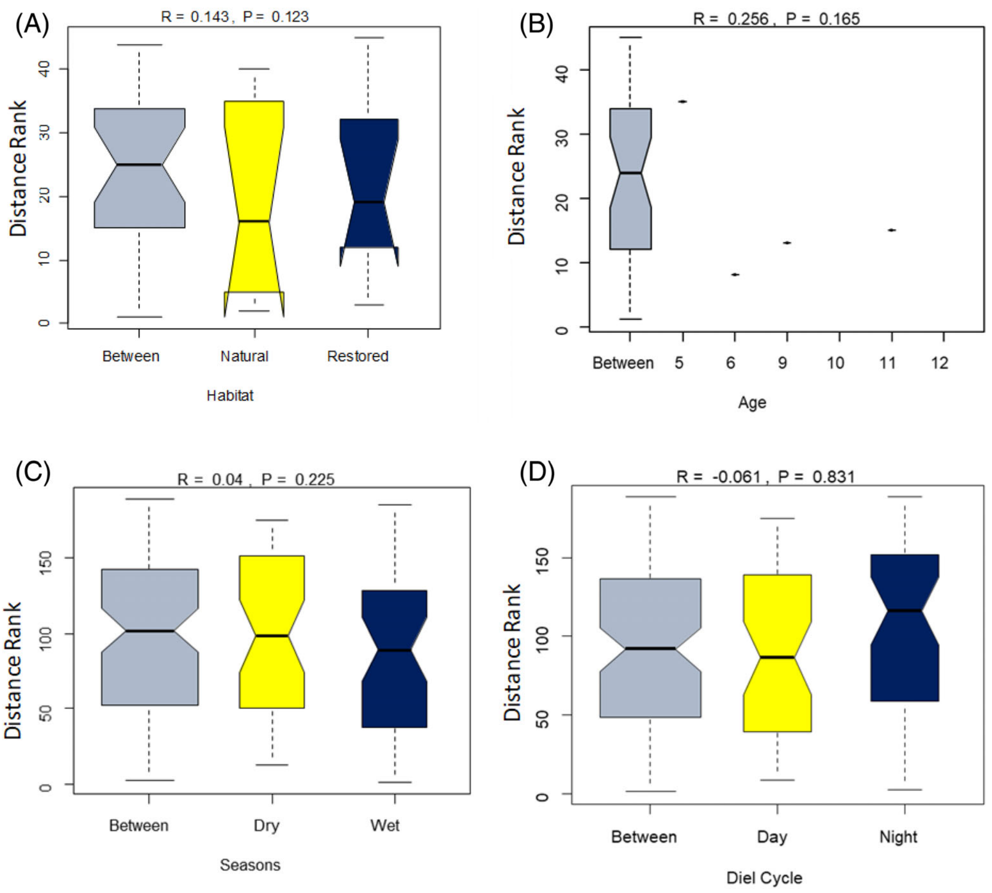

Figure 2. ANOSIM analysis. (A) Habitat, (B) age, (C) season, and (D) diel cycle. The y-axis represents the distance rank between samples, and the x-axis represents the results between both groups. Intra-group results are shown for each group. In the plot, the R-value was not close to 1, indicating that the inter-group differences were less than the intra-group differences.

between the diameter of restored and natural mangroves ($p < 0.01$).

Discussion

Many studies suggest that as restored mangroves mature, they facilitate the return of some faunal species, occasionally reaching levels comparable to natural mangroves (Bosire et al. 2008; Ferreira et al. 2015; Zimmer et al. 2022). We also observed this pattern with no notable differences in fish assemblages between restored and natural mangrove habitats. This suggests that restored mangroves can provide comparable habitat conditions to natural mangroves, supporting similar fish communities. The lack of significant differences may be attributed to similar structural complexity, environmental conditions, and resource availability between the two habitat types. This has important implications for coastal conservation as it reinforces the ecological value of mangrove restoration in maintaining fish biodiversity.

As restored or natural mangrove forests grow older, their structural complexity and biomass increase (Salmo et al. 2013; Ferreira et al. 2015; Azman Mohd et al. 2021), which provides suitable habitat and food for the recruitment of different organisms (Cannicci et al. 2008; Nagelkerken et al. 2008). Changes in faunal density, biomass, and species composition are expected to change with the age of the mangrove stands (Salmo et al. 2017). We did not observe this trend since the younger stands had the highest fish abundance, species richness, and diverse assemblages. Therefore, our hypothesis that fish abundance and richness would increase as restored and natural mangrove vegetation matured was rejected. Some studies in the Philippines also did not find a correlation between fish abundance and mangrove restoration age (Peralta-Milan & Salmo 2013; Salmo et al. 2018), suggesting that other important factors such as water quality, habitat structure, anthropogenic and natural activities are influencing the fish abundance and age of restored and natural mangroves (Enchelmaier et al. 2020; O'Connell et al. 2021; Kitchingman et al. 2023).

Restored mangrove habitats can support fish assemblages similar to natural mangrove habitats (Lewis & Gilmore 2007; Salmo et al. 2018; Ram et al. 2021). The restored mangroves here had approximately 90% of the fish species found in the natural mangroves, suggesting that mangrove restoration is highly effective at providing similar vegetation structure and fish

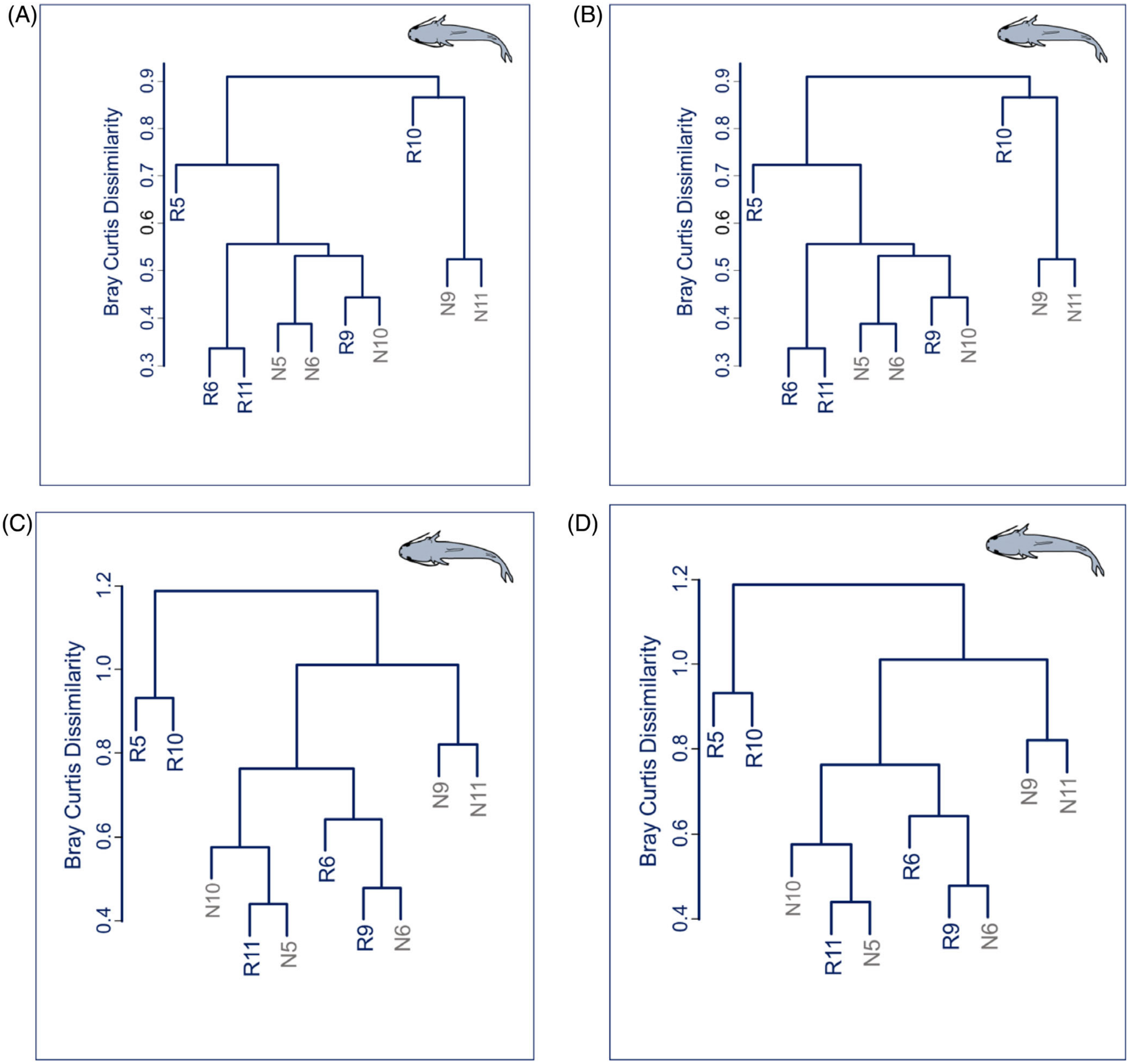

Figure 3. Cluster dendrogram of site dissimilarity of fish species composition between (A) habitats, (B) age, (C) seasons, and (D) diel cycle.

assemblages as natural mangroves. The homogeneity of fish species in natural habitats may be related to a similar structural composition of the mangroves and species-specific environmental adaptation. *Sciades couma* was the most abundant fish species recorded across the restored and natural mangrove habitats—a finding consistent with earlier reports in Guyana from Ram et al. (2021) and Dookram et al. (2017). This estuarine benthophagous species was associated with all mangrove stands, implying that age does not influence its presence. The northern Atlantic mangroves are ideal transitional zones between freshwater and marine environments, which seemingly provide a favorable estuarine habitat for *Sciades couma* (Barletta & Blaber 2007; Dantas et al. 2010).

Many studies have reported higher fish abundance at night than during the day in the intertidal mangrove creeks and estuaries, which seems to be associated with nocturnal foraging behavior (Krumme 2004; Ley & Halliday 2007; Castellanos-Galindo & Krumme 2013; Ramirez-Martínez et al. 2016; Pülmanns et al. 2018). Nocturnal feeding, reduced predation risk, and changes in prey availability may have contributed to the higher fish abundance at night than during the day in our study. Krumme (2004) found that the night assemblages in Northern

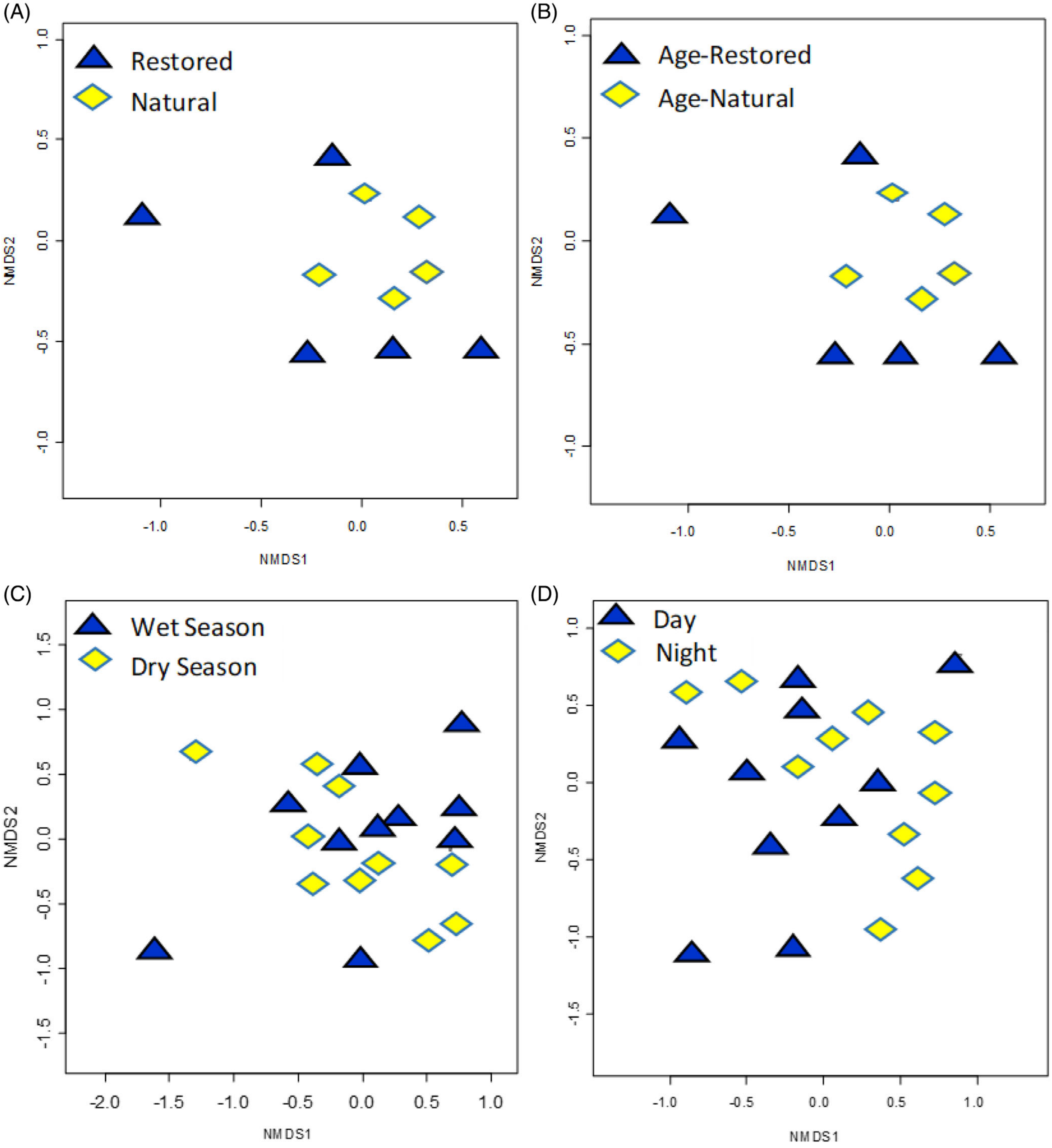

Figure 4. NMDS analysis of fish species composition in restored and natural mangroves: (A) habitat, (B) age, (C) seasons, and (D) diel cycle.

Brazil were dominated by Ariidae and Sciaenidae, and daytime assemblages were more diverse—a finding similar to our study.

Seasonal variations in fish abundance and composition within mangrove ecosystems are common in tropical and subtropical regions (Ikejima et al. 2003; Brenner & Krumme 2007; Barletta et al. 2008; Kamrani et al. 2016). Fluctuations in species richness and abundance between seasons may mirror shifts in the reproductive behaviors of fish and variations in food availability within the estuarine environment (Strydom 2015; Whitfield 2017; Zhou et al. 2019). We also observed seasonal variations in fish abundance and composition between the dry and wet seasons. We recorded higher species richness in the

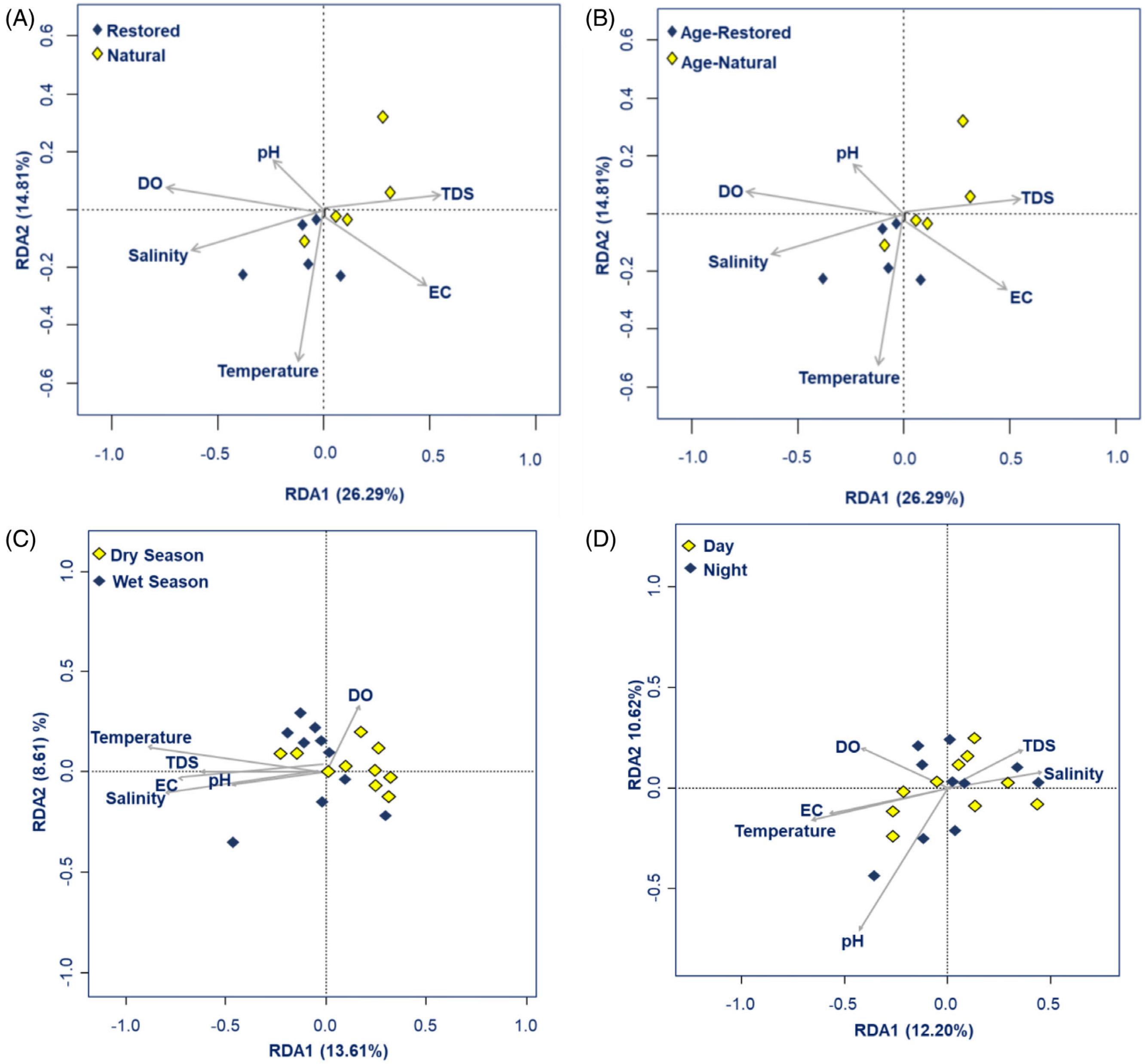

Figure 5. RDABiplot of fish species and their associations with the environmentalvariables in different: (A) habitats, (B) ages, (C) seasons and (D) diel cycle. Percentages inaxes labels refer to the explained proportion of constrained variance.

wet season, which is in line with previous studies by Aheto et al. (2014), Barletta et al. (2003), Ikejima et al. (2003), and Wu et al. (2018). Higher species richness in the wet season can be attributed to increased habitat availability and interconnectivity between freshwater and water areas since the rains facilitate the migration of different fish species to mangrove habitats. Estuarine fishes typically exhibit migratory behavior, moving out of the estuarine system toward adjacent coastal areas in response to shifts in salinity, temperature, and food availability, which vary significantly between seasons (Barletta et al. 2003, 2005; Dantas et al. 2010). We recorded higher fish abundance in the dry season similar to Barletta-Bergan et al. (2002), Giarrizzo and Krumme (2009), Mwandya et al. (2010), and Wu et al. (2018). The higher fish abundance in the dry season may have resulted from the concentration effect, increased prey availability, and seasonal migration.

Changes in fish composition are associated with the physical structure, maturity, and age of mangrove forests (Nagelkerken et al. 2008; Hutchison & Spalding 2014; Kiruba-Sankar et al. 2018). As mangroves mature, their structural complexity increases, which has been found to influence the fish species that inhabit these areas (Blaber 2007; Lewis & Gilmore 2007; Dubuc et al. 2019). Young mangroves examined here had less developed root systems and sparser canopy cover, offering fewer

Table 2. GLMM results for the effects of mangrove habitats, age, seasons, diel cycle, DBH and canopy as predictors of fish species richness and abundance.

Factor	*Estimate*	*SE*	p-*Value*
Species richness			
Habitat	−0.007	0.068	0.27
Age	−0.007	0.068	0.27
Season	−0.001	0.256	0.95
Diel cycle	−0.027	0.220	0.09
DBH	−0.311	0.332	0.44
Canopy	−0.240	0.058	0.05
Fish abundance			
Habitat	−0.001	0.005	0.07
Age	−0.001	0.005	0.71
Season	−0.001	0.006	0.84
Diel cycle	−0.004	0.005	0.42
DBH	0.300	0.242	0.34
Canopy	−0.014	0.025	0.62

sheltered spaces for juvenile fish or species that depend on structural features for protection from predators (Nagelkerken et al. 2000; Blaber 2007; Dubuc et al. 2019). Therefore, long-term monitoring is necessary to track changes in the fish assemblages as mangrove forests mature. By understanding how fish assemblages respond to forest maturation, restoration practitioners can make more informed decisions to enhance the ecological success of future mangrove restoration projects that aim to enhance fisheries.

Our findings reveal a similarity in the composition and structure of fish communities between restored and natural mangrove habitats, age, seasons, and age. Our study suggests that mangrove restoration positively impacts the availability of habitats for fish communities, promoting the recruitment of fish populations. Future research should explore long-term trends and functional connectivity between restored and natural mangroves to assess their ecological equivalency.

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Supporting Information

The following information may be found in the online version of this article:

Table S1: SIMPER analysis (analysis of similarities) in groups outlined by ANOSIM, showing the fish species that most contributed to the observed differences among groups between restored and natural mangrove habitats.

Table S2: SIMPER analysis (analysis of similarities) in groups outlined by ANOSIM, showing the fish species that most contributed to the observed differences among groups between ages of restored and natural mangrove habitats.

Table S3: SIMPER analysis (analysis of similarities) in groups outlined by ANOSIM, showing the fish species that most contributed to the observed differences among groups between wet and dry season.

Table S4: SIMPER analysis (analysis of similarities) in groups outlined by ANOSIM, showing the fish species that most contributed to the observed differences among groups between day and night.

Table S5: NMDS stress values for fish community ordination across different factors.

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