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RESEARCH ARTICLE

Tracking the long-term vegetation and soil characteristics of restored mangroves: a case study from Guyana's coast

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The global urgency to halt and reverse mangrove loss has led to the implementation of numerous initiatives to protect and restore mangroves and recover critical ecological functions and services. Restoration success is assessed by estimating mangrove survival, while diversity, vegetation structure, and soil characteristics are often overlooked with no long-term monitoring. Here, we investigated long-term changes in vegetation and soil characteristics of *Avicennia germinans*-dominated stands planted along Guyana's coast between 5 and 11 years old. A chronosequence approach was used to examine changes in vegetation and soil parameters in restored mangrove stands of different ages compared to natural stands of the same ages. Tree height, diameter, and aboveground biomass were inconsistent between restored and natural mangrove stands. Redundancy analysis (RDA) revealed that the soil properties were the important factors influencing both the restored and natural mangrove communities. There were no clear trajectories between the vegetation and soil characteristics with age, possibly due to site-specific and hydrodynamic environmental factors, such as tidal dynamics, riverine inputs, and climatic variations. While there were some equivalent vegetation and soil characteristics at the end of the first decade after restoration, the restored mangroves may require a longer timespan (approximately 25 years) than the period overserved in our study to be entirely identical to the natural mangroves. This case study from Guyana provides valuable insights into the ecological processes driving mangrove recovery dynamics, growth patterns, and restoration effectiveness and offers reliable data needed to inform future restoration projects.

Key words: chronosequence, indicators, mangrove forests, soil properties, trajectory

Implications for Practice

- Examining vegetative and soil characteristics allows restoration practitioners to evaluate how restored areas recover over time.
- Restored mangroves can achieve similar vegetation and soil characteristics to natural mangroves but may require longer timescales than natural mangroves of the same age.
- Understanding restored mangrove growth patterns can significantly improve the design and success of future restoration projects.

Introduction

Due to widespread mangrove degradation and increased awareness of harmful environmental and societal concerns, mangrove restoration is now highly prioritized by conservation organizations and Governments (Duncan et al. 2016; Ilman et al. 2016; Worthington & Spalding 2018). This has led to the implementation of many restoration projects to reestablish degraded mangrove ecosystem services and recover biodiversity (Bosire et al. 2006; Datta & Deb 2012; Worthington & Spalding 2018). Ecological restoration of degraded mangroves is a commonly used method for recovering coastal wetlands and associated ecosystem services (Lewis 2005; Ellison et al. 2020; Liu & Ma 2024). Ecological restoration aims to restore the integrity of ecological systems by enhancing ecosystem health, biodiversity, and ecosystem services while promoting sustainable interactions between humans and the environment (SER 2004). Many mangrove restoration goals and ambitious pledges have been made in line with the 2021–2030 United Nations Decade on Ecosystem Restoration (UNDER), a global campaign enacted to halt this destruction and accelerate global restoration efforts (Waltham et al. 2020).

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The Global Mangrove Alliance has also set an ambitious goal to restore half (4092 km^2) of the total restorable mangroves (8183 km^2) by 2030 (Leal & Spalding 2022). However, increasing investment in restoration requires evidence of the effectiveness of past restoration projects (Suding 2011; Ntshotsho et al. 2015; Friberg et al. 2016).

Mangrove restoration is usually conducted along coastal fringes, which are characterized by low nutrient availability as well as many stresses, including inundation, high salinity water, erosion, wind, sand, waves, and storms (Primavera & Esteban 2008; Samson & Rollon 2008; Kamali & Hashim 2011). The concentrations of organic carbon (OC), macronutrients, nitrogen, and available phosphorus and microbial enzymes' activity are essential factors influencing the growth and development of mangrove forests (Reef et al. 2010; Chowdhury et al. 2019*a*, 2019*b*; Alongi 2021). Although there is an understanding of the relationship between vegetation and soil in natural mangrove forest areas (Gleason et al. 2003; Salmo et al. 2013; Peters et al. 2020; Ahmed et al. 2023), studies examining if the same relationship exists between growth in restored mangrove forests and soil characteristics remain limited (Salmo et al. 2013). Changes in soil conditions, such as salinity or sediment composition alterations, can impact the health and resilience of mangrove ecosystems (Salmo et al. 2013; Chowdhury et al. 2019*a*, 2019*b*; Ahmed et al. 2022). Effective conservation and restoration strategies must consider the intricate relationship between mangrove plants and the soil environment (Ellison 2000; Holguin et al. 2001; Salmo et al. 2013).

Some researchers suggest that restored mangroves might achieve biomass, stand structure, and productivity levels of natural forests in 20–55 years after restoration (Salmo et al. 2013; Osland et al. 2020; Azman et al. 2021). The supporting empirical data for such assertions, however, remain limited. A critical factor in determining the success of mangrove planting initiatives is the rate and time for restored stands to achieve similar forest structure, biomass, and soil characteristics of natural mangroves (Ellison 2000; Salmo et al. 2013; Lewis et al. 2019).

Despite the surge of mangrove restoration projects, long-term monitoring to assess the successful or unsuccessful outcomes of these programs is rarely conducted (Ellison 2000; Biswas et al. 2009; Worthington & Spalding 2018). Evaluating the success of restoration projects is extremely challenging since using one metric over another can result in different outcomes (Block et al. 2001; Suding 2011; Baldera et al. 2018). This has important consequences for management decisions, stakeholder actions, and decision-makers regarding restoration projects. In the marine environment, most studies focus on rudimentary performance metrics, such as the survival rate of the individuals restored (Baggett et al. 2015; Bayraktarov et al. 2016; Cadier et al. 2020). Monitoring seedling survival rate is a short-term approach to assessing restoration success as it indicates planting method success, not ecosystem recovery (Hagen & Evju 2013; Wortley et al. 2013; Méndez-Toribio et al. 2021). Therefore, long-term monitoring of the restored mangrove growth trajectories and ecosystem functions, such as nutrient availability and cycling, are better ecological indicators of restoration success.

Limited evidence demonstrates how closely restored areas mimic naturally regenerated mangroves' growth rate and structure (Duke et al. 2007; Ram et al. 2021; Su et al. 2021). The influence of mangrove age on structure and function has been disregarded and poorly described (Azman et al. 2021). Soil physiochemical characteristics and nutrient status have also been overlooked, even though they are important indicators of mangrove growth and development (Barnuevo & Asaeda 2018). Though these details are crucial to advance our understanding of how mangrove forests change over time by monitoring vegetation structure, tree diversity, and biomass of different stand ages, this long-term monitoring is absent from many restoration programs, for example, the Guyana Mangrove Restoration Program (GMRP) (Azman et al. 2021).

In Guyana, there has been no long-term assessment of restored mangrove areas, even though the country has been funding this work since 2010, spending approximately 4,469,878 USD on restoration projects (Global Climate Change Alliance Plus (GCCA +) 2018). Monitoring has been short-term and focused on a few parameters, including site elevation, sediment salinity, seedling height, diameter, percent cover, and photos from permanent points (NAREI 2014). Most of the mangrove monitoring activities have been restricted to the planted areas with no comparison to reference sites, and there has been no attempt to evaluate the long-term success of these replanted sites. Furthermore, most studies that have compared results to replanted forest patches, do not provide an estimate of recovery over time (Salmo et al. 2013; Azman et al. 2021, 2023). Therefore, the degree of mangrove forest structure change with stand age remains unclear post-restoration.

Here, we assessed the forest structure and soil characteristics of restored mangroves of different ages (restored system) to estimate the time over which planted mangroves approach similar characteristics to that of natural mangrove forests (reference system) in Guyana. Evaluating the changes in restored mangrove vegetation and soil over time provides a better understanding of mangrove restoration evolution and serves as possible indicator parameters for evaluating the progress or success of mangrove restoration programs. Understanding the time required for restored mangroves to attain comparable structure and biomass as natural mangroves is useful for managers responsible for approving, funding, and designing mangrove restoration projects and achieving multiple ecosystem service outcomes.

Methods

Study Area

This study was conducted along Guyana's Atlantic coast, which forms a part of the North Brazil Shelf. The country has a tropical climate dominated by north-easterly trade winds with periods between 8 and 10 seconds and heights between 1 and 1.7 m (Winterwerp et al. 2020). Approximately 90% of Guyana's population lives along its low coastal plain, concentrated between the Essequibo and Berbice Rivers (Government of Guyana 2012). Earthen dams and concrete seawalls have been engineered along most of the coast to protect this area from storm surges and rising sea levels (Winterwerp et al. 2020).

Guyana's coast forms part of a 1600 km-long muddy coastal system dominated by massive mud banks that migrate from the mouth of the Amazon River to that of the Orinoco (Venezuela) within a unique geological system (Anthony et al. 2010). The morphodynamics of Guyana's coast hinges on pulses of mud abundance or relative scarcity embedded in multi-year cycles of mud bank activity and inter-bank phases (Anthony et al. 2010). Over time, the rhythmic nature of these alternating phases leads to rapid shoreline accretion, erosion, and major ecological changes involving the development and destruction of mangrove forests (Anthony et al. 2014). Guyana's coastal system is characterized by a semi-diurnal tide with a 1–3 m range at neap and spring tide, respectively (Anthony et al. 2014). The coastal fringe of Guyana has a mangrove forest community dominated by Black mangroves (*Avicennia germinans*), Red mangroves (*Rhizophora mangle*), White mangroves (*Laguncularia racemosa*), and Buttonwood (*Conocarpus erecta*) (Toorman et al. 2018; Ram et al. 2021).

In 2010, Guyana's government initiated the GMRP with funding from the European Union under the (GCCA+ 2018) scheme (Landell Mills Limited 2013). GMRP was implemented to increase mangrove forest cover, reestablish ecosystem services, increase coastal protection, and provide sustainable livelihood opportunities for coastal communities while mitigating climate change (Landell Mills Limited 2013). The GMRP was vital to protect the country's coast, which is 1–3 m below sea level at high tide. That project planted over 500,000 mangrove *A. germinans* seedlings at 19 locations along 8 km of Guyana's coast. A total of 17 areas were replanted between 2010 and 2013 under the European Union funding scheme, which ended in 2014. NAREI continues to advance active and passive mangrove restoration in Guyana. The survival rates were low initially, leading to a revision of the method used for restoration and greater success (Fig. 1) (Landell Mills Limited 2013).

Study Design

This study employed a chronosequence design of the current restored mangroves in Guyana of different ages, creating a space-for-time (SFT) chronosequence of restored mangrove vegetation and soil trajectories. The restored site (restored system) data were compared to natural mangroves (reference system). The SFT substitution approach infers temporal trends of diverse stand ages to create trajectory patterns for the restored ecosystem (Pickett 1989). The type of disturbance, initial colonization conditions, the longevity of pioneer species, the establishment of dominant species, and random processes can affect the temporal relationship between young and old sites, and nullify the prospects of using chronosequence here (Walker & del Moral 2003; Boyes et al. 2011; Chazdon 2017). As such, restoration programs using the chronosequence method may incorrectly infer the processes that cause vegetation change and imperial restoration efforts (Walker & del Moral 2003). In this study, those limitations were overcome by selecting sites of dissimilar ages, convergent successional trajectories, rapid species turnover, and low disturbance frequency.

Determination of Stand Age

In this study, 10 sites were selected via a stratified random approach, made up of five natural and restored mangrove forests. Natural mangroves are mangrove forests that have naturally colonized migrating mudflats or recolonized disturbed areas, while restored stands are monocultures of Black mangroves (*A. germinans*) planted between 2010 and 2018. Restored mangrove sample plots were classified into five different stand ages based on the date of planting: 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 as the restored mangroves. These sites were verified using satellite imagery to estimate the natural growth of mangrove forests from 5, 6, 9, 10, to 11 years ago.

Plant Measurements

Field data were collected between September to November 2022. Permanent circular plots (radius = 10 m) were established via stratified sampling with varying distances from the shoreline ($n = 3$ per site) (Kauffman & Donato 2012). For 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 (Kauffman & Donato 2012). Following the classification of Kauffman and Donato (2012), trees (>5 cm DBH) were measured in 10-m radius circular plots, saplings (<5 to 1.5 cm DBH and height >1.36 m) in a smaller 3 m circular subplot nested within the larger 10-m plot and seedlings (≤1.5 cm DBH) were also measured within a 2 m radius subplot. The tree height was determined using a Nikon Forestry Pro II Laser Rangefinder. The most important species were determined using the importance value index (IVI), which was calculated by adding the relative density, relative dominance, and relative frequency equation. The aboveground biomass (AGB) of all trees was calculated using species-specific allometric equations: *A. germinans* ($B = 0.14D2.4$), *L. racemosa* ($B = 1.03.3D2.5$), and *R. mangle* ($B = 0.1282D2.6$) (Fromard et al. 1998).

Soil Analysis

Triplicate soil samples were collected in each plot at low tide for physicochemical and nutrient analysis. Samples were collected from the core at 0–10, 10–20, 20–30, 30–40, and 40–50 cm depth with a polyvinyl chloride soil corer. The soil salinity/electrical conductivity (EC) were measured with a Fdit EC-3185 Soil Tester Kit. The pH and temperature were measured using an Aqua-pH Waterproof meter. Soil samples collected were analyzed at the NAREI laboratory for total nitrogen (N) and available phosphorus (P) contents using the Walkley Black method (Walkley & Black 1934), the digestion method (Sommers & Nelson, 1972), and the Bray method (Bray &

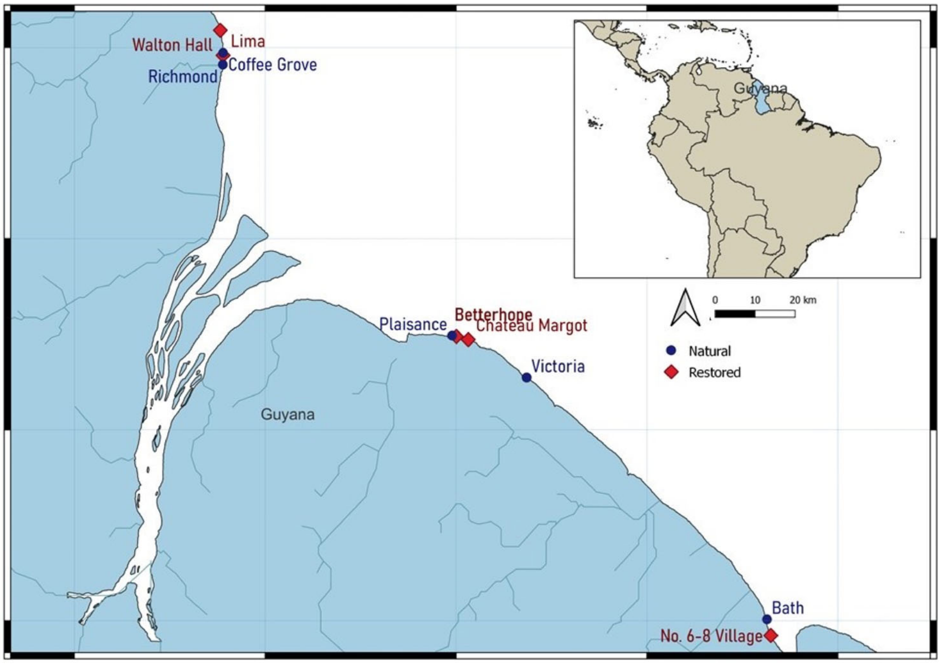

Figure 1. Location of study sites (blue circles are natural areas where mangrove forests have naturally colonized migrating mudflats or recolonized disturbed areas and red diamonds are restored areas replanted by the GMRP-NAREI).

Kurtz, 1945), respectively. A GBC 9000 model flame atomic absorption spectrophotometer was used to test the concentration of magnesium (Mg), potassium (K), sodium (Na), copper (Cu), manganese (Mn), iron (Fe), and zinc (Zn).

Statistical Analyses

Stand attributes were calculated as the mean and standard deviation. Shapiro–Wilk tests with the base function of the Rstudio shapiro.test was done to determine if our data was normally distributed. Even after the log 10 transformation, our vegetation data did not follow a normal distribution, requiring nonparametric tests ($p < 0.001$). A Levene's test was done using the levene. test function in Rstudio to assess the equality of variance between the restored and natural mangrove abundance and age ($p < 0.05$). A Wilcoxon test using the function wilcox.test was run in R Studio to compare the abundance between restored and natural mangroves. A nonparametric Kruskal–Wallis was used to examine the individual effects of age, treatment, and species and their interactions on the height, diameter, and AGB variables. The Kruskal–Wallis test with Dunn's post hoc analysis was done in RStudio using the kruskal.test and dunn.test functions, and results were considered significant if the p-value was less than an alpha level of 0.05. A general linear mixed model (GLMM) with Poisson regression was used to investigate the fixed and random factors impacting the mangrove species abundance in the restored and natural mangroves. Abundance was used as the response variable, while the "Age," "Forest Type," "Species," and "Location" were used as the predictors. Different variable transformations, distributions, and links were tested. Selection criteria for the GLMM included conditional Akaike Infromation Criterion, log-likelihood scores, and overdispersion ratios. The model was built using the "glmm" package in RStudio (Knudson et al. 2018). Redundancy analysis (RDA) was used to assess the relationship between mangrove abundance and different soil parameters. The soil characteristics 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 Analysis of Variance based on 999 permutations of residuals.

Results

Species Composition and Abundance

Three mangrove species (*Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*) were recorded at the restored and natural mangrove stands. *Avicennia germinans* was the most dominant species at all stands, except the 5-year-old restored stand where *L. racemosa* was more abundant. *Avicennia germinans* and *L. racemosa* were 84.2 and 11.6% more abundant in the restored mangroves than in the natural stands. *Rhizophora mangle* had a 52.1% higher abundance in natural mangroves than in restored mangroves. The restored stands were 50.1% more abundant than the natural stands, but there were no significant differences ($p > 0.05$) between the age and abundance of restored and natural mangroves (Table 1). The 6-year-old restored and 6-year-old natural stands had the highest

Table 1. Structural composition of restored and natural mangroves, where R5 (5 years old), R6 (6 years old), R9 (9 years old), R10 (10 years old), and R11 (11 years old) are restored mangroves, and N5 (5 years old), N6 (6 years old), N9 (9 years old), N10 (10 years old), and N11 (11 years old) are natural mangroves.

Mangrove forest type	*Mangrove species*	*Density (n/ha)*	*Basal area (m^2/ha)*	*Relative density (%)*	*Relative frequency (%)*	*Relative dominance (%)*	*Importance value (IV)*
R5	*Avicennia germinans*	28	10.98	20.74	0.21	0.46	31.93
	Laguncularia racemosa	99	12.97	73.33	0.73	0.54	87.04
	Rhizophora mangle	8	—	5.93	0.06	—	—
R6	*Avicennia germinans*	355	90.19	96.99	0.97	0.87	188.15
	Laguncularia racemosa	10	0.04	2.73	0.03	0.00	2.80
	Rhizophora mangle	1	—	0.27	0.00	—	—
R9	*Avicennia germinans*	63	27.25	82.89	0.83	0.96	110.97
	Laguncularia racemosa	11	—	14.47	0.14	—	
	Rhizophora mangle	2	1.24	2.63	0.03	0.05	3.90
R10	*Avicennia germinans*	89	36.99	91.75	0.92	0.98	129.66
	Laguncularia racemosa	2	0.62	2.06	0.02	0.02	2.71
	Rhizophora mangle	6	—	6.19	0.06	—	—
R11	*Avicennia germinans*	221	51.57	99.55	1.00	0.99	152.12
	Laguncularia racemosa	1	0.57	0.45	0.00	0.01	1.02
N5	*Avicennia germinans*	26	43.58	78.79	0.79	0.89	123.16
	Laguncularia racemosa	5	0.28	15.15	0.15	0.01	15.59
	Rhizophora mangle	2	—	6.06	0.06	—	—
N6	*Avicennia germinans*	82	55.32	97.56	1.00	1.00	153.88
N9	*Avicennia germinans*	41	18.73	42.71	0.43	0.61	61.86
	Laguncularia racemosa	52	0.21	54.17	0.54	0.01	54.92
	Rhizophora mangle	3	0.04	3.13	0.03	0.00	3.19
N10	*Avicennia germinans*	92	71.49	97.87	0.98	0.97	170.34
	Laguncularia racemosa	2	1.87	2.13	0.02	0.03	4.02
N11	*Avicennia germinans*	66	26.77	50.38	0.50	0.64	77.66
	Laguncularia racemosa	48	11.62	36.64	0.37	0.28	48.63
	Rhizophora mangle	17	3.72	12.98	0.13	0.09	16.83

mangrove abundance (Table 1). The seedling abundance was significantly ($p < 0.001$) higher in the restored mangroves (525 seedlings) compared to the natural mangroves (115 seedlings) (Table S1). The 6-year-old restored mangroves had the highest seedling abundance (253 seedlings), followed by the 11-year-old (177 seedlings) and 5-year-old stands (47 seedlings) (Table S1). The 9-year-old natural mangroves had the highest seedlings abundance (65 seedlings), followed by the 10-year-old (32 seedlings) and 5-year-old stands (11 seedlings) (Table S1). The sapling abundance was not significantly greater ($p > 0.05$) in the natural mangroves (100 saplings) compared to the restored mangroves (70 saplings) (Table S1). The 11-year-old natural mangroves had the highest sapling abundance ($n = 82$), followed by the 9-year-old ($n = 16$) and 5-year-old stands ($n = 2$) (Table S1).

GLMMs revealed that age influenced the restored mangrove's abundance (Est = −5.04; $p > 0.05$), leading to a species-specific decline, with *R. mangle* having the highest decline (Est = −147; $p < 0.05$). A similar trend was observed with the natural mangroves (Est = 27.05, $p > 0.05$), but the decline rate was lower than in the restored mangroves. However, age was not a significant ($p > 0.05$) predictor of mangrove species abundance in the restored and natural mangrove stands.

The restored mangroves had a 50.1% higher density than the natural mangroves, with the 6-year-old restored stand being the densest. The total basal area was slightly higher for the restored mangroves than the natural mangroves, with the 6-year-old stand having the highest (90.23 m^2/ha) (Table 1). *Avicennia germinans* had the highest relative density, relative frequency, relative dominance, and importance at all stands except for the 5-year-old restored stand, where *L. racemosa was* denser, more frequent, dominant, and important (Table 1).

Growth Patterns

The average height of the mangroves in natural stands (12.52 ± 0.65 m) was greater than at the restored stands (11.00 ± 0.78 m) by 13.81% (Fig. 2). The average height of the restored mangroves ranged between 10.10 and 13.57 m while it was 10.9–14.70 m in the natural stands. The 11-year-old mangroves were the tallest in the restored strands, while the 9-year-old mangroves were the tallest in the natural stands. There was a significant difference ($p < 0.01$) between tree age and height, but no significant difference ($p > 0.05$) between the height of restored and natural mangroves.

The average DBH in the natural mangrove stands (15.50 ± 1.80 cm) was greater than in the restored stands (12.90 ± 1.27 cm) by 20.16% (Fig. 3). The average DBH ranged between 9.10 and 16.50 cm in the restored stand and 12.20 and 18.60 cm in the natural stands. The 9-year-old mangroves had the highest DBH for the restored stands, while the 6-year-old mangroves had the highest DBH for the natural stands. There was a significant difference ($p < 0.01$) between tree age and diameter, and between the diameter of restored and natural mangroves ($p < 0.01$).

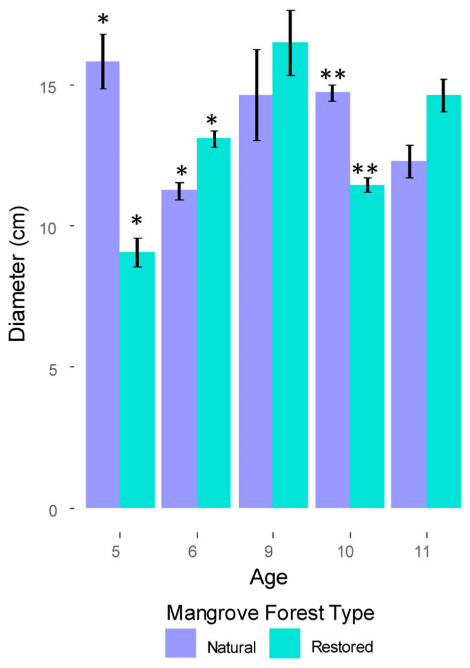

Figure 2. Tree height of restored and natural mangroves of different ages. The error bars indicate ± SD. *$p < 0.05$, **$p < 0.01$.

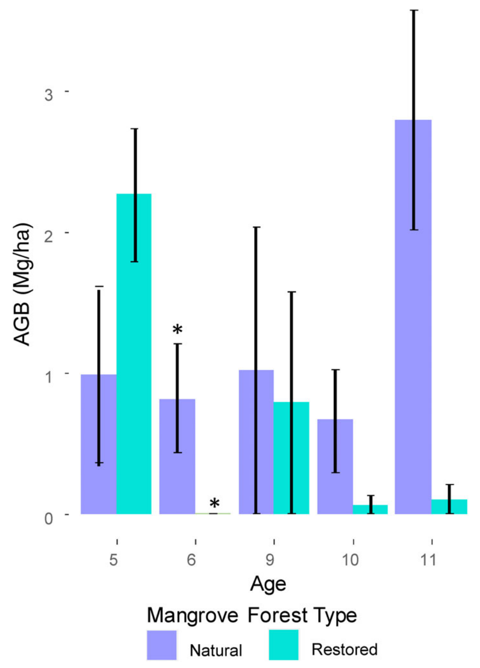

Figure 4. Aboveground biomass of restored and natural mangroves of different ages. The error bars indicate ± SD. *$p < 0.05$.

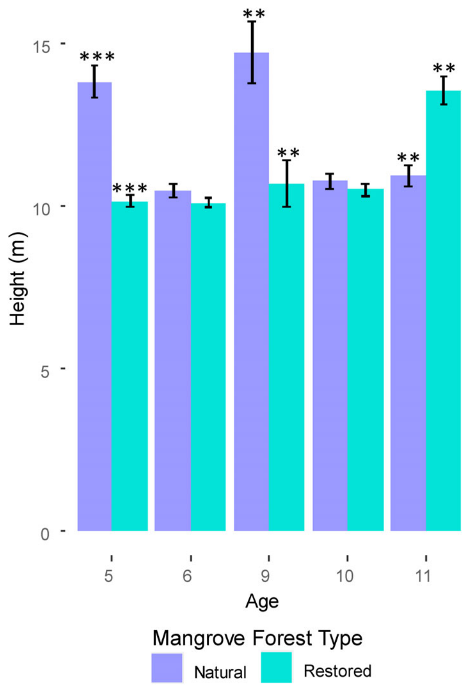

Figure 3. Tree diameter of restored and natural mangroves of different ages. The error bars indicate ± SD. **$p < 0.01$, ***$p < 0.001$.

The average AGB was greater in the natural mangrove stands (1.25 Mg/ha) than in the restored stands (0.52 Mg/ha) by 140.38% (Fig. 4). The average AGB of the restored mangroves ranged between 0.01 and 2.91 and 0.82–7.80 Mg/ha in the natural stands. The 9-year-old mangroves had the highest AGB for restored stands, while the 11-year-old natural mangroves had the highest for the natural stands. There was a significant difference ($p < 0.01$) between tree age and AGB, but no significant difference ($p > 0.05$) between the AGB of restored and natural mangroves.

Table 2. Soil physicochemical parameters from restored and natural mangroves of different ages (mean ± standard deviation) ($n = 3$).

Mangrove forest type	*EC (mS/cm)*	*pH*	*Organic carbon (%)*
R5	9.03 ± 3.32	7.02 ± 0.21	4.78 ± 0.00
R6	28.30 ± 2.06	7.08 ± 0.04	5.18 ± 0.22
R9	17.49 ± 0.80	7.13 ± 0.45	4.78 ± 0.00
R10	15.23 ± 1.94	7.47 ± 0.32	4.86 ± 0.00
R11	22.80 ± 5.21	7.60 ± 0.09	4.78 ± 0.18
N5	6.64 ± 1.69	7.46 ± 1.60	7.46 ± 0.09
N6	33.36 ± 1.60	7.22 ± 3.98	7.22 ± 0.33
N9	15.58 ± 3.98	7.50 ± 1.62	5.50 ± 3.02
N10	12.99 ± 1.90	6.49 ± 0.61	5.18 ± 0.28
N11	2.35 ± 1.70	6.45 ± 0.64	4.38 ± 0.00

Soil Physicochemical Characteristics

The soil pH ranged between 6.4 and 7.6 (Table 2). The restored mangrove soil pH was higher than the natural mangrove soils. The 11-year-old restored mangroves had the highest pH (7.6),

Table 3. Soil nutrient content in the restored and natural mangroves of different ages (mean ± standard deviation) ($n = 3$).

Mangrove forest type	P (mg/kg)	Concentration (mg/kg)				N (mg/L)	Base sat (%)	Conc. ppm		
		Mg	K	Na	Ca		Cu	Mn	Fe	Zn
R5	1.36 ± 0.12	7232.52 ± 609.70	6708.00 ± 609.67	8272.00 ± 628.37	972.80 ± 44.35	2499.45 ± 264.73	0.02 ± 0.05	4.68 ± 0.95	2.43 ± 0.41	0.92 ± 0.42
R6	2.11 ± 0.21	4420.00 ± 118.46	9336.00 ± 270.34	8352.00 ± 2369.38	1034.42 ± 27.49	2162.31 ± 174.73	1.87 ± 0.03	8.12 ± 1.33	1.04 ± 0.09	0.83 ± 0.18
R9	0.85 ± 0.10	6434.20 ± 45.65	6668.00 ± 129.65	8418.00 ± 482.29	1071.07 ± 65.75	1995.06 ± 102.27	0.05 ± 0.01	3.61 ± 1.11	4.94 ± 0.89	3.34 ± 0.97
R10	1.91 ± 0.18	5317.16 ± 97.32	6889.60 ± 461.21	8030.00 ± 552.74	901.09 ± 552.74	2179.44 ± 190.05	0.06 ± 0.01	3.48 ± 1.82	7.07 ± 0.71	2.36 ± 0.54
R11	3.42 ± 0.070	4630.00 ± 130.73	10,152.00 ± 849.93	8094.00 ± 289.39	1016.70 ± 222.30	2277.11 ± 180.19	1.94 ± 0.01	2.59 ± 0.79	0.95 ± 0.05	0.75 ± 0.26
N5	0.76 ± 0.13	2492.98 ± 593.13	727.87 ± 80.06	527.10 ± 132.89	20,325.00 ± 132.89	11,900.00 ± 3286.73	0.02 ± 0.01	0.32 ± 0.05	0.06 ± 0.01	0.14 ± 0.04
N6	0.66 ± 0.18	3651.60 ± 610.51	1763.33 ± 261.83	2032.47 ± 331.09	5024.16 ± 331.09	11,671.67 ± 4907.38	0.07 ± 0.07	0.33 ± 0.10	0.09 ± 0.04	0.14 ± 0.05
N9	0.73 ± 0.37	2990.76 ± 272.30	1445.67 ± 1336.76	962.00 ± 219.45	4920.82 ± 219.45	17,550.00 ± 4812.07	0.08 ± 0.03	0.16 ± 0.05	0.10 ± 0.05	0.13 ± 0.03
N10	1.43 ± 0.33	5567.80 ± 123.00	6512.00 ± 156.44	8580.00 ± 468.92	903.37 ± 67.25	1983.77 ± 160.42	0.09 ± 0.01	6.10 ± 2.23	6.47 ± 0.32	1.69 ± 1.28
N11	1.85 ± 0.57	4868.00 ± 792.55	9218.00 ± 377.25	7028.00 ± 387.65	840.68 ± 71.49	1966.04 ± 204.08	1.96 ± 0.01	2.81 ± 0.88	1.02 ± 0.17	0.14 ± 0.25

while the 5-year-old natural mangroves had the highest pH (7.4). The soil EC ranged between 2.35 and 33.60 S/cm (Table 2). The restored mangrove soil EC was higher than the natural mangrove soils. The 6-year-old restored mangroves had the highest EC (28.30 mS/cm), while the 6-year-old natural mangroves had the highest EC (33.60 mS/cm). The OC ranged between 4.38 and 7.46% (Table 3). The restored mangrove soil OC was higher than the natural mangrove soil. The 6-year-old restored mangroves had the highest OC (5.18%), while the 5-year-old natural mangroves had the highest OC (7.46%) (Table 2).

Soil Nutrient Status

The nutrient concentrations vary across restored and natural mangroves, with inconsistent patterns. The restored mangroves had higher concentrations of P, K, Na, and Zn, while the natural mangroves had higher concentrations of Ca, except for the 11-year-old stand (Table 3). The younger restored mangrove stands (R5 and R6) had higher levels of Mg, K, Na, Ca, N, and Mn than the older stands, which had higher levels of Cu, Fe, Zn, and P (Table 3). In contrast, the older mangrove natural stands (N10 and N11) had higher levels of Mg, K, Na, N, Cu, Mn, Fe, and Zn than the younger stands (N5 and N6), which had higher levels of P and Ca (Table 3). Most soil nutrients from the restored and natural mangroves did not increase with age and were inconsistent across different stands, except for Cu in the natural mangrove stands.

The RDA revealed that K, P, pH, EC, and OC are soil parameters that positively correlate with the abundance of *A. germinans*, while N and Mg negatively correlate with the abundance of *L. racemosa* (Fig. 5). There was no correlation between the soil parameters and *R. mangle*. The cumulative percentage variance of the vegetation occurrence data explained by the first four axes of the RDA was 37%. The cumulative percentage variance of the mangrove–environment relationship on the first axis was 91.75%, whereas that on the second axis was 6.5%: the first and second axes explained 96.75% of the relationship between the mangroves and the environment, indicating that the vegetation and environment axes were highly correlated. The sampling sites clustered into four groups in the ordination, suggesting that stand ages in the same group share some similar characteristics. The first group comprises the 6-year-old restored and 11-year-old natural sites, the second group is 9-year-old restored and natural sites, the third group is the 5- and 6-year-old restored sites, and the 5- and 10-year-old natural sites and the fourth group consists of the 10 and 11 years old restored sites.

Discussion

Wetland restoration and creation often aim to replace ecosystem functions and services lost during degradation (Osland et al. 2012). Many wetland restoration and creation efforts are implemented under the assumption that once an area has been restored, it will develop along a predictable trajectory and become equivalent to a natural wetland at some point in the

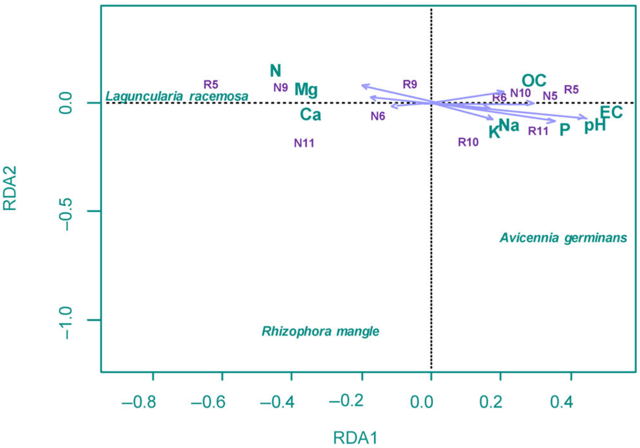

Figure 5. RDA plot of soil and vegetation patterns in restored and natural mangroves. Where R5 (5 years old), R6 (6 years old), R9 (9 years old), R10 (10 years old), and R11 (11 years old) restored mangroves, and N5 (5 years old), N6 (6 years old), N9 (9 years old), N10 (10 years old), and N11 (11 years old) natural mangroves. Arrows represent traits while its length is based on the contribution of each trait to separate the accessions. Nitrogen (N), organic carbon (OC), electrical conductivity (EC), power of hydrogen (Ph), calcium (Ca), magnesium (Mg), sodium (Na), potassium (K), and phosphorous (P).

future, thereby providing equivalent ecosystem functions or services (Choi 2004; Osland et al. 2012; Craft 2022). However, many of these efforts do not follow this predicted trajectory, which was the case in this study as well (Hossler et al. 2011; Suding 2011; Osland et al. 2012). While hydrological processes can be restored rapidly with proper design (e.g. within 1 year), soil-dependent properties and processes often require much more time (e.g. decades or centuries) to resemble natural or intact mangrove forest areas (Lewis 2005; Craft et al. 2003; Ballantine & Schneider 2009; Hossler & Bouchard 2010; Craft 2022). Unfortunately, a disproportionate number of studies exist on the rate and trajectory of wetlands ecosystem development post-restoration, even though these data are crucial for informing future restoration projects and practices, which are becoming common in coastal areas.

Once established, monospecific restored mangrove plantations undergo rapid growth and succession during early development, which is then followed by the recruitment of other species and convergence into natural forests (Proffitt & Devlin 2005; Bosire et al. 2008; Samson & Rollon 2008; Salmo et al. 2013). We observed a similar trend here, where restored stands started as *Avicennia germinans* monoculture plantations and were later colonized by *Laguncularia racemosa* and *Rhizophora mangle*. This trend indicates that the environment was conducive for new species, and the restored stand appears to be converging toward a natural mangrove stand. We observed low species richness, which was expected since only four mangrove species are adapted to the unstable substrates, mud bank movement, and variable salinities in the South American region (Fromard et al. 2004; Toorman et al. 2018; Ram et al. 2021). *Laguncularia racemosa*, a fast-growing pioneer species, is often replaced by *A. germinans*, which dominates the South American coast (Fromard et al. 2004). Multi-species mangrove stands can lead to wider niche differentiation than monocultures and increased total resource use, which provides multiple trophic pathways to sustain richer faunal communities (Bosire et al. 2006). *Avicennia germinans* was the most dominant species, probably because it is well adapted to the saline conditions experienced along the Central and South American coasts (Fromard et al. 1998; Nettel & Dodd 2007; Ram et al. 2021), and because of their ability to be one of the first species to colonize newly formed mudflat areas (Toorman et al. 2018; Triest et al. 2021; Aye et al. 2023). While there were a few *R. mangle* seedlings, no trees were present at the restored stands, possibly due to the saline conditions, different tidal inundation, low freshwater influence, and unfavorable topography (Duke & Allen 2006; Djamaluddin et al. 2023).

Restored mangrove seedling survival rate is a crucial factor influencing tree abundance in coastal ecosystems (Minchinton 2001; Bosire et al. 2008; Lewis 2005). In our study, the restored mangrove stands had a higher tree density than the natural mangrove stands. The higher restored mangrove density is likely due to more planted mangroves and favorable hydrological conditions for mangrove colonization and growth. We observed a similar restored mangrove tree density pattern to Azman et al. (2021) and Fromard et al. (1998), where these authors reported higher densities from younger, pioneer-stage mangrove stands than mature stands. However, in our study, the older natural stands had higher tree density than the younger pioneering stages (seedlings and saplings), indicative of a low regeneration potential. This finding conflicts with Goessens et al. (2014) and Khan et al. (2013), where these authors reported that tree density decreased with age in natural mangrove stands. The 6-year-old restored stand had the highest mangrove abundance, possibly due to higher survival rates and seedling abundance. The density of adult restored and natural mangrove trees was still increasing after the first decade of the chronosequence, indicating that these mangrove forests are not yet fully developed. As individual trees mature, the mangrove forest begins to self-thin, and adult tree densities usually decline (Bosire et al. 2008; Salmo et al. 2013; Azman et al. 2021).

Restored mangrove tree height, size, and density may require several decades, much longer than examined here, to be equivalent to natural mangroves (Proffitt & Devlin 2005). The natural mangroves at our sites were taller than the restored mangroves, except for the 11-year-old stand. Several factors may have contributed to this pattern, such as favorable environmental conditions and higher levels of essential nutrients such as Ca, Mg, N, P, K, and Na in this restored site than in the 11-year-old natural stand (Reef et al. 2010; Lovelock et al. 2014; Romero-Mujalli & Melendez 2023). The 9-year-old natural mangrove stand was the tallest, potentially due to higher observed Ca and N levels promoting increased plant growth. Our findings contradict those of Azman et al. (2021) and Ferreira et al. (2015), who found that the intact/natural forest stands were shorter than the younger planted mangroves in their studies. The dominance of the species restored (*Rhizophora* sp.) in those studies compared to the species restored in our study (*Avicennia* sp.) may have accounted for the difference in growth rates. Our findings are consistent with Dookie et al. (2022), who reported that the restored mangrove ecosystem had taller trees than natural and degraded ecosystems in Guyana. The younger restored mangroves had homogenous tree height and density, common in young tree plantations where planted seedlings are not yet exposed to strong competition (Niklas et al. 2003).

Mangrove tree diameter usually increases with stand age following self-thinning (Deshar et al. 2012; Kamara et al. 2012). In our study, the restored mangrove tree diameter did not increase, which may be due to site-specific environmental factors, competition, and varying nutrient availability (Kamara et al. 2012). The 9-year-old natural mangrove stand had the greatest diameter, which may be driven by the presence of multiple mangrove species and higher observed Ca and N concentration levels compared to the other stands. Our study supports previous findings that higher N levels increase mangrove growth rates and cover (Alongi 2017, 2021; Dangremond et al. 2020). The 5-year-old restored mangrove stand had the lowest diameter, probably because the trees in this stand were mostly immature. Even though it is estimated that restored mangrove trees can achieve diameters similar to those of natural mangroves between 25 and 55 years post-planting (Osland et al. 2012), some of the restored mangrove tree diameters were equivalent and even greater than those of some natural mangrove stands in the first decade of the chronosequence.

Mangrove forest age is known to influence AGB and belowground biomass carbon stocks (Salmo et al. 2013; Adame et al. 2018; Azman et al. 2021). Our study showed a nonlinear relationship between the restored and natural mangrove AGB and forest age. We found a higher total AGB in the natural mangroves (288.01 Mg/ha) than in the restored mangroves (137.83 Mg/ha). These findings conflict with earlier estimates by Ram et al. (2021), where they reported higher AGB in the restored stands (103 Mg/ha) than the intact stands (89.4 Mg/ha), possibly due to a different study design with larger plots and more sampling stands with several mangrove species. We assume that the difference between the restored and natural mangrove AGB may be due to multiple mangrove species (*L. racemosa* and *R. mangle*) in natural mangrove stands than monospecific restored stands. The growth rate of different mangrove species may also influence biomass accumulation in differently aged mangroves (Wang et al. 2021; Azman et al. 2023; Ray et al. 2023). Salmo et al. (2013) reported that younger plantations in the Philippines initially had low AGB but rapidly increased in 12-year-old stands. In contrast, in our study, the youngest plantation (5 years old) had the highest AGB due to the fast-growing nature of pioneer vegetation and the presence of other mangrove species (*L. racemosa*) with higher wood density values than *A. germinans*. Azman et al. (2021) found that the restored mangroves had two times more AGB biomass than naturally regenerated mangrove stands in Malaysia. This is contrary to the findings of our study but may be related to the high wood density of the *Rhizophora* sp. Meanwhile, the 9-year-old natural mangroves had the highest AGB and were also dominated by *L. racemosa*. Most of the restored mangrove stands AGB were not equivalent to natural mangrove stands in the first decade of the chronosequence. Therefore, the restored mangrove forests require more time to attain biomass equivalent to natural mangroves, which can take as long as 40 years (Azman et al. 2021).

There are often significant differences between restored, created, and natural wetland soils, and many studies indicate that it may take even decades or centuries for created and restored wetlands to develop soil properties equivalent to those of natural wetlands (Ball 2002; Proffitt & Devlin 2005; Hossler & Bouchard 2010; Hossler et al. 2011). Even though we expected distinct soil properties and higher nutrient levels in the natural mangroves, we found that a higher concentration of P, K, Na, and Zn in the restored mangroves is likely caused by a higher level of leaf litter degradation, organic matter decomposition, and nutrient regeneration in the restored mangroves (Bosire et al. 2005). The RDA revealed that the soil properties were the important factors influencing restored and natural mangrove communities. Increasing sediment organic matter content, salinity, P and N content, and other macronutrients are indicators of successful mangrove reestablishment (Grueters et al. 2021). Mangrove restoration usually increases soil nutrient accumulation during the first few years after restoration, followed by a steep decline as forests mature (Salmo et al. 2013; Shao et al. 2014; Zimmer et al. 2022). Salmo et al. (2013) reported a similar trend, with a clear progression between soil characteristics (P, N, and redox potential) and forest age. We did not observe this trend, indicating that site-specific factors such as soil composition, hydrology, and geomorphology may have influenced nutrient accumulation in restored and natural mangroves. Despite inconsistent patterns with the soil properties and age of the restored and natural mangrove stands in our study, the restored mangroves achieved higher levels of P, K, Na, and Zn at the end of the first decade of the chronosequence, suggesting successful nutrient accumulation in the restored ecosystem over time.

The rate and trajectory of ecosystem development vary due to wetland type, landscape position, land use history, and site-specific conditions (Proffitt & Devlin 2005; Ballantine & Schneider 2009; Suding 2011). The absence of clear trajectories between mangrove age, vegetation, and soil characteristics in our study might be attributed to the dynamic nature of Guyana's coastline. Guyana's coast is created by the mobile mud banks formed by the sedimentary environment due to the massive sediment loads discharged from the Amazon (Fromard et al. 2004). These changes might be important in determining mangrove forest survival, growth, structure, and composition here (Fromard et al. 2004; Anthony et al. 2010). Environmental factors, including tidal dynamics, riverine inputs, and climatic variations, might also influence Guyana's mangrove forests (Fromard et al. 2004; Anthony et al. 2014; Toorman et al. 2018). These complexities contribute to spatial divergence, where mangrove stands along the coast may experience distinctly different environmental conditions, thereby influencing developmental trajectories. Guyana's mixed mangrove species, each with unique adaptive strategies, further complicates any possible linear relationship between age, vegetation composition, and soil properties. Natural disturbances like storms, erosion, and accretion may also disrupt developmental patterns, leading to the non-uniform trajectories observed across mangrove stands here. Changes in river flow patterns are influenced by local activities and rainfall, which affect nutrient availability and sedimentation rates, impacting mangrove growth and development trajectories. Mangrove stands close to each other showed comparable vegetation and soil characteristics, irrespective of mangrove age and type.

The emergence of clear trends between age, vegetation, and soil characteristics may also require a longer timeframe than that examined in our study, which is consistent with data emerging from studies elsewhere. Mangrove forests have gradual and intricate growth patterns reaching maturity between 20 and 30 years (Jimenez et al. 1985; Alongi 2002; Osland et al. 2020), which might not manifest in distinctly similar trends between natural and restored sites within the relatively shorter time frame, following the intervention examined here. Some researchers propose that restored mangroves can achieve structural complexity and biomass like natural mangroves between 20 and 55 years post-restoration, provided that the biophysical conditions are conducive for growth (Salmo et al. 2013; Osland et al. 2020). Despite the lack of clear trajectories, this case study demonstrated that the restored mangrove forests developed some vegetation and soil characteristics but were not entirely equivalent to natural mangrove forests, indicating a positive recovery model post-planting. Our study provides valuable insights into the ecological processes driving mangrove recovery dynamics, growth patterns, and restoration effectiveness and offers reliable data needed to inform future restoration projects. It also provides a reliable timeline for the recovery of restored mangrove vegetation, which translates to ecosystem services and functions that support the well-being and resilience of local communities. Mangrove restoration practitioners and investors should consider these outcomes when planning or investing in future restoration projects.

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Supporting Information

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

Table S1. Stem density (ha^{-1}) of different mangrove species.

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