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Mangrove tree growth, diversity, and distribution in tropical coastline ecosystems

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ABSTRACT Mangrove trees are subject to several environmental stresses, often associated with the prevailing conditions of their ecosystems. We analysed the density, diversity, distribution, and biophysical measurements of more than 900 trees throughout nine natural, degraded, and restored tropical coastline ecosystems in Guyana. A one-year period of systematic sampling was carried out using the point-centred quarter method (PCQM) throughout two clearly defined wet and dry seasons. Significant variations in the distribution, diversity, and spatial arrangement of trees were observed within both the restored and degraded mangrove habitats. The study revealed notable discrepancies in the biophysical measurements of trees [$df = 8$, $p < 2.2e\text{-}16$], which were further found to have positive correlations [$p < 0.05$, $rs < 0.5$] and relationships with their corresponding ecosystem types. The presence of substantial tree species with larger growth measurements in both natural and restored ecosystems indicate a heightened capacity for ecological resistance and resilience in the face of environmental stresses, in contrast to the degraded ecosystems that now exhibit states of vulnerability due to low ecological resistance and resilience attributed to prevailing anthropogenic disturbances.

KEY WORDS Ecosystems; Guyana; mangroves; trees; tropical coastline.

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INTRODUCTION

Mangrove forests are found along the boundary between land and sea, resulting in their presence in terrestrial as well as aquatic settings. As a result, mangrove forests provide crucial functions in both domains along with a wide range of ecosystem services, including coastal protection, carbon sequestration, and the promotion of biodiversity (Rog et al., 2016). Nevertheless, the provision of these services is diminishing due to the depletion of mangrove forests, resulting in significant ecological and economic consequences for the dependent species and human populations (Ahmed et al., 2023). The expansion of coastal populations and the rise in sea levels are exerting pressure on mangrove forests, leading to their reduction in size and extent. The pressures encompass a range of factors, such as the combined effects of seawall building, aquaculture practices, excessive fishing, rising sea levels, extreme weather conditions, ecological invasion, and pollution (Wang et al., 2020). The mangrove forests located in the coastal areas of Guyana have seen a reduction of over 35% since the year 1980. The primary cause of this decline can be attributed to the intrusion of human activities, which has a detrimental impact on the functionality, diversity, and productivity of the three prevailing species present in this region, specifically *Avicennia germinans* (L.) L., *Laguncularia racemosa* (L.) C.F. Gaertn., and *Rhizophora mangle* L. (Dookie et al., 2022).

In light of the dynamic nature of the environment, a fundamental characteristic of an ecosystem lies in its capacity to restore itself following a disturbance. Different reactions to a disturbance may be classified as resistance, resilience, or sensitivity. Resistance refers to the capacity to endure perturbations in the face of a disruption. Resilience, on the other hand, pertains to the ability to recover after being affected by a disturbance. Lastly, sensitivity refers to the lack of capacity to endure or recover following a disturbance (Meredith et al., 2018). Moreover, alterations in the frequency or intensity of recurrent disturbances in these ecosystems can potentially exert a more immediate and apparent ecological influence on the structure and composition of forests compared to gradual climate changes. This can significantly contribute to the creation of irregularities and heterogeneity within a mangrove vegetation community (Zhang et al., 2016). The stability of mangrove ecosystems is heavily influenced by the integrity of forest structure, which is often assessed by measuring species diversity and population densities (Capdeville et al., 2019). Furthermore, the primary factors contributing to the resilience of established mangrove ecosystems include sediment accretion, surface elevation increases in relation to sedimentation and freshwater inputs, and the presence of well-maintained vegetative coverage (Duncan et al., 2018). Nonetheless, mangrove ecosystems that undergo degradation may have diminished resistance and resilience as a result of alterations in landscape structure, the influence of upstream factors on sediment and the transportation of nutrients, and disturbances to the environment that impact habitat interconnectivity. The presence of disturbances can have various effects on water and material movement, hinder the migration of plants and/or animals, and contribute to the disintegration of habitats and the creation of gaps in forests (Day et al., 2018).

Numerous studies have been conducted on the ecological dimensions of mangrove forests. However, the precise understanding of the correlation between various ecosystem types and their influence on tree growth and development remains limited, particularly in the context of tropical coastal environments. It is well recognised that the examination of mangrove trees in many ecological contexts holds significant value in terms of forecasting the dynamics and feedback mechanisms of various nutrient cycles as well as determining their level of resistance and resilience in the face of environmental stressors. Therefore, we formulated the hypothesis that substantial variations exist in the distribution, density, diversity, and growth parameters of trees seen in the different mangrove ecosystem types along the Guyana coastline. Our research has focused on three distinct ecosystem types: natural ecosystems (N), degraded ecosystems (D), and restored ecosystems (R). Natural ecosystems are characterised by a state of equilibrium in which the influence of human activities is either on par with or less than that of other indigenous species. These ecosystems have remained largely unaffected by human actions, preserving their original structure. On the other hand, restored ecosystems have experienced a process of restoration following their destruction, mostly as a result of human involvement. In contrast, ecosystems that have undergone degradation exhibit diminished levels of habitat quality, structure, and usefulness as a result of both natural and anthropogenic disturbances (Hobbs & Cramer, 2008). The present study's findings are expected to enhance the scientific community's understanding of the current status of mangrove trees in diverse ecosystem types found in tropical coastal locations. This information might be valuable for aiding environmental administrators and scientific investigators in accurately evaluating and devising strategies for potential projects focused on the restoration and preservation of mangrove forests.

MATERIAL AND METHOD

Study area

A total of nine mangrove locations were chosen along the coastal regions spanning from the East

Coast of Demerara to East Berbice, Corentyne (Fig. 1, Table 1). Out of the nine selected sites, three were identified as natural mangrove ecosystems, namely Novar (NOV), Number 27 Village (Bushlot) (NO27), and Kilmernock (KIL). Additionally, three sites were classified as degraded, which included Hope (HOPE), Greenfield (GREN), and Wellington Park (WPP). Lastly, the remaining three sites were categorised as restored, specifically Chateau Margot (CM), Number 6 Village (NO6), and Number 7 Village (NO7) (Figs. 2-10). The data collection process spanned twelve (12) months and was divided into four distinct phases. Phase 1 (P1) took place in August 2022 during the dry season (DS), followed by phase 2 (P2) in December 2022 during the wet season (WS). Phase 3 (P3) occurred in April 2023 during the dry season (DS), and finally, phase 4 (P4) was conducted in July 2023 during the wet season (WS). The restored areas include juvenile mangrove trees that have not yet attained complete maturity, sometimes referred to as "young forests." The Guyana Mangrove Restoration Project, implemented by the Ministry of Agriculture in 2016, involved the deliberate reestablishment of these ecosystems more than ten years ago. The natural mangrove ecosystems consist of long-standing, fully developed trees that experience minimal disturbances (Dookie et al., 2022) with little disturbances recorded (Table 2). In contrast, the selected degraded mangrove habitats have undergone significant deterioration, primarily caused by extensive erosion resulting from both natural and human activities, such as improper disposal of waste and evident pollution within and surrounding these forested areas (Table 2).

Experimental design and tree sampling

Biophysical assessments were conducted on approximately 100 mangrove trees in each location using the point-centred quarter method (PCQM) (Cottam & Curtis, 1956). At each of the nine research locations, a fixed 250 m line transect was established with survey points positioned at 10 m intervals. Every point represented where the four cardinal directions (North, South, East, and West) intersected, resulting in the division of each sample point into four quadrants. The measurement of the distance between the sample point and the closest reported mangrove tree within a 5 m radius was done for each quadrant. The tree species, the distance to each sample point, and the quadrat number were recorded. In cases where a tree was absent

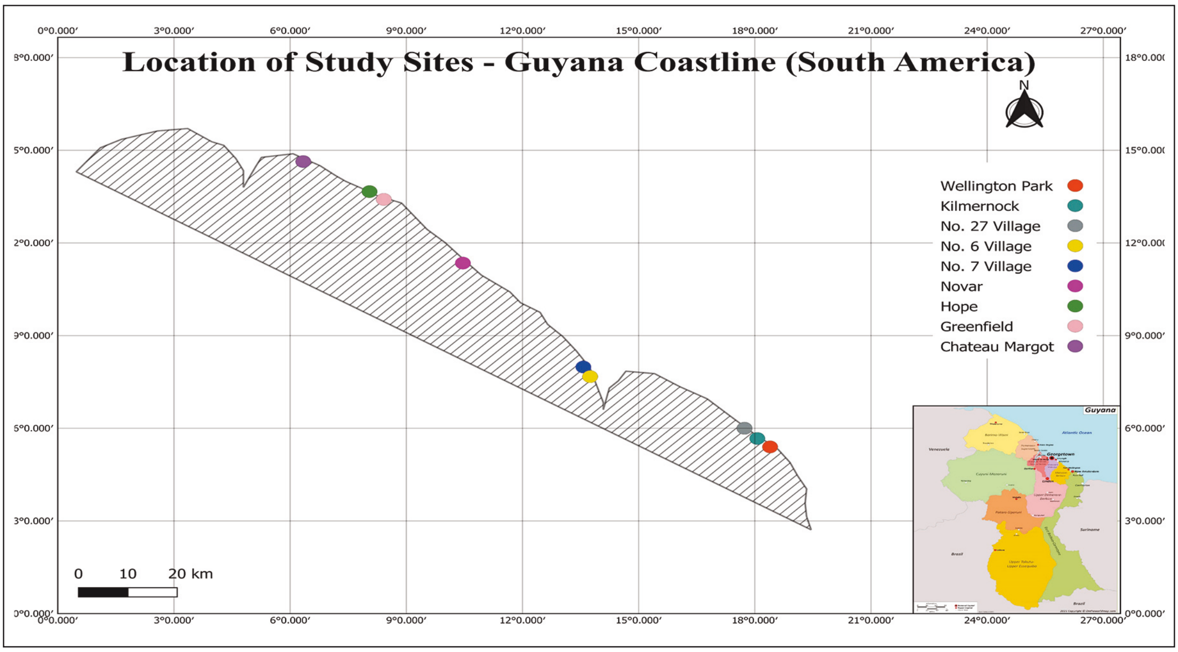


Figure 1. Map of the Guyana coastline showing the location of the nine mangrove sites under study.

Location	Latitude	Longitude
Chateau Margot	N 6°49'0.02374"	W 58°3'51.00106"
Hope	N 6°44'32.07628"	W 57°57'6.41812"
Greenfield	N 6°43'53.49443"	W 57°56'17.4772"
No. 6 Village	N 6°19'28.40228"	W 57°33'37.49807"
No. 7 Village	N 6°19'36.42726"	W 57°33'41.70874"
Novar	N 6°34'0.59128"	W 57°45'39.4853"
Wellington Park	N 6°10'53.69905"	W 57°14'9.4088"
Kilmernock	N 6°11'24.81158"	W 57°14'45.41302"
No. 27 Village Bushlot	N 6°12'27.7722"	W 57°15'52.46186"

Table 1. Geolocation information (GPS Coordinates) for all sites under study (Google Maps, 2023).

or deceased within a designated quarter, subsequent measurements of new trees were recorded. The following measurements were then obtained from the trees:

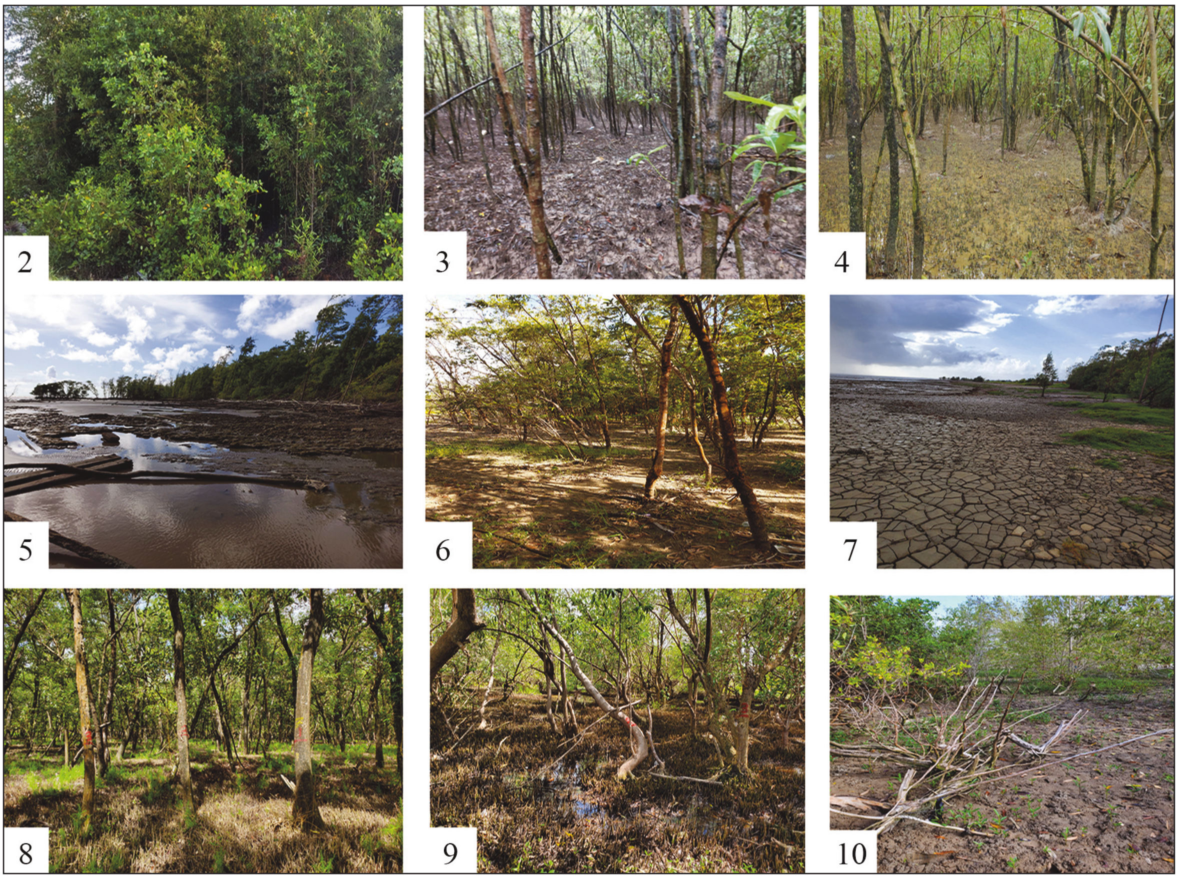
1. The height (HT) of the trees (in m) was measured using a Nikon Forester Pro II rangefinder using the three-point mode following the cosine rule.

2. The diameter at breast height (DBH) (in cm) was measured using a DBH tape 1.3 m from the base of the trees following the method outlined by Jaikishun et al. (2017):

i. If the tree was on a slope, the DBH was measured on an upward slope.

ii. If the tree was slanting, the DBH tape was wrapped at an angle to the tree's inclination rather than straight across parallel to the land.

iii. The measurement was taken just underneath



Figures 2–10. The three types of mangrove ecosystems: restored, Chateau Margot (Fig. 2), Number 7 Village (Fig. 3), Number 6 Village (Fig. 4); degraded, Hope (Fig. 5), Greenfield (Fig. 6), Wellington Park (Fig. 7), and natural, Novar (Fig. 8), Number 27 Village (Fig. 9), Kilmernock (Fig. 10).

Location			Chateau Margot (CM)	No. 6 Village (NO6)	No. 7 Village (NO7)	Hope (HOPE)	Greenfield (GREN)	Wellington Park (WEP)	Novar (NOV)	Kilmernock (KIL)	No. 27 Village (NO27)
Ecosystem Type			**Restored**			**Degraded**			**Natural**		
			EXTENT OF DISTURBANCES								
TYPES OF DISTURBANCES	**NATURAL**	Plant infestation	++	++	++	+	+	+	+++	++	+++
		Storms/ Tides	++	++	++	++++	++++	++++	++	++	++
		Erosion	++	++	++	+++++	++++	+++++	++	++	++
		Insect Infestation	+	++++	++++	+	+	+	++	++	++
		Sargassum invasion	++	++	++	++++	++++	+++++	++	++	++
	ANTHROPOGENIC	Bark Stripping	+	+	+	+++	++	++	+	+	+
		Grazing	+	++	++	++	++	+++	+++	++	+++
		Cutting	+	+	+	+++	+++	++++	++	++	++
		Sand Mining	+	+	+	++	++	++	+++	++	++
		Burning	+	+	+	++++	++++	++	+++	++	++
		Fishing activities	+++	++	++	+++++	+++++	+++	+++	+++	++
		Garbage Dumping	+	+	+	+++++	+++++	++++	++++	+++	+++
		Marine & coastal litter	++	+	+	++++	+++++	+++++	+++++	+++	+++
		Infrastructure Development	++	+	+	+++	++++	+++	++	++	++
		Lumbering (sawdust)	+	+	+	+	+	++++	+	+	+
		Seashell mining	++	+	+	++++	++++	++	+++	+	+

Table 2. Extent and types of natural and anthropogenic disturbances found in each mangrove ecosystem under study during the one-year period.

the fork point if the tree was forked at DBH. If measuring below the fork is impractical, the calculation of two trees was made.

iv. If a tree had fallen over but is still intact, the measuring stick was positioned at the bottom and the DBH will be estimated as if it were standing upright. If there are green leaves on a tree, it is considered to be alive.

v. The DBH of all trees measured were categorised into diameter classes of >5-10 cm, >10-20 cm, >20-30 cm, >30-40 cm, and >40 cm.

3. The Basal Area (BA): was calculated in m^2 using the recorded DBH values of the trees. (pi = 3.142) (Bettinger et al., 2017).

$$BA\ (m^2) = \frac{pi \times DBH\ (cm^2)}{40{,}000}$$

$$Stand\ Basal\ Area\left(\frac{m2}{ha}\right) = \frac{sum\ of\ BA\ of\ each\ area\ in\ the\ plot}{area\ of\ the\ plot\ (ha)}$$

Density, diversity, and distribution analysis

Using the information gathered using PCQM, the following parameters were analyzed:

1. Absolute and Relative Frequency (Cottam & Curtis, 1956; Mitchell, 2015)

$$\mathrm{F} = \frac{\text{No. of sample points with a species}}{\text{Total number of sample points}} \times 100.$$

$$\mathrm{RF} = \frac{\text{Absolute frequency of a species}}{\text{Total frequency of all species}} \times 100.$$

2. Relative Cover (Cottam & Curtis, 1956):

$$\mathrm{RC}\,(\text{Species } k) = \frac{\text{Total basal area of species } k \text{ along transect}}{\text{Total basal area of all species along transect}} \times 100.$$

3. Absolute density (AD) (λ_k):

The absolute density (λ_k) of each mangrove species was found by using the following formula:

$$(\mathrm{AD})\ \hat{\lambda}_k = \frac{\text{Quarters with species } k}{4n} \times \hat{\lambda}$$

Where all quarters with species 'k' in them are multiplied by the absolute density (λ_k) determined for all trees. A correction factor (CF) was applied to the existing density formula to account for vacant quarters.

$$\bar{r}' = \frac{\sum_{m=1}^{4n-n_0} R_m}{4n-n_0}$$

$$\text{AD (corrected)} = \hat{\lambda}_c = \frac{1}{(\bar{r}')^2} \cdot \mathrm{CF}$$

Where CF = $1 - \frac{n_0}{4n}$

n = the number of sampling points, $4n$ = the number of quarters, n_0 = the number of vacant quarters.

4. Relative Density (RD) (Mitchell, 2015):

$$\text{RD (Species k)} = \frac{\text{Quarters with species k}}{4\text{n}} \times 100$$

5. Importance Value (IV):

IV = relative density + relative frequency + relative cover

Diversity, evenness, and richness indices

1. Shannon- Weiner Diversity Index (H^1):

$$H' = -\sum_{i=1}^{s} p_i \ln p_i$$

Where s denotes the number of species, and Pi denotes the ratio of species individuals divided by the total number of individuals n of all species.

2. Shannon Equitability Index (E):

$$\mathrm{E} = -\Sigma \mathrm{pi} * \ln(\mathrm{pi})$$

3. The Margalef Richness Index (DMA): (Margalef, 1963)

$$DMA = \frac{(\mathrm{S}-1)}{\ln(\mathrm{N})}$$

Where S is the total number of species in the area sampled and N is the total number of individuals observed.

4. Simpson's Diversity Index (D*):* (Roswell et al., 2021)

$$D = \frac{1}{\sum_{i=1}^{s} p_i^2}$$

Where p is the proportion (n/N) of individuals of one particular species found (n)divided by the total number of individuals found (N), Σ is still the sum of the calculations, and s is the number of species.

5. Simpson's Reciprocal Index (1/D):

$$1/\mathrm{D} = \frac{\mathrm{N(N-1)}}{\sum \mathrm{n(n-1)}}$$

Where 1/D = Simpson reciprocal diversity index, N = the total number of organisms of all species found n = number of individuals of a particular species.

Data analysis

The datasets were analysed using a combination of Microsoft Excel and RStudio programming tools (version 2023.06.1+524) at a significance level of $p < 0.05$. The following statistical tests were applied:

i. Shapiro-Wilk test of normality: to determine the normality of datasets. Non-parametric tests were employed with a significance level of $p < 0.05$ due to the extremely skewed nature of the datasets, even after log10 transformations.

ii. Kruskal-Wallis test: to determine if there were significant differences in the tree growth measurements among the various mangrove locations.

iii. Dunn's test of multiple comparisons: to identify which ecosystem type had significant differences in the parameters measured.

iv. Spearman rank correlation coefficients: to assess the degree of association among tree growth measures and their locations.

v. Multiple regression analysis (generalised linear model): to ascertain the extent of linear associations between mangrove trees and their corresponding ecosystem types.

RESULTS

Distribution, diversity, and density of mangrove trees

The transect lines that were established across the nine mangrove sites during one year successfully documented the presence of the three dominant mangrove species – *A. germinans* (B), *L. racemosa* (W), and *R. mangle* (R) – only within two restored ecosystems (NO6 and NO7). *A. germinans* exhibited the highest level of dominance across all nine locations, with *L. racemosa* and *R. mangle* following in succession (Table 3). The majority of the sites examined exhibited the coexistence of two or more mangrove species. However, two specific natural sites, namely KIL and NO27, documented the presence of a single species throughout the transect line - *A. germinans.*

The diversity indices calculated from all sites revealed that the restored ecosystems had greater species diversity, evenness and richness followed by the degraded ecosystems, then the natural ecosystems. NO6 and NO7 ecosystems possessed greater species diversity and richness when compared to CM. However, CM possessed greater species evenness than the other two restored ecosystems (Fig. 11).

Location	**Ecosystem Type**	**Species Detected**	**Relative Cover**	**Relative Frequency**	**Relative Importance**	**Importance Value**	**Relative Density**		**Absolute Density (ha)**	
							Min	**Max**	**Min**	**Max**
Chateau Margot	**R**	B	80.03	60.00	71.34	214.03	74.00	74.00	2660.37	2660.37
		W	19.97	25.00	20.99	62.97	18.00	18.00	647.11	647.11
Number 6 Village	**R**	B	81.76	56.82	72.19	216.58	78.00	78.00	3131.38	3139.94
		W	9.02	18.18	12.06	36.21	9.00	9.00	361.31	362.30
		R	9.21	15.91	11.05	33.12	8.00	8.00	321.16	332.05
Number 7 Village	**R**	B	84.01	55.81	71.94	215.83	76.00	76.00	2183.03	2183.03
		W	6.68	11.63	8.11	24.31	6.00	6.00	172.34	172.34
		R	9.30	16.28	11.19	33.58	8.00	8.00	229.79	229.79
Novar	**N**	B	88.70	56.82	74.17	222.53	77.00	77.00	1113.30	1122.62
		R	11.31	18.18	13.16	39.48	10.00	10.00	144.58	145.79
Number 27 Village	**N**	B	100.00	67.57	100.00	300	84.00	84.00	635.28	635.28
Kilmernock	**N**	B	100.00	69.44	100.00	300	88.00	88.00	737.92	740.80
Greenfield	**D**	B	84.29	41.42	56.49	169.46	38.00	51.00	620.26	673.58
		W	15.70	15.07	12.90	38.78	7.00	9.00	111.65	124.44
Hope	**D**	B	88.83	50.92	64.84	194.53	48.00	65.00	639.76	1103.37
		R	11.03	12.43	9.94	29.83	6.00	7.00	68.89	137.92
Wellington Park	**D**	B	89.99	31.25	49.74	149.24	20.00	31.00	428.35	1126.88
		W	10.01	5.51	5.84	17.52	2.00	2.00	27.63	56.56

Table 3. Distribution and density of mangrove tree species present in all nine mangrove sites.

Figure 11. Diversity indices for the tree species present in the restored ecosystems.

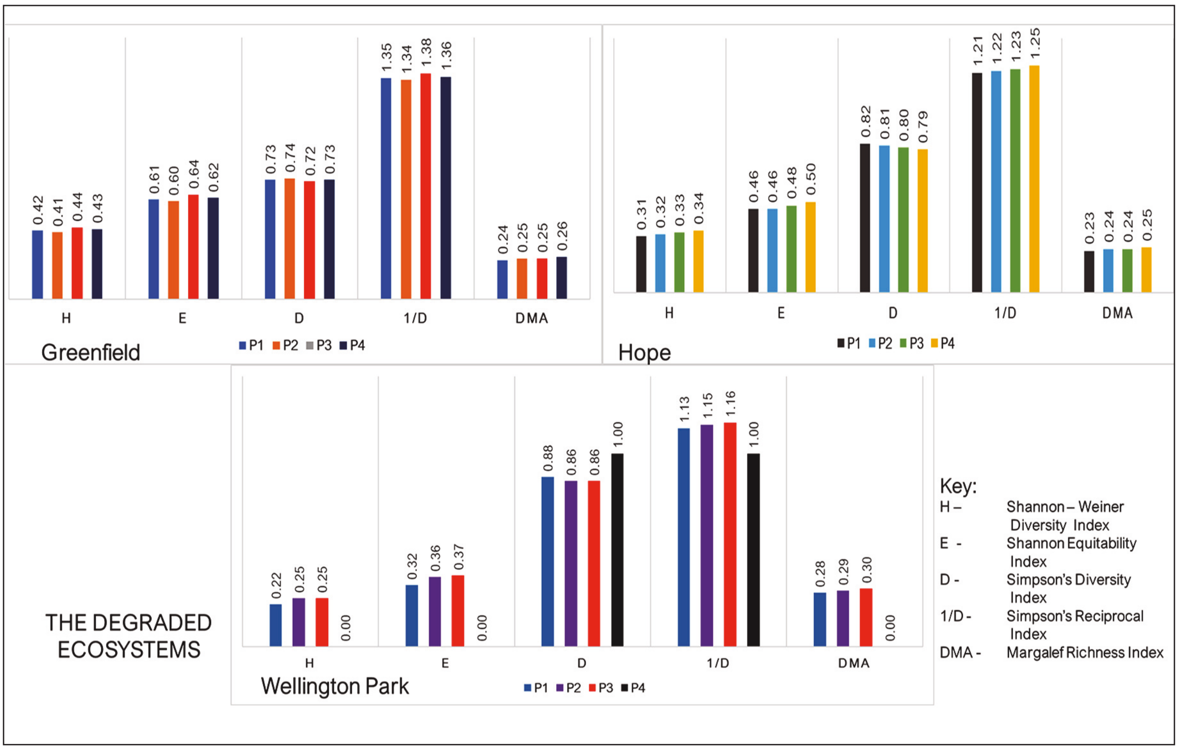


Figure 12. Diversity indices for the tree species present in the degraded ecosystems.

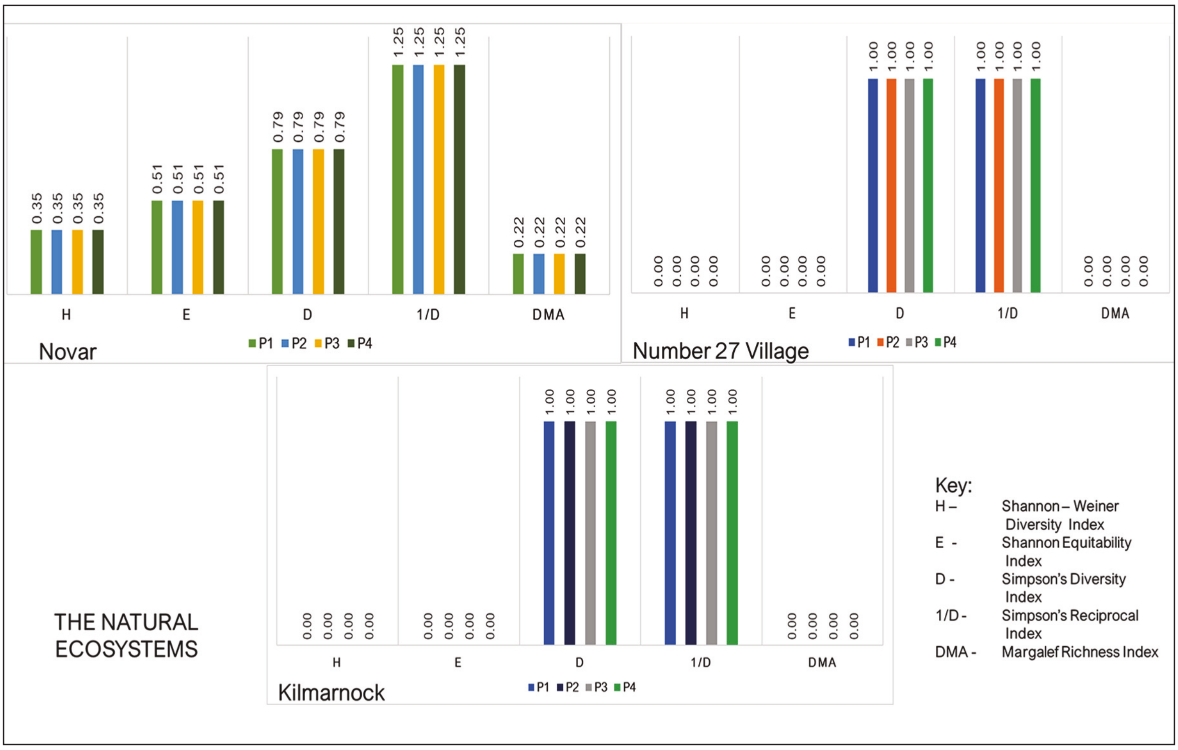


Figure 13. Diversity indices for the tree species present in the natural ecosystems.

Within the degraded ecosystems, GREN possessed mangrove species with greater diversity and evenness when compared to HOPE and WEP. However, low species richness was documented for all three degraded areas (Fig. 12). However, within the natural ecosystems, NOV documented greater species diversity, richness and evenness when compared to KIL and NO27. Due to the presence of only one prominent species, the diversity, evenness and richness indices for both NO27 and KIL were significantly low. With the exception of the degraded ecosystems, the diversity indices of all other mangrove sites were stable during the study period (Fig. 13).

The total density (per ha) calculations reported that overall, the restored ecosystems had greater tree densities, followed by the natural ecosystems, then the degraded ecosystems. In the restored ecosystems, NO6 recorded the highest tree density (4025.58 individuals/ha), followed by CM (3595.10 individuals/ha), then NO7 (2871.91 individuals/ha). Within the natural ecosystems, NOV recorded higher densities (1445.85 individuals/ha) than KIL (841.82 individuals/ha) and NO27 (individuals/ha). The densities of all tree species within the natural and restored ecosystems were stable throughout the one-year period. However, within the degraded areas, the tree densities declined significantly with values fluctuating between HOPE (708.65 – 1241.29 individuals/ha), WEP (455.98 – 1183.44 individuals/ha) and GREN (731.91 – 798. 02 individuals/ha). At the end of the year period, WEP possessed the lowest tree densities when compared to all other mangrove sites (Table 3).

Biophysical measurements of trees

Height (HT)

The natural ecosystems possessed taller trees, followed by the restored areas, and then the degraded areas. Within the natural areas, NOV possessed taller trees (HT_{max} = 11.20 ± 0.14 m) when compared to NO27 (HT_{max} = 10.25 ± 0.12 m) and KIL (HT_{max} = 10.55 ± 0.15 m) (Table 3 summarises the heights per species). In the restored areas, CM (HT_{max} = 10.60 ± 0.17 m) reported taller trees when compared to the other two restored ecosystems NO6 (HT_{max} = 9.82 ± 0.15 m) and NO7 (HT_{max} = 10.13 ± 0.34 m). However, in the degraded areas, HOPE (HT_{max}

= 9.97 ± 0.20 m) reported taller trees when compared to WEP (HT_{max} = 9.78 ± 0.34 m) and GREN (HT_{max} = 9.75 ± 0.21 m). Growth increments in tree heights, however, were greater in the restored areas (1.30 – 1.88 m) when compared to the natural (0.67 – 0.79 m) and degraded areas (0.65 – 1.15 m) of this study. Furthermore, Kruskal – Wallis tests reported significant differences between tree heights and their

Location	Ecosystem Type	Species Detected	Height (m)					DBH (cm)					Stand Basal Area (m^2/ha)		
			P1	P2	P3	P4	DT	P1	P2	P3	P4	DT	Min	Max	DT
Chateau Margot	R	B	9.23 ± 1.88	9.72 ± 0.18	10.17 ±0.19	10.60 ± 0.17	H	11.67 ± 0.31	12.08 ± 0.30	12.53 ± 0.32	12.95 ± 0.29	A	0.25	5.14	D
		W	9.13 ± 0.44	9.60 ± 0.45	10.08 ± 0.46	10.55 ± 0.44		11.86 ± 0.59	12.29 ± 0.57	12.71 ± 0.59	13.14 ± 0.58		0.73	1.31	
Number 6 Village	R	B	7.94 ± 0.15	8.60 ± 0.16	9.21 ±0.14	9.82 ± 0.15	C	8.23 ± 0.19	9.02 ± 0.18	9.75 ± 0.17	10.49 ± 0.16	F	2.62	3.53	F
		W	8.01 ± 0.55	8.54 ± 0.54	9.25 ±0.56	9.83 ± 0.57		8.05 ± 0.57	8.81 ± 0.58	9.55 ± 0.56	10.30 ± 0.59		0.40	2.43	
		R	7.90 ± 0.53	8.56 ± 0.55	9.15 ± 0.54	9.75 ± 0.56		8.78 ± 0.47	9.53 ± 0.45	10.29 ± 0.47	11.06 ± 0.46		0.40	2.51	
Number 7 Village	R	B	8.34 ± 0.14	8.88 ± 0.12	9.46 ± 0.11	9.98 ± 0.13	B	9.26 ±0.11	9.77 ± 0.12	10.27 ± 0.13	10.73 ± 0.10	C	2.65	3.53	E
		W	8.48 ± 0.37	9.03 ± 0.35	9.59 ± 0.36	10.13 ±0.34		9.22 ± 0.56	9.78 ± 0.55	10.32 ± 0.57	10.78 ± 0.54		0.21	0.29	
		R	8.45 ± 0.54	9.02 ± 0.55	9.59 ± 0.53	10.12 ± 0.56		9.55 ± 0.33	10.03 ± 0.34	10.56 ±0.32	11.01 ± 0.35		0.30	0.39	
Novar	N	B	10.41 ± 0.15	10.69 ± 0.14	10.94 ±0.16	11.20 ±0.14	E	19.50 ± 0.33	19.64 ± 0.34	19.87 ± 0.32	20.09 ± 0.31	G	12.19	22.76	E
		R	10.20 ± 0.34	10.61 ± 0.33	10.72 ± 0.32	10.97 ± 0.31		19.25 ± 0.92	19.53 ± 0.94	19.72 ± 0.92	19.94 ± 0.93		1.17	1.62	
Number 27 Village	N	B	9.58 ± 0.08	9.83 ± 0.09	10.04 ± 0.10	10.25 ± 0.12	D	26.13 ± 0.50	26.34 ± 0.51	26.55 ±0.52	26.76 ± 0.49	E	23.66	24.81	G
Kilmernock	N	B	9.81 ± 0.12	10.04 ± 0.14	10.29 ± 0.12	10.55 ± 0.15	B	18.16 ± 0.69	18.43 ± 0.68	18.71 ±0.65	18.96 ±0.68	B	13.05	14.09	A
Greenfield	D	B	8.60 ± 0.17	8.96 ± 0.19	9.41 ± 0.20	9.75 ± 0.21	A	9.33 ± 0.27	9.67 ± 0.28	9.77 ± 0.30	10.14 ±0.33	C	1.54	1.82	A
		W	7.95 ± 0.39	8.57 ± 0.44	9.06 ± 0.45	9.57 ± 0.47		8.93 ± 0.82	9.58 ± 0.86	9.94 ± 0.88	10.52 ± 0.97		0.31	0.33	
Hope	D	B	9.20 ± 0.18	9.52 ± 0.17	9.85 ± 0.16	9.97 ± 0.20	F	11.32 ± 0.44	11.66 ± 0.49	12.17 ±0.48	12.61 ± 0.50	C	3.28	3.67	C
		R	8.73 ± 0.39	8.99 ± 0.46	9.19 ± 0.45	9.38 ± 0.47		11.89 ± 0.89	12.68 ± 0.80	13.22 ± 0.81	13.59 ± 0.83		0.41	0.45	
Wellington Park	D	B	8.28 ± 0.24	8.56 ±0.27	8.83 ± 0.28	9.18 ± 0.34	G	10.13 ± 0.45	10.43 ± 0.46	10.74 ±0.48	10.65 ± 0.57	D	0.95	4.47	B
		W	7.31	7.53 ± 0.45	7.74 ± 0.51	0.00		12.94 ± 2.06	13.46 ± 2.08	13.57 ± 2.06	0.00		0.14	0.15	

Table 4. Biophysical measurements of trees found in all nine mangrove sites (Mean ± SE).

locations (df = 8, $p < 2.2e\text{-}16$) throughout this study. Furthermore, Dunn's test revealed that the heights of trees found in GREN, NO6, NO7, and NO27 significantly differed ($p < 0.05$) from all other ecosystems (Table 4).

Diameter at Breast Height (DBH)

The average DBH values differed among the three types of ecosystems, with the natural ecosystems possessing trees with greater values when compared to the other two ecosystem types. Within the natural ecosystems, NO27 possessed greater DBH values (DBH_{max} = 26.76 ± 0.49 cm) than NOV (DBH_{max} = 20.09 ± 0.31 cm) and KIL (DBH_{max} = 18.96 ± 0.68 cm). In the restored areas, CM possessed greater DBH values (DBH_{max} = 13.14 ± 0.58 cm). when compared to NO6 (DBH_{max} = 11.06 ± 0.46 cm) and NO7 (DBH_{max} = 11.01 ± 0.35 cm). However, in the degraded areas, smaller DBH values were recorded within HOPE (DBH_{max} = 13.59 ± 0.83cm), WEP (DBH_{max} = 13.57 ± 2.06cm), and GREN (DBH_{max} = 10.52 ± 0.97 cm). However, DBH growth increments were greater in the restored areas (1.28 – 2.25 cm) when compared to the natural (0.59 – 0.80 cm) and degraded areas (0.52 – 1.59 cm) during the one-year period. Additionally, Kruskal – Wallis tests reported significant differences between tree DBH and their locations (df = 8, $p < 2.2e\text{-}16$) throughout this study. Dunn's test revealed that the DBH of trees found in CM, KIL, GREN, HOPE, and WEP significantly differed ($p < 0.05$) from all other ecosystems (Table 4).

Basal Area (BA)

Further calculations revealed that, similar to the DBH values, the natural ecosystems possessed greater BA (stand) when compared to the other ecosystem types. Within the natural ecosystems, NO27 reported larger BA values (24.81 m^2/ha) when compared to NOV (24.38 m^2/ha) and KIL (14.09 m^2/ha). Furthermore, within the restored ecosystems, NO6 possessed greater BA values (8.47 m^2/ha) when compared to CM (6.45 m^2/ha) and NO7 (4.21 m^2/ha). Additionally, the degraded ecosystems recorded smaller BA values within WEP (4.62 m^2/ha), HOPE (4.12 m^2/ha) and GREN (2.15 m^2/ha) (Table 3 gives BA per species). Kruskal – Wallis tests reported significant differences between the SBA of the different ecosystem types (df = 8, $p < 2.2e\text{-}16$) throughout this study. Dunn's test revealed that the BA of trees found in KIL, GREN, HOPE, and WEP significantly differed ($p < 0.05$) from all other ecosystems (Table 4).

Correlation and regression analysis

The Spearman rank correlation coefficients (r_S) tabulated for the tree biophysical parameters [HT ~ DBH], [HT ~ SBA], and [DBH ~ SBA] revealed positive correlations within all nine sites and phases ($p < 0.05$, $r_S > 0.05$). The strongest positive correlations between tree HT - DBH, and HT - BA were seen among the degraded ecosystems (WEP: $0.92 \leq r_S \leq 0.98$, HOPE: $0.50 \leq r_S \leq 0.81$, GREN: $0.84 \leq r_S \leq 0.92$), followed by the natural ecosystems (NO27: $0.46 \leq r_S \leq 0.47$, KIL: $0.49 \leq r_S \leq 0.51$, NOV: $0.37 \leq r_S \leq 0.41$), then the restored ecosystems showcasing weaker, positive correlations which fluctuated throughout the study period (NO7: $0.34 \leq r_S \leq 0.36$, NO6: $0.18 \leq r_S \leq 0.23$, CM: $0.29 \leq r_S \leq 0.31$). It was also observed that there was a very strong positive correlation ($0.81 \leq r_S \leq 1.00$) between DBH and BA in all nine mangrove sites throughout this study.

Furthermore, repeated multiple regression analyses (generalized linear model) further provided enough evidence that indicated statistically significant relationships ($p < 0.05$) between tree HT, DBH, and BA in all of their respective locations. However, while all other locations reported strong positive Est and t-values throughout repeated analyses for P1 - P4, NO6 and NO7 coefficients were inconsistent with this trend, reporting weak positive values. This indicated that for every unit increase in the intercept, values for NO6 and NO7 may decrease.

DISCUSSION

Distribution, diversity, and density of mangrove trees

The recorded distribution pattern of mangrove species across all nine sites is consistent with the findings reported by Jaikishun et al. (2017) and Dookie et al. (2022). The observed increase in species diversity, richness, and densities in the restored ecosystems can be attributed to various factors, such as the deliberate choice of species, appropriate planting density and distance, effective replanting techniques, and proficient management methods employed during the restoration process of these forests. These strategies have facilitated the establishment of high densities of mixed mangrove species (Xiong et al., 2019). Nonetheless, the observed scarcity of species and low diversity indices in the natural forests might perhaps be attributed to the age of the trees and the established zonation patterns, wherein *A. germinans* is found in closest proximity to the coastline (Bovell, 2011). Due to their advanced stage of development and few disturbances, trees within natural ecosystems possess the capacity to endure severe environmental stresses that might otherwise impact tree populations in susceptible regions. Although the densities of the natural ecosystems in this study are lower, they exhibit more stability compared to the tree densities seen in the degraded regions, which experienced a dramatic decline over a single year. The reduced density, diversity, and species richness observed in the degraded areas can potentially be attributed to the prevalent anthropogenic conditions, as evidenced by the cutting and burning activities documented in Table 2. Additionally, natural disturbances such as erosion and rising sea levels may also contribute to the alteration of zonation patterns and vegetation assemblages in these areas.

Biophysical measurements

The trees in the natural ecosystems exhibited significantly greater heights, DBH, and basal areas compared to the trees present in the restored and degraded environments. One potential contributing aspect is the age of the trees. The process of mangrove development into mature trees with dominating branches and stronger trunks is sometimes observed to last several decades, as evidenced by an increase in stand basal area (Scales & Friess, 2019). Furthermore, trees exhibiting larger biophysical parameters serve as an indicator of the prevailing environmental circumstances, which, in this particular scenario, are conducive to the development and production of trees. This ecosystem type exhibited minimal perturbations, resulting in reduced impediments to tree growth caused by significant anthropogenic disturbances. These disturbances are well documented to impact soil water and nutrient availability, plant development and growth rates, as well as tree mortality (Glasby et al., 2019).

The trees within the restored regions exhibited reduced height as well as diminished DBH and stand basal areas. This phenomenon may be attributed to the age of the trees, especially in the case of the restored mangrove forests that were replanted less than 15 years ago and have not yet attained complete maturity. According to Osland et al. (2020), the process of attaining equivalence between mature mangrove trees at restored sites and the native species found in mangrove forests typically spans roughly 55 years. Nevertheless, based on the findings of this study, it is evident that the growth rates seen in this particular environment might lead to the establishment of a comparable state to that of natural ecosystems in terms of herbaceous and juvenile vegetation layers within a time frame of < 15 years. A higher density of trees in an area with limited plant spacing implies increased competition for essential resources required for plant growth, including light, water, soil nutrients, and others. This heightened competition acts as a constraining factor in the growth and development of trees (Magalhães et al., 2021). The observed variances may be attributed to the disparity in soil formation between restored regions and established mangrove ecosystems, with the former often requiring a longer time for this process to occur. The observed phenomenon might potentially be attributed to the origins of nutrient influx, such as the presence of leaf litter and the breakdown of organic material which may be diminished in recently rehabilitated bare soils (Thura et al., 2022).

However, the observed decrease in heights, DBH, and stand basal areas in the degraded sites might be attributed to many reasons that impose constraints on the availability of resources necessary for optimal plant growth and development. The mangroves within this particular ecosystem have experienced excessive exploitation due to a range of economic factors, such as their use as fuel, construction materials, fishing, industrial purposes, and the establishment of agricultural farmlands (as indicated in Table 2). Mangrove trees are subject to extensive exploitation, leading to the destruction of the mangrove forest ecosystem, leaving a significant portion of these stands in a condition of serious deterioration. The reduction of mangroves and the subsequent impact on related biodiversity can be attributed, in part, to pollution originating from anthropogenic sources. Nunoo and Agyekumhene (2022) also made comparable findings, affirming that mangroves in these regions exhibited inhibited development characterised by reduced girth size and height, as well as diminished richness of the surrounding vegetation and animals. The diminishment of trees in both size and quantity within this specific ecological category can result in soil erosion and reduced water availability. These effects arise from a combination of factors, including decreased transpiration, heightened evaporation, and the difficulty to access deep soil water owing to the absence of extensive root systems (Dai et al., 2023). Consequently, the escalating salinity gradients and diminished flow of essential soil nutrients and water necessary for the thriving of mangroves result in a state of deprivation sometimes referred to as 'starvation.'

Correlation and regression analysis

The correlation coefficients and regression analysis conducted in this study align with the findings of Trettin et al. (2015) and Purnamasari et al. (2020). These previous studies found favourable associations between tree height and DBH in their respective study areas. In contrast to the correlations reported in both natural and degraded ecosystems, the restored area exhibits small positive correlations between these growth metrics. This may indicate an unequal distribution of tree structural factors within the restored region. Marziliano et al. (2019) propose that the decline in height growth among trees may be attributed to age and diameter development, but the variation in tree size within a stand might be influenced by factors such as drought, extreme temperatures, and wind. Competition and architectural development are mutually influencing and dynamic processes within ecosystems that have undergone restoration. As a plant undergoes growth, its structural composition undergoes modifications, thereby influencing its immediate surroundings and modifying the available resources for both the plant itself and neighbouring organisms. In conjunction with the struggle for resources, such as light, the structure of trees undergoes a steady transformation, wherein larger trees exhibit enhanced development, hence surpassing smaller trees in competitive advantage (Ford et al., 2014). It is important to acknowledge that the correlation between DBH and BA is mostly attributed to the observation that BA is dependent on DBH, meaning that they exhibit a direct proportional association (Chukwu & Osho, 2018).

CONCLUSIONS

The findings of our study validate our hypothesis since there are considerable variations in tree growth, density, variety, and distribution across different types of mangrove ecosystems throughout the coastline of Guyana. Significant discrepancies were observed in the diversity, density, and distribution patterns between the restored and degraded habitats. However, variations in the biophysical characteristics were mostly visible in the natural and degraded ecosystems. In general, trees within both natural and restored ecosystems exhibit higher levels of ecosystem resistance and resilience in comparison to the degraded regions. The findings of our study provide additional evidence to support the idea that assessing the occurrence of mangrove vegetation, particularly trees, in different types of ecosystems over a period of time can serve as an indicator of their ecological state as well as their ability to withstand and recover from environmental stresses.

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