

CARBON STOCK UNVEILS THE CAPACITY OF MANGROVE RESILIENCE AT SUNGAI PULAI (JOHOR), MALAYSIA

Wolswijk G^{1, 2}, Satyanarayana B^{1, 3, 4, 5, *}, Ibrahim SA¹, Muhammad Naim NA¹, Zamri NAS Z¹, Idris I¹, Redzuan NS², Baharuddin N², Mohd-Taib FS⁶, Neela V⁷, Dahdouh-Guebas F^{3, 4, 8}

¹Mangrove Research Unit (MARU), Institute of Oceanography and Environment (INOS), Universiti Malaysia Terengganu (UMT), Kuala Nerus 21030, Malaysia

²Faculty of Science and Marine Environment (FSSM), Universiti Malaysia Terengganu (UMT), Kuala Nerus 21030, Malaysia

³Mangrove Specialist Group (MSG), Species Survival Commission (SSC), International Union for the Conservation of Nature (IUCN), c/o Zoological Society of London, London, United Kingdom

⁴Systems Ecology and Resource Management Research Unit (SERM), Université Libre de Bruxelles-ULB, 1050 Brussels, Belgium

⁵Global Mangrove Alliance—Malaysia Chapter (GMA-MC), Jalan Damansara, Taman Tun Dr. Ismail, 60000 Kuala Lumpur, Malaysia

⁶Department of Biological Sciences and Biotechnology, Universiti Kebangsaan Malaysia (UKM), Bangi, Selangor 43600, Malaysia

⁷Department of Medical Microbiology, Faculty of Medicine and Health Sciences, Universiti Putra Malaysia (UPM), Serdang, 43400 Selangor, Malaysia

⁸Ecology & Biodiversity Research Unit, Department of Biology, Vrije Universiteit Brussel-VUB, 1050 Brussels, Belgium

*satyam2149@gmail.com

Submitted November 2025; accepted January 2026

Mangrove forests are critical blue carbon ecosystems, yet their carbon stocks are influenced by both natural growth and human disturbance. This study presents one of the first comprehensive evaluations of tree structural parameters (density, basal area) and biomass carbon across a disturbance gradient in the Sungai Pulai Forest Reserve, Johor in Malaysia. Six sites were surveyed, ranging from undisturbed upstream (Sungai Redan) to downstream areas affected by infrastructure development, using 10 × 10 m plots along 100 m transects. *Rhizophora apiculata* dominated most sites, while *Bruguiera cylindrica*, *Ceriops tagal*, and *Xylocarpus granatum* were less frequent. Carbon stocks did not vary markedly with disturbance, suggesting resilience and comparable sequestration potential across the sites. Interspecific variation was evident, with *Sonneratia* and *Avicennia* spp. storing the highest per-tree carbon due to their large trunk diameter and basal area characteristics. These species-specific differences underscore the importance of maintaining diversity and structural integrity. Our findings provide valuable baseline data for national blue carbon accounting and conservation planning. In order to safeguard the climate mitigation role of Sungai Pulai, further clearing of mangroves must be avoided, and management activities should focus on long-term monitoring to detect subtle ecological changes over time.

Keywords: Mangrove forest, biomass carbon, anthropogenic disturbance, vegetation structure, blue carbon

INTRODUCTION

Mangrove forests play a critical role in global carbon cycling, serving as one of the most carbon-dense ecosystems on Earth. Through their high rates of primary productivity and efficient carbon burial in anoxic sediments, mangroves contribute significantly to climate regulation and coastal resilience (Alongi 2020, Donato et al. 2011). Beyond their role as a carbon sink, mangrove forests also provide a wide range of ecosystem goods and services vital for coastal environments

and human well-being (Dabalà et al. 2023). They act as natural barriers, protecting shorelines from erosion, storm surges, and waves (Dahdouh-Guebas et al. 2005), while supporting nursery and feeding grounds of diverse sedimentary, aquatic and tree hosting fauna (Cannicci et al. 2008, Reid et al. 2008, Dash et al. 2021, Wolswijk et al. 2025). Additionally, mangroves filter pollutants and trap sediments, thereby improving coastal water quality (Lewis et al. 2015). Both the ecological

and socioeconomic importance of mangroves underscore the need to conserve remaining natural stands and restore degraded areas as integral components of coastal management and blue carbon initiatives.

Globally, the mangrove cover has declined significantly, with a loss of 8600 km² between 1990 and 2020 (Bhowmik et al. 2022), due to both natural and anthropogenic disturbances such as sea level rise, extreme weather events, deforestation, and land conversion (Akram et al. 2023). In Peninsular Malaysia, Johor is the state with the second largest mangrove cover, totaling approximately 26,818 ha (Parlan et al. 2021). Much of Johor's mangrove forests are gazetted as Permanent Reserved Forests or Forest Reserves, including ~9126 ha of Ramsar Site within the Sungai Pulai forest. However, the rapid industrialisation, together with coastal urban development, aquaculture, and agricultural activities, caused an immense loss to this mangrove ecosystem (OECD 2018). Among others, the establishment of Tanjung Pelepas port in 2000, Tanjung Bin power plant in 2006–2007, ATB crude oil terminal in 2012, and Forest City in 2016, in the downstream of Sungai Pulai, are prominent. Meanwhile, changes in the hydrological conditions, sedimentation, and nutrient inputs are also bound to affect the overall stability and carbon storage of the mangrove ecosystems (Allais et al. 2024).

Despite the ecological importance of Sungai Pulai Forest Reserve, comprehensive assessments of mangrove species composition, vegetation structural characteristics, and biomass carbon remain limited. In this study, we aim to provide an updated and detailed evaluation of these parameters along the gradient of less to more disturbed habitat conditions, thereby validating mangrove vegetation structure versus carbon stock in Sungai Pulai. Specifically, the main objectives include - (i) to evaluate spatial variations in species composition and forest structural parameters (density, basal area, etc.) at selected sites between the upstream and the downstream, and (ii) to quantify aboveground and belowground biomass carbon stocks linked to the mangrove vegetation structure.

We hypothesise that the sampling sites in close proximity to the human encroachments would exhibit less forest structural complexity and reduced biomass carbon stocks, and the species

composition would vary along the gradient of disturbance between the upstream and the downstream locations.

MATERIALS AND METHODS

Study area

This study was conducted in the Sungai Pulai Forest Reserve, located in the southwestern region of Johor of Peninsular Malaysia (1°21'–1°26' N, 103°30'–103°37' E). The Sungai Pulai estuarine complex hosts one of the largest and best-preserved mangrove ecosystems in Malaysia, representing a critical component of the country's southern coastal wetland network. The area is characterised by a tropical humid climate, with a mean annual temperature of around 27 °C and average annual rainfall exceeding 2,000 mm (Nojumuddin et al. 2015). Six sampling sites were established between Sungai Redan in the upstream to Sungai Pulai in the downstream (Figure 1). The upstream sites (Sts. 1–2) are rather located in a pristine zone, dominated by *Rhizophora apiculata* Blume and *R. mucronata* Lam. stands, with no physical infrastructure developments or human encroachments nearby. In contrast, the downstream sites (Sts. 5–6) are close to several industrial establishments (port, power plant, oil terminal) and land conversion (Forest City) episodes, which could bring significant alterations to hydrological and sediment conditions. The intermediate sites (Sts. 3–4) can represent a transition zone, exhibiting mixed species composition and moderate disturbance levels in the vicinity (Figure 1).

Vegetation inventory

At each site, a 100 m transect with four 10 m × 10 m plots at 20 m intervals, was established from the waterfront to the back mangrove. Within each plot, all mangrove trees with a diameter > 2.5 cm at 1.3 m above the ground were identified to species level (Tomlinson 2016). The trunk diameter (D_{130}) was measured using a diameter tape, while tree height was estimated with a clinometer (Suunto PM-5, Finland). In order to assess natural regeneration inside the plot, four 1 m × 1 m subplots were placed at the corners, and the number of seedlings per species was counted.

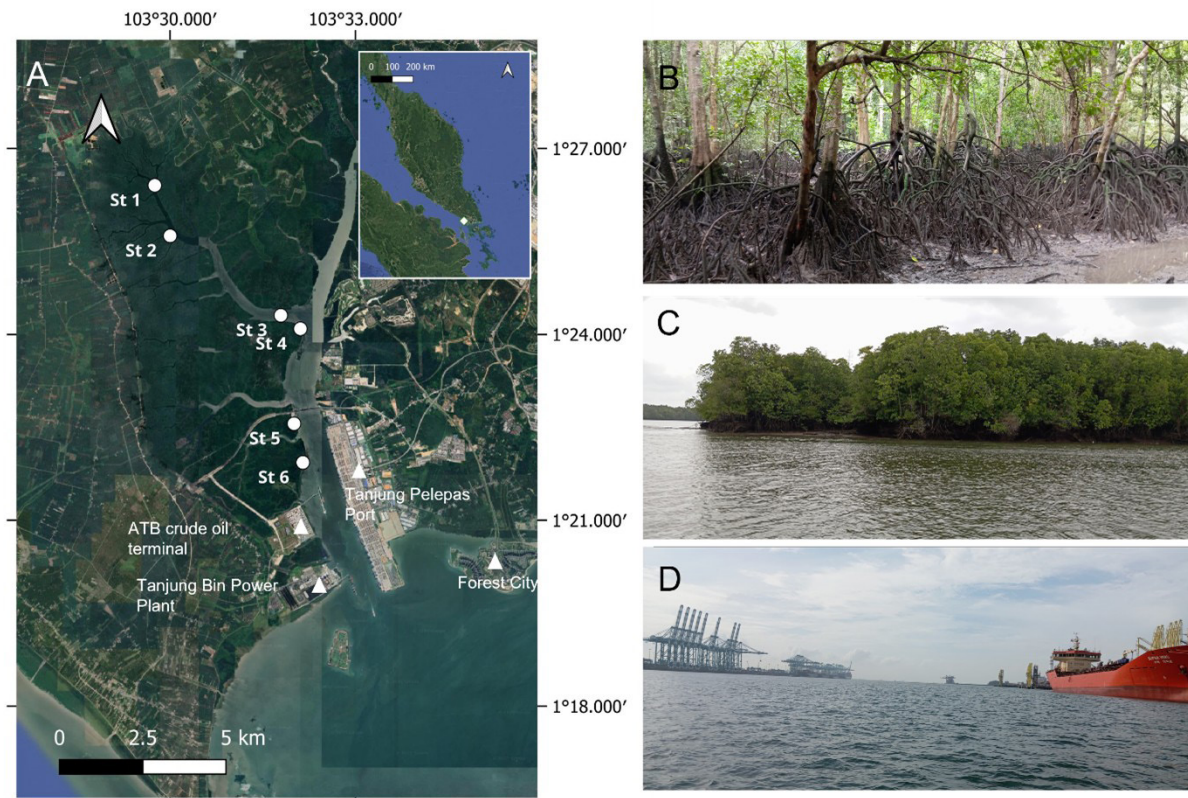


Figure 1 (A) Location of the sampling sites covering Sungai Redan in the upstream and Sungai Pulai in the downstream at Johor, Malaysia; (B) Dense *Rhizophora* stands at Sungai Redan (Sts. 1–2); (C) Mixed mangrove species composition in the intermediate location (Sts. 3–4); (D) Transshipment port and crude oil terminal on the banks of Sungai Pulai (Sts. 5–6) (photos by Behara Satyanarayana) (Base map: Google Satellite imagery © Google Earth, 2025. Map created using QGIS.)

Data analyses

The vegetation structure of the forest was evaluated by calculating the density and basal area of each species in the sampling sites through the following equations (Ellison 2012):

$$\text{Density (stems ha}^{-1}\text{)} = \frac{\text{number of stems/trees}}{\text{plot area (m}^2\text{)}} 10,000 \quad (1)$$

$$\text{Basal area (cm}^2\text{)} = \frac{\pi(D_{130})^2}{4} \frac{0.0001}{\text{plot area (m}^2\text{)}} \quad (2)$$

where, D_{130} stands for the stem diameter at 130 cm above the ground. In order to calculate the values of each variable per site, the average of the values per plot over the total number of plots was considered. For basal area, the unit was further converted into $\text{m}^2 \text{ ha}^{-1}$, taking into account the plot size of 100 m^2 .

In order to derive the species’ importance value (IV), relative density, relative dominance, and relative frequency were calculated per site for each species as follows (Dahdouh-Guebas & Koedam 2006):

$$\text{Relative density (\%)} = \frac{\text{number of trees of each species}}{\text{total number of trees}} 100 \quad (3)$$

$$\text{Relative dominance (\%)} = \frac{\text{Basal Area of each species}}{\text{total Basal Area}} 100 \quad (4)$$

$$\text{Relative frequency (\%)} = \frac{\text{frequency of a species}}{\text{frequency of all species}} 100 \quad (5)$$

where, the frequency of each species was calculated as follows:

$$\text{Frequency} = \frac{\text{number of plots with a species}}{\text{total number of plots}} \quad (6)$$

$$\text{Importance Value} = \text{R. density} + \text{R. dominance} + \text{R. frequency} \quad (7)$$

The complexity index of each site was then calculated by integrating the number of species, stand density, basal area, and mean tree height (Holdridge et al. 1971). To assess compositional similarity among sites, a non-metric multidimensional scaling (NMDS) ordination was conducted based on Bray–Curtis dissimilarity using the vegan package (Oksanen et al. 2022) in R version 4.5.1 (R Core Team 2024).

Both aboveground biomass (AGB) and belowground biomass (BGB) were estimated using the general allometric equations from Komiyama et al. (2008) as follows:

$$\text{AGB} = 0.251 \rho_w D_{130}^{2.46} \quad (8)$$

$$\text{BGB} = 0.199 (\rho_w 0.899) D_{130}^{2.22} \quad (9)$$

where, ρ_w is the species-specific wood density as found in the literature (Table 1) and D_{130} is the diameter at 130 cm from the base of the tree.

Finally, the biomass carbon was calculated using a carbon conversion factor of 0.47 for AGB and 0.39 for BGB (Kauffman & Donato 2012).

In order to evaluate differences among the sites, statistical analyses were performed on tree height, diameter, and biomass carbon. Data normality was tested using the Shapiro–Wilk test. As the data were not normally distributed, non-parametric analyses were applied, including the Kruskal–Wallis test followed by a post-hoc test for pairwise comparisons. All statistical analyses were carried out using Microsoft Excel and R software version 4.5.1.

Table 1 Wood density (ρ_w) values used for species-level biomass estimates at Sungai Pulai, Johor

Species	ρ_w (g cm ⁻³)	Source
<i>Rhizophora apiculata</i>	0.770	Komiyama et al. 2005
<i>Rhizophora mucronata</i>	0.701	Komiyama et al. 2005
<i>Bruguiera cylindrica</i>	0.749	Komiyama et al. 2005
<i>Bruguiera gymnorhiza</i>	0.699	Komiyama et al. 2005
<i>Bruguiera parviflora</i>	0.540	Ismail et al. 2015
<i>Xylocarpus granatum</i>	0.528	Komiyama et al. 2005
<i>Ceriops tagal</i>	0.746	Komiyama et al. 2005
<i>Sonneratia alba</i>	0.475	Komiyama et al. 2005
<i>Avicennia</i> spp.	0.506	Komiyama et al. 2005

RESULTS

A total of nine mangrove species were recorded across the six sampling stations in the Sungai Pulai Forest Reserve (Table 1). Tree density ranged from 1550 trees ha⁻¹ (St. 4) to 3675 trees ha⁻¹ (St. 5), while basal area varied between 14.0 m² ha⁻¹ (St. 5) and 29.8 m² ha⁻¹ (St. 2). *Rhizophora apiculata* exhibited the highest densities at most sampling sites, reaching 1775 trees ha⁻¹ (St. 1) and contributing basal areas up to 15.5 m² ha⁻¹ (St. 2). Other common species included *Bruguiera cylindrica* (L.) Blume (up to 2500 trees ha⁻¹ in St. 5) and *B. parviflora* (Roxb.) Wight & Arn. ex Griff. (up to 800 trees ha⁻¹ in St. 6). Importance Value (IV) scores ranged from 5.6 (*B. gymnorhiza* (L.) Lam. at St. 1) to 127.5 (*B. cylindrica* at St. 5), indicating a wide variation in species-level dominance among the sites. Mangrove richness per site varied from 5 to 9 species, with the highest diversity at St. 4 (Table 2).

The complexity index varied among six sampling sites (Figure 2), with the highest being found at St. 2 (88.22), followed by St. 4 (70.24) and St. 1 (65.03), and the lowest at St. 3 (29.50).

Table 2 Tree structural parameters of the mangrove vegetation at six sampling sites in Sungai Pulai Forest Reserve

	Density (stems ha ⁻¹)	basal area (m ² ha ⁻¹)	Rel. Den. (%)	Rel. Dom. (%)	Freq.	Rel. Freq. (%)	IV	Rank
Station 1								
<i>R. apiculata</i>	1775	14.4	44.9	55.7	1.0	20.0	120.7	1
<i>X. granatum</i>	450	6.5	11.4	23.3	1.0	20.0	54.7	2
<i>R. mucronata</i>	525	3.4	13.3	14.0	0.8	15.0	42.3	3
<i>C. tagal</i>	500	1.1	12.7	4.1	1.0	20.0	36.7	4
<i>B. parviflora</i>	650	0.6	16.5	2.3	0.8	15.0	33.8	5
<i>B. cylindrica</i>	25	0.1	0.6	0.5	0.3	5.0	6.1	6
<i>B. gymnorhiza</i>	25	0.0	0.6	0.0	0.3	5.0	5.6	7
Station 2								
<i>R. apiculata</i>	1300	15.5	39.7	51.1	1.0	21.1	111.8	1
<i>B. gymnorhiza</i>	700	2.8	21.4	9.2	1.0	21.1	51.6	2
<i>B. cylindrica</i>	800	2.1	24.4	6.9	0.8	15.8	47.1	3
<i>X. granatum</i>	250	6.1	7.6	20.2	0.8	15.8	43.7	4
<i>C. tagal</i>	75	1.5	2.3	4.8	0.8	15.8	22.9	5
<i>B. parviflora</i>	100	1.9	3.1	6.2	0.3	5.3	14.5	6
<i>R. mucronata</i>	50	0.5	1.5	1.6	0.3	5.3	8.4	7
Station 3								
<i>R. apiculata</i>	700	6.0	25.0	34.5	0.8	13.0	72.5	1
<i>B. gymnorhiza</i>	525	4.3	18.8	24.3	1.0	17.4	60.5	2
<i>R. mucronata</i>	450	2.6	16.1	14.9	0.8	13.0	44.0	3
<i>B. cylindrica</i>	550	0.7	19.6	3.9	1.0	17.4	41.0	4
<i>X. granatum</i>	175	2.9	6.3	16.8	0.8	13.0	36.1	5
<i>C. tagal</i>	200	0.9	7.1	5.0	1.0	17.4	29.5	6
<i>B. parviflora</i>	200	0.1	7.1	0.6	0.5	8.7	16.4	7
Station 4								
<i>B. parviflora</i>	725	3.6	19.7	16.8	1.0	13.8	50.3	1
<i>R. mucronata</i>	550	4.5	15.0	20.9	1.0	13.8	49.6	2
<i>R. apiculata</i>	650	3.4	17.7	15.6	1.0	13.8	47.1	3
<i>B. gymnorhiza</i>	475	2.4	12.9	11.2	1.0	13.8	37.9	4
<i>C. tagal</i>	650	0.9	17.7	4.4	1.0	13.8	35.9	5
<i>X. granatum</i>	300	2.4	8.2	10.9	1.0	13.8	32.8	6
<i>B. cylindrica</i>	225	1.4	6.1	6.6	0.8	10.3	23.1	7
<i>S. alba</i>	50	1.9	1.4	8.7	0.3	3.4	13.6	8
<i>Avicennia</i> spp.	50	1.1	1.4	4.9	0.3	3.4	9.7	9
Station 5								
<i>B. cylindrica</i>	2500	6.6	68.5	28.2	1.0	30.8	127.5	1
<i>R. apiculata</i>	775	15.4	21.2	65.2	1.0	30.8	117.2	2
<i>B. sexangula</i>	100	1.1	2.7	4.8	0.8	23.1	30.7	3
<i>X. granatum</i>	200	0.1	5.5	0.6	0.3	7.7	13.7	4
<i>B. gymnorhiza</i>	75	0.3	2.1	1.1	0.3	7.7	10.9	5

	Density (stems ha ⁻¹)	basal area (m ² ha ⁻¹)	Rel. Den. (%)	Rel. Dom. (%)	Freq.	Rel. Freq. (%)	IV	Rank
Station 6								
<i>R. apiculata</i>	1000	12.2	31.5	54.5	1.0	25.0	111.0	1
<i>B. cylindrica</i>	1075	4.9	33.9	21.8	0.8	18.8	74.4	2
<i>B. parviflora</i>	800	2.9	25.2	13.0	0.8	18.8	56.9	3
<i>B. gymnorhiza</i>	200	0.6	6.3	2.9	0.8	18.8	27.9	4
<i>Avicennia</i> spp.	50	1.5	1.6	6.9	0.3	6.3	14.7	5
<i>R. mucronata</i>	25	0.2	0.8	0.9	0.3	6.3	7.9	6
<i>C. tagal</i>	25	0.0	0.8	0.1	0.3	6.3	7.1	7

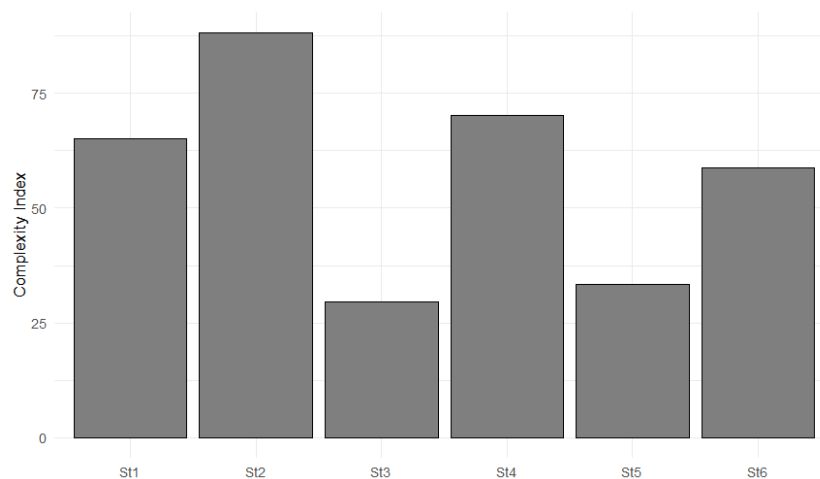


Figure 2 Complexity index of the six sampling sites (Sts. 1–6) at Sungai Redan and Sungai Pulai in Johor

The non-metric multidimensional scaling (NMDS) ordination revealed distinct clustering patterns among the six sampling sites (Figure 3). While Sts. 5–6 were positioned separately on the right side of the ordination space, indicating their species' compositional differences, Sts. 1–2 clustered near Sts. 3–4 on the left side, reflecting similarity in their community structure.

Mean stem diameter and height (Figure 4) showed some variation among the sites, with St. 2 and St. 6 being significantly different (Table S1) from the others (Kruskal-Wallis test, χ^2 (chi-squared) = 59.93, df = 5, p-value = 1.31×10^{-11} for diameter, and χ^2 (chi-squared) = 49.22, df = 5, p-value = 1.91×10^{-9} for height).

The aboveground biomass (AGB) and belowground biomass (BGB) (Figure 5) showed variation among plots across sites, resulting in total carbon stocks ranging from 98.45 to 150.95 Mg C ha⁻¹, with the lowest values at St. 3 and the highest at St. 1, respectively. However, median carbon stocks among the six sites did not differ significantly (Kruskal-Wallis test, χ^2 = 6.54, df = 5, p = 0.2572).

On the other hand, the individual tree carbon stock across species (Figure 6) revealed significant differences (Kruskal-Wallis, χ^2 = 136.87, df = 9, p = 2.2×10^{-16}). Pairwise comparisons found that *R. apiculata*, *Avicennia* spp., and *S. alba* J.Sm. had significantly higher mean carbon stocks compared to most other species (Table S2). However, the higher standard error for the latter two species indicates a greater variation among their individual trees.

Juvenile density varied markedly among species and sites (Figure 7). *B. cylindrica* showed the highest overall density, reaching up to 18,750 ind. ha⁻¹ at St. 6, followed by *B. parviflora* and *R. apiculata*, with peak values equal to 18,125 ind. ha⁻¹ and 8,125 ind. ha⁻¹, respectively. In contrast, the juveniles of *Avicennia* spp., *S. alba*, and *B. sexangula* were either absent or recorded at very low densities across most sites. St. 2, St. 4, and St. 6 exhibited the highest total juvenile densities, while St. 1 and St. 3 had the lowest.

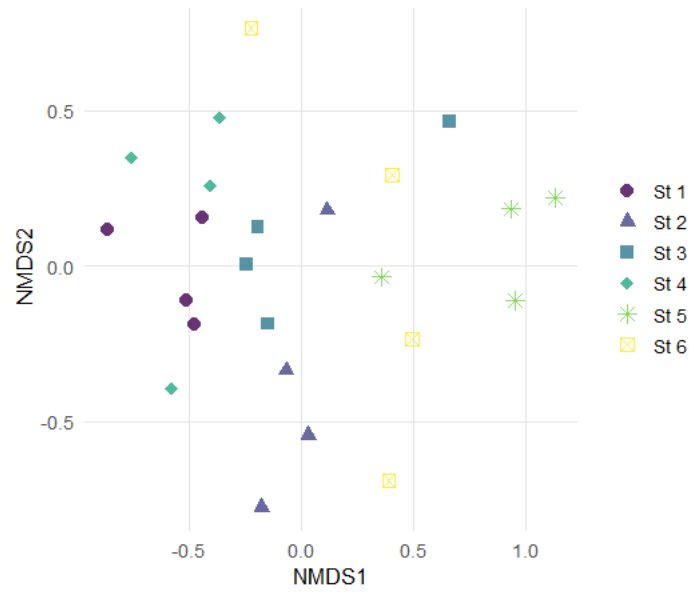


Figure 3 Non-metric multidimensional scaling (NMDS) ordination of the six sampling sites in Sungai Pulai Forest Reserve based on mangrove species composition data (Each point represents one sampling plot, and symbols denote different sites, as in the legend. The stress value = 0.23 shows a fair representation of the overall community structure in reduced-dimensional space)

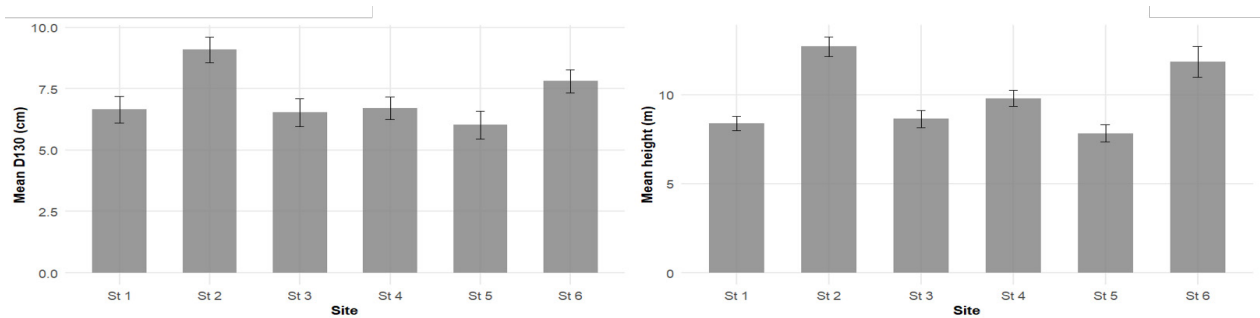


Figure 4 Mean diameter and height of the mangrove trees at six sampling sites in Sungai Pulai Forest Reserve (Error bars indicate standard errors and the statistical differences are reported in Table S1)

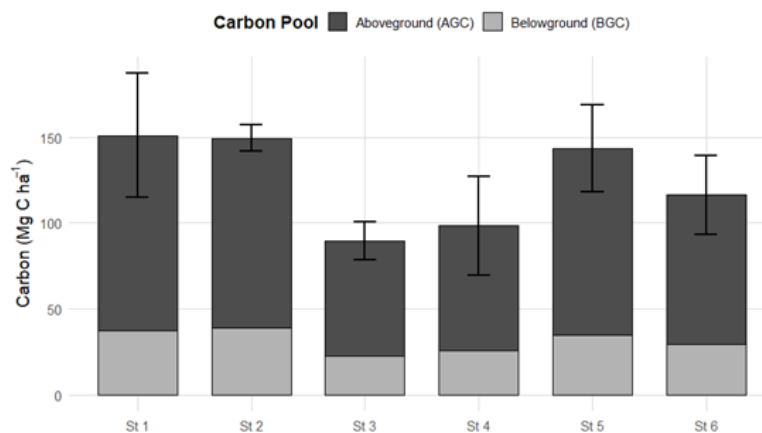


Figure 5 Average carbon stock at the six sampling sites in Sungai Pulai Forest Reserve (Error bars indicate standard error calculated on aboveground (AGC) and belowground carbon (BGC) combined)

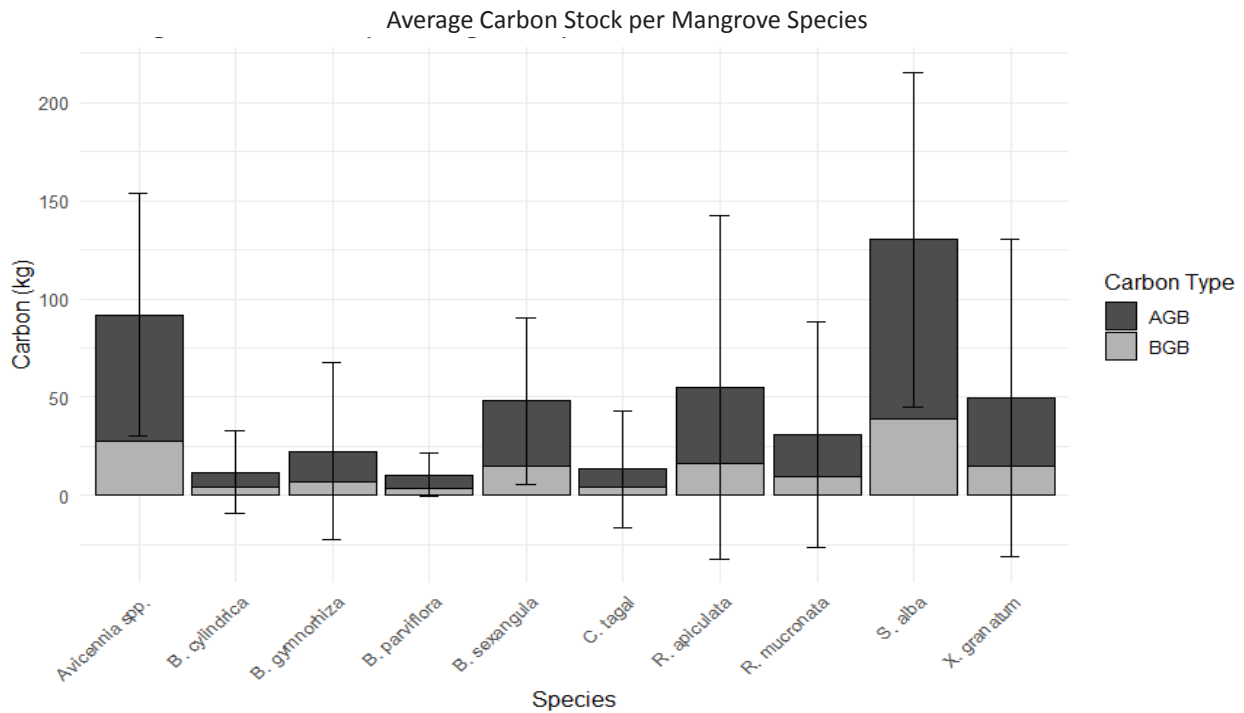


Figure 6 Mean carbon stock of different mangrove species at Sungai Pulai Forest Reserve (Error bars indicate standard error on the AGC and BGC combined)

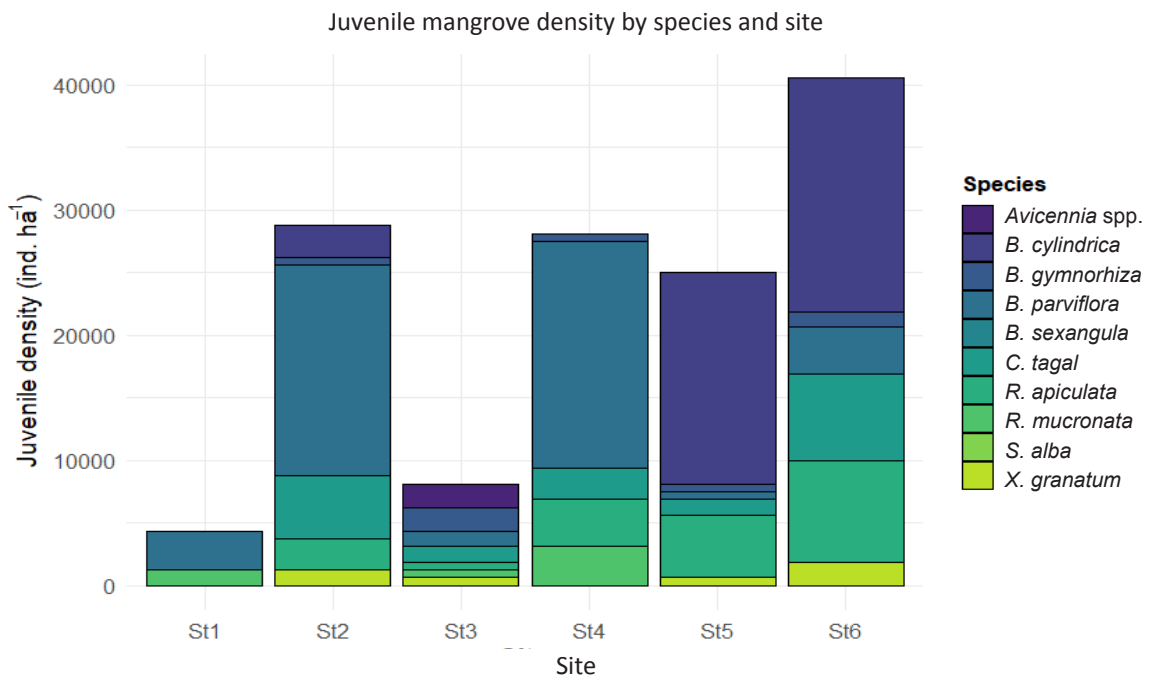


Figure 7 Density of mangrove juveniles of the different species present across the six sampling sites at Sungai Pulai Forest Reserve (ind.: individuals)

DISCUSSION

The present study examined the relationship between mangrove vegetation structure and carbon storage across six sites within the Sungai Pulai Forest Reserve, Johor. Overall, the results highlighted variations in stand structure and species composition strongly influence the spatial patterns of aboveground and belowground carbon stocks. Despite differences in proximity to anthropogenic features, there was no consistent pattern of decline in carbon stock along the gradient of less disturbed upstream sites to the more disturbed downstream sites. The study suggested that carbon storage in these mangrove stands was influenced by a combination of site-specific characteristics, such as species composition, stand age/maturity, and hydrological connectivity, rather than proximity to established buildouts alone. Local hydrodynamics, soil properties, and regeneration history are likely to maintain relatively stable carbon across the vast areas (Saavedra-Hortua et al. 2023). Accordingly, the first hypothesis proposing a directional decline in carbon stock along the disturbance gradient was not supported.

The grouping of sampling sites in the NMDS can be further explained by their species composition as well as biomass carbon. For instance, both *R. apiculata* and *X. granatum* J. Koenig in the less disturbed Sungai Redan (Sts. 1–2) contributed substantially to the total carbon due to their large stem diameter and basal area characteristics. In contrast, the sites dominated by *B. gymnorhiza* and *B. parviflora* or by a mix of smaller-statured *B. cylindrica* and *Ceriops tagal* (Perr.) C.B.Rob. species, particularly in the intermediate location (Sts. 3–4), exhibited lower carbon values. These results also supported the second hypothesis, which implied that species composition and structural attributes were key determinants of carbon stock. However, the co-dominance of *R. apiculata* and *B. cylindrica* in the downstream of Sungai Pulai (Sts. 5–6), where sedimentation is active, could reflect their capacity for natural regeneration and structural recovery with a steady carbon stock. The structural parameters, such as density and basal area, are important for understanding the vegetation growth dynamics (Satyanarayana et al. 2009), and its successful adaptation process

allows carbon accumulation to persist even in the moderately altered surroundings.

Although *S. alba* and *Avicennia* spp. were only recorded as a few individuals, both species exhibited the highest carbon per individual tree. These genera typically occupy seaward or more open zones, where their exposure to tidal action and salinity promotes the development of massive trunks, spreading crowns, and extensive root systems (Twomey & Lovelock 2025). Such morphological traits also result in high individual biomass even at low densities. Similar observations have been reported from Malaysia as well as other Southeast Asian countries (Anjum et al. 2025, Bui et al. 2025, Suhaili et al. 2024, Azman et al. 2021, Ahmed et al. 2021) and support the idea that pioneer species can make substantial per-tree contributions to carbon pools, even if they do not contribute significantly to the total stand storage. Overall, mangrove species composition at Sungai Pulai played a central role in explaining the variability of the carbon stock.

Most recently, Khan et al. (2025) also evaluated the mangrove biomass within Sungai Pulai and reported a total carbon stock of 91.01 Mg C ha⁻¹. However, their lower estimates, in contrast to the present study, were attributable to a different sampling design and spatial coverage. Importantly, they considered only the trees above 5 cm in diameter; unlike the present study, which measured all live mangroves with a diameter >2.5 cm as adult vegetation (Kairo et al. 2002, Goessens et al. 2014). Additionally, their (Khan et al. 2025) sampling approach represents mixed mangrove stands along the main (Sungai Pulai) channel, which might have missed the structural heterogeneity and mature stands of the other locations within the forest reserve. These results underscore the importance of extensive spatial sampling to accurately characterize the carbon storage capacity of mangrove ecosystems, especially in heterogeneous landscapes such as Sungai Pulai. Our total carbon stocks recorded are comparable to previously reported ranges in Malaysia, including up to 219.4 Mg C ha⁻¹ in Matang Mangrove Forest Reserve (Wolswijk et al. 2022) and 99.18 Mg C ha⁻¹ in Delta Kelantan (Rozainah et al. 2018). These values demonstrate that the mangrove forests of southern Peninsular Malaysia continue to serve as significant carbon reservoirs.

While *Rhizophora* species dominate overall carbon stocks, the high individual carbon content of *Sonneratia* and *Avicennia* underlines the ecological and functional value of maintaining diverse zonation patterns. Management efforts should therefore focus on conserving mixed-species stands, which collectively support mangrove resilience and carbon sequestration under the increasing anthropogenic pressure and climate change scenarios.

This structural and compositional diversity is further reflected in the regeneration dynamics across the sites, where patterns of juvenile distribution mirror the adult stand composition and local environmental conditions. Sites dominated by *R. apiculata* and *Bruguiera* spp., such as St. 2 and St. 6, also supported higher densities of conspecific juveniles, suggesting their promising natural recruitment and stable stand dynamics. In contrast, the low juvenile density at St. 1, despite the high adult basal area of *R. apiculata*, may indicate limited propagule establishment or higher seedling mortality, possibly due to altered microtopography or reduced tidal flushing (Van der Stocken et al. 2015). The occurrence of *C. tagal* and *X. granatum* juveniles in mixed stands (e.g., St. 4) points to a diverse regeneration pool that supports structural heterogeneity across the forest. These findings are consistent with previous observations that regeneration success in mangroves depends not only on seed availability but also on hydrological and sedimentary conditions that mediate propagule retention and early growth phenomena (Van der Stocken et al. 2019, Sousa et al. 2007). Overall, the congruence between dominant adult and juvenile taxa suggests that Sungai Pulai is still maintaining an active regeneration process, with the potential to sustain its current community structure and carbon storage capacity despite varying levels of anthropogenic interference.

CONCLUSION

This study provides an updated assessment of mangrove species composition, stand structure, and carbon stocks in the Sungai Pulai Forest Reserve. Despite variation in species composition and structural complexity among sampling sites, the higher total carbon storage at disturbed downstream locations suggest that natural forest dynamics and hydrodynamic processes remain

crucial in buffering the impacts of adjacent land use. The dominance of *R. apiculata* across most sites reflects ecological maturity and resilience, while the high per-tree carbon in *S. alba* and *Avicennia* spp. highlights the role of large, dense-wooded pioneers in biomass accumulation. Continuous monitoring, alongside strict protection against further mangrove loss, is essential to sustain productivity in Sungai Pulai. The integration of site-specific data into local conservation strategies will not only enhance ecosystem resilience but also reinforce Malaysia's coastal protection and climate mitigation commitments.

ACKNOWLEDGEMENTS

This study was fully supported by the Universiti Malaysia Terengganu (UMT) through the Inter-Disciplinary Impact-Driven Research Grant (ID2RG) for the “Mapping the effects of pollutants on mangrove biodiversity at Sungai Pulai (Johor) in relation to (un)disturbed environmental settings” project (Vot No. 55514). The authors gratefully acknowledged UMT science officers Tan Hock Seng, Che Mohd Kamarul Anuar bin Che Abdullah and Azahari bin Muda for their invaluable assistance during fieldwork. We also extend our appreciation to the financial authorities at UMT for their support, and to the Johor Forestry Department for granting permission to conduct this research.

REFERENCES

- AHMED S & KAMRUZZAMAN M. 2021. Species-specific biomass and carbon flux in Sundarbans mangrove forest, Bangladesh: Response to stand and weather variables. *Biomass and Bioenergy* 153: 106215. <https://doi.org/10.1016/j.biombioe.2021.106215>
- AKRAM H, HUSSAIN S, MAZUMDAR P, CHUA KO, BUTT TE & HARIKRISHNA JA. 2023. Mangrove health: a review of functions, threats, and challenges associated with Mangrove Management Practices. *Forests* 14: 1698. <https://doi.org/10.3390/f14091698>
- ALLAIS L, THIBODEAU B, KHAN NS, CROWE SA, CANNICCI S & NOT C. 2024. Salinity, mineralogy, porosity, and hydrodynamics as drivers of carbon burial in urban mangroves from a megacity. *Science of the Total Environment*. 912: 168955. <https://doi.org/10.1016/j.scitotenv.2023.168955>
- ALONGI DM. 2022. Impacts of climate change on blue carbon stocks and fluxes in mangrove forests. *Forests* 13: 149. <https://doi.org/10.3390/f13020149>
- ANJUM S, HOSSEN N, ISLAM T & KAMRUZZAMAN M. 2025. Stand structure, species composition and carbon accumulation in the polyhaline zone of the

- Sundarbans mangrove forest, Bangladesh. *Journal of Tropical Forest Science* 37: 118–129. <https://doi.org/10.26525/jtfs2025.37.1.118>
- AZMAN MS, SHARMA S, HAMZAH ML, ZAKARIA RM, PALANIVELLO K & MACKENZIE RA. 2023. Total ecosystem blue carbon stocks and sequestration potential along a naturally regenerated mangrove forest chronosequence. *Forest Ecology and Management* 527: 120611. <https://doi.org/10.1016/j.foreco.2022.120611>
- BHOWMIK AK, PADMANABAN R, CABRAL P & ROMEIRAS MM. 2022. Global mangrove deforestation and its interacting social-ecological drivers: A systematic review and synthesis. *Sustainability* 14(8): 4433. <https://doi.org/10.3390/su14084433>
- BUI KNT, VIEN NN, NGUYEN NT & HUYNH HD. 2025. Biomass, carbon stock, carbon uptake, and oxygen production of *Sonneratia alba*. *Journal of Tropical Forest Science* 37: 463–474. <https://doi.org/10.26525/jtfs2025.37.4.463>
- CANNICCI S, BURROWS D, FRATINI S, SMITH III TJ, OFFENBERG J & DAHDOUH-GUEBAS F. 2008. Faunal impact on vegetation structure and ecosystem function in mangrove forests: a review. *Aquatic botany* 89: 186–200. <https://doi.org/10.1016/j.aquabot.2008.01.009>
- DABALÀ A, DAHDOUH-GUEBAS F, DUNN DC ET AL. 2023. Priority areas to protect mangroves and maximise ecosystem services. *Nature communications* 14: 5863. <https://doi.org/10.1038/s41467-023-41333-3>
- DAHDOUH-GUEBAS F, JAYATISSA LP, DI NITTO D, BOSIRE JO, SEEN DL & KOEDAM N. 2005. How effective were mangroves as a defence against the recent tsunami? *Current biology* 15: R443–R447. <https://doi.org/10.1016/j.cub.2005.06.008>
- DAHDOUH-GUEBAS F & KOEDAM N. 2006. Empirical estimate of the reliability of the use of the Point-Centred Quarter Method (PCQM): Solutions to ambiguous field situations and description of the PCQM+ protocol. *Forest Ecology and Management* 228: 1–18. <https://doi.org/10.1016/j.foreco.2005.10.076>
- DASH B, ROUT SS, LOVARAJU A ET AL. 2021. Macrobenthic community of a tropical bay system revisited: Historical changes in response to anthropogenic forcing. *Marine Pollution Bulletin* 171: 112775. <https://doi.org/10.1016/j.marpolbul.2021.112775>
- DONATO DC, KAUFFMAN JB, MURDIYARSO D, KURNIANTO S, STIDHAM M & KANNINEN M. 2011. Mangroves among the most carbon-rich forests in the tropics. *Nature geoscience* 4(5): 293–297. <https://doi.org/10.1038/ngeo1123>
- ELLISON JC. 2012. *Climate Change Vulnerability Assessment and Adaptation Planning for Mangrove Systems*. World Wildlife Fund, Washington, DC.
- GOESSENS A, SATYANARAYANA B, VAN DER STOCKEN T ET AL. 2014. Is Matang Mangrove Forest in Malaysia sustainably rejuvenating after more than a century of conservation and harvesting management? *PloS One* 9(8): e105069. <https://doi.org/10.1371/journal.pone.0105069>
- HOLDRIDGE LR & GRENKE WC. 1971. *Forest environments in tropical life zones: a pilot study*. FAO-AGRIS. Pergamon press, Oxford.
- ISMAIL MH, ZAKI PH & HAMED AA. 2015. Wood density and carbon estimates of mangrove species in Kuala Sepetang, Perak, Malaysia. *Malaysian Forester* 78: 115–124.
- KAIRO JG, DAHDOUH-GUEBAS F, GWADA PO, OCHIENG C & KOEDAM N. 2002. Regeneration status of mangrove forests in Mida creek, Kenya: a compromised or secured future? *AMBIO: A Journal of the Human Environment* 31: 7–8. <https://doi.org/10.1579/0044-7447-31.7.562>
- KAUFFMAN JB & DONATO DC. 2012. *Protocols for the measurement, monitoring and reporting of structure, biomass and carbon stocks in mangrove forests*. Vol. 86, p. 7. CIFOR. Bogor, Indonesia.
- KHAN WR, GIANI M, BEVILACQUA S ET AL. 2025. Derivation of allometric equations and carbon content estimation in mangrove forests of Malaysia. *Environmental and Sustainability Indicators* 26: 100618. <https://doi.org/10.1016/j.indic.2025.100618>
- KOMIYAMA A, ONG JE & POUNGPARN S. 2008. Allometry, biomass, and productivity of mangrove forests: A review. *Aquatic Botany* 89: 128–137. <https://doi.org/10.1016/j.aquabot.2007.12.006>
- KOMIYAMA A, POUNGPARN S & KATO S. 2005. Common allometric equations for estimating the tree weight of mangroves. *Journal of Tropical Ecology* 21: 471–477. <https://doi.org/10.1017/S0266467405002476>
- LEWIS MA & RUSSELL MJ. 2015. Contaminant profiles for surface water, sediment, flora and fauna associated with the mangrove fringe along middle and lower eastern Tampa Bay. *Marine Pollution Bulletin* 95: 273–282. <https://doi.org/10.1016/j.marpolbul.2015.04.001>
- NOJUMUDDIN N S, YUSOF F & YUSOP Z. 2015. Identification of rainfall patterns in Johor. *Applied Mathematical Sciences* 9: 1869–1888. <http://dx.doi.org/10.12988/ams.2015.5133>
- OECD. 2018. *Building Resilient Cities: An Assessment of Disaster Risk Management Policies in Southeast Asia*. OECD Green Growth Studies. OECD Publishing, Paris.
- OKSANEN J, BLANCHET FG, FRIENDLY M ET AL. 2022. Vegan: Community Ecology Package. *R Package Version 2.6-4*. <https://CRAN.R-project.org/package=vegan>
- PARLAN I, HUSIN TM & HUSIN HIM. 2021. *An Overview of Wetlands in Malaysia*. Forest Research Institute Malaysia (FRIM), Malaysia.
- R CORE TEAM. 2024. R: A language and environment for statistical computing. *R Foundation for Statistical Computing*, Vienna, Austria. <https://www.R-project.org/>
- REID DG, DYAL P, LOZOUET P, GLAUBRECHT M & WILLIAMS ST. 2008. Mudwhelks and mangrove: the evolutionary history of an ecological association (Gastropoda: Potamididae). *Molecular Phylogenetics and Evolution* 47: 680–699. <https://doi.org/10.1016/j.ympev.2008.01.003>
- ROZAINAH MZ, NAZRI MN, SOFAWI AB, HEMATI Z & JULIANA WA. 2018. Estimation of carbon pool in soil, above and below ground vegetation at different types of mangrove forests in Peninsular Malaysia. *Marine Pollution Bulletin*. 37: 237–245. <https://doi.org/10.1016/j.marpolbul.2018.10.023>

- SAAVEDRA-HORTUA D, NAGELKERKEN I, ESTUPINAN-SUAREZ L M & GILLIS LG. 2023. Effects of connectivity on carbon and nitrogen stocks in mangrove and seagrass ecosystems. *Science of the Total Environment* 896: 164829. <https://doi.org/10.1016/j.scitotenv.2023.164829>
- SATYANARAYANA B, RAMAN AV, MOHD-LOKMAN H, DEHAIRS F, SHARMA VS & DAHDOUH-GUEBAS F. 2009. Multivariate methods distinguishing mangrove community structure of Coringa in the Godavari Delta, East coast of India. *Aquatic Ecosystem Health & Management* 12: 401–408. <https://doi.org/10.1080/14634980903334074>
- SOUSA WP, KENNEDY PG, MITCHELL BJ & ORDÓÑEZ LBM. 2007. Supply-side ecology in mangroves: do propagule dispersal and seedling establishment explain forest structure? *Ecological Monographs* 77: 53–76. <https://doi.org/10.1890/05-1935>
- SUHAILI NS, HATTA SM, SALLEH E & BESAR NA. 2024. Estimating the total carbon stock in the mangrove forest of Kota Marudu, Sabah, Malaysia. *Journal of Sustainability Science and Management* 19: 202–214. <http://doi.org/10.46754/jssm.2024.07.012>
- TOMLINSON PB. 2016. *The botany of mangroves*. Cambridge University Press, Cambridge.
- TWOMEY AJ & LOVELOCK CE. 2025. Variation in mangrove geometric traits among genera and climate zones. *Estuaries and Coasts* 48: 55. <https://doi.org/10.1007/s12237-025-01487-3>
- VAN DER STOCKEN T, DE RYCK DJ, VANSCHOENWINKEL B ET AL. 2015. Impact of landscape structure on propagule dispersal in mangrove forests. *Marine Ecology Progress Series* 524: 95–106. <https://doi.org/10.3354/meps11206>
- VAN DER STOCKEN T, WEE AK, DE RYCK DJ ET AL. 2019. A general framework for propagule dispersal in mangroves. *Biological Reviews* 94: 1547–1575. <https://doi.org/10.1111/brv.12514>
- WOLSWIJK G, BARRIOS TRULLOLS A, HUGÉ J ET AL. 2022. Can mangrove silviculture be carbon neutral? *Remote Sensing* 14: 2920. <https://doi.org/10.3390/rs14122920>
- WOLSWIJK G, BERNARD T, SLEUTEL J ET AL. 2025. Avifaunal communities as indicators of silvicultural impacts in mangrove forests. *Journal of Environmental Management* 383: 125414. <https://doi.org/10.1016/j.jenvman.2025.125414>

SUPPLEMENTARY INFORMATION

Table S1 Pairwise comparison (Wilcoxon Test) for D_{130} and Height among all the sampling sites (ns: not significant)

Comparison	D_{130} p-value	Height p-value	Significance
St 1 – St 2	4.6e-06	2.7e-08	Different
St 1 – St 3	0.737	0.665	ns
St 1 – St 4	0.244	0.029	Significant for Height
St 1 – St 5	0.303	0.146	ns
St 1 – St 6	0.00015	6.0e-06	Significant
St 2 – St 3	4.3e-05	3.4e-06	Significant
St 2 – St 4	0.00014	0.00012	Significant
St 2 – St 5	1.9e-08	7.1e-10	Significant
St 2 – St 6	0.126	0.073	ns
St 3 – St 4	0.371	0.089	ns
St 3 – St 5	0.190	0.054	ns
St 3 – St 6	0.00036	3.6e-05	Significant
St 4 – St 5	0.013	0.00021	Significant
St 4 – St 6	0.0083	0.010	Significant
St 5 – St 6	7.0e-08	5.9e-09	Significant

Table S2 Pairwise Wilcoxon Results for Total Biomass Carbon (by Species)

Comparison	p-value	Significance
<i>Avicennia</i> spp. – <i>B. cylindrica</i>	0.0416	Significant
<i>Avicennia</i> spp. – <i>B. gymnorhiza</i>	0.0538	ns
<i>Avicennia</i> spp. – <i>B. parviflora</i>	0.0416	Significant
<i>Avicennia</i> spp. – <i>B. sexangula</i>	0.6858	ns
<i>Avicennia</i> spp. – <i>C. tagal</i>	0.0359	Significant
<i>Avicennia</i> spp. – <i>R. apiculata</i>	0.2772	ns
<i>Avicennia</i> spp. – <i>R. mucronata</i>	0.1581	ns
<i>Avicennia</i> spp. – <i>S. alba</i>	0.6000	ns
<i>Avicennia</i> spp. – <i>X. granatum</i>	0.1286	ns
<i>B. cylindrica</i> – <i>C. tagal</i>	5.1e-05	Highly significant
<i>B. cylindrica</i> – <i>R. apiculata</i>	1.6e-15	Highly significant
<i>B. cylindrica</i> – <i>R. mucronata</i>	3.5e-06	Highly significant
<i>B. cylindrica</i> – <i>S. alba</i>	0.0471	Significant
<i>B. cylindrica</i> – <i>X. granatum</i>	0.636	ns
<i>C. tagal</i> – <i>R. apiculata</i>	3.3e-12	Highly significant
<i>C. tagal</i> – <i>R. mucronata</i>	7.6e-08	Highly significant
<i>C. tagal</i> – <i>X. granatum</i>	0.0328	Significant
<i>R. apiculata</i> – <i>R. mucronata</i>	0.198	ns
<i>R. apiculata</i> – <i>X. granatum</i>	0.0179	Significant
<i>R. mucronata</i> – <i>X. granatum</i>	0.129	ns