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Mangrove species distribution across soil texture gradients in Benoa Bay and Nusa Lembongan, Bali Province, Indonesia

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Abstract. *Dharmayasa IGNP, Sugiana IP, Anantanasakul P. 2025. Mangrove species distribution across soil texture gradients in Benoa Bay and Nusa Lembongan, Bali Province, Indonesia. Biodiversitas 26: 2908-2915.* This study unveils the crucial role of mangrove ecosystems in enhancing coastal resilience and mitigating climate change through carbon sequestration and shoreline stabilization. This study identifies strong relationships between soil particle composition (sand, silt, clay, and gravel) and the distribution of mangrove species across five genera-dominated zones (*Rhizophora*, *Sonneratia*, *Avicennia*, *Bruguiera*, and *Ceriops*) in Bali, Indonesia. By establishing 20 plots at two sites, Benoa Bay and Nusa Lembongan, and quantitatively measuring stand structure (tree and sapling density, diameter, canopy cover, and Mangrove Health Index (MHI) and soil parameters (texture, pH, water content, bulk density, and total organic matter), this study revealed that *Ceriops tagal* dominates soils with 35-45% silt and clay content; *Bruguiera gymnorrhiza* thrives in sandy soils exceeding 60% sand; and *Sonneratia alba* is associated with substrates containing over 20% gravel. Principal component analysis and Pearson correlation reveal significant negative effects of gravel on canopy cover (r: -0.73, $p<0.01$) and MHI (r: -0.74, $p<0.01$), and a positive correlation between sand content and sapling density (r: 0.56, $p<0.01$). These findings not only underscore the critical role of soil texture in mangrove distribution and forest health but also emphasize the need to consider edaphic conditions in restoration and conservation strategies. This knowledge is vital for enhancing ecosystem sustainability and biodiversity.

Keywords: Bali, mangrove, restoration, soil particle composition, species distribution

INTRODUCTION

Mangrove ecosystems play a vital role in maintaining the ecological balance of coastal environments (Ramdhun and Appadoo 2020; Alongi 2021). These intertidal forests, composed of salt-tolerant tree species, serve as critical buffers against coastal erosion, nurseries for marine biodiversity, and reservoirs for blue carbon storage (Sasmito et al. 2020; Amorim et al. 2023). Despite their importance, mangroves remain under considerable threat from anthropogenic pressures such as land conversion, pollution, and climate change (Richards and Friess 2016; Arifanti et al. 2021). To ensure effective conservation and restoration strategies, it is essential to understand the environmental factors that influence the distribution and composition of mangrove species (Sugiana et al. 2022).

One of the primary abiotic factors affecting mangrove distribution is soil characteristics, particularly soil texture or soil fraction (Marchand 2017; Xiong et al. 2018). Soil fraction refers to the relative proportions of sand, silt, and clay particles within the soil matrix (Matus 2021). These components determine several key soil properties, including porosity, permeability, aeration, moisture retention, and nutrient availability (Amorim et al. 2023). In coastal and estuarine zones where mangroves thrive, soil properties can vary significantly across spatial gradients, influencing species occurrence and ecological zonation (Prinasti et al. 2020).

Each mangrove species exhibits specific ecological preferences for certain edaphic conditions. For instance, *Rhizophora* species are typically found in low-energy environments with fine-textured, waterlogged soils dominated by silt and clay, which offer high moisture retention and organic matter accumulation (Gabi et al. 2021; Sugiana et al. 2021). On the other hand, *Avicennia* species can tolerate more saline and aerated conditions, often inhabiting higher intertidal zones with coarser, sandy substrates (Siregar et al. 2022). *Sonneratia* and *Bruguiera* species also demonstrate variable responses to soil texture, highlighting the complex interplay between soil fraction and species adaptability (Nurdiansah and Dharmawan 2021a; Sugiana et al. 2022).

Previous studies in Southeast Asia and other tropical regions have shown strong correlations between soil texture and mangrove species distribution (Lewerissa et al. 2018; Prinasti et al. 2020). However, such studies are still limited, and there remains a gap in understanding these relationships within Indonesian coastal ecosystems, particularly in Bali. Bali presents a unique ecological setting with a mosaic of mangrove habitats ranging from natural, undisturbed stands to areas undergoing active rehabilitation (Andiani et al. 2021). The region's coastal geomorphology, shaped by volcanic activity and tidal influences, contributes to diverse soil profiles and species assemblages (Prinasti et al. 2020; Sugiana et al. 2021).

Understanding the relationship between soil fraction and mangrove species distribution in Bali, Indonesia, is not only ecologically significant but also practical. As mangrove restoration efforts continue across Indonesia, especially in regions affected by land-use change and coastal development, identifying suitable soil conditions for each species can improve planting success and ecological resilience (Kusmana 2014). Moreover, such knowledge can inform spatial planning and ecosystem-based management, ensuring that restoration aligns with the natural edaphic requirements of native mangrove species (Nurdiansah and Dharmawan 2021a).

In addition to soil fraction, other parameters such as pH, water content, bulk density, and organic matter content may interact with soil texture to further influence plant growth and survival (Gao et al. 2019). For example, soils with high clay content often exhibit poor drainage and low oxygen diffusion, creating anoxic conditions that can limit seedling establishment unless matched with tolerant species (Hall et al. 2013; Luo et al. 2019). Conversely, sandy soils may drain quickly but offer low nutrient retention, which may only be suitable for species with adaptive root structures and efficient nutrient uptake mechanisms (Li et al. 2018). Therefore, a comprehensive investigation that includes multiple soil parameters can provide deeper insights into the edaphic drivers of mangrove distribution.

Despite the ecological and management implications, studies specifically examining the role of soil fraction in shaping mangrove species distribution in Bali are scarce (Nurdiansah and Dharmawan 2021b). Most existing research in the region has focused on biodiversity assessments, carbon stock estimations, or the impacts of pollution, while edaphic controls on vegetation patterns remain understudied (Dewi et al. 2021; Sugiana et al. 2022). Given the urgency of mangrove conservation and the increasing emphasis on evidence-based restoration, addressing this knowledge gap is both timely and necessary.

This study aims to analyze the influence of soil fraction on the distribution of mangrove species across selected sites in Bali. By examining variations in sand, silt, and clay content alongside species composition, we seek to identify specific edaphic preferences and potential thresholds for species occurrence. Additional parameters such as soil pH, water content, bulk density, and organic matter content will also be measured to contextualize the findings and assess their potential interactions with soil fraction. The outcomes of this research are expected to contribute to a better understanding of soil-vegetation relationships in mangrove ecosystems and offer practical recommendations for restoration initiatives in Bali and other tropical coastal regions. Ultimately, this study supports broader environmental objectives by promoting ecosystem resilience, enhancing biodiversity, and reinforcing coastal protection through scientifically informed mangrove management.

MATERIALS AND METHODS

Site description

This study was conducted in two locations: Benoa Bay (8.705181°S-8.794777°S, 115.173306°E-115.232200°E) and Nusa Lembongan (8.662261°S-8.691449°S, 115.449883°E-115.471856°E), Bali, Indonesia. Both mangrove ecosystems are predominantly dominated by five mangrove genera: *Rhizophora*, *Sonneratia*, *Avicennia*, *Bruguiera*, and *Ceriops*. The mangrove forest in Benoa Bay is managed by the Ngurah Rai Grand Forest Park Management Unit (UPTD TAHURA Ngurah Rai). In contrast, the mangrove forest in Nusa Lembongan is designated as a protected forest. In this study, we selected four sampling points from each genus-dominated zone (a total of 20 points), with 10 points located in Benoa Bay and 10 points in Nusa Lembongan (Figure 1).

Mangrove community structure measurement

The mangrove stand structure was evaluated through measurements conducted in 20 purposively distributed 10×10 m plots across five genera-dominated zones, with four plots allocated to each zone. Species identification followed standard botanical references (Dharmawan et al. 2020), and individuals were classified based on Diameter at Breast Height (DBH) into tree (≥5 cm) and sapling (<5 cm) categories. Structural parameters such as relative density, relative dominance, and relative frequency were used to calculate the Important Value Index (IVI), following the guidelines of Dharmawan et al. (2020), to provide insights into species dominance within each zone. Canopy cover was quantified through hemispherical photography, with nine images taken per plot using a smartphone with at least 3 MP resolution. ImageJ software was employed to analyze the photographs by calculating the proportion of vegetation pixels to total pixels (Dharmawan 2020). All field measurements were systematically recorded using the MonMang2.0 app (Sugiana et al. 2022).

Soil sampling and analysis

Soil samples were collected using a 5 cm-diameter soil auger at a depth of 0-100 cm, with three replicates taken at each site, approximately 5 meters apart. The collected soil was homogenized, and 200 g was stored in plastic containers for further analysis. Of this, 100 g was oven-dried at 70°C for about 48 hours to determine soil water content based on weight consistency, while another 100 g was dried at 105°C to calculate bulk density by comparing the dry weight to the auger volume. The dried samples were then used for particle size analysis (10 g) and Soil Organic Matter (SOM) assessment (3 g). Particle size distribution was determined using the dry sieve method following ASTM D422 (gravel: >2 mm, sand: 2 mm-75 μm) and the hydrometer method, also in accordance with ASTM D422, for separating silt and clay fractions. SOM was measured using the Loss on Ignition (LOI) method, in which samples were combusted at 550°C following the protocol of Chen et al. (2014).

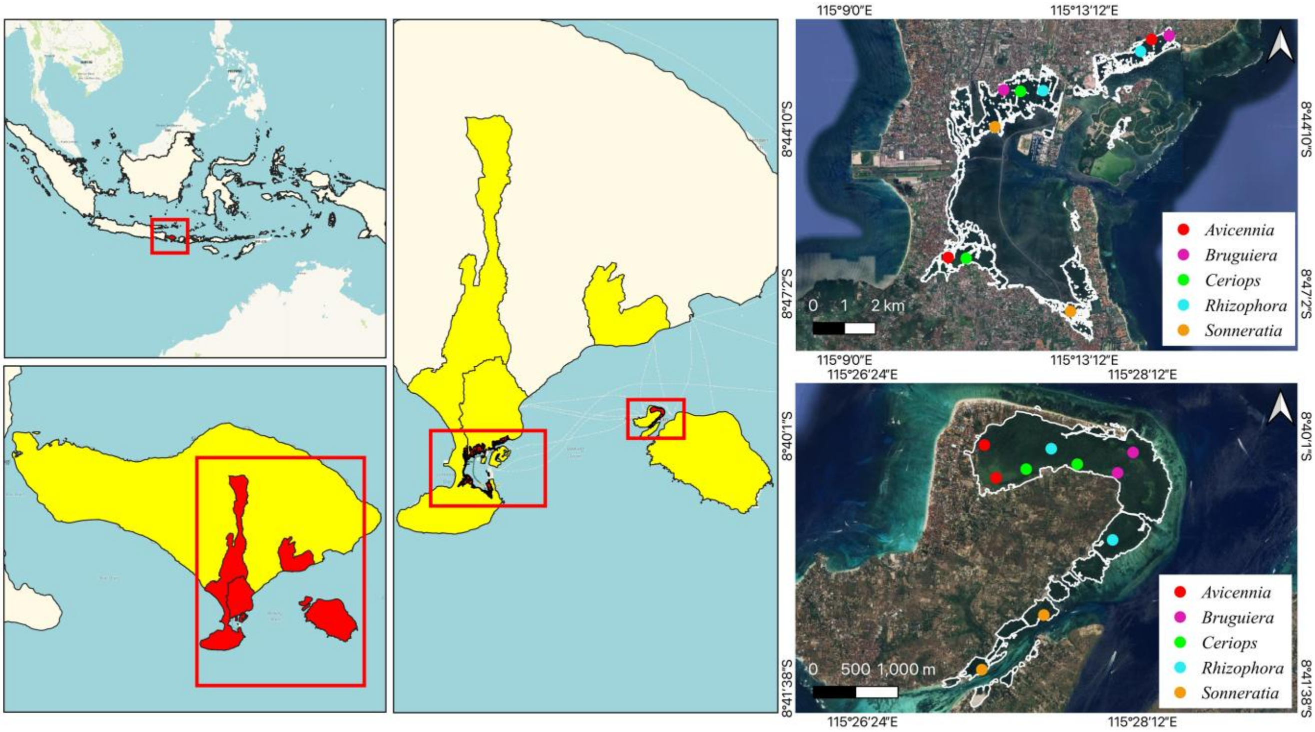

Figure 1. Research station and distribution of data collection plots

Statistical analysis

To evaluate whether significant differences existed in soil fraction and mangrove stand structure across different mangrove zones, an Analysis of Variance (ANOVA) was conducted. The Shapiro-Wilk test confirmed that all univariate data, including soil fractions, other soil properties, and structural parameters of mangroves, were normally distributed ($\rho > 0.05$). To identify which zones differed significantly, a Tukey Honestly Significant Difference (HSD) post hoc test was applied. In addition, the relationship between soil fraction and mangrove stand characteristics was assessed using Pearson correlation analysis, while spatial grouping of zones was explored through Principal Component Analysis (PCA). All statistical analyses, including tests of normality, ANOVA, correlation, and PCA, were carried out using RStudio version 4.0.2 and MVSPW software.

RESULTS AND DISCUSSION

Mangrove community structure

Mangrove stand structure showed significant variation across the five observed zones, with clear differences in tree density, sapling density, trunk diameter, canopy closure, and Mangrove Health Index (MHI) (Table 1). The Rhizophora zone exhibited the highest tree density at 3,895±256 ind ha^{-1}, followed by Bruguiera (2,964±386 ind ha^{-1}), while the *Sonneratia* zone had the lowest at 1,516±84 ind ha^{-1}. Sapling density was highest in *Bruguiera* (1,344±127 ind ha^{-1}) and lowest in *Sonneratia* (350±129 ind ha^{-1}). Despite the low density, *Sonneratia* stands had the largest average trunk diameter (11.5±0.8 cm), suggesting mature trees, whereas *Rhizophora* and *Bruguiera* zones had smaller diameters, consistent with denser and younger stands. Canopy closure was greatest in *Bruguiera* (77.0±1.6%) and *Ceriops* (74.8±1.7%) zones, significantly higher than *Sonneratia* (49.1±6.5%), mirrored by MHI values showing better forest health in *Bruguiera* and *Ceriops* compared to *Sonneratia*.

Table 1. The mangrove stands structure of each mangrove area

Parameters			**Area**		
	Rhizophora	***Sonneratia***	***Avicennia***	***Bruguiera***	***Ceriops***
Dominance species	*R. mucronata*	*S. alba*	*A. marina*	*B. gymnorrhiza*	*C. tagal*
Tree density (ind ha^{-1})	3895±256^{a}	1516±84^{c}	2763±125^{b}	2964±386^{b}	2800±65^{b}
Sapling density (ind ha^{-1})	1068±126^{b}	350±129^{d}	650±129^{c}	1344±127^{a}	570±96^{d}
Trunk diameter (cm)	8.2±0.2^{c}	11.5±0.8^{a}	9.8±0.3^{b}	8.5±0.3^{c}	8.9±0.1^{bc}
Canopy closure (%)	72.4±0.5^{a}	49.1±6.5^{c}	61.6±1.3^{b}	77.0±1.6^{a}	74.8±1.7^{a}
MHI (%)	52.1±0.6^{b}	38.0±3.2^{d}	43.7±1.7^{c}	57.6±1.2^{a}	53.0±1.8^{b}

Species composition analysis confirmed strong monodominance in each zone, with *Sonneratia alba* dominating *Sonneratia, Rhizophora mucronata* in *Rhizophora, Avicennia marina* in *Avicennia, Bruguiera gymnorrhiza* in *Bruguiera,* and *Ceriops tagal* in *Ceriops* zones (Figure 2). The Importance Value Index (IVI) reflected these patterns, with *Rhizophora* zones showing higher species diversity than the almost monodominant *Sonneratia* and *Avicennia* zones. The high densities in *Rhizophora* and *Bruguiera* align with their preference for muddy, low-salinity substrates common in landward areas (Primantara et al. 2019; Sugiana et al. 2021), and rehabilitation planting explains *Rhizophora*'s dense but smaller stems (Dharmawan et al. 2020; Andiani et al. 2021). Meanwhile, large trunk diameters but sparse trees in Sonneratia may result from natural dieback or allelopathic effects reducing regeneration (Zhang et al. 2018).

Canopy closure patterns correspond closely to species-specific traits, where *Bruguiera* and *Ceriops* form dense, compact canopies, while *Sonneratia* exhibits an open branching structure, resulting in lower canopy cover (Sugiana et al. 2021). These structural differences affect forest health, as reflected in the Mangrove Health Index (MHI), which integrates stem density and canopy cover (Nurdiansah and Dharmawan 2021a, b). The high stand density observed in *Rhizophora* and *Bruguiera* zones supports previous findings that these genera prefer muddy substrates and lower salinity conditions typical of landward zones (Primantara et al. 2019; Sugiana et al. 2021), with *R. mucronata* often planted in rehabilitation efforts, contributing to dense stands with smaller diameters (Dharmawan et al. 2020; Andiani et al. 2021). In contrast, *Sonneratia* zones display sparse tree density but larger trunk diameters, suggesting mature stands with limited regeneration, potentially due to dieback or allelopathic effects (Zhang et al. 2018). Compositionally, the Importance Value Index (IVI) highlights monodominance of *S. alba* and *C. tagal* in their respective zones, while the *Rhizophora* zone shows greater intra-genus diversity, comprising *R. mucronata*, *R. stylosa*, and *R. apiculata*. These patterns are consistent with previous studies that associate *S. alba* with high-salinity, sandy or gravelly substrates, and *Rhizophora* and *Ceriops* with transitional salinity and finer soil textures (Kusmana 2014; Pillai and Harilal 2016; Andiani et al. 2021). Collectively, these findings emphasize the importance of matching restoration strategies to local species composition and site-specific edaphic and hydrological conditions to maintain biodiversity and ecosystem resilience.

Soil fraction and other properties

Soil fraction composition varied significantly among the five mangrove zones (Figure 3). The *Bruguiera* zone exhibited the highest sand content at 65%, markedly higher than the *Ceriops* zone, which had the lowest sand proportion at 23%. In contrast, *Ceriops* soils contained the highest levels of silt and clay, reaching 35% and 18%, respectively, compared to *Bruguiera*'s minimal fine fractions (silt 10%, clay 5%). Gravel content was greatest in the *Sonneratia* zone at 4.4%, significantly exceeding that of *Rhizophora* (2.8%) and *Ceriops* (2.5%) zones, reflecting *Sonneratia*'s proximity to coral reef-derived sediments (Jenoh et al. 2016; Nurdiansah and Dharmawan 2021a).

The observed variation in soil texture aligns with typical species preferences for substrate types. *Rhizophora* species, often found in low-energy muddy substrates, thrive in environments with intermediate levels of silt and clay (Sugiana et al. 2021). In contrast, the *Bruguiera* zone, characterized by extremely sandy soils, aligns with this genus's tolerance for coarser substrates and reduced inundation compared to *Rhizophora* (Primantara et al. 2019). *Ceriops*, which dominated in finer soils with higher silt and clay content, supports previous findings indicating its preference for moderately to poorly drained substrates (Gabi et al. 2021).

High gravel content in the *Sonneratia* zone may be associated with its proximity to open coastal or coral reef systems, where biogenic gravel accumulates, as reported in previous studies (Jenoh et al. 2016; Nurdiansah and Dharmawan 2021a). *Sonneratia alba*, in particular, has shown high tolerance to saline, sandy-gravel substrates with limited organic matter, suggesting an ecological adaptation to less stable but well-aerated soils (Pillai and Harilal 2016; Lewerissa et al. 2018). This may also explain the lower canopy closure and MHI in these zones due to physical constraints on growth.

Moreover, the fine fractions (silt and clay) observed in the *Ceriops* area support conditions conducive to organic matter retention and nutrient availability, which could influence vegetation density and diversity positively. Clay-rich soils, although less permeable, support prolonged water retention and microbial activity essential for biogeochemical processes (Amorim et al. 2023). These characteristics potentially offer a more stable rooting medium for *C. tagal* and may contribute to the higher canopy cover observed in this area (Marchand 2017).

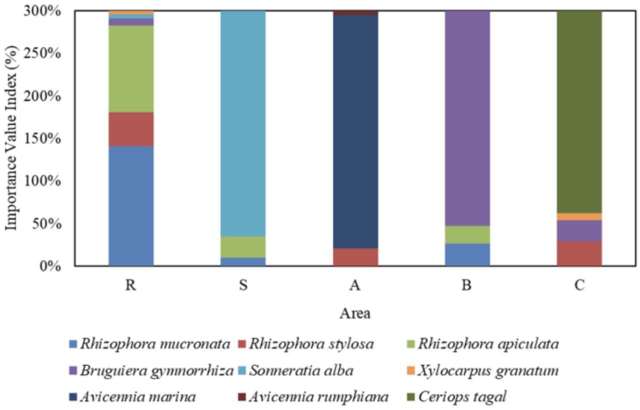

Figure 2. IVI of each mangrove area (R: *Rhizophora*, S: *Sonneratia*, A: *Avicennia*, B: *Bruguiera*, C: *Ceriops*)

The soil parameters showed noticeable differences across the five mangrove zones. The *Sonneratia* area had the most alkaline soil pH, while the *Rhizophora* zone exhibited the lowest value. Water content, a stable factor in mangrove ecosystems, was relatively high and consistent across areas, with *Sonneratia* having the highest average and *Rhizophora* the lowest. However, these differences were not statistically significant. Bulk density remained quite uniform across zones except for *Ceriops*, which showed a significantly lower value. Total Organic Matter (TOM) varied more distinctly; *Ceriops* had the highest TOM content, while *Bruguiera* recorded the lowest. Interestingly, *Rhizophora* and *Avicennia* areas had moderate TOM levels (Table 2).

The variation in soil parameters appears to reflect the distinct ecological preferences and substrate conditions observed in each mangrove zone. The *Sonneratia* zone, characterized by relatively higher pH and moisture, tends to grow on coarser sandy substrates with higher gravel content, suggesting a better drainage regime (Jenoh et al. 2016; Lewerissa et al. 2018). Despite favorable moisture conditions, its moderate TOM and lower silt-clay composition could explain the lower canopy coverage and limited species diversity found in this zone (Sugiana et al. 2021). In contrast, the *Rhizophora* zone had lower soil pH and moderate organic matter, associated with higher silt-clay content and dense stand structure, favoring species like *R. mucronata* that thrive in fine-textured, waterlogged soils (Pillai and Harilal 2016; Marchand 2017).

The *Ceriops* zone stood out with the highest TOM and relatively high silt and clay fractions, indicating a substrate with good nutrient-holding capacity. This might support species like *C. tagal,* which are known to prefer finer substrates with stable water retention (Amorim et al. 2023). Interestingly, although *Bruguiera* had one of the densest canopies and tree populations, its soil TOM was the lowest, suggesting that high tree density and closed canopy might lead to intense competition and slower litter decomposition or lower input (Nurdiansah and Dharmawan 2021a). Altogether, the interplay between soil fraction (especially silt and clay), organic matter, and edaphic conditions plays a pivotal role in shaping mangrove community structure and distribution in these zones.

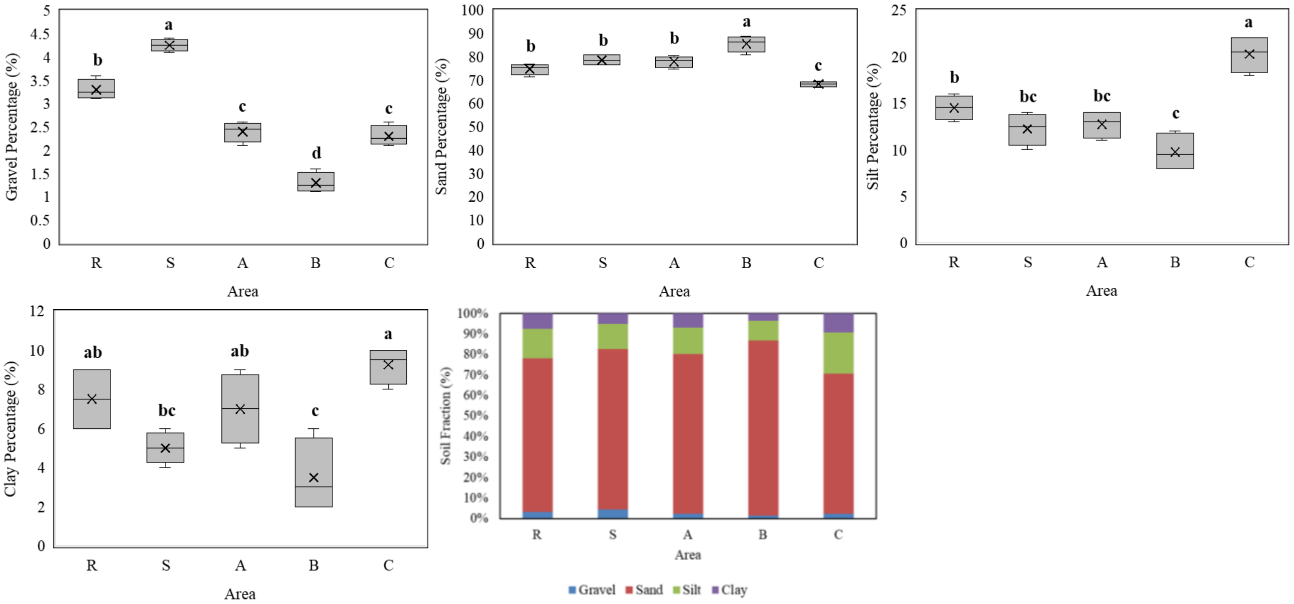

Figure 3. Soil fraction of each mangrove area (R: *Rhizophora*, S: *Sonneratia*, A: *Avicennia*, B: *Bruguiera*, C: *Ceriops*). Different lowercase letters (a, b, c) indicate significant differences among means based on ANOVA and Tukey HSD test at ρ≤0.05. Means sharing the same letter (e.g., ab or bc) are not significantly different from each other

Table 2. Soil properties of each mangrove area

Parameter	**Area**				
	Rhizophora	***Sonneratia***	***Avicennia***	***Bruguiera***	***Ceriops***
Soil pH	6.18±0.14^{c}	6.68±0.16^{a}	6.38±0.06^{ab}	6.25±0.18^{ab}	6.49±0.09^{bc}
Water content (%)	37±4^{a}	43±10^{a}	40±1^{a}	41±2^{a}	42±1^{a}
Bulk density (g cm^{-3})	0.62±0.03^{a}	0.65±0.03^{a}	0.63±0.02^{a}	0.65±0.02^{a}	0.57±0.01^{b}
TOM (%)	5.5±0.4^{b}	4.7±0.3^{bc}	5.1±0.4^{b}	4.0±0.6^{c}	6.8±0.2^{a}

Relationship between mangrove stand structure and soil fraction

Principal Component Analysis (PCA) explained 92.83% of the total variation in soil fraction data across mangrove zones, with Axis 1 accounting for 68.46% and Axis 2 for 24.37%. Axis 1 was negatively correlated with sand content and positively with silt and clay, while Axis 2 showed a strong negative loading of gravel. PCA scores clearly separated zones: *Ceriops* clustered on the positive side of Axis 1, indicating association with higher silt and clay; *Bruguiera* grouped on the negative sides of both axes, reflecting dominance of sandy soils; and *Sonneratia* aligned negatively on Axis 2, closely linked to gravel content. *Rhizophora* and *Avicennia* occupied intermediate positions, indicating adaptability to a broader range of soil textures (Figure 4).

The PCA ordination highlighted distinct ecological preferences among mangrove species based on edaphic conditions. The *Ceriops* zone, characterized by high silt and clay content, also exhibited the highest total organic matter (TOM) and the lowest bulk density. These fine-textured, nutrient-rich, and low-aeration soils create favorable conditions for *C. tagal*, a species known for its tolerance to soft, water-logged substrates (Sugiana et al. 2021; Yanti et al. 2021). Conversely, the *Bruguiera* zone, strongly associated with sandy soils, had the lowest TOM and moderately high bulk density, suggesting fast-draining substrates with limited nutrient retention. These conditions support species like *B. gymnorrhiza*, which are adapted to environments with higher oxygen availability and coarser particles (Kamruzzaman et al. 2017; Gabi et al. 2021).

The *Sonneratia* zone's association with gravel is aligned with the ecological traits of *S. alba*, a pioneer mangrove species commonly found on rocky, sandy, or coral-rubble substrates, often in higher salinity zones (Pillai and Harilal 2016). This species is also known to produce allelopathic substances that inhibit undergrowth, which may explain the low sapling density despite large trunk diameters (Xin et al. 2013). The zone also exhibited relatively low silt and clay content, contributing to reduced water and nutrient retention. On the other hand, the intermediate positioning of *Rhizophora* and *Avicennia* zones in the PCA space suggests that these genera can tolerate a broad range of soil textures. This edaphic flexibility explains their frequent occurrence in transitional or rehabilitated mangrove areas across Indonesia (Nurdiansah and Dharmawan 2021a; Sugiana et al. 2021) and supports their use in large-scale restoration efforts.

The Pearson correlation analysis revealed several notable relationships between mangrove stand structure and soil fractions. Gravel content was significantly positively correlated with trunk diameter yet showed strong negative correlations with canopy closure and MHI. Additionally, sapling density was negatively associated with gravel but positively correlated with sand content, while negatively correlated with silt (Table 3). These significant correlations suggest that different soil textures influence various aspects of mangrove stand dynamics.

Table 3. Relationship between mangrove stand structure and soil fraction (n: 20)

Parameter	Pearson correlation			
	Gravel	**Sand**	**Silt**	**Clay**
Tree density	-0.385	-0.044	0.083	0.140
Sapling density	-0.530^{*}	0.564^{**}	-0.504^{*}	-0.378
Trunk diameter	0.620^{**}	0.036	-0.110	-0.175
Canopy closure	-0.728^{**}	-0.124	0.268	0.188
MHI	-0.740^{**}	0.048	0.103	0.028

Note: **: Correlation is significant at the 0.01 level, *: Correlation is significant at the 0.05 level

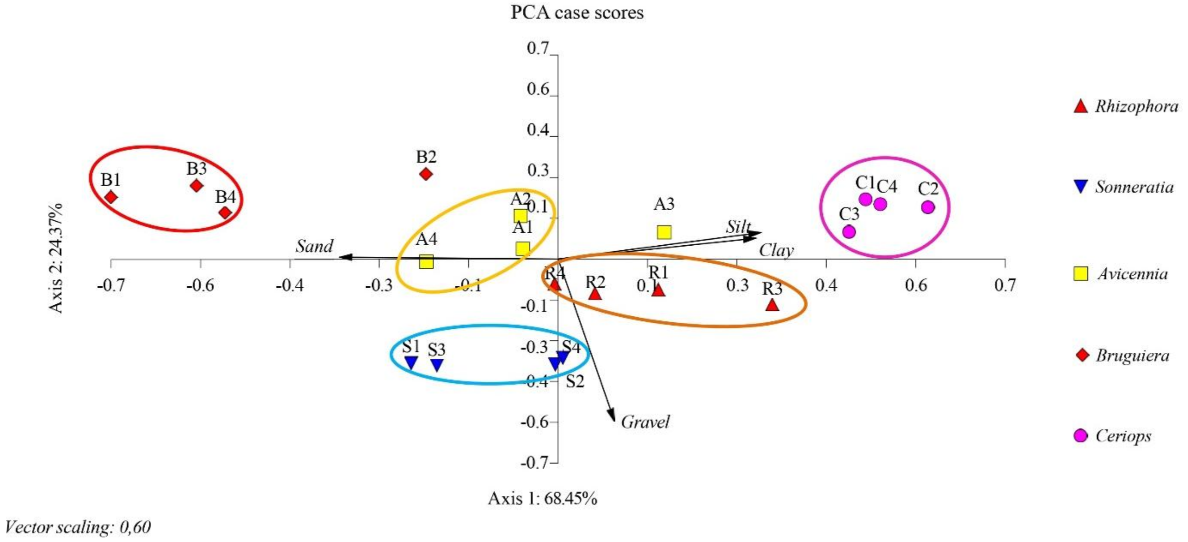

Figure 4. Principal component analysis result of the mangrove area and soil fraction

The strong positive correlation between gravel and trunk diameter suggests that coarse substrates may support larger individual mangrove trees, possibly due to reduced competition and better root penetration (Nurdiansah and Dharmawan 2021a). However, this comes at a cost—higher gravel content also correlates with reduced canopy closure and lower MHI, indicating that while individual trees may grow larger, overall forest health and density may decline in gravel-rich areas, likely due to poor water retention and limited nutrient availability (Xin et al. 2013; Gabi et al. 2021). The positive relationship between sand and sapling density implies that early-stage regeneration may be favored in more porous substrates. However, the concurrent negative association with silt suggests that nutrient-rich finer soils may hinder sapling establishment due to anoxic stress (Pillai and Harilal 2016). Overall, these correlations emphasize that mangrove structural parameters are closely linked with sediment properties, and understanding these relationships is essential for species-specific restoration strategies. While these correlations are statistically significant, it is important to acknowledge that they do not establish causation. Further studies are needed to examine how soil texture interacts with other environmental drivers such as salinity, hydrology, and nutrient dynamics to shape mangrove species distribution more comprehensively. In addition to edaphic factors, biotic interactions such as interspecific competition, facilitation, and species-specific ecological strategies may also influence mangrove distribution patterns. Integrating these biological aspects with abiotic variables into ecological models would offer a more holistic understanding of the mechanisms driving species zonation and forest dynamics.

Recommendation for future research

Given the observed relationships between soil fraction and mangrove stand characteristics, future studies are encouraged to implement a longitudinal monitoring framework. This will allow for a comprehensive examination of how seasonal and interannual variations influence mangrove dynamics. The gradual alterations in sediment deposition, tidal flushing, and storm events can change the proportions of sand, silt, clay, and gravel, thereby affecting species zonation and seedling survival. Understanding such temporal shifts will provide invaluable critical insight into how mangroves respond to both natural sediment dynamics and human-induced changes in coastal zones (Nardin et al. 2021).

In addition, future research should investigate physiological and biochemical adaptations of mangrove species to specific edaphic conditions. While this study identified ecological patterns, it remains important to clarify how traits like root plasticity, nutrient uptake efficiency, and salt regulation mechanisms allow certain species to thrive in distinct substrates (Pillai and Harilal 2016; Zhang et al. 2018). Molecular studies using genetic markers may reveal adaptive capacities of mangrove taxa that are otherwise not observable at the morphological or community level.

Expanding the scope of research to include integrated spatial modeling is also recommended. Incorporating variables such as salinity gradients, inundation frequency, land use, and anthropogenic pressures into geospatial models will enhance the accuracy of habitat suitability predictions. Remote sensing coupled with algorithms like Random Forest or PCA has shown promise in mapping mangrove zones and detecting early signs of degradation (Behera et al. 2021; Ghorbanian et al. 2021), thus supporting more strategic and resilient restoration planning in highly dynamic estuarine systems.

Although zones with higher silt and clay content (>25%) showed higher average canopy closure and MHI values, these associations were not statistically significant. In contrast, gravel content exhibited the strongest and most consistent negative correlations with canopy closure (r: -0.728, $p<0.01$) and MHI (r: -0.740, $p<0.01$), indicating that coarse substrates may limit mangrove forest health. Overall, soil texture, particularly the proportion of fine particles, remains an important factor influencing mangrove distribution and structural conditions. Future studies should adopt interdisciplinary approaches combining ecological, edaphic, physiological, and spatial data to better understand the complex drivers of mangrove zonation and health. While this study provides valuable insights from two representative sites, the limited number of study locations may constrain the generalizability of the findings. Therefore, expanding this research across a broader range of coastal ecosystems is necessary to validate and strengthen these conclusions. These efforts are critical to support sustainable mangrove management amid growing climate and development pressures.

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AUTHORS' STATEMENT

We acknowledge that the components of the Important Value Index (relative density, relative frequency, and relative dominance) were not fully elaborated in the Materials and Methods section. This decision was made because the underlying data are currently being utilized for further ongoing research and analysis. Nevertheless, should additional clarification be required for verification or academic purposes, we would be happy to provide the relevant information upon reasonable request via email at sugianaserangan@gmail.com.

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