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Edaphic and site-specific drivers of mangrove community assemblages: A case study from the southeastern coast of Sri Lanka

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ABSTRACT: Clear zonation from seaward to landward is absent in Sri Lankan mangroves. However, a patchy zonation within the mangroves can be observed. We hypothesized that this patchy distribution, in mangroves in Sri Lanka is caused by the variation in soil edaphic factors. A study was conducted on mangroves on the east coast of Sri Lanka using eighty-six 10 m × 10 m quadrates placed in five selected mangroves. Mangrove species >1cm dbh were identified and recorded. Soil samples were collected from each quadrat. Soil bulk density, salinity, pH and conductivity were measured with standard protocols. Differences in bulk density, pH, salinity and conductivity among sites were determined using ANOVA. Hierarchical agglomerative clustering (HAC) and non-metric multidimensional scaling (NMDS) were conducted to determine the plots with similar vegetation. Redundancy analysis (RDA) was used to identify the edaphic factors determining the plant assemblages. No significant differences were observed in edaphic factors among mangrove sites, except that the soil salinity of Pottuvil lagoon was significantly higher than that of other sites. HAC and NMDS both reveal six plant communities. RDA showed that salinity influenced mangrove community assemblages, although site had a stronger overall effect. The *Rhizophora–Lumnitzera–Excoecaria* community was associated with higher soil salinity compared to the *Lumnitzera–Excoecaria* and *Heritiera* communities. These results support the hypothesis of patchy zonation in Sri Lankan mangroves, with salinity and site-specific factors such as anthropogenic disturbance and hydrology shaping the observed community patterns.

KEY WORDS: Mangrove zonation, plant communities, soil Salinity, soil bulk density.

INTRODUCTION

Mangroves are ecosystems that thrive in the intertidal zones of tropical and subtropical coasts (Macnae, 1968; De Silva and De Silva, 2006). Plants in these ecosystems are highly adapted to harsh environmental conditions such as high salinity, physiological drought and unstable substrates (Tomlinson, 1994; Singh and Odaki, 2004). Despite these constraints, mangroves provide important ecosystem services, including coastal protection, nutrient cycling and climate regulation (Salem and Mercer, 2012; Getzner and Islam, 2020). They are among the highly productive terrestrial ecosystems (Behlinga *et al*., 2005; Granek and Ruttenberg, 2008) and among those with the highest carbon stocks (Mitra and Gatti, 2015; Kauffman *et al.,* 2020).

Mangrove zonation has historically been described as a seaward-to-landward gradient shaped by soil salinity, tidal inundation, estuarine location and climate factors (Snedaker, 1982; Satyanarayana *et al.*, 2009; Ward *et al*., 2016). However, in regions with low tidal ranges, such as much of Sri Lanka's coast, classical zonation is often weak or absent, and vegetation tends to display patchy, non-linear spatial patterns (Ranawana, 2017; Feller *et al*., 2017). Patchy community assemblages, including monotypic stands and abrupt transitions, have also been reported in other mangrove regions, indicating that local environmental heterogeneity can override classical zonation patterns (Youssef and Saenger, 1999; Ellison *et al*., 1999; Kathiresan and Bingham, 2001). Although there is much research available on the above objective, Krauss *et al*. (2008) proposed to conduct more comprehensive research to gain more insight into the zonation pattern of mangroves. Recent studies have highlighted the significant influence of edaphic factors on mangrove community structure. For instance, a study by Marpaung *et al*. (2022) identified that soil texture, water salinity, and nutrient concentrations (N-total, P, and K) significantly influenced mangrove species composition, explaining 37.2% of the overall variability. Similarly, a study by Athukorala *et al*. (2025) utilized remote sensing techniques to assess mangrove dynamics in Sri Lanka, revealing significant changes in mangrove distribution and structure due to anthropogenic and natural drivers.

We hypothesize that, although clear seaward-to-landward zonation may be limited in Sri Lankan mangroves, distinct patchy community assemblages still occur and are structured primarily by edaphic variation, particularly soil salinity. To test this hypothesis, we selected a connected network of mangroves on the eastern coast of Sri Lanka. Mangroves along the eastern coast of Sri Lanka remain understudied, largely due to restricted access during the civil conflict (Amarasinghe and Perera, 2017), and baseline data on species assemblages in this region are lacking.

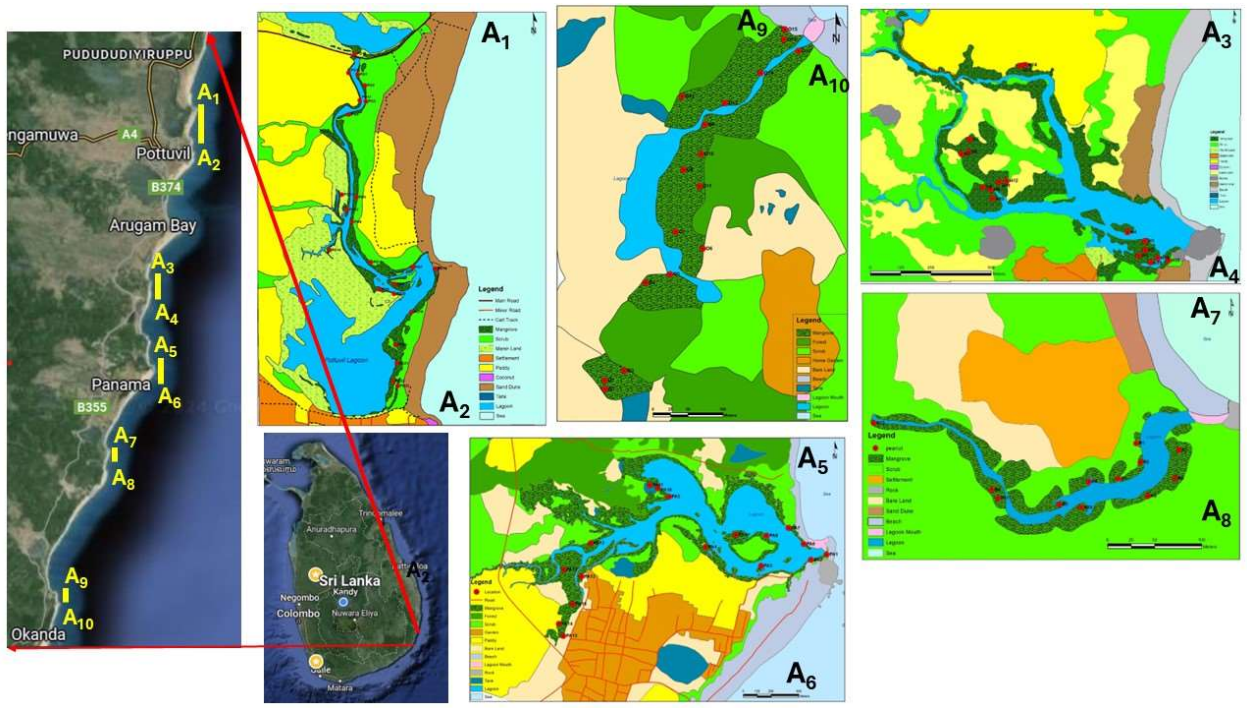

Fig. 1. Studied mangrove sites; **A_1-A_2**, Pottuvil lagoon; **A_3-A_4**, Hada Oya Estuary; **A_5-A_6**, Panama Lagoon; **A_7-A_8**, Ragamwela creek; and **A_9-A_{10}**, Okanda creek and the arrangement of plots within sites.

Site-specific factors such as historical land use, hydrological modifications, and anthropogenic disturbances can strongly influence mangrove community structure, even under similar microclimatic and edaphic conditions (Bosire *et al*., 2008; Friess and Webb, 2014). Understanding how these local drivers shape mangrove assemblages is critical for effective conservation planning (Duke *et al*., 2007), assessing species' adaptive potential to climate change (Gilman *et al*., 2008), and improving restoration outcomes, which have often failed in Sri Lanka due to neglect of site-specific species composition (Kodikara *et al*., 2017).

In this study, we examined mangrove plots across five ecologically distinct sites along the eastern coast of Sri Lanka to evaluate the influence of site-specific conditions on species assemblages and community structure. The data presented here provide baseline insights into the spatial organization of mangrove vegetation in an understudied region and contribute to understanding how local environmental factors drive patchy zonation in mangrove ecosystems.

MATERIALS AND METHODS

Study Sites

The study was conducted in five selected mangrove sites on the east coast of Sri Lanka: Pottuvil Lagoon, Panama Lagoon, Okanda Creek, Hada Oya estuary and Ragamwela Creek in Ampara District (Figure 1). Pottuvil is a large lagoon, and Panama is an estuarine lagoon, whereas others are comparatively small (area-wise).

Seasonal rains dominate the climate, with one prominent season with heavy rains from December to February (Northeast monsoon). The average annual rainfall of the sites ranges from 1200-1500 mm, and the mean annual temperature ranges from 30 – 32 ^{0}C (Jayasingam, 2008). Although these areas experienced very low tidal inundation during the rainy season and it was observed that the whole mangrove areas were submerged by floodwater.

Vegetation sampling

Eighty-six quadrates (10 m × 10 m) were placed randomly, covering all six study sites (Figure 1). Locations of the plots were recorded using a Magalan Explorist 600X GPS receiver. Individuals with >10 cm diameter at breast height (GBH) were identified to species level using the field guide "Guide to Mangroves of Sri Lanka" (Prasanna and Ranawana, 2014). Herbarium samples and necessary photographs were collected for further confirmation. The relative density of each species in each plot was calculated.

Edaphic factors

Five locations were selected randomly from each quadrat. Soil sample was taken from each selected location (5 samples from each quadrat × 86 quadrats = 420 samples) using a soil core from the top 0.45 m. All the collected samples were packed into polythene bags and properly labelled in the field. The samples were

transported to the Seed Science Laboratory of the Department of Botany, University of Peradeniya for analysis. All the samples were oven-dried at 105 ºC to a constant weight in wooden or plastic trays for 2-3 days. Properly dried soil samples were sieved using a 2 mm sieve (Darmakeerthi *et al*., 2007).

Oven-dried samples were weighed using a digital chemical balance to the nearest 0.01 g. Soil bulk density was calculated using the following equation (12), and only topsoil (first 30 cm) was used to determine the soil bulk density (Darmakeerthi *et al*., 2007).

$$Bulk\ densiy\ \ (P) = \frac{\text{Dry weight of Soil}}{\text{Volume of the Soil Core}}$$

Soil pH was measured by mixing 10 g each of air-dried and sieved soil samples with 25 ml of distilled water in a 50 ml glass beaker. Soil samples were stirred at regular intervals for 30 minutes and allowed to settle for 2 hrs. Later, the soil pH and soil conductivity were measured using a digital pH and conductivity meter (PCStestr 35, ®Thermo Scientific Inc.) (Darmakeerthi *et al*., 2007).

Soil salinity was measured using the suspension method. Ten grams of each air-dried soil sample were mixed with 50 ml (proportion is 1:5) of distilled water in a 100 ml Erlenmeyer flask, and the mixture was stirred intermittently for 30 min and kept for 2 hrs to settle. A calibrated digital electrical pH and conductivity meter (PC Stestr 35, ®Thermo Scientific Inc.) was used to measure the salinity (in ppm) to the nearest four decimals (Darmakeerthi *et al*., 2007).

Analysis of Data

Soil edaphic factor measurements (pH, salinity, bulk density, and organic carbon) collected from each mangrove plot were averaged to obtain a single representative value for each variable per plot.

To identify natural groupings of mangrove plots based on species composition, a Hellinger transformation was first applied to the species relative density data to minimize the influence of double zeros and prepare the data for ordination. To control potential site-level effects on community structure, a partial redundancy analysis (partial RDA) was performed with 'site' included as a conditioning variable. The residuals from this model, representing variation in species composition independent of site, were then used to calculate a Bray–Curtis dissimilarity matrix.

Hierarchical agglomerative clustering was subsequently carried out on the dissimilarity matrix using Ward's minimum variance method. To determine the optimal number of clusters, cluster solutions ranging from 2 to 20 were evaluated using average silhouette width as the selection criterion. The solution with the highest average silhouette width was chosen as optimal, reflecting the most internally consistent and ecologically meaningful community structure. Cluster validity was further examined using the cophenetic correlation coefficient, which measures the fidelity of the dendrogram in preserving original inter-plot dissimilarities.

Non-metric multidimensional scaling (NMDS) was employed to visualize patterns of species composition across mangrove plots based on Bray–Curtis dissimilarity. To assess the influence of edaphic variables on community structure, a permutational multivariate analysis of variance (PERMANOVA) was conducted using the Hellinger-transformed species data. The soil variables were included as predictors, and permutations were restricted within sites using the strata argument to control for spatial autocorrelation.

Additionally, redundancy analysis (RDA) was conducted to examine the relationship between environmental variables and species composition. In this model, environmental predictors (pH, salinity, bulk density, and organic carbon) were included as explanatory variables, while 'site' was treated as a covariate (conditioning variable) to account for spatial heterogeneity. The effect of 'site' on species composition was statistically removed, considering it as a covariate so that the influence of environmental variables, the main focus of this analysis, could be isolated. The statistical significance of the RDA model was evaluated through permutation testing (999 permutations). The results were visualized in an RDA triplot, with plots colored by cluster membership and ellipses indicating site-level groupings. Significant environmental vectors were overlaid to illustrate their correlations with patterns in species assemblage.

We used linear mixed-effects models (lmer in R) to assess the effects of soil pH, salinity, bulk density, and organic carbon on the relative density of each mangrove species. Plot was included as a random effect to account for within-site variation. Fixed-effect significance was evaluated using Satterthwaite's method (lmerTest). For species where the random effect variance was negligible (i.e., singular fit), models were refitted without the random effect. Predictor variables were standardized when necessary to improve model performance.

RESULTS

Mangrove diversity in the studied sites

Eight mangrove plant species were recorded in the studied quadrates allocated in different mangrove sites (Table 1). *Excoecaria agallocha* and *Lumnitzera racemosa* were present in all the study sites, while *Aegiceras corniculatum* was present only in the Pottuvil lagoon. The lowest number of mangrove species was recorded from Ragamwela Creek.

Table 1: Mangrove plant species recorded in quadrates in each study site

Mangrove site	Mangrove species								Species richness
	AECO	AVMA	BRGY	EXAG	HELI	LURA	RAAP	RAMU	
Pottuvil Lagoon	1	0	1	1	1	1	0	1	6
Panama Lagoon	0	1	1	1	0	1	1	1	6
Ocanda Creek	0	1	1	1	0	1	0	1	5
Hada Oya Estuary	0	0	1	1	1	1	1	1	6
Ragamwela Creek	0	1	0	1	0	1	0	0	3

AECO, *Aegiceras corniculatum*; AVMA, *Avicennia marina*; BRGY, *Bruguiera gymnorhiza*; EXAG, *Excoecaria agallocha*, HELI, *Heritiera littoralis*; LURA, *Lumintzera racemosa*; RAAP, *Rhizophora apiculata*; RAMU, *Rhizophora mucronata*; 1, present; 0, absent.

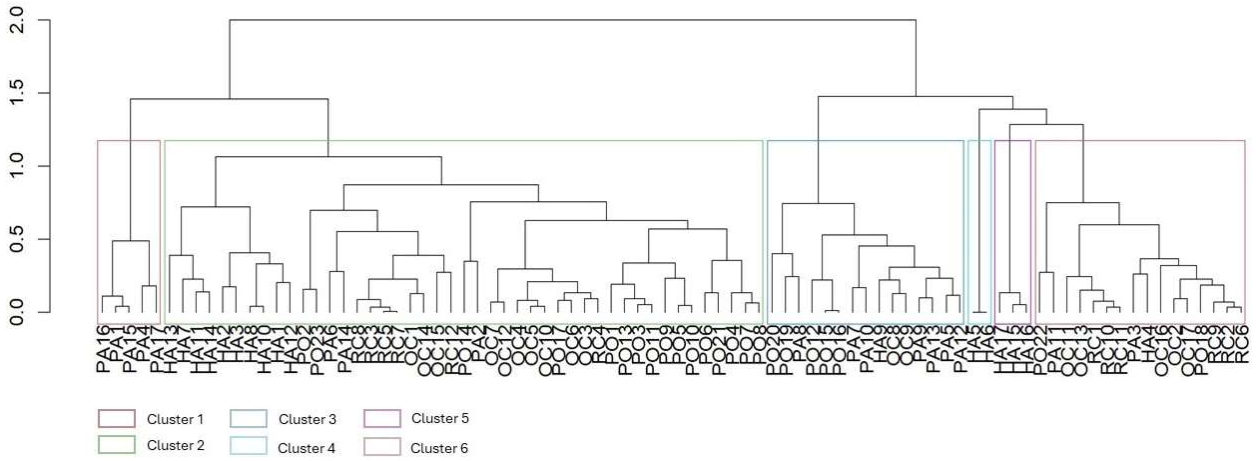

Fig. 2. Hierarchical agglomerative clustering (performed using Ward's minimum variance method) dendrogram of mangrove plots based on Bray–Curtis dissimilarities calculated from the residuals of a partial redundancy analysis (partial RDA), which accounted for site-level effects. The colored squares represent the final clusters identified. HA, Hada Oya Estuary; OC, Okanda Creek; PA, Panama Lagoon; PO, Pottuvil lagoon and RC, Ragamwela Creek.

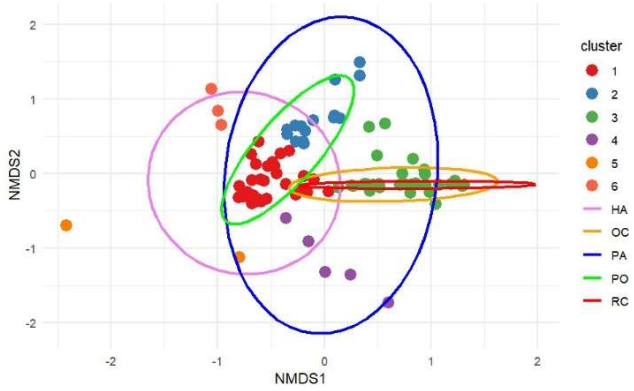

Fig. 3. Non-metric multidimensional scaling (NMDS) ordination of mangrove species composition across five study sites (HA, Hada Oya Estuary; OC, Okanda Creek; PA, Panama Lagoon; PO, Pottuvil lagoon and RC, Ragamwela Creek), showing site-wise clustering patterns. Ellipses represent 95% confidence intervals for each site, indicating site-level variation in species assemblages. Points are color-coded by cluster membership (Cluster 1, *Excoecaria agallocha*; Cluster 2, *Rhizophora* - *Lumnitzera* – *Excoecaria*; Cluster 3, *Lumnitzera* – *Excoecaria*; Cluster 4, *Avicennia* – *Excoecaria*; Cluster 5, *Bruguiera* – *Excoecaria*, and Cluster 6, *Heritiera littoralis* communities) as determined by hierarchical clustering based on Bray–Curtis dissimilarity.

Plant community assemblages

According to the results of silhouette width analysis, six clusters were identified as the optimum number. The average silhouette width and cophenetic correlation of the clusters were 0.26 and 0.42, respectively. The hierarchical clustering is shown in Figure 2. The NMDS ordination also supported this grouping, revealing the same six clusters (Figure 3). Nonetheless, NMDS revealed a tendency for site-specific clustering. Hada Oya estuary (pink) and Okanda creek (orange) show relatively distinct ellipses, while Panama lagoon (blue) and Pottuvil lagoon (green) have overlapping ellipses. Cluster 1 (red) is dense and central, Clusters 4 (purple) and 5 (orange) are more spread out or peripheral.

Indicator species analysis showed that *Excoecaria agallocha* occurred across all clusters (IndVal = 0.95, P = 0.018) except in cluster 5. Cluster 1 was dominated solely by *E. agallocha*. Cluster 2 was characterized by the dominance of *Rhizophora mucronata* (IndVal = 0.91, P = 0.001), *Lumnitzera racemosa* (IndVal = 0.84, P = 0.005), alongside *E. agallocha*. In Cluster 3, *L. racemosa* (IndVal = 0.84, P = 0.005) and *E. agallocha* were the dominant species. Clusters 4 and 6 were dominated by *Avicennia marina* (IndVal = 0.93, P = 0.002) and *Bruguiera gymnorhiza* (IndVal = 0.94, P = 0.001), respectively, together with *E. agallocha*. Cluster 5 was dominated by *Heritiera littoralis* (IndVal = 0.97, P = 0.001).

Table 2. Results of PERMANOVA and partial RDA

	Source	R^2	F	P value
PERMANOVA	Site	0.29	13.5	0.001***
	Salinity	0.07	6.8	0.028*
	pH	0.003	0.36	0.136
	Bulk density	0.02	1.67	0.56
	Organic Carbon	0.003	0.33	0.75
Partial RDA	Salinity		3.25	0.011*
	pH		1.15	0.31
	Bulk density		0.52	0.77
	Organic Carbon		0.42	0.84

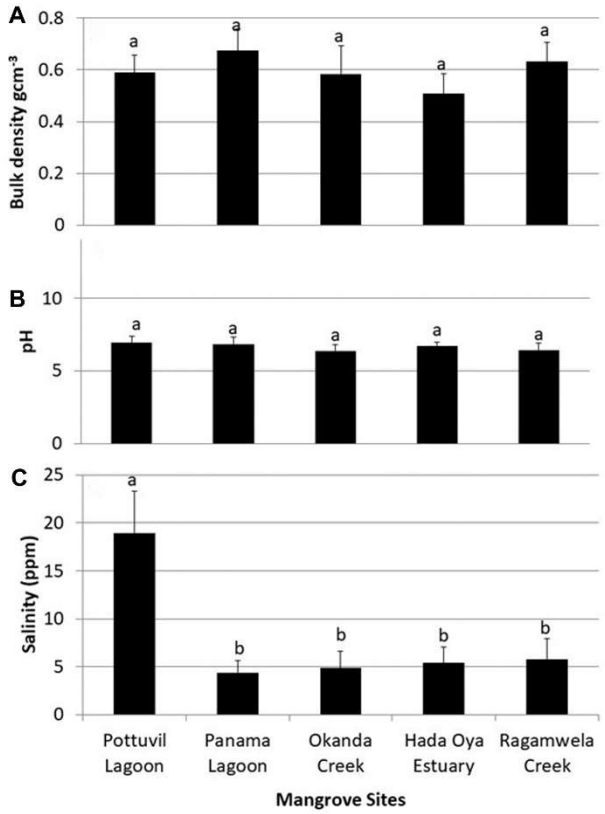

Fig. 4. Variation in edaphic parameters across five mangrove sites: Pottuvil Lagoon, Panama Lagoon, Okanda Creek, Hada Oya Estuary, and Ragamwela Creek. (A) Bulk density (g cm^{-3}), (B) soil pH, and (C) salinity (ppm). Pottuvil exhibited the highest soil salinity, which was significantly greater than that of the other sites, among which no significant differences were observed. Furthermore, no significant differences were observed in soil pH and bulk density across the sites. Error bars represent standard errors of the mean. Bars sharing the same lowercase letter are not significantly different ($p > 0.05$) according to Tukey's HSD test.

Soil edaphic factors of the mangrove sites

There were no significant differences in soil bulk density ($H(\chi^2) = 8.45$, $p = 0.07$) or pH ($H(\chi^2) = 7.6$, $p = 0.11$) among mangrove sites, Pottuvil Lagoon, Panama Lagoon, Ocanda Creek, Hada Oya Estuary and Ragamwela Creek (Figure 4). However, the soil salinity of the Pottuvil Lagoon was significantly higher than the other mangrove sites ($H(\chi^2) = 33.91$, $p < 0.001$).

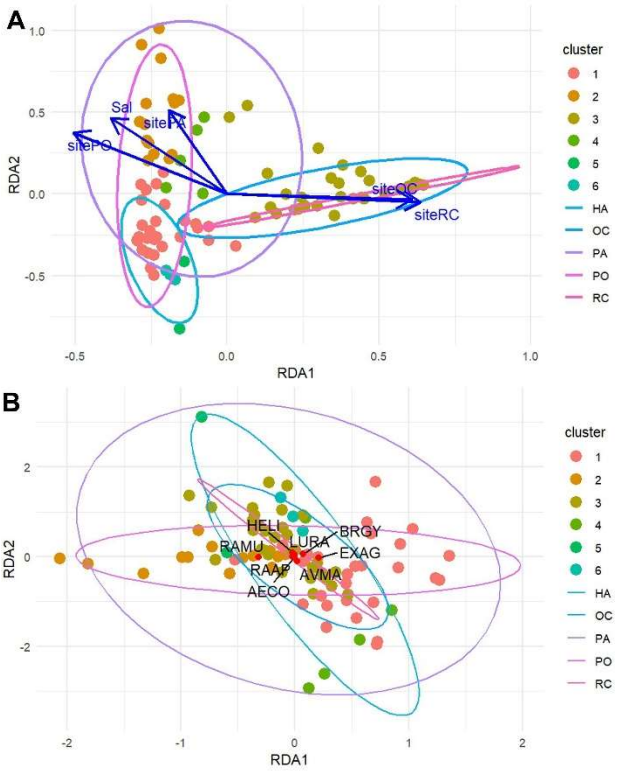

Fig. 5. Redundancy Analysis (RDA) ordination plots showing relationships among mangrove sites, environmental variables, and species composition. **A.** RDA biplot displaying the influence of environmental variables (Salinity [Sal], pH, bulk density, and organic carbon) and site vectors on plot-level species composition. Clusters represent distinct plant assemblages, while ellipses indicate 95% confidence intervals for each site. **B.** RDA species biplot showing the distribution of eight mangrove species (AECO: *Aegiceras corniculatum*, AVMA: *Avicennia marina*, BRGY: *Bruguiera gymnorhiza*, EXAG: *Excoecaria agallocha*, HELI: *Heritiera littoralis*, LURA: *Lumnitzera racemosa*, RAAP: *Rhizophora apiculata*, RAMU: *Rhizophora mucronata*) across environmental gradients.

Effect of edaphic factors on shaping the plant communities

PERMANOVA results indicated that both site ($F = 13.5$, $P = 0.001$) and soil salinity ($F = 2.8$, $P = 0.028$) had significant effects on mangrove species composition. The site explained 29% of the variation in species assemblages across quadrats, while environmental variables collectively accounted for 7% of the variation. The combined effect of site and environmental variables explained an additional 8% of the total variation in community composition. On the other hand, after partitioning the effect of the site through partial RDA, salinity had a significant effect on community assemblage (Table 2).

The RDA ordination diagram revealed clustering patterns that were broadly consistent with those identified in the NMDS analysis (Figure 5). According to the partial RDA results, salinity remained the primary environmental factor influencing species assemblages, even after accounting for site effects (Figure 5A). Nevertheless, the effect of the site was substantial and

Table 3. Coefficients and significance levels for the associations between soil edaphic factors and species densities, based on linear mixed-effects model analysis.

Edaphic Factors	AECO		AVMA		BRGY		EXAG		HELI		LURA		RAAP		RAMU	
pH	-0.302	0.763	-0.219	0.827	2.001	0.049	2.359	0.021	0.061	0.951	-2.435	0.017	-0.095	0.925	-1.326	0.189
Salinity	3.137	0.002	-1.082	0.282	-0.679	0.498	1.067	0.289	-1.608	0.112	-2.23	0.029	-0.609	0.544	4.992	<0.001
Bulk Density	1.339	0.184	2.192	0.031	-1.976	0.051	-0.167	0.868	-2.182	0.032	0.948	0.346	-1.032	0.305	-0.053	0.958
Soil Organic Carbon	2.896	0.005	-0.719	0.474	-0.106	0.916	0.232	0.817	0.24	0.811	0.117	0.907	-0.143	0.887	-0.145	0.885

AECO, *Aegiceras corniculatum*; AVMA, *Avicennia marina*; BRGY, *Bruguiera gymnorhiza*; EXAG, *Excoecaria agallocha*; HELI, *Heritiera littoralis*; LURA, *Lumnitzera racemosa*; RAAP, *Rhizophora apiculata*; RAMU, *Rhizophora mucronata*. Dark pink indicates a significant positive effect at $p < 0.01$., Light pink indicates a significant positive effect at $p < 0.05$. Light blue indicates a significant negative effect at $p < 0.05$.

appeared to mask the influence of salinity to some degree. Interestingly, environmental variables still showed associations with specific sites despite being conditioned in the model. For example, the Pottuvil site appeared to be characterized by higher salinity, as indicated by the alignment of the salinity and Pottuvil site vectors in the ordination space. The partial RDA also revealed distinct species–environment relationships. *Rhizophora apiculata* and *Aegiceras corniculatum* were associated with a similar set of environmental conditions, while *Bruguiera gymnorhiza* and *Excoecaria agallocha* were associated with contrasting environmental gradients (Figure 5B). In contrast, *Avicennia marina* and *Lumnitzera racemosa* clustered near the center of the ordination, suggesting they are ecological generalists capable of thriving across a broad range of environmental conditions.

Soil Variable Effects on Individual Mangrove Species

According to the results of the linear mixed-effects models, the relative densities of six mangrove species were significantly influenced by at least one of the studied edaphic variables (Table 3). Among these, salinity had a significant effect on three species. *Rhizophora mucronata* density increased with rising soil salinity, with salinity being the only significant factor affecting this species. *Aegiceras corniculatum* showed a similar positive response to salinity, and its density was also positively influenced by soil organic carbon. In contrast, both salinity and pH had a negative effect on the density of *L. racemosa*. Bulk density significantly influenced the densities of *A. marina* and *H. littoralis*, but in opposite directions; *A. marina* density increased with bulk density, while *H. littoralis* density decreased. The density of *E. agallocha* was positively associated with pH.

DISCUSSION

The most important finding in the study is the unravelling of the significance of soil salinity in determining the plant mangrove community assemblages on the southeastern coast of Sri Lanka. Although the significance of soil salinity in determining the distribution of mangrove species has been shown in several studies conducted in many mangroves (Snedaker, 1982; Josh and Ghose, 2003; Barik *et al*., 2018), this has not been shown in Sri Lanka experimentally. Mangrove ecosystems of Sri Lanka are confined to a narrow belt surrounding the brackish water sources, as the tidal inundation is very low (NARESA, 1991; Ranawana, 2017). Thus, the mangrove zonation from the seaward side to the landward side occurs due to variation in salinity, is not clear in most of the mangroves in Sri Lanka, except for the seaward zone consisting of *Rhizophora* spp. and *Avicennia* spp. (De Silva and Balasubramaniam, 1984-85). Although the classical landward-to-seaward linear zonation is not evident in the studied sites, our results support a pattern of patchy zonation, where discrete species assemblages are distributed irregularly across the landscape in response to local variations in edaphic conditions, particularly soil salinity. The concept of patchy zonation used here refers to the presence of discrete, often small-scale clusters of monospecific or mixed mangrove assemblages that do not follow a continuous gradient from seaward to landward. Instead, these patches appear to be shaped by localized edaphic heterogeneity, such as salinity micro-gradients, rather than broad tidal or estuarine zonation patterns typically described in classical models (e.g., Tomlinson, 1994). Nevertheless, as reported by De Silva and Balasubramaniam (1984-1985) for many mangrove sites in Sri Lanka, *Rhizophora* spp. were present on the seaward side of the mangrove but only restricted to about a 2-10 m narrow strip (observations by MGMP, KBR and KMGGJ). This pattern is supported by the results of our linear mixed-effects model, which showed a significant positive association between soil salinity and the relative density of *R. mucronata*.

The present work revealed six different mangrove plant communities, *Excoecaria agallocha*, *Rhizophora, Lumnitzera – Excoecaria*, *Lumnitzera - Excoecaria*, *Avicennia – Excoecaria, Bruguiera – Excoecaria, and Heritiera littoralis* communities. According to the RDA, the mixed mangrove community, which mainly consists of *Rhizophora, Lumnitzera - Excoecaria* has significantly higher salinity than the *Heritiera littoralis* community. Most of the plots with *Rhizophora, Lumnitzera - Excoecaria* community were on the seaward side and consisted of about a narrow 2 m stretch of a pure *Rhizophora mucronata* community. Although according

to the analysis, the *Avicennia* - *Excoecaria* community had been identified as a community with the slightest preference towards salinity, *Avicennia marina* has been identified as a salinity-loving species by many researchers (Tomlinson, 1994; Kathiresan, 2015). On the other hand, Tomlinson (1994) also reported that *A. marina* as a species occurs in a wide range of saline environments. Results of the linear mixed model analysis of the current study also did not support the fact that the *A. marina* distribution is affected by the salinity. Instead, *A. marina* density showed a positive association with soil bulk density. This finding contrasts with its commonly reported seaward distribution, as soil bulk density typically decreases from the landward to the seaward edge in mangrove ecosystems. However, several studies have noted the disjunct or patchy distribution of *A. marina*, with populations occurring on both seaward and landward fringes (Macnae, 1968; Johnstone, 1983; Dahdouh-Guebas *et al*., 2002). This phenomenon, often referred to as "double zonation" (Johnstone, 1983; Smith, 1992), suggests that *A. marina* may establish in distinct ecological niches within the same mangrove system. Dahdouh-Guebas *et al*. (2004), for example, found no genetic differences between seaward and landward populations in Kenya, indicating that local environmental factors, such as disturbance regimes, hydrological variation, or anthropogenic influence, rather than genetic divergence, may drive this unusual distribution pattern. Thus, the observed association with bulk density in our study may reflect such localized adaptations or site-specific environmental conditions, warranting further investigation.

Heritiera littoralis has been identified as a species on the landward side (Smith, 1992) of the mangrove and prefers comparatively low salinity (Paliyavuth *et al*., 2004). Consistent with these findings, the *H. littoralis* community in our study occurred away from the seaward side, and RDA revealed that these communities occur in low-salinity locations. Further, the linear mixed-effects model analysis showed that *H. littoralis* prefers soil with low bulk density. The *Lumnitzera – Excoecaria* community is also a community that occurs in a low to moderate salinity environment, as indicated by the RDA. The distribution of *Lumnitzera racemosa*, in particular, was strongly and negatively influenced by soil salinity, i.e., its density decreased as salinity increased. This pattern aligns with several previous studies reporting that *L. racemosa* has a limited tolerance for high salinity (Dangremond *et al*., 2015; Barik *et al*., 2018; Manohar, 2021). Even within the *Rhizophora–Lumnitzera–Excoecaria* community, *L. racemosa* typically occurs on the landward side. *Excoecaria agallocha* appears to exhibit a broad tolerance to salinity and is widely distributed across all plant communities. Consistent with this, our linear mixed-effects model did not detect a significant effect of salinity on the density of *E. agallocha*, although its density was positively associated with soil pH. The literature reports contrasting views on its salinity tolerance. Some studies suggest that it is distributed across a wide salinity gradient, from low to high salinity environments (Perera *et al*., 2013), while others provide evidence of high salt tolerance (Jenci and Natarajan, 2009; Mitra *et al*., 2010). However, no reports to date suggest that its distribution is influenced by soil pH.

Soil salinity level of sites in the Pottuvil Lagoon was higher than at the other mangrove sites studied. As concluded above, *Rhizophora – Lumnitzera* and *Excoecaria* community was associated with high-salinity environments, and this community type predominated at Pottuvil lagoon. In contrast, the Okanda Creek mangrove site, fed by freshwater runoff for much of the year, was characterized mainly by the *Lumnitzera* - *Excoecaria* community. A similar pattern was observed at the Ragamwela Creek site. In the Panama Lagoon and Hadaoya Estuary, a variety of mangrove communities were recorded, probably due to broad variation in salinity and other edaphic factors. Notably, *H. littoralis* was found only at the Hadaoya Estuary, which exhibited particularly high variability in salinity and soil characteristics. The site, along with the Panama Estuary, also recorded the highest levels of plant species richness among the studied locations.

The current work revealed that the plant community assemblages in the mangrove sites are determined mainly by the salinity. Similarly, Macnea (1968), Youssef and Saenger (1999), Raganas and Magcale-Macandog (2020) and Sreelekhsmi *et al.* (2020) suggested that salinity is the main driving force of mangrove community assemblies in the Indo-West-Pacific region. Youssef and Saenger (1999) also suggested that waterlogging conditions were a factor contributing to the assembly of mangrove species. Tidal flooding conditions (Snedaker, 1982; Satyanarayana *et al.*, 2009; Wang *et al*., 2019), waterlogging conditions (Matthijs *et al*., 1999) and soil nutrient content (Hilmi *et al*., 2021) have been identified as other factors determining the community assemblages. Soil salinity of the ecosystem could change with the change in hydrodynamics (Bricheno and Wolf, 2018) as well as with climate change (change in rainfall and increase in temperature). Thus, it is suggested that with climate change and the change in hydrodynamics, the community assemblages of mangroves could change.

On the other hand, our study also revealed a more pronounced effect of site on mangrove species composition than the measured edaphic factors, indicating strong spatial structuring likely driven by broader environmental, geographic, or historical differences among sites. This finding suggests that mangrove community assembly is influenced not only by local-scale abiotic conditions such as soil salinity, pH, bulk density, and organic carbon but also by larger-scale spatial and ecological processes. Factors such as hydrological connectivity, tidal regimes, freshwater inflow, propagule availability, disturbance history, and anthropogenic influences may differ significantly among

sites and exert substantial influence on community composition (Alongi, 2002; Feller *et al*., 2010; Friess *et al*., 2012). Furthermore, legacy effects from past land-use changes and natural and anthropogenic disturbances (e.g., cyclones or sedimentation) can leave lasting imprints on vegetation structure (Krauss *et al*., 2008). The strong site effect detected through ordination and statistical analyses (e.g., NMDS, PERMANOVA, and RDA) emphasizes the importance of incorporating spatial context and landscape-level drivers when interpreting patterns of mangrove biodiversity and planning for conservation or restoration interventions.

The findings from the linear mixed model and PERMANOVA analyses in this study provide valuable insights for mangrove restoration planning. The results revealed that the distribution of certain mangrove species is influenced by key edaphic factors such as salinity, pH, soil bulk density, and organic carbon content. Therefore, it is essential to consider these species–soil associations when selecting species for restoration efforts. In addition to edaphic factors, our analyses also indicate that species assemblages are shaped by site-specific conditions, including anthropogenic disturbances and other local environmental variables. These factors must be taken into account to ensure the success of restoration initiatives. Neglecting them may lead to restoration failures, as highlighted by Kodikara *et al*. (2017).

However, it is important to acknowledge that several key environmental factors were not assessed in the present study. For instance, specific hydrological patterns and detailed hydrological data were neither collected nor incorporated into the analysis. Nevertheless, hydrology is widely recognized as a critical driver of mangrove community structure, influencing salinity regimes, inundation frequency, and nutrient fluxes (Twilley and Rivera-Monroy, 2005; Krauss *et al*., 2008). Similarly, the micro- and macro-nutrient content of the soil was not measured, though soil nutrient availability can significantly influence plant community composition, particularly in terrestrial ecosystems (Tilman, 1982; Güsewell, 2004). However, the role of soil nutrient composition in shaping mangrove community assemblages remains less clearly established (Alongi, 2009). Additionally, site-specific factors such as anthropogenic disturbances and historical land-use patterns were not included in the analysis, though these could have contributed to the observed site effects, which were found to be significant in the present study (Ellison, 2000; Friess and Webb, 2014).

In conclusion, our study revealed six different plant communities from five different mangrove sites on the southeastern coast of Sri Lanka. Moreover, the analysis revealed that these plant communities are mainly determined by the soil salinity variations and other site-specific factors like hydrodynamics and disturbance regimes. These findings reinforce the idea that mangrove zonation in Sri Lanka is better characterized as patchy rather than continuous. Consequently, changes in site-specific drivers, such as hydrodynamics or land use. could alter localized salinity profiles, reshaping these patchily distributed assemblages.

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