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Research article

How biotic, abiotic, and functional variables drive belowground soil carbon stocks along stress gradient in the Sundarbans Mangrove Forest?

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ABSTRACT

Mangrove forests, some of the most carbon-dense ecosystems on Earth, play an important role in climate change mitigation through storing carbon in the soil. However, increasing anthropogenic pressures and sea level rise are likely to alter mangrove forest structure and functions, including the major source of carbon in mangrove ecosystems — below-ground soil carbon stocks (BSCS). Although estimating soil carbon stocks has been a popular practice in the mangroves, but poorly understood the (I) the linkage between BSCS and key ecosystem drivers (i.e., biotic, abiotic, and functional) and in (II) determining the pathways of how BSCS and multiple forest variables interact along stress gradients. This lack of understanding limits our ability to predict ecosystem carbon dynamics under future changes in climate. Here, we aimed to understand how abiotic factors (such as salinity, canopy gap fraction, nutrients, and soil pH), biotic factors (e.g., structural parameters, canopy packing, and leaf area index, LAI), and forest functional variables (e.g., growth and aboveground biomass stocks, AGB) affect BSCS (i.e., soil organic carbon, SOC, and root carbon, RC) using spatiotemporal data collected from the Sundarbans Mangrove Forest (SMF) in Bangladesh. We observed that BSCS decreased significantly with increasing salinity (e.g., from 70.6 Mg C ha^{-1} in the low-saline zone to 44.6 Mg C ha^{-1} in the high-saline zone). In contrast, the availability of several macronutrients (such as nitrogen, phosphorous, and potassium), LAI, species diversity, AGB, and growth showed a significant positive effect on SOC and RC. Stand properties, including tree height, basal area, density, canopy packing, and structural diversity, had a non-significant but positive impact on RC, while tree height and basal area significantly influenced SOC. Pathway analysis showed that salinity affects BSCS variability directly and indirectly by regulating stand structure and restricting nutrients and forest functions, although basal area, nutrients, and LAI directly enhance RC stocks. Our results indicate that an increase in nutrient content, canopy density, species diversity, and leaf area index can enhance BSCS, as they improve forest functions and contribute to a better understanding of the underlying mechanisms.

1. Introduction

Mangrove forests are one of the most carbon-rich ecosystems in the tropics containing on average 1,023 Mg carbon per hectare (Atwood et al., 2017; Donato et al., 2011; Friess, 2019; Sanderman et al., 2018). The ability of mangrove forests to store about five times more carbon (C) to soil than other terrestrial forests make them important C sinks. Therefore, preserving mangrove belowground soil C stocks for reducing

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or preventing greenhouse gas emissions is now recognized as one of the most low-cost mechanisms for mitigating climate change (Atwood et al., 2017). However, mangroves are amongst the most threatened and rapidly vanishing habitats on Earth with a 35% global coverage loss since the 1990s for land conversion, deforestation, and habitat degradation (Polidoro et al., 2010; Richards and Friess, 2016). Increasing human pressures and climate change-induced stresses such as sea-level rise (SLR), cyclones, salinization, etc. are likely to cause structural and functional imbalance of the remaining endangered mangrove forests (Carugati et al., 2018; Goldberg et al., 2020; Hamilton and Casey, 2016; Lee et al., 2021; Richards and Friess, 2016), For example, SLR-induced salinity rise has now been recognized as one of the key limiting factors for mangrove growth and development (Chen and Wang, 2017; Kirwan and Megonigal, 2013) in many parts of the world, including Sundarbans Mangrove forest (SMF) (Ahmed et al., 2022). Sea dominated Sundarbans delta is largely exposed to SLR (Banerjee et al., 2012; Mukhopadhyay et al., 2018) and the SLR rate along the Bangladesh coast (5.93 mm yr-1) was substantially higher than the global average (1.0–2.0 mm yr-1) in the 20th century, and the projected SLR is 32 cm by 2050 (Karim and Mimura, 2008). Soil salinity level has already increased by 60% in the SMF since 1980 (Aziz and Paul, 2015). The detrimental consequences of salinity rise on mangrove species distributions, diversity, forest structure and functions in the SMF are now well established (Ahmed et al., 2022). Furthermore, biotic homogenization has been underway in the Sundarbans (Sarker et al., 2019a). Continuation of such historical pressures may drastically alter the structure and functions of the SMF with direct effects on belowground soil carbon stocks (BSCS), the major source of C in mangrove ecosystems (Trettin et al., 2021). Therefore, a comprehensive understanding of how multiple abiotic, biotic and forest functional variables effects BSCS is crucial to comprehend future C dynamics under climate change scenarios.

BSCS consists of root and organic C (Alongi, 2012; Rasse et al., 2005), and contribute more than the aboveground biomass or carbon stocks in mangrove forests (Hamilton and Friess, 2018; Komiyama et al., 2008). Mangrove BSCS or BSCS can be determined by a diverse ecosystem components and variables, for example, stand age (Alongi et al., 2004; Marchand, 2017), sedimentation or siltation (Alongi et al., 2005; Sarker et al., 2019b), waterlogging conditions (Marchand, 2017), soil conditions (e.g., moisture, pH, salinity, salinity zones, bulk density, sand content) (Rahman et al., 2021b; Sanderman et al., 2018; Wang et al., 2021; Xiong et al., 2018), nutrient content (N, P, K) (Adame et al., 2013; Wang et al., 2021), and species diversity and distribution (Jardine and Siikamäki, 2014; Rahman et al., 2021b). More specifically, stand age and nutrients provide positive feedback while salinity, land use change and sand content may play negative roles in determining BSCS (Adame et al., 2013; Badarudeen et al., 1996; Lunstrum and Chen, 2014; Pekkan et al., 2021). Although, detrimental salinity impacts can be reduced by adopting different practices on a small scale (Cicek et al., 2022), which may improve the overall forest functions. However, interactions between abiotic and biotic factors in mangroves are largely controlled by nutrient availability, which can directly influence tree growth (Reef et al., 2010) and BSCS. In fact, multiple biotic and abiotic variables may simultaneously influence BSCS and forest functions through their interactive effects. To illustrate, biodiversity enhances forest productivity (Tilman et al., 1997) and correlated with the nutrient cycling (Ratcliffe et al., 2017; Tilman et al., 1997). Besides, vertical structural diversity (e.g., height diversity), a proxy of niche complementarity (Lee et al., 2022), helps to better predict ecosystem functions (LaRue et al., 2019; Tilman et al., 1997) which is further connected to diversity-productivity linkages (Zheng et al., 2019). Furthermore, salinity restricts the release of nutrients by impeding microbial decomposers, further affecting the composition and distribution of species (Alongi, 2018), which may affect BSCS as species distribution may affect the soil carbon (see above discussion). Hence, any changes of these factors would strongly affect BSCS, thus, uncovering the relationships between these potential driving variables and their effects on BSCS would improve our understanding of how ecosystems may function under stress (Huang et al., 2018).

A number of recent studies have assessed soil organic carbon, SOC, root carbon, RC stocks and its variation with salinity zones in the SMF (Ahmed et al., 2021, 2022; Rahman et al., 2015, 2021b). Besides, salinity, siltation, and soil pH were identified as the key limiting factors affecting mangrove biodiversity and productivity in the SMF (Rahman et al., 2015, 2021b; Sarker et al., 2019b). Although these studies eloquently describe the driving forces for mangrove biodiversity and productivity, and advance our knowledge on mangrove carbon distributions in different salinity zones, we still lack a quantitative understanding of what and how multiple variables i.e., biotic (3D forest structure), abiotic, and functional affect BSCS, and whether the effects are direct or indirect.

Understanding the relationships between belowground carbon in forests and climate change can inform strategies for mitigating and adapting to climate change and is important for predicting and mitigating the impacts on forests, which play a vital role in regulating the global climate. Although mangrove soil carbon is getting global attention and several studies have already made global estimations (Atwood et al., 2017; Kida et al., 2017; Sanderman et al., 2018), they are poorly focused at a regional level, specifically linking with the drivers. Regional data is critical to modelling future climate change impacts at a regional to global level (Alongi, 2012). However, we still know little about how rising salinity may affect BSCS at a regional level and its effect on individual species and communities (e.g., mangrove structure, functions, growth, and productivity) (Ahmed et al., 2022). Elucidating these questions would help us to better understand mangroves' carbon dynamics under changing climates.

In this study, we aimed to quantify how rising salinity, nutrient availability, stand structural properties, and forest functional variables influence mangrove forests' BSCS (SOC and RC). More precisely, we asked (QI): What ecosystem variables influence BSCS? or what are the relationships between biotic factors (e.g., 3D forest structure), abiotic factors, and functional variables with BSCS along the salinity gradient? (QII): How does increasing salinity regulate (directly and indirectly) BSCS via modifying site-specific ecosystem variables? We hypothesised that (HI) abiotic stressors such as salinity, pH, and canopy gap fraction (pink coloured) would have a negative effect on BSCS, whereas a mixture of biotic, functional, and soil nutrient variables would have a positive impact (grey coloured) (see more in Fig. 1). In summary, favourable environmental conditions (such as lower salinity and higher nutrient levels) primarily regulate BSCS directly or indirectly through stand structure, its diversity, and functional variables (HII). To test the hypotheses, we evaluated the forest structure, species and structural diversity, canopy packing, canopy gap fraction, leaf area index, soil salinity, pH, nutrients (N, P, and K), aboveground biomass, and growth variables, listed in Fig. 1.

2. Materials and methods

2.1. Study site

We conducted this study in the Sundarbans Mangrove Forest (SMF) (area of 6017 km^2), Bangladesh (21°30′-22° 30′ N, 89°00′-89°55′ E) (Fig. 2). Based on river water salinity the SMF is categorized into three ecological zones, namely, oligohaline (<14 ppt), mesohaline (14–25 ppt), and polyhaline >25 ppt) (Islam and Gnauck, 2009). According to Ahmed and Iqbal (2011), the plant community assemblages and distribution patterns are strongly determined by the different salinity ecological zones in the SMF.

2.2. Sampling framework and tree inventory

A total of 60 permanent sample plots (PSPs) were established from which we evaluated the carbon stocks and the required forest variables.

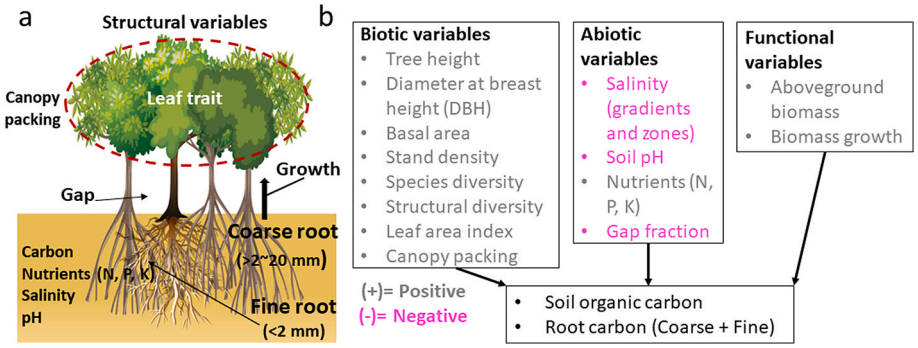

Fig. 1. Conceptualized biotic, abiotic, and functional variables' impact on belowground soil carbon stocks (BSCS) for hypotheses testing. (a) depicts evaluated variables; and (b) potential correlations between studied variables and BSCS.

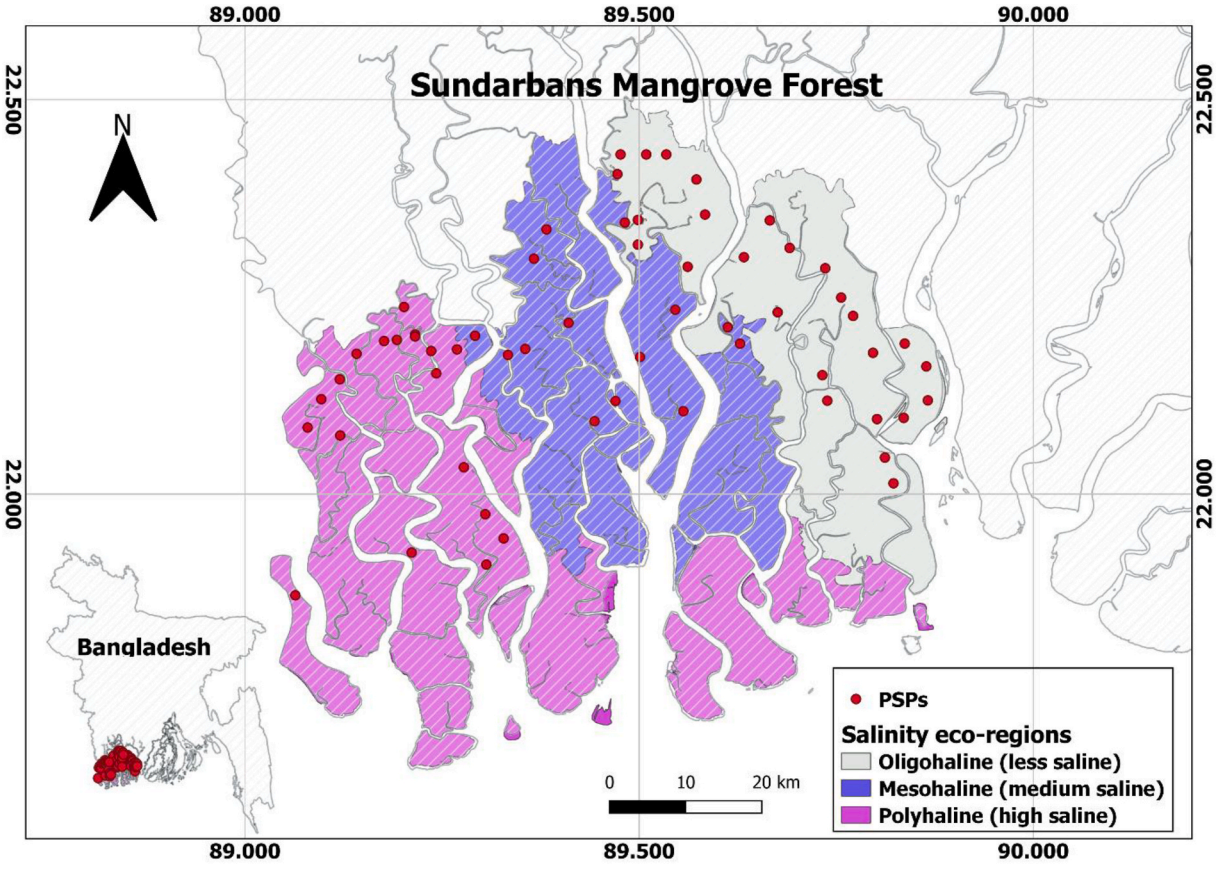

Fig. 2. Showing permanent sample plots (PSPs) locations across three salinity eco-zones in the Sundarbans Mangrove Forest (SMF), Bangladesh.

In each of the ecological zones, we employed the stratified random sampling technique to establish 20 PSPs measuring 0.01 ha each across the Sundarbans Mangrove Forest (SMF) in April 2018. We ensured that the plots we established were a true representation of the major forest types across the saline zones of the SMF (Iftekhar and Saenger, 2008) (Fig. 2). Using an aluminum tag, we tagged all the trees with a diameter at breast height thereafter DBH (1.3 m above the ground) of $\geq$ 5 cm. In addition, we measured tree heights using an electronic dendrometer (Criterion RD 1000, Laser Technology Incorporation, USA). Using a repeated measurement approach, in November 2020, we went back to all the PSPs and measured the DBH and heights of every tree (a total of 1378 tree) that were previously tagged to evaluate growth (biomass changes over time).

2.3. Stand structure and species composition

We used all trees to calculate the stand attributes such as stand density (stems ha^{-1}), mean tree height (m), quadratic mean DBH, and stand basal area ($m^2\ ha^{-1}$). We used the Shannon's diversity index (SDI) to estimate species diversity as a proxy of occupied niches by species (Turnbull et al., 2016)). Since the SDI equally weighs both species dominance and frequency, it prevents any species from being favored more than others (Hortal et al., 2010; Jost, 2006; Liu et al., 2018). To determine the structural diversity (i.e., vertical and horizontal), particularly tree size class distributions, the coefficients of variation of height (Hcv) and DBH (DBHcv) were used as a proxy for habitat quality (i.e., macro and micro) (Heym et al., 2021; Larrieu et al., 2014). In terms of understanding canopy packing (CP) or occupation (i.e., CP is a measure of how densely packed the forest canopy is with trees; a higher CP

indicates the use of a higher niche space) impact, we used a proxy of CP from the standard deviation (sd) of DBH and mean stand density (CP = sd of DBH * stand density) (Jucker et al., 2015; Pretzsch and Schütze, 2016; Williams et al., 2017). We also measured the leaf area index (LAI) and canopy gap fraction (the percentage of canopy foliage cover indicated by the quantity of sky that can be seen through the canopy, a proxy for the niche space availability, LaRue et al. (2019)), using the CI-100 plant canopy analyzer (CID Bio-Science, USA). We averaged five LAI and canopy gap fraction/transmission coefficient data points (four cardinal directions and the center) from each PSP in order to account for plot-level variability.

2.4. Aboveground biomass and carbon estimation

We estimated the aboveground biomass using a non-destructive method (e.g., allometry equations). Based on the newly proposed allometric equations by Rahman et al. (2021c) (see Table 1), we first estimated the dry biomass of all the tree species and then converted it into aboveground carbon (i.e., multiplying by 0.5) using the guidelines developed by Gifford (2000). We also calculated the annual AGB gains from biomass changes by dividing the biomass and structural measurements over the study period (~2.5 years).

2.5. Soil variables (salinity, nutrients, carbon)

We applied a specific soil sample design (see Ahmed et al., 2022 for more details) to identify the spatial variability in soil nutrients, and carbon storage (soil and root) and collected a total of seven soil samples from each PSP at varying depths (15 cm for nutrients; 50 cm for root and soil organic carbon (SOC)). In total, 420 soil samples were collected to estimate nutrients (n = 180), organic (n = 120) and living root carbon (n = 120).

2.5.1. Soil salinity and pH

The Sundarbans' salinity upsurge is often argued to be emanating from the joint effect of the sea-level rise and lower upstream fresh water flow, while anticipating an increase in salinization in the near future (The World Bank, 2017). To understand the relationship between belowground carbon stocks (BSCS) in forests and climate change drivers, we assessed plot level soil salinity in five random samples per year for three years (2018–2020). We took these samples in April (during the early rainy season) and November (during the early winter or dry season). In total, we collected 1800 soil samples over the course of the study. After collecting the samples, we first stratified them into five distinct categories (10 cm each). We then subsequently picked 5 mm of soil from each of the five sections to constitute composite soil samples.

After the tidal water level stabilized, we employed a soil conductivity meter (Extech 341350 A-P Oyster) to measure the in-situ soil salinity (as electrical conductivity, EC) in a 1:5 distilled water: soil dilution (used in Ahmed et al. (2022)). The pH of the soil was then measured in the field by using a digital soil pH meter.

Table 1
List of allometric equations used for aboveground biomass calculation (from Rahman et al. (2021c)). AGB, DBH, and H denote aboveground dry biomass (Kg), DBH (cm), and tree height (m).

Species	Equations
Avicennia spp.	ln (AGB) = −1.56 + 2.21 ln (DBH)
Bruguiera spp.	ln (AGB) = −1.45 + 2.29 ln (DBH)
Excoecaria agallocha	ln (AGB) = −2.57 + 0.862ln (DBH^2 H)
Hereteira fomes	ln (AGB) = −1.99 + 2.46ln (DBH)
Lumitzera racemosa	ln (AGB) = −2.12 + 2.42ln (DBH)
Rhizophoa spp.	ln (AGB) = −2.37 + 0.895 ln (DBH)
Sonneratia apetala	ln (AGB) = −2.89 + 0.917 ln (DBH^2 H)
Xylocarpus spp.	ln (AGB) = −1.92 + 2.31 ln (DBH)

2.5.2. Soil nutrients

In this study, we selected ammonia because it is the most dominant source of nitrogen through denitrification (the conversion of nitrate into ammonia) (discussed in Reef et al. (2010)). The selection and measurement of soil NH_4^+ (thereafter termed as N) concentration followed the Kjeldahl method (Bremner and Breitenbeck, 1983). We also measured total phosphorus (P) using the molybdovanadate technique and a 721 spectrophotometer. An atomic absorption spectrophotometer (AA-7000) was used to quantify the concentrations of potassium (K) in soil at the soil chemistry laboratory of the Civil and Environmental Engineering Department in the Shahjalal University of Science and Technology, Bangladesh.

2.5.3. Soil organic carbon stocks

To estimate the soil organic carbon stocks, we followed the guidelines provided by Howard et al. (2014) and Batjes (1996). In doing so, we collected two soil samples representing each plot by using an open-faced soil auger with a diameter of 5.6 cm and a length of 1.2 m. The samples were further grouped based on three major soil depth classes (0–10, 10–20, and 20–50 cm). We collected soil subsamples (2 mm) from the middle of each of the soil depth classes and mixed them to make a composite soil sample. All soil samples were sorted and refined to be free of stones, visible roots, etc. before being transferred into plastic zipper bags and finally stored in a in plastic box at a controlled temperature (<10 °C) (see details in Ahmed et al. (2022), before being sent to the laboratory for analysis. Details of laboratory analyses can be found in Ahmed et al. (2022). Finally, we converted the SOC density (gm cm^{-3}) to SOC content (Mg ha^{-1}) for the composite samples (see details in Howard et al. (2014)).

2.5.4. Soil root (coarse and fine) carbon stocks

Living tree root samples were obtained from the top soil at a depth of 50 cm using the soil-core method, based on which we estimated the belowground root carbon. We chose the soil-core method because of its cost-effectiveness and accuracy (Addo-Danso et al., 2016). Besides, due to its widespread recognition as the most active soil layer for the majority of mangrove root processes, a depth of 50 cm was chosen for this investigation (Castañeda-Moya et al., 2011; Komiyama et al., 1987). In each of the sample plots, we employed a stainless-steel corer (internal diameter of 12 cm and length 57 cm) to collect two soil cores, summing to a total of 120. The samples were promptly rinsed with 0.3 mm steel mesh and with river water, following which the cleaned roots were stored in polythene zipper bags and sent to the laboratory for analysis. The analysis process entailed soaking the roots in fresh water while flowing through different steel sieve meshes at the same time to separate the roots into two major size classes, namely ≤ 2 mm (fine root) and ≤ 20 mm (coarse root). Our process was entirely based on the protocols of Ahmed et al. (2021), involving the use of bare hands to differentiate living roots from dead roots. Sorted roots were weighed both before and after being, and all root biomass values were converted into carbon following Gifford (2000) and expressed as Mg C ha^{-1}.

2.6. Statistical analyses

To understand overall relationships (hypothesis HI) between belowground carbon stocks (BSCS) and forest variables, we used a double-level approach. At first, we developed a correlation matrix to assess which potential forest variables (biotic, abiotic, and functional) significantly influence BSCS. Second, we developed generalized linear mixed effects (glmm) models by using the "glmmTMB" package in R (Magnusson et al., 2017) to check how salinity in each of the eco-zones affects BSCS. Initially, all biotic, abiotic, and functional variables were included in the models as fixed effects. We only used variables with VIF >3 (variance inflation factor) to avoid multicolnierty. We used the "car" package to calculate VIF in R (Fox et al., 2012). Besides, to avoid temporal and spatial autocorrelation, we included salinity zones and plot

numbers as random effects. We then applied the "dredge" function from the "MuMin" package (Barton, 2010) for selecting the best model with the best combinations of fixed effect variables. The most parsimonious models were selected based on the Akaike Information Criterion (AIC) values, which were then visualized by "sjPlot" in R (Lüdecke and Lüdecke, 2015). Besides, we also used the "ggeffects" package to predict our models' output (Lüdecke et al., 2020). Our data was subjected to the Shapiro–Wilk normality test, followed by a log transformation of data that was not normally distributed.

Finally, we developed a structural equation model (SEM) using the "Lavaan" package in R (Rosseel, 2012) to understand the underlying pathways (direct and indirect with combining interactions and relations) between biotic, abiotic, and forest functional variables with belowground soil carbon stocks (hypothesis HII). Variables that significantly influenced belowground carbon in the correlation matrix were selected for SEM to increase model clarity. The final model was chosen based on the lowest AIC score, and goodness of fit statistics ((comparative fit index, CFI > 0.95, non-significant paths ($p > 0.05$), and the standardized root mean square residual (SRMR < 0.05)) (Schermelleh-Engel et al., 2003) were used to compare and reduce the models. All statistical analysis and visualizations were performed in the R environment (version 4.2.1) (R Core Team, 2021).

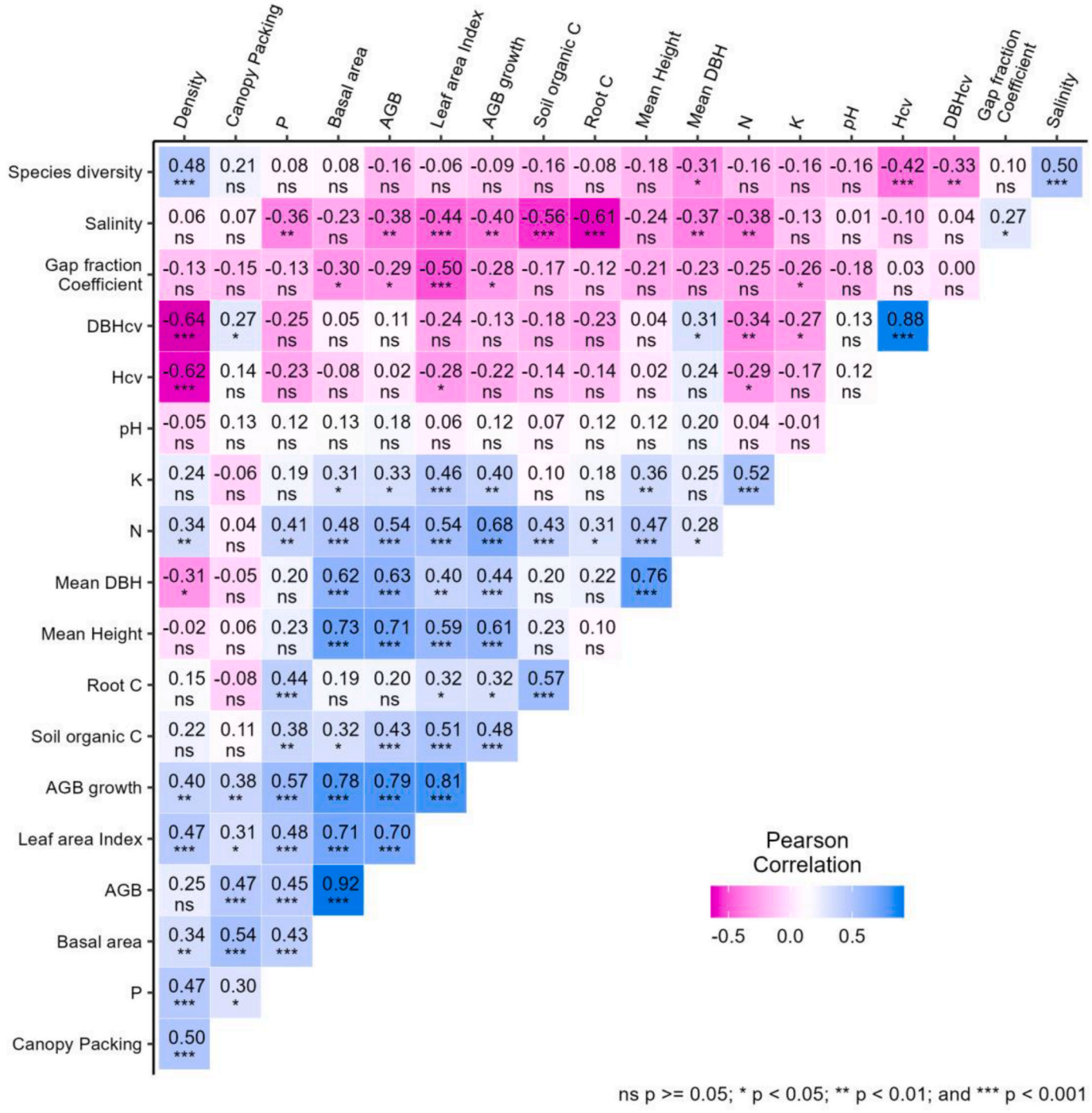

Fig. 3. Correlation matrix visualizes the overall linkage between biotic, abiotic, and forest functional variables with belowground soil carbon stocks (organic and root).

3. Results

Data on various biotic, abiotic, and functional variables in different salinity eco-zones are summarized and presented in Supplementary Table 1. Species-specific DBH distributions are shown in Supplementary Fig. 1.

3.1. Factors influencing belowground carbon stocks (BSCS) (HI)

The Pearson correlation analysis revealed significant positive relationships between belowground carbon (organic carbon and root carbon), nutrient availability, leaf area index (LAI), and functional variables such as aboveground biomass stocks (AGB) and growth ($p < 0.05$). Fig. 3 shows the correlation coefficients for these relationships. Salinity, in contrast, had a significant negative effect on BSCS ($p < 0.05$). Species and structural diversity (i.e., DBHcv and Hcv) and canopy gap fraction had non-significant but negative impacts on BSCS, while canopy packing (CP), mean DBH, and mean height showed non-significant but positive effects on BSCS. Although CP had no significant impact on BSCS, it was significantly correlated with BSCS-positive influencing factors such as basal area, AGB, growth, and LAI. Additionally, all stand structural variables, except mean stand height and basal area, showed non-significant effects on soil organic carbon (SOC) and root carbon (RC) (Fig. 3). Salinity and salinity-driven variables had a negative effect on overall ecosystem variables (correlation coefficients were negative in all cases).

Combining all the biotic, abiotic, and functional variables, we found that LAI and root carbon stocks (coarse and fine) positively affect SOC stocks (Fig. 4a), while species diversity and nutrient availability affect coarse and fine RC stocks ($p < 0.05$) (Fig. 4b and c). In contrast, the overall effect of salinity on BSCS was negative ($p < 0.05$) (Fig. 4a–c). Details of the fitted models are presented in Supplementary Table 2. Our

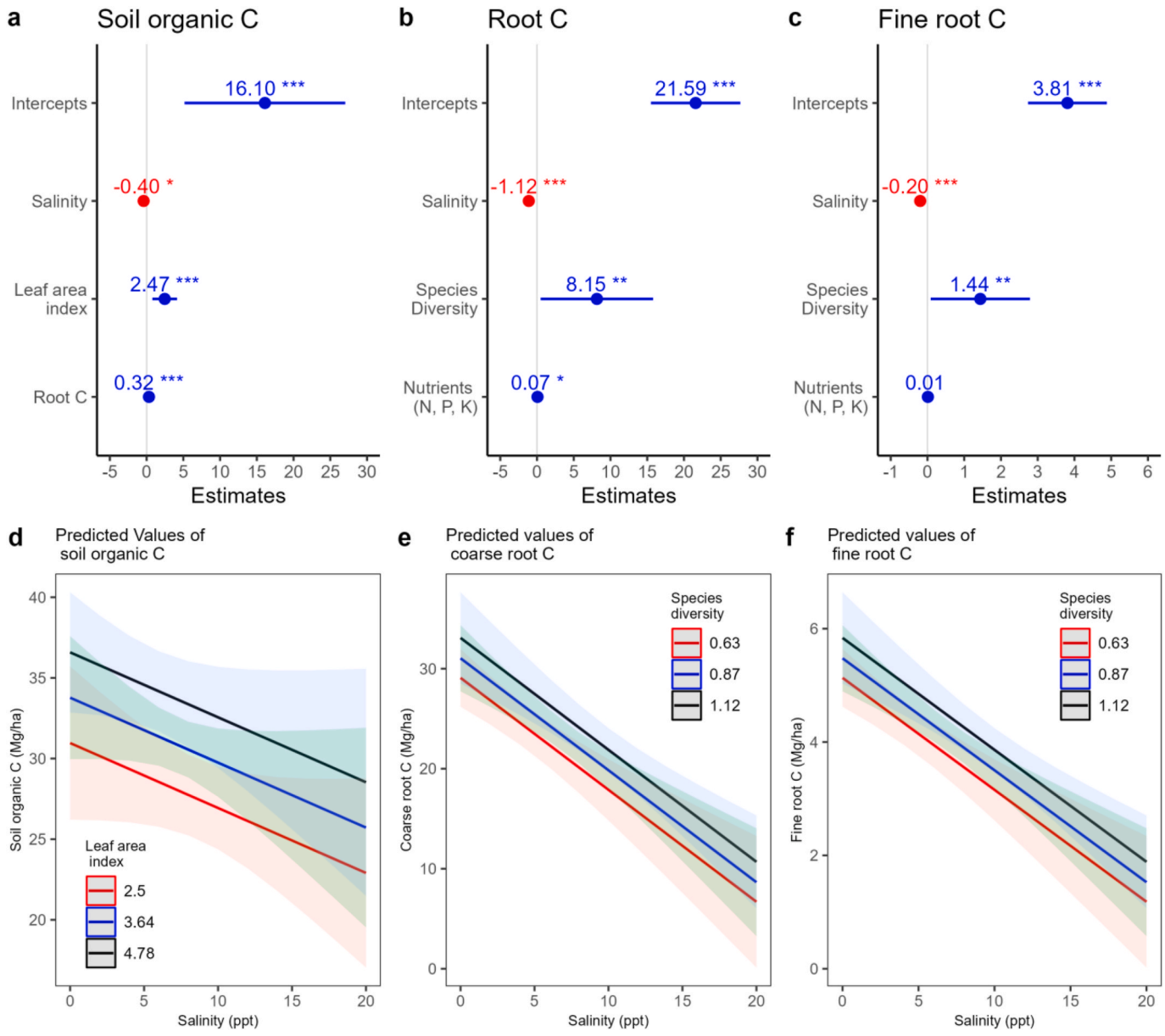

Fig. 4. Fitted linear mixed models presenting the estimates of the coefficients, where (a) showing best fitted model to predict soil organic carbon, (b) coarse root carbon and (c) fine root carbon. Blue indicates standardized values above the overall model estimate and red indicates standardized values below. Solid dots are mean estimates with 95% confidence interval (CI) and the numbers above indicate the coefficient values. The adjacent asterisk signs denote their significance level (***$p < 0.001$; **$p < 0.01$; *$p < 0.05$). Grey shaded vertical lines in top row indicate the reference value for the no effects (estimates = 0). Besides, (d–f) represent the predicted models the using variables of interests, here LAI and species diversity. Shaded areas denote the 95% confidence intervals.

predicted models revealed that LAI and species diversity strongly influence the BSCS (Fig. 4 d–f), indicating that increasing LAI changes intercept values while salinity maintains slopes roughly constant.

Moreover, strong variations in BSCS (organic, coarse roots, and fine roots carbon stocks) were observed across the salinity eco-zones, which decreased in the higher salinity zone ($p < 0.05$). The highest overall stocks of SOC and RC were found in the oligohaline ecozone. Similar results were observed for coarse and fine root stocks (see Supplementary Fig. 2).

3.2. Pathways of belowground soil carbon or interactions (direct vs. indirect) with factors (HII)

SEM results revealed interacting linkages between soil salinity, BSCS, and other forest-related factors (Supplementary Table 3, Fig. 5, Supplementary Fig. 3). Overall, data showed that soil salinity had a direct negative impact on BSCS and functional variables (i.e., AGB and growth). Besides, mean tree height (MH) showed indirect associations (Supplementary Fig. 3). The relationship between soil salinity and growth was shown to be directly non-significant; however, salinity had an indirect impact on growth by directly affecting nutrients, carbon, and LAI as well as by boosting canopy gap fraction (Fig. 5, Supplementary Table 3; Supplementary Fig. 3). Indirect and non-significant relationships are presented in Supplementary Fig. 3.

4. Discussion

We observed synergistic effects of multiple forest variables on the belowground soil carbon stocks (BSCS). Salinity, a large forest canopy gap, and a high magnitude of salinity (i.e., zones) are the primary stressors limiting BSCS, whereas higher nutrient (N, P, and K) levels, functional variables (AGB and growth), and leaf area index promote BSCS. Pathway analysis showed that salinity had a direct negative impact on BSCS, while stand structural attributes (such as height and basal area) and nutrients had a direct positive effect on BSCS (Figs. 3–5).

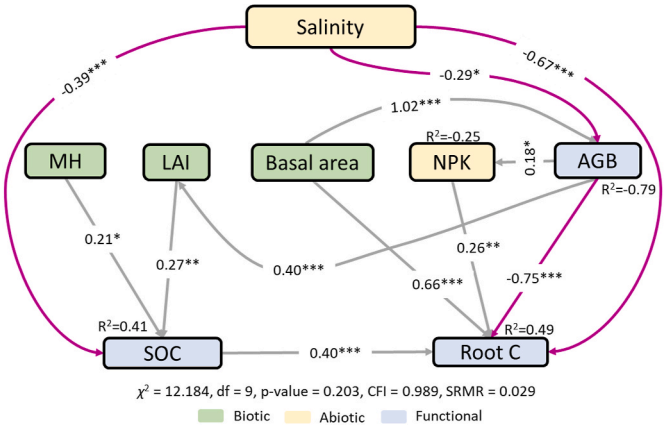

Fig. 5. Structural equation model (SEM) showing the diverse associations and pathways between biotic, abiotic, and functional variables with belowground carbon stocks. Developed SEM model goodness of fit tests, $\chi 2 = 12.184$, $p = 0.203$, with a comparative fit index (CFI) close to one (CFI = 0.99) (Bentler, 1990) and standardized root mean square residual (SMMR = 0.029), indicating no significant deviation from model datasets at 9 degrees of freedom. The grey and red arrows indicate the pathways of positive and negative effects between covariates, respectively. Arrows with numbers indicate the standardized association of predictors with dependent variables. The numbers in the above boxes indicate their explained variance (coefficient of determinant: R2 indicates the proportion of variance explained) by all the predictors. The adjacent path values indicate the standardized path coefficients indicated with their significance level (asterisk signs) (***$p < 0.001$; **$p < 0.01$; *$p < 0.05$). Only direct and significant relationships are shown. Please see Supplementary Fig. 3 for non-significant and indirect relationships.

4.1. Drivers of belowground soil carbon stocks (BSCS) (HI)

Salinity, structural variables (such as tree height, DBH), LAI (leaf arear index), nutrients, growth, and productivity collectively affect BSCS with multiple consequences in the SMF (Figs. 3 and 4). Stand structure (e.g., height, DBH, basal area), nutrient availability (N, P, and K), and forest functions (AGB and growth) positively affect soil organic carbon stocks (SOC). High saline conditions and low concentrations of several macronutrients (N, P, and K) contributed to reduce site quality in the SMF (Ahmed et al., 2022), which limits different aspects of forest functioning as observed in this study (Supplementary Table 1, Fig. 3). Furthermore, poor site quality may reduce soil microbial activity, resulting in decreased nutrient release and plant growth (Alongi, 2018; Yan et al., 2015). Because microbial activity is one of the primary processes for SOC formation (Jastrow et al., 2007), the reduction of microbial activity in high-salinity, nutrient-poor sites can strongly contribute to reduced BSCS.

Our study revealed an inverse relationship between salinity and BSCS in the SMF, which is in line with other mangrove studies across the globe, where they have also reported that high salinity retards mangrove productivity and carbon stocks (Ahmed et al., 2022; Lara and Cohen, 2006). Recently, Rahman et al. (2021b) and Ahmed et al. (2021) have observed a significantly reduced amount of soil carbon and fine root stocks in the high saline zones of the SMF, Bangladesh, which is also similar to our results. In contrast, in an earlier study, Rahman et al. (2015) compared belowground carbon stocks across the low, moderate, and high salinity zones in the SMF and reported a substantially lower BSCS in the low salinity zone compared to the high salinity zone. This could happen due to variations in sampling intensity and sampling sites, along with the species composition of the sampling sites, as Rahman et al. (2021b) observed species composition significantly influencing SOC stocks in the SMF. However, these contrasting results do not indicate that productivity will be automatically enhanced in low salinity zones because other habitat constraining factors for mangrove growth and development (such as nutrient limitation and siltation) in such areas may also limit mangrove growth and properties (Ahmed et al., 2022; Lamers et al., 2013). For example, we observed a declining trend in mean tree height for most of the observed trees in the mangroves with increasing salinity (see Supplementary Table 1 and Supplementary Fig. 1), which can ultimately contribute to ecosystem carbon loss. Sarker et al. (2021) have recently shown that increasing salinity results in dwarfism of the plant species in the SMF, and the effect is higher for the most carbon-contributing species (e.g., *Heritiera fomes)* in the SMF. High salinity also causes spatial variability in tidal water nutrients (Wahid et al., 2007), while we found decreasing patterns of nutrients at the plot level (Fig. 3). Another reason could be that the less saline benign mangrove sites are usually more diverse (i.e., heterogeneous species and structural composition) and productive, which promotes higher primary and secondary tree growth and thus contributes to higher biomass and carbon stocks than the highly saline stressed sites (Crooks et al., 2011; Kathiresan and Bingham, 2001).

Unfavorable site conditions, plant disease, and human exploitation have enhanced tree mortality in high-salinity areas and thereby the canopy gaps (Ahmed et al., 2022; Sarker et al., 2019a). We also observed that canopy gap fractions positively correlated with salinity (Fig. 3), which indicates that salinity could increase tree mortality and create gaps, which later negatively affect BSCS by changing forest structure. Besides, we expected that species diversity may positively enhance BSCS, which is commonly observed in other subtropical coastal regions (Li et al., 2020). However, our mixed effect models identified the significant impact of species diversity on BSCS (Fig. 4, Supplementary Table 2), albeit the correlation matrix showed non-significant results, which indicates that the influence of species diversity is plot- and zone-specific and partly supports our first hypothesis (HI). Rahman et al. (2021a) also mentioned that species richness or diversity in the SMF has a positive effect on SOC stocks. Additionally, Bai et al. (2021) found that

mangrove species diversity positively influences soil carbon storage on the Hainan Island of China. A more refined analysis of their study, however, indicated that the positive association was significantly more evident in the forest tree communities than the shrub communities or a mixture of forest and shrub communities. The reason for this observed pattern could be related to the higher species diversity and carbon storage in the SMF. Besides, we observed that species diversity positively correlated with salinity (Fig. 3). We argued that salinity may increase species diversity but decrease species productivity in high-saline areas, making them dwindle. Another possible reason is that high-saline areas are often close to the sea (Ahmed et al., 2021). This means this region is likely to face strong winds and saltier water from the sea flooding more often, which might raise the salinity level compared to other areas. Similarly, strong wind conditions may produce structurally diverse mangrove communities with high saline tolerant species (such as dwarf and bushy-like species such as *Ceriops decandra* growing in the SMF) (Ahmed et al., 2021), which may contribute less to BSCS, leading to lower BSCS stocks in high-saline and sea-exposed areas. Low productivity could occur due to high salt water, which may reduce fresh water availability for trees, create dry soil conditions, and increase the chance of hydraulic failure (HF). By closing stomata, plants can reduce the risk of failure, leading to lower C accumulation (Joshi et al., 2022), resulting in less productive species. Another reason could be to avoid HF in high salinity areas; trees might have adapted reduced leaf size (as we observed a decreasing trend of LAI with salinity) to avoid water loss via transpiration, as plants avoid HF by closing stomata (Joshi et al., 2022; Raschke, 1976). These conditions result in lower growth and, thereby, lower carbon stocks in higher saline areas of the SMF. However, the effects of species stomatal conductance, hydraulic capability including inundation (high salt water), and wind on BSCS, on the other hand, are largely unknown.

Furthermore, as the local setting (nutrient availability) may regulate species composition (Castañeda-Moya et al., 2013; Simard et al., 2019), this spatial variability in BSCS can be linked with spatial local dynamics at the plot-to-stand level. In this study, we recorded high carbon stocks in the low-saline ecozone, which could be the result of higher nutrients' availability and nutrient-induced species growth. These spatial dynamics may influence the stand structure (such as height, DBH, etc.), diversity, and their functions as well (Simard et al., 2019), all of which can be linked to BSCS (Figs. 3 and 4). Mangrove ecosystems usually experience a trade-off between salinity and the spatial assemblages of species as well as the functional growth and productivity of mangrove forests, thereby influencing the carbon stocks of such ecosystems (Crooks et al., 2011; Twilley and Chen, 1998). Our results suggest that the trees' functions are more saline sensitive, and they may lose functions (e.g., growth) more rapidly with increasing salinity, implying that the biomass accumulation rate may be slowed with rapid salinity changes, which may reduce the BSCS stocks by limiting root production. This implies that trees' functional relationship with salinity is species-specific, as some trees are salinity tolerant (e.g., *A. germinans*) and others are not (Devaney et al., 2021), which is identical to species-specific DBH responses to salinity in our study (see Supplementary Fig. 1).

4.2. Pathway analyses of belowground soil carbon stocks (BSCS) (HII)

Our SEM (structural equation model) analysis revealed that both biotic and abiotic variables influenced BSCS and forest functions (growth) either directly or indirectly. To illustrate, salinity has a direct negative impact on BSCS. In contrast, salinity indirectly affects growth by limiting LAI and nutrients (Fig. 5, Supplementary Fig. 2). SEM also depicted that the mangrove BSCS was linked (directly or indirectly) to the structural properties such as height, basal area, and AGB, which increased with basal area but decreased with tree density (Figs. 3 and 5, and Supplementary Table 3). These relationships have been well documented by others, who state that mangrove tree carbon sequestration increases significantly and continuously with tree size (Stephenson et al., 2014). SEM identified that soil nutrients were directly enhancing root stock and biomass growth (in a non-significant but positive way) (Supplementary Fig. 2). The underlying pathways or mechanisms of the relationships between diversity and carbon stocks might be linked with nutrient availability and climatic conditions. For example, diverse mangrove systems are characterized by higher nitrogen content and mean annual precipitation, both of which are positively linked to mangrove diversity and thus significantly increase mangrove carbon stocks (Osland et al., 2017; Simard et al., 2019). Therefore, it is generally suggested that spatial patterns of mangrove diversity and carbon storage are influenced by climate and soil resource-dependent mediating factors (mean annual precipitation and soil nitrogen, respectively). It is popularly argued that mangrove ecosystems are nitrogen-limiting plant communities (Reef et al., 2010), because higher nitrogen accumulation accounts for more soil nourishment that facilitates mangrove growth (Hamilton and Friess, 2018; Sasmito et al., 2019).

The influence of growth and AGB on BSCS was direct and negative but positively affecting NPK contents, which further benefit stand structure (e.g., basal area and height) and thereby rapid tree growth (Fig. 5). Temmerman et al. (2012) identified that rapid tree growth results in an increase in AGB stocks. This could also be linked with site-specific conditions, for example, nutrient availability and salinity (Twilley and Rivera-Monroy, 2009). Low nutrients and high salinity cause slower growth and a decline in species-specific forest structure (Ahmed et al., 2022; Devaney et al., 2021). In addition to the direct effect, lower carbon stocks in the high salinity eco-zone may occur as a result of the interactive effects of site-specific variables and species composition. In accordance with that notion, our study demonstrated that forest growth and soil carbon stocks were largely influenced by nutrients, salinity, and stand structure (Figs. 3 and 5, and Supplementary Fig. 2). Similar findings were reported by Chowdhury et al. (2019) for the Indian part of the Sundarbans, showing that soil with deficient nutrients and increased salinity significantly impacted the structure of the forest coverage. Thus, salinity-driven forest structural change might have a strong impact on BSCS.

However, we identified a direct negative link between root stocks and AGB stocks (Fig. 5), indicating rapid tree growth adds more AGB and carbon to this mangrove system but reduces belowground root production. The underlying mechanism could be closely related phylogenetic species that share the same niches and evolutionary history (Huang et al., 2020). Close phylogenetic species with higher wood density (e.g., *H. fomes*) are resistant to strong wind or stem breakage, forcing them to add a greater proportion of biomass to the stem (Chave et al., 2009). The SMF, which is largely exposed to the sea, is likely to face strong winds (see above discussion), which might force species to have more biomass in their stems than roots, specifically in the high saline zones (see Supplementary Fig. 2). Meanwhile, SOC is strongly linked with root growth, which contributes to SOC in the soil substrate (Rogers et al., 2019). Our SEM has also identified a strong and direct link between SOC and root stocks (Fig. 5). This indicates that forest growth contributes to SOC stocks through producing roots and their decomposition, or vice versa. Therefore, lower root production results in an overall lower BSCS.

Furthermore, organic carbon is a well-recognized soil fertility indicator (Begam et al., 2020), and poor sites (see above discussion) might contribute to reducing SOC (Kida et al., 2017). Low soil carbon burial could be another reason for low SOC in high-salinity areas, as sea-level rise reduces decomposition by increasing salinity and thereby influences soil carbon burial (Spivak et al., 2019). Our SEM showed that LAI and SOC are directly related, while higher salinity lowers LAI. This means that smaller leaves may contribute less leaf litterfall and litter carbon than larger leaves, which further increases the chance of reducing the availability of nutrients in the soil.

4.3. Study implications and future directions

Our results suggest that salinity, 3D forest structure (a combination of canopy packing and structural diversity), nutrient availability, and canopy gap fraction are important factors that can affect the growth and carbon stocks in the SMF. Specifically, low salinity and high nutrient availability appear to improve the ecological stability and belowground soil carbon stocks (BSCS) of the mangrove ecosystems. Additionally, species diversity and higher canopy packing through crown complementarity may be strong drivers of BSCS, indicating that 3D structure is crucial in determining BSCS, although vertical diversity may not have the same effect due to stress conditions. Failing to consider the three-dimensional structure of forests in modeling efforts may lead to inaccurate predictions of BSCS across salinity gradients, particularly when models are applied to sites that differ from the sites where BSCS was higher (i.e., sites with either high or low levels of salinity that are either poor or rich forests, respectively, according to Ahmed et al. (2022)). This could potentially lead to misleading conclusions about the impacts of salinity on these forested ecosystems in climate change scenarios. Therefore, it is important to carefully consider the 3D structure of forests when developing and applying modeling approaches in order to ensure that the results accurately reflect the complexity of these systems. In addition, the above discussions (sections 4.1 and 4.2) suggest that the mangrove ecosystem can be characterized by complex interactions among forest variables that may not be explained only by directional relationships. However, we anticipated that by comprehending the bi-directional (direct and indirect) relationship between BSCS and the related drivers, we may be able to more accurately predict how BSCS and ecosystem functions will react in the face of climate change, particularly in regions where salinity is a significant issue. So, this study lays the groundwork for using 3D structural modeling with BSCS through complex causal relationships in mangroves, which is something that doesn't happen very often. So, using data from terrestrial laser scanning could make it easier to describe the structure of a forest and link it to the belowground soil carbon stocks.

Finally, our results indicate the combined effect of low salinity, high nutrients, and 3D forest structure on BSCS. This recommends that maintaining upstream freshwater flow may help to preserve habitat suitability for certain species (Sarker et al., 2019a), while we observed that a major portion of species performed better in less saline areas (see DBH distribution), which could be a useful strategy for mitigating the negative effects of salinity (Ahmed et al., 2022; Cicek et al., 2022). Thus, this study provides valuable insights for the management of coastal ecosystems, including mangrove plantations, in the face of projected climate change. The results of this study have important implications for improving the ecological stability of coastal ecosystems by maintaining forest structure (e.g., DBH, tree height, canopy packing, etc.) and species composition (more productive species like *H. fomes*), which are becoming more and more recognized as important for protecting coastal areas and as possible tools for slowing down climate change.

5. Conclusions

This study examines the interplay of various biotic, abiotic, and functional forest variables on mangrove belowground carbon stocks (BSCS). We found that salinity has a negative impact on forest structure, growth, carbon stocks, and nutrient availability, potentially undermining the ecological stability and BSCS of the mangrove ecosystem. In contrast, low salinity and high nutrient availability appear to enhance the performance of the forest. We also observed that 3D forest structure (stand structure additively packed with canopy) and species diversity have a positive effect on BSCS. Although we mostly used proxy variables to characterize 3D forest structure, the use of advanced tools such as terrestrial laser scanners may yield more accurate results concerning the relationship between 3D forest structure and BSCS. These findings may be useful for predicting the impacts of climate change on coastal plantations and other coastal ecosystems. Our study was based on a natural forest, and future studies using coastal plantations and more advanced tools (like laser scanning data) may help to better explain how coastal mangrove forests work and incorporate our current findings.

Credit author statement

Conceptualization-SA. Data Collection- SKS (lead), SA, MK. Formal analysis- SA. Manuscript writing- SA and JAE. English Editing- CSSN and EC. Final review- HP, SKS, FIC and EC. All authors read and approved the final version of the manuscript.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data is shared with the manuscript

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Appendix A. Supplementary data

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