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Soil nutrients and leaf area index interact with species and structural diversity to buffer mangrove productivity against salinity

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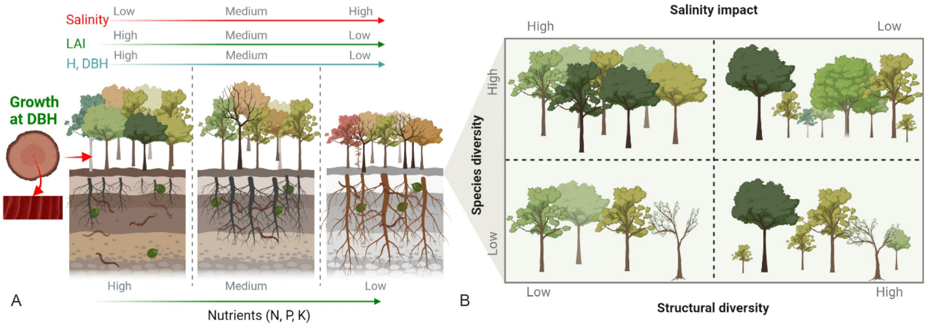
ABSTRACT

- The comparative roles of species and structural diversity in mitigating the impacts of salinity were evaluated.
- Greater diversity contributes to mitigating salinity impacts by interacting with nutrients and leaf functional trait.
- Nutrients and leaf functional trait (leaf area) significantly influenced the effects of salinity on mangrove growth.
- Future growth models should incorporate functional traits and nutrient availability to improve predictions of mangrove growth under saline conditions.



Mangroves show a biogenic response to adjust sea-level rise by accumulating sediment and carbon (vertical soil accretion), reshaping their structure and composition to minimize the effects. Additionally, the often-overlooked factors of soil nutrient availability, functional traits, and stand structure can alter the mangrove diversity-salinity-productivity link. However, how these multiple drivers interplay to maintain growth against salinity still needs to be better understood. Considering all these, we answered two questions: (QI) How do species diversity and structural heterogeneity modulate growth vs. salinity relationships? (QII) To what extent can structural heterogeneity and species diversity create optimal conditions by minimizing the adverse effects of salinity while concurrently maximizing forest growth? To comprehensively understand the interplay between structural and species diversity, nutrient availability, functional traits, and rising salinity, we examined a dataset from 60 permanent plots established in the Sundarbans mangrove forest in Bangladesh. Our results indicated that species diversity less directly contributed to forest growth than structural heterogeneity, nutrient availability (N, P, and K), and leaf area index. While forest structural and species diversity alone is unlikely to optimize growth, incorporating nutrients into the models showed a slight improvement in buffering against salinity. However, when nutrients were combined with the leaf area index, the models indicated a much stronger enhancement in the forest's resilience to salinity through interactions with these factors, allowing continued growth. In conclusion, our study highlights the relative contributions of species and structural diversity to mangrove growth under stress and the potential roles of nutrients and functional traits. These findings are valuable for forest growth modelling, informing conservation and management strategies for mangroves, particularly in coastal plantations facing environmental changes.

Keywords mangrove productivity, structure-functions relation, competition, density, sediment nutrients, functional traits, climate change

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1 Introduction

Mangrove forests, situated at the intersection of terrestrial and marine environments, hold a significant role in coastal ecosystems (Alongi, 2008). They offer many ecosystem services, including livelihoods to millions of coastal people, shoreline stabilization, protection of coastal communities from tidal surges and cyclones, habitats for various species, and sequestrate huge amounts of carbon per year (210 Tg C yr^{-1}) (Donato et al., 2011; Alongi, 2012, 2014; Yoshikai et al., 2021; Ahmed et al., 2023). However, these vital ecosystems are facing unprecedented challenges due to the impacts of climate change, in particular, the rising level of sea level and salinity and shifts in hydrological patterns (Lovelock et al., 2015; Singh, 2020). Global sea level rise, attributed to climate change, has resulted in extensive changes to mangrove habitats and coastal alterations (Sofawi et al., 2017). This phenomenon not only threatens water availability necessary for mangrove survival but also triggers complex ecological responses that intertwine with other intrinsic factors governing the growth of mangrove forests by reducing structure and changing species composition, which is now well recognized in the Indo-pacific regions (Lovelock et al., 2015; Yoshikai et al., 2021; Perri et al., 2023). Furthermore, the intensity of salinity is projected to increase and is identified as one of the most critical factors that may retard mangrove functional and physiological activities by reducing seed germination (Mitra et al., 2010), leaf size and shape (Mollick et al., 2021), fine root production (Ahmed et al., 2021), tree height (Perri et al., 2023), wood density (Rahman et al., 2021a), and site quality (Ahmed et al., 2022), for example. In response to climate change-induced sea level rise, mangroves adopt a biogenic approach by accumulating organic carbon and sediment (Saintilan et al., 2023). Although few studies explain species diversity through facilitation may help to reduce the salinity impacts (Huxham et al., 2010). However, less is understood regarding the biogenic response of mangroves to salinity, mainly how this response may involve changes in structural and species diversity combined with nutrients and functional traits for maintaining growth.

Biodiversity-productivity relationship is often observed in both tropical and temperate forests, as demonstrated by various studies (Vanelslander et al., 2009; Williams et al., 2017; Ali et al., 2019; Park et al., 2019; Zheng et al., 2019). The finding of this relationship plays a critical role in understanding the growth patterns against stress as tree productivity is mainly dependent on the structural and species diversity (Ahmed et al., 2023; Astigarraga et al., 2023; Pretzsch et al., 2023), while other driver effects can be manifested into accumulated tree structure. Forest stands with higher species and structural diversity facilitating each other through complementarity (Huxham et al., 2010; Jucker et al., 2015). Complementarity occurs when different species occupy different ecological niches, enabling efficient resource utilization by plants and increasing aboveground biomass (Paquette and Messier, 2011; Forrester et al., 2013; Fotis et al., 2018). This is achieved by reducing interspecific competition between species via stratification in crown and root areas (Riofrío et al., 2017; Condés et al., 2023). Several studies reported that structural diversity is more important than species diversity to maintain aboveground biomass growth (Ali et al., 2016; Dănescu et al., 2016; Park et al., 2019; Astigarraga et al., 2023), as species diversity impact can be mediated by structure (Park et al., 2019). Structural diversity is considered a reliable ecosystem function predictor (LaRue et al., 2019, 2023a, 2023b). In contrast, with the increasing of studies on the association of species diversity with forest growth in different locations and/or biomes, conflicting findings emerged-positive, negative, or even neutral (Cavard et al., 2010; Del Río et al., 2022), which initiates dispute among scientists (Dănescu et al., 2016). This debate is likely to occur due to inappropriate consideration of tree age, nutrients, stand density, and different aspects of biodiversity because these driving factors can define the structure and growth from the individual tree to the stand level under stress (Pretzsch, 2009; Condés et al., 2013; Ali et al., 2016; Schmied et al., 2023). In particular, when stand density is a critical factor that may increase competition and reduce growth (Pretzsch, 2005; Ng et al., 2016). When stand density is so high that light becomes a limiting factor, the significance of the tree's spatial arrangement in defining interspecific competition, relationships, and other competitive events may diminish (Amoroso and Turnblom, 2006). A recent experimental study has reported that constant tree growth in mixed forest stands under low to medium tree density (Thurm and Pretzsch, 2021).

Understanding the intricate dynamics influencing mangrove growth amid changing environmental conditions poses a significant challenge. The delicate interplay between rising salinity and density-induced competition is further complicated by the crucial role of nutrients—nitrogen (N), phosphorus (P), and potassium (K), with nitrogen identified as the primary growth-limiting factor for mangroves (Alongi, 2020). As salinity levels increase, nutrient availability tends to decrease, potentially leading to decreased site conditions and productivity (Ahmed et al., 2022), as productivity is strongly correlated to site conditions (Sun et al., 2017). To adjust the site conditions, plants modify the functional traits (Yaseen et al., 2023) and increase the functional trait variability (Price et al., 2014). Later, the modified functional traits will likely modulate plant dynamics (Pérez-Ramos et al., 2019). Despite the widespread acknowledgment of the adverse effects of increased salinity, the influence of diversity in associations with nutrients and functional traits on growth in mangroves remains a largely unexplored aspect. Notably, the role of density-modified structure and the buffering potential of nutrient availability among mangrove trees have received limited attention, even though they hold paramount importance in scientific research and management considerations. Adding to the complexity, the relative extent to which structural and species diversity act as buffers against salinity to optimize growth remains largely unexplored. Bridging these gaps in our understanding is crucial for comprehensive insights into mangrove ecosystems under changing conditions.

Several studies on a regional to global scale have demonstrated that species diversity, tree density management, and thinning can increase forest growth by lowering competition for resources like light, water, and nutrients (Miller, 1997; Zhang et al., 2012; LaManna et al., 2017; Güney et al., 2022; Qu et al., 2022). If forest growth needs to be sustained for a long time, management strategies must be modified in response to the effects of climate change (Millar et al., 2007). Long-term growth can be maximized by employing adaptive forest management techniques, including monitoring and modifying forest structure in response to changing conditions (Lindenmayer et al., 2011). By integrating these principles and practices into forest management, forest ecosystems' ecological health and resilience can be preserved while maximizing growth. Consequently, forest regions' future composition and growth will depend on how tree species respond to projected climate change and local environmental conditions. Despite the strong impact of species and structural diversity on forest functions in climate change scenarios, understanding their comparative role remains contentious.

After considering the above discussion, the overarching objective of this study is to gain a comprehensive understanding of the multifaceted interactions among structural diversity, species diversity, nutrient availability, density-induced competition, and rising salinity and how these interactions collectively or individually shape the growth patterns of mangrove forests (Fig. 1). To do this, we formulated two specific research questions and hypotheses.

(QI) How do species diversity and structural heterogeneity influence growth-salinity relationships? We hypothesized that (HI): Structural and species diversity has a buffering role in mitigating salinity impacts by interacting with nutrient availability and functional traits.

Moreover, (QII): To what extent does the structural heterogeneity and species diversity contribute to buffer forest conditions by minimizing the adverse effects of salinity while concurrently maximizing forest growth potential? To evaluate whether structural and species diversity can optimize growth by reducing salinity impacts, we hypothesized (HII) that the combined influence of structural heterogeneity, species diversity, nutrients, and functional traits would optimize growth. However, we also hypothesized that nutrients and functional characteristics might play a crucial role in enhancing the model's capability and potentially help to reduce salinity impacts.

To address our research questions, we employed a dataset from the Sundarbans Reserve mangrove Forest (SRF) of Bangladesh, one of the largest and most diverse mangrove forests in the world (Rahman et al., 2015; Islam et al., 2016). This dataset includes information on stand structural and compositional diversity, salinity gradients, and

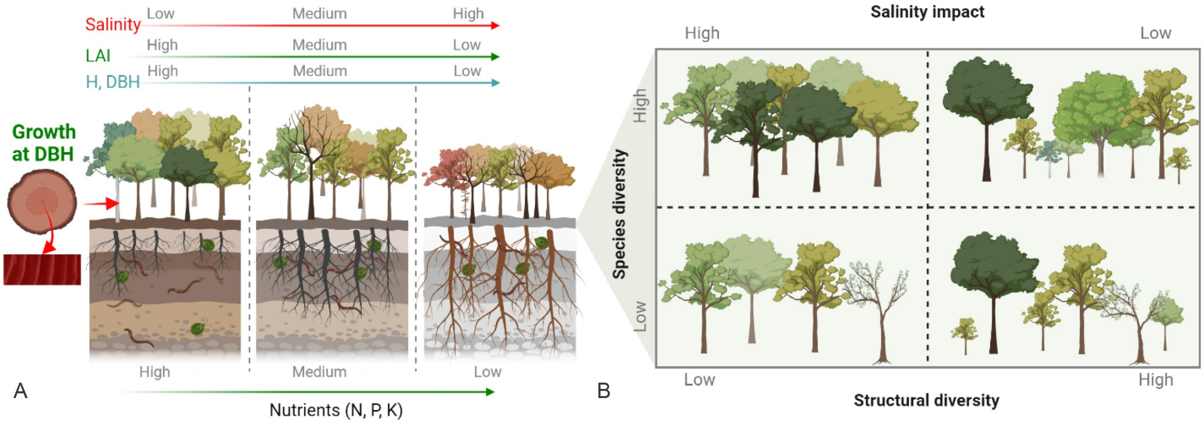


Fig. 1 Conceptual framework illustrating the influence of salinity on forest parameters and growth buffering mechanisms. (A) The variability of forest parameters across salinity levels and (B) the interaction of salinity and structural diversity, species diversity (proportional weight), and nutrients used in this study to describe growth differences and responses. The conceptual diagram explains that salinity stress actively reduces tree growth by limiting structure (tree height, H; diameter at breast height, DBH) and inhibiting resources (nutrients) and leaf functions (leaf area index, LAI). When the forest is structurally diverse in species and structure and resources are abundant, the stress impacts are buffered and promote growth. In panel A, darker soil color indicates higher availability of nutrients (N, P, and K).

nutrients (N, P, and K). We chose this dataset because of the ecological significance of the Sundarbans, which encompasses a large area and is located in an active delta (Bangladesh part: 6 017 km^2). The SRF exhibits salinity gradients species diversity and plays a significant role in mitigating climate change through sequestering and storing atmospheric carbon and addressing natural calamities like tropical cyclones (Rogers and Goodbred, 2014; Akber et al., 2018; Sarker et al., 2019a, 2019b; Ahmed et al., 2022). This region, in turn, holds the potential to inform evidence-based strategies for conserving and managing these crucial coastal ecosystems in the face of dynamic global changes. By enhancing our understanding of the intricate interactions between ecological variables, this research could contribute to scientific knowledge and offer practical guidance for safeguarding endangered mangrove ecosystems from future threats and degradation.

2 Materials and methods

2.1 Study site description and tree inventory

This research was carried out within the unique ecosystem of the Sundarbans Reserve Mangrove Forest (SRF) in Bangladesh, as illustrated in Fig. S1. SRF is located in an active delta (Rogers and Goodbred, 2014) and faces increasing salinity challenges (Lovelock et al., 2015; Ahmed et al., 2022). Due to increasing salinity, SRF loses productive species or less salinity-tolerant species (Sarker et al., 2019a), which makes SRF less productive in high-salinity areas by restricting tree height growth (Ahmed et al., 2022; Perri et al., 2023). SRF has been classified as three saline zones based on river water salinity levels, namely oligohaline (<14 ppt), mesohaline (14–25 ppt), and polyhaline (>25 ppt) (Ahmed et al., 2022). To comprehensively assess the forest's structure, species composition, and carbon storage, we established 60 permanent sample plots (PSPs). Each of these plots covered an area of 0.01 hectares. Our sampling strategy involved the creation of 20 PSPs within each of the three salinity eco-regions. This allocation was achieved through a stratified random sampling approach, ensuring representation across the salinity zones. This first fieldwork was conducted in April 2018.

To document the tree diversity, we identified and labeled all trees with a minimum diameter at breast height (DBH) of 4.6 cm, measured at 1.3 meters from the ground. Aluminum tags were affixed to these trees for identification purposes. Concurrently, tree heights were measured utilizing an electrical Dendrometer, specifically the Criterion RD 1 000 model from Laser Technology Incorporation in the USA. Adopting the 4.6 cm DBH criterion is in line with historical practice, dating back to the 1900s, and is particularly suited to mangroves given their relatively slow aboveground growth pattern.

In November 2020, we revisited all 60 PSPs to remeasure and assess the biomass growth patterns of the tagged trees—data collection involved measuring the DBH and heights of all the 1 378 trees tagged in 2018. However, we excluded all dead trees during the growth (aboveground biomass changes) calculation.

2.2 Stand structure, species composition, nutrients, and biomass estimation

We utilized various tree measurements to assess the characteristics of the forest stand (Table 1). These measurements included stand density (number of stems per hectare), mean

Table 1 List of plot-level variables used in this study.

Variables and metrics names	Abbreviated form	Unit/calculation
Mean diameter at breast height	DBH	cm
Horizontal diversity (coefficient of variation of DBH)	cv of DBH	variation of DBH (cv of DBH=sd DBH/mean DBH)
Mean tree height	H	m
Vertical diversity (coefficient of variation of H)	cv of H	variation of H (cv of H=sd H/mean H)
Initial stand density	Density	stems ha^{-1}
Aboveground biomass stocks	AGB	mg ha^{-1} (biomass equation adopted from Ahmed et al. (2022))
Aboveground biomass changes over time	AGB growth or increment	mg ha^{-1} yr^{-1}
Species diversity	Shannon diversity	Shannon's index
Ammonia (NH_4^+) termed as nitrogen	N	mg kg^{-1}
Phosphorus	P	mg kg^{-1}
Potassium	K	mg kg^{-1}
Nutrients	Nutrients	Total nutrients=N+P+K
PAR leaf area index	LAI	(m^2 m^{-2})

tree height in meters, and the quadratic mean diameter at breast height (DBH), i.e., 130 cm. We employed Shannon's index to evaluate species diversity (our survey covered 13 species). We calculated the coefficient of variation of H and DBH to analyze structural diversity, specifically the distribution of tree sizes. We also determined the Leaf Area Index (LAI) to check the impacts of functional traits on tree growth. We collected five LAI readings from each plot to determine potential tree variability. Lastly, we estimated tree aboveground biomass non-destructively using allometric equations, which had been developed locally to estimate dry biomass for all tree species (Rahman et al., 2021b) (Table S1). Additionally, to assess the influence of nutrient availability, we examined the presence of nitrogen, phosphorus, and potassium within the top 50 cm of soil depth. The above methodology employed is based on the approach outlined in Ahmed et al. (2022).

2.3 Statistical analyses

In our analyses, we started by checking the normality of our dataset using a Shapiro–Wilk normality test. To address any deviations from the distribution of variables, we made a logarithmic transformation to align them with the assumptions of normality and homogeneity, if necessary. Moving on to exploring the first research question (QI), we initially looked at how forest growth, salinity, density, structural diversity, and species richness correlate through linear regression using the “lm” function in R.

Furthermore, to elucidate the relative impacts of species diversity and structural diversity (direct vs. indirect) on mitigating salinity effects on AGB growth across varying nutrient levels, we employed a structural equation model (SEM) utilizing the “lavaan” package (Rosseel, 2012) and plotted the model by “tidySEM” package Van Lissa (2020). To determine the most suitable model, we employed various fit indices, including the chi-square (χ^2) test (with the criteria of $0 \leqslant \chi^2/\mathrm{df} \leqslant 2$), the comparative fit index (CFI) (requiring CFI>0.95), the standardized root mean square residual (SRMR<0.05), and the significance of paths ($p>0.05$), as recommended by Schermelleh-Engel et al. (2003). We calculated the indirect and total association of sediment salinity and Shannon diversity with aboveground biomass growth by following Rahman et al. (2021a).

As we delved deeper into our analysis to test HII, we performed several multiple linear models (MLM) using the “lm” function (global model) by choosing variables from the SEM in a progressive way. We employed an MLM with standardized predictor variables. Standardization was performed using the formula $f(x) = (x_i - x_{min})/(x_{max} - x_{min})$, where x_i represented the variables with their respective maximum (x_{max}) and minimum (x_{min}) values. This approach facilitated a direct comparison of effect sizes, thereby enhancing the interpretability of the model (Schielzeth, 2010). Finally, we optimized all models to maximize the growth by reducing salinity impacts. We used “optim” functions with advanced optimization methods “L-BFGS-B” in base R. Similar to model fitting, we first tried to optimize the model without considering nutrients and leaf area index , as forest structure and species composition management are easily attainable through management (Pretzsch, 2009). We expected that the impact of nutrients might manifest in structure and diversity. In the second and third optimization steps, we included nutrients and leaf area index in the model. We compared the model's performance (i.e., with vs. without nutrients and leaf area index based on AIC values by using the “performance” functions from the “performance” package (Lüdecke et al., 2021). Besides, all the visualizations were done by using the “ggplot2” package (Wickham, 2011).

All statistical analyses and visualizations were performed in R (version 4.3.1) (R Core Team, 2023).

3 Results

3.1 Patterns and distribution of species and structural diversity across salinity, nutrient availability, and density gradients

Stand structure, species diversity, and growth varied across salinity zones and levels as well as stand density (Fig. 2). Most structural diversity, such as H, DBH, cv of H, and DBH, were higher, and distributions were skewed towards the oligohaline and mesohaline zones. In contrast, species diversity tends to be higher in the polyhaline salinity zones (Fig. 2A–2E). Stand structural properties and forest growth (above-ground biomass changes over time) varied across salinity and density gradients (Fig. 2). Forest growth was reduced with salinity. In contrast, growth increased with nutrient availability and density (see the trend in Fig. 2F–2H).

3.2 Role of structural and species diversity in modulating salinity impacts on growth via nutrient availability and functional traits (Q1)

Species diversity enhanced growth across salinity levels but declined under varying nutrient regimes and density gradients (Fig. 3, right column). Structural diversity (measured as the coefficient of variation of DBH) positively influenced growth across nutrient regimes and density gradients but decreased with increasing salinity levels (compare the trends, Fig. 3, middle column). Additionally, AGB growth increased with AGB stocks (Fig. S2). Growth responses to structure and species density across salinity zones are presented in Fig. S3.

Figure 4 shows that growth response varies by species

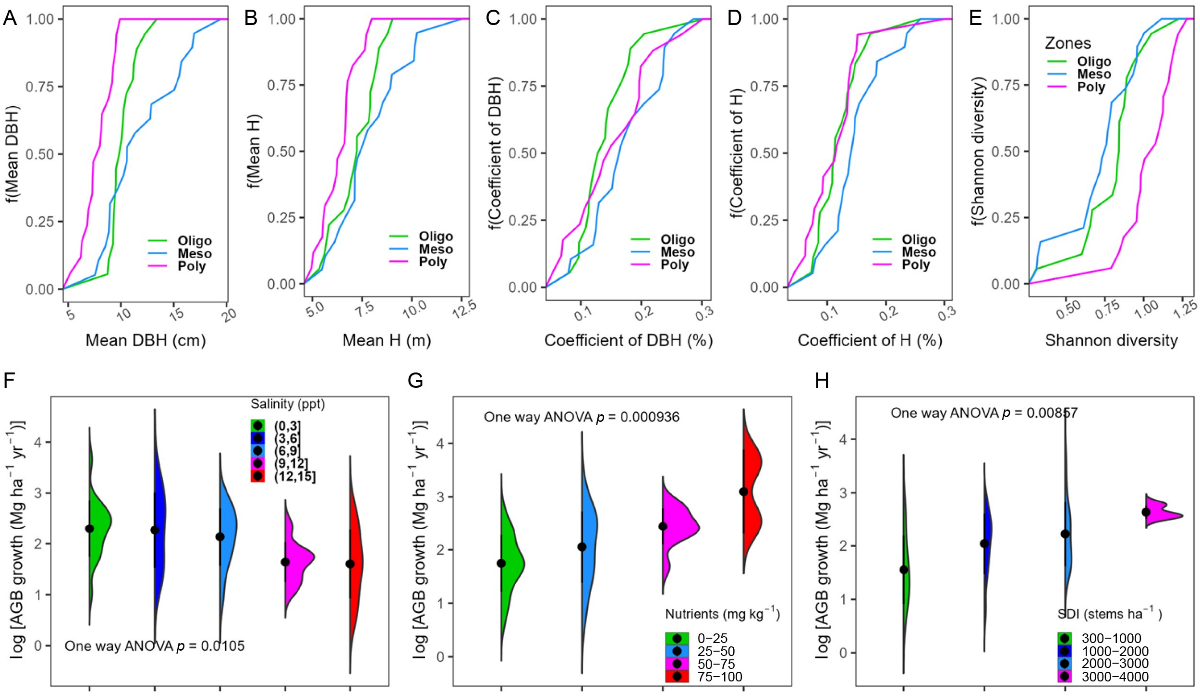


Fig. 2 The descriptive representations of patterns of structure and AGB growth. Top row: (A–E) shows cumulative density distributions of structural properties (A) mean DBH, (B) mean height, (C) horizontal diversity or coefficient of DBH, (D) mean coefficient of height, (E) Shannon species diversity. In the Bottom row, figures (F–H) show growth response. (F) growth response to different salinity levels, (G) growth response to nutrient availability, and (H) growth variability with different stand density levels. In Fig. F–H, vertical solid lines indicate a 95% confidence interval and black circles indicate median values.

and is influenced by functional traits. Growth was positively correlated with mean tree height (H), diameter at breast height (DBH), and LAI, with species-specific variations observed across nutrient availability and salinity levels.

Our Structural Equation Model (SEM) demonstrated a good fit (χ^2=12.889, p=0.301), providing insights into how species diversity and structural diversity influence the relationship between salinity and growth via nutrient availability and leaf area index (see Fig. 5). The SEM accounted for 84% of the variation in Aboveground Biomass (AGB) growth. Specifically, species diversity had a significant direct effect on growth (β=0.16, p<0.01) and an indirect impact by improving leaf trait levels (β=0.10, p>0.05). In contrast, structural diversity showed a positive and statistically significant direct effect on growth (β=0.23, p<0.01).

As expected, salinity was found to be negatively correlated with nutrient availability (β=−0.34, p<0.001) and showed a weak, non-significant direct effect on AGB growth (β=−0.02, ns). This suggests that salinity indirectly affects AGB growth by reducing nutrient availability and LAI rather than having a pronounced direct impact. The LAI had a strong, positive, and statistically significant direct effect on AGB growth (β=0.71, p<0.001), while LAI elevated with nutrients (β=0.40, p<0.001).

The total effect of sediment salinity was negative (β=−0.309, p<0.01), while species diversity (β=0.07, p>0.05) and nutrients (β=0.156, p>0.05) had positive but not significant effects (see Table 2).

3.3 Role of structural heterogeneity and species diversity to create optimal growth conditions (Q2)

The optimized model's results, as shown in Fig. 6, highlight how—species diversity, structural diversity, nutrients, and LAI—influence forest growth in the presence of salinity stress. Fig. 6A shows that predictions fall below zero when only species diversity and cv of DBH are included in the model. Fig. 6B indicates a reduction in the negative trend when nutrients are added, with predictions hovering near the zero line. Figure 6C demonstrates that including LAI results in most predictions exceeding zero.

4 Discussion

Our results indicate that structural and species diversity reduces salinity impacts by associating with nutrient availability and leaf area index. More precisely, structural diversity is more effective in low-salinity areas where competition for light is intense. Species diversity matters more in high-salinity areas where usable water for trees is scarce. Besides, nutrient availability improves forest condi-

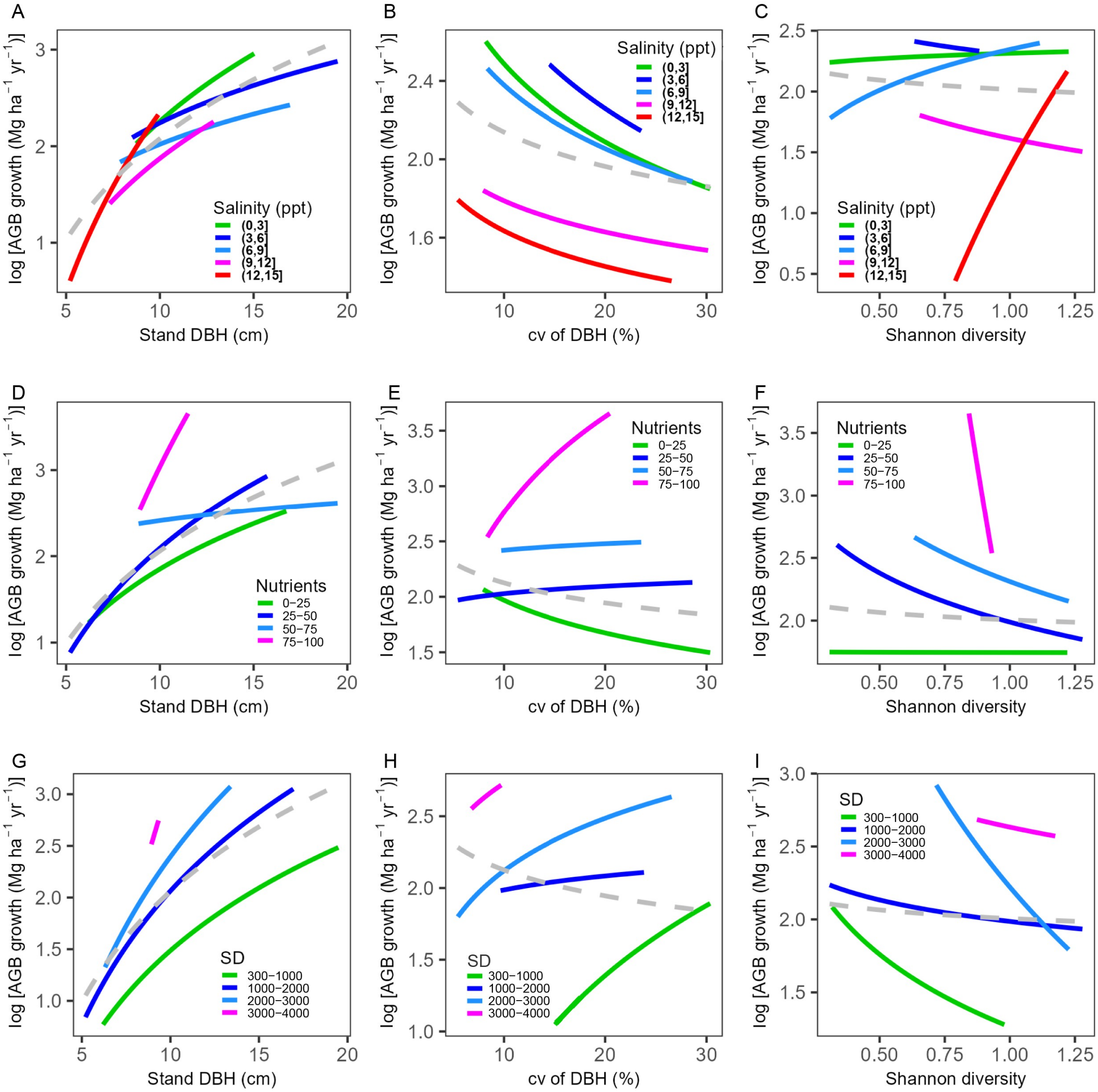


Fig. 3 Growth response to stand structure and species diversity across different salinity, nutrients, and stand density levels. SD indicates stand density (stems ha^{-1}). The Grey dashed line indicates the mean trend line.

tions by helping leaf function traits, further helps the forest reduce salinity stress and competition for light by modifying structure and species.

4.1 Role of structural and species diversity in modulating salinity impacts on growth via nutrients, functional traits, and stand density (Q1)

Our results indicate that forest growth predominantly occurred in lower salinity areas (Fig. 2), driven by salinity's impact on stand structural diversification. High salinity areas showed lower overall growth, likely due to reduced hydraulic conductivity and water availability (Lovelock et al., 2006). Besides, it could also be possibly due to low stand dominant height and stocking degrees (Condés et al., 2013) in high salinity areas.

Mangrove growth's multidimensional response to salinity was observed through tree structure (DBH, cv of DBH), species diversity, nutrient availability, and stand density (Figs. 3−4). Bivariate relationships showed species diversity had a negative and insignificant impact across salinity gradients, but SEM indicated a positive impact on AGB growth when interacting with nutrients and leaf area index. High salinity may increase mortality and create gaps, potentially filled by saline-tolerant species like *C. decandra* (Ahmed et al., 2023), increasing species diversity without enhancing growth. Nutrient levels did not increase with species diversity as expected, possibly due to flash flooding or distinct pheno-

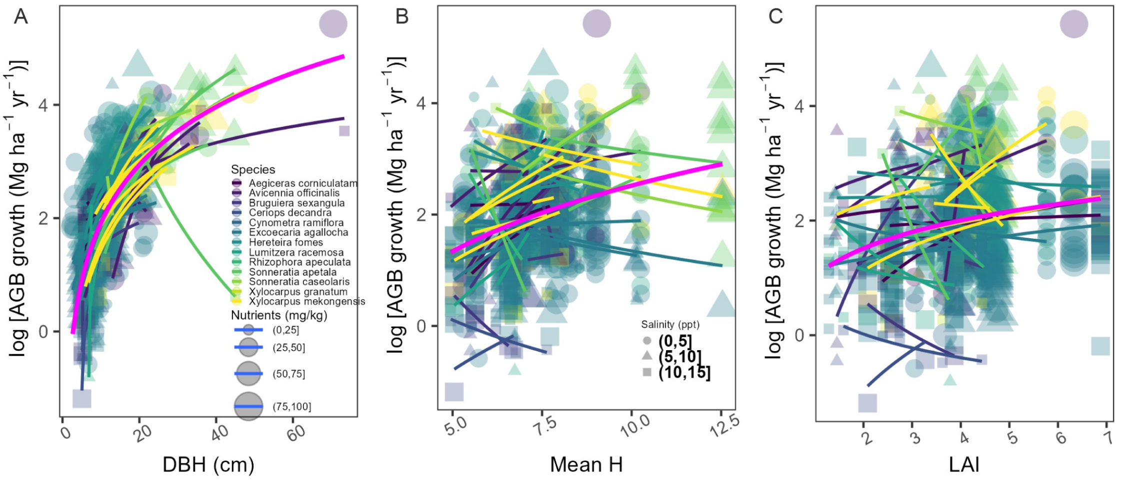
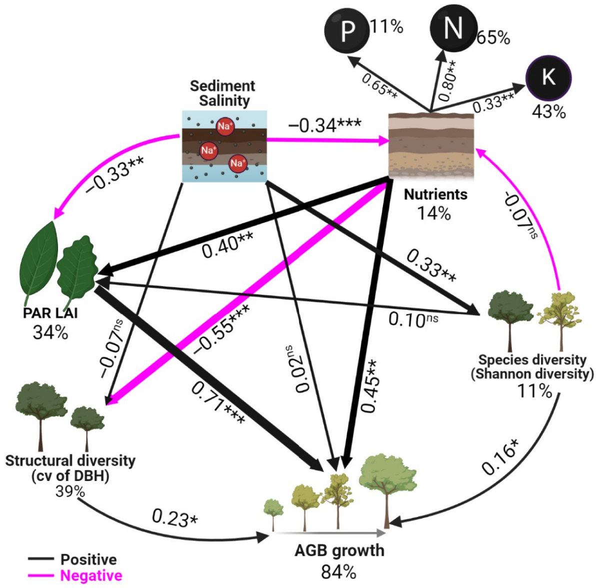


Fig. 4 The changes in AGB growth concerning tree and species level structure (H, DBH), leaf area index (LAI), and varying levels of salinity and nutrient availability. The pink color indicates the mean trend line. Legends are applicable for all sub-figures.



χ^2 = 12.889, *p* = 0.301, DF=11, CFI=0.988, RMSEA=0.053, SRMR=0.066

Fig. 5 The Structural Equation Model (SEM) illustrating the nuanced contributions, both direct and indirect, of species diversity and structural diversity in mitigating the impact of salinity on growth along varying nutrient gradients. The goodness-of-fit tests for the model produced the following outcomes: χ^2=12.889, *p*=0.301, indicative of a commendable fit with the data. Moreover, the Comparative Fit Index (CFI) registered at CFIc 0.988, while the Root Mean Square Error of Approximation (RMSEA) and Standardized Root Mean Square Residual (SRMR) were 0.053 and 0.066, respectively, signifying no significant deviations from the model's underlying dataset. These assessments were conducted with a degree of freedom of two. The numerical values on the arrows denote the standardized strength of the relationships between the predictors and the dependent variables. The figures adjacent to the variables signify the proportion of variance accounted for, quantified as the coefficient of determination (R^2) is denoted by %, by all the predictors. The thickness of the lines signifies the magnitude or robustness of the relationships. Moreover, the proximate path values indicate standardized path coefficients and incorporate significance levels denoted by asterisks (ns>0.05; **p*<0.05; ***p*<0.01; and ****p*<0.001). ns, not significant.

logical patterns or terrestrial inputs. We expected continuous litterfall from various species most likely enriched the soil with nutrients (Ahmed and Kamruzzaman, 2021), and diverse root depths allowed better nutrient utilization (Soethe et al., 2006). This variation could be attributed to differences in nutrient availability across salinity gradients. A previous study highlighted that highly saline, less-diverse Sundarbans mangroves are characterized by elevated phosphorus (P) and potassium (K) levels, whereas less saline, more diverse mangrove communities exhibit higher nitrogen (N) levels. Notably, nitrogen appears to have minimal influence on community diversity (Sarker, 2017). These patterns are likely associated with the location of these areas—lower salinity zones are typically situated near estuaries that receive terrestrial nutrient inputs, while higher salinity zones are found along open coasts with limited or no terrestrial nutrient inputs. Additionally, litterfall decomposition rates and microbial activity tend to be higher in lower salinity areas (Khan et al., 2009; Alongi, 2011), contributing to enhanced nutrient availability.

Besides, these contrasting results indicate that forest functions might species specific and their response to with disturbance or stress type (i.e., competition for nutrients, light or salinity) (see Figs. 3, 4 and Sarker et al. (2021)).

Structural diversity positively correlated with AGB growth but negatively with nutrient levels, suggesting smaller trees benefit more from nutrients. Structural diversity and functional traits had a more substantial influence on biomass growth than species diversity (Fig. 5), possibly due to synchrony or disturbances like cyclones. Species diversity's weak correlation with biomass growth may explain species loss with stand maturity in high saline areas (Schall et al., 2018; Sarker et al., 2019a; Ahmed et al., 2022). LAI strongly influenced AGB growth, enhanced by nutrient availability (Pérez-Ramos et al., 2019; Yaseen et al., 2023), which is consistent with our results.

Table 2 Indirect and total standardized association of sediment salinity, nutrients, functional traits, species, and structural diversity on forest increment.

Indirect and total association pathways	Increment	
	std. as	*p*-value
Indirect association of sediment salinity through Shannon diversity	0.052	0.105
Indirect association of sediment salinity through LAI	−0.232	**0.016**
Indirect association of sediment salinity through nutrients	−0.153	0.062
Indirect association of sediment salinity through cv of DBH	−0.015	0.623
Indirect association of sediment salinity through Shannon diversity and LAI	0.022	0.432
Indirect association of sediment salinity through Shannon diversity and cv of DBH	0.007	0.454
Indirect association of sediment salinity through Shannon diversity and nutrient	−0.01	0.646
Indirect association of sediment salinity through Shannon diversity, nutrient, and LAI	−0.007	0.647
Indirect association of sediment salinity through Shannon diversity, nutrient, and cv of DBH	0.003	0.654
Indirect association of Shannon diversity through cv of DBH	−0.095	**0.045**
Indirect association of Shannon diversity through LAI	0.068	0.411
Indirect association of Shannon diversity through nutrients	−0.05	0.639
Indirect association of Shannon diversity through nutrients and LAI	−0.02	0.642
Indirect association of Shannon diversity through nutrients and cv of DBH	0.009	0.65
Indirect association of nutrients through cv of DBH	−0.127	**0.084**
Indirect association of nutrients through LAI	0.283	**0.004**
Total association of sediment salinity	−0.309	**0.008**
Total association of Shannon's diversity	0.071	0.552
Total association of nutrients	0.156	0.17

The indirect and total associations of sediment salinity, nutrients, and Shannon diversity were based on structural equation models. The significant standardized associations (std. as) have a *p*-value<0.05.

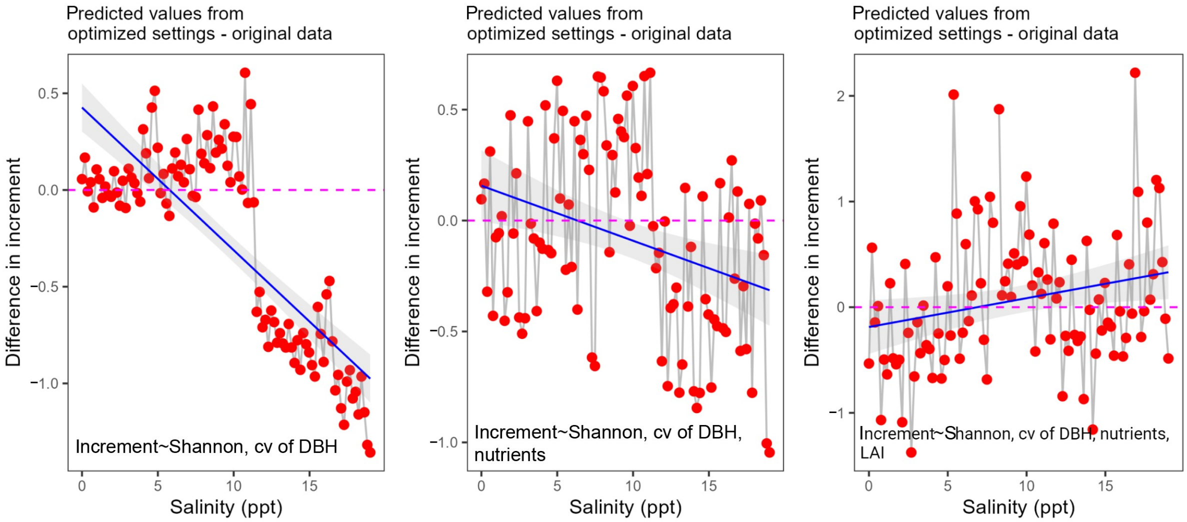


Fig. 6 Model optimization to maximize forest increment or AGB growth. In A–C, the *x*-axis represents the salinity values, and the *y*-axis represents the difference in increment values (the predicted growth values obtained from the optimized settings for a specific set of predictor variables−the actual AGB growth values or the original data). The blue line shows how the contrast changes as salinity changes. The magenta dashed line at *y*=0 indicates where the optimized and actual increment values are equal. If the blue line exceeds the red dashed line, optimized settings reduce salinity's impact on AGB growth; minimal difference suggests predictor variables have limited influence on the outcome. In the subset, respective models optimize the settings, and predictions are presented.

Growth increased with forest stand density, despite SEM not including density in the final model. Higher density fostered greater height growth in young trees, especially in high salinity areas (Fig. 2). Heightened competition for light among densely packed trees led to increased aboveground biomass (López-Hoffman et al., 2006; Peng et al., 2022). Biodiversity and nutrient richness in densely populated stands also contributed to growth (Vanelslander et al., 2009; Cleland, 2011).

However, structural diversity, nutrients and leaf trait positively buffered salinity impacts, while they are interacting together.

4.2 Role of structural heterogeneity and species diversity to create optimal growth conditions (Q2)

Our model optimization settings explain that combined structural diversity and species proportions may not maximize forest growth. However, adding nutrients to optimization settings enabled the forest to buffer a bit (until a certain salinity level was reached). Still, when added functional trait optimization showed the forest to sustain its growth against salinity (see Fig. 6). These results indicate that a nutrient-free setting may not mitigate salinity impacts and nutrient availability most likely trees to capture light and accumulate biomass efficiently through functional traits. However, continuously increasing salinity led to a reduction in growth, eventually reaching the zero line. This supports our second hypothesis (HII). These results additionally indicate that species diversity and structural diversity, coupled with canopy complementarity, assist trees in effectively utilizing the available nutrients and mitigating the impacts of salinity. This could be related to more plastic and extensive crown space occupation by species-diverse stands compared to less diverse stands, which could increase aboveground biomass in higher salinity stands. It could be attributed to species diversity and density, which increased canopy packing, reduced crown shyness, and enhanced light use efficiency, leading to increased growth (Pretzsch, 2014; Jucker et al., 2015). However, the mean line suggests that better outcomes (growth) may be attainable by adjusting predictor variables, i.e., increasing canopy packing through mixing. Several studies have demonstrated that tree density management and thinning can increase forest growth by lowering competition for resources like light, water, and nutrients (Miller, 1997; Güney et al., 2022; Qu et al., 2022).

Nevertheless, sustainable forest growth needs modified management strategies in response to the effects of climate change (Millar et al., 2007; Lindenmayer et al., 2011). Our model optimizations also indicate that structure and the growth of stands can be enhanced under stress by applying suitable silvicultural strategies. By integrating these principles and practices into forest management, forest ecosystems' ecological health and resilience can be preserved while maximizing growth. However, large-scale datasets or more studies are required to conclude.

5 Research implications and future directions

The findings of our study shed light on the crucial role of species and structural diversity in mitigating the impact of salinity, particularly in regions with higher salinity levels. We observe a buffering effect in the areas where species diversity is naturally more abundant. This suggests that the functional differences between species, specifically their varying levels of salt tolerance, work synergistically to support continued forest growth.

Conversely, in regions with lower salinity levels but higher structural diversity, we see a different dynamic at play. Here, the growth persists, indicating that species diversity might not be the primary driver. Instead, less salty areas and salt-tolerant species, while maintaining structural diversity, tend to utilize crown space more extensively through denser canopy packing. This might lead to an increase in aboveground biomass growth.

Besides, in the case of the natural mangrove forest, managing both the structure and species composition becomes critical due to its vast expanse. However, this insight is particularly relevant in specific natural forest parts where natural mortality rates tend to be higher (could be due to salinity, biological age, or natural calamities). More precisely, stands-dominated pioneer species like *Sonneratia apetala* and *Avicennia officinalis* often experience frequent mortality due to their biological age, or diseases like dying back increase mortality (Giri et al., 2007; Rahman et al., 2010) and form significant gaps. Furthermore, the Sundarbans region is prone to tropical cyclones, which lead to tree mortality by causing severe damage, further creating gaps, especially in areas with higher salinity levels, which are more exposed to the coasts with little or no terrestrial nutrient inputs. Introducing different species in these gaps could be beneficial in expediting forest recovery and enhancing resilience against future climatic events (natural calamities and salinity).

This research holds strong applicability in coastal single species-based plantation efforts to mixing plantations, especially when the objective is to safeguard coastal areas while simultaneously harnessing the co-benefits of carbon sequestration (growth under salinity stress) in the face of cyclones. It underscores the potential of nature-based solutions in fortifying our coastal belts against environmental challenges.

However, our study was conducted in a single mangrove forest (Sundarbans), which may limit generalizability to other regions. Examining multiple sites across varying salinity gradients could strengthen conclusions. Besides, we expect some interplay between water depth and seasonal rainfall patterns due to storms effect on salinity level and impacts, which could be interesting to explore. However, our dataset could not capture any disturbance (e.g., cyclones) effect on growth across species within study periods (~2.5 years). Overall, the study takes an essential first step in highlighting biodiversity's role in increasing mangrove resilience to salinity stress. However, ongoing research across broader spatial scales and including additional functional measures is needed. For example, the mechanisms underlying diversity-productivity relationships still need to be fully elucidated.

Further research into functional traits and niche differentiation could provide more mechanistic explanations. Translation to the application requires examining feasibility constraints. A systems perspective incorporating socio-ecological factors could maximize conservation impact. While promising, the findings represent an early stage in fully elucidating diversity's multifaceted influence.

6 Conclusion

This study evaluated the comparative role of structural and species diversity in modulating salinity impacts on growth. We also assessed how some growth-modifying factors, for example, nutrient availability, and leaf functional traits, modulate the salinity-growth relationships. Our analyses revealed that the growth of mangrove forests is strongly controlled by salinity, with its effects mediated by structural heterogeneity, nutrient dynamics, and leaf functional traits. Conversely, the leaf area index emerged as the primary facilitator of forest growth in areas marked by elevated salinity and limited water access. While species diversity may influence growth indirectly through its interaction with forest structure, structural diversity, including variations in stand size classes and horizontal heterogeneity. These insights are vital for improving mangrove growth modelling, enhancing ecological understanding, and informing coastal forest conservation and management strategies.

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Authors contributions

Conceptualization: SA; Data collection: SA, SKS (lead) and MK; Data analysis: SA (lead), MMR; Manuscript writing: SA (lead), RH, NT, SP; Manuscript revision: MMR, HP, SKS, SP, TH, TTA, EU, CSSN; Supervision: HP (lead), SKS

Competing interest

The authors declare no competing interest.

Data and code availability

Data is available in Ahmed et al. (2022). All R code is available from the corresponding author upon request.

Electronic supplementary material

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References

Ahmed, S., Kamruzzaman, M., 2021. Species-specific biomass and carbon flux in Sundarbans mangrove forest, Bangladesh: response to stand and weather variables. Biomass and Bioenergy 153, 106215.

Ahmed, S., Kamruzzaman, M., Azad, M.S., Khan, M.N.I., 2021. Fine root biomass and its contribution to the mangrove communities in three saline zones of Sundarbans, Bangladesh. Rhizosphere 17, 100294.

Ahmed, S., Sarker, S.K., Friess, D.A., Kamruzzaman, M., Jacobs, M., Islam, M.A., Alam, M.A., Suvo, M.J., Sani, M.N.H., Dey, T., Naabeh, C.S.S., Pretzsch, H., 2022. Salinity reduces site quality and mangrove forest functions. From monitoring to understanding. Science of the Total Environment 853, 158662.

Ahmed, S., Sarker, S.K., Friess, D.A., Kamruzzaman, M., Jacobs, M., Sillanpää, M., Naabeh, C.S.S., Pretzsch, H., 2023. Mangrove tree growth is size-dependent across a large-scale salinity gradient. Forest Ecology and Management 537, 120954.

Akber, M.A., Patwary, M.M., Islam, M.A., Rahman, M.R., 2018. Storm protection service of the Sundarbans mangrove forest, Bangladesh. Natural Hazards 94, 405–418.

Ali, A., Lin, S.L., He, J.K., Kong, F.M., Yu, J.H., Jiang, H.S., 2019. Tree crown complementarity links positive functional diversity and aboveground biomass along large-scale ecological gradients in tropical forests. Science of the Total Environment 656, 45–54.

Ali, A., Yan, E.R., Chen, H.Y.H., Chang, S.X., Zhao, Y.T., Yang, X.D., Xu, M.S., 2016. Stand structural diversity rather than species diversity enhances aboveground carbon storage in secondary subtropical forests in Eastern China. Biogeosciences 13, 4627–4635.

Alongi, D.M., 2008. Mangrove forests: resilience, protection from tsunamis, and responses to global climate change. Estuarine, Coastal and Shelf Science 76, 1–13.

Alongi, D.M., 2011. Patterns of mangrove wood and litter production within a beach ridge-fringing reef embayment, Northern Great Barrier Reef Coast. Estuaries and Coasts 34, 32–44.

Alongi, D.M., 2012. Carbon sequestration in mangrove forests. Carbon Management 3, 313–322.

Alongi, D.M., 2014. Carbon cycling and storage in mangrove forests. Annual Review of Marine Science 6, 195–219.

Alongi, D.M., 2020. Nitrogen cycling and mass balance in the world's mangrove forests. Nitrogen 1, 167–189.

Amoroso, M.M., Turnblom, E.C., 2006. Comparing productivity of pure and mixed Douglas-fir and western hemlock plantations in the Pacific Northwest. Canadian Journal of Forest Research 36, 1484–1496.

Astigarraga, J., Calatayud, J., Ruiz-Benito, P., Madrigal-Gonzalez, J., Tijerin-Trivino, J., Zavala, M.A., Andivia, E., Herrero, A., 2023. Forest structural diversity determines tree growth synchrony in response to climate change. bioRxiv, 2023–2003.

Cavard, X., Bergeron, Y., Chen, H.Y.H., Paré, D., 2010. Mixed-species effect on tree aboveground carbon pools in the east-central boreal forests. Canadian Journal of Forest Research 40, 37–47.

Cleland, E.E., 2011. Biodiversity and ecosystem stability. Nature Education Knowledge 3, 14.

Condés, S., Del Rio, M., Sterba, H., 2013. Mixing effect on volume growth of *Fagus sylvatica* and *Pinus sylvestris* is modulated by stand density. Forest Ecology and Management 292, 86–95.

Condés, S., Pretzsch, H., del Río, M., 2023. Species admixture can increase potential tree growth and reduce competition. Forest Ecology and Management 539, 120997.

Dănescu, A., Albrecht, A.T., Bauhus, J., 2016. Structural diversity promotes productivity of mixed, uneven-aged forests in southwestern Germany. Oecologia 182, 319–333.

Del Río, M., Pretzsch, H., Ruiz-Peinado, R., Jactel, H., Coll, L., Löf, M., Aldea, J., Ammer, C., Avdagić, A., Barbeito, I., Bielak, K., Bravo, F., Brazaitis, G., Cerný, J., Collet, C., Condés, S., Drössler, L., Fabrika, M., Heym, M., Holm, S.O., Hylen, G., Jansons, A., Kurylyak, V., Lombardi, F., Matović, B., Metslaid, M., Motta, R., Nord-larsen, T., Nothdurft, A., Den Ouden, J., Pach, M., Pardos, M., Poeydebat, C., Ponette, Q., Pérot, T., Reventlow, D.O.J., Sitko, R., Sramek, V., Steckel, M., Svoboda, M., Verheyen, K., Vospernik, S., Wolff, B., Zlatanov, T., Bravo-oviedo, A., 2022. Emerging stability of forest productivity by mixing two species buffers temperature destabilizing effect. Journal of Applied Ecology 59, 2730–2741.

Donato, D.C., Kauffman, J.B., Murdiyarso, D., Kurnianto, S., Stidham, M., Kanninen, M., 2011. Mangroves among the most carbon-rich forests in the tropics. Nature Geoscience 4, 293–297.

Forrester, D.I., Kohnle, U., Albrecht, A.T., Bauhus, J., 2013. Complementarity in mixed-species stands of *Abies alba* and *Picea abies* varies with climate, site quality and stand density. Forest Ecology and Management 304, 233–242.

Fotis, A.T., Murphy, S.J., Ricart, R.D., Krishnadas, M., Whitacre, J., Wenzel, J.W., Queenborough, S.A., Comita, L.S., 2018. Above-ground biomass is driven by mass-ratio effects and stand structural attributes in a temperate deciduous forest. Journal of Ecology 106, 561–570.

Giri, C., Pengra, B., Zhu, Z.L., Singh, A., Tieszen, L.L., 2007. Monitoring mangrove forest dynamics of the Sundarbans in Bangladesh and India using multi-temporal satellite data from 1973 to 2000. Estuarine, Coastal and Shelf Science 73, 91–100.

Güney, D., Atar, F., Turna, I., Günlü, A., 2022. Effects of precommercial thinning intensity on growth of *Fagus orientalis* Lipsky stands over 6 years. Journal of Forestry Research 33, 937–947.

Huxham, M., Kumara, M.P., Jayatissa, L.P., Krauss, K.W., Kairo, J., Langat, J., Mencuccini, M., Skov, M.W., Kirui, B., 2010. Intra- and interspecific facilitation in mangroves may increase resilience to climate change threats. Philosophical Transactions of the Royal Society B: Biological Sciences 365, 2127–2135.

Islam, S., Feroz, S.M., Ahmed, Z.U., Chowdhury, A.H., Khan, R.I., Al-Mamun, A., 2016. Species richness and diversity of the floristic composition of the Sundarbans mangrove reserve forest, Bangladesh in relation to spatial habitats and salinity. The Malaysian Forester 79, 7–38.

Jucker, T., Bouriaud, O., Coomes, D.A., 2015. Crown plasticity enables trees to optimize canopy packing in mixed-species forests. Functional Ecology 29, 1078–1086.

Khan, M.N.I., Suwa, R., Hagihara, A., 2009. Biomass and above-ground net primary production in a subtropical mangrove stand of *Kandelia obovata* (S. , L.) Yong at Manko Wetland, Okinawa, Japan. Wetlands Ecology and Management 17, 585–599.

LaManna, J.A., Mangan, S.A., Alonso, A., Bourg, N.A., Brockelman, W.Y., Bunyavejchewin, S., Chang, L.W., Chiang, J.M., Chuyong, G.B., Clay, K., Condit, R., Cordell, S., Davies, S.J., Furniss, T.J., Giardina, C.P., Gunatilleke, I.A.U.N., Gunatilleke, C.V.S., He, F.L., Howe, R.W., Hubbell, S.P., Hsieh, C.F., Inman-Narahari, F.M., Janík, D., Johnson, D.J., Kenfack, D., Korte, L., Král, K., Larson, A.J., Lutz, J.A., Mcmahon, S.M., Mcshea, W.J., Memiaghe, H.R., Nathalang, A., Novotny, V., Ong, P.S., Orwig, D.A., Ostertag, R., Parker, G.G., Phillips, R.P., Sack, L., Sun, I.F., Tello, J.S., Thomas, D.W., Turner, B.L., Vela Díaz, D.M., Vrška, T., Weiblen, G.D., Wolf, A., Yap, S., Myers, J.A., 2017. Plant diversity increases with the strength of negative density dependence at the global scale. Science 356, 1389–1392.

LaRue, E.A., Fahey, R.T., Alveshere, B.C., Atkins, J.W., Bhatt, P., Buma, B., Chen, A.P., Cousins, S., Elliott, J.M., Elmore, A.J., Hakkenberg, C.R., Hardiman, B.S., Johnson, J.S., Kashian, D.M., Koirala, A., Papeş, M., St Hilaire, J.B., Surasinghe, T.D., Zambrano, J., Zhai, L., Fei, S.L., 2023a. A theoretical framework for the ecological role of three-dimensional structural diversity. Frontiers in Ecology and the Environment 21, 4–13.

LaRue, E.A., Hardiman, B.S., Elliott, J.M., Fei, S.L., 2019. Structural diversity as a predictor of ecosystem function. Environmental Research Letters 14, 114011.

LaRue, E.A., Knott, J.A., Domke, G.M., Chen, H.Y.H., Guo, Q.F., Hisano, M., Oswalt, C., Oswalt, S., Kong, N., Potter, K.M., Fei, S.L., 2023b. Structural diversity as a reliable and novel predictor for ecosystem productivity. Frontiers in Ecology and the Environment 21, 33–39.

Lindenmayer, D.B., Likens, G.E., Haywood, A., Miezis, L., 2011. Adaptive monitoring in the real world: proof of concept. Trends in Ecology & Evolution 26, 641–646.

López-Hoffman, L., DeNoyer, J.L., Monroe, I.E., Shaftel, R., Anten, N.P.R., Martínez-Ramos, M., Ackerly, D.D., 2006. Mangrove seedling net photosynthesis, growth, and survivorship are interactively affected by salinity and light. Biotropica 38, 606–616.

Lovelock, C.E., Ball, M.C., Feller, I.C., Engelbrecht, B.M.J., Ling Ewe, M., 2006. Variation in hydraulic conductivity of mangroves: influence of species, salinity, and nitrogen and phosphorus availability. Physiologia Plantarum 127, 457–464.

Lovelock, C.E., Cahoon, D.R., Friess, D.A., Guntenspergen, G.R., Krauss, K.W., Reef, R., Rogers, K., Saunders, M.L., Sidik, F., Swales, A., Saintilan, N., Thuyen, L.X., Triet, T., 2015. The vulnerability of Indo-Pacific mangrove forests to sea-level rise. Nature 526, 559–563.

Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., Makowski, D., 2021. performance: an R package for assessment, comparison and testing of statistical models. Journal of Open Source Software 6, 3139.

Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications 17, 2145–2151.

Miller, D.R., 1997. Forest stand dynamics. Agricultural and Forest Meteorology 86, 139–140.

Mitra, A., Chowdhury, R., Sengupta, K., Banerjee, K., 2010. Impact of salinity on mangroves of Indian Sundarbans. Journal of Coastal Research 1, 71–80.

Mollick, A.S., Sultana, R., Azad, M.S., Khan, M.N.I., 2021. Leaf morphological plasticity in three dominant tree species in the Sundarbans mangrove forest of Bangladesh in different salinity zones. Wetlands Ecology and Management 29, 265–279.

Ng, C.W.W., Ni, J.J., Leung, A.K., Zhou, C., Wang, Z.J., 2016. Effects of planting density on tree growth and induced soil suction. Géotechnique 66, 711–724.

Paquette, A., Messier, C., 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. Global Ecology and Biogeography 20, 170–180.

Park, J., Kim, H.S., Jo, H.K., Jung, I.I.B., 2019. The influence of tree structural and species diversity on temperate forest productivity and stability in Korea. Forests 10, 1113.

Peng, D., Guo, H.Y., Armitage, A.R., Pennings, S.C., 2022. Competition and abiotic stress affect the size of mangroves near their geographic range limit. Journal of Plant Ecology 15, 129–140.

Pérez-Ramos, I.M., Matías, L., Gómez-Aparicio, L., Godoy, Ó., 2019. Functional traits and phenotypic plasticity modulate species coexistence across contrasting climatic conditions. Nature Communications 10, 2555.

Perri, S., Detto, M., Porporato, A., Molini, A., 2023. Salinity-induced limits to mangrove canopy height. Global Ecology and Biogeography 32, 1561–1574.

Pretzsch, H., 2005. Stand density and growth of Norway spruce (*Picea abies* (L.) Karst.) and European beech (Fagus sylvatica L.): evidence from long-term experimental plots. European Journal of Forest Research 124, 193–205.

Pretzsch, H., 2009. Forest dynamics, growth, and yield. In: Pretzsch, H., ed. Forest Dynamics, Growth and Yield. Berlin, Heidelberg: Springer, 1–39.

Pretzsch, H., 2014. Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. Forest Ecology and Management 327, 251–264.

Pretzsch, H., Ahmed, S., Rötzer, T., Schmied, G., Hilmers, T., 2023. Structural and compositional acclimation of forests to extended drought: results of the KROOF throughfall exclusion experiment in Norway spruce and European beech. Trees 37, 1443–1463.

Price, J.N., Gazol, A., Tamme, R., Hiiesalu, I., Pärtel, M., 2014. The functional assembly of experimental grasslands in relation to fertility and resource heterogeneity. Functional Ecology 28, 509–519.

Qu, Y.C., Wang, H.C., Dean, T.J., Zhang, J.G., Zhang, X.Q., 2022. Growth dominance and growth efficiency in response to thinning treatments in Chinese fir plantations with long-term spacing trials. Forest Ecology and Management 521, 120438.

R Core Team, 2023. R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing.

Rahman, M.M., Rahman, M.M., Islam, K.S., 2010. The causes of deterioration of Sundarban mangrove forest ecosystem of Bangladesh: conservation and sustainable management issues. Aquaculture, Aquarium, Conservation & Legislation 3, 77–90.

Rahman, M.M., Zimmer, M., Ahmed, I., Donato, D., Kanzaki, M., Xu, M., 2021a. Co-benefits of protecting mangroves for biodiversity conservation and carbon storage. Nature Communications 12, 3875.

Rahman, M.S., Donoghue, D.N.M., Bracken, L.J., Mahmood, H., 2021b. Biomass estimation in mangrove forests: a comparison of allometric models incorporating species and structural information. Environmental Research Letters 16, 124002.

Rahman, M.S., Hossain, G.M., Khan, S.A., Uddin, S.N., 2015. An annotated checklist of the vascular plants of Sundarban Mangrove Forest of Bangladesh. Bangladesh Journal of Plant Taxonomy 22, 17–41.

Riofrío, J., del Río, M., Pretzsch, H., Bravo, F., 2017. Changes in structural heterogeneity and stand productivity by mixing Scots pine and Maritime pine. Forest Ecology and Management 405, 219–228.

Rogers, K.G., Goodbred, S.L., 2014. The Sundarbans and Bengal

Delta: the world's largest tidal mangrove and delta system. In: Kale, V.S., ed. Landscapes and Landforms of India. Dordrecht: Springer, 181–187.

Rosseel, Y., 2012. lavaan: an R package for structural equation modeling. Journal of Statistical Software 48, 1–36.

Saintilan, N., Horton, B., Törnqvist, T.E., Ashe, E.L., Khan, N.S., Schuerch, M., Perry, C., Kopp, R.E., Garner, G.G., Murray, N., Rogers, K., Albert, S., Kelleway, J., Shaw, T.A., Woodroffe, C.D., Lovelock, C.E., Goddard, M.M., Hutley, L.B., Kovalenko, K., Feher, L., Guntenspergen, G., 2023. Widespread retreat of coastal habitat is likely at warming levels above 1.5°C. Nature 621, 112–119.

Sarker, S.K., 2017. Spatial and temporal patterns of mangrove abundance, diversity and functions in the Sundarbans. Ph.D. Dissertation. University of Glasgow, Glasgow, UK.

Sarker, S.K., Matthiopoulos, J., Mitchell, S.N., Ahmed, Z.U., Al Mamun, M.B., Reeve, R., 2019a. 1980s–2010s: the world's largest mangrove ecosystem is becoming homogeneous. Biological Conservation 236, 79–91.

Sarker, S.K., Reeve, R., Matthiopoulos, J., 2021. Solving the fourth-corner problem: forecasting ecosystem primary production from spatial multispecies trait-based models. Ecological Monographs 91, e01454.

Sarker, S.K., Reeve, R., Paul, N.K., Matthiopoulos, J., 2019b. Modelling spatial biodiversity in the world's largest mangrove ecosystem—the Bangladesh Sundarbans: a baseline for conservation. Diversity and Distributions 25, 729–742.

Schall, P., Schulze, E.D., Fischer, M., Ayasse, M., Ammer, C., 2018. Relations between forest management, stand structure and productivity across different types of Central European forests. Basic and Applied Ecology 32, 39–52.

Schermelleh-Engel, K., Moosbrugger, H., Müller, H., 2003. Evaluating the fit of structural equation models: tests of significance and descriptive goodness-of-fit measures. Methods of Psychological Research 8, 23–74.

Schielzeth, H., 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1, 103–113.

Schmied, G., Hilmers, T., Mellert, K.H., Uhl, E., Buness, V., Ambs, D., Steckel, M., Biber, P., Šeho, M., Hoffmann, Y.D., Pretzsch, H., 2023. Nutrient regime modulates drought response patterns of three temperate tree species. Science of the Total Environment 868, 161601.

Singh, J.K., 2020. Structural characteristics of mangrove forest in different coastal habitats of Gulf of Khambhat arid region of Gujarat, west coast of India. Heliyon 6, e04685.

Soethe, N., Lehmann, J., Engels, C., 2006. The vertical pattern of rooting and nutrient uptake at different altitudes of a south ecuadorian montane forest. Plant and Soil 286, 287–299.

Sofawi, A.B., Nazri, M.N., Rozainah, M.Z., 2017. Nutrient variability in mangrove soil: anthropogenic, seasonal and depth variation factors. Applied Ecology and Environmental Research 15, 1983–1998.

Sun, L., Gong, L., Zhu, M.L., Xie, L.N., Li, H.L., Luo, Y., 2017. Leaf stoichiometric characteristics of typical desert plants and their relationships to soil environmental factors in the northern margin of the Tarin Basin. Chinese Journal of Ecology 36, 1208–1214.

Thurm, E.A., Pretzsch, H., 2021. Growth–density relationship in mixed stands–results from long-term experimental plots. Forest Ecology and Management 483, 118909.

Van Lissa, C.J., 2020. tidySEM: Tidy Structural Equation Modeling. R Package Version 0.1 1.

Vanelslander, B., De Wever, A., Van Oostende, N., Kaewnuratchadasorn, P., Vanormelingen, P., Hendrickx, F., Sabbe, K., Vyverman, W., 2009. Complementarity effects drive positive diversity effects on biomass production in experimental benthic diatom biofilms. Journal of Ecology 97, 1075–1082.

Wickham, H., 2011. ggplot2. WIREs Computational Statistics 3, 180–185.

Williams, L.J., Paquette, A., Cavender-Bares, J., Messier, C., Reich, P.B., 2017. Spatial complementarity in tree crowns explains overyielding in species mixtures. Nature Ecology & Evolution 1, 0063.

Yaseen, M., Khan, W.R., Bahadur, S., Batool, F., Khalid, F., Ahmed, U., Ashraf, M., 2023. Intra- and inter-specific responses of plant functional traits to environmental variables: implications for community ecology in the tropical monsoonal dwarf forest on Hainan Island. Frontiers in Forests and Global Change 6, 1198626.

Yoshikai, M., Nakamura, T., Suwa, R., Sharma, S., Rollon, R., Yasuoka, J., Egawa, R., Nadaoka, K., 2021. Predicting mangrove forest dynamics across a soil salinity gradient using an individual-based vegetation model linked with plant hydraulics. Biogeosciences Discussions, 1–34.

Zhang, Y., Chen, H.Y.H., Reich, P.B., 2012. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. Journal of Ecology 100, 742–749.

Zheng, L.T., Chen, H.Y.H., Yan, E.R., 2019. Tree species diversity promotes litterfall productivity through crown complementarity in subtropical forests. Journal of Ecology 107, 1852–1861.