Mangrove tree growth is size-dependent across a large-scale salinity gradient

Shamim Ahmed [a,b,*], Swapan Kumar Sarker [d], Daniel A. Friess [c], Md. Kamruzzaman [b], Martin Jacobs [a], Mériadec Sillanpää [e], Clement Sullibie Saagulo Naabeh [f], Hans Pretzsch [a]

[a] Chair of Forest Growth and Yield Science, Department of Life Science Systems, School of Life Sciences, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany
[b] Forestry and Wood Technology Discipline, Khulna University, Khulna 9208, Bangladesh
[c] Department of Earth and Environmental Sciences, Tulane University, 6823 St Charles Ave, New Orleans, LA 70118, USA
[d] Department of Forestry and Environmental Science, Shahjalal University of Science and Technology, Sylhet, Bangladesh
[e] Department of Geography, 1 Arts Link, National University of Singapore, Singapore 117570
[f] Institute of Environment and Sanitation Studies, University of Ghana, International Programmes Office, MR39+C4X, Annie Jiagge Rd, Accra, Ghana

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ABSTRACT

Salinity-influenced ecosystems are projected to face a tree to stand level growth reduction as a response to climate change. Although large and mature trees play a central role in defining carbon dynamics and site conditions, their eco-physiological and functional responses to increasing salinity remain poorly understood. Therefore, we test our hypotheses, i.e., large-diameter trees are predominantly contributing to above-ground biomass (AGB) stocks, whilst small-diameter trees are mainly contributing to AGB growth or gain (biomass changes over time) in higher salinity areas of the Sundarbans mangrove forest, Bangladesh. It can further be expressed by a growth dominance coefficient (GDC) that turns negative (a negative GDC indicates small trees proportionately contribute more to growth) in high-salinity areas while remaining positive in lower-salinity areas. We also hypothesized that species and structural diversity positively influence AGB stocks and gain. To test our hypotheses, we employed data from 60 permanent sample plots installed in the Sundarbans mangrove forest to estimate size-dependent functions by examining tree size, diversity, and growth dominance patterns to salinity gradients. Trees in higher salinity areas showed negative or reverse growth dominance patterns, indicating large trees contributed less to forest growth, which means smaller trees were disproportionately responsible for growth within the stand. Across the salinity zones, large-diameter (>20 cm in diameter at breast height, DBH) trees contributed primarily to AGB stocks, while small-diameter (<20 cm in DBH) trees contributed more to forest growth. We observed species diversity had no significant influence, whilst vertical diversity (height diversity) had a significant positive influence on AGB stocks and gain. Forest functioning (e.g., biomass accumulation rate) is more asymmetric (higher growth of small trees vs. low growth of large trees) in poor sites (i.e., high salinity), as poor site quality favors small trees to grow but not the large-diameter trees, which indicates large trees are more sensitive to high salinity as they lose growth. Our results indicate the size-dependent tree functions also depend on biotic and abiotic factors in mangroves. Increased structural diversity and removing mature trees to allow small trees to grow may benefit mangrove forest functioning (biomass stocks and growth), but species diversity may not.

1. Introduction

Although mangrove forests cover only 0.1% of the Earth's surface (Hamilton and Casey, 2016), they play a crucial role in climate change mitigation and adaptation, for example, storing up to five times more carbon per hectare than tropical rainforests (Donato et al., 2011).

Located at the interface of land and sea, mangroves are exposed to a range of climate change stressors such as sea-level rise and changes in precipitation, which can lead to changes in variables such as salinity that are known to affect mangrove growth (Chen and Wang, 2017). Salinity changes can greatly affect the growth and development of mangroves, likely favoring dwarf mangroves (Feller, 1995; Ball, 2002; Lovelock et al., 2005) and may force the forest into homeostatic collapse by affecting functional processes such as growth (Chowdhury et al., 2019). Although mangroves can show morphological plasticity or resistance to some environmental changes (Vovides et al., 2014), Sarker et al. (2021) predicted a 50% salinity increase in the Sundarbans by 2050, likely to reduce overall ecosystem productivity by 30%.

Tree size is a crucial factor in evaluating site conditions and dynamics of biomass and carbon, and ecosystem-level response to environmental forcing factors, many of which will be altered under climate change (Piponiot et al., 2022). Larger trees in forests play a keystone role (Lindenmayer et al., 2012) and strongly influence biomass and carbon stocks (Lutz et al., 2012; Ali et al., 2019). For example, large trees in natural forests across the globe cumulatively contribute around 50% of forest biomass (Lutz et al., 2018). Large-diameter trees are more exposed to the micro-climate (e.g., direct exposure to light in respective stands) (Kimmins, 1987), which may further help us to understand size-dependent functions of any environmental change (Ali et al., 2019), denoting the ecological significance of large-diameter trees. In addition, in wetter (i.e., swamp or wetlands) forests, small-sized trees (1–10 cm in diameter) can contribute to growth and biomass, emphasizing the necessity of considering these trees in forest dynamics evaluations (Piponiot et al., 2022).

Despite having a significant ecological role, little is known about how changes in tree size classes, along with abiotic and biotic factors, influence biomass and carbon dynamics (Yuan et al., 2021). Therefore, to better explain growth dynamics in mangroves, relationships between biotic (i.e., species richness, stand structure) and abiotic (i.e., salinity) factors with forest functions (i.e., AGB stocks and gain) are critical. It is well recognized that biotic and abiotic factors largely affect forest functions. For example, species diversity increases forest productivity (Tilman et al., 1997), while structural heterogeneity enhances mechanical stability and helps to better predict ecosystem functions under stress (Tilman et al., 1997; LaRue et al., 2019; Pretzsch et al., 2022). Hence, uncovering the relationships between biotic and abiotic factors with growth partitioning is crucial for gaining a comprehensive understanding of how the ecosystem functions under stress (Huang et al., 2018). However, the underlying mechanisms and the complex interactions between these factors in mangroves are yet to be understood. Besides, information related to the relative role and contribution of large and mature trees and associated small and medium-diameter trees to mangrove growth and productivity is scarce. Furthermore, it is still unclear whether large or small trees suffer more from salinity stress in mangrove forests. We are therefore interested in understanding stand growth pattern changes with salinity (i.e., abiotic), in addition to size dependent functions and effects of species and structural diversity (i.e., biotic) on biomass and carbon dynamics at the stand level.

At the stand-level, trees may exhibit species-specific growth dominance patterns; large-sized trees may contribute proportionally more to growth rather than biomass, whereas small-sized trees contribute more to biomass rather than growth (Binkley, 2004; Binkley et al., 2006). Growth dominance patterns are well documented for temperate forests (i.e., Pine forests) and *Eucalyptus* plantations (Binkley et al., 2004; Doi et al., 2010; Fernández et al., 2011; Fernández-Tschieder and Binkley, 2018; Fernández-Tschieder et al., 2020). However, growth dominance patterns have mostly remained unexplored for mangroves. We thus applied the growth dominance patterns approach (Binkley et al., 2006) to understand size-dependent growth patterns across a key environmental gradient (e.g., salinity) and uncover the relationship with biotic and abiotic variables. Using these approaches, we predict that (HI) salinity shifts the growth dominance patterns from positive to negative, i.e., larger trees dominate the biomass (symmetric biomass allocation) but smaller trees contribute disproportionately to growth with increasing salinity (asymmetric growth allocation). Hence, we assume overall biomass stocks and gain will decline with increasing salinity when growth partitioning is shifted towards small size classes of trees, and (HII) the salinity-driven growth dominance pattern has a direct negative impact on aboveground biomass (AGB) stocks and AGB gain. In contrast, structural diversity and species diversity would have a direct positive impact on functional variables such as above ground biomass and gain (biomass changes over time), while salinity should have a direct negative impact on functional variables (i.e., AGB stocks and gain).

To test the hypotheses, we evaluated size-dependent tree growth and performance across the salinity zones and salinity gradient in the Sundarbans mangrove forest to better understand how the growth of large trees is influenced by changes in salinity. Previous studies observed the influence of salinity on mangrove growth (Rahman et al., 2020; Siddique et al., 2021), productivity and composition (Sarker et al., 2019a; Sarker et al., 2019b; Rahman, 2020) with limited or no focus on growth partitioning and size-dependent tree functions. Therefore, we also looked at how species and structural diversity together influence AGB stocks and gain to better understand the effects of growth dominance patterns on mangrove functions. The knowledge of how AGB stocks are influenced by structural diversity and the mass-ratio effect (i.e., dominant traits) is critical for a better understanding of ecosystem functions (Fotis et al., 2018). This study could further improve our understanding of the underlying mass-ratio effect and ecological aspects (i.e., the relative driving role of dominant and large-sized trees on ecosystem functions) of the mangrove ecosystem to predict future growth patterns.

2. Materials and methods

2.1. Study site and tree inventory

We conducted the study in the Sundarbans mangrove forest in Bangladesh (21○30′–22○ 30′ N, 89○00′-89○55′ E, area of 6017 km²) (Supplementary Fig. 1). The Sundarbans present extensive variability in environmental variables, such as salinity. Based on river water salinity, the ecosystem is classified into three distinct ecozones: oligohaline (salinity < 14 ppt), mesohaline (salinity < 14–25 ppt), and polyhaline (>25 ppt) (Islam and Gnauck, 2009). Salinity differs mostly due to upstream freshwater flow, which causes lower salinity in the east of the Bangladesh Sundarbans and higher salinity in the west (Wahid et al., 2007). These salinity ecozones or gradients largely determine the heterogeity of plant communities in the Sundarbans (Ahmed and Iqbal, 2011). Management and conservation decisions are made based on the status of tree growth and forest stocks in these ecological zones (Sarker et al., 2019a).

Mean annual rainfall and temperature vary between 1640 and 2000 mm and 21 to 30 °C in the study area (Rahman and Asaduzzaman, 2010). To evaluate forest structure and above ground biomass (AGB) stocks, we established a total of 60 permanent sample plots randomly, with 20 in each ecozone (100 m² each) across the Bangladesh Sundarbans in April 2018 (Supplementary Fig. 1). All PSPs were established at least 200 m away from the river to avoid destruction by river erosion. We identified and tagged all the trees just above the DBH point (which allowed us to remeasure at the same point) with a DBH ≥ 4.6 cm (diameter at breast height – 1.3 m from the ground) with an aluminum tag. Because of the slow growth of mangroves in this region, DBH ≥ 4.6 has been used to understand above-ground growth in mangroves since the 1980 s (Iftekhar and Saenger, 2008), and has since been used in other studies (Sarker et al., 2019b; Ahmed et al., 2022). We also measured tree heights using an electrical dendrometer (Criterion RD 1000, Laser Technology Incorporation, USA). We revisited all the plots in November 2020 and measured DBH and heights of all trees tagged in 2018 to evaluate growth or biomass gain (changes in biomass between

two measurements) and changes in growth dominance pattern. In addition, we measured plot-level soil salinity by taking five random samples (within 15 cm of soil depth) in each plot (600 samples in total in each year) during April (early rainy season) and November (early winter or dry season) each year throughout the study period 2018–2020. As mean plot level salinity was used in all cases, our observed salinity may vary from river-based salinity classes. Furthermore, to avoid the overall rainfall effect on salinity, we sampled salinity twice (before and after the rainy season). During sampling, we noticed no notable changes in inundation levels, indicating that tidal height remained nearly constant in the respective zones throughout the research periods.

2.2. Stand structure, species diversity and growth dominance patterns

We used all measured (DBH $\geq$ 4.6 cm, as per Iftekhar and Saenger (2008)) trees to calculate stand characteristics such as the stand density (stems ha^{-1}), mean plot height (m), mean DBH (cm), and basal area (m^2 ha^{-1}). To characterize species diversity, we used the Shannon's index because this index gives similar weights on both species frequency and dominancy, thus not favoring any species disproportionately (Jost, 2006; Hortal et al., 2010; Liu et al., 2018). For structural diversity (vertical and horizontal tree size class distributions, i.e., variations in height and DBH), we used the coefficient of variance (CV) of height and DBH, and the ratio of height and DBH (Ht/DBH). To understand the relative contributions of different size classes of trees to biomass and growth, we classified the DBH into three classes: <10 cm: small trees; 10–20 cm: medium trees; >20 cm: large or mature trees. Because our observed mean DBH values across salinity zones ranged from 7.81 to 11.7 cm (see Table 1).

To evaluate growth dominance patterns, we adopted the methodology from Binkley (2004) and Binkley et al. (2006), plotting the cumulative gain (biomass changes over time, Mg ha yr^{-1}) against the cumulative stem biomass of trees arranged from the smallest to the largest DBH. We estimated a Growth Dominance Coefficient (GDC), identical to the Gini coefficient (the difference is that GDC values range between − 1 to 1 whereas the Gini coefficients cannot be negative), to quantify the dominance level by adopting the equation from Fernández et al. (2011) (Eq.1).

$$GDC = \frac{\sum_{i=1}^{n-1} Cb_i - Cg_i}{\sum_{i=1}^{n-1} Cb_i} \tag{1}$$

where Cb_i and Cg_i denote the cumulative aboveground biomass and cumulative aboveground growth or gain up to the ith individual in relation to total biomass and growth, respectively. A stand could be displaying null (GDC = 0), positive (GDC > 0) and negative (GDC < 0) growth dominance, where individuals' proportional growth and biomass are identical, with large trees contributing more to growth than biomass, and small trees contributing more to growth than biomass, respectively (see details in Fernández-Tschieder and Binkley (2018)).

Table 1
List of allometric equations used for above ground biomass calculation (adapted from Rahman et al. (2021)). AGB, DBH, and H denote aboveground dry biomass (Kg), diameter at breast height (cm), and height (m), respectively.

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)
Aegiceras corniculatam	$\sqrt{}$(AGB) = 0.48 DBH-0.13

2.3. Above ground biomass estimations

We estimated tree dry aboveground biomass (AGB) following species-specific allometric equations (Table 1) for the Sundarbans compared and proposed by Rahman et al. (2021). We also computed yearly AGB gain from biomass changes by dividing the biomass and structural measurements by the study duration (~2.5 years).

2.4. Statistical analyses

To test our first hypothesis (HI) that the salinity gradient across eco-zones has an impacts on size-specific contributions to AGB stocks and AGB gain, we compared the variation of the cumulative contribution of size classes between the tree size classes and salinity zones by undertaking a two-way ANOVA (analysis of variances) followed by a post-hoc Tukey HSD test. Data normality was assessed by the Shapiro–Wilk test, with log transformed data being used when necessary. In addition, we conducted bivariate regression analyses to assess the salinity impacts on forest functions and GDC. Through bivariate relationships, we also checked how AGB stocks and AGB gain respond to salinity and stand variables (such as stand structure, structural diversity, GDC, etc.). In addition, we predict AGB stocks and gain a response to salinity and GDC by using the 'ggeffects' package (Lüdecke et al., 2020).

In addition to checking the individual effect, we reduced the explanatory variables aiming to increase the clarity of the structural equations model (SEM) that we used to test our second hypothesis (HII). In our analysis of bivariate relationships, the variables that showed a significant association with either AGB stocks or AGB gain were included in the SEM (i.e., salinity, CV of H, stand density, H/DBH ratio, and GDC). Through SEM, we tried to understand the complex interactions (i.e., direct or indirect) between biotic and abiotic variables, as SEM depicts direct and indirect relationships (Grace et al., 2012). SEM was implemented using the 'Lavaan' package in R-studio (Rosseel, 2012). We initially normalized the data (i.e., log transformed) as SEM requires all the data to be normalized. The R statistical software version 4.2.1 (r-project.org) was used for all statistical analysis and visualizations.

3. Results

3.1. Size dependent functions to salinity gradients and eco-zones

Stand structural variables, AGB stocks and AGB gain varied across the salinity eco-zones in the Bangladesh Sundarbans (Table 2). Most of the variables (e.g., mean height, mean DBH, basal area, AGB stocks and gain) showed significantly higher values in the less salinity areas (i.e., oligohaline and mesohaline ecozones) compared to the high salinity areas (i.e., polyhaline ecozone) (Table 2; Supplementary Fig. 2a). In addition, pioneer species (i.e., *Avicennia officinalis* and *Sonneratia apetala*) showed higher DBH values (Supplementary Fig. 2b, c).

We detected negative growth dominance patterns in high salinity (polyhaline) ecozone plots (Fig. 1). In contrast, trees in the lower salinity (oligohaline) ecozone mostly displayed a positive growth dominance pattern (Fig. 1). Growth dominance patterns reveal that large tree growth was restricted but small-sized tree growth continued in highly saline eco-zones and along the salinity gradient (Fig. 1). Besides, GDC values have significantly declined (become negative) in high salinity areas, implying that the growth dominance line in higher salinity areas is strongly skewed upward direction (Fig. 1).

In addition, our bivariate correlation analysis showed that AGB stocks and AGB gain declined significantly at higher salinities at the plot to tree level (Fig. 2 a, b, and Supplementary Fig. 3), demonstrating the influence of rising salinity in slowing down the AGB stocks and gain in the polyhaline zone. Our prediction model produced similar effects on AGB stocks and gains for salinity and GDC (Fig. 2 f, g). AGB stocks decreased as the H/DBH (height diameter ratio) proportion grew

Table 2
Summary of the studied variables (mean ± SD) evaluated in this study across salinity eco-zones. Where CV, H, and DBH denote the coefficient of variation, height, and diameter at breast height, respectively. Similar letters represent no significant difference (adopted from Post-hoc Tukey test).

| Types	Variables / Zones	Oligohaline	Mesohaline	Polyhaline	Mean
Environmental variables	Salinity (ppt)	2.15 ± 0.24a	6.79 ± 0.46b	13.08 ± 0.48c	7.29 ± 0.63
Stand structure and structural diversity	Species diversity	0.82 ± 0.05b	0.72 ± 0.05b	1.06 ± 0.03a	0.87 ± 0.03
	Species no.	3.9 ± 1.83b	3.75 ± 0.85b	5.7 ± 1.3a	4.45 ± 1.63
	Mean Height (m)	7.24 ± 0.24a	7.81 ± 0.40a	6.40 ± 0.19b	7.19 ± 0.18
	CV of Ht	0.12 ± 0.01a	0.15 ± 0.01a	0.12 ± 0.01a	0.13 ± 0.01
	Mean DBH (cm)	10.07 ± 0.30a	11.68 ± 0.80a	7.81 ± 0.28b	9.91 ± 0.36
	CV of DBH	0.14 ± 0.01a	0.18 ± 0.01a	0.16 ± 0.02a	0.16 ± 0.01
	Basal area (m^2 ha^{-1})	27.19 ± 3.41a	27.57 ± 3.39a	17.47 ± 2.74b	24.47 ± 1.91
	Density (stems ha^{-1})	2405.0 ± 168.2a	2005.3 ± 245.4b	2273.7 ± 189.4a	2251.7 ± 118.0
Biomass (Mg ha^{-1}) and growth (Mg ha^{-1} yr^{-1})	Above ground	368.2 ± 45.97a	382.06 ± 49a	166 ± 33b	307.92 + 27.76
	Biomass growth/gain	24.8 ± 3.62a	19.54 ± 2.1b	11.1 ± 1.34c	18.66 + 1.62
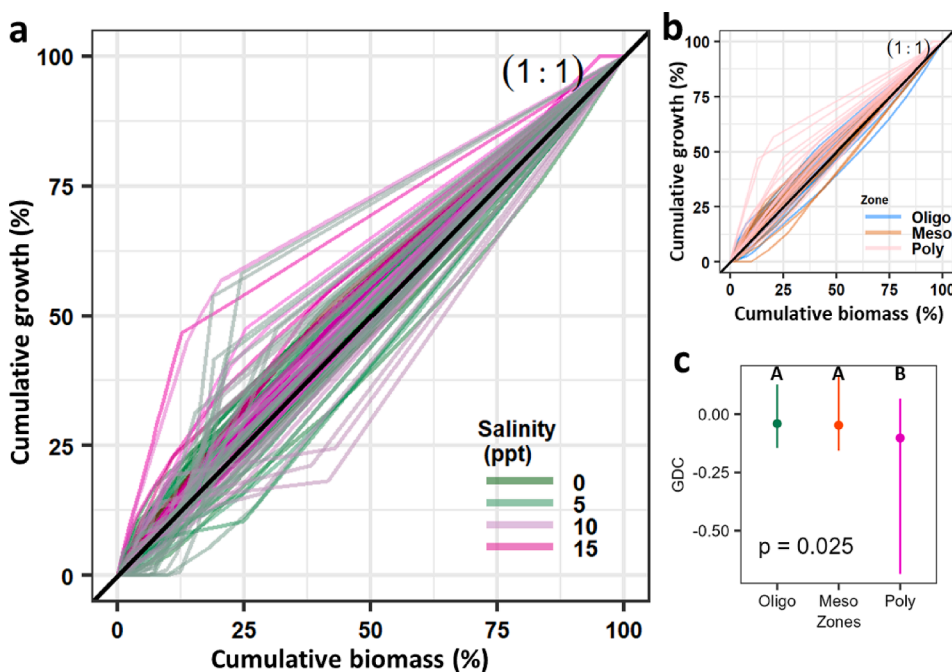
Fig. 1. Variations in growth dominance patterns along the (a) salinity gradient and (b) across the salinity eco-zones. Lines above the black solid lines (1:1) denote negative growth dominance, lines below the solid line (1:1) signify positive growth dominance, and identical lines 1:1 represent zero or null growth dominance. (c) GDC (growth dominance coefficient) comparison between salinity zones. Solid circles denote the mean values while vertical lines indicate 95% confidence interval. P-value showing the levels of significance and similar letters represent no significant difference between zones (adopted from one-way analysis of variance and Post-hoc Tukey test). Fig. a and b modified from Ahmed et al., 2022.

(Supplementary Fig. 4 a), whereas AGB growth increased when vertical diversity (CV of Ht) and stem density increased (Supplementary Fig. 5 a, b). In addition, GDC values show a decreasing trend with increasing salinity (Fig. 2 c, h) and negative GDC values contributed to a sharp decline in AGB stocks (Fig. 2 d, i) and AGB gain (Fig. 2 e, j).

Large-sized trees (>20 cm) contributed significantly more to AGB stocks than other tree-size classes (Fig. 3 A), while medium-sized (10–20 cm) trees contributed significantly more to AGB gain (Fig. 3 B) across the salinity ecozones. Furthermore, biomass stocks and gains increased significantly with tree size across the salinity eco-zones (Fig. 3 C and D). In terms of AGB gain, regression lines show a declining trend in high salinity areas, whereas in less salinity areas, relative biomass (%) gain shows a significantly increasing trend with increasing tree size.

3.2. SEM: Direct and indirect relationships between biotic, abiotic and functional variables

Our SEM depicts the various interacting links between biotic (i.e., structural variables including stand density, height-to-DBH ratio, vertical diversity, and GDC), abiotic (salinity), and forest functions such as AGB stocks and AGB gain (Fig. 4). Overall, SEM revealed that soil salinity had a strong negative effect on GDC, AGB, and AGB gain (Fig. 4). Furthermore, GDC has a negative impact on AGB stocks and gains, thus providing strong support to our second hypothesis (HII). Indirect

relationships exist between the H/DBH ratio and forest factors such as vertical diversity and stand density (Fig. 4). However, no significant relationship was observed between soil salinity and coefficient of variation of height (CV of Ht). Both AGB stocks and gains are directly affected by one another (Fig. 4).

4. Discussion

4.1. Salinity driven stand structure and growth dominance pattern impacts on AGB stocks and gain

Changes in stand structure are critical as they largely define how the forest functions (Ali, 2019). We observed that salinity critically changed stand structure (e.g., H, DBH, diversity, etc.) and functions (AGB stocks and gain) across salinity eco-zones. Our results show that the size-dependent AGB distributions and growth are significantly different among salinity eco-zones. We detected a positive growth dominance pattern in low salinity areas while detecting a reversed or negative growth pattern in areas of higher salinity. Hence, large trees proportionately contributed more and less to growth than smaller trees in low and higher salinity areas, respectively, thus denoting asymmetric growth distribution (Fig. 1, Supplementary Fig. 2) and providing strong support for our first hypothesis (HI).

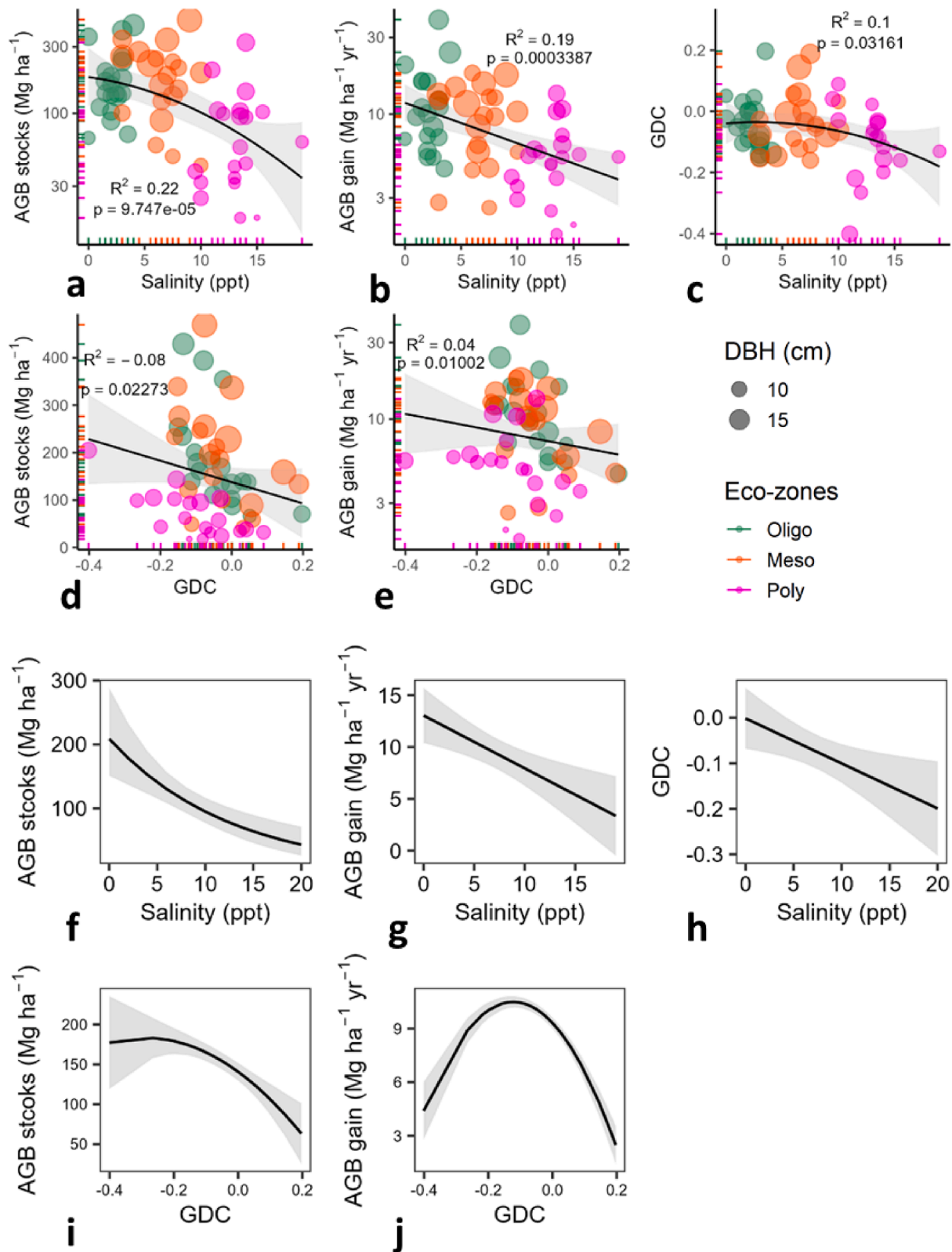Generally, larger trees have more access to light, allowing them to

Fig. 2. Bivariate relationships between the environmental, structural and functional variables. (a-c) show the effects of salinity on aboveground biomass (AGB) stocks, AGB gains, and GDC. (d-e) show the effects of GDC on AGB stocks and gain across salinity zones, as well as mean tree sizes. (f-j) shows the predicted response plots of salinity and growth dominance coefficient on AGB stocks and AGB growth or gain. All response plots are significant (p < 0.05). To increase the clarity, the rug along the axis margin shows the data distribution with zero-width bins. The shaded area denotes the 95% confidence interval. The p-value indicates the significance level. Others with non-significant relationships are shown in Supplementary Figs. 4 and 5.
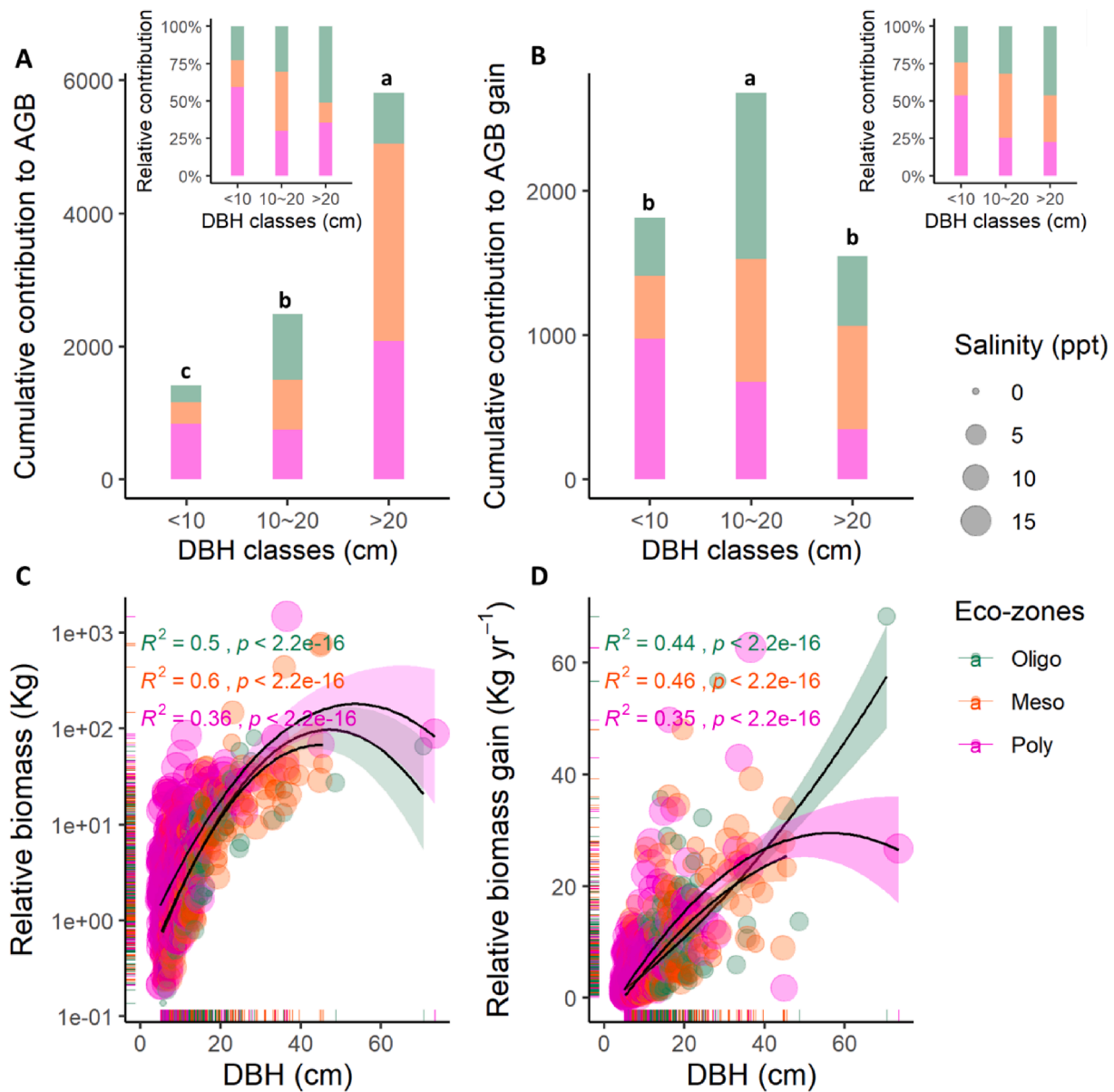
Fig. 3. Aboveground biomass stocks and gains changes with tree size classes and salinity eco-zones. (a) cumulative contribution to AGB (b) the total contribution of classified tree size classes to AGB gain. Inset plots show the respective relative contributions of specific size classes. (c) Changes in relative AGB stock [Y-axis log scaled] and (d) changes in relative AGB gain with tree size and salinity. The 95% confidence interval is denoted by a colored shaded area. The small letters in Figs. a and b show the results of the post-hoc Tukey test. There are no significant differences between the letters.

higher growth (Stark et al., 2012), but smaller trees are more prone to suffering from competition (i.e., reduced carbon accumulation as biomass) (McDowell et al., 2018). High access to light and less competition for large trees than for small-sized trees might help large trees perform better in less salinity areas. Growth reduction in small trees might also happen due to dominance of the suppressing tree characteristics (as small trees are suppressed by dominant trees), while large trees are proportionately benefitted by their size. In contrast, large trees might not effectively utilize resources (such as nutrients) and were unable to dominate the growth in the community, especially in high salinity areas, thereby reducing the overall growth efficiency of the stand. This, despite the fact that large trees devote a greater amount of their resources to reproduction than small trees do (Thomas, 2011), results in lower carbon stocks and gain in higher salinity areas (Table 1). Resource utilization may also depend on nutrient availability in soil, suggesting that in higher salinity areas, nutrients might be lower. Another critical reason could be the inundation and flooding (Crase

et al., 2013). Several studies have found that flooded soil reduces sap flow and thus growth (Krauss et al., 2007). Mangrove growing conditions and habitat (salinity and inundation tolerances) are regularly inundated by salt water, which manipulates tree functions. Again, mangroves inundation tolerance ability regulates species-specific water use efficiency and productivity (Lovelock et al., 2016). High salinity areas are more exposed to the sea and have a greater chance of being flooded compare to other salinity zones. Therefore, frequent saltwater flooding might make the soil more anaerobic, which limits mangrove growth because of reduced sap flow, stomatal conductance, freshwater availability, and plant water uptake ability. Reef et al. (2015) observed a threefold increase in the water uptake capacity of *A. marina* with enhanced stomatal conductance in a relatively benign environment (less saline). Although mangroves use both saline and fresh water for metabolic functions, availability of fresh water largely enhances mangrove growth (Santini et al., 2015).

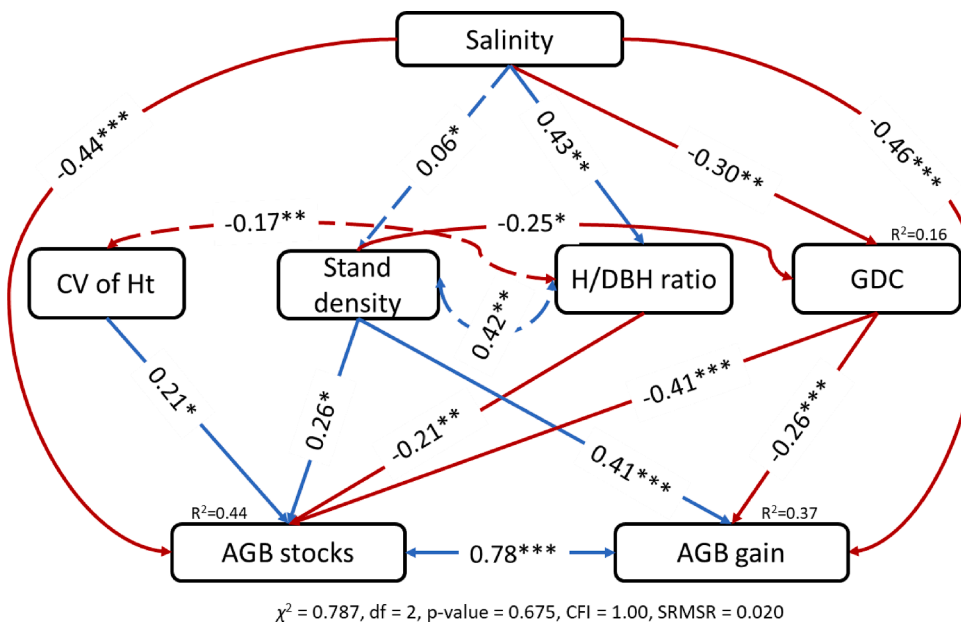We found that large-sized trees dominated the AGB stocks across the

Fig. 4. Structural equation models (SEMs) showing the diverse interactive associations with forest growth, aboveground biomass stocks (AGB), growth (i.e., AGB gain), and stand structures. Developed SEM model's goodness of fit statistics: $\chi^2 = 0.787$, p = 0.675, with a comparative fit index (CFI) of one (CFI = 1.00) (Bentler, 1990), and standardized root mean square residual (SRMSR = 0.02), indicating no significant deviation from model datasets at 2 degrees of freedom. The blue 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. Coefficient of determinant: R^2 (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 significant relationships are shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

salinity gradient, but their growth patterns were negative in higher salinity areas (Fig. 2), as expected. This finding is inconsistent with the assumption of Binkley (2004) that when large trees dominate a forest stand, GDC values get higher, i.e., from zero to positive. However, Binkley's (2004) hypothesis was consistent with the growth pattern in comparatively low salinity areas. We observed AGB stocks in lower salinity areas to be dominated by large trees while GDC values were mostly positive (Fig. 1; Fig. 3 c). Besides correlations between size and growth, growth dominance can also be determined by the distribution of stand tree size (Forrester, 2019). These variations in growth dominance in the Sundarbans might also be affected by tree size distributions and structural diversification, such as the sporadic distribution of large trees in high salinity areas (Table 1 and Supplementary Figs. 2 a, c).

We observed a cumulative contribution of tree size classes to biomass stocks and gain and found mid-sized (10–20 cm) trees and trees in moderate salinity areas held higher biomass gain, implying better growth. Hence, small or mid-size trees surpassed the cumulative contribution of large trees to AGB gain (Fig. 2 b), indicating large trees are losing growth. This finding corresponds to the global carbon distribution in tree size classes, where Piponiot et al. (2022) observed small-sized trees contributed more to growth than large trees. These findings suggest that small-sized trees contribute significantly to biomass stocks and growth, and that small-sized trees should be considered when evaluating growth dynamics. Contribution differences between tree size classes may occur as a result of slower photosynthetic rates under rapid changes in salinity and increasing tree size (Drake et al., 2010) under rapid changes in salinity and increasing tree size. Due to higher salinity, surviving large trees might become physiologically restricted in stomatal conductance and photosynthesis, indicating they are facing difficulties in maintaining their physiological functions and thereby growth (also discussed above). This could also happen due to the combined effects of a tree's biological age, species composition and increased competition for limited resources. For example, Bradford et al. (2010) observed decreasing growth dominance patterns with increasing stand age. We observed higher stem density in the polyhaline zone, which might also enhance species-species competition, and limits trees' resource exploitation efficiency and physiological functions, thereby leading to reverse growth dominance as discussed by Bradford et al. (2010).

Bivariate relationships detected that salinity had a negative effect on both functional variables (here AGB stocks and gain) and growth

dominance patterns (Fig. 3). This salinity-driven negative GDC had a significant direct negative effect on AGB stocks and gain, while structural diversity (i.e., vertical) positively influenced AGB stocks identified by the SEM model (Fig. 4), which partly supports our second hypothesis (HII). We could not identify any significant direct effects of species richness on AGB stocks and gain (see Supplementary Fig. 4d, 5c). This might have happened due to the co-occurrence of a higher number of dwarf trees in high salinity areas (see Table 2). This also suggests that poor sites (high salinity areas) favored the growth of small trees, not big trees, which ultimately decreased overall stand growth and associated biomass stocks. In contrast, vertical structural diversity and stand density had a positive effect on AGB stocks and gain across the salinity zones (Fig. 4).

Higher structural diversity produces more stable stands (Pretzsch et al., 2022). The deltaic Sundarbans mangrove forest is heavily exposed to the sea and experiences tropical cyclones regularly, which may force them to develop structurally diverse stands with complex root system (for example, different species have different root modifications such as buttresses and pneumatophores in *Heritiera fomes*, aerial roots, and knee roots in *Bruguiera sexangula*) for stabilization and protection against the wind, potentially allowing the mangrove plant communities to maintain their ecological functions. Also, salinity strongly influenced the size of trees (increased H/DBH ratio or slenderness ratio) and species composition (Table 1, Fig. 4), which further negatively impacted tree functions. This might have occurred because of higher densities (Fig. 4), which might lower stand stability (by increasing competition and making trees narrower). For example, when H/DBH ratio increases with salinity, stability might decrease, and thereafter, the stand might be unable to perform better physiologically, which affects functional variables. The density driven H/DBH ratio could be physiologically restricted by soil nutrients and light availability of the stand. Although, we were unable to detect how nutritional availability mediates the effects of salinity on growth dominance, we anticipate that increased nutrient availability may buffer the effects of salinity and, as a result, growth dominance may improve (shift from negative to positive).

4.2. Potential impacts of climate change on growth dominance, forest functions and management

We found reduced size-dependent functions and negative growth dominance patterns along the salinity gradient, which suggests that

climate change may potentially shape the growth and development of the mangrove forest through rising sea levels. Karim and Mimura (2008) have predicted 32 cm of sea level rise along the Bangladeshi coast by 2050, which may change the whole structure of the forest and its functions. Due to climate change, high salinity areasmay expand and encroach on areas of previously lower salinity; therefore, trees in lower salinity areas will face similar consequences to trees in high-salinity areas. Thus, we assume that due to the growth reduction of trees, the AGB stocks and belowground carbon stocks may also be affected in other ways. For example, when growth rates declined in higher salinity areas, it may have happened due to fewer physiological functions (e.g., lower photosynthesis rate). As we observed in higher salinity areas, reverse growth patterns occur, which further indicates less functional capability. Consequently, lower photosynthesis activities of large trees result in trees producing fewer leaves, which indirectly contributes to less litterfall and, ultimately, may affect nutrient cycling. Thus, although salinity changes in overall ecosystems are generally slow, climate change records suggest salinity may change rapidly, which could threaten the ecosystem stability and functions of mangrove forests. In fact, the average salinity level in the Sundarbans has already increased by 60% since 1980, and geomorphological or hydrological prediction models have projected a 5 – 10% decadal increase in salinity (Sarker et al., 2021). Tree size-dependent and structural diversity-related functions help to predict future growth and carbon dynamics (Zuidema et al., 2013; Ali et al., 2019). Our results suggest that large trees' growth is declining (meaning climax communities, for example, *H. fomes)* and that small and medium trees (most of them may be locally invasive, *E. agallocha*) are contributing to forest growth. Overall forest growth is reduced in high salinity areas. Therefore, our size-dependent study related to biomass dynamics and partitioning across the salinity gradients could help to predict future carbon dynamics for climate change feedbacks in mangroves.

5. Conclusion

This study highlights the growth performance of large and mature trees, as these trees predominantly contribute to biomass. We found salinity as a key limiting factor, reducing overall ecosystem functioning by diminishing forest structural variables and shifting the growth pattern from positive to negative. The negative growth dominance patterns and size-dependent functional capability of trees indicate large trees are losing growth but still dominantly contributing to the aboveground biomass stocks. Negative growth patterns also characterize the limited functional capability of large trees, which additionally explains the higher functional capability of associated small trees, particularly in high salinity areas. Similarly, as tree size distributions are strongly influenced by salinity, thereby influencing aboveground biomass stocks and growth. Overall, salinity, tree size, and growth dominance patterns determine AGB stocks and gain in the Sundarbans mangrove forest. However, we were unable to detect overall site conditions (i.e., nutrient availability) effects on growth partitioning. Our results provide a valuable comparative benchmark of size-dependent tree performance and their contributions to carbon dynamics in mangrove ecosystems while responding to salinity and climate change. Therefore, this information is useful to predict the future growth performance of trees and overall ecosystem consequences. Although our research shows how shifting growth patterns affect aboveground biomass and growth, the mechanisms underlying these effects have yet to be found. Therefore, we suggest for future studies that focus on the underlying mechanisms of growth and root partitioning across site settings (i.e., nutrient availability). In addition, given the projected consequences of climate change on the coastal forests, we need to further study how sea-level rise will change mangrove biomass dynamics with their distributions in tree size classes at a global scale.

Data and code availability
Summary data shared with the manuscript (.csv). All R code is

available from the corresponding author upon request.

CRediT authorship contribution statement

Shamim Ahmed: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Visualization, Writing – review & editing. **Swapan Kumar Sarker:** Methodology, Resources, Supervision, Writing – review & editing. **Daniel A. Friess:** Writing – original draft, Writing – review & editing. **Md. Kamruzzaman:** Resources, Writing – review & editing. **Martin Jacobs:** Writing – review & editing. **Mériadec Sillanpää:** Writing – review & editing. **Clement Sullibie Saagulo Naabeh:** Writing – review & editing. **Hans Pretzsch:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing – review & editing.

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

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.120954.

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