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Aboveground carbon sequestration of *Cunninghamia lanceolata* forests: Magnitude and drivers



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ABSTRACT

Understanding the spatial variation, temporal changes, and their underlying driving forces of carbon sequestration in various forests is of great importance for understanding the carbon cycle and carbon management options. How carbon density and sequestration in various *Cunninghamia lanceolata* forests, extensively cultivated for timber production in subtropical China, vary with biodiversity, forest structure, environment, and cultural factors remain poorly explored, presenting a critical knowledge gap for realizing carbon sequestration supply potential through management. Based on a large-scale database of 449 permanent forest inventory plots, we quantified the spatial-temporal heterogeneity of aboveground carbon densities and carbon accumulation rates in *Cunninghamia lanceolata* forests in Hunan Province, China, and attributed the contributions of stand structure, environmental, and management factors to the heterogeneity using quantile age-sequence analysis, partial least squares path modeling (PLS-PM), and hot-spot analysis. The results showed lower values of carbon density and sequestration on average, in comparison with other forests in the same climate zone (i.e., subtropics), with pronounced spatial and temporal variability. Specifically, quantile regression analysis using carbon accumulation rates along an age sequence showed large differences in carbon sequestration rates among underperformed and outperformed forests (0.50 and 1.80 Mg·ha⁻¹·yr⁻¹). PLS-PM demonstrated that maximum DBH and stand density were the main crucial drivers of aboveground carbon density from young to mature forests. Furthermore, species diversity and geotopographic factors were the significant factors causing the large discrepancy in aboveground carbon density change between low- and high-carbon-bearing forests. Hotspot analysis revealed the importance of culture attributes in shaping the geospatial patterns of carbon sequestration. Our work highlighted that retaining large-sized DBH trees and increasing shade-tolerant tree species were important to enhance carbon sequestration in *C. lanceolata* forests.

1. Introduction

Forest ecosystems function is a major component of global carbon sequestration (Friedlingstein et al., 2022). Globally, forests absorb an estimated 35% of the total carbon dioxide emissions in the atmosphere and constitute nearly 25% of the total carbon in terrestrial ecosystems (Beer et al., 2010; Luysaert et al., 2007). Aboveground biomass (AGB)

represents a significant and visible carbon reservoir in forest ecosystems (Pan et al., 2011). Forest carbon density and carbon accumulation from biomass exhibit high spatial and temporal variability across large areas, and their dynamics are affected by biodiversity, stand structure, and environment attributes at different scales (Clark, 2010; Stephenson et al., 2014). Therefore, exploring the distribution and underlying mechanisms of carbon density and carbon accumulation change is particularly

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important for effective forest management to mitigate global climate change. While the distribution of aboveground carbon density and carbon accumulation across landscapes has been well reported (Ouyang et al., 2019; Zhang and Chen, 2015), their underlying drivers remain inadequately understood, especially at the local to landscape scale.

During the last decade, numerous studies utilizing forest inventory data have explored the conceptual model of the relationships between species diversity and AGB, spanning from positive effects to no-significance and even negative effects (Gamfeldt et al., 2013; Gao et al., 2021; Morin et al., 2011). Two primary mechanisms, the niche complementarity effect and the selection effect, are used to evidence these positive correlations. The niche complementarity effect suggests that species with different niches efficiently utilize available resources, thereby enhancing aboveground biomass or carbon accumulation (Tilman, 1999). However, the selection effect assumes that greater species richness boosts AGB density by increasing the probability of containing highly productive or ecologically important species (Loreau and Hector, 2001). In addition to the positive relationships, the insignificant or negative correlation between species diversity and forest AGB may be attributed to competitive exclusion and uneven competition for light (Ali et al., 2016; Szwagrzyk and Gazda, 2007). Furthermore, species diversity can indirectly influence community-level AGB by affecting stand density or tree size inequality via mechanisms of plant interactions and species coexistence (Ali et al., 2016; Liang et al., 2007).

Multiple stand structure attributes, including large-diameter trees, stand stem density, and individual tree size inequality, exhibit more frequent and significant direct associations with AGB compared to species diversity (Forrester et al., 2018; Ouyang et al., 2019; Zhang and Chen, 2015). Large-diameter trees, for instance, serve as crucial drivers in determining AGB in forests as they occupy the majority of the growth space in the upper canopy layer (Lutz et al., 2018; Slik et al., 2013). Tree size variation can either reduce or increase AGB and carbon stocks, partly attributed to alterations in the efficient partitioning of light resources between individual trees (Ullah et al., 2021; Zhang and Chen, 2015). Similarly, higher tree densities can improve forest AGB and carbon storage by promoting greater canopy packing, leading to improved light harvesting (Ali et al., 2019c; Jucker et al., 2015). In addition, stand age is considered a key predictor of aboveground biomass and carbon accumulation as it influences plant diversity and stand structure in the tree community (Lee et al., 2023; Liu et al., 2018a, b; Poorter et al., 2016).

It is important to note that environmental variations (e.g., geotopographic, climatic, and soil factors) and anthropogenic attributes determine aboveground biomass and carbon accumulation in forests (Jucker et al., 2016; Poorter et al., 2015; Zhu et al., 2022). Latitudinal and elevational gradients, including climate, soil, resource utilization, biogeography, cultural factors, and history, can influence the spatial distribution of tree species, forest structure, species diversity, forest biomass, and carbon stocks (Chu et al., 2019). Furthermore, soil properties may have direct influence on plant growth and productivity by affecting their ability to retain water and supply nutrients, which in turn can affect AGB or carbon density (Ali et al., 2020). Precipitation, temperature, and solar radiation are also recognized as potential drivers of aboveground carbon stock and carbon accumulation change across climatic zones or ecoregion (Ali et al., 2020; Fang et al., 2012; Jucker et al., 2016). In addition to these natural environmental factors, cultural factors, including religious beliefs, lifestyle habits, and aesthetic preferences, can also influence afforestation preferences, management strategies, and the preservation of old trees, consequently impacting forest carbon density (Måren and Sharma, 2021; Yu et al., 2021). Environment and anthropogenic factors, therefore, need to be considered when testing the drivers of aboveground carbon density and carbon accumulation in forests.

Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook) is a crucial coniferous species used for timber production and is widely distributed in subtropical China (Zhao et al., 2009). To meet the increasing demand for timber, millions of hectares of *C. lanceolata* monocultures have been

established in Hunan Province since the 1950s, with an increasing number of areas being replanted for second or subsequent rotations. However, *C. lanceolata* plantations in subsequent successive rotations lead to decreased soil fertility and diminished ecosystem productivity (Ma et al., 2003). Moreover, younger forest stands have undergone more rapid turnover, while old-growth forests have diminished due to decades of excessive logging and poorly regulated forests management (Yu et al., 2017). The majority of the existing *C. lanceolata* forests in Hunan Province consist of young and middle-aged forests with relatively poor stand quality. They suffer serious degradation, deforestation, and fragmentation, which heavily inhibit their carbon sequestration potential. The distribution of forest carbon sequestration in Hunan Province exhibits spatial unevenness (Chen et al., 2019). Maintaining or restoring standing *C. lanceolata* forests is an achievable goal to enhance carbon sequestration potential (Seddon et al., 2020). Therefore, exploring the characteristics and drivers of carbon density change in various *C. lanceolata* forests can help provide specific management strategies for maintaining or restoring standing *C. lanceolata* forests in degraded areas.

How carbon density and carbon accumulation rates in various *C. lanceolata* forests in subtropical China vary with diversity, stand structure, environment factors, and cultural factors in space remain poorly explored, presenting a critical knowledge gap for realizing carbon sequestration supply potential through management. In this research, we quantified the spatial and temporal heterogeneity of forest carbon densities and carbon accumulation rates in *C. lanceolata* forests in Hunan Province, China, based on a large-scale database of 449 permanent forest inventory plots, and attributed the contributions of tree diversity, stand structure, environmental, and management factors to the heterogeneity using quantile age-sequence analysis, multiple linear regression, partial least squares path modeling, and hot spot analysis. We aimed to (1) estimate changes of aboveground carbon density and carbon accumulation rate across different *C. lanceolata* forests; (2) quantify the relative contributions of tree species diversity, stand structure, and environmental attributes to aboveground carbon density change across various *C. lanceolata* forests; as well as (3) analyze various factors directly and indirectly affecting aboveground carbon density in various *C. lanceolata* forests, and offer management options accordingly.

2. Material and methods

2.1. Study area

The research region is situated in Hunan Province, central subtropical China, spanning from 108°47' to 114°15' E longitude and 24°38' to 30°08' N latitude, covering a total area of 21.18×10^4 km² (Fig. 1). This region features a continental humid mid-subtropical monsoon climate. The annual total precipitation ranges from 1,200 to 1,700 mm (rainfall mostly occurs in April–October) and the annual average temperature falls between 16 and 18 °C (Huang et al., 2014). The region is abundant in forest resources, boasting a forest coverage rate of 59% (Ouyang et al., 2019).

2.2. Forest inventory and climate data

Forest stand data utilized in our study were obtained from the permanent sample plots, measuring 25.82 m × 25.82 m in size, located in Hunan Province. These plots were established and sampled in accordance with national forest continuous inventory protocols during the fifth National Forest Inventory of China (1999–2004). We selected 449 plots with *C. lanceolata* as the dominant tree species. Plot-level data included stand structural attributes (age group, stand age, and stand density), geotopographic factors (latitude, longitude, altitude, and slope), soil factors (soil thickness, humus layer thickness, and litter thickness). The tree species name and the diameter at breast height (DBH, DBH ≥ 5 cm) for each stem in every plot were individually documented. For this study, the sample plots dominated by *C. lanceolata* covered young-aged (<10 years

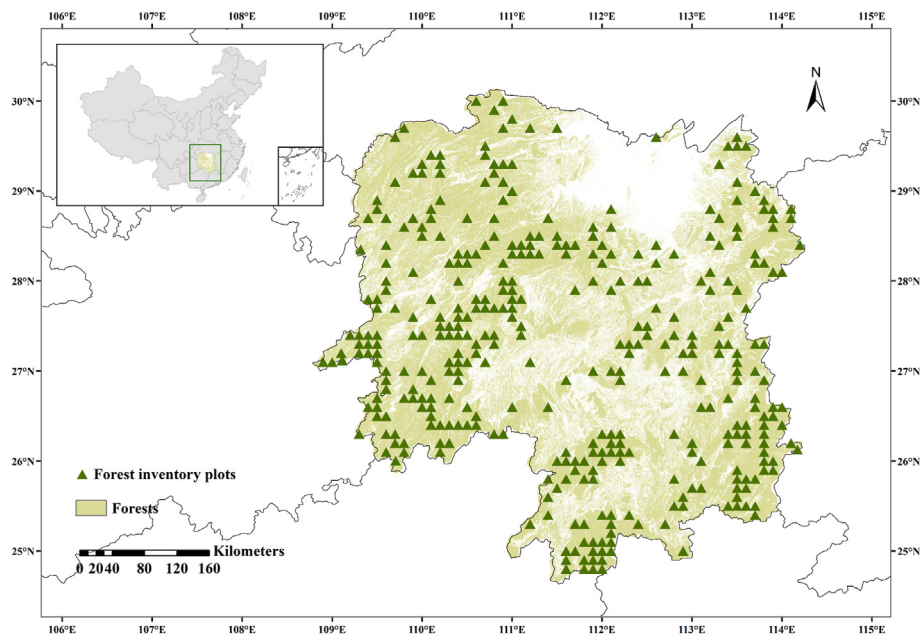


Fig. 1. The distribution of forest inventory plots used in this study.

old), middle-aged (11–20 years old), near-mature (21–25 years old) and mature groups (26–35 years old) for *C. lanceolata* forests. The classification of age groups within the *C. lanceolata* forests was determined according to the criteria outlined in the Operational Guidelines for the Seventh Round of Continuous Forest Resources Inventory in Hunan Province.

The climate factors analyzed in our study included mean annual temperature (MAT), mean annual precipitation (MAP), and solar radiation. Utilizing the plots' geographical location, we obtained 1 km MAT and MAP data and 10 km annual total solar radiation data from the National Tibetan Plateau Data Center (<http://data.tpdc.ac.cn>), and utilized the average values of these variables spanning 1987 to 2004 for analysis (Ding and Peng, 2020; Peng, 2019, 2020; Peng et al., 2019; Peng et al., 2017; Peng et al., 2018; Feng and Wang, 2021).

2.3. Calculations of aboveground carbon density

The aboveground biomass of all live trees (DBH \geq 5 cm) within each plot was calculated by applying species-specific allometric equations based on DBH as a predictor. These equations were obtained from Luo et al. (2020) and Zhou et al. (2018) (Table S1). For the less common species and a small fraction of trees identified as softwood or hardwood broadleaf species, we calculated their biomass values using general equations for hardwood or softwood species (Table S1) (Cai et al., 2014; Wang et al., 2019). We calculated the total aboveground biomass per plot by summing the aboveground biomass of all trees, and then converted this value to tons per hectare ($\text{Mg}\cdot\text{ha}^{-1}$). The aboveground carbon density (AGCD) of each plot was computed by multiplying the total aboveground biomass per unit area ($\text{Mg}\cdot\text{ha}^{-1}$) by the carbon conversion coefficient (a factor of 0.47) (Luo et al., 2020).

2.4. Computation of stand structure variables

We computed stand structure variables to evaluate their impacts on AGCD and elucidate underlying mechanisms. To estimate the impact of large trees on carbon density, we first estimated the maximum DBH for each plot using the top 1% (99th percentile) DBH calculated from the DBH frequency distribution (Lutz et al., 2018; Slik et al., 2013). We selected the Shannon-Wiener diversity index and DBH variation as measures of stand structure diversity. The Shannon-Wiener diversity

index (Eq. 1), accounts for both species richness and evenness within each plot, was utilized to quantify species diversity, employing the 'vegan' package for R 4.2.1. (Ali et al., 2016; Zhang et al., 2012).

$$H_s = - \sum_{i=1}^S P_i \times \ln(P_i) \quad (1)$$

where, P_i is the ratio of the number of the i -th species to the total number of all species in the sample plot, while S is the number of tree species.

The DBH variation among individual trees serves as an indicator to reflect the extent of realized niche differentiation facilitated by positive plant interactions (Zhang and Chen, 2015). To quantify DBH variation, we calculated the coefficient of variation of DBH at the plot-level, which was calculated by dividing the standard deviation of all DBH measurements by the mean DBH (Clark, 2010). This calculation was carried out using the 'raster' package for R 4.2.1.

2.5. Statistical analysis

2.5.1. Quantile age-sequence analysis

One effective way to understand the carbon sequestration potential and the management options is to contrast low-carbon-bearing forests (low carbon accumulation rate forests) with high-carbon-bearing forests (high carbon accumulation rate forests). In our study, the low-carbon-bearing and high-carbon-bearing forests were defined as forests with AGCD lower than the 10th or higher than the 90th quantiles of AGCD, respectively, along the age sequence. Quantile age-sequence analysis was used to obtain the mean aboveground carbon accumulation rate (AGCR, $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) across the chronosequences of low- and high-carbon-bearing forests, respectively. The mean rate of carbon accumulation was determined by calculating the slopes obtained from regression lines of carbon density vs. forest age at the 10th, 30th, 50th, 70th, and 90th quantiles, respectively (Hooker and Compton, 2003).

2.5.2. Importance of predictors for aboveground carbon density

We utilized multiple linear regression to construct models for predicting AGCD and applied a multi-model inference approach to select the best model, which was the basis for estimating the importance of predictors. Before constructing any linear model, we evaluated the normality of all predictor variables (except for longitude and latitude), applying the

Shapiro-Wilk goodness-of-fit test. We transformed non-normally distributed continuous variables using natural logarithms and standardized them to enhance linearity and normality (Grace et al., 2016). To address multicollinearity issues, we calculated Variance Inflation Factors (VIF) and systematically eliminated independent variables exhibiting severe multicollinearity until $VIF < 5$. The full model included five stand structure variables (species diversity, stand age, maximum DBH, stand density, and DBH variation), four geo-topographic variables (latitude, longitude, altitude, and slope), three soil variables (soil thickness, humus layer thickness, and litter thickness), and three climatic variables (MAT, MAP, and solar radiation). Due to the intimate connection between geographical elements (longitude and latitude) and cultural influences, these elements were recognized as potential cultural factors associated with AGCD within forests. We controlled for five stand structure variables. The best average models were then selected and calculated applying a multi-model inference approach relied on the corrected Akaike information criterion (AICc) with a criterion of $\Delta AICc < 2$. This analysis was performed using the R package ‘MuMIn’ (Barton, 2016). As a result, we obtained standardized coefficients for the explanatory variables via the process of model averaging. Then, we evaluated the relative importance of the considered variables in influencing AGCD by determining the proportion of variance they accounted for or by comparing the absolute values of average parameter estimates (standardized regression coefficients) with the sum of all parameter estimates from the model predictors. All statistical analyses were done in R 4.2.1.

2.5.3. Partial least squares path model

We employed the partial least squares path model (PLS-PM) to assess both the direct and indirect key drivers of AGCD. This method offers distinct benefits over conventional structural equation models by requiring a smaller sample size and avoiding assumptions about data distribution, rendering it particularly well-suited for exploratory analysis (Ren et al., 2023). To ensure comparability among various *C. lanceolata* forests and assess model goodness of fit, we selected only the most crucial variables determined by the average models obtained through multiple linear regression to construct the models using the “plsmpm” package in R 4.2.1 (Sanchez, 2013).

2.5.4. Hot-spot analysis

In order to assess the spatial variation of AGCD in the study region, we conducted a hot spot analysis (Getis-Ord G_i^*) to investigate the spatial distribution pattern of AGCD (Sun et al., 2020). This analysis can help differentiate clusters of comparable values that are significantly different from the average, assisting in identifying spatial hot- and cold-spots. Hot spots were classified using the Z-score obtained from the test. In cases with significant positive Z-scores, a higher Z-score suggests a more pronounced concentration of high values, signifying stronger hot spots. On the contrary, significant negative Z-scores with lower values suggest stronger cold spots. Z-scores that are “not significant” indicate the lack of spatial autocorrelation (Manepalli et al., 2011). The analysis was conducted using ArcGIS 10.7.

3. Results

3.1. Aboveground carbon density and carbon accumulation rate

The AGCD of *C. lanceolata* forests varied from 0.25 to 83.20 $\text{Mg}\cdot\text{ha}^{-1}$, with an average value of 20.33 $\text{Mg}\cdot\text{ha}^{-1}$. The average AGCD in young, middle-age, near-mature, and mature age groups were 8.78, 20.40, 29.20, and 32.80 $\text{Mg}\cdot\text{ha}^{-1}$, respectively (Fig. 2a). The AGCD of *C. lanceolata* forests significantly varied among forest ages ($P < 0.001$) (Fig. 2b). The AGCRs were 0.50, 0.78, 1.10, 1.40, and 1.80 $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ at the 10th, 30th, 50th, 70th, and 90th quantiles, respectively (Fig. 2b).

When considering different age forests, almost all stand structural attributes showed significantly positive correlations with AGCD and these correlations were notably stronger compared to most environment attributes (Fig. S1). Specially, AGCD was significantly positively correlated with stand density, maximum DBH, and DBH variation across four age forests. Species richness was significantly positively related with AGCD in young ($p < 0.01$), middle-aged ($p < 0.01$), and near-mature forests ($p < 0.05$). Among the environmental variables, soil thickness was significantly positively correlated with AGCD in young ($p < 0.001$) and middle-aged ($p < 0.01$) forests. MAT had a weak positive correlation with AGCD in young forests ($p < 0.05$). Solar radiation had a positive correlation with AGCD in young forests ($p < 0.05$), middle-aged forests ($p < 0.001$), and near-mature forests ($p < 0.05$). However, latitude only had significantly negatively correlation with AGCD in young ($p < 0.05$), middle-aged ($p < 0.001$), and near-mature forests ($p < 0.01$).

When considering different carbon-bearing forests, both the maximum DBH and DBH variation had significant positive correlations with AGCD (Fig. S2). Additionally, in low-carbon-bearing forests, the AGCD was significantly correlated positively with stand density ($p < 0.05$) and MAP ($p < 0.05$). Furthermore, significant positive relationships of AGCD were observed with species richness ($p < 0.01$) and altitude ($p < 0.001$), in high-carbon-bearing forests.

3.2. Relative importance of stand structure and environment attributes on aboveground carbon density

Multiple linear models suggested that stand structure, geo-topographic, soil, and climate attributes together explained 57%–78% of the variance in AGCD across various *C. lanceolata* forests (Fig. 3). Overall, stand structure attributes consistently accounted for a larger proportion of the variance in AGCD compared to geo-topographic, soil, and climate factors across various *C. lanceolata* forests.

When considering different age forests, the maximum DBH showed a large effect on AGCD in general and across different age forests (accounting for 41%, 33%, 40%, 40%, and 35% of the variance) (Tables S2 and S3). Stand density had the next strong effect on AGCD in general and across different age forests (accounting for 27%, 19%, 33%, 21%, and 29% of the variance) (Tables S2 and S3). Species diversity had a relatively strong effect on AGCD in near-mature (explained 10% of the variance; Fig. 3d) and mature forest (explained 11% of the variance;

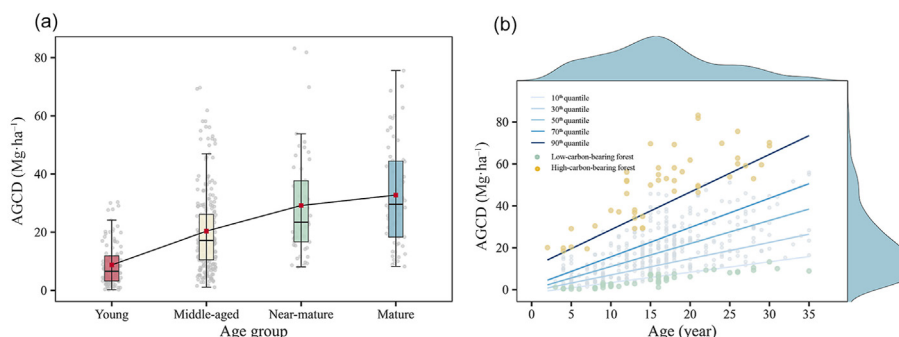


Fig. 2. Aboveground carbon density among age groups (a) and with forest age among five quantiles (b).

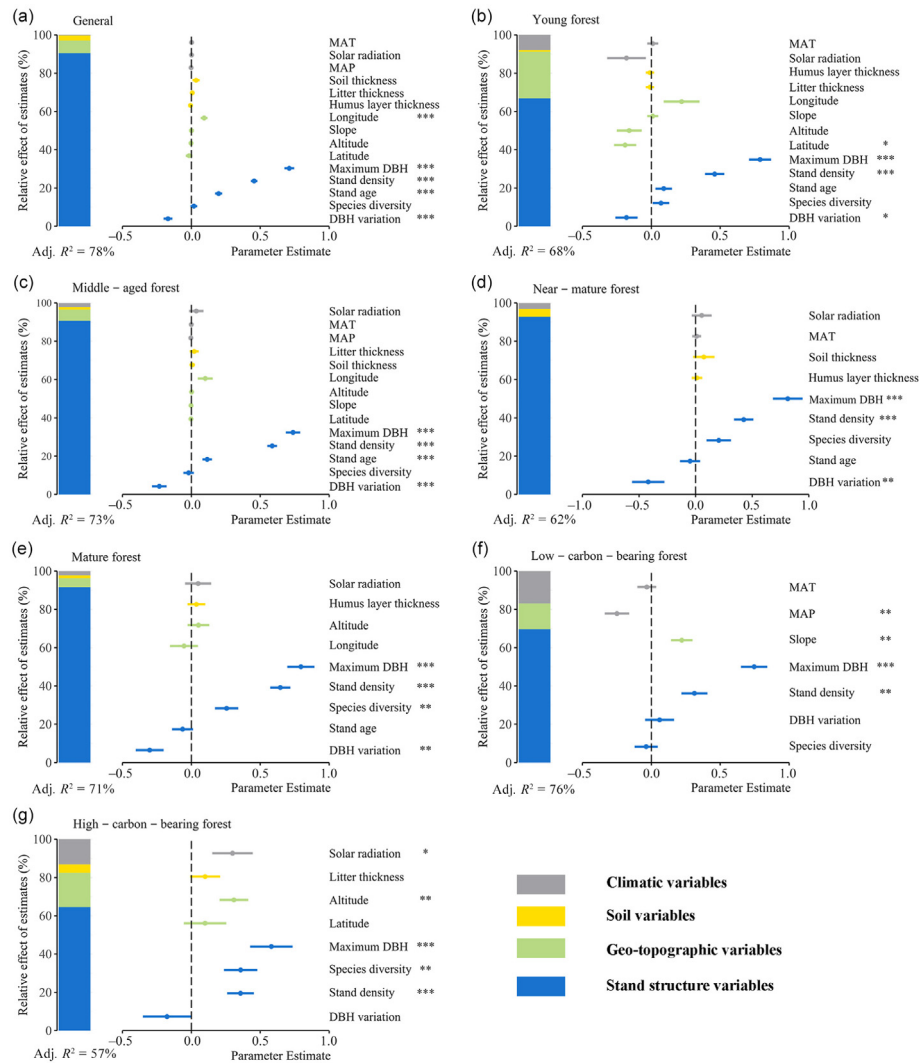


Fig. 3. Standardized estimates (mean \pm SE) of stand structure and environment attributes on aboveground carbon density for *C. lanceolata* forests based on multiple linear models. The p -value of each predictor were given as: * $p < 0.050$; ** $p < 0.010$; *** $p < 0.001$.

Fig. 3e). Stand age exhibited a significant positive correlation with AGCD in general (explained 12% of the variance; Fig. 3a) and middle-aged forests (explained 6% of the variance; Fig. 3c). Conversely, DBH variation had a significant negative effect on AGCD in general (explained 10% of the variance; Fig. 3a), young (explained 8% of the variance; Fig. 3b), middle-aged (explained 12% of the variance; Fig. 3c), near-mature (explained 20% of the variance; Fig. 3d), and mature forests (explained 14% of the variance; Fig. 3e). Among the environment attributes, only longitude exhibited a significantly positive relationship with AGCD in general (explained 5% of the variance; Fig. 3a). Conversely, latitude demonstrated a significantly negative relationship with AGCD in young forests (explained 8% of the variance; Fig. 3b).

When considering low- and high-carbon-bearing forests, maximum DBH and stand density also had the greatest effects on AGCD (Fig. 3f and g, Table S4). However, species diversity had a strong positive effect on AGCD in high-carbon-bearing forests (accounting for 16% of the variance; Fig. 3g) compared to the negative effect in low-carbon-bearing forests (accounting for 2% of the variance; Fig. 3f). Then, MAP and slope also had a weak effect on AGCD in low-carbon-bearing forests (Fig. 3f). Altitude and solar radiation had a weak effect on AGCD in high-carbon-bearing forests (Fig. 3g).

3.3. Direct and indirect effects of main drivers on aboveground carbon density

The direct or indirect effects of stand structure attributes and environment attributes on AGCD were examined across various *C. lanceolata* forests. PLS-PM analysis revealed that the best model for AGCD explained variances ranging from 67% to 81% across various *C. lanceolata* forests (Fig. 4), suggesting that the key variables could explain the majority of AGCD variation in *C. lanceolata* forests.

AGCD was mainly directly influenced by maximum DBH and stand density in general and across different age forests (standardized path coefficient: 0.31–0.76; Fig. 4). Species diversity significantly and directly influenced AGCD in mature forests (standardized path coefficient: 0.27; Fig. 4e). Species diversity also had an indirect positive effect via maximum DBH or DBH variation on AGCD in general and across different age forests. Stand age directly influenced AGCD in general and middle-aged forests (standardized path coefficient: 0.21 and 0.12), and it also had an indirect positive effect via maximum DBH, stand density, or species diversity on AGCD in general, young, and mature forests. However, DBH variation directly negatively influenced AGCD in general (standardized path coefficient: -0.17 ; Fig. 4a), middle-aged (standardized path coefficient: -0.22 ; Fig. 4c), near-mature (standardized path coefficient: -0.41 ; Fig. 4d), and mature (standardized path coefficient: -0.30 ; Fig. 4e) forests. Stand density had an indirect effect on AGCD via

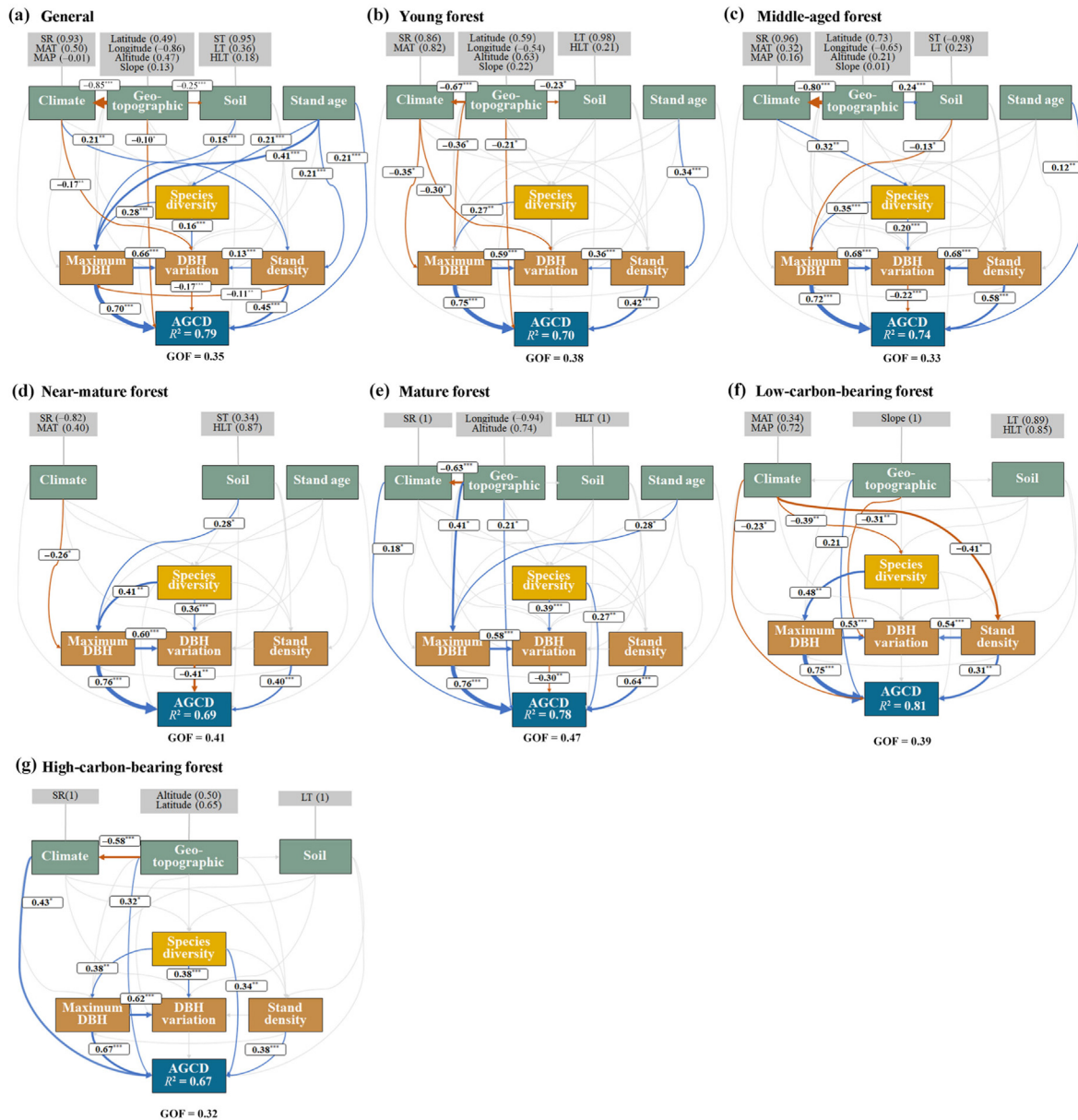


Fig. 4. The PLS-PM explaining the direct and indirect effects of primary stand structure and environment attributes on AGCD. Blue and orange lines denote positive and negative significant relationships, respectively, while gray lines indicate non-significant relationships; the thickness of the blue and orange lines signify the strength of the causal relationship, supplemented by a standardized path coefficient. The p -value of each predictor were given as: * $p < 0.050$; ** $p < 0.010$; *** $p < 0.001$. (SR-solar radiation, ST-Soil thickness, LT-Litter thickness, HLT- Humus layer thickness). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

maximum DBH and DBH variation in general. AGCD showed a direct correlation with a combination of geo-topographic in general (e.g., latitude, longitude, slope and altitude), young (e.g., longitude, latitude, slope and altitude), and mature (longitude and altitude) forests. Climate, geo-topographic, and soil factors also had an indirect effect via maximum DBH on AGCD in forests, even though the relationship varied among different forests.

For low-carbon-bearing forests, AGCD was significantly positively influenced by maximum DBH and stand density (standardized path coefficients: 0.75 and 0.31; Fig. 4f), and it exhibited a significant correlation with geo-topographic and climatic factors (standardized path coefficients: 0.21 and -0.23; Fig. 4f). Species diversity and climate factors had significant indirect effects on AGCD via maximum DBH or stand density. For high-carbon-bearing forests, maximum DBH, species diversity, and stand density had strong positive direct effects on AGCD

(standardized path coefficients: 0.67, 0.34, and 0.38; Fig. 4g), while a combination of geo-topographic and climate attributes exhibited a significant correlation with AGCD (standardized path coefficients: 0.32 and 0.43; Fig. 4g). Species diversity had a significant indirect effect on AGCD through maximum DBH.

4. Discussion

4.1. Relatively low carbon sequestration of *C. lanceolata* forests in Hunan Province, China

A range of 0.25–83.20 Mg·ha⁻¹ for AGCD in *C. lanceolata* forests was found, which was lower than the values of previous studies conducted in a similar climate zone. The AGCD of the young to mature forests in the *C. lanceolata* forest ranged from 8.78 to 32.80 Mg·ha⁻¹, narrower than

previous estimates in similar climate zones (Fig. S3a). For example, the AGCD estimated in northern Guangxi Province (29.42–105.10 Mg·ha⁻¹) (Lan et al., 2016) and Fujian Province (69.94–131.81 Mg·ha⁻¹) (Fu, 2016) were all higher than our results. Our AGCD was considerably lower than the global averages for *C. lanceolata* plantations (18.89–63.77 Mg·ha⁻¹) (Bukoski et al., 2022) (Fig. S3a).

Similarly, AGCR estimated for the *C. lanceolata* chronosequences of various quantiles (0.50–1.80 Mg·ha⁻¹·yr⁻¹) were far lower than the averages of *C. lanceolata* plantations in the world (2.09 Mg·ha⁻¹·yr⁻¹) (Bukoski et al., 2022) and southern China (2.40 Mg·ha⁻¹·yr⁻¹) (Yu et al., 2020) in the same climate zone (Fig. S3b). Although the AGCR of the best *C. lanceolata* forests (i.e., above the 90th quantile) was similar to the estimated value of coniferous forest in Guangdong Province (1.23 Mg·ha⁻¹·yr⁻¹) (Zhou et al., 2008) and white pine in Rhode Island, USA (1.38 Mg·ha⁻¹·yr⁻¹) (Hooker and Compton, 2003), it was lower than the averages of *C. lanceolata* plantations found in other places, indicating that the *C. lanceolata* forests in Hunan Province have a large potential for increasing AGCD.

The relatively low AGCDs and AGCRs of *C. lanceolata* forests observed in our study could be ascribed to various attributes, including data source. Estimates obtained from forest inventories tend to be lower than those derived from experimental sites because the latter must be well maintained and representative to be considered (Orihuela-Belmonte et al., 2013; Sun and Liu, 2020). However, the large-scale forest inventory unbiasedly covers all kinds of forests in the region, thereby it is more regionally representative. This study utilized forest inventory data to help differentiate low- and high-carbon-bearing forests to find the characteristics and drivers of the AGCD change between low-carbon-bearing and high-carbon-bearing forests, which is valuable for proposing different management strategies to maintain or restore *C. lanceolata* forests. In addition, the lower AGCDs and AGCRs observed may be attributed to the predominance of young and middle-aged forests, constituting 75% of the stands in our study. Nonetheless, as the young and middle-aged forests continue to mature over time, we anticipate a future increase in AGCD within *C. lanceolata* forests in Hunan.

4.2. Stand structural attributes more important in determining aboveground carbon density sequestration

This study showed how the relationships among stand age, species richness, maximum DBH, stand density, DBH variation, and AGCD vary across various *C. lanceolata* forests. Our analysis revealed that stand structure attributes were robust predictors of AGCD across various *C. lanceolata* forests, while environmental factors made a relatively smaller contribution (Figs. 3 and 4).

Our findings showed that large-diameter trees exerted the most significant direct positive impact on AGCD compared to other individual predictors across various *C. lanceolata* forests (Figs. 3 and 4), indicating that the prominent role of large-diameter trees as a driver of AGCD in *C. lanceolata* forests (Ali et al., 2019b; Lutz et al., 2018). These results aligned with earlier findings, which emphasized the significance of big-sized and dominant trees in determining AGCD in forests, supporting the selection effect (Ali et al., 2019b; Loreau and Hector, 2001; Wu et al., 2022). In general, aboveground biomass experiences exponential growth or follows a power-function relationship with respect to tree diameter at the individual tree scale. As a result, larger trees in stands make a disproportionately greater contribution to the overall forest aboveground biomass compared to medium- and small-sized trees (Ali and Mattsson, 2017; Stephenson et al., 2014).

Our results demonstrated that stand density was another important predictor of AGCD, which was in agreement with prior studies in both temperate forests (Gao et al., 2021; Ullah et al., 2021) and subtropical forests (Ouyang et al., 2019; Wu et al., 2022). The positive relationship between stand density and AGCD can be primarily attributed to increasing canopy packing, which enhances resource utilization and ultimately leads to higher AGCD (Ali et al., 2020; Forrester et al., 2018).

Moreover, our results also supported the species-energy hypothesis, indicating that higher stand density contributes to greater AGB due to increased energy availability (Ali et al., 2020; Ullah et al., 2021). However, there was a contrasting perspective suggesting that increasing stand density could foster both intraspecific and interspecific competition, driven by resource limitations, which might ultimately result in a decline in AGB (Bourdier et al., 2016). This might explain our additional results, which suggested that stand density had an indirect negative effect on AGCD via maximum DBH in general forests.

In addition, AGCD generally increased with forest stand age in our study. This strong positive effect on AGCD can be attributed to the cumulative growth of trees over ecosystem succession (Poorter et al., 2016; Lee et al., 2023; Liu et al., 2018a,b; Xu et al., 2018). We also found that stand age has an indirect impact on AGCD through changes in stand density, maximum DBH, or species diversity in general, young, and mature forests (Fig. 4). The positive links between diversity and age were usually found in early successional stages or before canopy closure (Ouyang et al., 2019). However, this relationship tends to diminish in later successional stages and post-canopy closure, and intensified competition (Zhang and Chen, 2015). Given that the majority of the forests in our study were young (age < 35 years), the observed positive association between diversity, age, and aboveground carbon suggests their potential for greater carbon absorption through future growth. However, a negative correlation between stand age and AGCD was found in near-mature and mature forests (Fig. 3d and e), likely attributable to human interference, such as the high-intensity illegal logging of large-sized trees, leading to significant carbon stock losses as stand age (Aryal et al., 2014; Pyles et al., 2022).

Interestingly, our results showed a strong direct positive correlation between species diversity and AGCD in high-carbon-bearing forests compared to low-carbon-bearing forests (Fig. 4f and g), and this positive relationship was consistent in mature forests (Fig. 4e). Our results suggested that, relative to other stand structure variables, species diversity was the significant factor in predicting AGCD and AGCR in high-carbon-bearing and mature *C. lanceolata* forests. Hence, it demonstrated that the niche complementarity effect was at play in high-carbon-bearing and mature *C. lanceolata* forests (Gao et al., 2021; Liang et al., 2016; Poorter et al., 2016). The niche complementarity effect stated that a varied species community enhances efficient use of resources by capitalizing on complementarity mechanisms among coexisting species, thereby leading to increase AGB (Poorter et al., 2015). It can be concluded that in high-carbon-bearing and mature *C. lanceolata* forests, the increase in tree species diversity has a more significant effect on increasing AGCR and AGCD than the size and abundance of the dominant tree species (*C. lanceolata* in our study). Moreover, the PLS-PM analysis revealed that species diversity had an indirect positive effect on AGCD via increasing stand density and maximum DBH across different age groups (Fig. 4). This suggested that the relationship between species diversity and AGCD was associated with other stand structure attributes (Ouyang et al., 2019).

We found that DBH variation had negative or negligible relationships across different *C. lanceolata* forests, except for low-carbon-bearing forests (Figs. 3 and 4). This finding did not support the niche complementarity hypothesis related to tree sizes. The negative influence of DBH variation on AGCD may be attributed to the predominance of *C. lanceolata* trees in our studied forests (Ali et al., 2019a; Zhang and Chen, 2015). Our findings confirmed earlier results suggesting that tree size inequality has either a negative or non-significance effect on AGB in stands dominated by coniferous species, such as the single-species stands of ponderosa pine, silver fir, and European beech (Bourdier et al., 2016; Cordonnier and Kunstler, 2015). The PLS-PM analysis suggested that AGCD substantially increased with maximum DBH, stand density, and species diversity rather than DBH variation across various *C. lanceolata* forests. This was more likely due to competitive exclusion, where big-sized trees tend to disproportionately monopolize light resources relative to their size (Ali et al., 2016; Bourdier et al., 2016; Szwagrzyk

and Gazda, 2007). In this way, an increase in *C. lanceolata* trees density might not significantly enhance aboveground biomass, as high planting densities could lead to reduced photosynthesis and biomass due to self-shading in fast-growing plants (Dong et al., 2016). Pretzsch (2005) demonstrated that productivity levels were greater in mixtures with stratified canopies, where the upper canopy was occupied by intolerant species, in comparison to monocultures (Pretzsch, 2005). Increasing the diversity of shade-tolerant tree species positively impacted aboveground biomass (Morin et al., 2011).

From a practical standpoint, the observed positive correlations between maximum DBH, stand density, and species diversity and AGCD provided a viable strategy for forest management and the realization of carbon density potential within the framework of ecological mechanisms (Ali et al., 2019b; Zhang and Chen, 2015). Maximum DBH and stand density were the most important drivers on AGCD in general and across different age forests, as well as in different carbon-bearing forests. Furthermore, our study also showed that species diversity dominance of high-carbon-bearing forests was the main structural driver of AGCD compared to low-carbon-bearing forests. Our results provided evidence on the importance of the presence of large-sized or large biomass trees in enhancing aboveground biomass and carbon density (Cavanaugh et al., 2014; Lutz et al., 2018). Therefore, extending the rotation length of *C. lanceolata* is crucial, promoting the production of large-diameter timber and ensuring continuous carbon sequestration in trees (Diao et al., 2022; Yu et al., 2020). Additionally, maintaining complex stand structures and increasing other shade-tolerance tree species could prove beneficial in achieving management objectives related to aboveground biomass and carbon accumulation for *C. lanceolata* forests (Zhu et al., 2022).

4.3. The influence of cultural factors on the formation of geospatial patterns of aboveground carbon sequestration

The AGCD of various *C. lanceolata* forests showed a clear spatial dependence in our study. We discovered that longitude showed a significant positive correlation with AGCD in general *C. lanceolata* forests (Fig. 3a), while latitude showed a significant negative correlation with AGCD in young to near-mature forests in a bivariate relationship (Table S2). The geospatial patterns in AGCD can be related to the cultural factors (Mären and Sharma, 2021). These findings were further supported by spatial analysis, which revealed that AGCD hotspots of various *C. lanceolata* forests were mainly distributed in the southeast and southwest regions of Hunan Province (Fig. S4). As shown in Fig. S4f and 4g, compared to the dispersed spatial pattern of low-carbon-bearing forests, the high-carbon-bearing forests were distributed in the southwest (Huaihua, Suining, Chengbu, and Dongkou counties) and southeast (Chaling, Ling, Anren, and Yongxing counties) regions of the province. The history of planting *C. lanceolata* for timber production in these regions can be dated back 600 years, as *C. lanceolata* is known as 'all-purpose wood' and 'authentic wood', widely used for building houses and furniture. As a result, *C. lanceolata* in these regions has received higher attention and better management from the locals compared to other regions. While more *C. lanceolata* forests with high AGCD and AGCR distributed in these areas may seem counterintuitive in the context of traditional forest use, the traditional culture in these regions has led to a preference for large-diameter trees and the habit of retaining old trees. If these forests were harvested, forest carbon density would be reduced, thereby rational harvesting strategies can reduce carbon density loss.

Additionally, we found altitude had a significant effect on AGCD in high-carbon-bearing forests (Fig. 3g) compared to low-carbon-bearing forests, which also can be attributed to human disturbance. Steeper terrain at higher altitudes can restrict entry and provide protection against human interference, contributing to higher carbon storage in these areas (Spracklen and Righelato, 2014). Furthermore, our results showed that stand structure and environment variables accounted for only 57%–78% of the variation in AGCD across *C. lanceolata* forests,

suggesting that the larger unexplained variation may be related to cultural and management factors, not considered in our models.

Our results also suggested that solar radiation had a significantly direct effect on AGCD in high-carbon-bearing forests (Fig. 4g). The increased availability of light notably contributes to the growth and biomass of *C. lanceolata* forests (Liu et al., 2018a,b). MAP and slope had a significantly negatively direct/indirect effect on the AGCD (Fig. 4f) in low-carbon-bearing forests. This may be attributed to unfavorable topographic and climatic conditions limiting the accumulation of *C. lanceolata* forest biomass by limiting soil nutrients, water, light, and wind velocity (Chen et al., 2023; Moeslund et al., 2013). Furthermore, the patterns of aboveground biomass were ultimately influenced by a combination of soil, climatic, and biotic attributes along spatial gradients (e.g., latitude and longitude) (Ali et al., 2020; Chu et al., 2019; Fang et al., 2012). However, we found that soil and climatic factors had little or no significant direct/indirect effect on AGCD in most *C. lanceolata* forests (Fig. 4). This could be due to the masking effect of the extensive temporal and spatial heterogeneity across a wide geographic area on the impact of environmental attributes on aboveground biomass and carbon stocks (Ouyang et al., 2019; Xu et al., 2018).

5. Conclusion

We found that mean aboveground carbon densities ranged from 8.78 to 32.80 Mg·ha⁻¹ from young to mature forests in *C. lanceolata* forests in Hunan Province. The results showed low values of carbon density and carbon accumulation rate on average, in comparison with other forests in the same climate zone, with pronounced temporal variability, suggesting a large potential for carbon sequestration if the carbon density in low-carbon-bearing forests can be improved through management practices. Specifically, quantile age-sequence analysis using carbon accumulation rates along an age sequence showed large differences in carbon sequestration rates among underperformed and outperformed forests (i.e., 0.50 and 1.80 Mg·ha⁻¹·yr⁻¹ at the 10th and 90th quantiles, respectively). Alarming, even with the best forests at the 90th quantile, the carbon sequestration rate was very low compared with other plantations in the subtropics.

We explored the drivers of AGCD in *C. lanceolata* forests, using the multiple linear regression models, PLS-PM analysis, and hot-spot analysis. Our findings indicated that maximum DBH and stand density were the primary drivers of AGCD across various *C. lanceolata* forests. We found direct and indirect effects of species diversity on AGCD across various *C. lanceolata* forests, and hence confirming the niche complementarity effect. Meanwhile, we observed a stronger positive effect of species diversity on AGCD in high-carbon-bearing forests compared to low-carbon-bearing forests, suggesting that an increase in species diversity may strongly impact AGCD in *C. lanceolata* dominated forests. However, we found negative or negligible interactions between DBH variation and AGCD across various forests (except for low-carbon-bearing forests), due to competitive exclusion. Hotspot analysis revealed the importance of culture attributes in shaping the geospatial patterns of carbon sequestration. Our findings provided strong evidence for forest management to protect large-sized DBH trees and increase shade-tolerant tree species to enhance their carbon sequestration in *C. lanceolata* forests.

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Authors' contribution

Chen Wang: Methodology, Data Curation, Writing – original draft, methodology, Visualization. Shuguang Liu: Conceptualization, Methodology, Writing – review & editing, and Supervision, Funding acquisition. Yu Zhu: Formal analysis, Resources, Writing – review and editing, Funding acquisition. Andrew R. Smith: Writing – review & editing. Ying Ning: Writing – review & editing. Deming Deng: Data curation.

Data availability

Data are available on request from the authors.

CRedit authorship contribution statement

Chen Wang: Writing – original draft, Visualization, Methodology, Data curation. **Shuguang Liu:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Yu Zhu:** Writing – review & editing, Resources, Funding acquisition. **Andrew R. Smith:** Writing – review & editing. **Ying Ning:** Writing – review & editing. **Deming Deng:** Data curation.

Declaration of competing interest

The authors declare that they have no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fecs.2024.100165>.

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