Stand structural diversity rather than species diversity enhances aboveground carbon storage in secondary subtropical forests in Eastern China

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Abstract

Stand structural diversity, typically characterized by variances in tree diameter at breast height (DBH) and total height, plays a critical role in influencing aboveground carbon (C) storage. However, few studies have considered the multivariate relationships of aboveground C storage with stand age, stand structural diversity, and species diversity in natural forests. In this study, aboveground C storage, stand age, tree species, DBH and height diversity indices, were determined across 80 subtropical forest plots in Eastern China. We employed structural equation modeling (SEM) to test for the direct and indirect effects of stand structural diversity, species diversity, and stand age on aboveground C storage. The three final SEMs with different directions for the path between species diversity and stand structural diversity had a similar goodness of fit to the data. They accounted for 82% of the variation in aboveground C storage, 55-59% of the variation in stand structural diversity, and 0.1% to 9% of the variation in species diversity. Stand age demonstrated strong positive total effects, including a positive direct effect (β = 0.41), and a positive indirect effect via stand structural diversity (β = 0.41) on aboveground C storage. Stand structural diversity had a positive direct effect on aboveground C storage (β = 0.56), whereas there was little total effect of species diversity as it had a negative direct association with, but had a positive indirect effect, via stand structural diversity, on aboveground C storage. The negligible total effect of species diversity on aboveground C storage in the forests under study may have been attributable to competitive exclusion with high aboveground biomass, or a historical logging preference for productive species. Our analyses suggested that stand structural diversity was a major determinant for variations in aboveground C storage in the secondary subtropical forests in Eastern China. Hence, maintaining tree DBH and height diversity through silvicultural operations might constitute an effective approach for enhancing aboveground C storage in these forests.

Key words: biodiversity; carbon storage; evergreen broadleaved forests; species diversity; stand structure; structural equation model.

1 Introduction

Subtropical forests in the East Asian monsoon region comprise a significant carbon (C) sink, likely due to young stand ages coupled with high nitrogen deposition, sufficient water, and heat availability (Yu et al., 2014). Although C tends to accumulate as forest age (Poorter et al., 2016), we still lack a complete understanding of the determinants/mechanisms of C accumulation in these subtropical forests.

Stand structural diversity and species diversity have strong links to aboveground biomass or C storage in forest ecosystems (Dănescu et al., 2016; Wang et al., 2011; Zhang et al., 2012). The structural and species diversity of stands depend to a large extent on the stand age (Lei et al., 2009; Wang et al., 2011; Zhang and Chen, 2015). However, associations between stand structural diversity, species diversity, and C storage, or productivity of stands remain debated (e.g., Dănescu et al., 2016; Poorter et al., 2015). This is, to some extent, the case, as the well-documented effects of stand age (a critical driver for individual species dynamics, aboveground C storage and productivity), has not often been explicitly considered (but see Zhang and Chen, 2015).

Multilayered stand structures have been theorized to increase the capture and efficient utilization of light (Yachi and Loreau, 2007), and empirical evidence has indicated that stand structural diversity is positively associated with aboveground biomass or C storage. Hence, we hypothesized that stand structural diversity has a positive direct effect on the aboveground storage of C (Fig. 1a). On the other hand, the direct relationships between species diversity and aboveground biomass or C, have been reported to be either positive (Dayamba et al., 2016; Wang et al., 2011), negative (Szwagrzyk and Gazda, 2007), or insignificant (Vilà et al., 2003). A recent analysis suggests that tree species diversity increases structural diversity of a stand, and as a consequence, enhances the aboveground biomass (Zhang and Chen, 2015). In the meantime, both stand structure and species diversity are influenced by stand age

(Brassard et al., 2008; Zhang and Chen, 2015), which lead to the indirect effects of stand age via stand structural diversity and species diversity, on aboveground C storage (Fig. 1a). Alternately, the stand structural diversity may be critical to species coexistence (Clark, 2010), and in turn may impart a positive indirect effect on the aboveground C storage (Zhang and Chen, 2015) (Fig. 1b). Moreover, species diversity and stand structural diversity may provide positive feedback to each other (Fig. 1c).

In this study, we aimed to investigate the effects of stand structural diversity and species diversity on aboveground C storage, while accounting for the effects of stand age. We employed structural equation models (SEMs; Malaeb et al., 2000) to analyze data from 80 structurally diverse and mixed subtropical forest plots in Eastern China. Specifically, we tested the following hypotheses, represented by SEMs paths: 1) the effects of stand age on aboveground C storage, species diversity, and stand structural diversity, 2) the indirect effect of stand age on aboveground C storage via stand structural and species diversity, and 3) the direct effects of stand structural and species diversity, as well as the indirect effect of species diversity via stand structural diversity on aboveground C storage (Fig. 1). Due to the complex interactions between species diversity and stand structural diversity (Clark, 2010; Zhang and Chen, 2015), we also investigated alternative pathways between the two (Figs. 1b and 1c).

2 Materials and methods

2.1 Study area, sites, and plots

This study was conducted in the lower eastern extension of the Tiantai and Siming Mountains (29º41-50´N, 121º36-52´E) located near Ningbo City, Zhejiang Province, in Eastern China. This region has a typical subtropical monsoon climate with a hot and humid summer and a dry cold winter. The highest peak in this area reaches 800 m above sea level, while most other reliefs are in the 70-500 m range (Yan et al., 2013). The soils in these areas were classified as Ferralsols according to the FAO soil classification system (World Reference Base for Soil Resources, 2006), with the parent materials consisting mostly of Mesozoic sedimentary rocks, some acidic igneous rocks, and granite residual weathered material (Yan et al., 2013).

Five study sites were selected within the study area, including Tiantong National Forest Park, Ruiyan Forest Park, Dongqian Lake Landscape Area, Shuangfeng Mountain, and Nanshan Mountain. The studied region had been subjected to both anthropogenic and natural disturbances such as logging, land-use conversion, windthrow via typhoon, and variable intensities of human disturbances in its history; however, it has been protected from anthropogenic activity for the last 25 years or more. Consequently, forests in the region contained stands with different levels of degradation (Wang et al., 2007; Yan et al., 2009). Although forests across the study areas are considered as secondary subtropical forests, the mature forests around a Buddhist temple in the center of the Tiantong National Forest Park approximate to climax monsoon evergreen broadleaved forests, as they have been protected from complete clearance for centuries.

We selected stands that had recovered naturally from logging in the study areas, with no human disturbances for more than three decades. We established a total of 80 plots, including young forests (n = 21), premature forests (n = 39), and mature forests (n = 20) (Yan et al., 2013). The measurement of the plots was carried out through forest inventories and ground based surveys, which were conducted between 2010 and 2013, and based on Forestry Standards for 'Observation Methodology for Long-term Forest Ecosystem Research' of the People's Republic of China (LY/T 1952-2011). Each plot (20 × 20 m) was located at a distance of least 100 m from stand edges in order to minimize edge effects. For each sample stand, we determined the stand age as the number of years since the last stand replacing disturbance, i.e., clearcut harvesting (e.g., Wang et al., 2007; Yan et al., 2009). The official records of the Ningbo Forestry Bureau, Zhejiang Province, were reviewed to extract stand age data.

In each plot, the basal diameter (diameter at 5 cm above the root collar) and the diameter at breast height (DBH) were measured for trees taller than 1.50 m, while the basal diameter and diameter at 45 cm height above ground level were measured (with a diameter tape) for trees that were shorter than 1.50 m. The total tree height for each tree was measured with a telescopic pole for heights of up to 15 m, and with a clinometer for heights of >15 m. The studied plots contained between 6 and 46 tree species per plot, and among them, deciduous species such as *Liquidambar formosana* and *Quercus fabri*, and evergreen species such as *Lithocarpus glaber* were the dominant species in young forests. Evergreen species such as *Choerospondias axillaris* and *Schima superba* dominated in the premature forests, while *Castanopsis fargesii* and *Castanopsis carlesii* dominated in the mature forests.

2.2 Estimation of aboveground carbon storage

The AGB of individual trees (AGB*t*) having DBH ≥ 5 cm was calculated using the general allometric equation (eqn 1; Chave et al., 2014) based on tree DBH (cm), height (H, m) and species' wood density (ρ, g cm^{-3}).

$$\mathrm{AGB}t = 0.0673 \times (\rho \times \mathrm{DBH}^2 \times \mathrm{H})^{0.976} \qquad \text{eqn 1}$$

We estimated the AGB of individual shrubs and small trees having a DBH of < 5 cm (AGB*s*) using a multi-species allometric equation (eqn 2) (developed locally), based on DBH, height and species' wood density (Ali et al., 2015).

$$\mathrm{AGBs} = 1.460 \times \exp\{-3.23 + 2.17 \times \mathrm{Ln(D)}\} \qquad \text{eqn 2}$$

The total AGB per plot was the sum of the AGB*t* and AGB*s*. Subsequently, we converted AGB to aboveground C storage (Mg ha^{-1}) by multiplying AGB with a conversion factor of 0.5, assuming that 50% of the total tree biomass is C (Dixon et al., 1994).

2.3 Quantification of species diversity and stand structural diversity

We used the Shannon-Wiener biodiversity index to quantify tree species diversity (Magurran, 2004) and tree-size variations (i.e., tree DBHs and heights) within each plot as stand structural diversity. With the Shannon-Wiener index, the DBH and height were grouped into different discrete classes in order to evaluate which combination of discrete classes for DBH and height diversity indices best predicted aboveground C storage in secondary subtropical forests. For DBH, 2, 4, 6, and 8 cm classes were tested, while for height, 2, 3, 4, and 5 m classes were tested. Tree species, DBH and height diversity indices were calculated for each plot using equations 3, 4, and 5, respectively (Buongiorno et al., 1994; Magurran, 2004; Staudhammer and LeMay, 2001). Similar to other studies in forests (Finegan et al., 2015; Prado-Junior et al., 2016; Zhang and Chen, 2015), we used the relative basal area to represent the proportions of individual species, DBH class, or height class within each sample plot,

$$\mathrm{H_s} = -\sum_{i=1}^{s} \mathrm{p}_i \times \ln(\mathrm{p}_i) \qquad \text{eqn 3}$$

$$\mathrm{H_d} = -\sum_{j=1}^{d} \mathrm{p}_j \times \ln(\mathrm{p}_j) \qquad \text{eqn 4}$$

$$\mathrm{H_h} = -\sum_{k=1}^{h} \mathrm{p}_k \times (\ln \mathrm{p}_k) \qquad \text{eqn 5}$$

where p_i, p_j, and p_k are the proportion of basal areas of *i*th species, *j*th DBH classes and *k*th height classes, respectively, while *s*, *d*, and *h* are the number of tree species, DBH classes, and height classes, respectively. The calculations on the Shannon-Weiner indices were performed using the *vegan* package for the R 3.2.2 (Oksanen et al., 2015; R Development Core Team, 2015).

2.4 Statistical analyses

As recommended (Grace et al., 2016), we constructed three SEMs based on known theoretical multivariate causes of forest diversity and aboveground C storage in natural forests (Fig. 1). We used stand structural diversity as a latent variable by incorporating two observable variables, tree DBH diversity and height diversity, which are highly correlated based on different discrete classes (r = 0.34 to 0.60, P = 0.002 to < 0.001). To assess how DBH and height classes affected the prediction of aboveground C storage, we tested 48 SEMs employing different combinations of discrete classes of tree DBH diversity (2, 4, 6, and 8 cm classes) and height diversity (2, 3, 4, and 5 m classes) based on the three conceptual models (Table S1).

For the interpretation of results (Grace et al., 2016), we identified bivariate relationships between each of the hypothesized causal paths according to our hypothesis in Fig. 1, using Pearson's correlation and regression analysis. Specifically, we fit each pair of variables using simple linear and multiple linear regressions, through the addition of quadratic and cubic polynomial terms to test for bivariate relationships of aboveground C storage. Stand age, species diversity, DBH, and height diversity indices were included based on their various discrete classes. We also tested the bivariate relationships between stand age and species diversity, DBH, and height diversity indices based on their various discrete classes. Our analyses indicated that simple linear regression analysis was optimal in describing bivariate relationships based on the Akaike information criterion (AIC). Pearson's correlations coefficients between all tested variables are listed in Table S2

The Shapiro-Wilk goodness-of-fit test was utilized to assess the normality of all variables. As recommended (Grace et al., 2016), all numerical variables, including aboveground C storage, species diversity, stand age, and DBH and height diversity indices, were natural-logarithm transformed and standardized in order to meet the assumptions of normality and linearity, and to allow comparisons among multiple predictors and models (Zuur et al., 2009).

For the selection of the best SEM, several tests were used to assess the model fit of all SEMs (Malaeb et al., 2000), i.e., the Chi-square (χ^2) test, goodness-of-fit index (GFI), comparative fit index (CFI), standardized root mean square residual (SRMR), and AIC. We used the χ^2 test, representing the maximum likelihood estimation, to assess how well the 48 hypothesized SEMs fit the data (Table S3). Indicators for a good model fit to the data included an insignificant ($P > 0.05$) χ^2 test statistic, SRMR < 0.05, and both GFI and CFI > 0.90 (Malaeb et al., 2000). Among all acceptable models, we selected those with the lowest AICs as our final models. Tree DBH diversity based on 8 cm, and height diversity based on the 2 m class were selected as the stand structural diversity (a latent variable), as this combination resulted in the SEM with the lowest AIC, with a *P*-value of the χ^2 test for the total model fit greater than 0.05 (Table S3). The SEMs based on combinations of 4 cm or 6 cm discrete classes for DBH diversity, and the 2 m class for height diversity were also accepted ($P > 0.05$), whereas the SEMs based on all other combinations of discrete classes for DBH and height diversity indices were rejected ($P < 0.05$; Table S3).

The indirect effect of a predictor was calculated by multiplying the standardized effects of all paths on one route, from one predictor to mediator, and then to aboveground C storage, while total effect was calculated by adding standardized direct and indirect effects (Grace et al., 2016). The SEM was implemented using the *lavaan* package (Rosseel, 2012) in R 3.2.2 (R Development Core Team, 2015).

3 Results

Bivariate relationships indicated that aboveground C storage increased with tree DBH diversity, height diversity, and stand age, but had no association with species diversity (Fig. 2). Both tree DBH diversity and height diversity increased with stand age, whereas none of the other bivariate relationships were statistically significant (Fig. 2).

The final SEMs with the three directions for the path between species diversity and stand structural diversity had a similar good-fit to the data (Fig. 3). These SEMs accounted for 82% of the variation in aboveground C storage, 55% to 59% of the variation in stand structural diversity, and 0.1% to 9% of the variation in species diversity (Fig. 3). Stand structural diversity had the strongest positive direct effect on aboveground C storage (β = 0.56, P = 0.001), followed by the positive effect of stand age (β = 0.41, P = 0.003), and negative effect of species diversity (β = -0.23, P < 0.001) in these SEMs (Table 1; Fig. 3). There was a significantly positive direct effect of stand age on stand structural diversity, but an insignificant effect on species diversity (Fig. 3). Species diversity and stand structural diversity had a significant positive direct effect on each other (Fig. 3)

Stand age had a strong indirect effect via stand structural diversity (β = 0.41, P = 0.002; Table 1) and insignificant indirect effects via species diversity (β = -0.10, P = 0.357) on aboveground C storage in all three SEMs (Fig. 3, Table 1). The indirect effects of stand structural diversity via species diversity were insignificant regardless of SEMs, while species diversity had a marginally significant positive indirect effect via stand structural diversity (β = 0.11, P = 0.059, Table 1). The total (direct + indirect) effects of stand age, stand structural diversity, and species diversity were 0.82, 0.56, and -0.12, respectively, on aboveground C storage (Fig. 3a; Table 1). In the alternative SEMs (Figs. 3b and 3c), the total effect of stand age, stand structural diversity, and species diversity on aboveground C storage were quite similar to the SEM in Fig. 3a (Table 1).

4 Discussion

To the best of our knowledge, this is the first study to analyze the multivariate relationships between aboveground C storage and its drivers (stand age, stand structural diversity, and species diversity) in secondary subtropical forests in China. We found a positive relationship between stand structural diversity and aboveground C storage, but a negative relationship between species diversity and aboveground C storage, while accounting for the considerable positive influence of stand age in our study. Our results revealed that the positive relationships reported in previous studies, between stand structural diversity and aboveground C storage, in boreal and temperate forest ecosystems (e.g., Dănescu et al., 2016; Zhang and Chen, 2015), may be extended to subtropical forests.

Our results indicated that tree DBH and height diversity indices were significantly positively related to aboveground C storage across plots; these relationships likely resulted from increased light capture and light use efficiencies in association with complex tree sized structures (Dănescu et al., 2016; Yachi and Loreau, 2007; Zhang and Chen, 2015). Forest communities possessing variable diameters and heights are likely to also have their own set of habitat requirements for water and soil nutrients (Lei et al., 2009; Wang et al., 2011). Our results, as well as those from previous studies, collectively suggest that a multilayered forest structure allows for the more efficient utilization of light, water, and soil nutrients at the stand level (Poorter et al., 2015), and as a result increases the aboveground C storage (Buongiorno et al., 1994; Dănescu et al., 2016; Wang et al., 2011; Zhang and Chen, 2015).

Our bivariate analysis indicated that there was minimal association between species diversity and aboveground C storage, while the result of the structural equation model showed that species diversity had a direct negative effect, augmented by a positive indirect effect, via stand structural diversity, yielding a negligible total effect of species diversity on aboveground C storage. Although forest productivity may increase with species richness and evenness (e.g., Zhang et al., 2012), the lack of positive effects of species diversity on aboveground C storage might be attributable to competitive exclusion (e.g., high stand biomass may exclude weak competitors) (Grace et al., 2016; Grime, 1973). Alternatively, the dominance of productive species has a potent impact on aboveground biomass or C storage

(Cardinale et al., 2011; Lasky et al., 2014; Prado-Junior et al., 2016; Tobner et al., 2016). Our findings of the positive indirect effect of species diversity via stand structural diversity, and stand structural diversity via species diversity on aboveground C storage were consistent with previous studies (Vilà et al., 2013; Zhang and Chen, 2015). These findings indicated that species diversity promoted stand structural diversity (Brassard et al., 2008; Zhang and Chen, 2015), and that stand structural diversity increased the coexistence of species (Clark, 2010), and in either case, increased aboveground C storage.

The strong positive contribution of stand age to aboveground C storage was attributable to cumulative tree growth over time (Lei et al., 2009; Poorter et al., 2016). Stand age may also indirectly impact aboveground C storage through directional changes in stand structural and/or species diversity that take place during the course of forest succession (Becknell and Powers, 2014; Zhang and Chen, 2015). As hypothesized, we found that stand age was significantly positively related to stand structural diversity, which had a strong direct effect on aboveground C storage. Our findings were consistent with the notion that complementarity effects increase over time via increasing stand structural diversity (Zhang and Chen, 2015).

In the forest stands under study, we found there to be a minimal direct impact of stand age on tree species diversity, and an indirect effect of stand age via species diversity on aboveground C storage. It remains intensely debated as to how stand age, as a measure of disturbance frequency, affects tree species diversity across forest landscapes with diverse localized conditions (Connell, 1978; Yeboah et al., 2016). For instance, disturbances of intermediate intensity may selectively remove specific species; hence, decrease species diversity (Yeboah and Chen, 2016). Our findings of the weak direct effect of stand age on species diversity, and indirect effect of stand age via species diversity on aboveground C storage, as well as the negative direct effect of species diversity on aboveground C storage, might have resulted from historical human disturbances, which may have selectively harvested productive species in the study region. Future research will be required to improve our conceptual model through the inclusion of the effects of disturbance history on tree species diversity and its influence on aboveground C storage.

5 Concluding remarks

Our study elucidated a number of complex relationships that exist among aboveground C storage, stand age, stand structural diversity, and species diversity, of secondary subtropical forests across Eastern China. We found that aboveground C storage increased with stand age and stand structural diversity; however, it was not altered via species diversity. Our structural equation model analysis indicated that stand age possessed the largest total positive effect, followed by stand structural diversity, on aboveground C storage, while the total effect of species diversity was negligible. The minimal total effect of species diversity on aboveground C storage in the forest stands under study might have been attributable to competitive exclusion, with high aboveground biomass, or historical logging preferences for productive species.

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Table 1. The direct, indirect, and total standardized effects on aboveground C storage based on structural equation models (SEMs). The indirect effect was calculated by multiplying the standardized effects of all paths on one route, from one predictor to mediator, and then to aboveground C storage, while the total effect was calculated by adding standardized direct and indirect effects, presented in Fig. 3.

Predictor	Pathway to aboveground C storage	Model 3a		Model 3b		Model 3c	
		Effect	*P*-value	Effect	*P*-value	Effect	*P*-value
Stand age	Direct effect	0.41	0.003	0.41	0.003	0.41	0.003
	Indirect effect via species diversity	-0.005	0.827	0.07	0.199	-0.005	0.827
	Indirect effect via stand structural diversity	0.41	0.002	0.41	0.002	0.41	0.002
	Total effect	0.82	<0.001	0.89	<0.001	0.82	<0.001
Species diversity	Direct effect	-0.23	<0.001	-0.23	<0.001	-0.23	<0.001
	Indirect effect via stand structural diversity	0.11	0.059	----	----	----	----
	Total effect	-0.12	0.056	-0.23	<0.001	-0.23	<0.001
Stand structural diversity	Direct effect	0.56	0.001	0.56	0.001	0.56	0.001
	Indirect effect via species diversity	----	----	-0.10	0.357	----	----
	Total effect	0.56	0.001	0.46	0.011	0.56	0.001

Figure Legends

Fig. 1 Conceptual models for the prediction of aboveground C storage in secondary subtropical forests of Eastern China, showing hypothesized relationships of how stand age impacts forest diversity, and how stand age and forest diversity concomitantly impact aboveground C storage. Forest diversity is characterized by the magnitude of relevant factors (e.g., species diversity) and their variations in forest stand structures (e.g., DBH and height diversity; a latent variable). Three conceptual models were proposed based on different direct effects of forest diversity components on each other; a) stand structural diversity → species diversity; b) species diversity → stand structural diversity; and c) species diversity ↔ stand structural diversity.

Fig. 2 Bivariate relationships between endogenous (dependent) and exogenous (independent) variables (n = 80), for all hypothesized causal paths in the final selected structural equation models (SEMs). All numerical variables were natural log-transformed and standardized. (a)-(d) Aboveground carbon (AGC) storage (Mg ha^{-1}) vs. height diversity (Hh, 2 m class), DBH diversity (Hd, 8 cm class), stand age (SA) and species diversity (Hs), respectively; (e-g) Diversity (Hh, Hd, and Hs) vs. stand age (SA); (h)-(i) DBH diversity (Hd, 8 cm class) and height (Hh, 2 m class) diversity vs. species diversity (Hs); and (j)-(k) species diversity (Hs) vs. DBH diversity (Hd, 8 cm class) and height (Hh, 2 m class) diversity. All fitted regressions are significant at $P < 0.001$ and the relationships without fitted lines are insignificant at $P > 0.05$.

Fig. 3 The final best-fit structural equation models (SEMs) relating aboveground C storage to stand age, stand structural diversity, and species diversity. Solid arrows represent significant ($P < 0.05$) paths and dashed arrows represent non-significant paths ($P > 0.05$). For each path the standardized regression coefficient is shown. R^2 indicates the total variation in a dependent variable that is explained by the combined independent variables. The final three SEMs have a similar good-fit to the data (Table S3).

Fig. 1

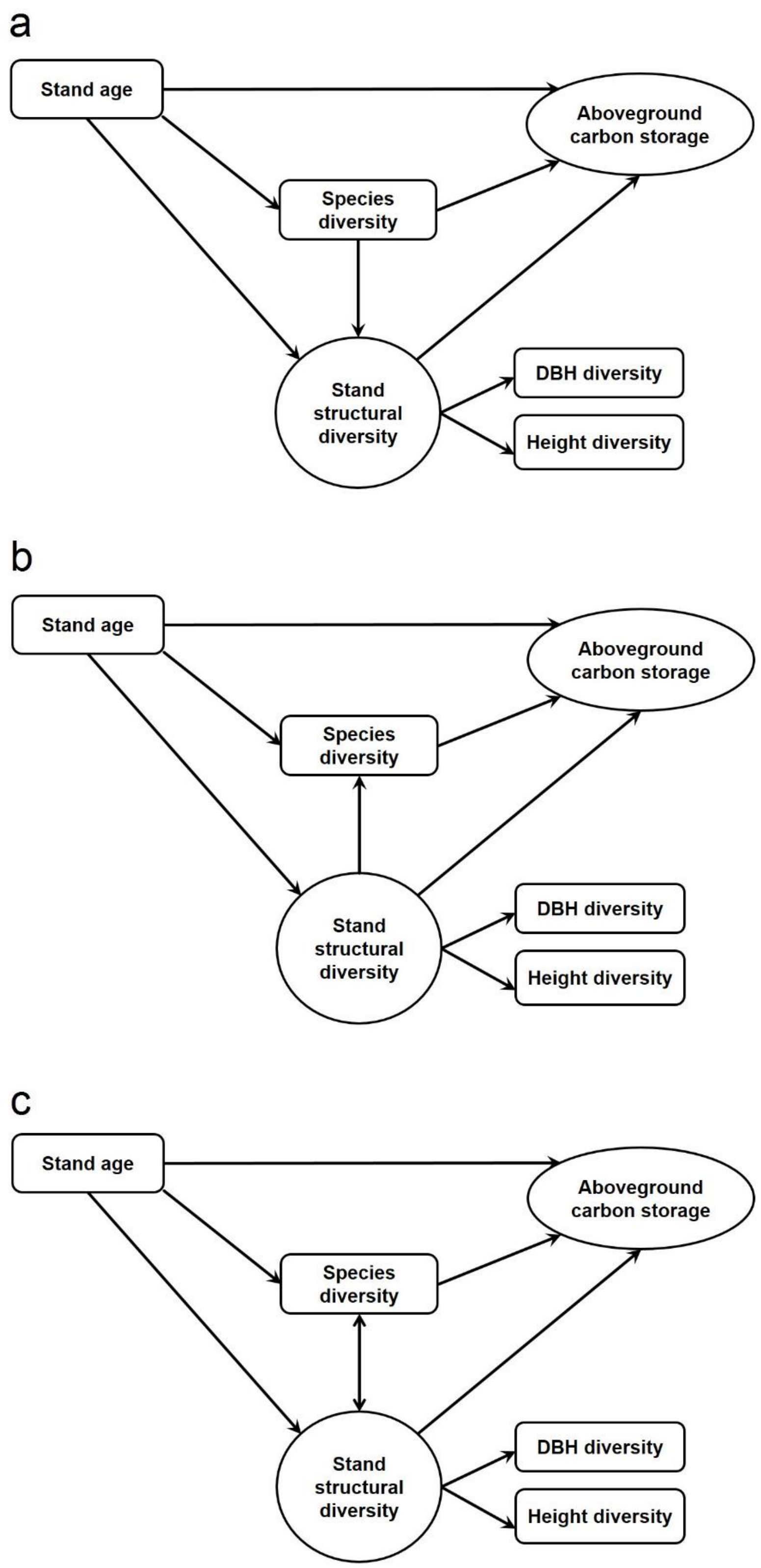

a
Stand age
Aboveground carbon storage
Species diversity
Stand structural diversity
DBH diversity
Height diversity
b
Stand age
Aboveground carbon storage
Species diversity
Stand structural diversity
DBH diversity
Height diversity
c
Stand age
Aboveground carbon storage
Species diversity
Stand structural diversity
DBH diversity
Height diversity

Fig. 2

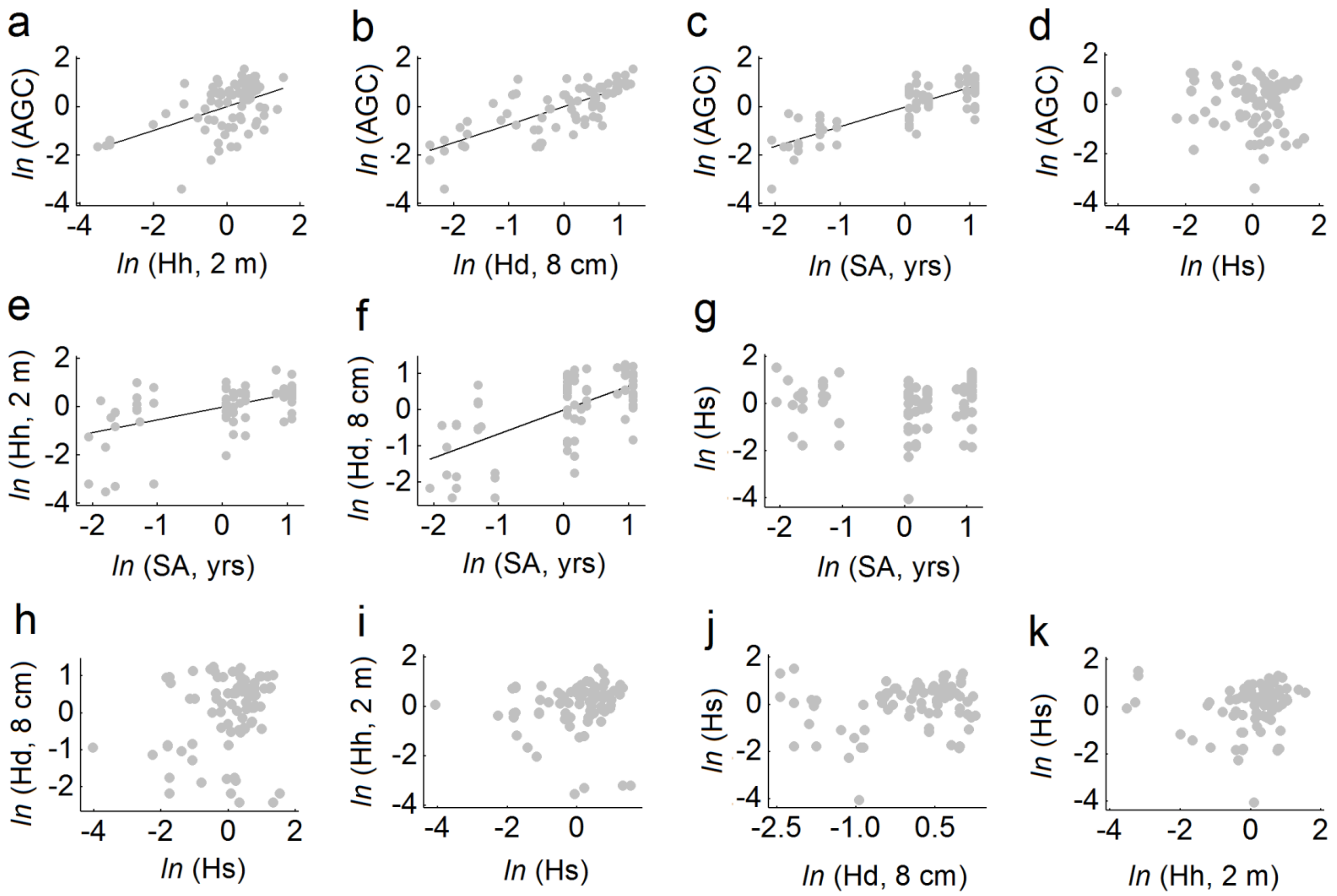
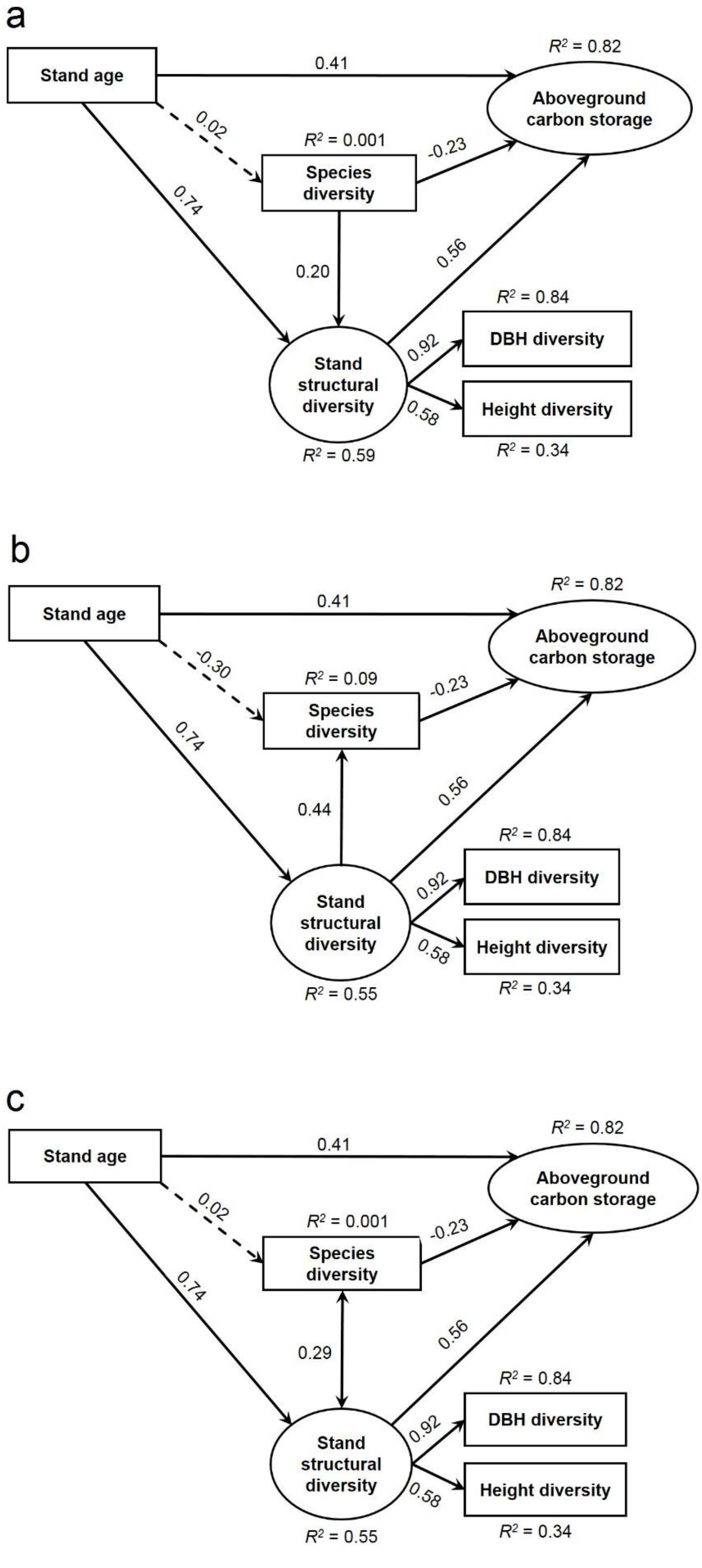

a
ln (AGC)
ln (Hh, 2 m)
b
ln (AGC)
ln (Hd, 8 cm)
c
ln (AGC)
ln (SA, yrs)
d
ln (AGC)
ln (Hs)
e
ln (Hh, 2 m)
ln (SA, yrs)
f
ln (Hd, 8 cm)
ln (SA, yrs)
g
ln (Hs)
ln (SA, yrs)
h
ln (Hd, 8 cm)
ln (Hs)
i
ln (Hh, 2 m)
ln (Hs)
j
ln (Hs)
ln (Hd, 8 cm)
k
ln (Hs)
ln (Hh, 2 m)

Fig. 3


a
Stand age
0.41
R² = 0.82
Aboveground carbon storage
0.02
R² = 0.001
-0.23
Species diversity
0.74
0.20
0.56
R² = 0.84
DBH diversity
0.92
Stand structural diversity
0.58
Height diversity
R² = 0.59
R² = 0.34
b
Stand age
0.41
R² = 0.82
Aboveground carbon storage
-0.30
R² = 0.09
-0.23
Species diversity
0.74
0.44
0.56
R² = 0.84
DBH diversity
0.92
Stand structural diversity
0.58
Height diversity
R² = 0.55
R² = 0.34
c
Stand age
0.41
R² = 0.82
Aboveground carbon storage
0.02
R² = 0.001
-0.23
Species diversity
0.74
0.29
0.56
R² = 0.84
DBH diversity
0.92
Stand structural diversity
0.58
Height diversity
R² = 0.55
R² = 0.34

Supplementary information

Table S1. Summary of plot variables used in the bivariate relationship and structural equation models (SEMs) for the quantification of forest diversity and aboveground C storage in the secondary subtropical evergreen broadleaved forests of Eastern China. *n* = 80; ln = natural log.

Variable	Unit	Transformation	Minimum	Maximum
Dependent variable				
Aboveground C (AGC) storage	Mg ha^{-1}	ln and standardized	-3.42	1.58
Explanatory variables				
Stand age (SA)	years	ln and standardized	-2.06	1.07
Tree species diversity (Hs)	unitless	ln and standardized	-4.06	1.54
Tree DBH diversity (Hd, 2 cm)	unitless	ln and standardized	-3.27	1.30
Tree DBH diversity (Hd, 4 cm)	unitless	ln and standardized	-3.02	1.14
Tree DBH diversity (Hd, 6 cm)	unitless	ln and standardized	-4.07	1.17
Tree DBH diversity (Hd, 8 cm)	unitless	ln and standardized	-2.44	1.26
Tree height diversity (Hh, 2 m)	unitless	ln and standardized	-3.53	1.55
Tree height diversity (Hh, 3 m)	unitless	ln and standardized	-4.20	1.22
Tree height diversity (Hh, 4 m)	unitless	ln and standardized	-2.87	1.70
Tree height diversity (Hh, 5 m)	unitless	ln and standardized	-4.16	1.45

DBH, tree diameter at breast height

Table S2. Pearson's correlation coefficients between variables used in this study for testing structural equation models (SEMs) of aboveground C storage. The highlighted gray portion in the table indicates the variables used in the selected SEMs (see Fig. 2). All variables were natural log transformed and standardized. Coefficients are significant at $P < 0.05$ (*), < 0.01 (**), and < 0.001 (***). See Table S1 for abbreviations and units of variables.

	Hs	Hh (2 m)	Hd (8 cm)	SA	AGC	Hh (3 m)	Hh (4 m)	Hh (5 m)	Hd (2 cm)	Hd (4 cm)	Hd (6 cm)
Hs											
Hh (2 m)	0.05										
Hd (8 cm)	0.21	0.53***									
SA	0.02	0.52***	0.66***								
AGC	-0.10	0.49***	0.74***	0.82***							
Hh (3 m)	-0.06	0.94***	0.59***	0.56***	0.50***						
Hh (4 m)	0.02	0.89***	0.58***	0.60***	0.53***	0.90***					
Hh (5 m)	-0.02	0.80***	0.60***	0.59***	0.51***	0.84***	0.87***				
Hd (2 cm)	0.28*	0.40***	0.80***	0.51***	0.62***	0.38***	0.34***	0.38***			
Hd (4 cm)	0.27*	0.50***	0.94***	0.63***	0.71***	0.52***	0.52***	0.56***	0.93***		
Hd (6 cm)	0.24*	0.42***	0.89***	0.61***	0.69***	0.45***	0.47***	0.50***	0.87***	0.95***	

Table S3. Model selection of good-fit structural equation model (SEM) for aboveground carbon storage. Model fit summary, particularly AIC, was employed to determine the best-fit SEM model. Selected models, based on three conceptual models in the study, are highlighted in bold. All possible combinations of discrete classes for DBH and height diversity along with stand age and species diversity were tested. (see Figure 1 for conceptual models). df: degrees of freedom; CFI: comparative fit index; GFI: goodness of fit index; SRMR: standardized root mean square residual; AIC: Akaike information criterion; R^2 indicates the total variation in aboveground C storage that is explained by the combined independent variables. Note: df is based on the number of 'knowns' minus the number of free parameters in the model, not on the sample size.

Conceptual model	Discrete classes used for stand structure indices		df	Model fit summary						Model remarks based on chi-square test, selection based on lowest AIC and other parameters
	Height (class in m)	DBH (class in cm)		CFI	GFI	SRMR	AIC	R^2	Chi-square (P-value)	
1a	2	2	2	0.97	0.97	0.05	33.25	0.88	7.25 (0.027)	Rejected
1b	2	2	2	0.97	0.97	0.05	33.25	0.88	7.25 (0.027)	Rejected
1c	2	2	2	0.97	0.97	0.05	33.25	0.88	7.25 (0.027)	Rejected
1a	2	4	2	0.98	0.98	0.04	31.27	0.83	5.27 (0.072)	Accepted
1b	2	4	2	0.98	0.98	0.04	31.27	0.83	5.27 (0.072)	Accepted
1c	2	4	2	0.98	0.98	0.04	31.27	0.83	5.27 (0.072)	Accepted
1a	2	6	2	0.99	0.98	0.04	30.20	0.90	4.20 (0.123)	Accepted
1b	2	6	2	0.99	0.98	0.04	30.20	0.90	4.20 (0.123)	Accepted
1c	2	6	2	0.99	0.98	0.04	30.20	0.90	4.20 (0.123)	Accepted
1a	**2**	**8**	**2**	0.99	0.98	0.03	**30.18**	**0.82**	**4.18 (0.124)**	**Accepted & selected**
1b	**2**	**8**	**2**	0.99	0.98	0.03	**30.18**	**0.82**	**4.18 (0.124)**	**Accepted & selected**
1c	**2**	**8**	**2**	0.99	0.98	0.03	**30.18**	**0.82**	**4.18 (0.124)**	**Accepted & selected**
1a	3	2	2	0.92	0.94	0.07	40.87	0.88	14.87 (0.001)	Rejected
1b	3	2	2	0.92	0.94	0.07	40.87	0.88	14.87 (0.001)	Rejected
1c	3	2	2	0.92	0.94	0.07	40.87	0.88	14.87 (0.001)	Rejected
1a	3	4	2	0.94	0.94	0.07	39.78	0.80	13.78 (0.001)	Rejected
1b	3	4	2	0.94	0.94	0.07	39.78	0.80	13.78 (0.001)	Rejected
1c	3	4	2	0.94	0.94	0.07	39.78	0.80	13.78 (0.001)	Rejected
1a	3	6	2	0.95	0.95	0.06	37.45	0.83	11.45 (0.003)	Rejected
1b	3	6	2	0.95	0.95	0.06	37.45	0.83	11.45 (0.003)	Rejected
1c	3	6	2	0.95	0.95	0.06	37.45	0.83	11.45 (0.003)	Rejected
1a	3	8	2	0.95	0.94	0.07	38.75	0.78	12.75 (0.002)	Rejected
1b	3	8	2	0.95	0.94	0.07	38.75	0.78	12.75 (0.002)	Rejected
1c	3	8	2	0.95	0.94	0.07	38.75	0.78	12.75 (0.002)	Rejected
1a	4	2	2	----	----	----	----	----	----	Bad-fit
1b	4	2	2	----	----	----	----	----	----	Bad-fit

1c	4	2	2	----	----	----	----	----	----	Bad-fit
1a	4	4	2	0.96	0.95	0.05	36.45	0.83	10.45 (0.005)	Rejected
1b	4	4	2	0.96	0.95	0.05	36.45	0.83	10.45 (0.005)	Rejected
1c	4	4	2	0.96	0.95	0.05	36.45	0.83	10.45 (0.005)	Rejected
1a	4	6	2	0.96	0.96	0.05	34.75	0.87	8.75 (0.013)	Rejected
1b	4	6	2	0.96	0.96	0.05	34.75	0.87	8.75 (0.013)	Rejected
1c	4	6	2	0.96	0.96	0.05	34.75	0.87	8.75 (0.013)	Rejected
1a	4	8	2	0.96	0.96	0.04	35.44	0.81	9.44 (0.009)	Rejected
1b	4	8	2	0.96	0.96	0.04	35.44	0.81	9.44 (0.009)	Rejected
1c	4	8	2	0.96	0.96	0.04	35.44	0.81	9.44 (0.009)	Rejected
1a	5	2	2	0.93	0.94	0.07	41.01	0.91	15.01 (0.001)	Rejected
1b	5	2	2	0.93	0.94	0.07	41.01	0.91	15.01 (0.001)	Rejected
1c	5	2	2	0.93	0.94	0.07	41.01	0.91	15.01 (0.001)	Rejected
1a	5	4	2	0.94	0.94	0.07	40.81	0.79	14.81 (0.001)	Rejected
1b	5	4	2	0.94	0.94	0.07	40.81	0.79	14.81 (0.001)	Rejected
1c	5	4	2	0.94	0.94	0.07	40.81	0.79	14.81 (0.001)	Rejected
1a	5	6	2	0.95	0.95	0.06	38.27	0.81	12.27 (0.002)	Rejected
1b	5	6	2	0.95	0.95	0.06	38.27	0.81	12.27 (0.002)	Rejected
1c	5	6	2	0.95	0.95	0.06	38.27	0.81	12.27 (0.002)	Rejected
1a	5	8	2	0.95	0.94	0.06	39.71	0.79	13.07 (0.001)	Rejected
1b	5	8	2	0.95	0.94	0.06	39.71	0.79	13.07 (0.001)	Rejected
1c	5	8	2	0.95	0.94	0.06	39.71	0.79	13.07 (0.001)	Rejected