

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

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25 **Contribution of the co-authors:** AA, ERY and HYHC conceived and designed the study. ERY coordinated the
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Abstract

30 Stand structural diversity, typically characterized by variances in tree diameter at breast height (DBH) and height, plays an important role in influencing aboveground 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 and tree species, DBH and height diversities, 35 were determined across 80 subtropical forest plots in Eastern China. We used structural equation modeling (SEM) to test for direct and indirect effects of 48 combinations of discrete classes of DBH diversity (2, 4, 6 and 8 cm classes) and height diversity (2, 3, 4 and 5 m classes), species diversity and stand age on aboveground C storage. The three selected SEMs with any direction for the path between species diversity and stand structural diversity had a 40 similar goodness of fit to the data. The three SEMs explained 82% of the variation in aboveground C storage, 55-59% of the variation in stand structural diversity and negligible variation in species diversity. Stand structural diversity had the strongest direct and positive effect on aboveground C storage ($\beta = 0.56$, $P = 0.001$), followed by a positive effect of stand age ($\beta = 0.41$, $P = 0.003$) and a negative effect of species diversity ($\beta = -0.23$, $P < 0.001$). 45 Stand age had also a strong effect on stand structural diversity ($\beta = 0.74$, $P < 0.001$), but a weak effect on species diversity. Our analyses suggest that stand structural diversity is a major determinant for the variation in aboveground C storage in the secondary subtropical forests in Eastern China. Maintaining tree DBH diversity and height diversity through silvicultural operations could be an effective approach for enhancing aboveground C storage 50 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 play a critical role in global carbon (C) cycling, capture more C than previously thought (Yu et al., 2014). Despite their importance (Niu et al., 2012; Wang et al., 2014), we still lack a complete understanding of how aboveground C storage vary with stand age, and changes in species diversity and stand structural diversity in these forests (see the conceptual models in Fig. 1). Aboveground C storage in forest ecosystems is directly impacted by tree species diversity and stand structural diversity (Dănescu et al., 2016; Wang et al., 2011). In addition, stand age, as an indicator for stand development following disturbances, has been identified as a primary factor that influences aboveground biomass (AGB) in both even-aged (Böttcher et al., 2008) and uneven-aged (Becknell and Powers, 2014; Poorter et al., 2016) forest stands. Moreover, variability in stand structural diversity and species diversity depends to a large extent on stand age (Lei et al., 2009; Wang et al., 2011; Zhang and Chen, 2015). Therefore, stand age may directly and indirectly affect aboveground C storage, via changes in stand structural diversity and species diversity in forest ecosystems (Fig. 1). Surprisingly few studies have teased apart the direct and indirect effects of stand age, species diversity and stand structural diversity on aboveground C storage in complex natural forests (but see Dănescu et al., 2016; Zhang and Chen, 2015).

There has been a reinvigorated research interest on how AGB (thus aboveground C storage) varies with stand age, species composition, and abiotic factors, in both managed plantations and natural secondary forests (Becknell and Powers, 2014; Clark and Clark, 2000; Poorter et al., 2016; Zhang et al., 2012); however, discrepancies among studies remain unresolved. For instance, some studies have documented that the relationship between species diversity and AGB was either positive (Dayamba et al., 2016; Wang et al., 2011; Zhang and Chen, 2015), negative (Szwagrzyk and Gazda, 2007), or non-significant (Vilà et

al., 2003). We hypothesize that species diversity has a direct effect on aboveground C storage in subtropical forests (Fig. 1a). Species diversity may also affect aboveground C storage via stand structural diversity (Poorter et al., 2015; Zhang and Chen, 2015).

The importance of stand structural diversity to aboveground C storage has recently been recognized (e.g., Dănescu et al., 2016; Poorter et al., 2015; Zhang and Chen, 2015). Multi-layered stand structure may be theorized to enhance light capture and increase light use efficiency (Yachi and Loreau, 2007). Stand structural diversity, which varies strongly within communities (due to disturbances) and across communities (due to environmental gradients), may have a large direct effect on aboveground C storage (Poorter et al., 2015). Stand structure attributes such as tree size (DBH and/or height) inequality among and within species are critical toward maintaining species diversity (Clark, 2010), and in turn affect aboveground C storage (Fig. 1a; Zhang and Chen, 2015). The effects of tree species diversity on aboveground C storage may be partly attributable to stand structural diversity because tree size variation helps maintain species diversity (Fig. 1b; Clark, 2010). Alternatively, species diversity and stand structural diversity provide positive feedback to each other (Fig. 1c).

The influence of species and structural diversity on aboveground C storage or productivity remains debated (e.g., Dănescu et al., 2016; Poorter et al., 2015), in part because a well-documented coupling factor such as stand age, which is a critical driver for individual species dynamics, aboveground C storage and productivity (Zhang and Chen, 2015), has not often been explicitly considered. We hypothesize that stand age has a strong influence on aboveground C storage, species diversity and structural diversity in secondary subtropical forests. The effects of stand age may be direct (Becknell and Powers, 2014) or indirect, via stand structural diversity and/or species diversity, on aboveground C storage (Fig. 1).

In this study, we aim to investigate the effects of stand structural diversity and species diversity on aboveground C storage, while accounting for the effects of stand age. We used

structural equation models (SEMs; Grace et al., 2016) to analyze data from 80 structurally
diverse and mixed subtropical forest plots in Eastern China. Specifically, we tested the
105 following 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 diversity and/or species diversity, and 3) the direct and indirect effects of
stand structural diversity and species diversity on aboveground C storage (Fig. 1). Because of
the complex interactions between species diversity and stand structural diversity (Clark,
110 2010; Zhang and Chen, 2015), we tested the influence of stand structural diversity and
species diversity on each other (Fig. 1c).

2 Materials and methods

2.1 Study site, plots and forest structure

115 The study was conducted in the lower eastern extension of the Tiantai and Siming Mountains
(29°41-50 N, 121°36-52 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
120 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 in the study area, including Tiantong National Forest Park,
125 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 by typhoon, and different

intensities of human disturbances in the history, but has been protected from anthropogenic activities for the last more than 25 years. Consequently, forests in the region contained stands with different levels of degradation (Wang et al., 2007; Yan et al., 2009). Although forests in the study areas are thought to be 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 have naturally recovered without human disturbances for more than three decades in the study areas. 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 plots was carried out through forest inventory and ground based survey, which were conducted between 2010 and 2013, 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. We acknowledge that our plot sizes were quite small; however, similar to other regions, secondary forest patches often occur in smaller tracts than is the case with primary forests (Becknell and Powers, 2014).

In each plot, the basal diameter (diameter at 5 cm above root collar) and DBH were measured for trees taller than 1.50 m, while the basal diameter and diameter at 45 cm above the ground were measured (with a diameter tape) for trees that were shorter than 1.50 m. Total tree height for each tree was measured with a telescopic pole for the height of up to 15 m, and with a clinometer for heights of >15 m. The studied plots had 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, with evergreen species such as *Choerospondias axillaris* and *Schima*

superba dominating in the premature forests, while *Castanopsis fargesii* and *Castanopsis carlesii* dominated in the mature forests.

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2.2 Estimation of aboveground carbon storage

The AGB of individual tree (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).

$$160 \quad \text{AGB}_t = 0.0673 \times (\rho \times \text{DBH}^2 \times H)^{0.976} \quad \text{eqn 1}$$

We estimated AGB of individual shrubs and small trees having DBH < 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).

$$\text{AGB}_s = 1.460 \times \exp\{-3.23 + 2.17 \times \ln(D)\} \quad \text{eqn 2}$$

165 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 Explanatory variables

170 Our conceptual models include four explanatory variables for predicting aboveground C storage (Fig. 1): stand age, species diversity, DBH diversity and height diversity. In this study, stand age represents the number of years since the stand replacing disturbance (e.g., Wang et al., 2007; Yan et al., 2009). The official records of Ningbo Forestry Bureau, Zhejiang Province, were reviewed to collect relevant data about the disturbances in the study
175 area.

We used the Shannon-Wiener biodiversity index to quantify tree species, DBH and height diversities (Magurran, 2004). We quantified tree-size variation (i.e., tree DBHs and heights)

within each plot as structural diversity at the stand level. With the Shannon–Wiener index, DBH and height were grouped into different discrete classes in order to evaluate which combination of discrete classes for DBH and height diversities best predict 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 in order to assess the different variations in DBH and height diversities. Similar to species diversity, DBH diversity and height diversity were calculated by replacing the number of species with the number of DBH or height classes of tree individuals. Based on basal area proportions, tree species, DBH and height diversities were calculated for each plot using equations 3, 4 and 5, respectively (Buongiorno et al., 1994; Magurran, 2004; Staudhammer and LeMay, 2001).

$$H_s = - \sum_{i=1}^s p_i \times \ln(p_i) \quad \text{eqn 3}$$

$$H_d = - \sum_{j=1}^d p_j \times \ln(p_j) \quad \text{eqn 4}$$

$$H_h = - \sum_{k=1}^h p_k \times (\ln p_k) \quad \text{eqn 5}$$

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 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 affect the prediction of aboveground C storage, we tested 48 SEMs

using 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 (Fig. 1).

For the interpretation of results (Grace et al., 2016), we conducted bivariate relationships between each 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 regression and multiple linear regressions by adding quadratic and cubic polynomial terms to test for bivariate relationships of aboveground C storage with each of stand age, species diversity, and DBH and height diversities based on their various discrete classes. We also tested the bivariate relationships between stand age and species diversity, and DBH and height diversities based on their various discrete classes. Our analyses indicated that simple linear regression analysis was the best in describing bivariate relationships based on the Akaike information criterion (AIC). A summary of variables used in the statistical analyses is listed in Table S1. Bivariate relationships for all hypothesized causal paths in the final SEMs are shown in Fig. 2 and Pearson's correlations coefficients between all tested variables are listed in Table S2.

Shapiro-Wilk goodness-of-fit test was used to assess the normality for all variables. As recommended (Grace et al., 2016), all numerical variables including aboveground C storage, species diversity, stand age, and DBH and height diversities 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. 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., 230 2016). The SEM was implemented using the *lavaan* package (Rosseel, 2012) in R 3.2.2 (R Development Core Team, 2015).

3 Results

Tree DBH diversity based on 8 cm and height diversity based on 2 m class were selected as 235 the stand structural diversity (a latent variable) because this combination resulted in the best-fit SEM that had the lowest AIC, with a P -value of χ^2 test for the overall model fit greater than 0.05 (Table S3; Fig. 3). The SEMs based on combinations of 4 cm or 6 cm discrete class for DBH diversity and 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 diversities 240 were rejected ($P < 0.05$; Table S3).

The selected 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; Table S3). The three final SEMs all accounted for 82% of the variation in aboveground C storage, 55% to 59% of the variation in stand structural diversity and negligible variation in species diversity (Fig. 3). 245 Stand structural diversity had the strongest positive direct effect on aboveground C storage ($\beta = 0.56$, $P = 0.001$), followed by positive effect of stand age ($\beta = 0.41$, $P = 0.003$) and negative effect of species diversity ($\beta = -0.23$, $P < 0.001$) 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 in these SEMs (Fig. 3). Species diversity and stand 250 structural diversity had a significant positive direct effect on each other (Fig. 3) Stand age had a strong indirect effect via stand structural diversity ($\beta = 0.41$, $P = 0.002$; Table 1) and insignificant indirect effects via species diversity ($\beta = -0.10$, $P = 0.357$) 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 ($\beta = 0.11$, $P = 0.059$, 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 almost similar to 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 strong positive influence of stand age in our study. Our results indicate 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) can be extended to subtropical forests.

Our results showed that tree DBH and height diversities were strongly positively related with aboveground C storage across plots; those relationships likely resulted from increased light capture and light use efficiencies in association with complex tree size structures (Dănescu et al., 2016; Zhang and Chen, 2015). Forest communities possessing different diameters and heights may also have their own set of habitat requirements for water and soil nutrients (Wang et al., 2011). The maintenance of high stand structural diversity supports

species may increase complementarity effects (Lei et al., 2009). Our results and those from previous studies collectively suggest that a multilayered forest structure allows for more efficient utilization of light, water and soil nutrients at the stand level (Poorter et al., 2015), and as a result increases the accumulation of aboveground C storage (Buongiorno et al., 1994; Wang et al., 2011; Zhang and Chen, 2015).

We found that species diversity had an insignificant negative relationship with aboveground C storage in our studied forests. Although AGB is expected to increase with species richness and evenness (e.g., Zhang et al., 2012), the lack of positive effect of species diversity on aboveground C storage might be attributable to species redundancy in the studied forests. Since forests in the study area are already diverse, an increase in species richness may lead to niche overlap, instead of niche differentiation, causing negative interspecific interactions through competition (Walker, 1992). Moreover, in contrast with previous studies that have showed strong indirect effects of species diversity via stand structural diversity, or indirect effect of stand structural diversity via species diversity, on aboveground C storage or productivity (Vilà et al., 2013; Zhang and Chen, 2015), our study showed weak associations between species diversity and stand structural diversity, indicating that intraspecific size variation is the primary cause for stand structural diversity (Clark, 2010) and its positive effects on aboveground C storage in our study forests.

The strong positive contribution of stand age to aboveground C storage is attributable to the accumulation of tree growth and increased structural complexity over time. Stand age can also indirectly impact aboveground C storage through the directional changes in stand structural and/or species diversity during 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 are consistent with the idea that the complementarity

effects increase through time via increasing stand structural diversity (Zhang and Chen, 2015).

305 We found little direct effect of stand age on tree species diversity and indirect effect of stand age via species diversity on aboveground C storage in our study forests. It is highly debated how stand age as a measure of disturbance frequency affects tree species diversity across forest landscapes with diverse local site conditions (Yeboah et al., 2016). For instance, disturbances of intermediate intensity may selectively remove specific species, and hence
310 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 might have selectively harvested certain species in the study region. Future research is needed to
315 improve our conceptual model by including the effects of disturbance history on tree species diversity and its influence on aboveground C storage.

5 Conclusions

This study has presented and articulated the inherent complexities of variation, as relates to
320 aboveground C storage, by utilizing stand age, stand structural diversity and species diversity of secondary subtropical forests across eastern China. We found that 82% of variations in aboveground C storage could be explained by stand characteristics in these heterogeneously aged forests. Stand age had strong direct effect on stand structural diversity but weak effect on species diversity, and therefore strongly indirectly affect, via stand structural diversity,
325 aboveground C storage. Stand structural diversity is a major determinant for the variation in aboveground C storage in the secondary subtropical forests in Eastern China. Maintaining

tree DBH diversity and height diversity through silvicultural operations could be an effective approach for enhancing aboveground C storage in these forests.

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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	<i>P</i> -value	Effect	<i>P</i> -value	Effect	<i>P</i> -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 predicting aboveground C storage in secondary subtropical forests in Eastern China, showing hypothesized relationships of how does stand age affect forest diversity, and how do stand age and forest diversity together affect aboveground C storage. Forest diversity is characterized by their magnitude (e.g., species diversity) and variation in stand structure (e.g., DBH and height diversity; a latent variable). Three conceptual models are 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 other fitted regressions are significant at $P < 0.001$ with exception of fitted regressions in panels' (d), (g), (h)-(k) ($P > 0.05$).

Fig. 3 The final best-fit structural equation models (SEMs) relating aboveground C storage to stand age and forest diversity (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. Final SEMs (a, b and c) are consistent with conceptual models in Figure 1. The summary of model selection of best-fit SEM for aboveground C storage is provided in Table S3.

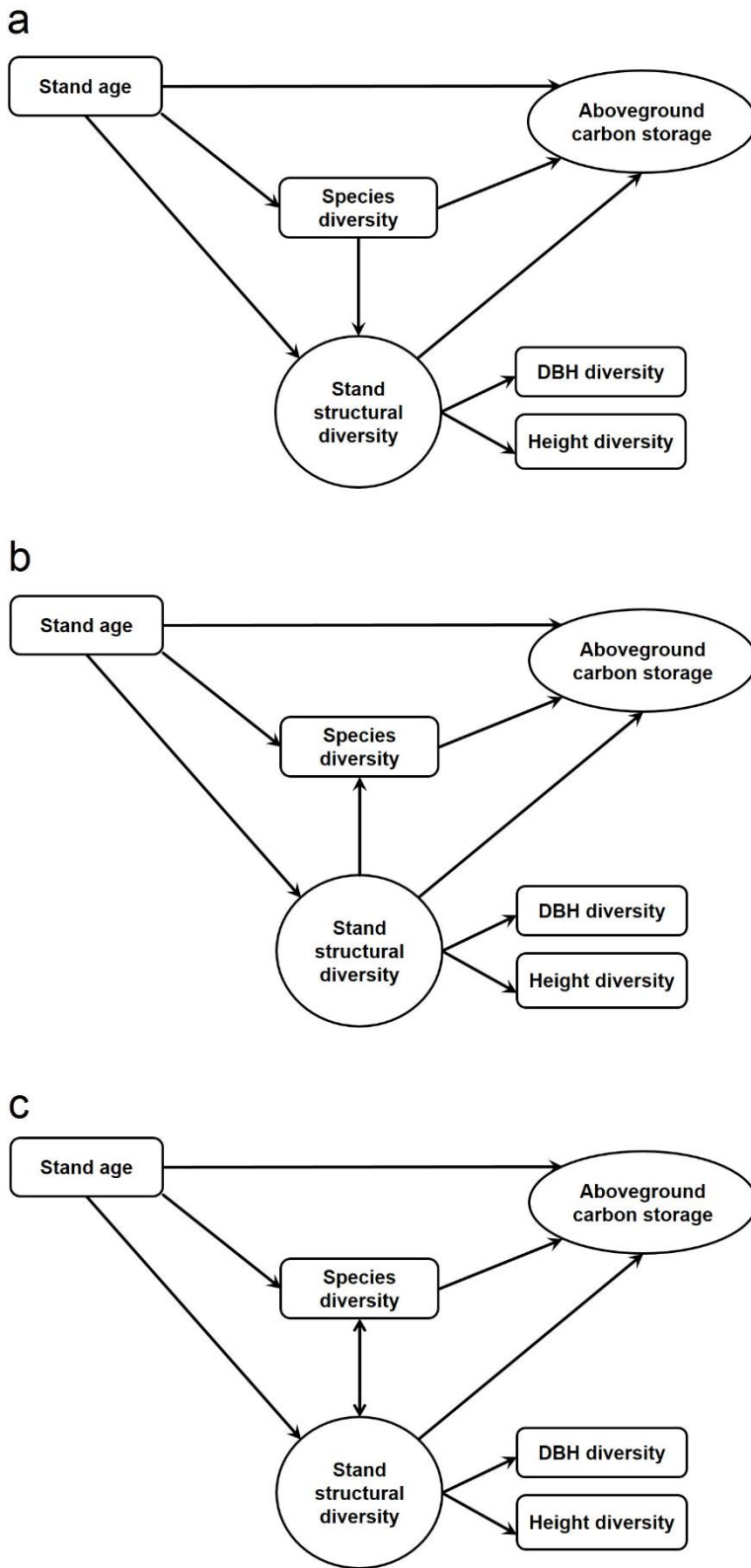


Fig. 2

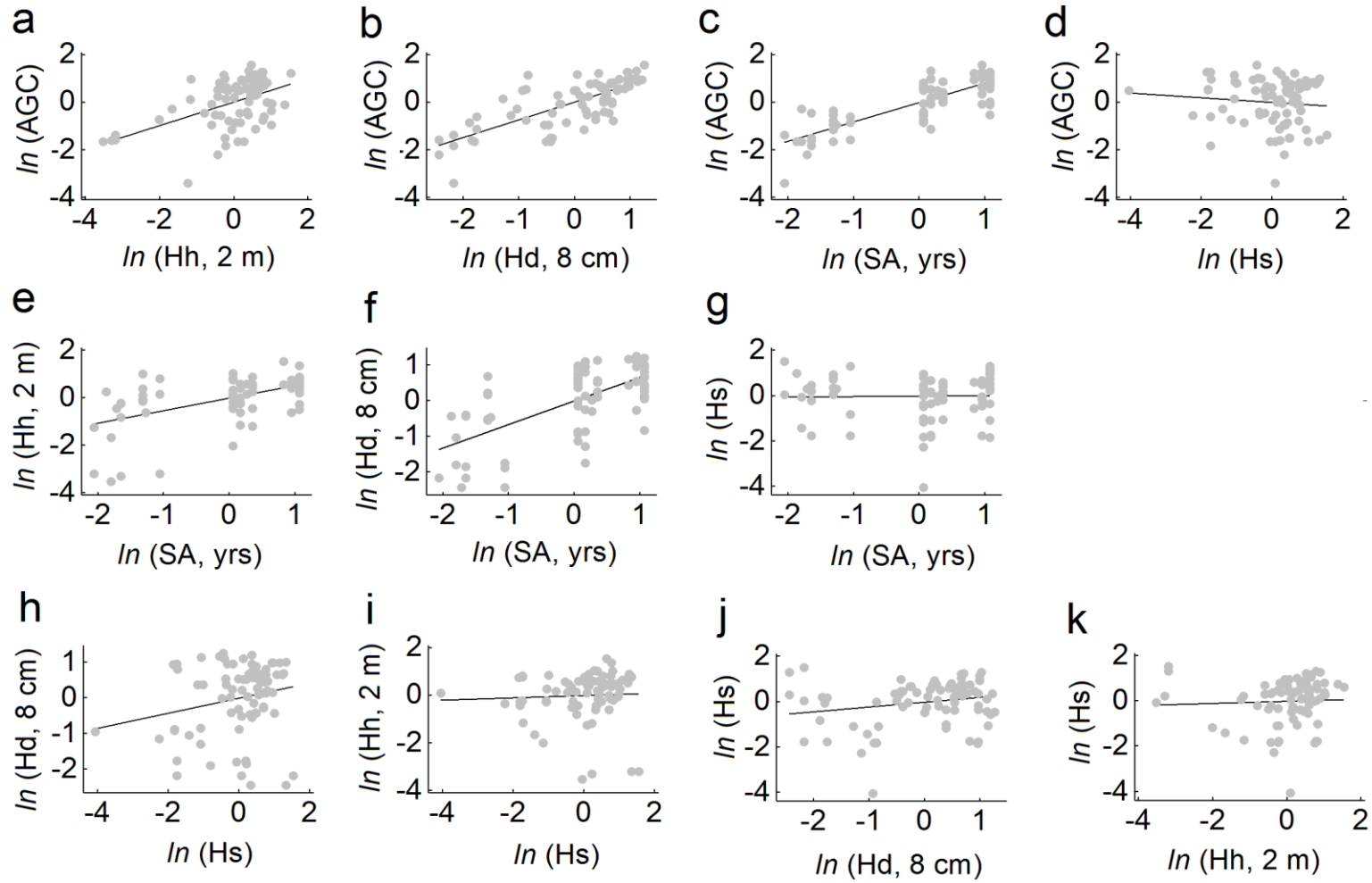


Fig. 3

