

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

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19 **Running title:** Forest diversity and aboveground carbon storage

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21 Text pages: (without references, and Tables and Figures): 15

22 Tables: 1      Figures: 3      References: 41

23 Supplementary information: Tables: 3

24

25 **Contribution of the co-authors:** AA, ERY, and HYHC conceived and designed the study. ERY coordinated  
26 the research project. AA, YTZ, XDY, and MSX conducted sampling design, field and lab work. AA analyzed  
27 the data. AA and ERY wrote the paper. HYHC and SXC reviewed, commented on and edited the drafts. All co-  
28 authors reviewed and approved the final manuscript.

29 The authors declare that they have no conflict of interest.

30

## 31 **Abstract**

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

56 **Key words:** biodiversity; carbon storage; evergreen broadleaved forests; species diversity;

57 stand structure; structural equation model.

58

## 59 **1 Introduction**

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

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

74 Multilayered stand structures have been theorized to increase the capture and efficient  
75 utilization of light (Yachi and Loreau, 2007), and empirical evidence has indicated that stand  
76 structural diversity is positively associated with aboveground biomass or C storage. Hence,  
77 we hypothesized that stand structural diversity has a positive direct effect on the aboveground  
78 C storage (Fig. 1a). On the other hand, the direct relationships between species diversity and  
79 aboveground biomass or C, have been reported to be either positive (Dayamba et al., 2016;  
80 Wang et al., 2011), negative (Szwagrzyk and Gazda, 2007), or insignificant (Vilà et al.,  
81 2003). A recent analysis suggests that tree species diversity increases structural diversity of a  
82 stand, and as a consequence, enhances the aboveground biomass (Zhang and Chen, 2015). In  
83 the meantime, both stand structure and species diversity are influenced by stand age

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

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

101

## 102 **2 Materials and methods**

### 103 **2.1 Study area, sites, and plots**

104 This study was conducted in the lower eastern extension of the Tiantai and Siming Mountains  
105 (29°41-50'N, 121°36-52'E) located near Ningbo City, Zhejiang Province, in Eastern China.  
106 This region has a typical subtropical monsoon climate with a hot and humid summer and a  
107 dry cold winter. The highest peak in this area reaches 800 m above sea level, while most  
108 other reliefs are in the 70-500 m range (Yan et al., 2013). The soils in these areas were

109 classified as Ferralsols according to the FAO soil classification system (World Reference  
110 Base for Soil Resources, 2006), with the parent materials consisting mostly of Mesozoic  
111 sedimentary rocks, some acidic igneous rocks, and granite residual weathered material (Yan  
112 et al., 2013).

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

124         We selected stands that had recovered naturally from logging in the study areas, with no  
125 human disturbances for more than three decades. We established a total of 80 plots, including  
126 young forests ( $n = 21$ ), premature forests ( $n = 39$ ), and mature forests ( $n = 20$ ) (Yan et al.,  
127 2013). The measurement of the plots was carried out through forest inventories and ground  
128 based surveys, which were conducted between 2010 and 2013, and based on Forestry  
129 Standards for 'Observation Methodology for Long-term Forest Ecosystem Research' of the  
130 People's Republic of China (LY/T 1952-2011). Each plot ( $20 \times 20$  m) was located at a  
131 distance of least 100 m from stand edges in order to minimize edge effects. For each sample  
132 stand, we determined the stand age as the number of years since the last stand replacing  
133 disturbance, i.e., clearcut harvesting (e.g., Wang et al., 2007; Yan et al., 2009). The official

134 records of the Ningbo Forestry Bureau, Zhejiang Province, were reviewed to extract stand  
135 age data.

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

146

## 147 **2.2 Estimation of aboveground carbon storage**

148 The AGB of individual trees (AGB<sub>t</sub>) having DBH ≥ 5 cm was calculated using the general  
149 allometric equation (Eq. (1):Chave et al., 2014) based on tree DBH (cm), height (H, m) and  
150 species' wood density (ρ, g cm<sup>-3</sup>).

$$151 \quad \text{AGB}_t = 0.0673 \times (\rho \times \text{DBH}^2 \times H)^{0.976} \quad (1)$$

152 We estimated the AGB of individual shrubs and small trees having a DBH of < 5 cm  
153 (AGB<sub>s</sub>) using a multi-species allometric equation (developed locally; Eq. (1)), based on  
154 DBH, height and species' wood density (Ali et al., 2015).

$$155 \quad \text{AGB}_s = 1.460 \times \exp\{-3.23 + 2.17 \times \ln(D)\} \quad (2)$$

156 The total AGB per plot was the sum of the AGB<sub>t</sub> and AGB<sub>s</sub>. Subsequently, we converted  
157 AGB to aboveground C storage (Mg ha<sup>-1</sup>) by multiplying AGB with a conversion factor of  
158 0.5, assuming that 50% of the total tree biomass is C (Dixon et al., 1994).

159

### 160 **2.3 Quantification of species diversity and stand structural diversity**

161 We used the Shannon-Wiener biodiversity index to quantify tree species diversity (Magurran,  
162 2004) and tree-size variations (i.e., tree DBHs and heights) within each plot as stand  
163 structural diversity. With the Shannon-Wiener index, the DBH and height were grouped into  
164 different discrete classes in order to evaluate which combination of discrete classes for DBH  
165 and height diversity indices best predicted aboveground C storage in secondary subtropical  
166 forests. For DBH, 2, 4, 6, and 8 cm classes were tested, while for height, 2, 3, 4, and 5 m  
167 classes were tested. Tree species, DBH and height diversity indices were calculated for each  
168 plot using Eq. (3), (4), and (5), respectively (Buongiorno et al., 1994; Magurran, 2004;  
169 Staudhammer and LeMay, 2001). Similar to other studies in forests (Finegan et al., 2015;  
170 Prado-Junior et al., 2016; Zhang and Chen, 2015), we used the relative basal area to represent  
171 the proportions of individual species, DBH class, or height class within each sample plot,

$$172 \quad H_s = -\sum_{i=1}^s p_i \times \ln(p_i) \quad (3)$$

$$173 \quad H_d = -\sum_{j=1}^d p_j \times \ln(p_j) \quad (4)$$

$$174 \quad H_h = -\sum_{k=1}^h p_k \times (\ln p_k) \quad (5)$$

175 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  
176 height classes, respectively, while  $s$ ,  $d$ , and  $h$  are the number of tree species, DBH classes,  
177 and height classes, respectively. The calculations on the Shannon-Weiner indices were  
178 performed using the *vegan* package for the R 3.2.2 (Oksanen et al., 2015; R Development  
179 Core Team, 2015).

180

### 181 **2.4 Statistical analyses**

182 As recommended (Grace et al., 2016), we constructed three SEMs based on known  
183 theoretical multivariate causes of forest diversity and aboveground C storage in natural



184 forests (Fig. 1). We used stand structural diversity as a latent variable by incorporating two  
185 observable variables, tree DBH diversity and height diversity, which are highly correlated  
186 based on different discrete classes ( $r = 0.34$  to  $0.60$ ,  $P = 0.002$  to  $< 0.001$ ). To assess how  
187 DBH and height classes affected the prediction of aboveground C storage, we tested 48  
188 SEMs employing different combinations of discrete classes of tree DBH diversity (2, 4, 6,  
189 and 8 cm classes) and height diversity (2, 3, 4, and 5 m classes) based on the three conceptual  
190 models (Table S1).

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

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

208 For the selection of the best SEM, several tests were used to assess the model fit of all  
209 SEMs (Malaeb et al., 2000), i.e., the Chi-square ( $\chi^2$ ) test, goodness-of-fit index (GFI),  
210 comparative fit index (CFI), standardized root mean square residual (SRMR), and AIC. We  
211 used the  $\chi^2$  test, representing the maximum likelihood estimation, to assess how well the 48  
212 hypothesized SEMs fit the data (Table S3). Indicators for a good model fit to the data  
213 included an insignificant ( $P > 0.05$ )  $\chi^2$  test statistic, SRMR  $< 0.05$ , and both GFI and CFI  $>$   
214  $0.90$  (Malaeb et al., 2000). Among all acceptable models, we selected those with the lowest  
215 AICs as our final models. Tree DBH diversity based on 8 cm, and height diversity based on  
216 the 2 m class were selected as the stand structural diversity (a latent variable), as this  
217 combination resulted in the SEM with the lowest AIC, with a  $P$ -value of the  $\chi^2$  test for the  
218 total model fit greater than 0.05 (Table S3). The SEMs based on combinations of 4 cm or 6  
219 cm discrete classes for DBH diversity, and the 2 m class for height diversity were also  
220 accepted ( $P > 0.05$ ), whereas the SEMs based on all other combinations of discrete classes  
221 for DBH and height diversity indices were rejected ( $P < 0.05$ ; Table S3).

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

227

### 228 **3 Results**

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

233           The final SEMs with the three directions for the path between species diversity and  
234 stand structural diversity had a similar good-fit to the data (Fig. 3). These SEMs accounted  
235 for 82% of the variation in aboveground C storage, 55% to 59% of the variation in stand  
236 structural diversity, and 0.1% to 9% of the variation in species diversity (Fig. 3). Stand  
237 structural diversity had the strongest positive direct effect on aboveground C storage ( $\beta =$   
238 0.56,  $P = 0.001$ ), followed by the positive effect of stand age ( $\beta = 0.41$ ,  $P = 0.003$ ), and  
239 negative effect of species diversity ( $\beta = -0.23$ ,  $P < 0.001$ ) in these SEMs (Table 1; Fig. 3).  
240 There was a significantly positive direct effect of stand age on stand structural diversity, but  
241 an insignificant effect on species diversity (Fig. 3). Species diversity and stand structural  
242 diversity had a significant positive direct effect on each other (Fig. 3)

243           Stand age had a strong indirect effect via stand structural diversity ( $\beta = 0.41$ ,  $P =$   
244 0.002; Table 1) and insignificant indirect effects via species diversity ( $\beta = -0.10$ ,  $P = 0.357$ )  
245 on aboveground C storage in all three SEMs (Fig. 3, Table 1). The indirect effects of stand  
246 structural diversity via species diversity were insignificant regardless of SEMs, while species  
247 diversity had a marginally significant positive indirect effect via stand structural diversity ( $\beta$   
248 = 0.11,  $P = 0.059$ , Table 1). The total (direct + indirect) effects of stand age, stand structural  
249 diversity, and species diversity were 0.82, 0.56, and -0.12, respectively, on aboveground C  
250 storage (Fig. 3a; Table 1). In the alternative SEMs (Figs. 3b and 3c), the total effect of stand  
251 age, stand structural diversity, and species diversity on aboveground C storage were quite  
252 similar to the SEM in Fig. 3a (Table 1).

253

## 254 **4 Discussion**

255 To the best of our knowledge, this is the first study to analyze the multivariate relationships  
256 between aboveground C storage and its drivers (stand age, stand structural diversity, and  
257 species diversity) in secondary subtropical forests in China. We found a positive relationship

258 between stand structural diversity and aboveground C storage, but a negative relationship  
259 between species diversity and aboveground C storage, while accounting for the considerable  
260 positive influence of stand age in our study. Our results revealed that the positive  
261 relationships reported in previous studies, between stand structural diversity and aboveground  
262 C storage, in boreal and temperate forest ecosystems (e.g., Dănescu et al., 2016; Zhang and  
263 Chen, 2015), may be extended to subtropical forests.

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

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

283 (Cardinale et al., 2011; Lasky et al., 2014; Prado-Junior et al., 2016; Tobner et al., 2016). Our  
284 findings of the positive indirect effect of species diversity via stand structural diversity, and  
285 stand structural diversity via species diversity on aboveground C storage were consistent with  
286 previous studies (Vilà et al., 2013; Zhang and Chen, 2015). These findings indicated that  
287 species diversity promoted stand structural diversity (Brassard et al., 2008; Zhang and Chen,  
288 2015), and that stand structural diversity increased the coexistence of species (Clark, 2010),  
289 and in either case, increased aboveground C storage.

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

299         In the forest stands under study, we found there to be a minimal direct impact of stand  
300 age on tree species diversity, and an indirect effect of stand age via species diversity on  
301 aboveground C storage. It remains intensely debated as to how stand age, as a measure of  
302 disturbance frequency, affects tree species diversity across forest landscapes with diverse  
303 localized conditions (Connell, 1978; Yeboah et al., 2016). For instance, disturbances of  
304 intermediate intensity may selectively remove specific species; hence, decrease species  
305 diversity (Yeboah and Chen, 2016). Our findings of the weak direct effect of stand age on  
306 species diversity, and indirect effect of stand age via species diversity on aboveground C  
307 storage, as well as the negative direct effect of species diversity on aboveground C storage,

308 might have resulted from historical human disturbances, which may have selectively  
309 harvested productive species in the study region. Future research will be required to improve  
310 our conceptual model through the inclusion of the effects of disturbance history on tree  
311 species diversity and its influence on aboveground C storage.

312

## 313 **5 Concluding remarks**

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

324

## 325 **Acknowledgements**

326 This work was supported by the National Natural Science Foundation of China (Grant No.  
327 31228004 and 31270475) and the CFERN & GENE Award Funds on Ecological Papers. We  
328 thank Professor Xuhui Zhou (East China Normal University) for his comments on an earlier  
329 draft. Constructive comments from two anonymous reviewers helped to substantially  
330 improve an earlier version of this manuscript.

331

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465

**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

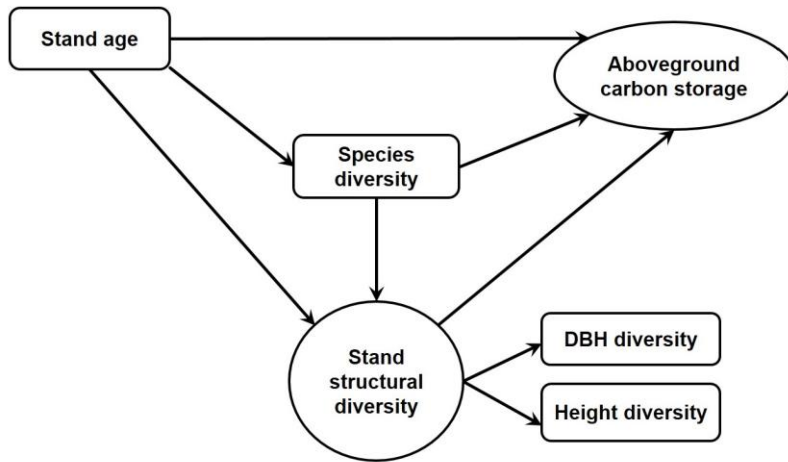
**Fig. 1** Conceptual models for the prediction of aboveground C storage in secondary subtropical forests of Eastern China, showing hypothesized relationships of how stand age impacts forest diversity, and how stand age and forest diversity concomitantly impact aboveground C storage. Forest diversity 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 ( $\text{Mg ha}^{-1}$ ) 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  $P > 0.05$ .

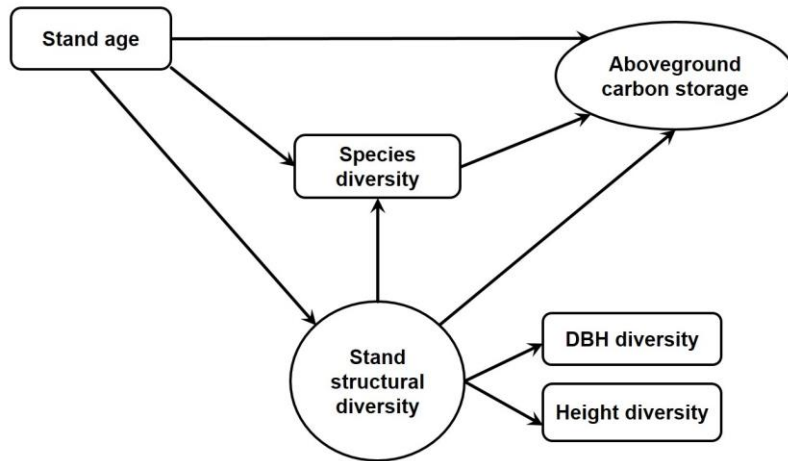
**Fig. 3** The final best-fit structural equation models (SEMs) relating aboveground C storage to stand age, stand structural diversity, and species diversity. Solid arrows represent significant ( $P < 0.05$ ) paths and dashed arrows represent non-significant paths ( $P > 0.05$ ). For each path the standardized 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



b



c

