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13th July, 2016

Dr. Anja RammigAssociate Editor
Biogeosciences
European Geosciences Union

**Re: Submission of revised manuscript**

Dear Dr. Anja Rammig,

Please find attached our revised manuscript (bg-2016-6) "**Stand structural diversity rather than species diversity enhances aboveground carbon storage in secondary subtropical forests in Eastern China**", submitted as a research paper for *Biogeosciences.*

We are indeed grateful for your patience and helpful suggestions during the review process. We also greatly appreciate the comments from the two reviewers. Please find our point-by-point responses attached in the file "Response to referees".

The coauthors have did revision without track changes in the manuscript. We have highlighted the changes in red color. Meanwhile, we also asked a native speaker (Frank Boelm, c/o NanoApps Consulting, 270 Ray Court, Thunder Bay, ON, Canada) to revise (please find his track changes) the manuscript. As a consequence, our manuscript has been considerably improved.

Yours sincerely,

Dr. En-Rong Yan
Professor in Vegetation and Functional Ecology

## Response to referee #1

*The manuscript has improved significantly, and all of the issues I raised previously have been addressed. The manuscript is now much more concise and focused. Only one question remains open (see below) and a few language-related issues should be fixed prior to publication.*

=> Thank you for your positive comment on our revised manuscript (MS). We have revised the manuscript according to your comments.

*Model selection: can you explain your model selection strategy in more detail, especially why you prefer models with a Chi-square test resulting in $p > 0.05$, which seems counterintuitive to me.*

=> We have explained our model selection strategy in more detail in the revised MS. Please see lines 218-221.

*Fig 1.: The difference between the three plots is not directly visible. Have you experimented with different arrow sizes or colors?*

=> We have explained the differences among three models in the caption. Species diversity and stand structural diversity were experimented with based on their different effects on each other. Thank you.

*Language issues:*

*L55: cycling, *and* capture*

*L57: C storages va*ies*, no comma after stand age*

*L68: "teased apart" is maybe not the correct wording; how about "few studies have separated the direct and indirect..."*

*L129: activities for more than the last 25 years*

*L277: Sentence starting with "The maintenance" seems incomplete*

*L310: Our findings of *a* weak direct effect*

*L324: and therefore strongly affects aboveground C storage indirectly, via stand structural diversity*

=> We have corrected these mistakes. Thank you.

## Response to referee #2

*I consider the authors have done a good job dealing with previous comments. The new version of the manuscript is much more clear and focused on what the authors actually can do: test forest attributes as predictors of forest biomass. I consider the manuscript will be a very valuable contribution to the scientific literature on the relation between biodiversity and ecosystem function. However, I still have some concerns about the framing of the problem, the methods, the discussion and the presentation, which I consider deserve further (but minor) work:*

=> We are grateful to you for reviewing our MS once again, and providing constructive comments. We have revised our MS according to your comments, which we believe has substantially improved our MS. Thank you.

*1. Problem statement is still a bit confusing. I provide further suggestions on the attached file to reorganize some ideas/sentences.*

=> We have followed your comments and revised the MS accordingly. Please find below our responses to each specific comment.

*2. Authors still do not provide a clear definition on how was stand age defined. They talk about several kinds of disturbance in the region, but they do not define explicitly in relation to which disturbance was age defined.*

=> We have now explicitly defined stand age. Please see lines 129-130 and 137-140 in the revised MS.

*3. Discussion is yet not fully satisfactory. Particularly, the relevant result on the negative relation between biomass and species diversity is poorly explained. This kind of results have* *relevant implications for the scientific literature. I provide further suggestions on the attached file.*

=> We have revised the discussion as suggested. Please see lines 264-267 and 282-298 in the revised MS. Thank you.

*4. I think the manuscript requires careful revision by a native English editor to identify and correct some minor mistakes. I have provided some observations through the text.*

=> We have asked a native English speaker to edit the language. Thank you.

*Specific comments:*

*L 48-50. This is not discussed, but merely said in the conclusions section. I suggest to emphasize here the negative effect of diversity.*

=> Revised as suggested. Please see lines 44-55 in the revised MS. Thank you.

*Introduction: Authors have done a well job in focusing the introduction towards the main theme of the MS: the contribution of stand age, species diversity and stand diversity. However, the presentation of the concepts is still confusing. Probably, reordering some of the sentences would improve this section. I suggest they follow this order:*

*1. South East Asian forest are important for C cycling (c capture), probably associated to the high representation of young stands in the region (Yu et al.) C accumulates as forest age, but we still lack a complete understanding of the determinants (mechanisms) of carbon accumulation. Tree species diversity and stand structural diversity have been proposed as factors driving C storage....*

*2. A paragraph on the evidence of stand structural diversity and C stocks and on the evidence of tree diversity and C stocks.*

*3. The interrelation between forest age, structure and tree diversity. Therefore the need to have integrative tests of those mechanisms: Then present their model (Figure 1) and explain it briefly based.*
*4. The aim of the work on how to test the model.*

=> Thank you for your comments. We have followed your suggested theme and revised the entire introduction accordingly.

*L 55. Capturing?*

=> Corrected.

*L 55. Here there is a sentence that is lacking: why the effects of should stand age and species diversity be tested for this forests? Are East Asian forests impacted by human activities? Are secondary forests a common feature of this region?*

=> Revised as suggested. Thank you.

*L 57. ..., and of changes in... Wording is not adequate*

=> Corrected in the revised MS.

*L 58. It should not be cited here*

=> Deleted in the revised MS.

*L 60. The do refer to stand structural diversity, not tree species diversity*

=> Revised

*L 71-80. The paragraph have the main ideas on which the work is based on, but they are poorly presented*

=> Revised as suggested.

*L 78-80. Too simple: why do you expect that? Which direction should it be?*

=> We have now elaborated further in the revised MS. The introduction has been reorganized and rewritten, as suggested.

*L 90-92. You just said the same three lines before*

=> Deleted

*L 93-94. Isn´t it the same in line 74-75?*

=> Deleted.

*L 95. This sentence is the same you have said previously. Please consider moving it to the end of the first paragraph*

=> Revised

*L 103. This is not an adequate citation for SEM, since Grace et al´s paper in Nature is not a methodological paper nor provides new analytical approaches*

=> Revised

*L 105. Hypothesis, represented by paths?*

=> Revised as recommended

*L 129. Odd wording*

=> Corrected.

*L 136-137. Ages are of forest recovery from what kind of disturbance? In the previous paragraph they talked about logging, land-use conversion and wind throw. Is this work mixing plots coming from different kinds of disturbances? If it is, please at least say it explicitly. Moreover, in the response letter...*

=> We have now explicitly stated this in the revised MS. Please see lines 129-130 and 137-140 in the revised MS.

*L 143-144. If plots were at least 100m from stand edges, therefore stands were not as small as authors suggest. I suggest to simply not include any kind of argument relative to plot size.*

=> Revised as suggested. Thank you.

*L 171-175. This should be in the previous section on general site characteristics. And again, it is not clear which disturbance was it.*

=> Revised as suggested. Thank you.

*L 182-183. Sobra*

=> unnecessary phrase deleted

*L 185-186. Why basal area proportions? Why not simply number of individuals?*

=> We have explained this in the revised MS. Please see line 176 in the revised MS.

*L 208-212. But this should be partial correlations to tease apart the independent effects of each variable*

=> Because variables are highly dependent on each other, it was not possible to find independent effects of each variable. Alternatively, we used structural equation models to examine cause-effect relationships among the variables as we hypothesized. We used bivariate relationships to augment SEMs.

*L 244. Strange*

=> revised.

*L 249. Delete*

=> Deleted.

*Discussion: I found the discussion of the two main results disappointing. How can stand structural diversity favor grater C stocks? Authors talk about one mechanisms: enhanced light use. But how does that work? Does higher light use efficiency means greater capacity to stock C? The other relevant results is that on the negative effect of species diversity. Given the central role it has been given to diversity for ecosystem functioning, I think authors should do a better work to argue why the found the reverse. Now the just have a spuriously presented argument of strong functional redundancy. Previous meta-analysis on the effect of species richness on forest AGB (both temperate and tropical) show species richness may have no or negative effect (Cardinale et al. 2011 Amer. J. Bot). Authors should review such previous work.*

=> Thank you for your constructive comments on the discussion section. As suggested, we have thoroughly revised and reorganized the discussion section. By following your suggestions, we believe the MS has been significantly improved.

*L 277-278. Not well written. What do you mean?*

=> Revised.

*L 281. The accumulation of C storage? Isn´t it just C storage? You are assessing C stocks and therefore storage, rather than accumulation (a rate, which you did not measured here).*

=> Revised.

*L 283. In a statistical sense? Your results show it is significant. Moreover, it is negative, contrary to expectations from previous studies!*

=> We apologize for the error. Yes, the effect is significant. We have further discussed the negative effect of species diversity on aboveground C storage.

*L 287-289. Then why other species richer systems shows positive effects of species diversity on AGB (e.g. Poorter et al. 2015)? I find this argument not well sustained*

=> We agree with you and have revised the corresponding text.

*L 292-293. Weak? Compared to what?*

=> Revised and clarified. Please see lines 373-381. Thank you.

L 307. Stand age is not a measure of disturbance frequency

=> Based on the original definition (Connell, 1978), stand age represents disturbance frequency

*L 310-314. Previously, you have said that the negative direct effect of species diversity on AGB may be due to strong functional redundancy. From that, one would expect that removing certain species may favor C accumulation by reducing competition. But here you suggest that selective harvest may have caused the negative association between diversity and AGB. Aren´t those two arguments contradictory?*

=> We agree with you. Species redundancy is not the reason for the lack of diversity effect on aboveground C. We believe that the selective removal of productive species (thus reducing competitive exclusion==high diversity) leads to minimal or negative effects of species diversity on aboveground C. We have carefully revised the Discussion for consistency.

L 319. Related?

=> Corrected.

L 321. Variation

=> Corrected.

L 382. Capitalize first letter

=> Corrected.

Fig. 2 caption. Drop "other"

=> Corrected.

Fig. 2 I suggest to indicate significant relationships with a continuous fitted line, and non-significant with a discontinuous one. Alternatively, do not present the fitted line for those non-significant cases.

=> Revised as suggested. Please see revised Fig. 2.

Fig. 3 caption. How to show that. Please present Chi-2 test results associated to each model

=> Revised as suggested. Please Fig. 3 caption in the revised MS. Thank you.

Connell, J. H.: Diversity in tropical rain forests and coral reefs - High diversity of trees and corals is maintained only in a non-equilibrium state, Science, 199, 1302-1310, 1978.

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

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

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

Tables: 1 Figures: 3 References: ~~38~~41

Supplementary information: Tables: 3

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

# Abstract

Stand structural diversity, typically characterized by variances in tree diameter at breast height (DBH) and total height, plays a critical~~n important~~ 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, ~~and~~ tree species, DBH and height diversity indices, were determined across 80 subtropical forest plots in Eastern China. We ~~used~~ 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~~ing~~ 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 ~~had~~ demonstrated strong positive total effects, including a positive direct effect ($\beta$ = 0.41), and a positive indirect effect via stand structural diversity ($\beta$ = 0.41) on aboveground C storage. Stand structural diversity had a positive direct effect on aboveground C storage ($\beta$ = 0.56), whereas there ~~is~~ was little total effect of species diversity as ~~species diversity~~it had a negative direct association with, but had a positive indirect effect, via stand structural diversity, on aboveground C storage. The ~~little~~negligible total effect of species diversity on aboveground C storage in the forests under~~our~~ study ~~forests~~ may have been attributable to competitive exclusion ~~in the forest~~ with high aboveground biomass, or a historical logging preference for productive species. Our analyses suggested that stand structural diversity ~~is~~ was a ~~a~~ major determinant for va~~the va~~riations in aboveground C storage in the secondary subtropical forests in Eastern China. Hence, maintaining ~~. Maintaining~~ tree DBH ~~diversity~~ and height

diversity through silvicultural operations could might constitutebe a 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 ~~are~~ comprise a ~~strong~~ significant carbon (C) sink, ~~probably~~ 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~~s~~ 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). ~~Stand~~ The structural ~~diversity~~ and species diversity of s~~-~~tands depend to a large extent on the stand age (Lei et al., 2009; Wang et al., 2011; Zhang and Chen, 2015). However, ~~the~~ associations ~~among~~ 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,~~, in part because~~ as the ~~a~~ well-documented~~the~~ effects of stand age (~~, which is~~ a critical driver for individual species dynamics, aboveground C storage and productivity), has not often been explicitly considered (but see Zhang and Chen, 2015).

M~~M~~ulti~~-~~layered stand structures ~~has~~ have been theorized to increase the~~light capture~~ capture and efficient utilization of light ~~and light use efficiency~~ (Yachi and Loreau, 2007), and ~~, and~~ empirical evidence ~~shows~~ has indicated that stand structural diversity is positively associated with aboveground biomass or C storage~~-~~(e.g., Dănescu et al., 2016; Poorter et al., 2015; Zhang and Chen, 2015). Hence, w~~We~~ ~~thus~~ hypothesized that ~~stand~~ stand structural diversity has a positive direct effect on the aboveground storage of C ~~storage~~ (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 ~~stand~~ structural diversity of a stand, and ~~in~~ as a consequence, ~~increase~~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~~ing~~ to the indirect effects of stand age via stand structural diversity and species diversity, on aboveground C storage (Fig. 1a). Alternatel~~ively~~y, the stand structural diversity may be critical to species coexistence (Clark, 2010), and in turn ~~has~~ may impart a positive indirect effect on the aboveground ~~C~~ 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 ~~used~~ 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 ~~diversity~~ and species diversity, and 3) the direct effects of stand structural ~~diversity~~ and species diversity, as well as ~~and~~ the indirect effect of species diversity via stand structural diversity on aboveground C storage (Fig. 1). ~~Because of~~ Due to the complex interactions between species diversity and stand structural diversity (Clark, 2010; Zhang and Chen, 2015), we also ~~tested~~investigated ~~the~~ alternative pathways between the two ~~stand structural diversity and species diversity~~ (Figs. 1b and 1c).

## 2 Materials and methods

## 2.1 Study area, sites, and plots

~~The~~ This 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 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 ~~by~~ via typhoon, and ~~different~~ variable intensities of ~~human~~ human disturbances in its history ~~in the history~~; however, it ~~,~~ ~~but~~ has been protected from anthropogenic activity~~ies~~ for the last ~~more than~~ 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 ~~in~~ across the study areas are ~~thought to be~~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 ~~have~~ had ~~naturally~~ recovered naturally from logging in the study areas, ~~and have not had~~with no ~~any~~ 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 the plots was carried out through forest ~~inventory~~ inventories and ground based ~~survey~~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 ~~collect~~ 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 ~~the~~ ground level were measured (with a diameter tape) for trees that were shorter than 1.50 m. The t~~T~~otal tree height for each tree was measured with a telescopic pole for ~~the~~ heights of up to 15 m, and with a clinometer for heights of >15 m. The studied plots contained~~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.~~,~~ E~~with e~~vergreen species such as *Choerospondias axillaris* and *Schima superba* ~~dominating~~ 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 ~~using~~ 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 ~~conducted~~ 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 ~~regression~~ and multiple linear regressions, ~~by~~ through the addition of~~ng~~ quadratic and cubic polynomial terms to test for bivariate relationships of aboveground C storage. ~~with each of~~ S~~s~~tand age, species diversity, ~~and~~ 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, ~~and~~ DBH, and height diversity indices based on their various discrete classes. Our analyses indicated that simple linear regression analysis was optimal~~the best~~ 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~~sed~~ to assess the normality ~~for~~ of all variables. As recommended (Grace et al., 2016), all numerical variables, including aboveground C storage, species diversity, stand age, and ~~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 ($\chi^2$) test, goodness-of-fit index (GFI), comparative fit index (CFI), standardized root mean square residual (SRMR), and AIC. We used the $\chi^2$ 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 ($P > 0.05$) ~~(~~$\chi^2$ test statistic, SRMR < 0.05, and both GFI and CFI > 0.90 (Malaeb et al., 2000). Among all acceptable models, we selected ~~the models~~ 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 ~~because~~ this combination resulted in the SEM with the lowest AIC, with a *P*-value of the $\chi^2$ test for the ~~overall~~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~~ 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 showed 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 all 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 ($\beta$ = 0.56, $P$ = 0.001), followed by the 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 (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 ($\beta$ = 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~~ total effect of stand age, stand structural diversity, and species diversity on aboveground C storage were ~~almost~~ 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 ~~strong~~ considerable positive influence of stand age in our study. Our results ~~indicate~~ 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), ~~can~~ may be extended to subtropical forests.

Our results ~~showed~~ indicated that tree DBH and height diversity indices were ~~strongly~~ significantly positively related ~~with~~ to aboveground C storage across plots; ~~those~~ 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 ~~different~~ variable diameters and heights ~~may~~ 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 ~~and~~ 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 ~~is~~ was ~~little~~ 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 ~~little total~~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 ~~strong~~ 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, ~~or~~ and stand structural diversity via species diversity~~,~~ on aboveground C ~~storage~~storage ~~is~~ were consistent with previous studies (Vilà et al., 2013; Zhang and Chen, 2015). These~~is~~ findings indicated~~s~~ that species diversity ~~promotes~~ promoted stand structural diversity (Brassard et al., 2008; Zhang and Chen, 2015), and that ~~or~~ stand structural diversity ~~increases~~ increased the coexistence of species ~~coexistence~~ (Clark, 2010), and in either case, ~~increases~~ increased aboveground C storage.

The strong positive contribution of stand age to aboveground C storage ~~is~~ was attributable to ~~the ac~~cumulati~~on~~ve ~~of~~ tree growth over time (Lei et al., 2009; Poorter et al., 2016). Stand age ~~can~~ may also indirectly impact aboveground C storage through ~~the~~ 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 ~~are~~ were consistent with the ~~idea~~ notion that ~~the~~ complementarity effects increase ~~through~~ over time via increasing stand structural diversity (Zhang and Chen, 2015).

In the forest stands under study, ~~We~~ we found ~~little~~ there to be a minimal direct ~~effect~~ impact of stand age on tree species diversity, and an indirect effect of stand age via species diversity on aboveground C storage ~~in our study forests~~. It ~~is~~ remains intensely~~highly~~ debated as to how stand age, as a measure of disturbance frequency, affects tree species diversity across forest landscapes with diverse localized ~~site~~ conditions (Connell, 1978; Yeboah et al., 2016). For instance, disturbances of intermediate intensity may selectively remove specific species; ~~, and~~ 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 ~~might~~ may have selectively harvested productive species in the study region. Future research ~~is~~ will be ~~needed~~ required to improve our conceptual model ~~by~~ through the inclusion of~~ding~~ the effects of disturbance history on tree species diversity and its influence on aboveground C storage.

## 5 Concluding remarks~~sion~~

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


## Acknowledgements

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**Table 1.** The direct, indirect, and ~~total~~ 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~~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~~ng~~ aboveground C storage in secondary subtropical forests ~~in~~ of Eastern China, showing hypothesized relationships of how ~~does~~ stand age ~~affect~~ impacts forest diversity, and how ~~do~~ stand age and forest diversity ~~together~~ concomitantly ~~affect~~ impact aboveground C storage. Forest diversity is characterized by ~~their~~ 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 ~~are~~ 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

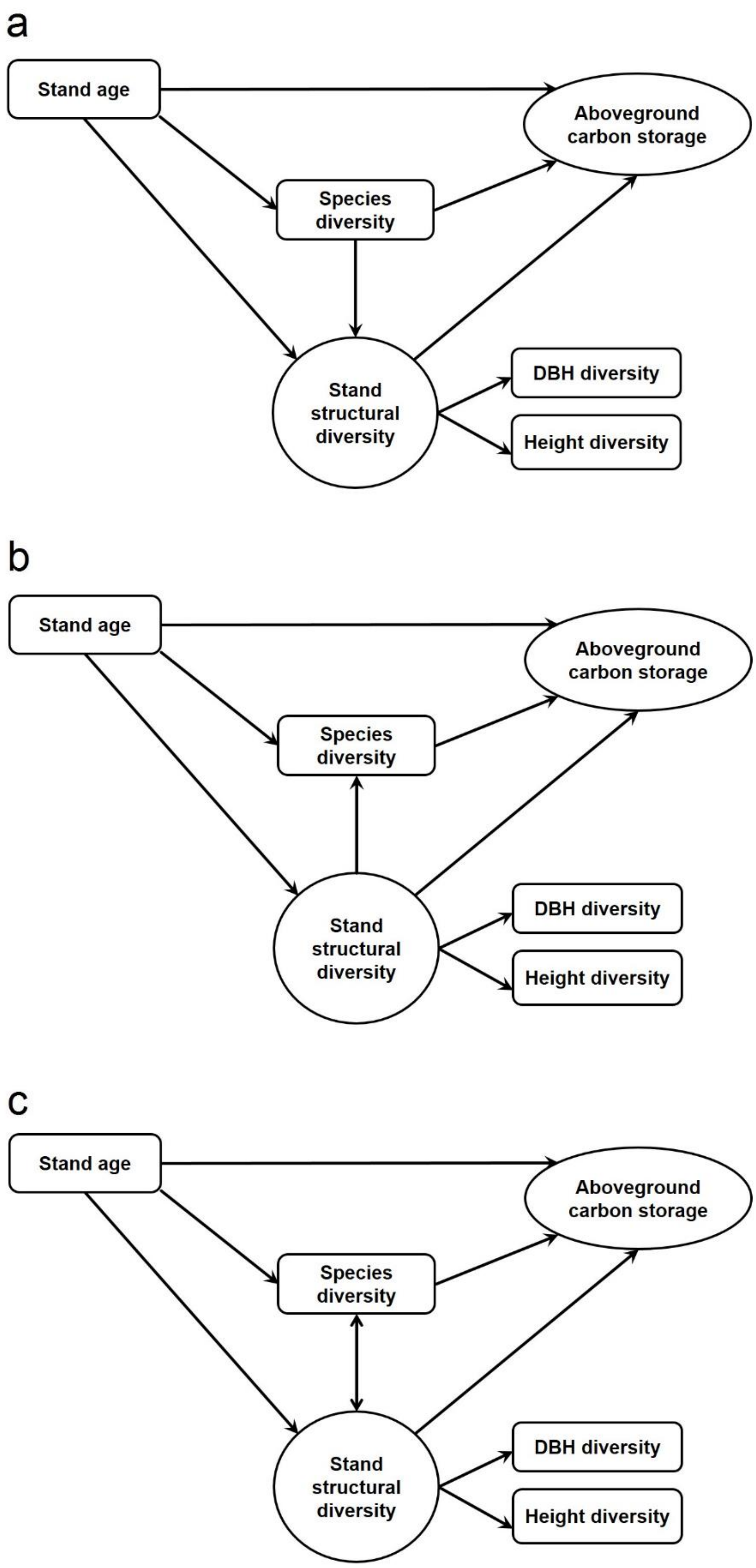
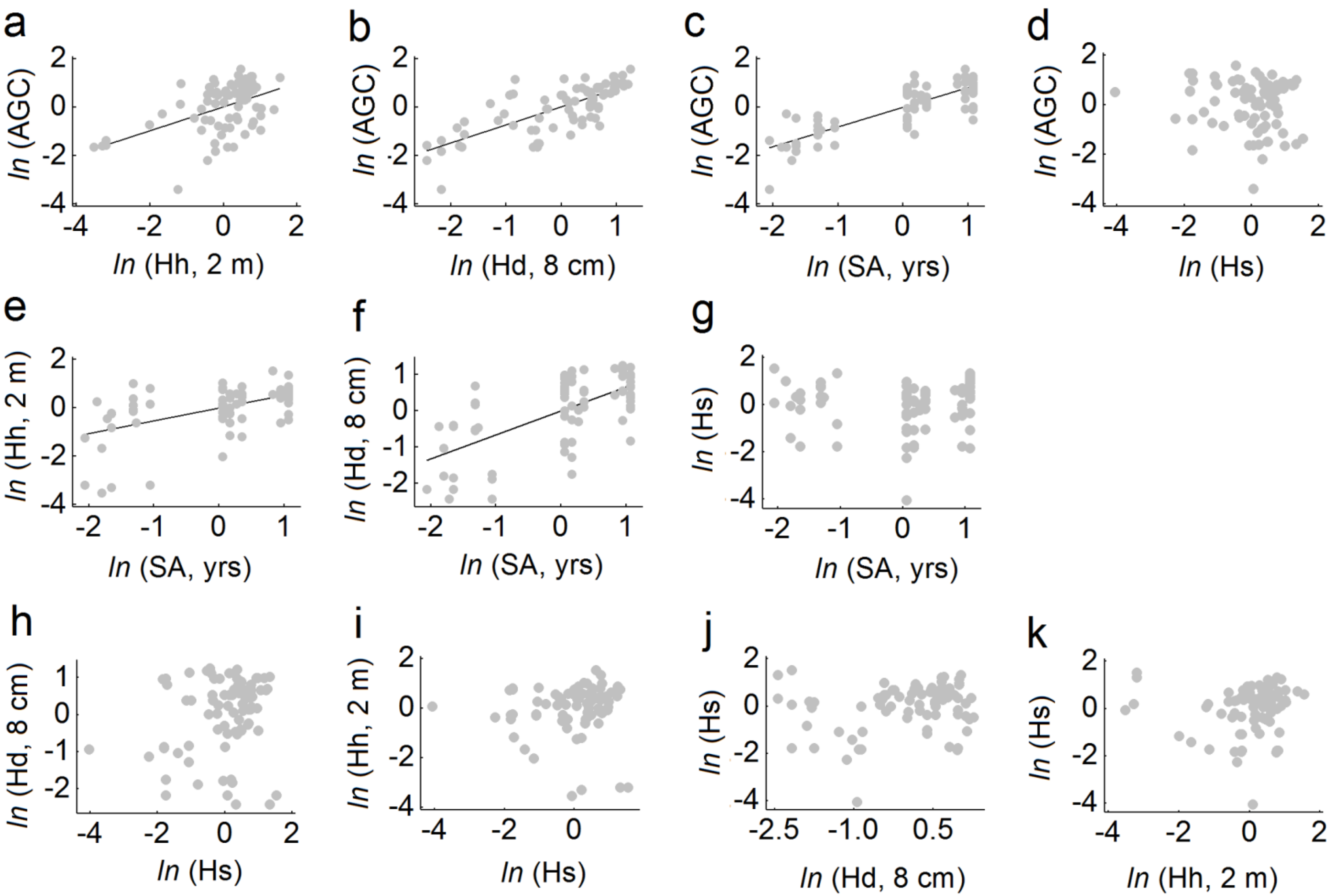
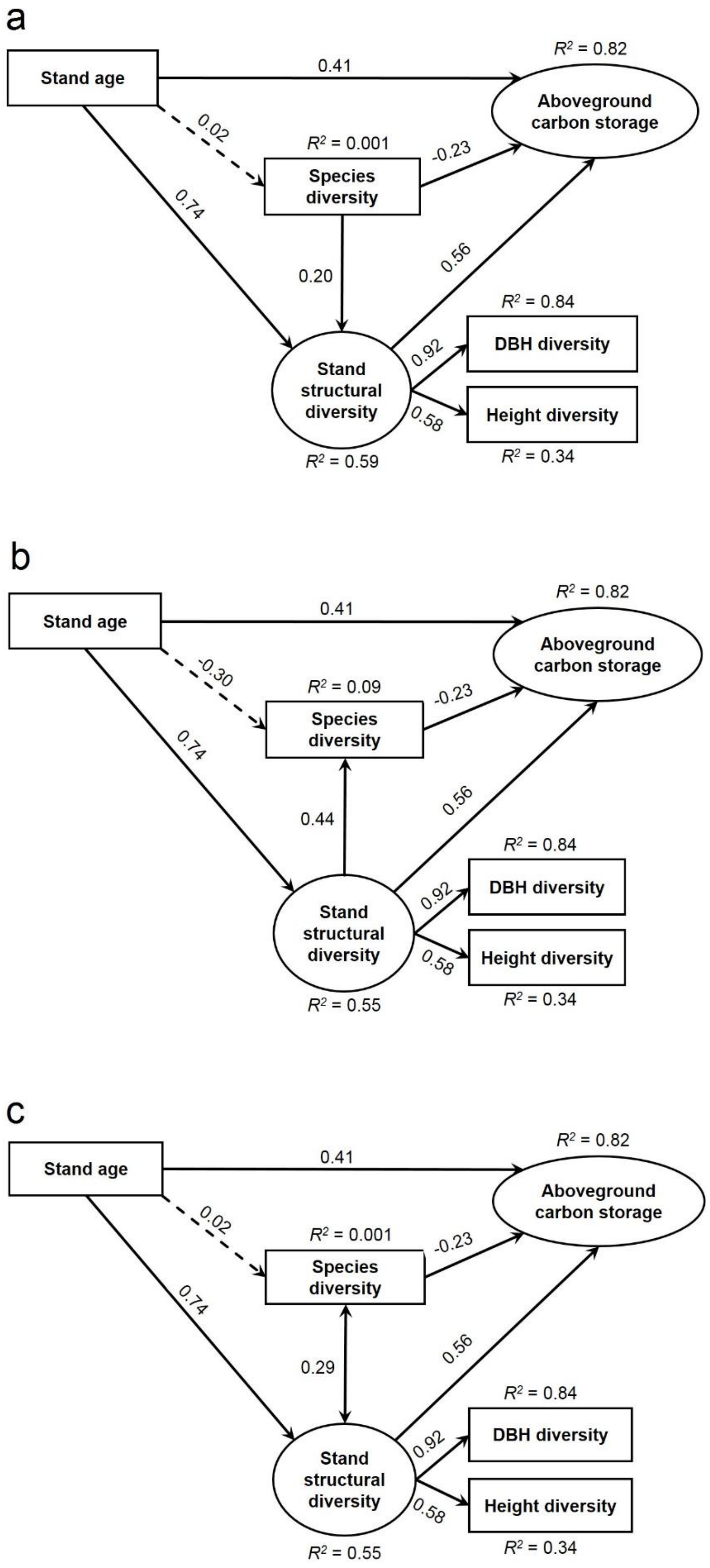

a
Stand age
Aboveground carbon storage
Species diversity
Stand structural diversity
DBH diversity
Height diversity
b
Stand age
Aboveground carbon storage
Species diversity
Stand structural diversity
DBH diversity
Height diversity
c
Stand age
Aboveground carbon storage
Species diversity
Stand structural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

30

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