Drivers of tree carbon storage in subtropical forests

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### HIGHLIGHTS

- Biodiversity enhances tree carbon storage in subtropical forests.
- Niche complementarity and mass-ratio effect both play a role in maintaining ecosystem functioning.
- Stand age, stand structure and environmental conditions all affect tree carbon storage.

### ABSTRACT

Tropical and subtropical forest ecosystems play an important role in the global carbon regulation. Despite increasing evidence for effects of biodiversity (species diversity, functional diversity and functional dominance), stand structural attributes, stand age and environmental conditions (climate and topography) on tree carbon storage, the relative importance of these drivers at large scale is poorly understood. It is also still unclear whether biodiversity effects on tree carbon storage work through niche complementarity (i.e. increased tree carbon storage due to interspecific resource partitioning) or through the mass-ratio effect (tree carbon storage regulated by dominant traits within communities). Here we analyze tree carbon storage and its drivers using data from 480 plots.
1. Introduction

The relationships between biodiversity and ecosystem functioning (B-EF) have received considerable attention during the past two decades, largely because ecosystem functions and biodiversity of natural systems play an important role in providing goods and services (De Deyn et al., 2008; Isbell et al., 2011; Cardinale et al., 2012; Zhang et al., 2012). Numerous manipulative experiments have demonstrated positive relationships between plant diversity and productivity or aboveground biomass (Hector et al., 1999; Tilman et al., 2001; Cardinale et al., 2007). Evidence for correlations between plant diversity and tree carbon storage in natural forests is rapidly increasing. Although many studies have found a positive relationship across boreal forests (Paquette and Messier, 2011; Zhang and Chen, 2015), temperate forests (Paquette and Messier, 2011; Ruiz-Benito et al., 2014), and tropic and subtropical forests (Cavanaugh et al., 2014; Poorter et al., 2015), there are also many inconsistent results (Vilà et al., 2003; Ruiz-Jaen and Potvin, 2011; Ali et al., 2016; Fotis et al., 2018; van der Sande et al., 2017). These equivocal results reveal our limited knowledge in understanding multivariate mechanisms that simultaneously affect biodiversity and ecosystem functioning in natural ecosystems (Zhang et al., 2012). These divergent results also may reveal methodological differences among studies, particularly differences in the geographical scale, as the relationship between tree carbon storage and biodiversity may be more prevalent at larger scales, as is also observed within (Paquette and Messier, 2011; Isbell et al., 2018). Much research, therefore, is still needed to improve our understanding of the patterns and causes of B-EF relationships in natural ecosystems at large scales, particularly in species-rich tropical or subtropical forests (Cavanaugh et al., 2014; Poorter et al., 2015).

Much debate has centered on the mechanisms behind observed positive B-EF relationships. The two commonly tested mechanisms are the niche complementarity hypothesis (Tilman et al., 1997; Loreau and Hector, 2001) and the mass-ratio hypothesis (Grime, 1998). The niche complementarity hypothesis states that functionally diverse species assemblages can better utilize a pool of limiting resources, and as a consequence, increasing tree diversity and productivity, which is known to be a critical driver for individual species dynamics and tree carbon storage (Chen and Taylor, 2012; Pretzsch et al., 2014; Chen et al., 2016; Poorter et al., 2016). Stand age can also indirectly affect tree carbon storage by influencing plant diversity or stand structure in the community (Becknell and Powers, 2011; Zhang and Chen, 2015). Environmental conditions may have direct effect on tree carbon storage through their effect on nutrient and water availability (de Castilho et al., 2006; Alves et al., 2010; Poorter et al., 2015). Mean annual precipitation (MAP) and actual evapotranspiration (AET), for example, are recognized as primarily responsible for ecosystem development at large scales (Fang et al., 2012; Poorter et al., 2017). Environmental conditions may also have indirect influence (Paquette and Messier, 2011; Jucker et al., 2016) through shifting species distributions and abundance, and stand structure, along environmental gradients (Cavanaugh et al., 2014; Murphy et al., 2015; Poorter et al., 2015).

Although multiple drivers affect tree carbon storage (Paquette and Messier, 2011; Ali et al., 2016; Fotis et al., 2018), few studies have simultaneously tested these biotic (biodiversity, stand age and structural attributes) and abiotic (environmental conditions) factors on tree carbon storage in species-rich subtropical or tropical forests. The objective of this study is to test how tree carbon storage is driven by these biotic and abiotic factors across species-rich subtropical forests in China. Specifically, we address the following three questions: First, how do biotic (biodiversity, stand age and structural attributes) and abiotic (environmental conditions) factors drive tree carbon storage? We hypothesize that biodiversity, high stem density and tree size variation enhance tree carbon storage, and that tree carbon storage relates to stand age and environmental conditions. Second, what is the relative
strengths of these factors on tree carbon storage? We hypothesize that tree carbon storage is most strongly affected by stand age, followed by environmental conditions, biodiversity (through niche complementarity or mass-ratio effect) and stand structural attributes. Third, how do these variables directly and/or indirectly affect tree carbon storage? We hypothesize that (1) biodiversity, structural attributes, environmental conditions and stand age have direct effects on tree carbon storage; 2) environmental conditions and stand age also have indirect effects via biodiversity and structural attributes on tree carbon storage; 3) biodiversity also has indirect effect on tree carbon storage through its effect on structural attributes; we also tested the influence of stand structural attributes on biodiversity, because structural attributes might play a role in maintaining biodiversity (Clark, 2010). We address these questions using 480 forest inventory plots sampled across species-rich subtropical forests in China.

2. Materials and methods

2.1. Study area and forest inventory data

We sampled 480 plots with size of 0.06 ha from China’s subtropical forests, all undisturbed, not managed and located at least 100 m from the nearest edge or road, to reduce edge effects. These plots spanned a geographic range from 27.01° to 34.73° N in latitude, and from 100.33° to 121.06° E in longitude, across seven provinces in China (Fig. 1), with an annual mean temperature from 3.2 to 19.5 °C, an annual mean precipitation from 636 to 1926 mm and a slope from 0 to 64°. All stems ≥3 cm in DBH in each plot were individually recorded, measured, and identified to species-level in the field between 2011 and 2012. Taxonomic names were verified against Catalogue of Life China (Checklist 2015, http://www.sp2000.org.cn/) and Flora of China (http://flora.eflora.cn/). The plots together contained 455 species belonging to 181 genera and 68 families. For each plot, we determined stand age according to last growth ring, which represents net productivity accumulated from stand establishment (Chisholm et al., 2013; Michaletz et al., 2014), using the relevant allometric equations with diameter at breast height and tree height as predictors (Ecosystem Carbon Sequestration Project, 2015) (Table S2). Live tree biomass was converted to tree carbon storage by multiplying the standard conversion of 0.5 g carbon per gram of dry woody plant biomass (Brown, 1997) (Table S1).

2.2. Tree carbon storage estimation

We estimated live tree biomass (stem + branches + foliage + roots) of each plot, which represents net productivity accumulated from stand establishment (Chisholm et al., 2013; Michaletz et al., 2014), using the relevant allometric equations with diameter at breast height and tree height as predictors (Ecosystem Carbon Sequestration Project, 2015) (Table S2). Live tree biomass was converted to tree carbon storage by multiplying the standard conversion of 0.5 g carbon per gram of dry woody plant biomass (Brown, 1997) (Table S1).

2.3. Biodiversity metrics

In this study, we calculated three dimensions of biodiversity: species diversity, functional diversity and functional dominance. We used the Shannon-Wiener biodiversity index as a proxy of species diversity to account for species richness and evenness, two important aspects of species diversity in B-EF relationships studies (Zhang et al., 2012; Zhang and Chen, 2015). The Shannon-Wiener biodiversity index was calculated as $H_s = \sum_{i=1}^{S} p_i \times \ln(p_i)$, where $p_i$ is the proportion of individuals of species $i$ in the plot, while $S$ is the number of tree species (Table S1).

We used maximum diameter and wood density to calculate functional diversity and dominance, as these traits can represent differential life-history strategies and are commonly used in B-EF studies (Whitmore, 1998; Díaz et al., 2007; Cavanaugh et al., 2014). Maximum diameter can serve as an important indicator of the light capture strategy (Falster and Westoby, 2005; Kraft et al., 2008). The maximum diameter of each species was determined from our dataset, with values assigned equal to the largest diameter value in the data set for a given species (following Cavanaugh et al., 2014). Wood density is a good indicator of life-history strategy and varies from low wood density indicating fast growth and early reproduction to high wood density indicating slow growth and high resistance to environmental hazards (Chave et al., 2006). The wood density for most species (75%), which made up at least 95% of the basal area across all the plots, were quantified on five to seven individuals between 10 and 20 cm DBH that were exposed to sunlight or high lateral light levels. Wood density was measured using the density of the nearest branch attached to the main trunk, which has been shown to be a strong indicator of the main stem wood density.
(Swenson and Enquist, 2008). The branch wood density was calculated as oven-dried mass (80 °C, 48 h) divided by water-displaced volume of three to five segments cutting from three separate branches for each tree (Liu et al., 2016). For a few species (20%), wood density was gleaned from literature for the major tree species in China (Zhang et al., 2011) and the global wood density data base (Chave et al., 2009). When wood density was lacking for a particular species, we used the corresponding genus or family mean wood density (calculated from our region’s data). For functional diversity, we used the functional dispersion (FDIs) which sums weighted distances from the centroid of all species in a community (Laliberté and Legendre, 2010). FDIs can flexibly handle different trait types and work with any distance (Laliberté and Legendre, 2010). For functional dominance, we estimated the community weighted mean for wood density (CWMWD) and maximum diameter (CWMMD). The CWM of each trait in a given plot was calculated as the mean trait value of each species weighted by the relative abundance of the species (Cavannaugh et al., 2014). Although stem diameter was used to estimate tree carbon storage at the stem level, plot CWMWD still is a relatively independent predictor of plot tree carbon storage (Ruiz-Jaen and Potvin, 2011; Cavannaugh et al., 2014).

Shannon-Wiener biodiversity index was calculated using the ‘vegan’ package and functional diversity and dominance using ‘FD’ package in R 3.2.5 (R Development Core Team, 2016) (Table S1).

2.4. Structural attributes

We used stem density and tree size variation within each plot as stand structural attributes (Table S1). DBH variation among individuals, a surrogate of tree size variation, represents the degree of the realized niche differentiation via positive plant interactions in a community (Yachi and Loreau, 2007; Chu et al., 2009; Clark, 2010). We used the coefficient of variation (CV) of DBH to represent DBH variation within each plot (Brassard et al., 2008; Zhang and Chen, 2015).

2.5. Environmental factors

We used the mean annual precipitation (MAP), a good indicator for water availability (Obrien, 1993), and actual evapotranspiration (AET), a widely accepted proxy for plant productivity (Gastone, 2000), which are often thought to be closely related to species diversity and forest biomass (Gaston, 2000; Fang et al., 2012) (Table S1). The data for MAP data were downloaded from the WorldClim database with a resolution of 30 arc sec (Hijmans et al., 2005) and AET data from CGIAR-CSI with the resolution of 30 arc sec (http://www.cgiar-csi.org). We also included slope and aspect of each plot in our analysis (Table S1), as these factors can directly or indirectly affect forest biomass (de Castilho et al., 2006; Fotis et al., 2018). Slope and slope aspect were measured by GPS (Garmin, Rino-130) and Abney’s level in each plot. Based on previous studies (e.g. Sharma et al., 2011), we classified each plot into four categories of aspect: northeast (NE, 0°–89°), northwest (NW, 90°–179°), southeast (SE, 180°–269°) and southwest (SW, 270°–359°).

2.6. Statistical analyses

We first used Pearson correlation coefficients to test the pair-wise relationships between plot tree carbon storage and each predictor of biodiversity (species diversity, functional diversity, functional dominance), structural attributes (DBH variation, stem density) and environmental factors (MAP, AET, slope). We also used analysis of variance to test the differences in plot tree carbon storage among four aspect categories. Tree carbon storage, DBH variation, stem density, stand age, CWMWD and Shannon-Wiener index were natural logarithm-transformed before analyses to improve normality and linearity.

We used multiple linear regressions to analyze the relationship between dependent and explanatory variables. Multiple regression models are commonly used to predict the value of a variable based on the value of two or more other variables in this field of research (e.g. Yuan et al., 2016; Fotis et al., 2018). As the two climate variables (MAP and AET) are strongly correlated (Table S3), we thus only put MAP and other variables in the full model. We compared all possible models according to corrected Akaike information criterion (AICc), and candidate models were those with an AICc value close to the most parsimonious model (ΔAICc < 2) (Burnham and Anderson, 2002). The weighted averaged coefficient were the calculated based on these candidate models (Burnham and Anderson, 2002). Model selection and weighted averaging were conducted using the ‘MuMIn’ package (Bartoň, 2016).

The partial least squares path model (PLS-PM), which has been widely used to study complex multivariate relationships among variables (e.g. Wagg et al., 2014; Luo et al., 2017), was performed to infer potential direct and indirect effects of biodiversity, stand structure, stand age and environmental factors on tree carbon storage (Sanchez, 2013). The PLS-PM differs from the conventional covariance-based path analysis, and does not impose any distributional assumptions on the data which is usually difficult to meet (Sanchez, 2013; Luo et al., 2017). Based on expected relationship between tree carbon storage and key drivers, we established a base model that linked stand age, environmental conditions, biodiversity and structural attributes to tree carbon storage. To examine whether structural attributes simultaneously impact species diversity and tree carbon storage, we also fitted a model with opposite direction of the path between species diversity and structural attributes. In the PLS-PM, we used latent variable by incorporating two indicator variables, AET and MAP, to represent climate. The latent variable (climate) is a linear combination of the standardized indicator variables (MAP and AET) (Sanchez, 2013). We used a non-parametric bootstrapping (1000 resamples in this study) to estimate the precision of the PLS parameter estimates. The 95% bootstrap confidence interval was used to judge whether estimated path coefficients were significant. Path coefficient represents the direction and strength of direct effect between two variables. The PLS-PM was performed using the package ‘plspm’ in R 3.2.5 (R Development Core, 2016). The adjust p values of multiple comparisons were calculated based on Benjamini–Hochberg multiple-testing correction by false discovery rate (FDR) (Benjamini and Hochberg, 1995; Pike, 2011).

3. Results

3.1. Bivariate relationship between tree carbon storage and individual predictor variables

Tree carbon storage varied by an order of magnitude across subtropical forests in China, ranging from 15.4 Mg/ha to 214.9 Mg/ha. Stand age had the strongest positive relationship with tree carbon storage among the individual predictor variables ($R^2 = 0.32, P < 0.001$; Table S3), with DBH variation being second ($R^2 = 0.12, P < 0.001$). Stem density had a weak negative correlation ($R^2 = 0.02, P = 0.01$). MAP had a weak positive correlation with tree carbon storage ($R^2 = 0.01, P = 0.04$) and was the only environmental variable significantly related to tree carbon storage (Table S3, Fig. S1, S2). Among biodiversity variables, the Shannon’s index ($R^2 = 0.08, P < 0.001$) and functional dispersion ($R^2 = 0.03, P < 0.001$) had positive correlations with tree carbon storage, while CWMWD had negative correlation with tree carbon storage ($R^2 = 0.01, P = 0.02$) (Fig. 2) and CWMMD was unrelated (Table S3, Fig. S1).

3.2. The relative importance of biotic and abiotic factors for tree carbon storage

In contrast to the bivariate relationship between tree carbon storage and individual predictors, the final multiple regression models included 9 predictors, accounted for 43% of the variation in tree carbon storage (Fig. 3). Stand age still had the strongest effect on tree carbon storage. Among the biodiversity variables, Shannon’s index and CWMWD had a positive effect, CWMMD had a negative effect on tree carbon storage.
and functional dispersion had a neutral effect on tree carbon storage. Of the stand structural attributes, DBH variation had a strong positive effect on tree carbon storage, while stem density had neutral effects. Among the environmental variables, MAP had a strong positive effect on tree carbon storage, while all the other predictors did not have effects (Fig. 3). Replacing MAP with AET resulted in almost no changes to these results (Fig. S3).

3.3. The direct and indirect effect of all predictor variables on tree carbon storage

The partial least squares path model indicated that all predictor variables together explained 42% of variations in tree carbon storage ($R^2 = 0.42$, Fig. 4a). Stand age, climate, species diversity, DBH variation and CWMDIA all had significant positive direct effects on tree carbon storage, whereas CWMWD had a significant negative direct effect (Fig. 4a, Table 1). Stand age also had a positive indirect effect via species diversity and DBH variation, and a negative indirect effect through CWMDIA. Climate factors had a positive indirect effect via species diversity and negative indirect effects via CWMWD and DBH variation. Species diversity also had a positive indirect effect via DBH variation on tree carbon storage.

The alternative model with altered direction for the path between species diversity and DBH variation also accounted for 42% of the variation in tree carbon storage ($R^2 = 0.42$, Fig. 4b). Similar to the model in Fig. 4a, stand age and climate factors had significant effects on DBH variation. DBH variation had positive effects on not only tree carbon storage but also diversity (Fig. 4b).

4. Discussion

Tropical and sub-tropical forests store a significant part of global carbon and biodiversity (Bonan, 2008). We show that species diversity and functional dominance enhance tree carbon storage in subtropical forests, even after having controlled for stand age and environmental conditions as confounding factors, supporting both niche complementarity and mass-ratio effect hypotheses. Our large-scale study shows that positive biodiversity effects on ecosystem functioning found by
Much debate has centered around whether biodiversity plays an important role in promoting productivity or carbon storage in species-rich tropical and sub-tropical forests (Cavanaugh et al., 2014; Finegan et al., 2015; Poorter et al., 2015; Wu et al., 2014; Ali et al., 2016). We hypothesized that biodiversity enhances tree carbon storage after accounting for stand age and environmental conditions because of niche complementarity and mass-ratio effect. As expected, we found that species diversity had a significant positive effect on tree carbon storage, which is consistent with other studies conducted in tropical (Cavanaugh et al., 2014; Poorter et al., 2015), temperate (Vílás et al., 2007; Paquette and Messier, 2011), boreal forests (Paquette and Messier, 2011; Zhang and Chen, 2015). Species diversity also had an indirect effect on tree carbon storage via increasing DBH variation. Higher DBH variation, resulting from differences within and among species (Clark, 2010; Morin et al., 2011), indicates greater spatial packing of different tree canopy heights promoting above-ground light capture and light-use efficiency within communities (Yachi and Loreau, 2007; Forrester, 2014; Zhang and Chen, 2015). This indicates that niche complementarity, the ability of hyper-diverse communities to better use the limited resources, may be a mechanism promoting tree carbon storage in subtropical forests. Additionally, we found that species diversity and DBH variation increased with stand age, in agreement with the idea that the complementarity effects increase with succession (Reich et al., 2012; Zhang et al., 2012; Zhang and Chen, 2015). Our alternative PLS-PM model (Fig. 4b) shows a significant positive effect of DBH variation on species diversity, in line with the earlier finding that individual variation plays an important role in species coexistence (Clark, 2010). This result suggests niche complementarity to be not only a mechanism underlying a positive B-EF relationship, but also underlying maintenance of species diversity in natural forests (Clark, 2010; Zhang and Chen, 2015).

While species diversity was positively related to tree carbon storage, functional diversity had a weak positive effect in bivariate relationship (Fig. 2), but a neutral independent effect on tree carbon storage after other variables were accounted for (Fig. 3), not consistent with the niche complementarity hypothesis (Tilman et al., 1997). A possible explanation is that we did not select the most important traits related to complementary resource allocation in our functional diversity metric (Petchey and Gaston, 2006). We focused on two wood related traits (wood density and maximum diameter) ignoring possibly better suited functional traits (e.g. specific leaf area, leaf nitrogen content and minimum rooting depth) for which we did not have data.

Apart from the positive impact of species diversity, also CWM$_{WD}$, a measure of functional dominance, significantly impacted tree carbon storage. Forests with a higher CWM$_{WD}$ had greater tree carbon storage after stand age and environmental variables accounted for, in line with our prediction. This is similar to the result reported by Cavanaugh et al. (2014) for natural tropical forests on a global scale, and it is not surprising considering that maximum diameter is a good predictor of tree carbon storage (Kraft et al., 2008).

We found that CWM$_{WD}$ was negatively related to tree carbon storage, contrary to our expectation and to previous studies (Bunker et al., 2005; Prado-Junior et al., 2016; Poorter et al., 2017, but see Stegen et al., 2009). Generally, higher wood density indicates higher biomass per unit volume, thus leading to higher tree carbon storage (Bunker et al., 2005; Poorter et al., 2017). However, species with lower wood density may have a higher diameter growth rate (Chave et al., 2008), leading to a negative correlation between CWM$_{WD}$ and basal area. Indeed, we found such a negative relationship ($r = -0.13$, $P = 0.004$), suggesting lower CWM$_{WD}$ plots to have higher rates of biomass accumulation, leading to higher tree carbon storage. These results support the mass-ratio hypothesis, which emphasizes the importance of the traits of dominant species in maintaining ecosystem functions (Grime, 1998). Our overall results show that both niche complementarity and mass-ratio effect contribute to tree carbon storage in hyper-diverse ecosystems, in accordance with the results of a meta-analysis of manipulative studies showing that both these effects average accounted for 50% of the B-EF relationship (Cardinale et al., 2011).

4.2. How do stand age and environmental conditions affect tree carbon storage?

We hypothesized that tree carbon storage increases with forest stand age within a wide range of variation in environmental conditions. The strong positive relationship we found is consistent with previous studies (Zhang and Chen, 2015; Ali et al., 2016; Poorter et al., 2016), supporting our hypothesis. This strong positive effect is the result of cumulative tree growth over ecosystem succession (Lei et al., 2009; Poorter et al., 2016). As hypothesized, stand age also has an indirect effect on tree carbon storage via species diversity, CWM$_{WD}$, CWM$_{WD}$ and forest structural attributes (e.g. DBH variation). This result is in accordance with previous findings that stand age indirectly influences tree biomass storage via changes in forest composition and trait distribution during forest succession (Campetella et al., 2011; Becknell and Powers, 2014; Zhang and Chen, 2015; Ali et al., 2016; Ali et al., 2017). We hypothesized that tree carbon storage relates to environmental conditions, and indeed found significant relationships with climate factors, but not topographic variables (e.g. slope and aspect), partly supporting our hypothesis. This result is in agreement with previous studies where climate factors (e.g. AET, MAP) had positive effect on forest productivity or carbon storage (Poorter et al., 2015; Poorter et al., 2017; Jucker et al., 2016). Mean annual precipitation correlated with the length of the growing season (Toledo et al., 2011), hence, higher mean annual precipitation indicate longer period of individual tree growth, resulting...
in a larger biomass accumulation over time (Poorter et al., 2015; Poorter et al., 2017). Suitable temperature and sufficient water can initiate photosynthesis and meet evaporative needs, which are important for tree growth, and hence promote tree carbon storage. Environmental conditions strongly influence species diversity and compositions of plant communities, and thus ecosystem functioning (Poorter et al., 2015; Poorter et al., 2017). As expected, environmental conditions also have an indirect effect on tree carbon storage via species diversity, forest structural attributes and CWM of trait values, consistent with previous studies (Becknell and Powers, 2014; Poorter et al., 2015; Poorter et al., 2017). We used partial least squares path model to control other potentially confounding factors, finding that both species diversity and functional dominance had significant relationships with tree carbon storage in natural, hyper-diverse communities, but correlation does not necessarily mean causation (Poorter et al., 2017). This limitation of our study call for manipulative experiments and modeling studies to provide further support for a causal relationship between biodiversity and tree carbon storage in natural, hyper-diverse communities. It should be noted that we did not measure other ecosystem functions (e.g. tree productivity), which is not necessarily interchangeable with tree carbon storage (Chisholm et al., 2013). More studies are required to investigate the biodiversity effects on different forest ecosystem functions simultaneously at large scale in the future, as biodiversity effects differed markedly among ecosystem functions (Poorter et al., 2017).

5. Conclusions

Using the large-scale observational data from 480 plots with variable stand age and environmental conditions, our results indicate that in subtropical forests, species diversity, functional dominance, stand age and climate factors all drive variation in tree carbon storage at large scale. We found that stand age most strongly influenced tree carbon storage, followed by climate. While species diversity, CWM_DIA and DBH variation had independent positive effects on tree carbon storage, CWM_WD had an independent negative effect and topography had a neutral effect. Therefore, our results suggest that niche complementarity as well as mass-ratio effect play an important role in maintaining tree carbon storage in subtropical forests. Our result further indicate that conserving biodiversity and maintaining complex stand structure can maximize tree carbon storage in subtropical forests.

Fig. 4. The most parsimonious path model illustrating the potential direct and indirect effects of biodiversity, stand structure, stand age and environmental variables on tree carbon storage in subtropical forests. (a) Species diversity has an effect on DBH variation. (b) The alternative model with DBH variation has an effect on species diversity. Climate is a latent variable by incorporating MAP and AET. Single-headed arrows represent hypothesized causal relationships between variables. Black solid lines indicate significant relationships. The coefficients are standardized prediction coefficients for each causal path. $R^2$ indicates the total variation of a dependent variable is explained by independent variables.
Table 1

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.11.024.

References


Brassard, B.W., Chen, H.Y.H., Wang, J.R., Duinker, P.N., 2008. Effects of time since stand age, climate, species diversity and CWM traits on tree carbon storage base on partial least squares path modeling (PLS-PM). Significant effects are at P < 0.05 (*), 0.01 (**), and 0.001 (***).


