



## Drivers of tree carbon storage in subtropical forests



Yin Li<sup>a,b</sup>, Weikai Bao<sup>c</sup>, Frans Bongers<sup>d</sup>, Bin Chen<sup>e</sup>, Guoke Chen<sup>a</sup>, Ke Guo<sup>a</sup>, Mingxi Jiang<sup>f</sup>, Jiangshan Lai<sup>a</sup>, Dunmei Lin<sup>g</sup>, Chunjiang Liu<sup>h</sup>, Xiaojuan Liu<sup>a</sup>, Yi Liu<sup>a,b</sup>, Xiangcheng Mi<sup>a</sup>, Xingjun Tian<sup>i</sup>, Xihua Wang<sup>j</sup>, Wubing Xu<sup>a,b</sup>, Junhua Yan<sup>k</sup>, Bo Yang<sup>l</sup>, Yuanrun Zheng<sup>a</sup>, Keping Ma<sup>a,b,\*</sup>

<sup>a</sup> State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China

<sup>b</sup> University of Chinese Academy of Sciences, Beijing 100049, China

<sup>c</sup> Key Laboratory of Mountain Ecological Restoration and Bioresource Utilization, Ecological Restoration and Biodiversity Conservation Key Laboratory of Sichuan Province, Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu, China

<sup>d</sup> Forest Ecology and Forest Management Group, Wageningen University, PO Box 47, 6700 AA Wageningen, the Netherlands

<sup>e</sup> Shanghai Chenshan Botanical Garden, Shanghai 200062, China

<sup>f</sup> Key Laboratory of Aquatic Botany and Watershed Ecology, Chinese Academy of Sciences, Wuhan 430074, China

<sup>g</sup> Key Laboratory of the Three Gorges Reservoir Region's Eco-Environment, Ministry of Education, Chongqing University, Chongqing 400045, China

<sup>h</sup> Department of Landscape Architecture and Engineering, College of Agriculture and Biology, Shanghai Jiao Tong University, 2678 Qixin Road, Shanghai 201101, China

<sup>i</sup> School of Life Sciences, Nanjing University, Nanjing 210093, China

<sup>j</sup> School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200062, China

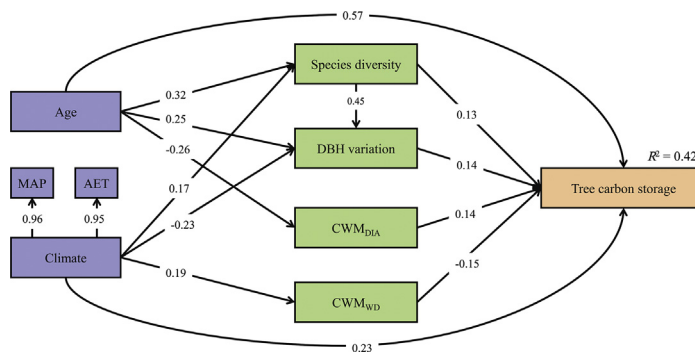
<sup>k</sup> South China Botanic Garden, Chinese Academy of Science, Guangzhou 510650, China

<sup>l</sup> Key Laboratory of Plant Resources and Biodiversity of Jiangxi Province, Jingdezhen University, 838 Cidu Avenue, Jingdezhen, Jiangxi 333000, China

### 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.

### GRAPHICAL ABSTRACT



### ARTICLE INFO

#### Article history:

Received 18 August 2018

Received in revised form 30 October 2018

Accepted 2 November 2018

Available online 05 November 2018

Editor: Elena PAOLETTI

### 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 of 480 plots

\* Corresponding author at: State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, 20 Nanxincun, Xiangshan, Beijing 100093, China.

E-mail addresses: [liyin@ibcas.ac.cn](mailto:liyin@ibcas.ac.cn) (Y. Li), [baowk@cib.ac.cn](mailto:baowk@cib.ac.cn) (W. Bao), [frans.bongers@wur.nl](mailto:frans.bongers@wur.nl) (F. Bongers), [chenbin@csnbgsh.cn](mailto:chenbin@csnbgsh.cn) (B. Chen), [chengk@ibcas.ac.cn](mailto:chengk@ibcas.ac.cn) (G. Chen), [guoke@ibcas.ac.cn](mailto:guoke@ibcas.ac.cn) (K. Guo), [mixiang@wbjcas.cn](mailto:mixiang@wbjcas.cn) (M. Jiang), [lai@ibcas.ac.cn](mailto:lai@ibcas.ac.cn) (J. Lai), [lindunmei@cqu.edu.cn](mailto:lindunmei@cqu.edu.cn) (D. Lin), [chjliu@sjtu.edu.cn](mailto:chjliu@sjtu.edu.cn) (C. Liu), [liuxiaojuan06@ibcas.ac.cn](mailto:liuxiaojuan06@ibcas.ac.cn) (X. Liu), [liuyi@ibcas.ac.cn](mailto:liuyi@ibcas.ac.cn) (Y. Liu), [mixiangcheng@ibcas.ac.cn](mailto:mixiangcheng@ibcas.ac.cn) (X. Mi), [tianxj@nju.edu.cn](mailto:tianxj@nju.edu.cn) (X. Tian), [xhwang@des.ecnu.edu.cn](mailto:xhwang@des.ecnu.edu.cn) (X. Wang), [xuwubing@ibcas.ac.cn](mailto:xuwubing@ibcas.ac.cn) (W. Xu), [jhyan@scib.ac.cn](mailto:jhyan@scib.ac.cn) (J. Yan), [zhengyr@ibcas.ac.cn](mailto:zhengyr@ibcas.ac.cn) (Y. Zheng), [kpma@ibcas.ac.cn](mailto:kpma@ibcas.ac.cn) (K. Ma).

**Keywords:**

Biodiversity–ecosystem function  
Niche complementarity  
Mass-ratio effect  
Stand age  
Environmental conditions  
Stand structure

sampled across subtropical forests in China. We use multiple regression models to test the relative effects of biodiversity, stand structural attributes, stand age and environmental conditions on tree carbon storage, and use a partial least squares path model to test how these variables directly and/or indirectly affect tree carbon storage. Our results show that tree carbon storage is most strongly affected by stand age, followed by climate, biodiversity and stand structural attributes. Stand age and climate had both direct and indirect (through species diversity, functional dominance and stand structural attributes) effects. We find that tree carbon storage correlates with both species diversity and functional dominance after stand age and environmental drivers are accounted for. Our results suggest that niche complementarity and the mass-ratio effect, not necessarily mutually exclusive, both play a role in maintaining ecosystem functioning. Our results further indicate that biodiversity conservation might be an effective way for enhancing tree carbon storage in natural, species-rich forest ecosystems.

© 2018 Elsevier B.V. All rights reserved.

## 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 above-ground 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 than at smaller scales (Waide et al., 1999; Isbell et al., 2018). Much research, therefore, is still needed to improve our understanding about the patterns and causes of B-EF relationships in natural ecosystems at large scale, 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 total ecosystem functioning, than less diverse communities (Loreau, 2000; Morin et al., 2011). This would result in a strong positive relationship between tree carbon storage and functional diversity, as well as species diversity (Zhang and Chen, 2015). The mass-ratio hypothesis proposes that ecosystem functions are driven by the traits of dominant species in the community (Grime, 1998) and predicts a significant correlation between tree carbon storage and functional dominance (e.g. community-weighted mean of trait values) (Diaz et al., 2007). Previous studies have found that tree carbon storage was positively related to community weighted mean of potential maximum diameter (Cavanaugh et al., 2014; Sullivan et al., 2017), due to tree potential maximum diameter to be linked to the ability of a species to capture light and compete against neighbors (Kraft et al., 2008). Community-weighted mean of wood density has also been considered to affect tree carbon storage (Bunker et al., 2005; Chave et al., 2009; Prado-Junior et al., 2016; Poorter et al., 2017). Which mechanism (niche complementarity vs. mass-ratio hypotheses) would underlie

the positive B-EF relationship in forest ecosystems? Several studies have found that niche complementarity was the underlying mechanism for the positive B-EF relationship (Morin et al., 2011; Zhang et al., 2012), while others argued that the mass-ratio effect was leading (Lin et al., 2016; Lohbeck et al., 2016; Fotis et al., 2018) or also played an important role in promoting ecosystem functioning (Cavanaugh et al., 2014; Ruiz-Benito et al., 2014; Ali et al., 2017).

Not only species diversity but also forest structural attributes, such as tree size variation and stem density determine forest biomass, resource capture and productivity (Poorter et al., 2015; Zhang and Chen, 2015; Ali et al., 2016; Fotis et al., 2018). Tree size variation links to forest diversity and aboveground biomass in natural forests (Zhang and Chen, 2015) through better spatial packing of different tree crowns and thus more efficient utilization of light (Yachi and Loreau, 2007). Similarly, higher stem densities have been shown to enhance tree carbon storage via greater canopy packing which leads to more light capture and higher wood production (Morin, 2015). In addition, tree size variation and stem density are at the same time influenced by species diversity (Zhang and Chen, 2015; Chiang et al., 2016). Such structural attributes of stands need to be included when testing B-EF relationships in forest.

Besides forest structural attributes, stand age and environmental conditions (e.g. climate, topographic heterogeneity) play a role in the relationships between biodiversity and natural forest tree carbon storage (Ali et al., 2016; Poorter et al., 2016; Sullivan et al., 2017). Stand age 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, 2014; Zhang and Chen, 2015). Environmental conditions may have direct effect on tree carbon storage through their influence 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 scale (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  $\geq 3$  cm in DBH in each plot were individually recorded, measured, and identified to species-level in the field between 2011 and 2012. For species that could not be identified in the field, specimen were collected and identified by relevant experts in the lab. Taxonomic names were verified against *Catalogue of Life China* (Checklist 2015, <http://www.sp2000.org.cn/>) and *Flora of China* (<http://foc.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 stand-replacing data extracted from the records of the local Forestry Bureau or by coring the fifth largest tree of each plot (Bruehlheide et al., 2011), where the number of tree rings provided a conservative estimate of stand age. The stand characteristics of the subtropical forests in China are shown in 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  $H_s = -\sum_i^S p_i \times \ln(p_i)$ , 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

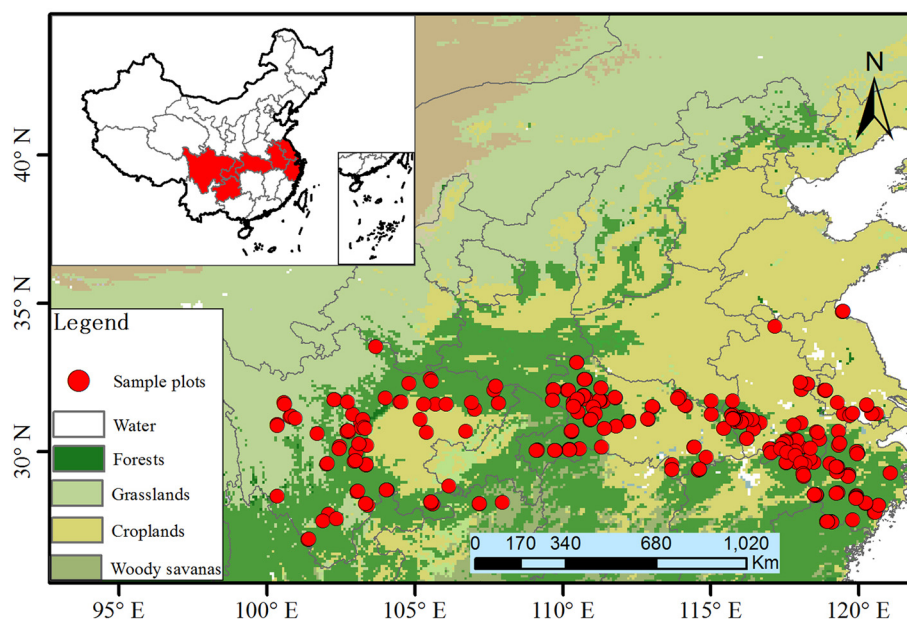


Fig. 1. Locations of the 480 sample plots across subtropical forests in China. The base vegetation map is modified from the 2012 MODIS global land cover map ([www.landcover.org/data/lc/](http://www.landcover.org/data/lc/)) with IGBP Land Cover Type Classification.



(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 ( $CWM_{WD}$ ) and maximum diameter ( $CWM_{DIA}$ ). 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 (Cavanaugh et al., 2014). Although stem diameter was used to estimate tree carbon storage at the stem level, plot  $CWM_{DIA}$  still is a relatively independent predictor of plot tree carbon storage (Ruiz-Jaen and Potvin, 2011; Cavanaugh 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 (O'Brien, 1993), and actual evapotranspiration (AET), a widely accepted proxy for plant productivity (Gaston, 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,  $CWM_{DIA}$  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 ( $AIC_c$ ), and candidate models were those with an  $AIC_c$  value close to the most parsimonious model ( $\Delta AIC_c < 2$ ) (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 (Bartoń, 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 'plsmp' 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).

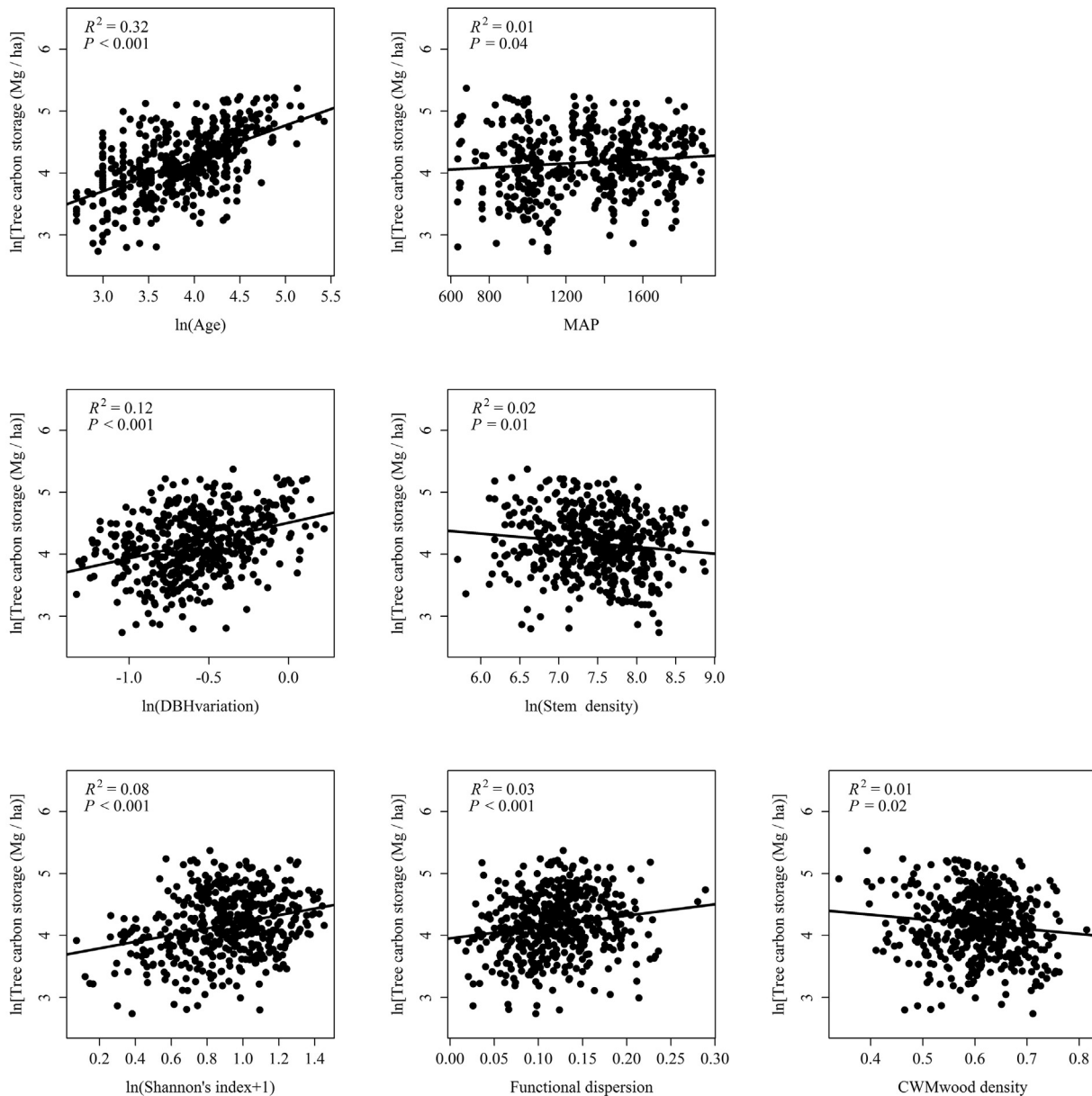
### 3. Results

#### 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  $CWM_{WD}$  had negative correlation with tree carbon storage ( $R^2 = 0.01$ ,  $P = 0.02$ ) (Fig. 2) and  $CWM_{DIA}$  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  $CWM_{DIA}$  had a positive effect,  $CWM_{WD}$  had a negative effect on tree carbon storage



**Fig. 2.** Bivariate relationships between tree carbon storage and biodiversity (Shannon's index, functional dispersion and  $CWM_{WD}$ ), stand structure (DBH variation and stem density), stand age and environmental variables (MAP) ( $N = 480$ ).

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

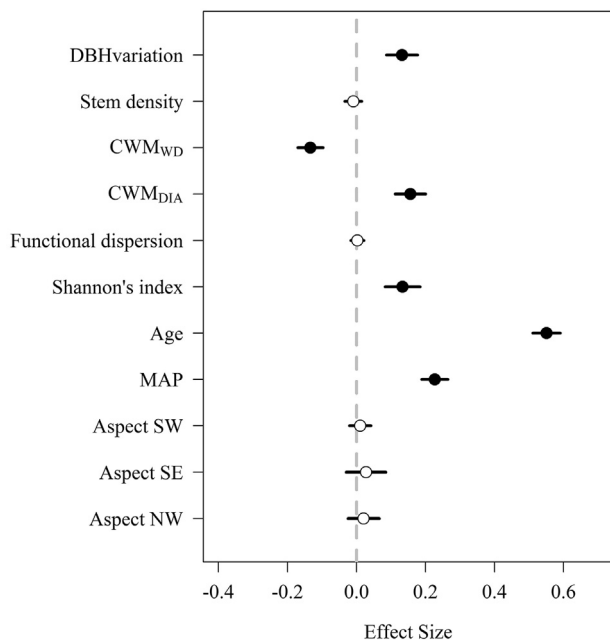
The partial least squares path model indicated that all predictor variables together explained 42% of variations in tree carbon storage ( $R^2 = 0.42$ , Fig. 4a). Stand age, climate, species diversity, DBH variation and  $CWM_{DIA}$  all had significant positive direct effects on tree carbon storage,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

negative indirect effects via  $CWM_{WD}$  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



**Fig. 3.** Multiple regression model results of tree carbon storage using biodiversity, stand structure, stand age and environmental variables. Each variable was standardized and their effect sizes (circles) were compared to determine differences in the strength of predictor variables on tree carbon storage. Closed circles indicate significant effects on tree carbon storage ( $P < 0.05$ ), and Means  $\pm$  1 SE (standard error) are shown.

experimental studies (Huang et al., 2018; Niklaus et al., 2017) and relatively simple boreal (Paquette and Messier, 2011; Zhang and Chen, 2015) and temperate forests (Paquette and Messier, 2011) can also be extended to natural, species-rich (sub)tropical forest ecosystems.

#### 4.1. How does biodiversity promote tree carbon storage in subtropical forests?

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 (Vilà 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 hyperdiverse 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).

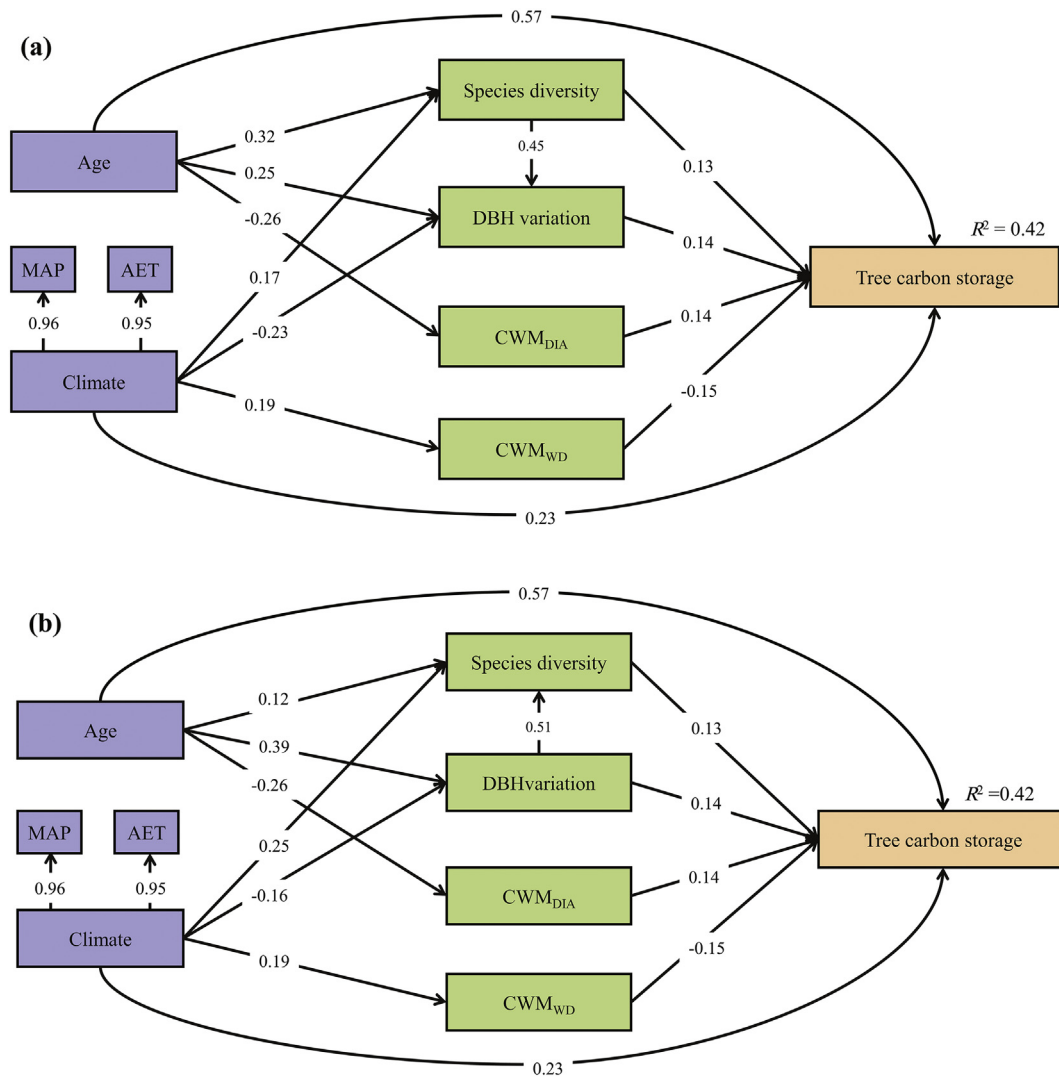
While species diversity was positively related to tree carbon storage, functional diversity had a weak positive effect in bivariate relationship (Fig. 2), but a neutral independent effect on tree carbon storage after other variables were accounted for (Fig. 3), not consistent with the niche complementarity 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<sub>DIA</sub>, a measure of functional dominance, significantly impacted tree carbon storage. Forests with a higher CWM<sub>DIA</sub> 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<sub>WD</sub> 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., 2009), leading to a negative correlation between CWM<sub>WD</sub> and basal area. Indeed, we found such a negative relationship ( $r = -0.13$ ,  $P = 0.004$ ), suggesting lower CWM<sub>WD</sub> 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 averaged 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<sub>DIA</sub>, CWM<sub>WD</sub> 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



**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.

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<sub>DIA</sub> and DBH variation had independent positive effects on tree carbon storage, CWM<sub>WD</sub> 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.



**Table 1**

Direct, indirect and total standardized effects of stand age, climate, species diversity and CWM of trait values on tree carbon storage base on partial least squares path modeling (PLS-PM). Significant effects are at  $P < 0.05$  (\*),  $< 0.01$  (\*\*), and  $< 0.001$  (\*\*\*)

Predictor	Pathway to tree carbon storage	Effect	
		Model in Fig. 4a	Model in Fig. 4b
Stand age	Direct effect	0.57***	0.57***
	Indirect through species diversity	0.04**	0.02*
	Indirect through DBH variation	0.04**	0.06**
	Indirect through CWM <sub>DIA</sub>	-0.04**	-0.04**
	Total effect	0.61	0.61
Climate	Direct effect	0.23***	0.23***
	Indirect through species diversity	0.02*	0.03*
	Indirect through DBH variation	-0.04**	-0.02**
	Indirect through CWM <sub>WD</sub>	-0.03**	-0.03**
	Total effect	0.18	0.21
Species diversity	Direct effect	0.13**	0.13**
	Indirect through DBH variation	0.06**	-
	Total effect	0.19	0.13
DBH variation	Direct effect	0.14**	0.14**
	Indirect through species diversity	-	0.07**
	Total effect	0.14	0.21
CWM <sub>DIA</sub>	Direct effect	0.14**	0.14**
	Indirect effect	-	-
	Total effect	0.14	0.14
CWM <sub>WD</sub>	Direct effect	-0.15**	-0.15**
	Indirect effect	-	-
	Total effect	-0.15	-0.15

## Acknowledgements

We are grateful to all the field investigators. We would also like to thank Prof. Bernhard Schmid, Ms. Yanhong Bing, Dr. Yuanjie Xu and many others for their help. This work was financially supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDA19050404, XDA05050204).

## 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

- Ali, A., Yan, E.R., Chen, H.Y.H., Chang, S.X., Zhao, Y.T., Yang, X.D., Xu, M.S., 2016. Stand structural diversity rather than species diversity enhances aboveground carbon storage in secondary subtropical forests in eastern China. *Biogeosciences* 13, 4627–4635.
- Ali, A., Yan, E.R., Chang, S.X., Cheng, J.Y., Liu, X.Y., 2017. Community-weighted mean of leaf traits and divergence of wood traits predict aboveground biomass in secondary subtropical forests. *Sci. Total Environ.* 574, 654–662.
- Alves, L.F., Vieira, S.A., Scaranello, M.A., Camargo, P.B., Santos, F.A.M., Joly, C.A., Martinelli, L.A., 2010. Forest structure and live aboveground biomass variation along an elevational gradient of tropical Atlantic moist forest (Brazil). *For. Ecol. Manage.* 260, 679–691.
- Bartoň, K., 2016. MuMIn: Multi-Model Inference. R package version 1.15.6. Retrieved from <https://CRAN.R-project.org/package=MuMIn>.
- Becknell, J.M., Powers, J.S., 2014. Stand age and soils as drivers of plant functional traits and aboveground biomass in secondary tropical dry forest. *Can. J. For. Res.* 44, 604–613.
- Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. Soc. B. Methodol.* 57, 289–300.
- Bonan, G.B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320, 1444–1449.
- Brassard, B.W., Chen, H.Y.H., Wang, J.R., Duinker, P.N., 2008. Effects of time since stand-replacing fire and overstory composition on live-tree structural diversity in the boreal forest of Central Canada. *Can. J. For. Res.* 38, 52–62.
- Brown, S., 1997. Estimating Biomass and Biomass Change of Tropical Forests: A Primer. FAO, Rome, Italy.
- Bruelheide, H., Böhnke, M., Both, S., Fang, T., Assmann, T., Baruffol, M., Bauhus, J., Buscot, F., Chen, X.Y., Ding, B.Y., Durka, W., Erfmeier, A., Fischer, M., Geißler, C., Guo, D.L., Guo, L.D., Härdtle, W., He, J.S., Hector, A., Kröber, W., Kühn, P., Lang, A.G., Nadrowski, K., Pei, K.Q., Scherer-Lorenzen, M., Shi, X.Z., Scholten, T., Schuldt, A., Trogisch, S., von Oheimb, G., Welk, E., Wirth, C., Wu, Y.T., Yang, X.F., Zeng, X.Q., Zhang, S.R., Zhou, H.Z., Ma, K.P., Schmid, B., 2011. Community assembly during secondary forest succession in a Chinese subtropical forest. *Ecol. Monogr.* 81, 25–41.

- Bunker, D.E., DeClerck, F., Bradford, J.C., Colwell, R.K., Perfecto, I., Phillips, O.L., Sankaran, M., Naeem, S., 2005. Species loss and aboveground carbon storage in a tropical forest. *Science* 310, 1029–1031.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*. Springer, New York.
- Camptella, G., Botta-Dukát, Z., Wellstein, C., Canullo, R., Gatto, S., Chelli, S., Mucina, L., Bartha, S., 2011. Patterns of plant trait–environment relationships along a forest succession chronosequence. *Agric. Ecosyst. Environ.* 145, 38–48.
- Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S., Loreau, M., Weis, J.J., 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proc. Natl. Acad. Sci. U. S. A.* 104, 18123–18128.
- Cardinale, B.J., Matulich, K.L., Hooper, D.U., Byrnes, J.E., Duffy, E., Gamfeldt, L., Balvanera, P., O'Connor, M.I., Gonzalez, A., 2011. The functional role of producer diversity in ecosystems. *Am. J. Bot.* 98, 572–592.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. *Nature* 486, 59–67.
- de Castilho, C.V., Magnusson, W.E., de Araújo, R.N.O., Luizão, R.C.C., Luizão, F.J., Lima, A.P., Higuchi, N., 2006. Variation in aboveground tree live biomass in a central Amazonian Forest: effects of soil and topography. *For. Ecol. Manage.* 234, 85–96.
- Cavanaugh, K.C., Gosnell, J.S., Davis, S.L., Ahumada, J., Boundja, P., Clark, D.B., Mugerwa, B., Jansen, P.A., O'Brien, T.G., Rovero, F., Sheil, D., Vasquez, R., Anelman, S., 2014. Carbon storage in tropical forests correlates with taxonomic diversity and functional dominance on a global scale. *Glob. Ecol. Biogeogr.* 23, 563–573.
- Chave, J., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., Steege, H.t., Webb, C.O., 2006. Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecol. Appl.* 16, 2356–2367.
- Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. *Ecol. Lett.* 12, 351–366.
- Chen, H.Y.H., Taylor, A.R., 2012. A test of ecological succession hypotheses using 55-year time-series data for 361 boreal forest stands. *Glob. Ecol. Biogeogr.* 21, 441–454.
- Chen, H.Y.H., Luo, Y., Reich, P.B., Searle, E.B., Biswas, S.R., 2016. Climate change-associated trends in net biomass change are age dependent in western boreal forests of Canada. *Ecol. Lett.* 19, 1150–1158.
- Chiang, J.M., Spasojevic, M.J., Muller-Landau, H.C., Sun, I.F., Lin, Y., Sus, S.H., Chen, Z., Chen, C.T., Swenson, N.G., McEwan, R.W., 2016. Functional composition drives ecosystem function through multiple mechanisms in a broadleaved subtropical forest. *Oecologia* 182, 829–840.
- Chisholm, R.A., Muller-Landau, H.C., Abdul Rahman, K., Bebb, D.P., Bin, Y., Bohlman, S.A., Bourg, N.A., Brinks, J., Bunyavechewin, S., Butt, N., Cao, H., Cao, M., Cárdenas, D., Chang, L.W., Chiang, J.M., Chuyong, G., Condit, R., Dattaraja, H.S., Davies, S., Duque, A., Fletcher, C., Gunatilleke, N., Gunatilleke, S., Hao, Z., Harrison, R.D., Howe, R., Hsieh, C.F., Hubbell, S.P., Itoh, A., Kenfack, D., Kiratiprayoon, S., Larson, A.J., Lian, J., Lin, D., Liu, H., Lutz, J.A., Ma, K., Malhi, Y., McMahon, S., McShea, W., Meegaskumbura, M., Mohd. Razman, S., Morecroft, M.D., Nytch, C.J., Oliveira, A., Parker, G.G., Pulla, S., Puchi-Manage, R., Romero-Saltos, H., Sang, W., Schurman, J., Su, S.H., Sukumar, R., Sun, I.F., Suresh, H.S., Tan, S., Thomas, D., Thomas, S., Thompson, J., Valencia, R., Wolf, A., Yap, S., Ye, W., Yuan, Z., Zimmerman, J.K., 2013. Scale-dependent relationships between tree species richness and ecosystem function in forests. *J. Ecol.* 101, 1214–1224.
- Chu, C.J., Weiner, J., Maestre, F.T., Xiao, S., Wang, Y.S., Li, Q., Yuan, J.L., Zhao, L.Q., Ren, Z.W., Wang, G., 2009. Positive interactions can increase size inequality in plant populations. *J. Ecol.* 97, 1401–1407.
- Clark, J.S., 2010. Individuals and the variation needed for high species diversity in forest trees. *Science* 327, 1129–1132.
- De Deyn, G.B., Cornelissen, J.H., Bardgett, R.D., 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecol. Lett.* 11, 516–531.
- van der Sande, M.T., Peña-Claros, M., Ascarrunz, N., Arets, E.J.M.M., Licona, J.C., Toledo, M., Poorter, L., 2017. Abiotic and biotic drivers of biomass change in a Neotropical forest. *J. Ecol.* 105, 1223–1234.
- Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., Robson, T.M., 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proc. Natl. Acad. Sci. U. S. A.* 104, 20684–20689.
- Ecosystem Carbon Sequestration Project, 2015. *Observation and Investigation for Carbon Sequestration in Terrestrial Ecosystems by Technical Manual Writing Group of Ecosystem Carbon Sequestration Project*. Science Press, Beijing.
- Falster, D.S., Westoby, M., 2005. Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. *J. Ecol.* 93, 521–535.
- Fang, J., Shen, Z., Tang, Z., Wang, X., Wang, Z., Feng, J., Liu, Y., Qiao, X., Wu, X., Zheng, C., 2012. Forest community survey and the structural characteristics of forests in China. *Ecography* 35, 1059–1071.
- Finegan, B., Peña-Claros, M., de Oliveira, A., Ascarrunz, N., Bret-Harte, M.S., Carreño-Rocabado, G., Casanoves, F., Díaz, S., Velepucha, P.E., Fernandez, F., Licona, J.C., Lorenzo, L., Salgado Negret, B., Vaz, M., Poorter, L., 2015. Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. *J. Ecol.* 103, 191–201.
- Forrester, D.I., 2014. The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. *For. Ecol. Manage.* 312, 282–292.
- Fotis, A.T., Murphy, S.J., Ricart, R.D., Krishnadas, M., Whitacre, J., Wenzel, J.W., Queenborough, S.A., Comita, L.S., 2018. Above-ground biomass is driven by mass-ratio effects and stand structural attributes in a temperate deciduous forest. *J. Ecol.* 106, 561–571.
- Gaston, K.J., 2000. Global patterns in biodiversity. *Nature* 405, 220–227.
- Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* 86, 902–910.



- Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Höglberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Körner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prins, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.D., Siamantziouras, A.S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S., Lawton, J.H., 1999. Plant diversity and productivity experiments in European grasslands. *Science* 286, 1123–1127.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978.
- Huang, Y.Y., Chen, Y.X., Castro-Izaguirre, N., Baruffol, M., Brezzi, M., Lang, A., Li, Y., Härdtke, W., von Oheimb, G., Yang, X.F., Liu, X.J., Pei, K.Q., Both, S., Yang, B., Eichenberg, D., Assmann, T., Bauhus, J., Behrens, T., Buscot, F., Chen, X.Y., Chesters, D., Ding, B.Y., Durka, W., Erfmeier, A., Fang, J.Y., Fischer, M., Weigelt, A., Wu, L.D., Guo, D.L., Gutknecht, J.L.M., He, J.S., He, C.L., Hector, A., Hönl, L., Hu, R.Y., Klein, A.M., Kühn, P., Liang, Y., Li, S., Michalski, S., Scherer-Lorenzen, M., Schmidt, K., Scholten, T., Schuldt, A., Shi, X.Z., Tan, M.Z., Tang, Z.Y., Trogisch, S., Wang, Z.W., Welk, E., Wirth, C., Wubet, T., Xiang, W.H., Yu, M.J., Yu, X.D., Zhang, J.Y., Zhang, S.R., Zhang, N.L., Zhou, H.Z., Zhu, C.D., Zhu, L., Bruelheide, H., Ma, K.P., Niklaus, P.A., Schmid, B., 2018. Impacts of species richness on productivity in a large-scale subtropical forest experiment. *Science* 362, 80–83.
- Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., Scherer-Lorenzen, M., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B.J., Zavaleta, E.S., Loreau, M., 2011. High plant diversity is needed to maintain ecosystem services. *Nature* 477, 199–202.
- Isbell, F., Cowles, J., Dee, L.E., Loreau, M., Reich, P.B., Gonzalez, A., Hector, A., Schmid, B., 2018. Quantifying effects of biodiversity on ecosystem functioning across times and places. *Ecol. Lett.* 21, 763–778.
- Jucker, T., Avăcăriței, D., Bărnoaiea, I., Duduman, G., Bouriaud, O., Coomes, D.A., 2016. Climate modulates the effects of tree diversity on forest productivity. *J. Ecol.* 104, 388–398.
- Kraft, N.J.B., Valencia, R., Ackerly, D.D., 2008. Functional traits and niche-based tree community assembly in an amazonian forest. *Science* 322, 580–582.
- Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91, 299–305.
- Lei, X., Wang, W., Peng, C., 2009. Relationships between stand growth and structural diversity in spruce-dominated forests in New Brunswick, Canada. *Can. J. For. Res.* 39, 1835–1847.
- Lin, D., Anderson-Teixeira, K.J., Lai, J., Mi, X., Ren, H., Ma, K., 2016. Traits of dominant tree species predict local scale variation in forest aboveground and topsoil carbon stocks. *Plant Soil* 409, 435–446.
- Liu, X.J., Swenson, N.G., Lin, D.M., Mi, X.C., Umaña, M.N., Schmid, B., Ma, K.P., 2016. Linking individual-level functional traits to tree growth in a subtropical forest. *Ecology* 97, 2396–2405.
- Lohbeck, M., Bongers, F., Martínez-Ramos, M., Poorter, L., 2016. The importance of biodiversity and dominance for multiple ecosystem functions in a human-modified tropical landscape. *Ecology* 97, 2772–2779.
- Loreau, M., 2000. Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* 91, 3–17.
- Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412, 72–76.
- Luo, Z.K., Feng, W.T., Luo, Y.Q., Baldock, J., Wang, E.L., 2017. Soil organic carbon dynamics jointly controlled by climate, carbon inputs, soil properties and soil carbon fractions. *Glob. Chang. Biol.* 23, 4430–4439.
- Michaletz, S.T., Cheng, D., Kerkhoff, A.J., Enquist, B.J., 2014. Convergence of terrestrial plant production across global climate gradients. *Nature* 512, 39–43.
- Morin, X., 2015. Species richness promotes canopy packing: a promising step towards a better understanding of the mechanisms driving the diversity effects on forest functioning. *Funct. Ecol.* 29, 993–994.
- Morin, X., Fahse, L., Scherer-Lorenzen, M., Bugmann, H., 2011. Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecol. Lett.* 14, 1211–1219.
- Murphy, S.J., Audino, L.D., Whitacre, J., Eck, J.L., Wenzel, J.W., Queenborough, S.A., Comita, L.S., 2015. Species associations structured by environment and land-use history promote beta-diversity in a temperate forest. *Ecology* 96, 705–715.
- Niklaus, P.A., Baruffol, M., He, J.S., Ma, K.P., Bernhard, S., 2017. Can niche plasticity promote biodiversity–productivity relationships through increased complementarity? *Ecology* 98, 1104–1116.
- Obrien, E.M., 1993. Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa's woody flora. *J. Biogeogr.* 20, 181–198.
- Paquette, A., Messier, C., 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. *Glob. Ecol. Biogeogr.* 20, 170–180.
- Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. *Ecol. Lett.* 9, 741–758.
- Pike, N., 2011. Using false discovery rates for multiple comparisons in ecology and evolution. *Methods Ecol. Evol.* 2, 278–282.
- Poorter, L., van der Sande, M.T., Thompson, J., Arets, E.J.M.M., Alarcón, A., Álvarez-Sánchez, J., Ascarrunz, N., Balvanera, P., Barajas-Guzmán, G., Boit, A., Bongers, F., Carvalho, F.A., Casanoves, F., Cornejo-Tenorio, G., Costa, F.R.C., de Castilho, C.V., Duivenvoorden, J.F., Dutrieux, L.P., Enquist, B.J., Fernández-Méndez, F., Finegan, B., Gormley, L.H.L., Healey, J.R., Hoosbeek, M.R., Ibarra-Manríquez, G., Junqueira, A.B., Levis, C., Licona, J.C., Lisboa, L.S., Magnusson, W.E., Martínez-Ramos, M., Martínez-Yrizar, A., Martorano, L.G., Maskell, L.C., Mazzei, L., Meave, J.A., Mora, F., Muñoz, R., Nytych, C., Pansonato, M.P., Parr, T.W., Paz, H., Pérez-García, E.A., Rentería, L.Y., Rodríguez-Velázquez, J., Rozendaal, D.M.A., Ruschel, A.R., Sakschewski, B., Salgado-Negret, B., Schiatti, J., Simões, M., Sinclair, F.L., Souza, P.F., Souza, F.C., Strapp, J., ter Steege, H., Swenson, N.G., Thonicke, K., Toledo, M., Uriarte, M., van der Hout, P., Walker, P., Zamora, N., Peña-Claros, M., 2015. Diversity enhances carbon storage in tropical forests. *Glob. Ecol. Biogeogr.* 24, 1314–1328.
- Poorter, L., Bongers, F., Aide, T.M., Zambrano, A.A.M., Balvanera, P., Becknell, J.M., Boukili, V., Brancalion, P.H., Broadbent, E.N., Chazdon, R.L., Craven, D., de Almeida-Cortez, J.S., Cabral, G.A., de Jong, B.H., Denslow, J.S., Dent, D.H., DeWalt, S.J., Dupuy, J.M., Durán, S.M., Espirito-Santo, M.M., Fandino, M.C., César, R.G., Hall, J.S., Hernandez-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher, S.G., Licona, J.C., Lohbeck, M., Marín-Spiotta, E., Martínez-Ramos, M., Massoca, P., Meave, J.A., Mesquita, R., Mora, F., Muñoz, R., Muscarella, R., Nunes, Y.R., Ochoa-Gaona, S., de Oliveira, A.A., Orihuela-Belmonte, E., Peña-Claros, M., Pérez-García, E.A., Piotta, D., Powers, J.S., Rodríguez-Velázquez, J., Romero-Pérez, I.E., Ruíz, J., Saldarriaga, J.G., Sanchez-Azofeifa, A., Schwartz, N.B., Steininger, M.K., Swenson, N.G., Toledo, M., Uriarte, M., van Breugel, M., van der Wal, H., Veloso, M.D., Vester, H.F., Vicentini, A., Vieira, I.C., Bentes, T.V., Williamson, G.B., Rozendaal, D.M., 2016. Biomass resilience of Neotropical secondary forests. *Nature* 530, 211–214.
- Poorter, L., van der Sande, M.T., Arets, E.J.M.M., Ascarrunz, N., Enquist, B., Finegan, B., Licona, J.C., Martínez-Ramos, M., Mazzei, L., Meave, J.A., Muñoz, R., Nytych, C.J., de Oliveira, A.A., Pérez-García, E.A., Prado-Junior, J., Rodríguez-Velázquez, J., Ruschel, A.R., Salgado-Negret, B., Schiavini, I., Swenson, N.G., Tenorio, E.A., Thompson, J., Toledo, M., Uriarte, M., van der Hout, P., Zimmerman, J.K., Peña-Claros, M., 2017. Biodiversity and climate determine the functioning of Neotropical forests. *Glob. Ecol. Biogeogr.* 26, 1423–1434.
- Prado-Junior, J.A., Schiavini, I., Vale, V.S., Arantes, C.S., van der Sande, M.T., Lohbeck, M., Poorter, L., 2016. Conservative species drive biomass productivity in tropical dry forests. *J. Ecol.* 104, 817–827.
- Pretzsch, H., Biber, P., Schütze, G., Uhl, E., Rötzer, T., 2014. Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nat. Commun.* 5, 4967.
- R Development Core Team, 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria <https://www.r-project.org/>.
- Reich, P.B., Tilman, D., Isbell, F., Mueller, K., Hobbie, S.E., Flynn, D.F.B., Eisenhauer, N., 2012. Impacts of biodiversity loss escalate through time as redundancy fades. *Science* 336, 589–592.
- Ruiz-Benito, P., Gómez-Aparicio, L., Paquette, A., Messier, C., Kattge, J., Zavala, M.A., 2014. Diversity increases carbon storage and tree productivity in Spanish forests. *Glob. Ecol. Biogeogr.* 23, 311–322.
- Ruiz-Jaen, M.C., Potvin, C., 2011. Can we predict carbon stocks in tropical ecosystems from tree diversity? Comparing species and functional diversity in a plantation and a natural forest. *New Phytol.* 189, 978–987.
- Sanchez, G., 2013. PLS Path Modeling with R. Trowchez Editions, Berkeley.
- Sharma, C.M., Giroloa, S., Baduni, N.P., Ghildiyal, S.K., Suyal, S., 2011. Variation in carbon stocks on different slope aspects in seven major forest types of temperate region of Garhwal Himalaya, India. *J. Biosci.* 36, 701–708.
- Stegen, J.C., Swenson, N.G., Valencia, R., Enquist, B.J., Thompson, J., 2009. Above-ground forest biomass is not consistently related to wood density in tropical forests. *Glob. Ecol. Biogeogr.* 18, 617–625.
- Sullivan, M.J., Talbot, J., Lewis, S.L., Phillips, O.L., Qie, L., Begne, S.K., Chave, J., Cuni-Sanchez, A., Hubau, W., Lopez-Gonzalez, G., Miles, L., Monteagudo-Mendoza, A., Sonke, B., Sunderland, T., ter Steege, H., White, L.J., Affum-Baffoe, K., Aiba, S.I., de Almeida, E.C., de Oliveira, E.A., Alvarez-Loayza, P., Davila, E.A., Andrade, A., Aragao, L.E., Ashton, P., Aymard, C.G., Baker, T.R., Balinga, M., Banin, L.F., Baraloto, C., Bastin, J.F., Berry, N., Bogaert, J., Bonal, D., Bongers, F., Brienen, R., Camargo, J.L., Cerón, C., Moscoso, V.C., Chezeaux, E., Clark, C.J., Pacheco, A.C., Comiskey, J.A., Valverde, F.C., Coronado, E.N., Dargie, G., Davies, S.J., De Canniere, C., Djuikouo, K.M., Doucet, J.L., Erwin, T.L., Espejo, J.S., Ewango, C.E., Fauser, S., Feldpausch, T.R., Herrera, R., Gilpin, M., Gloor, E., Hall, J.S., Harris, D.J., Hart, T.B., Kartawinata, K., Kho, L.K., Kitayama, K., Laurance, S.G., Laurance, W.F., Leal, M.E., Lovejoy, T., Lovett, J.C., Lukas, F.M., Makana, J.R., Malhi, Y., Maracahipes, L., Marimon, B.S., Junior, B.H., Marshall, A.R., Morandi, P.S., Mukendi, J.T., Mukinzi, J., Nilus, R., Vargas, P.N., Camacho, N.C., Pardo, G., Peña-Claros, M., Pétronelli, P., Pickavance, G.C., Poulsen, A.D., Poulsen, J.R., Primack, R.B., Priyadi, H., Quesada, C.A., Reitsma, J., Réjou-Méchain, M., Restrepo, Z., Rutishauser, E., Salim, K.A., Salomão, R.P., Samsodin, I., Sheil, D., Sierra, R., Silveira, M., Slik, J.W., Steel, L., Taedoung, H., Tan, S., Terborgh, J.W., Thomas, S.C., Toledo, M., Umuunay, P.M., Gamarra, L.V., Vieira, I.C., Vos, V.A., Wang, O., Willcock, S., Zedler, L., 2017. Diversity and carbon storage across the tropical forest biome. *Sci. Rep.* 7, 39102.
- Swenson, N.G., Enquist, B.J., 2008. The relationship between stem and branch wood specific gravity and the ability of each measure to predict leaf area. *Am. J. Bot.* 95, 516–519.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277, 1300–1302.
- Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T., Lehman, C., 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294, 843–845.
- Toledo, M., Poorter, L., Peña-Claros, M., Alarcón, A., Balcázar, J., Leão, C., Licona, J.C., Llanque, O., Vroomans, V., Zuidema, P., Bongers, F., 2011. Climate is a stronger driver of tree and forest growth rates than soil and disturbance. *J. Ecol.* 99, 254–264.
- Vilà, M., Vayreda, J., Gracia, C., Ibáñez, J.J., 2003. Does tree diversity increase wood production in pine forests? *Oecologia* 135, 299–303.
- Vilà, M., Vayreda, J., Comas, L., Ibáñez, J.J., Mata, T., Obón, B., 2007. Species richness and wood production: a positive association in Mediterranean forests. *Ecol. Lett.* 10, 241–250.
- Wagg, C., Bender, S.F., Widmer, F., van der Heijden, M.G.A., 2014. Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proc. Natl. Acad. Sci. U. S. A.* 111, 5266–5270.
- Waide, R.B., Willing, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P., Parmenter, R., 1999. The relationship between productivity and species richness. *Annu. Rev. Ecol. Syst.* 30, 257–300.

- Whitmore, T.C., 1998. *An Introduction to Tropical Rain Forests*. Oxford University Press, Oxford.
- Wu, X., Wang, X., Tang, Z., Shen, Z., Zheng, C., Xia, X., Fang, J., 2014. The relationship between species richness and biomass changes from boreal to subtropical forests in China. *Ecography* 38, 602–613.
- Yachi, S., Loreau, M., 2007. Does complementary resource use enhance ecosystem functioning? A model of light competition in plant communities. *Ecol. Lett.* 10, 54–62.
- Yuan, Z., Wang, S., Gazol, A., Mellard, J., Lin, F., Ye, J., Hao, Z., Wang, X., Loreau, M., 2016. Multiple metrics of diversity have different effects on temperate forest functioning over succession. *Oecologia* 182, 1175–1185.
- Zhang, Y., Chen, H.Y.H., 2015. Individual size inequality links forest diversity and above-ground biomass. *J. Ecol.* 103, 1245–1252.
- Zhang, S.B., Slik, J.W.F., Zhang, J.L., Cao, K.F., 2011. Spatial patterns of wood traits in China are controlled by phylogeny and the environment. *Glob. Ecol. Biogeogr.* 20, 241–250.
- Zhang, Y., Chen, H.Y.H., Reich, P.B., 2012. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *J. Ecol.* 100, 742–749.