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# Community-weighted mean of leaf traits and divergence of wood traits predict aboveground biomass in secondary subtropical forests



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## HIGHLIGHTS

## GRAPHICAL ABSTRACT

- Aboveground biomass is associated with functional divergence of wood traits.
- Aboveground biomass is associated with community-weighted mean of leaf traits.
- Leaf and wood economics are decoupled for influencing ecosystem functioning.
- Community-weighted mean of leaf and divergence of wood traits alone and jointly affect aboveground biomass.
- Both the mass ratio and niche complementarity hypotheses regulate aboveground biomass.



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# ABSTRACT

Subtropical forests are globally important in providing ecological goods and services, but it is not clear whether functional diversity and composition can predict aboveground biomass in such forests. We hypothesized that high aboveground biomass is associated with high functional divergence (FDvar, i.e., niche complementarity) and community-weighted mean (CWM, i.e., mass ratio; communities dominated by a single plant strategy) of trait values. Structural equation modeling was employed to determine the direct and indirect effects of stand age and the residual effects of CWM and FDvar on aboveground biomass across 31 plots in secondary forests in subtropical China. The CWM model accounted for 78, 20, 6 and 2% of the variation in aboveground biomass, nitrogen concentration in young leaf, plant height and specific leaf area of young leaf, respectively. The FDvar model explained 74, 13, 7 and 0% of the variation in aboveground biomass, plant height, twig wood density and nitrogen concentration in young leaf, respectively. The variation in aboveground biomass, CWM of leaf nitrogen concentration in young leaf, respectively. The variation in aboveground biomass, CWM of leaf nitrogen concentration in young leaf, respectively. The variation in aboveground biomass, CWM of leaf nitrogen concentration in young leaf respectively. The variation in aboveground biomass, was negatively direct effect but low indirect positive effects on aboveground biomass. Aboveground biomass was negatively

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related to CWM of nitrogen concentration in young leaf, but positively related to CWM of specific leaf area of young leaf and plant height, and FDvar of plant height, twig wood density and nitrogen concentration in young leaf. Leaf and wood economics spectra are decoupled in regulating the functionality of forests, communities with diverse species but high nitrogen conservative and light acquisitive strategies result in high aboveground biomass, and hence, supporting both the mass ratio and niche complementarity hypotheses in secondary subtropical forests.

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#### 1. Introduction

Understanding the relationship between the plant functional trait diversity and aboveground biomass is important for managing carbon storage in aboveground biomass and mitigating the increasing atmospheric CO<sub>2</sub> concentration (Díaz et al., 2011). When compared to species and/or structural diversity - aboveground biomass relationships (Ali et al., 2016; Dănescu et al., 2016), our understanding of how functional trait diversity and composition influence aboveground biomass in forest ecosystems remains poor. Plant functional traits affect plant fitness and performance directly or indirectly (Violle et al., 2007), trait-based approaches thus are rapidly emerging as a promising way to understand underlying ecological mechanisms that operate in plant communities. Functional divergence (FDvar, referring to niche complementarity) and community-weighted mean (CWM, or mass ratio, referring to the degree of a communities dominated by a single plant strategy) are two independent measures of biodiversity (Diaz et al., 2007). It is becoming increasingly evident that functional trait composition (i.e., CWM) rather than functional trait diversity (i.e., FDvar) strongly affects aboveground biomass in tropical forests (Becknell and Powers, 2014; Conti and Díaz, 2013; Finegan et al., 2015). However, relationships between functional traits and aboveground biomass may be fundamentally different among forest types because resource limitations to plant growth are specific in different types of forests (Lohbeck et al., 2013). In addition, aboveground biomass, and CWM and FDvar of plant trait values are at the same time influenced by stand age (Becknell and Powers, 2014). Stand age, hence, may directly and indirectly affect aboveground biomass via CWM and FDvar of trait values (Fig. 1). To date, our understanding of how FDvar and CWM of trait values predict aboveground biomass in forest communities remains unclear when stand age is considered.

The mass ratio hypothesis postulates that ecosystem processes are driven by the (traits of the) most abundant species in plant communities (Grime, 1998). According to this hypothesis, communities dominated by plants with a single resource use strategy have high aboveground biomass. If the mass ratio mechanism plays a role, aboveground biomass should be closely associated to CWM of trait values (Fig. 1a), a community metric that weighs species trait values by the relative abundance of the species in a community (Conti and Díaz, 2013; Diaz et al., 2007; Garnier et al., 2004). However, the relationship between CWM of trait values and aboveground biomass may be fundamentally dependent on stand age (Fig. 1). The niche complementarity hypothesis states that functional traits can mediate niche partitioning and lead to different resource utilization by plants across space (Petchey and Gaston, 2006); for example, through the formation of stratified mixtures of sun- and shade-adapted species in a community. Therefore, it is expected that a forest community with high aboveground biomass has a diverse group of species with a high variety of functional strategies (Zhang and Chen, 2015; Zhang et al., 2012; Fig. 1b).

In natural forests, the importance of functional trait diversity and composition to aboveground biomass has recently been recognized and debated (Becknell and Powers, 2014; Conti and Díaz, 2013; Finegan et al., 2015). The opposite relationships between aboveground biomass and CWM and/or FDvar of trait values in forest communities might be attributed primarily to weak relationships between individual traits and broad functional strategies, particularly trade-offs between 'grow fast and die young' versus 'grow slow and live long', as suggested by leaf (Wright et al., 2004), wood (Chave et al., 2009), and whole-plant (Reich, 2014) economics spectra. In addition, relationships between functional traits are measured, because functional strategies of different organs are not necessarily coordinated, and leaf and stem



**Fig. 1.** Conceptual models for the prediction of aboveground biomass in secondary subtropical forests of eastern China, showing hypothesized relationships of how stand age affects functional divergence (FDvar) and community-weighted mean (CWM) of functional traits, and how stand age, FDvar and CWM concomitantly affect aboveground biomass. Three conceptual models were proposed based on individual and joint effects of FDvar and CWM of trait values, after accounting for the effects of stand age; a) MRH (mass ratio hypothesis) model; b) NCH (niche complementarity hypothesis) model; and c) joint model of MRH and NCH. The positive (+) and negative (-) signs indicate the direct effect of exogenous (independent) on endogenous (dependent) variables.

economics spectra can be decoupled (Baraloto et al., 2010). Moreover, the shift in functional strategies of plants with forest succession (Yan et al., 2006) might also lead to uncertain relationships between growth/turnover rates and aboveground biomass in different aged forests. In this context, we hypothesize that aboveground biomass increases with stand age, and the residual variation in aboveground biomass can be individually (Fig. 1a and b) and jointly (Fig. 1c) explained by FDvar and CWM of trait values in secondary forest communities. We predict that high aboveground biomass shall be associated with the divergence and/or dominance (on average) of conservative or acquisitive leaf and wood traits.

We have recently reported that stand structural diversity rather than species diversity is a major determinant of aboveground carbon storage in secondary subtropical forests (Ali et al., 2016). In this study, we aim to investigate the individual and joint residual effects of CWM and FDvar of trait values on aboveground biomass, after considering for the effects of stand age (Fig. 1), across 31 plots in secondary subtropical forests in eastern China. We asked the following three questions to evaluate whether the relationships reported for tropical moist, wet and dry forests also hold for secondary subtropical forests: 1) how are CWM and FDvar of trait values associated with aboveground biomass in secondary forests with a range of stand ages? 2) which mechanism - the mass ratio or the niche complementarity alone or jointly would explain the residual variation in aboveground biomass? and 3) what are the relative effect (measured in the form of standardized coefficients) of each predictor for predicting aboveground biomass, after the direct effect of stand age on each predictor (CWM and/or FDvar of traits) is accounted for?

## 2. Materials and methods

#### 2.1. Study sites

The study was conducted in the lower eastern extension of the Siming Mountain (29°41–50′N, 121°36–52′E), Zhejiang Province, in eastern China. Under a warm and humid subtropical monsoon climate, the area has an average temperature of 28.1 °C and 4.2 °C in the warmest and coldest months, respectively. The mean annual precipitation is 1374.7 mm with most of that occurs between May and August, the mean annual evaporation is 1320.1 mm, and the mean annual relative humidity is 82% (Yan et al., 2013). The soils in these areas were classified as Ferralsols according to the FAO soil classification system (World Reference Base for Soil Resources, 2006), with the parent materials consisting mostly of Mesozoic sedimentary rocks, some acidic igneous rocks, and granite residual weathered material (Song and Wang, 1995).

#### 2.2. Disturbance history of study areas and selection of forest plots

We selected three study areas: Tiantong National Forest Park, Ruiyan Forest Park and Dongqian Lake Landscape Area. The studied region had been subjected to both anthropogenic and natural disturbances such as logging, land-use conversion, windthrow caused by typhoon, and variable intensities of human disturbances in its history. However, the studied forest sites had been protected from anthropogenic activity for the last 25 years or more (e.g., Wang et al., 2007). Consequently, forests in the region contained stands with different successional status (Wang et al., 2007; Yan et al., 2009). Although forests across the study areas are considered as secondary subtropical forests, mature forests around a Buddhist temple in the center of the Tiantong National Forest Park approximate to climax monsoon evergreen broadleaved forests, as they have been protected from clearance for centuries (Wang et al., 2007).

We selected 31 stands (i.e., plots) that had naturally recovered without human disturbances for more than three decades in the study areas. Each plot  $(20 \times 20 \text{ m})$  was located at a distance of least 100 m from stand edge in order to minimize the edge effect. For each stand, we determined stand age as the number of years since the last stand replacing disturbance, i.e., clearcut harvesting (Ali et al., 2016; Wang et al., 2007; Yan et al., 2009). The official records of the Ningbo Forestry Bureau, Zhejiang Province, were reviewed to extract stand age data. A description of the vegetation in each studied plot is provided in Table S1.

#### 2.3. Estimation of aboveground biomass

In each plot, diameter at breast height (DBH) for individuals taller than 1.50 m, while diameter at 45 cm height ( $D_{45}$ ) or at the midheight of tree were measured for those individuals having height <1.50 m. The height of trees up to 15 m was measured with a telescopic pole, while a clinometer was used for trees having heights >15 m (Ali et al., 2016).

The aboveground biomass of individual trees (AGB*t*) having DBH  $\geq$  5 cm was calculated using the global allometric equation (Eq. (1); Chave et al., 2014) based on tree DBH (cm), height (H, m) and species' wood density ( $\rho$ , g cm<sup>-3</sup>).

$$AGBt = 0.0673 \times \left(\rho \times DBH^2 \times H\right)^{0.976}$$
(1)

The aboveground biomass of individual shrubs and small trees (AGBs) was estimated using a multi-species allometric equation (Eq. (2)) developed locally, based on stem diameter (D), height and species' wood density (Ali et al., 2015). Here, D was DBH < 5 cm for individuals having heights > 1.50 m or D<sub>45</sub> for those having heights < 1.50 m.

$$AGBs = 1.34 \times exp\{-5.40 + 1.65 \times ln(D) + 0.885 \times ln(H) + 3.31 \times \rho\}$$
(2)

#### 2.4. Measurements of plant functional traits

For measuring functional traits, 3-6 healthy mature plants per species were randomly selected in sunlit positions, preferably totally unshaded or minimally shaded (in order to avoid the effect of light) (Cornelissen et al., 2003). Those individuals were marked in each plot at peak biomass in the growing season, and species identity and its coverage was recorded to estimate the relative abundance of different species. Then leaf, twig and stem samples were collected in the summer (i.e., July to August) of 2008 when plants had fully developed leaves. In total, we sampled 96 species (72 evergreen and 24 deciduous), 933 trees, 4665 twigs and 9330 leaves. By following the recommended methodology (Cornelissen et al., 2003), we measured 14 functional traits for each sampled plant, including leaf dry matter content (LDMC), specific leaf area (SLA), leaf nitrogen (N) and phosphorus (P) concentrations in both mature and young leaves, twig dry matter content, twig wood density, stem wood density, stem N and P concentrations, and plant height. In each plot, the most abundant woody species, i.e., species with >75% of cumulative abundance, were selected to assess trait variation among species within a community (Tables S1 and S2; Cornelissen et al., 2003; Pakeman and Quested, 2007). Since leaf longevity is strongly correlated with major trade-offs in plant functional traits (Aerts et al., 2000; Cornelissen et al., 2003), here we focus on leaf traits in both mature (leaves formed in the previous year or earlier) and young leaves (current year leaves). For more details about the method please see Kang et al. (2014) and Yan et al. (2013).

In the field, five branches were collected from five different positions in each sampled plant, i.e., from the four sides and the upper position of the sunlit side of the tree crown. After that the current year twigs were separated from the collected branches according to the terminal set of internodes. Approximately 20 mature leaves without visible damage were collected per twig, and then one current year twig without visible leaf loss was sampled from each branch. Each sample was covered in a moist paper towel and stored in a sealed plastic bag and kept cool until the samples were brought back to the laboratory for further analysis. In the laboratory, the leaves were separated from the twig, then twig length and twig diameter at the midpoint along the length were measured using an electronic vernier caliper (accurate to 0.1 mm). For the purpose of calculating twig wood density, twig cross-sectional area was calculated from the diameter while twig volume was calculated assuming that the twigs had a cylindrical shape (Cornelissen et al., 2003; Yan et al., 2013). At the same time, 20 mature leaves from each branch and all young leaves attached on the selected current year twig were collected to form separate samples. The leaves were then scanned using a leaf area meter (LI-3100C, Li-Cor, USA) to determine the mean leaf area for each mature and current year leaf. For compound leaves, we considered a leaflet as the laminar unit. Then twig and leaf samples were dried at 75 °C for 48 h in an oven to determine twig and leaf dry mass, for calculating twig dry matter content, LDMC, SLA and twig wood density. The SLA was calculated as the one-sided area of a leaf divided by its oven-dried mass, and LDMC as the oven-dried mass of a leaf divided by its water-saturated fresh mass. Twig dry matter content was calculated as the oven-dried mass of a twig divided by its water-saturated fresh mass, and twig wood density as the oven-dried mass of a twig divided by its fresh volume (Cornelissen et al., 2003). Finally, the leaf samples were ground to determine leaf N and P concentrations using a flow-injection auto-analyzer (Skalar-1000, The Netherlands).

We also collected a wood core sample from the same 3–6 individuals per species that were selected for sampling with a 5-mm diameter increment corer at the same position of each tree to determine stem wood density. In the laboratory, the length and diameter (at three points) of the wood core sample were measured using an electronic vernier caliper, and then the volume of the wood core sample was calculated. Next, core samples were dried at 75 °C in an oven for 72 h to determine dry mass to calculate stem wood density, as described above for twig (Cornelissen et al., 2003). Finally, the wood core samples were ground to determine stem N and P concentrations as described above.

The field sampling and laboratory work were conducted using the protocol of Forestry Standards for 'Observation Methodology for Long-term Forest Ecosystem Research' of the People's Republic of China (LY/T 1952–2011).

2.5. Quantification of community-weighted mean and functional divergence

As recommended by empirical studies (Conti and Díaz, 2013; Pakeman and Quested, 2007), we used plant abundance instead of basal area to determine species abundance because it avoids potential circularity derived from using DBH for calculating both functional trait diversity and aboveground biomass. The relative abundance of each species was estimated through its relative density, i.e., the number of individuals of one species as a percentage of the total number of individuals of all species in each plot (e.g., Conti and Díaz, 2013). The relative abundance of each species in each type of forest community used in the study is detailed in Table S2.

Two attributes of biodiversity were used to test the strength of the relationship between forest diversity and aboveground biomass in subtropical forests. This framework distinguishes two different generic attributes of forest diversity in a community, the dominant (most abundant) trait values and the variety (divergence) of trait values (e.g., Conti and Díaz, 2013). First, CWM of a single trait (Eq. (3)) was calculated as the average trait value in the community, weighted by the species abundance (Garnier et al., 2004). This metric represents the expected functional trait value of a specific community (Diaz et al., 2007).

$$CWM_x = \sum_{i=1}^{s} p_i t_i$$
(3)

where CWM<sub>x</sub> is the CWM for trait x, s is the number of species in the community,  $p_i$  is the relative abundance of the *i*th species in the community and  $t_i$  is the trait value for the *i*th species.

Second, FDvar of a single trait was calculated based on Eq. (4), which represents the variance in trait values weighted by the abundance of each species in the community (Mason et al., 2003).

$$FDvar = {^2/_{\pi} \arctan(5V)} \text{ And } V = \sum_{i=1}^{s} p_i (lnx_i - lnx)^2$$
(4)

where  $x_i$  is the trait value for the *i*th species,  $p_i = a_i / \sum_{n=1}^{s} a_i$  and  $\ln x =$ 

 $\sum_{i=1}^{s} p_i \ln x_i$ , where  $a_i$  is the relative abundance of the *i*th species in the community. FDvar values range between 0 (low or no trait diversity) and 1 (high trait diversity). The calculations on the FDvar and CWM indices were performed using the *vegan FD*, *dbFD* and *functcomp* packages in R 3.2.2 (R Development Core Team, 2015).

#### 2.6. Statistical analyses

We constructed three metamodels based on known theoretical multivariate causes of forest diversity (i.e., CWM and/or FDvar of trait values) and aboveground biomass in natural forests, with the addition of stand age in the structural equation models (SEMs) (Fig. 1). To construct a good-fit SEM for each of CWM (Fig. 1a), FDvar (Fig. 1b) and joint (CWM plus FDvar; Fig. 1c) effect, we first conducted three ordinary least squares multiple regression analyses in order to find the best subset of predictors for each of the CWM effect (the first analysis: testing the mass ratio hypothesis), the FDvar effect (the second analysis: testing the niche complementarity hypothesis), and the joint effect (the third analysis: testing the two hypotheses jointly) on aboveground biomass. The purpose of conducting three series of multiple regression analyses was to reduce the number of predictors and to avoid the confounding multicollinearity effect of CWM and FDvar of trait values on each other, as they are expected to be highly correlated (Conti and Díaz, 2013; Finegan et al., 2015). Therefore, we first decomposed the total variations explained by both CWM and FDvar values on aboveground biomass by analyzing them individually, and then tested them jointly for comparison. Regression analyses were conducted for aboveground biomass and predictor variables by starting from all 14 potential predictor variables (14 CWM or 14 FDvar indices) without interactions, resulting in a total of 16,383 possible models for each of CWM and FDvar. With respect to the combined effects of CWM and FDvar on each response variable, we used only those predictor variables retained in the best models of CWM and FDvar. This is due to the fact that the combination of 28 indices (14 CWM and 14 FDvar indices) yields a total of 268,435,455 possible models, which were beyond the capability of the MuMIn package in R, even without considering interactions between variables. Thus, a total of 63 models, with possible combinations of 3 CWM and 3 FDvar indices, were tested for aboveground biomass. From all subsets of regression analysis we selected the best-fit model for the construction of SEMs that had the lowest Akaike Information Criterion (AICc; Wagenmakers and Farrell, 2004), for each of CWM, FDvar, and CWM plus FDvar series of analyses. Linear models were tested using the stats package and all subset regression analyses were conducted using the MuMIn package in R 3.2.2 (Bartoń, 2016).

In addition, multicollinearity diagnosis was performed in multiple regression analyses using the variance inflation factor (VIF), as multicollinearity larger than 10 could cause inaccurate model parameterization and decrease statistical power, and exclude significant predictor variables (Graham, 2003). It was noted that all VIF values were lower than the critical heuristic value of 10, suggesting that collinearity among predictor variables did not strongly affect our result. Also, a modeling averaging approach (synthetic model) was developed in the *MuMIn* package in R to evaluate which predictor variable contributed consistently across all models and to avoid the multicollinearity in the

model. For this, regression coefficients of each predictor were averaged across all models, weighted by their Akaike Information Criterion weight (AICc-wi), which represents the likelihood of a given best fit model relative to all other models (Wagenmakers and Farrell, 2004). An importance value was calculated by adding the AICc-wi values of the models in which the variables were present (e.g., Ali et al., 2016; Finegan et al., 2015). Importance values range between zero (low importance) and one (high importance).

For the interpretation of results from SEM (Grace et al., 2016), we analyzed bivariate relationships between each of the hypothesized causal paths according to our hypothesis, using simple regression analyses. Specifically, we fit each pair of variables using a simple linear regression analysis to test for bivariate relationships of aboveground biomass with each of stand age, and CWM and FDvar of trait values. We also tested the bivariate relationships between stand age and CWM and FDvar of trait values.

Several tests were used to assess the model fit of SEM (Malaeb et al., 2000), i.e., the Chi-square ( $\chi^2$ ) test, goodness-of-fit index (GFI), comparative fit index (CFI), standardized root mean square residual (SRMR), and AIC. The indirect effect of the stand age was calculated by multiplying the standardized effects of all paths on one route, from stand age to each mediator (CWM and/or FDvar of trait values), and then to aboveground biomass, while the total effect was calculated by adding standardized direct and indirect effects (Ali et al., 2016; Grace et al., 2016). The SEM was implemented using the *lavaan* package (Rosseel, 2012) in R 3.2.2 (R Development Core Team, 2015).

The variables of each studied plot used in the analysis are listed in Table S3. Based on Kendall's (tau) correlation, there were relatively weak correlations among all pairs of CWM and/or FDvar of trait values, and most of them were nonsignificant (Table S4). The best multiple regression models are provided in Table S5, and the synthetic models are shown in Table S6.

## 3. Results

Bivariate relationships showed that aboveground biomass significantly increased with stand age (Fig. 2a). The CWM of N concentration in young leaves significantly decreased (Fig. 2b), whereas FDvar of plant height significantly increased with stand age (Fig. 2c). Aboveground biomass significantly decreased with increasing CWM of leaf N concentration in both mature and young leaves, LDMC of young leaves, and stem N concentration (Fig. 2d–g). However, aboveground biomass significantly increased with high CWM of P concentration and SLA of young leaves (Fig. 2h–i). With respect to FDvar, aboveground biomass significantly increased with increasing divergence of plant height and twig dry matter content (Fig. 2g–h). The other CWM and FDvar of trait values were not significantly related to aboveground biomass or to stand age (Table S7).

The SEMs for CWM, FDvar and CWM + FDvar had similar good-fits to the data, with joint SEM of CWM + FDvar explained a slightly greater amount of the variation in aboveground biomass (Fig. 3). The three SEMs were good-fits to the data without any correlations between pairs of CWM and/or FDvar of trait values (Fig. 3), indicating that leaf and stem economics spectra were decoupled, and that those traits were independent predictors for aboveground biomass (Table S4).

The CWM (the mass ratio hypothesis) model accounted for 78, 20, 6, and 2% of the variation in aboveground biomass, CWM of N concentration in young leaves, plant height, and SLA of young leaves, respectively (Fig. 3a). The CWM of SLA of young leaves had the strongest positive direct effect on aboveground biomass ( $\beta = 0.33$ , P < 0.001), followed by the negative effect of CWM of N concentration in young leaves ( $\beta = -0.24$ , P = 0.011), and positive effect of CWM of plant height ( $\beta = 0.22$ , P = 0.010; Table 1). There was a significant negative direct effect of stand age on CWM of N concentration in young leaves ( $\beta = -0.44$ , P = 0.007), but a nonsignificant positive effect on CWM of SLA of young leaves and plant height (Fig. 3a).

With respect to the niche complementarity hypothesis, the FDvar model explained 74, 13, 7, and 0% of variation in aboveground biomass, FDvar of plant height, twig wood density, and N concentration in young leaves, respectively (Fig. 3b). The FDvar of N concentration in young leaves had the strongest positive direct effect on aboveground biomass ( $\beta = 0.23, P = 0.011$ ), followed by the positive effects of FDvar of plant height ( $\beta = 0.20, P = 0.044$ ) and FDvar of twig wood density ( $\beta = 0.19, P = 0.044$ ; Table 1). There was a significantly positive direct effect of stand age on FDvar of plant height ( $\beta = 0.36, P = 0.034$ , Fig. 3b).

In testing the joint effect of the mass ratio and niche complementarity mechanisms, the SEM accounted for 86, 20, 13, 7, 2, and 0% of the variation in aboveground biomass, CWM of N concentration in young leaves, FDvar of plant height, FDvar of twig wood density, CWM of SLA of young leaves, and FDvar of N concentration in young leaves, respectively (Fig. 3c). The CWM of N concentration in young leaves had the strongest negative direct effect on aboveground biomass ( $\beta = -0.30$ , P < 0.001), followed by the positive effect of CWM of SLA of young leaves ( $\beta = 0.28$ , P < 0.001), FDvar of N concentration of young leaves ( $\beta = 0.26$ , P < 0.001), FDvar of twig wood density ( $\beta = 0.23$ , P = 0.001) and FDvar of plant height ( $\beta = 0.20$ , P = 0.005; Table 1). There was a significant negative direct effect of stand age on CWM of N concentration in young leaves ( $\beta = -0.44$ , P = 0.007) and a positive direct effect on FDvar of plant height ( $\beta = 0.36$ , P = 0.034; Fig. 3c).

Stand age had mostly a nonsignificant indirect positive effect via CWM and/or FDvar of traits values on aboveground biomass in all three SEMs (Fig. 3, Table 1), with the exception of significant effect via CWM of N concentration in young leaves in the joint SEM ( $\beta = 0.24$ , P = 0.013). The total (direct + indirect) effect of stand age on aboveground biomass was quite similar in SEMs on CWM ( $\beta = 0.77$ , P < 0.001), FDvar ( $\beta = 0.79$ , P < 0.001), and CWM + FDvar ( $\beta = 0.75$ , P < 0.001; Table 1).

### 4. Discussion

Subtropical forests in the East Asian monsoon region play a critical role in providing ecosystem services and functions such as carbon cycling (Ali et al., 2016; Niu et al., 2012; Wang et al., 2014). This study highlights the fundamental role of CWM and FDvar of trait values for predicting aboveground biomass in secondary subtropical forests. In agreement with our hypothesis, this study showed that aboveground biomass increases with stand age, and the residual variation in aboveground biomass is explained by CWM and FDvar alone (Fig. 3a and b) and jointly (Fig. 3c) of leaf and wood traits. The main novelty of this study is determining that high aboveground biomass in secondary subtropical forests is associated with both niche complementarity (in terms of FDvar of plant height and twig wood density) and mass ratio (N conservative and effective light acquisition strategies of leaf traits) mechanisms. Our findings contrast with those who found no support to either the niche complementarity hypothesis (Conti and Díaz, 2013; Finegan et al., 2015) or the mass ratio hypothesis (Conti and Díaz, 2013).

The contrasting relationships of aboveground biomass with CWM and FDvar values in relation to different functional traits in SEMs suggest that communities consisting of species with dominant nutrientuse strategies by young leaves and divergent wood economics spectra had higher aboveground biomass in the studied forests. The dominant effect of the leaf nutrient-use strategies on aboveground biomass may be related to the plant's leaf economics spectrum (e.g., Garnier et al., 2004). For instance, the leaf economics spectrum ranges from exploitative plants characterized by N rich leaves, high SLA and fast nutrient acquisition and turnover, thus being conducive to fast growth and high aboveground biomass, to conservative plants with nutrient-poor leaves and slower growth associated with slow nutrient and biomass turnover (Wright et al., 2004).

Of the tested leaf trait values, two CWM and one FDvar of traits of young leaves, were significant predictors of aboveground biomass after explicitly considering the effects of stand age, when the ecological



**Fig. 2.** Bivariate relationships between endogenous (dependent) and exogenous (independent) variables (n = 31), for all hypothesized casual paths in structural equation models. Only significant relationships (see Table S7) are shown here. (a–c) Aboveground biomass (AGB), community-weighted mean (CWM) of nitrogen concentration in young leaves (LNC-Y), and functional divergence (FDvar) of plant height (H) versus stand age, respectively; (d–i) aboveground biomass versus CWM of nitrogen concentration in mature leaves (LNC-M), CWM of LNC-Y, CWM of dry matter content in young leaves (LDMC-Y), CWM of stem nitrogen concentration (CWM SNC), CWM of phosphorus concentration in young leaves (CWM LPC-Y), and CWM of specific leaf area of young leaves (SLA-Y), respectively; and (j–k) aboveground biomass versus FDvar H (height), and FDvar of twig dry matter content (FDvar TDMC), respectively.

mechanisms were tested individually and jointly. On the one hand, the negative association of CWM of N concentration in young leaves with aboveground biomass indicates an N conservative strategy. On the other hand, the positive association of CWM of SLA of young leaves with aboveground biomass implies an acquisitive strategy across the studied species within communities. These results are in agreement with previous studies in tropical wet and moist forests (Finegan et al., 2015; Malhi et al., 2004) and herbaceous vegetation under secondary succession in the temperate region (Garnier et al., 2004), which suggest that expectations derived from the leaf economics spectrum (Wright et al., 2004) will scale up to the level of canopy properties and ecosystem

processes. Further, high SLA tends to have high aboveground biomass and that CWM of SLA indeed indicates stand-level carbon gain (e.g., Finegan et al., 2015). Another explanation for the positive association of CWM of SLA of young leaves with aboveground biomass would be that the studied forests with complex vertical structures (i.e., high FDvar of plant height) have a lot of unshaded leaves, which result mainly from the few dominant canopy species that are effective in light acquisition. Although forests with complex structure should have more shaded plants in the understory, canopy tree species that effectively intercept light are larger than understory species. Therefore, communities with a high proportion of unshaded leaves have high aboveground biomass.



**Fig. 3.** The best-fit structural equation models (SEMs) relating aboveground biomass to stand age, community-weighted mean (CWM), functional divergence (FDvar) of functional traits. Solid arrows represent significant (P < 0.05) paths and dashed arrows represent non-significant paths (P > 0.05). For each path the standardized regression coefficient is shown.  $R^2$  indicates the total variation in a dependent variable that is explained by the combined independent variables. Model-fit statistics are shown in the figure. For abbreviations, see Table 1.

In this study, the significant positive associations of FDvar of plant height, twig wood density, and N concentration in young leaves with aboveground biomass across stand ages (Fig. 3b) indicate the positive role of a diverse N acquisitive strategy along with tree size diversity (Ali et al., 2016; Zhang and Chen, 2015; Zhang et al., 2012). The positive relationship between CWM of plant height and aboveground biomass (Fig. 3a), indicates that high aboveground biomass might be associated with tall or fast growing tree species (on average) in the studied forests. Again species that are effective in light acquisition are fast growing. It is logical that a forest community containing fast-growing species with functionally diverse wood syndromes, e.g., a diverse array of plant height and other wood attributes (e.g., wood density), can lead to a complex stand structure, and hence higher aboveground biomass (Ali et al., 2016; Cavanaugh et al., 2014). Therefore, coexisting fast growing species being divergent in plant height and wood density in an ecosystem could be more efficient for accessing and utilizing light, and for

#### Table 1

The direct, indirect, and total standardized effects on aboveground biomass based on structural equation models (SEMs). The indirect effect of stand age was calculated by multiplying the standardized effects of all paths on one route, from stand age to mediator (CWM or FDvar of trait value), and then to aboveground biomass, while the total effect was calculated by adding standardized direct and indirect effects, as presented in Fig. 3. Abbreviations: CWM, community-weighted mean; FDvar, functional divergence; H, plant height; LNC-Y, leaf nitrogen concentration in young leaves; SLA-Y, specific leaf area of young leaves; TWD, twig wood density.

Predictor	Pathway to aboveground biomass	CWM model (Fig. 3a)		FDvar model (Fig. 3b)		Joint model (Fig. 3c)	
		Effect	P-value	Effect	P-value	Effect	P-value
Stand age	Direct effect	0.56	< 0.001	0.65	< 0.001	0.43	< 0.001
	Indirect effect via CWM H	0.05	0.222	-	-	-	-
	Indirect effect via CWM LNC-Y	0.10	0.063	-	-	0.24	0.013
	Indirect effect via CWM SLA-Y	0.05	0.392	-	-	0.04	0.391
	Indirect effect via FDvar H	-	-	0.07	0.141	0.07	0.088
	Indirect effect via FDvar TWD	-	-	0.05	0.236	0.07	0.172
	Indirect effect via FDvar LNC-Y	-	-	0.01	0.792	0.01	0.791
	Total effect	0.77	< 0.001	0.79	< 0.001	0.75	< 0.001
CWM H	Direct effect	0.22	0.010	-	-	-	-
CWM LNC-Y	Direct effect	-0.24	0.011	-	-	-0.30	< 0.001
CWM SLA-Y	Direct effect	0.33	< 0.001	-	-	0.28	< 0.001
FDvar H	Direct effect	-	-	0.20	0.044	0.20	0.005
FDvar TWD	Direct effect	-	-	0.19	0.044	0.26	< 0.001
FDvar LNC-Y	Direct effect	-	-	0.23	0.011	0.23	0.001

constructing tissues per wood volume, thus increasing aboveground biomass (Cavanaugh et al., 2014; Chave et al., 2009; Ruiz-Benito et al., 2014).

The results from the three SEM models demonstrate that, in this study, the joint model, which combines CWM and FDvar of trait values, could significantly improve the predicting power of aboveground biomass, in addition to the effects of stand age. This supports, therefore, our prediction that CWM of leaf traits and FDvar of wood traits jointly explain the residual variation in aboveground biomass in secondary subtropical forests (Fig. 3c). The high functional trait diversity (plant height, twig wood density and leaf N concentration) and high CWM of SLA and low CWM of leaf N concentration suggest that in high biomass stands, plot basal area is concentrated by diverse species, but with dominant (on average) light acquisition and N conservation strategies in the studied forests. Our results are in contrast to the recent studies that provide strong evidence for the mass ratio hypothesis only in tropical forests (Conti and Díaz, 2013; Finegan et al., 2015). In this study, the individual and joint effects of CWM of leaf traits and FDvar of wood traits on predicting aboveground biomass suggest that the two mechanisms work together to regulate aboveground biomass in secondary subtropical forests. This explanation is supported by findings from a recent meta-analysis of manipulative studies where niche complementarity and mass ratio effects together contribute about 50% to the biodiversity – ecosystem function relationship (Cardinale et al., 2011).

It should be noted that trait diversity and aboveground biomass should be interactively correlated to stand age. In this study, we only found a significant direct effect of stand age on CWM of N concentration in young leaves and FDvar of plant height, and a low indirect effect of stand age via CWM and/or FDvar of trait values on aboveground biomass. The strong directional shift in CWM of N concentration in young leaves and FDvar of plant height with stand age is consistent with the productivity filtering hypothesis (Grime, 2006). The low indirect effect of stand age via CWM and/or FDvar of trait values on biomass might be attributable to complex mechanisms, as change patterns of functional trait diversity across successional forests are also affected by stand properties such as soil moisture content and fertility, community structure, and even disturbance intensity (Yeboah and Chen, 2016). We anticipate that our results encourage further studies on the inclusion of the effects of environment properties, disturbance history on CWM and FDvar of trait values and its influence on aboveground biomass. In addition, soil carbon is highly related to the decomposability of leaf and wood litters that are contributed by leaf and wood economics spectra. Consequently, it would be interesting to study how plant functional trait diversity affects soil and even total ecosystem carbon storage (aboveground plus soils) in subtropical forests.

#### 5. Concluding remarks

We conclude that, first, in testing the mass ratio and niche complementarity hypotheses for predicting aboveground biomass, the role each hypothesis or mechanism plays depends on the functional trait of concern. For example, higher aboveground biomass was mostly driven by the CWM of young leaf traits (i.e., the mass ratio hypothesis) and FDvar of wood traits (i.e., the niche complementarity hypothesis), indicating that leaf and stem economics spectra are decoupled. Second, to understand changes in aboveground biomass, it is important to measure functional traits on different organs of a plant, in order to represent both the conservative and acquisitive strategies of the whole-plant economics spectrum. Third, from a functional point of view, functional traits of secondary subtropical forests have different relationships with aboveground biomass than what have previously been shown for wet, moist and dry tropical forests. In subtropical forests, communities with an array of species having a diverse syndrome, but on average, dominated by both N conservative and light acquisitive strategies, rather than of only acquisitive or conservative strategies alone, have high aboveground biomass. In addition, relationships of CWM of leaf traits with aboveground biomass are consistent with tropical moist and wet forests. Overall, this study advances our understanding of mechanisms affecting aboveground biomass in secondary subtropical forests, and can help predict the response of these forests to future climate change.

## Data availability

The dataset used for this paper is available as supplementary files (Tables S1, S2, and S3). More information about the dataset is available upon request to the corresponding author.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx. doi.org/10.1016/j.scitotenv.2016.09.022.

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