Forest Ecology and Management 401 (2017) 125–134

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

The forest strata-dependent relationship between biodiversity and aboveground biomass within a subtropical forest

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A R T I C L E I N F O

Article history:
Received 16 March 2017
Received in revised form 19 June 2017
Accepted 19 June 2017
Available online 15 July 2017

Keywords:
Ecosystem function
Evergreen broadleaf forest
Forest strata
Niche complementarity effect
Soil nutrients
Species diversity
Stand structure
Structural equation modelling

A B S T R A C T

The relationships between biodiversity and aboveground biomass in forest ecosystems have been intensively studied in recent decades. Still, the mechanisms that underlie it remain highly debated. We hypothesized that overstorey species diversity and individual tree size variation contribute to aboveground biomass and understorey species diversity through the niche complementarity effect, while weaken the relationship between understorey aboveground biomass and individual tree size variation due to the mixed effects of tree development, biotic interaction and reduced available resources by overstorey strata. The integrative relationships of species diversity and tree size variation (variation in diameter at breast height-DBH) with aboveground biomass were analysed at overstorey and understorey strata across 125 plots in a 5-ha subtropical forest in Eastern China. For comparison, we tested these relationships at individual strata (isolation modelling), and whole-community level, by using linear structural equation model while accounting for the effects of soil nutrients. The integrative modelling accounted for 35, 31, 16, 12, 4, and 0% of the variation in understorey aboveground biomass, overstorey aboveground biomass, overstorey DBH variation, overstorey species diversity, understorey species diversity, and understorey DBH variation, respectively. Overstorey DBH variation and species diversity had the positive direct effects on overstorey aboveground biomass. Overstorey species diversity significantly promoted the understorey species diversity, but DBH variation and aboveground biomass of overstorey strata had negligible effects on the diversity and aboveground biomass of understorey strata. Soil nutrients had positive direct effect on overstorey DBH variation, but negative direct effects on overstorey and understorey aboveground biomass and overstorey species diversity. These results provide strong evidence for the niche complementarity effect for driving positive relationships of species diversity and individual tree size variation with aboveground biomass at overstorey strata. The strong and consistent negative effects of soil nutrients on overstorey aboveground biomass and species diversity suggest an important mechanism that high species diversity of overstorey strata with great tree size variation on nutrient-poor soils is crucial for driving high aboveground biomass in subtropical forest ecosystems. In conclusion, this study suggests that no sole and ubiquitous relationship between biodiversity and aboveground biomass exists in a structurally complex forest, but rather that the magnitude and direction of this relationship is greatly dependent on the forest strata where available resources shift substantially. We argue that ecological models for predicting aboveground biomass would be improved by including separate effects of overstorey and understorey diversity.

1. Introduction

Previous studies have suggested that the positive relationships between forest diversity (e.g., species diversity and individual tree size variation) and aboveground biomass are essential to the ability of forests to provide goods and services (Wang et al., 2014; Poorter et al., 2015; Zhang and Chen, 2015; Ali and Mattsson, 2017). Due to the dominant role of overstorey strata on the available resource and their influences on various ecological processes, the diversity and aboveground biomass of understorey strata are substantially influenced by overstorey trees in forests (Barbier et al., 2008). However, in most of the empirical studies, the effects of forest strata (e.g., overstorey and understorey) on the relationship

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http://dx.doi.org/10.1016/j.foreco.2017.06.056
0378-1127/

between biodiversity and aboveground biomass are often ignored, making it impossible to assess the effects of overstorey trees on the patterns of biodiversity and aboveground biomass of understorey in forest ecosystems (Cavanaugh et al., 2014; Poorter et al., 2015; Zhang and Chen, 2015; Ali and Mattsson, 2017). Therefore, specific research is needed to improve our understanding about the patterns, magnitude and mechanisms of diversity – aboveground biomass relationships across forest strata in forests. Disentangling these ecological complexities requires integrative modelling considering how species diversity and tree size variation of overstorey and understorey strata affect their corresponding aboveground biomass, and at the same time how overstorey strata affect the diversity and aboveground biomass of understorey in species-rich forests (Fig. 1).

The positive relationships between biodiversity and ecosystem functions are often attributed to the niche complementarity hypothesis (Tilman et al., 2001), which postulates that species with different niches are able to use available resources more efficiently, and thus enhancing aboveground biomass or productivity (Zhang et al., 2012b). Species diversity and individual tree size variation are important for ecosystem functions because they can influence the efficiency of resource acquisition and utilization among and within component species in forests (Chu et al., 2009; Zhang and Chen, 2015). Species diversity generally interpreted as a result of niche differentiation and facilitation (i.e., species complementarity), is recognized to be responsible for the positive relationships between biodiversity and aboveground biomass in both experimental and natural environments, including forests (Loreau et al., 2001; Poorter et al., 2015; Zhang and Chen, 2015). Recent studies have suggested that multilayered stand structure also promotes aboveground biomass due to the niche complementarity effect in both natural forests and agroforests (Poorter et al., 2015; Zhang and Chen, 2015; Ali et al., 2016; Ali and Mattsson, 2017). Individual tree size variation is a key stand structural attribute being generally quantified by variances among all individual tree sizes across component species in a community (Clark, 2010; Zhang and Chen, 2015). Theoretically, individual tree size variation enhance aboveground biomass through complementary light-use (Yachi and Loreau, 2007; Zhang and Chen, 2015; Ali and Mattsson, 2017).

In forest ecosystems, overstorey strata store large quantities of aboveground biomass due to their high wood volumes and disproportionate contribution of large trees to the aboveground biomass at whole-community level (Slik et al., 2013). In contrast, understorey strata contribute much to the majority of biodiversity (Nilsson and Wardle, 2005; Gilliam, 2007; Barbier et al., 2008). Moreover, local environmental conditions strongly affecting plant performance (Barbier et al., 2008; Bartels and Chen, 2010, 2013), thus the ensuing patterns of species diversity and tree size variation across forest strata. Light, being one of the most important plant resources, is often limiting for understorey trees, while it is abundant for overstorey trees (Wright, 2002; Brenes-Arguedas et al., 2011). A dense forest with great aboveground biomass can positively contribute to ecosystem functions through large stem volumes of overstorey trees, but slows down ecosystem functioning rates in understorey due to low light availabilities (Slik et al., 2013; Poorter et al., 2015; Zhang et al., 2016). Additionally, species diversity of overstorey strata may promote species diversity in understorey strata as a result of reduced interspecific competition (Bartels and Chen, 2013; Zhang et al., 2016). Therefore, to understand the mechanism(s) by which aboveground biomass is

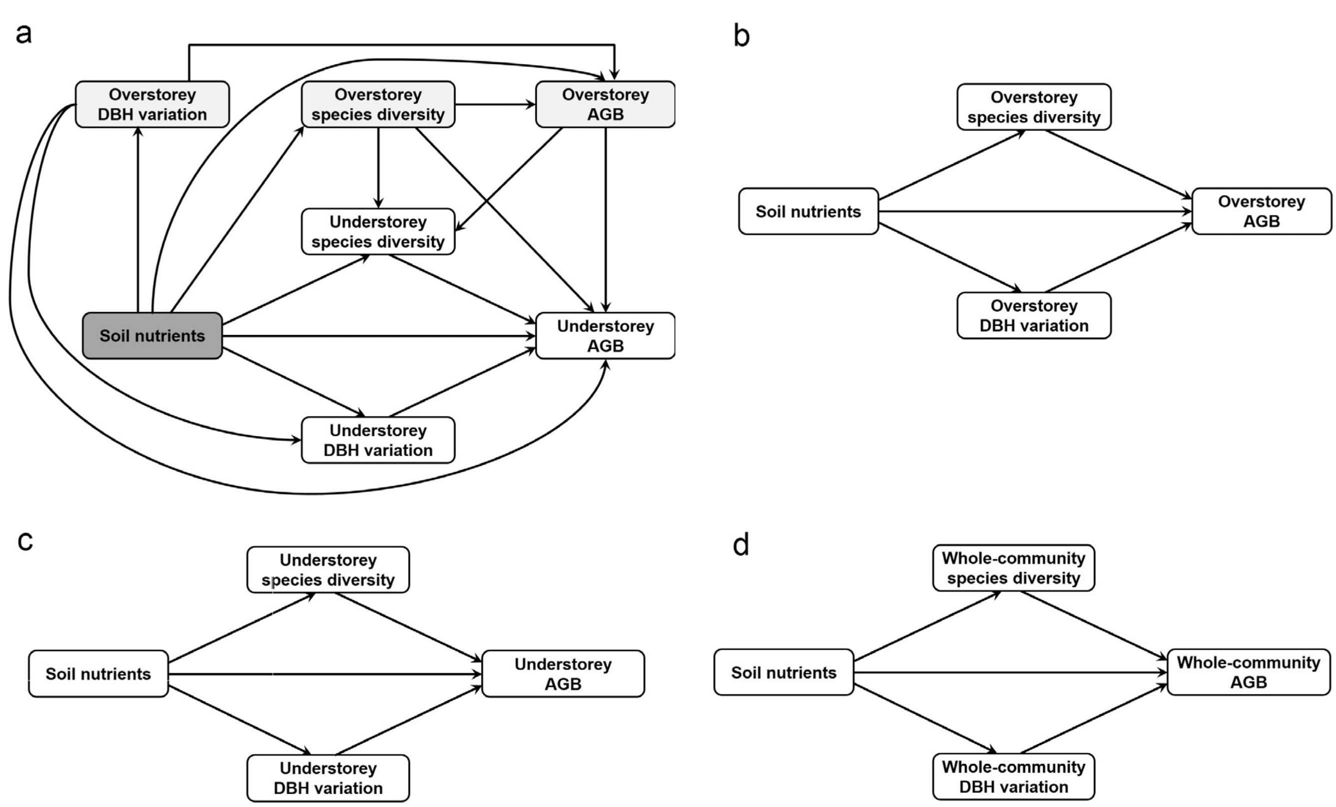

Fig. 1. Conceptual models for the relationships of aboveground biomass with species diversity and individual tree size variation (DBH variation) across forest strata in a subtropical evergreen broadleaf forest. (a) integrative modelling showing hypothesized relationships of how species diversity and individual tree size variation in overstorey and understorey strata affect their corresponding aboveground biomass, and at the same time how overstorey strata affects the diversity and aboveground biomass of understorey strata, in addition to the effects of soil nutrients. (b) and (c) isolation modelling showing hypothesized relationships of how species diversity and individual tree size variation of overstorey and understorey strata affect their corresponding aboveground biomass; and (d) whole-community modelling showing hypothesized relationships of how species diversity and individual tree size variation of whole-community affect whole-community aboveground biomass.

interactively affected by biodiversity in both overstorey and understorey strata within forests, it may be insightful to consider understorey and overstorey strata separately.

In this study, we tested hypothesis of the niche complementarity in terms of species diversity and individual tree size variation by using linear structural equation model (SEM) through analyzing biophysical data from 125 plots inside a 5-ha subtropical forest in Eastern China. Studies in tropical forests reveal that soil nutrients or physicochemical variables should be included when testing multivariate relationships between diversity and aboveground biomass because it determines nutrients availability which strongly influences the relationships between biodiversity and aboveground biomass (Poorter et al., 2015; Prado-Junior et al., 2016). Considering this, we constructed four conceptual frameworks for overstorey and understorey strata both in integration (Fig. 1a) and in isolation (Fig. 1b and c), as well as in whole-community (Fig. 1d). Specifically, we asked the following two questions. First, how do species diversity, individual tree size variation and soil nutrients relate with aboveground biomass across forest strata and whole-community level? With respect to the niche complementarity hypothesis, we predicted that species diversity and individual tree size variation have positive effects on aboveground biomass across forest strata alone and combined (Prediction 1). Considering the soil fertility hypothesis (Wright et al., 2011; Quesada et al., 2012), we predicted that aboveground biomass, species diversity and individual tree size variation increase with an improvement of soil nutrients in both overstorey and understorey strata, and in whole-community (Prediction 2).

The second question is whether species diversity, individual tree size variation and aboveground biomass of overstorey strata affect biodiversity and aboveground biomass of understorey strata, when soil nutrients are considered simultaneously? We predicted that overstorey strata would decrease aboveground biomass and individual tree size variation in understorey strata (Prediction 3), due to the dominant role of overstorey strata in competing and/or consuming available light and soil nutrients (Anderson et al., 1969; Bartels and Chen, 2010; Zhang et al., 2016). In addition, we predicted that species diversity of overstorey strata may promote species diversity of understorey (Prediction 4), due to increased resource heterogeneity and reduced interspecific competition in understorey (e.g., Gamfeldt et al., 2013; Zhang et al., 2016).

2. Materials and methods

2.1. Study site and forest plots

This study was conducted in a 5-ha subtropical forest plot in Tiantong National forest park (29°48′N, 121°47′E, 200 m a.s.l), located in Ningbo city, Zhejiang province, in Eastern China. The area is characterized by a warm and humid subtropical monsoon climate, and has an average temperature of 28 °C and 4.2 °C in the warmest and coldest months, respectively. The average annual precipitation is 1375 mm, most of which falls between May and August; annual evaporation is 1320 mm and annual relative humidity is 82% (Yan et al., 2013). The vegetation is characterized as a subtropical evergreen broadleaf forest, and the soils are classified as Ferralsols in the FAO soil classification system (World Reference Base for Soil Resources, 2006), with pH values that range from 4.4 to 5.1. The parental material is mostly composed of Mesozoic sediments and intrusive acidic rocks, including quartzite and granite (Yan et al., 2013).

The studied 5-ha forest plot is located in the center of the Park, and is divided into 125 subplots (20 × 20 m). The topography of the plot is very heterogeneous and rugged (Fig. S1), with elevation varying from 320.4 to 489.4 m a.s.l. The slopes of the subplots within the plot ranges from 13.8 to 43.9°. The altitude is more pronounced in the northern section than in the southern section of the plot. The western and eastern edges of the plot extended through two north–south oriented valleys, with the interior of the plot spanning two small northwest-to-southeast oriented ridges, approximately 100 m apart (Fig. S1).

All stems ≥ 1 cm diameter at breast height (DBH) were individually tagged, geo-referenced, measured for DBH using a diameter tape and identified to species-level in June to August 2009. A total of 20,253 stems were recorded belonging to 108 species, 76 genera and 43 families. This work was guided on "Observation Methodology for Long-term Forest Ecosystem Research" of National Standards of the People's Republic of China (GB/T 33027-2016). Vertical structure of community and species composition varied with changes in topography. In the ravine area, the canopy tree layer (∼15–20 m in height) was dominated by *Choerospondias axillaris*, which is a deciduous species, whereas the sub-canopy tree layer (4 < height < 15 m) was dominated by evergreen species such as *Machilus leptophylla*. The dominant species in the shrub layer (<4 m in height) was composed of evergreen species such as *Litsea elongate* and *Eurya loquaiana*. On slopes and ridge areas, the dominant species in the shrub layer was similar to the ravine area. In contrast, the canopy tree layer was occupied by evergreen species including *Lithocarpus harlandii* and *Cyclobalanopsis nubium*, and the sub-canopy tree layer was also dominated by evergreen species, such as *Lithocarpus harlandii*.

2.2. Quantification of forest diversity

Overstorey strata were defined as all individuals with DBH ≥ 10 cm in each forest plot, and understorey strata included trees with 1 ≤ DBH < 10 cm (Barrufol et al., 2013; Zhang et al., 2016). This resulted in a total of 3224 stems belonging to 75 species, 51 genera and 29 families in the overstorey strata, and a total of 17,025 stems belonging to 103 species, 65 genera and 37 families in the understorey strata across 125 plots in a 5-ha subtropical forest.

We used two measures of forest diversity that were quantified for overstorey and understorey strata separately: Shannon's species diversity and DBH variation. This resulted in four diversity measures per plot for integrative modelling analyses, while two measures per plot for whole-community level and forest strata level analyses. We used the Shannon-Wiener biodiversity index (Eq. (1)) to quantify tree species diversity at each plot (Magurran, 2004). The species' relative basal area (relative to the total understorey/ overstorey basal area) was used to weight the number of tree species at overstorey and understorey strata at each plot, because basal area is a better indicator of plant performance than abundance (Zhang and Chen, 2015; Ali et al., 2016). Similarly, the species' relative basal area (relative to the whole-community basal area) was used to weight number of tree species at whole-community level at each plot. We chose Shannon's species diversity index to account for species richness and evenness, two of the important aspects of species diversity in biodiversity – productivity studies (Zhang et al., 2012b).

$$\mathrm{H_s} = -\sum_{i=1}^{s} \mathrm{p}_i \times \ln(\mathrm{p}_i) \tag{1}$$

where p_i is the proportion of basal areas of ith species, while s is the number of tree species. The calculations on the Shannon-Weiner diversity index was performed using the *vegan* package (Oksanen et al., 2015).

We used DBH variation among individual trees within each plot as proxy of individual tree size variation (Zhang and Chen, 2015; Ali and Mattsson, 2017), because the overall DBH variation represents the degree of the realized niche differentiation via positive plant-plant interactions (Yachi and Loreau, 2007; Clark, 2010). Coefficient of variation of DBH (Eq. (2)), the ratio of the standard deviation of all DBH measurements to the mean DBH, was used to calculate DBH variation within each plot, expressed as percentage.

$$CV_j = \frac{s_j}{\bar{x}_j} \times 100 \tag{2}$$

where CV_j is the individual tree size (DBH) variation of all species within *j*th plot, s_j is the standard deviation of all DBH measurements within *j*th plot, i.e. $s_j = \sqrt{\frac{\Sigma(x_j - \bar{x}_j)^2}{n_i - 1}}$, $\bar{x}_j$ is the mean DBH of the *j*th plot, i.e. $\bar{x}_j = \frac{\sum_{i=1}^{n} x_i}{n_i}$, and x_j is the value of each individual tree DBH in the *j*th plot being averaged.

The calculations on the coefficient of variation was performed using *cv* function of *raster* package.

2.3. Soil physicochemical variables dataset

To take into account for the effects of soil variables (i.e., soil nutrients) on the relationships between biodiversity and aboveground biomass, the original dataset of soil physicochemical variables for each subplot within a 5-ha forest plot were obtained from the study of Zhang et al. (2012a). Soil physicochemical variables included soil carbon concentration, phosphorus concentration, nitrogen concentration, pH, volumetric soil water content, bulk density and humus depth. In order to reduce the number of local soil physicochemical variables and remove highly correlated variables (see Table S1 for correlations), we ran a principal component analyses (PCA) based on the soil physicochemical variables. The first multivariate axis of PCA (PC 1, 49%) was mostly defined by soil physicochemical variables including soil carbon content, pH, volumetric soil water content, bulk density and humus depth. The second multivariate axis of PCA (PC2, 27%) was mostly defined by soil nutrients including soil phosphorus and nitrogen contents in addition to the fair contribution of soil physicochemical properties. In all statistical analyses, we used PC2 values in the structural equation models, since it better represented soil nutrients variation (see Table S2).

2.4. Estimation of aboveground biomass

We calculated aboveground biomass for each tree with DBH $\geq$ 5cm (AGB*t*) using a global allometric equation (Eq. (3)) (Chave et al., 2014), which is based on tree DBH, site-specific environment stress factor (E) and species' wood density (ρ).

$$\begin{aligned} AGBt = \exp\{&-1.803 - 0.976(E) + 0.976 \times \ln(\rho) + 2.673 \\ &\times \ln(DBH) - 0.0299 \times (\ln(DBH))^2 \end{aligned} \tag{3}$$

where E for our study site was derived from Chave et al. (2014).

Applying generalized allometric equations developed for large trees (DBH $\geq$ 5cm) (Chave et al., 2014) to shrubs and small trees may overestimate or underestimate the actual biomass, because of their restriction in the DBH range, and different growth forms and physiognomies, as compared to large trees (Litton and Kauffman, 2008). Global allometric equation for trees with DBH $\geq$ 5cm (Chave et al., 2014) tended to overestimate, but to a very lesser extent, biomass of individual small trees and shrubs (DBH < 5 cm) as compared to the estimations obtained using Ali et al. (2015) site-specific equation for small trees and shrubs, but the results of the two equations were highly consistent ($R^2 = 0.96$, $P < 0.001$, PMSE = 0.01, $n = 13799$; Fig. S2). Therefore, we tried to accurately estimate the aboveground biomass of shrubs and small trees (AGB*s*) with DBH < 5 cm by using a general multispecies allometric equation (Eq. (4)) developed locally for small trees and shrubs (Ali et al., 2015), which is similarly based on tree DBH and species' wood density (ρ).

$$AGBs = 1.450 \times \exp\{-4.97 + 2.20 \times \ln(DBH) + 3.06(\rho)\} \tag{4}$$

2.5. Statistical analyses

Our study design may confound statistical results when there is spatial autocorrelation in the variables of interest. To account for this, we performed generalized least-squares (GLS) models (Pinheiro and Bates, 2016) by accounting for subplots with spatial autocorrelation (including subplots X and Y coordinates as a spatial effect) and without spatial autocorrelation (no reference to subplots X and Y coordinates) among subplots for all relationships between predictors and aboveground biomass (Chisholm et al., 2013; Yuan et al., 2016). In addition, forest strata may also confound the spatial autocorrelation in the variables of interest, as overstorey and understorey strata within a plot have similar spatial location (X and Y coordinates). We therefore explicitly accounted for the effect of vertical strata (overstorey and understorey) by using grouping variable on the relationship between predictor and aboveground biomass in both spatial (i.e., subplots X and Y coordinates are grouped within strata) and non-spatial (no reference to subplots X and Y coordinates within strata) GLS models. GLS model is a reliable method for testing whether subplots sharing similar abiotic conditions are independent from each other within a forest (Zuur et al., 2009). The goodness of fit of spatial and non-spatial GLS models was evaluated by AIC, and we found that models without spatial autocorrelation always had the lower AIC values (Table S3), which is similar to the recent observations in 25-ha broad-leaved Korean pine mixed forest and 5-ha secondary poplar-birch forest in northeastern China (Yuan et al., 2016).

Having confirmed that spatial autocorrelation is not likely to strongly confound our results, we employed linear SEM to examine the relationships of species diversity and DBH variation with aboveground biomass, in addition to the effects of soil nutrients. We constructed SEM based on known hypothetical multivariate causes of forest diversity and aboveground biomass within each vertical strata for integrative and isolation modelling, and also for whole-community level analyses (Fig. 1). Several tests were used to assess the goodness of fit for SEMs (Malaeb et al., 2000), i.e., the Chi-square (χ^2) test, goodness-of-fit index (GFI), comparative fit index (CFI), standardized root mean square residual (SRMR) and Akaike information criterion (AIC). Indicators for a best model fit to the data critically included an insignificant χ^2 test statistic ($P > 0.05$; indicates that sample and observed covariance matrices are statistically indistinguishable), SRMR < 0.08, and both GFI and CFI > 0.95 (Hoyle, 2012; Grace et al., 2016). We critically used χ^2 test, representing the maximum likelihood estimation, to assess how well the hypothesized SEM fits the data (Ali et al., 2016; Grace et al., 2016). The indirect effect of a predictor was calculated by multiplying the standardized effects of all paths on one route from one predictor to mediator and then to aboveground biomass, while total effect was calculated by adding standardized direct and indirect effects (Ali et al., 2016; Grace et al., 2016). The SEMs were employed using the *lavaan* package (Rosseel, 2012).

Shapiro-Wilk goodness-of-fit test was used to assess the normality for all variables. As recommended (Grace et al., 2016), all numerical variables including aboveground biomass, species diversity and DBH variation were natural-logarithm transformed and standardized in order to meet the assumptions of normality and linearity, and to allow comparisons among multiple predictors and models (Zuur et al., 2009). For the interpretation of results

(Grace et al., 2016), we conducted the bivariate relationships indicating each hypothesized path according to the conceptual model in Fig. 1, using Pearson's correlation and regression analyses. The complementary Pearson's correlations and bivariate relationships to the SEMs are provided in Table S4 and Figs. S3–S5, respectively. See Appendix S1 for the dataset used in the analyses. For all statistical analyses R 3.2.2 was used (R Development Core Team, 2015).

3. Results

According to the χ^2 test, the integrative SEM which included the overstorey and understorey strata in conjunction was accepted ($\chi^2 = 5.98$, $P = 0.425$). In comparison, the isolation SEMs for overstorey ($\chi^2 = 0.27$, $P = 0.605$) and understorey ($\chi^2 = 2.03$, $P = 0.155$) strata were also accepted, whereas the whole-community SEM was rejected ($\chi^2 = 4.72$, $P = 0.030$; Table 1). The goodness of fit for the integrative and forest strata SEMs showed that including overstorey and understorey trees in an integration (Fig. 2) or in isolation (Fig. 3a and b) performed equally well for predicting aboveground biomass (Tables 1 and 2).

The integrative SEM accounted for 35, 31, 16, 12, 4, and 0% of the variation in understorey aboveground biomass, overstorey aboveground biomass, overstorey DBH variation, overstorey species diversity, understorey species diversity, and understorey DBH variation, respectively (Fig. 2). Overstorey DBH variation ($\beta = 0.53$, $P < 0.001$) and species diversity ($\beta = 0.19$, $P = 0.016$) had positive direct effects on overstorey aboveground biomass. Overstorey species diversity had positive direct effect on species diversity ($\beta = 0.19$, $P = 0.046$), but not on aboveground biomass of understorey strata. Understorey species diversity and DBH variation did not significant affect understorey aboveground biomass. Soil nutrients had positive direct effect on overstorey DBH variation ($\beta = 0.39$, $P < 0.001$), but negative direct effects on aboveground biomass in both overstorey ($\beta = -0.34$, $P < 0.001$) and understorey ($\beta = -0.46$, $P < 0.001$), and on species diversity in overstorey ($\beta = -0.35$, $P < 0.001$). In contrast, soil nutrients did not directly affect understorey species diversity and DBH variation (Table 2; Fig. 2).

Overstorey species diversity, DBH variation and aboveground biomass did not indirectly affect understorey aboveground biomass via understorey species diversity and DBH variation (Table 2). Soil nutrients had indirect positive effect on overstorey aboveground biomass via overstorey DBH variation ($\beta = 0.21$, $P < 0.001$), while negative indirect effect on overstorey

Table 1
Model fit statistic summary of the structural equation models (SEMs) for the relationships of species diversity and individual tree size variation with aboveground biomass, in addition to the effects of soil nutrients, in a subtropical forest. SEMs were accepted or rejected based on χ^2 test.

Hypothesized model	*df*	Model fit statistics summary						Model remarks	SEM
		CFI	GFI	SRMR	AIC	R^2	χ^2 (*P*-value)		
Integrative model (Fig. 1a)	5	1.00	0.99	0.030	2456.07	0.31 (overstorey AGB) 0.35 (understorey AGB)	3.24 (0.664)	Accepted	Fig. 2
Overstorey strata model (Fig. 1b)	1	1.00	0.99	0.015	1426.38	0.31	0.27 (0.605)	Accepted	Fig. 3a
Understorey strata model (Fig. 1c)	1	0.98	0.99	0.040	1459.81	0.33	2.03 (0.155)	Accepted	Fig. 3b
Whole-community model (Fig. 1d)	1	0.96	0.98	0.064	1424.33	0.36	4.72 (0.030)	Rejected	Fig. S6

Note: *df* is based on the number of 'knowns' minus the number of free parameters in the model, not on the sample size.
Abbreviations: AGB, aboveground biomass; *df*, degrees of freedom; CFI, comparative fit index; GFI, goodness of fit index; SRMR, standardized root mean square residual; AIC, Akaike information criterion; χ^2, Chi-square test; R^2 indicates the total variation in aboveground biomass that is explained by the combined independent variables.

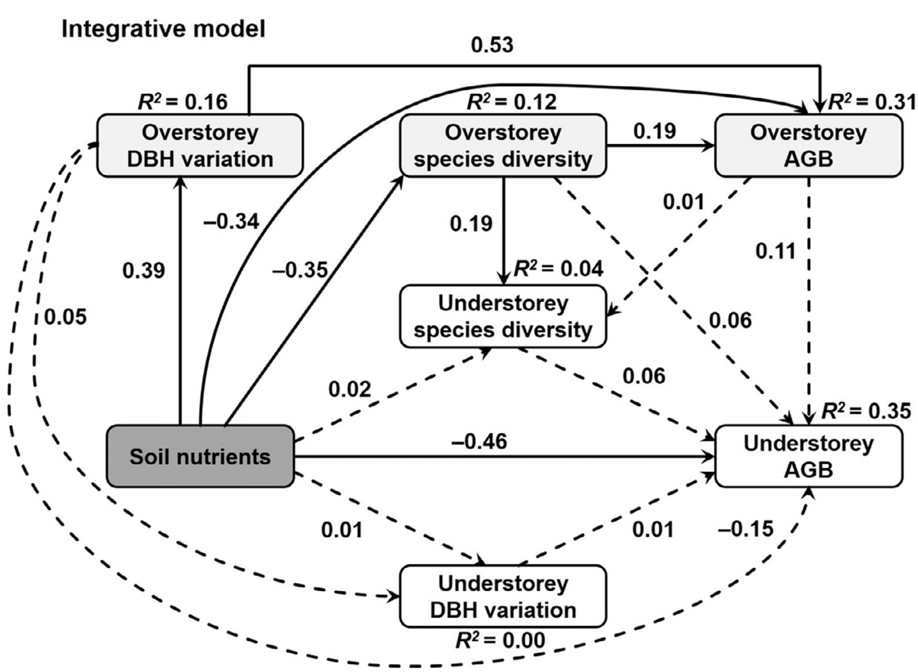

Fig. 2. The best-fit structural equation model for the integrative modelling of the relationships of species diversity and individual tree size variation in overstorey and understorey strata with their corresponding aboveground biomass, and the relationships of overstorey strata with understorey strata, in addition to the effects of soil nutrients. 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 Table 1. For abbreviations, see Table 2.

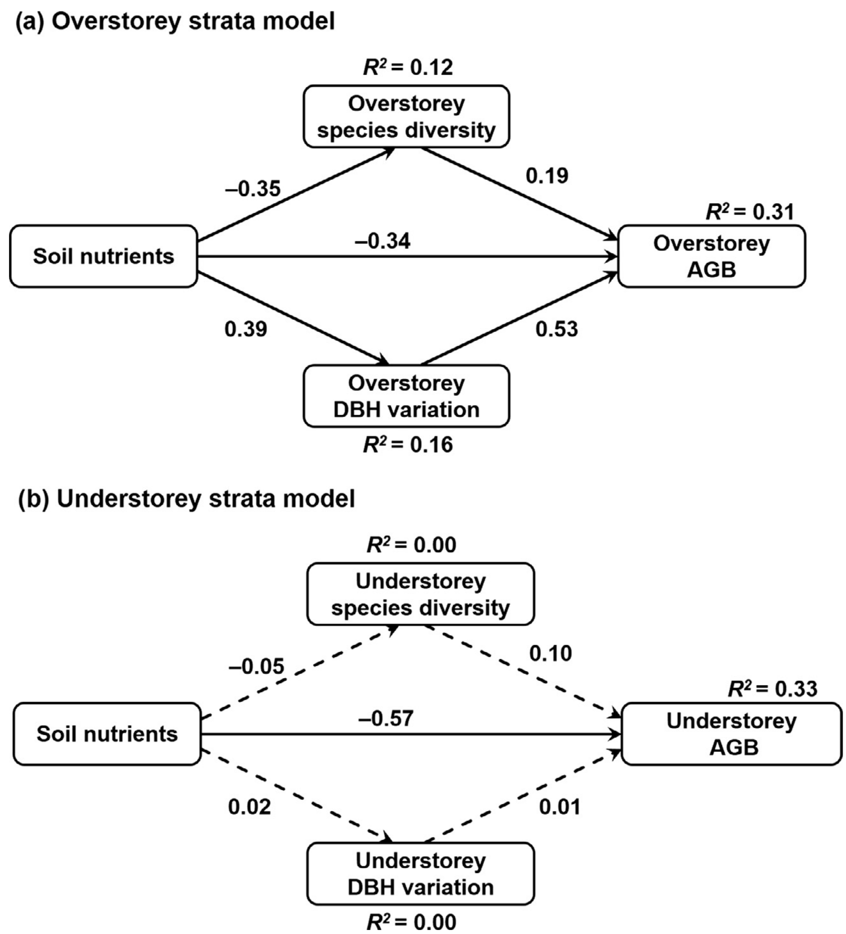

Fig. 3. The best-fit structural equation models for the isolation modelling of forests strata. (a) the relationships of species diversity and individual tree size variation with aboveground biomass at overstorey strata, and (b) understorey strata, in addition to the effects of soil nutrients. Solid arrows 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 Table 1. For abbreviations, see Table 2.

aboveground biomass via overstorey species diversity ($\beta = -0.07$, $P = 0.037$). The indirect effect of soil nutrients on understorey aboveground biomass was not found. There were significant total negative effects of soil nutrients on understorey and overstorey aboveground biomass, but the strength of the effect varied at understorey ($\beta = -0.58$, $P < 0.001$) and overstorey ($\beta = -0.20$, $P = 0.023$) strata (Table 2).

The overstorey SEM (Fig. 3a) showed that overstorey DBH variation ($\beta = 0.53$, $P < 0.001$) and species diversity ($\beta = 0.19$, $P = 0.016$) had positive direct effects on overstorey aboveground biomass (Fig. 3a). Soil nutrients had negative direct effects on overstorey aboveground biomass ($\beta = -0.34$, $P < 0.001$) and species diversity ($\beta = -0.35$, $P < 0.001$), but positive direct effect on overstorey DBH variation ($\beta = 0.39$, $P < 0.001$). Soil nutrients also had indirect positive effect via overstorey DBH variation ($\beta = 0.21$, $P < 0.001$) while negative indirect effect via overstorey species diversity ($\beta = -0.07$, $P = 0.037$) on overstorey aboveground biomass. The total effect of soil nutrients on overstorey aboveground biomass was significantly negative ($\beta = -0.20$, $P = 0.023$; Table 2).

The SEM for understorey strata (Fig. 3b) showed that species diversity and DBH variation did not directly affect aboveground biomass in understorey. Aboveground biomass significantly decreased with soil nutrients ($\beta = -0.57$, $P < 0.001$). Soil nutrients did not directly affect understorey species diversity and DBH variation. There were not significant indirect effects of soil nutrients via understorey species diversity and DBH variation on understorey aboveground biomass. The total effect of soil nutrients on aboveground biomass was relatively similar to the direct effect ($\beta = -0.57$, $P < 0.001$; Table 2). In comparison, the whole-community SEM (Fig. S6) showed almost similar results to the overstorey SEM (Fig. 3a), but the SEM was rejected based on χ^2 test ($P < 0.05$).

4. Discussion

Using both integration and isolation modelling, we assessed how species diversity and individual tree size variation drive aboveground biomass in overstorey and understorey strata, and whether overstorey species diversity and individual tree size variation affect understorey species diversity, tree size variation and aboveground biomass in a subtropical forest, when soil nutrients were considered simultaneously. In partial agreement with our Prediction 1 and Prediction 2, we found that aboveground biomass significantly increases with species diversity and individual tree size variation in overstorey strata, whereas the positive relationships are not statistically significant in understorey strata. With increase of soil nutrients, there is an increase of individual tree size variation in overstorey strata, but the decrease of overstorey species diversity and aboveground biomass in both forest strata. Our Prediction 3 was rejected, as we found that overstorey strata did not affect aboveground biomass and individual tree size variation in understorey strata. Markedly, species diversity of overstorey strata promotes species diversity of understorey, which is in full agreement with our Prediction 4.

Table 2
The direct, indirect, and total standardized effects on aboveground biomass based on structural equation models (SEMs). Effects values of accepted SEMs are shown here (see Table 1 for model fit statistics, and Figs. 2 and 3 for accepted SEMs). Significant effects are indicated in bold ($P < 0.05$). Abbreviations: DBH, diameter at breast height; AGB, aboveground biomass; S.E., standard error.

Predictor	Pathway to response variable	Response variable	Integrative model in Fig. 2			Overstorey strata model in Fig. 3a			Understorey strata model in Fig. 3b		
			Effect	S.E.	*P*-value	Effect	S.E.	*P*-value	Effect	S.E.	*P*-value
Soil nutrients	Direct effect	Overstorey AGB	−0.34	0.06	**<0.001**	−0.34	0.06	**<0.001**	–	–	–
	Direct effect	Understorey AGB	−0.46	0.06	**<0.001**	–	–	–	−0.57	0.05	**<0.001**
	Indirect effect via overstorey species diversity	Overstorey AGB	−0.07	0.02	**0.037**	−0.07	0.02	**0.037**	–	–	–
	Indirect effect via overstorey DBH variation	Overstorey AGB	0.21	0.04	**<0.001**	0.21	0.04	**<0.001**	–	–	–
	Indirect effect via overstorey species diversity	Understorey AGB	−0.02	0.02	0.460	–	–	–	–	–	–
	Indirect effect via overstorey DBH variation	Understorey AGB	−0.06	0.03	0.115	–	–	–	–	–	–
	Indirect effect via overstorey AGB	Understorey AGB	−0.04	0.02	0.222	–	–	–	–	–	–
	Indirect effect via understorey species diversity	Understorey AGB	0.00	0.00	0.853	–	–	–	−0.01	0.01	0.604
	Indirect effect via understorey DBH variation	Understorey AGB	0.00	0.00	0.964	–	–	–	0.00	0.00	0.925
	Total effect	Overstorey AGB	−0.20	0.06	**0.023**	−0.20	0.06	**0.023**	–	–	–
	Total effect	Understorey AGB	−0.58	0.06	**<0.001**	–	–	–	−0.57	0.05	**<0.001**
Overstorey species diversity	Direct effect	Overstorey AGB	0.19	0.08	**0.016**	0.19	0.08	**0.016**	–	–	–
	Direct effect	Understorey AGB	0.06	0.08	0.453	–	–	–	–	–	–
	Indirect effect via understorey species diversity	Understorey AGB	0.02	0.02	0.350	–	–	–	–	–	–
	Indirect effect via overstorey AGB	Understorey AGB	0.02	0.02	0.258	–	–	–	–	–	–
	Total effect	Overstorey AGB	0.19	0.08	**0.016**	0.19	0.08	**0.016**	–	–	–
	Total effect	Understorey AGB	0.10	0.08	0.217	–	–	–	–	–	–
Overstorey DBH variation	Direct effect	Overstorey AGB	0.53	0.08	**<0.001**	0.53	0.08	**<0.001**	–	–	–
	Direct effect	Understorey AGB	−0.15	0.09	0.095	–	–	–	–	–	–
	Indirect effect via understorey DBH variation	Understorey AGB	0.00	0.00	0.893	–	–	–	–	–	–
	Indirect effect via overstorey AGB	Understorey AGB	0.06	0.05	0.209	–	–	–	–	–	–
	Total effect	Overstorey AGB	0.53	0.08	**<0.001**	0.53	0.08	**<0.001**	–	–	–
	Total effect	Understorey AGB	−0.09	0.08	0.242	–	–	–	–	–	–
Understorey species diversity	Direct effect	Understorey AGB	0.08	0.07	0.291	–	–	–	0.10	0.07	0.188
Understorey DBH variation	Direct effect	Understorey AGB	0.01	0.07	0.888	–	–	–	0.01	0.07	0.920

4.1. The relationship between biodiversity and aboveground biomass depends on forest strata

The observed positive relationships of aboveground biomass with species diversity and individual tree size variation in overstorey strata might be attributable to the niche complementarity effect, which progressively leads to great site resource utilization (Díaz et al., 2011; Slik et al., 2013; Poorter et al., 2015; Zhang et al., 2016). Within forests, complex tree sized structures associate with increased light capture and light use efficiencies (Yachi and Loreau, 2007; Zhang and Chen, 2015; Dănescu et al., 2016; Ali and Mattsson, 2017). Tree species with high size variation or variable tree sizes in forest communities are likely to have their own set of habitat requirements for water and soil nutrients (Lei et al., 2009; Ali et al., 2016). Therefore, a multilayered forest structure allows for more efficient utilization of resources in species diverse forests, leading to enhance of aboveground biomass due to niche differentiation (Poorter et al., 2015; Zhang and Chen, 2015; Ali et al., 2016; Dănescu et al., 2016). Generally, aboveground biomass increases exponentially or power-functionally with tree diameter at tree scale (Chave et al., 2014; Ali et al., 2015), and large trees in overstorey strata thus contribute disproportionally to stand biomass compared with small trees in natural forests (Poorter et al., 2015) and agroforests (Ali and Mattsson, 2017).

We found that the magnitude of the effects of species diversity and individual tree size variation on aboveground biomass in understorey strata is relatively weaker compared to the observations at overstorey strata. The non-significant relationships between biodiversity and aboveground biomass in understorey strata might be attributable to developmental effect of tree species. Understorey strata include both shrub species and regeneration of canopy tree species, which are functionally different in coping with biotic interaction and resource competition. Regeneration of trees could have a different ecology than developed trees, as trees grow they may experience varying biomechanical burdens and environmental conditions, or pre-programmed ontogenetic switch, which can induce concomitant changes in tree structure and function (Meinzer et al., 2011). Therefore, the relationship between biodiversity and aboveground biomass might be weakened in understorey strata by the mixture effects of development or life stage and high degree of biotic interaction and resource heterogeneity. In addition, tree species in overstorey strata with high aboveground biomass and great tree size may consume a large part of resource, thus probably reducing resources availability to understorey species (Gilliam, 2007; Mason et al., 2011). As such, the dominant role of overstorey strata on the available resources likely weakens the biodiversity – aboveground biomass relationships in understorey strata (Hooper et al., 2005; Zhang et al., 2016). The strong response of overstorey species diversity and weak response of understorey species diversity to soil nutrients collectively suggest a dominant filtering role of the overstorey trees in shaping understorey structure and function (Zhang et al., 2016). Moreover, the absence of evidence for the effects of species diversity and individual tree size variation on aboveground biomass in understorey strata might be also attributable to the inability of diversity indices to gauge the actual range of positive interactions in the analysed understorey strata, rather than an intrinsic ecological mechanism (Dănescu et al., 2016).

In this study, we found that species diversity are positively related between overstorey and understorey strata. Understandably, if there are more seed trees of different species in overstorey strata, high species diversity in understorey strata is nursed and promoted due to abundant seed availability from different species. Moreover, overstorey or large tree species may adjust the habitat to sustain the suitability of understorey or small tree species (e.g., Gamfeldt et al., 2013; Lefcheck et al., 2015). For instance, high species diversity of overstorey strata may increase resource heterogeneity in the understorey strata or facilitate understorey trees, which in turn promotes understorey species diversity (Bartels and Chen, 2010, 2013; Zhang et al., 2016).

4.2. High species diversity and aboveground biomass on nutrient-poor soils

We found a clear trend toward high aboveground biomass across forest strata on nutrient-poor soils in the studied forest, with a high species diversity and low individual tree size variation in overstorey strata, and without any biodiversity mediation in understorey strata. This might be attributable to the specific adaptations of conservative species to the nutrient-poor soils that increase species longevity and biomass retention, thus enhancing the storage of aboveground biomass at the stand level (Poorter et al., 2015; Prado-Junior et al., 2016; Ali and Mattsson, 2017). Nutrient-poor soils are widely thought to be advantageous to species with conservative strategy, whereas nutrient-rich soils support species in favor of acquisitive strategy (Poorter and Bongers, 2006; Coomes et al., 2009; Fortunel et al., 2014; Reich, 2014). In the studied forest, the canopy trees or large trees and understorey trees are generally conservative evergreen species, which tend to dominate to infertile soils (Yan et al., 2006; Yan et al., 2009). Therefore, with slow growth and high longevity, they may accumulate and contribute to large part of aboveground biomass at the stand level (Prado-Junior et al., 2016).

Soil fertility hypothesis predicts that aboveground biomass or productivity increases with increasing soil nutrients availability, and plants grow fast when resource availability is high (Wright et al., 2011; Quesada et al., 2012). However, high nutrients availability may also lead to increased competition, and hence high mortality and biomass turnover rates of plants (Prado-Junior et al., 2016). Consequently, high aboveground biomass or productivity in (sub-) tropical forests associates often with nutrient-poor soils (Poorter et al., 2015; Chiang et al., 2016; Prado-Junior et al., 2016). In this study, we also found that nutrient enhancements depress species diversity in overstorey strata of the studied forest. This mismatch between conventional theory and empirical pattern is potentially due to an interaction between tree size and niche overlap among canopy tree species (Prado-Junior et al., 2016). Emergent tree species with large maximum size in overstorey strata can grow large and may integrate resource patches both above- and belowground by reducing the niche complementarity with functionally dissimilar species and by increasing niche overlap with functionally similar species (Walker, 1992; Prado-Junior et al., 2016). As such, species diversity in overstorey strata is depressed (e.g. Jucker et al., 2016).

5. Concluding remarks

Our results provide strong evidence for the forest strata-dependent relationship between biodiversity and aboveground biomass in a subtropical forest. Particularly, the integrative model of this study suggests the general notion that no sole and ubiquitous relationship between biodiversity and aboveground biomass exists, but rather that the magnitude and direction and the underlying mechanisms of this relationship is forest strata-specific where available resources shift greatly. In overstorey strata, the positive relationship of aboveground biomass with species diversity and individual tree size variation might be attributed to the niche complementarity effect. In understorey strata, the mixture effects of tree development, high degree of biotic interaction, and increased resource heterogeneity might complicate the relationship between biodiversity and aboveground biomass. Importantly, the positive association of species diversity between overstorey and understorey strata indicates a crucial role of taxonomic diversity in overstorey trees for fostering species diversity of understorey strata in a subtropical forest. The strong and consistent negative effects of soil nutrients on aboveground biomass and overstorey species diversity suggest an important mechanism that high species diversity of overstorey strata with great tree size variation on nutrient-poor soils is crucial for driving high aboveground biomass in subtropical forest ecosystems. Insightfully, ecological models for predicting aboveground biomass would be improved by including separate effects of overstorey and understorey diversity.

Statement of authorship

AA & ERY conducted research; AA compiled and analysed the data; AA & ERY designed the study and wrote the paper.

The authors declare no conflict of interest.

Acknowledgements

The authors would like to thank Min Guo, Qiang Zhong, Meng Kang, Yue Xu, Yilu Xu, Xiaodong Yang, Haixia Huang, Zhihao Zhang, Baowei Sun, Wenji Ma, Qingru Shi, Yantao, Zhao, Qingqing Zhang, Mingshan Xu, and Liuli Zhou for their assistance in the field and laboratory. We thank Professor Xi-Hua Wang for providing original dataset of soil physicochemical variables. This study was supported by the National Natural Science Foundation of China (Grant Nos. 31670438 and 31270475), and the CFERN & BEIJING TECHNO SOLUTIONS Award Funds on excellent academic achievements.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.06.056.

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