



Forest strata-dependent functional evenness explains whole-community aboveground biomass through opposing mechanisms

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ABSTRACT

A positive biodiversity – aboveground biomass relationship is often attributed to the niche complementarity hypothesis. This hypothesis has received much less support when based on functional trait diversity and when tested in complex natural forests. Here, we hypothesized that niche complementarity (high trait diversity) in the understorey and niche overlap (low trait diversity) in the overstorey would drive whole-community aboveground biomass. To test this hypothesis, we used multiple linear regression models to evaluate how functional trait diversity (functional richness, evenness, divergence and dispersion) of overstorey, understorey, and whole-community determine aboveground biomass across 125 plots in a 5-ha subtropical forest of Eastern China. A structural equation model was used to evaluate whether the functional trait diversity of overstorey affects the relationships between understorey functional trait diversity and whole-community aboveground biomass while considering for the effect of environmental factors. We additionally considered the effects of mass ratio (i.e. community-weighted mean of trait values) and stand structural complexity. The strong negative effect of overstorey functional evenness on aboveground biomass provides support to the functional dominance and/or niche overlap rather than niche complementarity effect. The negative effect of overstorey functional evenness on aboveground biomass was also partially mediated by its direct negative effect on understorey functional evenness. The weak positive effect of understorey functional evenness on aboveground biomass provides support to the niche complementarity effect. We conclude that functional evenness of overstorey and understorey strata affect whole-community aboveground biomass differently through opposing mechanisms, regardless of the effects of mass ratio and stand structural complexity.

1. Introduction

Understanding the ecological mechanisms for the relationships between biodiversity and ecosystem function has been a central debate in ecology for more than four decades (Grime, 1973). A number of ecological hypotheses exist on how the magnitude of ecosystem function would respond to variation in species and/or functional trait diversity (e.g., Naeem, 2002). A prominent hypothesis is the niche complementarity hypothesis predicting that communities with large numbers of species (i.e. species diversity) (Tilman, 1999) or varieties of functional traits (i.e. functional trait diversity) (Díaz et al., 2007) can efficiently utilize the available resources, and thereby increasing the realized degree of niche differentiation for determining high ecosystem

functions in forests (Zhang et al., 2012). Most of the recent studies found no or a little support for the niche complementarity hypothesis, based on functional trait diversity in forest ecosystems (Conti and Díaz, 2013; Finegan et al., 2015; Chiang et al., 2016; Fotis et al., 2017; van der Sande et al., 2017). Among these empirical studies, the relationships between functional trait diversity and aboveground biomass have been assessed at the level of either whole-community or overstorey stratum only. Natural forests, however, are always structurally complex and plant species with different functional strategies are generally assembled in different vertical layers or forest strata (i.e., overstorey and understorey) (Wright, 2002; Rüger et al., 2012).

Understorey stratum contributes much to the majority of biodiversity and has a high turnover rate in comparison with overstorey

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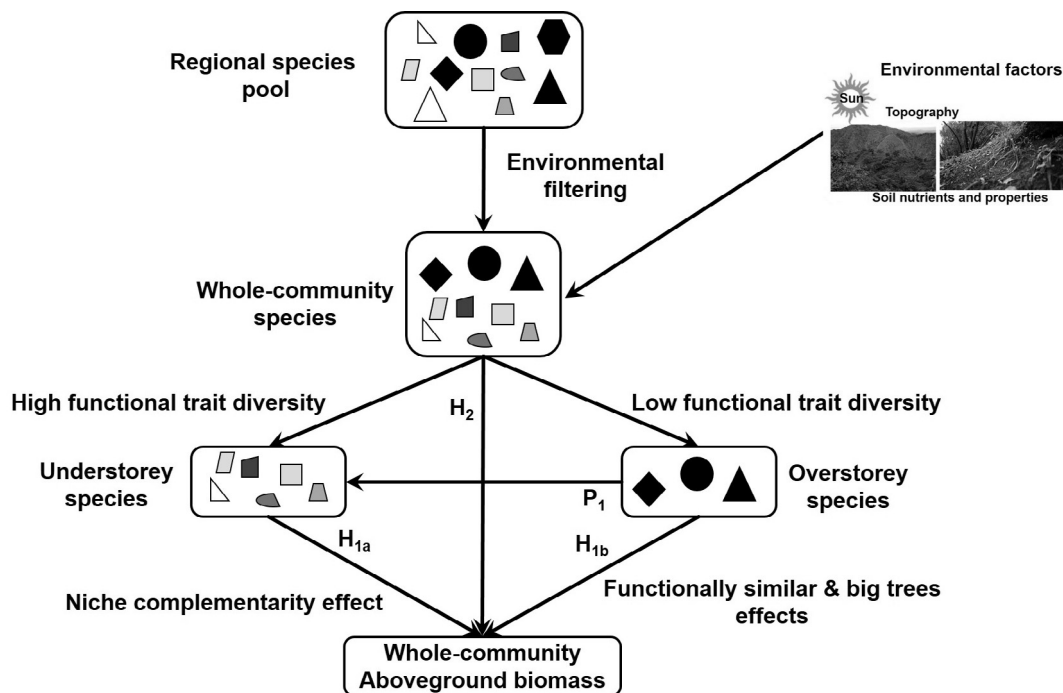


Fig. 1. A conceptual framework showing how changes in aboveground biomass are determined by underlying mechanisms (niche complementarity and/or niche overlap and big trees effects). Species pool having different symbols and colors represents different species and traits dissimilarity, respectively, while the size of the symbols represents the overstorey (big size) and understorey (small size) species. H_{1a} , H_{1b} , H_2 and P_1 indicate the proposed hypotheses, prediction or questions (see introduction section).

stratum (Nilsson and Wardle, 2005; Gilliam, 2007; Barbier et al., 2008). Overstorey stratum stores a large amount of aboveground biomass due to their large wood volumes and uneven contribution of large trees to the whole-community level aboveground biomass (Slik et al., 2013). Environmental conditions affecting plant performance can strongly differ across forest strata in natural forests, and therefore important resources like the light are often limiting in the understorey while abundant in overstorey stratum of forests (e.g., Wright, 2002; Brenes-Arguedas et al., 2011). Based on the functional trait diversity, the niche complementarity effect may be less crucial in the overstorey stratum probably due to the dominance of few large trees, and hence it is expected that low functional trait diversity or high functional dominance or niche overlap would drive aboveground biomass (Prado-Junior et al., 2016; Fotis et al., 2017). In understorey stratum, it is expected that high functional trait diversity would enhance aboveground biomass because strong interactions among coexisting species could lead niche differentiation, facilitation and competition in a more stressful and resource-limited environment (Paquette and Messier, 2011).

Despite many efforts in understanding the niche complementarity effect on ecosystem function, uncertainties still remain (Hooper et al., 2005; Díaz et al., 2007). For instance, the mass ratio and stand structural complexity also strongly influence ecosystem function (Chiang et al., 2016; Prado-Junior et al., 2016). The mass ratio hypothesis suggests that aboveground biomass or productivity is strongly driven by the functional identity or composition of the most dominant species or traits (Grime, 1998), which can be quantified in term of community-weighted mean (CWM) of a trait values (Garnier et al., 2004; Díaz et al., 2007; Finegan et al., 2015). By evaluating the mass ratio effect, we have previously reported that high aboveground biomass was markedly determined by the functional identity of overstorey tree height on nutrient-rich soils, whereas by understorey conservative traits on nutrient-poor soils (Ali and Yan, 2017b). Besides the mass ratio effect, stand structural complexity, quantified in terms of individual tree size inequality and species diversity, is also important for determining ecosystem function because it reflects the capability of resource acquisition

and utilization among component species and interacting individuals in natural forests (Fotis et al., 2017). Consequently, aboveground biomass increases with stand structural complexity in overstorey stratum but not in understorey stratum in a subtropical forest (Ali and Yan, 2017a). In sum, the niche complementarity and mass ratio effects, based on functional traits, on aboveground biomass or productivity are not necessarily mutually exclusive in natural forests (Conti and Díaz, 2013; Chiang et al., 2016; Prado-Junior et al., 2016). In this context, considering the confounding effects of mass ratio and stand structural complexity on ecosystem function may clarify the role of niche complementarity played for driving the relationships between functional trait diversity and aboveground biomass across forest strata. In addition, studies in (sub-) tropical forests also show that environmental factors such as topography and soil nutrients may modulate the multivariate relationships between functional trait diversity and ecosystem functions (Chiang et al., 2016; Prado-Junior et al., 2016; Ali and Yan, 2017b).

In this study, we were particularly interested to explore whether the functional (multivariate) trait diversity of overstorey and understorey strata have differential effects on the whole-community aboveground biomass while accounting for the effects of local environmental conditions. Using forest inventory, functional traits and environmental factors datasets across 125 plots in a 5-ha natural subtropical forest in Eastern China, we addressed the following three main questions with associated hypotheses or predictions. (1) How does functional trait diversity of overstorey and understorey strata, alone or jointly, affect whole-community (overstorey plus understorey strata) aboveground biomass (hereafter simply referred to ‘aboveground biomass’)? We hypothesize that high functional trait diversity of understorey stratum due to the niche complementarity (H_{1a}), while low functional trait diversity of overstorey stratum due to the presence of few large trees or niche overlap (H_{1b}) drives high aboveground biomass in a community (Fig. 1). In comparison, we hypothesize (H_2) that low functional trait diversity of whole-community drives high aboveground biomass in a community due to the dominant role of functionally-similar large trees

(i.e., overstorey) on understorey stratum and available resources (Fig. 1) (Bartels and Chen, 2010; Ali and Yan, 2017b; Zhang et al., 2017). (2) What is the contribution of functional trait diversity of overstorey and understorey strata to aboveground biomass? We predict (P_1) that functionally-similar big trees (i.e., overstorey stratum) have a larger contribution than functionally-dissimilar small trees (i.e., understorey stratum) on aboveground biomass due to the large stem volumes present in overstorey (Slik et al., 2013; Ali and Yan, 2017a). (3) Whether functional trait diversity of overstorey stratum affects functional trait diversity of understorey stratum and its relationship with aboveground biomass, after accounting for the effects of environmental factors in a subtropical forest? We hypothesize that functionally-similar big trees have negative effects on the functional trait diversity of understorey and hence may reduce the positive relationships between understorey functional trait diversity and aboveground biomass (Ali and Yan, 2017b; Zhang et al., 2017), which we call the big trees effect (H_{1a} , H_{1b} , P_1). In addition, we were interested to clarify whether the mass ratio and stand structural complexity effects change the hypothesized relationships (i.e. H_{1a} , H_{1b} , H_2) between functional trait diversity and aboveground biomass in each of individual forest stratum and whole-community.

2. Materials and methods

2.1. Available datasets: forest inventory, functional traits and environmental factors

In this study, we used the forest inventory, measured functional traits and environmental factors datasets from our previous studies (Ali and Yan, 2017a, b). These available datasets were collected across 125 (20 × 20 m) plots in a 5-ha subtropical evergreen broadleaf forest in center of the Tiantong National forest park, located in Ningbo city, Zhejiang province, in Eastern China (Yan et al., 2013).

All stems ≥ 1 cm diameter at breast height (DBH) and leaf physical functional traits including mean leaf area, specific leaf area and leaf dry matter content were measured for each of the 20,253 individuals of the 108-studied species across 125 plots. Leaf chemical traits, including leaf nitrogen and phosphorous concentrations, and wood density were measured for 98 species by randomly selecting seven healthy mature trees for each species (Cornelissen et al., 2003). The leaf chemical traits and wood density were missing for 10 rare or less abundant species (contributed less than 10% in most of the 20 observed plots) (Ali and Yan, 2017b), and hence 98 species (contributed $\sim 99\%$ of the 5-ha community coverage measured as the species' relative basal area) were used in this study. The plant maximum height was derived from the Chinese flora database. The detail description of the measurement of plant functional traits is provided in our previous study (Ali and Yan, 2017b).

To consider any effects of environmental conditions (see topographic heterogeneity in Fig. S1) on the relationships between functional trait diversity and aboveground biomass, we included the topographical properties and soil physicochemical properties as covariates (see a summary of the variables in Table S1). To avoid the strong correlations among local environmental conditions (see Table S2), we used the two axes of principal component analyses (PCA) for soil properties and for topographical variables (soil PC1, soil PC2, topography PC1 and topography PC2), separately (see Table S3).

2.2. Quantification of functional trait diversity and estimation of aboveground biomass

Overstorey stratum included all individuals with tree DBH ≥ 10 cm in each forest plot, and understorey stratum included woody vegetation with $1 \leq \text{DBH} < 10$ cm (Ali and Yan, 2017b, a). The overstorey stratum included tree species of the emergent, canopy and sub-canopy layers, whereas the understorey stratum included shrubs and small tree

species. The small tree species in the understorey stratum are the prospective species which are growing to occupy any respective layer of the overstorey stratum. The herbaceous ground vegetation was excluded in this study, due to the non-availability of the data and low species richness of herbaceous ground vegetation in the subtropical forests as compared to the boreal and temperate forests.

For calculation of functional trait diversity in overstorey, understorey, and whole-community within each plot, we used eight measured functional traits, including six leaf and two stem traits, that are crucial for aboveground biomass and productivity (Finegan et al., 2015; Prado-Junior et al., 2016). We used four multivariate-trait indices of functional trait diversity that were quantified for overstorey and understorey separately: functional evenness, functional richness, functional divergence and functional dispersion (Mason et al., 2005; Villéger et al., 2008; Laliberté and Legendre, 2010). This resulted in eight indices for functional trait diversity across forest strata, while four indices for whole-community level analyses within each plot. The species' relative basal area was used to weight species' traits across forest strata and at a whole-community level within each plot as suggested by a previous study (Prado-Junior et al., 2016). Functional trait values were standardized before the quantification of four functional diversity indices. Here, standardization of the functional trait values refers to a standardized variable (also called a z-score or a standard score), which has been rescaled to have a mean of 0 and a standard deviation of 1. The functional trait diversity indices were calculated using the *vegan* (Oksanen et al., 2015) and *FD* packages (Laliberté and Legendre, 2010).

We calculated aboveground biomass (AGBt) for each tree (DBH ≥ 5 cm) using a global allometric equation (Chave et al., 2014),

$$\text{AGBt} = \exp\{-1.803 - 0.976(E) + 0.976 \times \ln(\rho) + 2.673 \times \ln(\text{DBH}) - 0.0299 \times (\ln(\text{DBH}))^2\}$$

based on tree DBH and species' wood density (ρ), where E for our study site was derived from Chave et al. (2014). For aboveground biomass (AGBs) of shrubs and small trees (DBH < 5 cm), we used a locally developed multispecies generalized model (Ali et al., 2015), $\text{AGBs} = 1.450 \times \exp\{-4.97 + 2.20 \times \ln(\text{DBH}) + 3.06(\rho)\}$, based on small tree and shrub DBH or diameter at 45 cm height from the ground (Ali and Yan, 2017a, b). A summary of functional trait diversity and biomass values is listed in Table S1.

2.3. Statistical analyses

Multiple linear regressions models were used to evaluate how aboveground biomass (overstorey plus understorey) was driven by functional trait diversity (functional dispersion, functional divergence, functional richness and functional evenness) of overstorey and understorey strata across local environmental conditions (hereafter referred as 'forest strata model'). More specifically, we conducted three series of forest strata model in order to find the optimal subset of predictor(s) (i.e., optimal model) for each of the overstorey stratum effect (the first series; overstorey model), the understorey stratum effect (the second series; understorey model), and the joint effect of overstorey and understorey strata (the third series; joint model for forest strata), in addition to the local environmental factors, on aboveground biomass. For the first and second series of the forest strata model, we included functional trait diversity indices (4 indices) of overstorey and understorey stratum, respectively. With respect to the third series, we jointly included all indices of functional trait diversity (8 indices) for the purpose to evaluate the combined effects of overstorey and understorey strata on aboveground biomass. For comparison, we also evaluated how aboveground biomass was driven by whole-community functional trait diversity across local environmental conditions (hereafter referred as 'whole-community model'). In all models, we included local environmental factors, i.e. soil PC1, soil PC2, topography PC1 and PC2, as covariates.

We evaluated all possible subsets of regression models and selected

Table 1

Results of the forest strata optimal models (i.e., overstorey, understorey, and joint models) based on a series of multiple regression analyses for aboveground biomass and predictors (functional trait diversity and environmental factors). Relative contribution (RC in %), standardized regression coefficient, *t*-test and *P*-value are given. The coefficient of determination (R^2), *F*-test, *P*-value and Akaike Information Criterion (AICc) of the model are also given. *P* values < 0.05 are given in bold. *P* value > 0.05 for Moran's *I* test indicates no spatial autocorrelation in the residuals of the model. The gray portion in the table represents that variables were not included in the given model, whereas blank cells represent that variables were not retained in the selected optimal model.

Predictors	Overstorey FTD model				Understorey FTD model				Joint model (overstorey + understorey)			
	RC	Beta	<i>t</i>	<i>P</i>	RC	Beta	<i>t</i>	<i>P</i>	RC	Beta	<i>t</i>	<i>P</i>
Constant	----	0.00	9.77	<0.001	----	0.00	5.25	<0.001	----	0.00	6.07	<0.001
<i>Overstorey stratum FTD</i>												
Functional divergence												
Functional richness												
Functional evenness	71.99	-0.35	-4.20	<0.001					57.81	-0.32	-3.76	<0.001
Functional dispersion												
<i>Understorey stratum FTD</i>												
Functional divergence												
Functional richness												
Functional evenness					48.74	0.21	2.49	0.014	18.95	0.15	1.74	0.085
Functional dispersion												
<i>Environmental factors</i>												
Soil PC1												
Soil PC2	28.01	-0.20	-2.44	0.016	51.26	-0.22	-2.56	0.012	23.24	-0.19	-2.28	0.024
Topography PC1												
Topography PC2												
<i>Model statistics</i>												
<i>F</i> -test (<i>P</i> -value)	13.36				7.24				10.10			
	(<0.001)				(0.001)				(<0.001)			
R^2	0.18				0.11				0.20			
AICc	1149.8				1160.5				1148.9			
Moran's <i>I</i> -test (<i>P</i> -value)	0.04				0.07				0.05			
	(0.310)				(0.113)				(0.288)			

the most parsimonious optimal model that had lowest AICc (i.e. Akaike Information Criterion adjusted for small sample sizes) and lowest number of predictors (Bartoń, 2016). The percent variation explained by each predictor was represented by the relative contribution of that predictor to the total variation explained in term of the coefficient of determination (i.e., R^2), determined using the *relaimpo* package (Groemping, 2013). The importance of each predictor to the explained variance was assessed based on both relative contribution and the marginal effect of each predictor within the optimal model. Multiple linear regression models were performed using the *stats* package and all subsets regression analyses were evaluated in *MuMIn* package (Bartoń, 2016).

In addition, we employed structural equation model (SEM) in order to evaluate whether functional trait diversity of overstorey stratum affects understorey stratum and its relationship with aboveground biomass, after accounting for the effects of environmental factors. Here, we designed an SEM based on the following three hypothesized paths: (1) direct effect of overstorey functional trait diversity on understorey functional trait diversity; (2) indirect effects of overstorey functional trait diversity via understorey functional trait diversity on whole-community aboveground biomass; and (3) direct effects of overstorey functional trait diversity, understorey functional trait diversity and environmental factors on aboveground biomass. To provide almost

result with the optimal multiple linear regression models, we, therefore, selected the best predictors for aboveground biomass as suggested by the joint optimal model for forest strata (i.e. the third series of linear models). Best-fit SEM was assessed critically through the insignificant ($P > 0.05$) Chi-square (χ^2) test value while also considering the goodness-of-fit index (GFI), comparative fit index (CFI) and standardized root mean square residual (SRMR). The SEM was implemented using the *lavaan* package (Rosseel, 2012).

To account for spatial autocorrelation, we used generalized least-squares models (GLS) (Pinheiro and Bates, 2016). By plotting semi-variogram of the spatial GLS models with accounted for the nugget effect (intercept), we found no clear indication of spatial autocorrelation (Fig. S2), and hence the non-spatial models had the lower AIC values (Table S4) which agree with the recent findings in natural forests (Chiang et al., 2016; Ali and Yan, 2017b, a). We also used the Moran's *I* test for evaluating the spatial autocorrelation in the residuals of the selected optimal linear model (Fig. S3), using the *spdep* package (Bivand, 2016). The summary of predictors and aboveground biomass, used in the main analyses is listed in Table S1. The complementary Pearson's correlations and bivariate relationships to the general linear models are shown in Tables S5 and S6, and Figs. S4–S7, respectively.

To test the confounding effects of mass ratio and stand structural complexity, we conducted an additional analysis by including the CWM

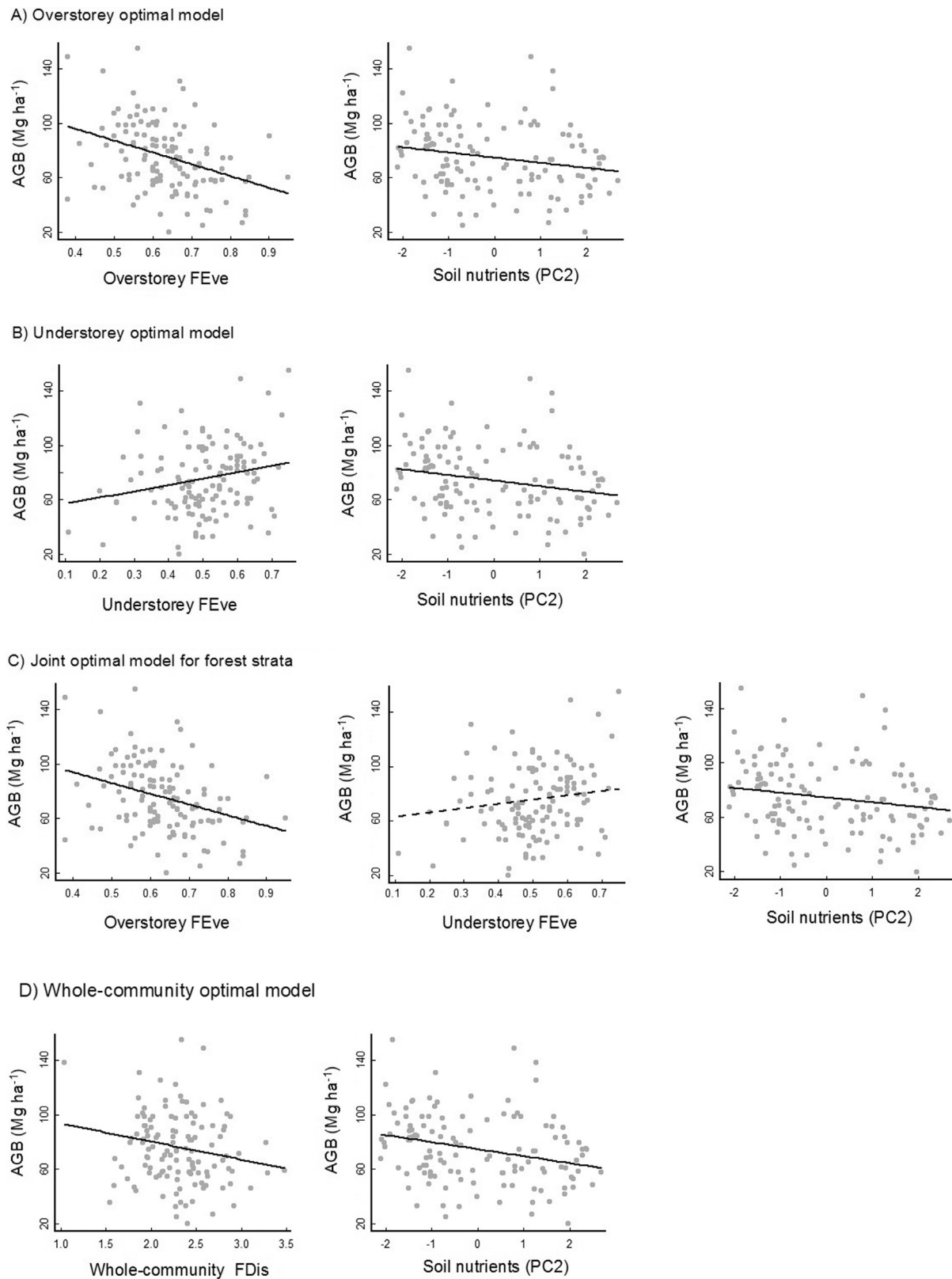


Fig. 2. The response of whole-community aboveground biomass to the retained predictors in the forest strata and whole-community optimal models (see Tables 1 and 2 for statistics). See Figs. S4–S7 for bivariate relationships.

indices, Shannon's species diversity and individual tree size inequality into the three series of forest strata optimal models, and the whole-community optimal model. In order to reduce the number of predictors, we included only those CWM indices (see Table S7) which had the

significant bivariate relationships with whole-community aboveground biomass (a variable of interest in this study), by following a standard approach of Conti and Díaz (2013). The detailed methods about the calculations of CWM and stand structural complexity indices, used in

the additional analyses for testing the mass ratio and stand structural complexity effects, are available in our previous studies (Ali and Yan, 2017a, b).

For all statistical analyses, R 3.4.2 was used (R Development Core Team, 2017).

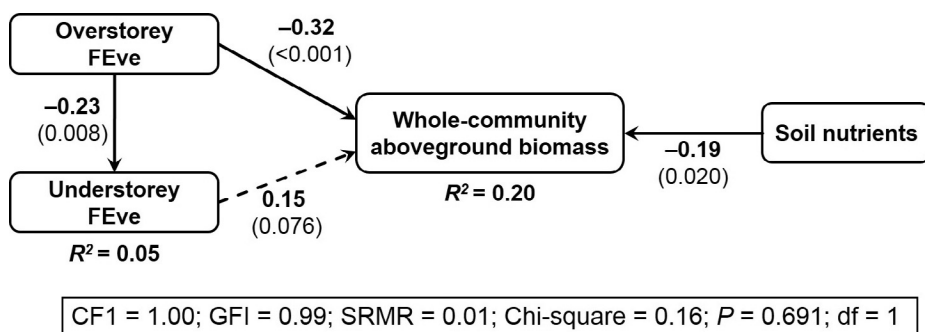
3. Results

In overstorey stratum, aboveground biomass was best predicted ($F = 13.36$, $P > 0.001$, $R^2 = 0.18$) by functional evenness ($\beta = -0.35$, $P < 0.001$; contributed 71.99%) and soil nutrients ($\beta = -0.20$, $P = 0.016$; contributed 28.01%), with no spatial autocorrelation in the residuals (Table 1, Fig. 2A). In understorey stratum, aboveground biomass was best predicted ($F = 7.24$, $P = 0.001$, $R^2 = 0.11$) by functional evenness ($\beta = 0.21$, $P = 0.014$; contributed 48.74%) and soil nutrients ($\beta = -0.22$, $P = 0.012$; contributed 51.26%), again with no spatial autocorrelation in the residuals (Table 1, Fig. 2B). The optimal joint model showed that aboveground biomass ($F = 10.10$, $P > 0.001$, $R^2 = 0.20$) was best predicted by overstorey functional evenness ($\beta = -0.32$, $P < 0.001$; contributed 57.81%), understorey functional evenness ($\beta = 0.15$, $P = 0.085$; contributed 18.95%) and soil nutrients ($\beta = -0.19$, $P = 0.024$; contributed 23.24%), without spatial autocorrelation in the residuals (Table 1, Fig. 2C).

The joint optimal model of overstorey and understorey strata showed that the direct effect of understorey functional evenness on aboveground biomass is no longer significant (Table 1; Fig. 2C), possibly weakened by the strong effect of overstorey functional evenness. The SEM showed that overstorey functional evenness had a strong direct negative effect on understorey functional evenness ($\beta = -0.23$, $P = 0.008$), and weakened the positive relationship between understorey functional evenness and aboveground biomass ($\beta = 0.15$, $P = 0.076$). Indirect effect of overstorey functional evenness via understorey functional evenness on aboveground biomass was non-significant ($\beta = -0.04$, $P = 0.117$), while total effect (direct + indirect effects) of overstorey functional evenness was significantly negative ($\beta = -0.37$, $P < 0.001$; Fig. 3).

At whole-community level, aboveground biomass ($F = 6.72$, $P = 0.002$, $R^2 = 0.20$) was best predicted by functional dispersion ($\beta = -0.20$, $P = 0.024$; contributed 32.05%) and soil nutrients ($\beta = -0.27$, $P = 0.002$; contributed 67.95%), with no spatial autocorrelation in the residuals (Table 2). This result demonstrates that aboveground biomass is high in plots with low functional dispersion, represents functionally similar average distance species to the basal-area weighted centroid of all species in community trait space, and located on soils with low soil nutrients (Fig. 2D).

The additional analysis regarding the inclusion of CWM, species diversity and individual tree size inequality showed that, although the added variables were retained in the models (Tables S8 and S9), whole-community aboveground biomass was still positively related to the



sions (see Table 1). Abbreviations: FEve, functional evenness; CFI, comparative fit index; GFI, goodness of fit index; SRMR, standardized root mean square residual; df, degree of freedom.

Table 2

Results of the whole-community optimal model based on aboveground biomass and predictors (functional trait diversity and environmental factors) using a multiple linear regressions model. General information is provided in Table 1. P values < 0.05 are given in bold. P value > 0.05 for Moran's I test indicates no spatial autocorrelation in the residuals of the model.

Predictor	RC	Beta	t	P
Constant	–	0.00	7.71	0.043
<i>Whole-community level FTD</i>				
Functional divergence				
Functional richness				
Functional evenness				
Functional dispersion	32.05	–0.20	–2.28	0.024
<i>Environmental factors</i>				
Soil PC1				
Soil PC2	67.95	–0.27	–3.12	0.002
Topography PC1				
Topography PC2				
<i>Model statistics</i>				
F-test (P-value)	6.72 (0.002)			
R ²	0.10			
AICc	1154.0			
Moran's I- test (P-value)	0.06 (0.183)			

functional trait diversity of understorey while negatively related to the functional trait diversity of overstorey stratum (Table S8). The additional optimal model for whole-community showed that unequal stand structure (i.e., individual tree size inequality) dominated by tall tree species with high leaf dry matter content had high whole-community aboveground biomass (Table S9).

4. Discussion

This study provides a strong evidence that separating functional trait diversity of overstorey and understorey strata improve predictions of aboveground biomass in a subtropical forest because overstorey and understorey strata have opposing effects on aboveground biomass. Our results support the hypotheses that high functional trait diversity of understorey stratum positively affects aboveground biomass due to the niche complementarity mechanism, while functional evenness of overstorey stratum negatively influences aboveground biomass due to the strong effect of a few dominant and functionally-similar tree species in overstorey stratum.

The main finding of this study is that high aboveground biomass in a community associates to different mechanisms where the niche complementarity (in terms of high functional trait diversity of understorey) and functionally-similar big trees effects (in terms of low functional trait diversity of overstorey, i.e., niche overlap) are at play (Figs. 1 and 3). Overstorey is the main contributor to aboveground biomass due to their large stem volumes, low functional trait diversity and high functional dominance (i.e., functional identity of tree height), hence

Fig. 3. Structural equation model linking functional trait diversity (i.e., functional evenness) of overstorey and understorey strata, and soil nutrients (soil PC2) with whole-community aboveground biomass. 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 and P -value in the bracket are shown. R^2 indicates the total variation in a dependent variable that is explained by the combined independent variables. Model-fit statistics are provided. The variables in the model were selected based on the final joint optimal model obtained from a series of multiple regressions

reflecting the mass ratio rather than niche complementarity effect (Prado-Junior et al., 2016; Ali and Yan, 2017b; Fotis et al., 2017). We also showed that the explained variance of aboveground biomass by overstorey stratum is higher than that by understorey stratum, probably due to the strong effects of stand structural complexity and mass ratio as compared to the niche complementarity (Ali and Yan, 2017b, a; Fotis et al., 2017; van der Sande et al., 2017). As such, understorey functional trait diversity has a weak positive effect on aboveground biomass probably due to the complementarity among slow-growing conservative species (Ali and Yan, 2017b).

The negative relationship between overstorey functional evenness and aboveground biomass suggests that aboveground biomass is high in communities where a constrained area of the multivariate-trait space is occupied by most of overstorey trees' basal area, contrary to the predictions by niche complementarity hypothesis (Prado-Junior et al., 2016). Indeed the few adult statures or species dominated by resource-acquisition or productivity-related traits may substantially contribute to the whole-community aboveground biomass in natural forests (Balvanera et al., 2005; Lohbeck et al., 2016; Ali and Yan, 2017b). Actually, the negative relationship between overstorey functional evenness and aboveground biomass substantiates the fact that high aboveground biomass can be maintained or built up by few functionally-similar dominant species through the process of niche overlap (species redundancy) and/or the mass ratio effect (e.g., Prado-Junior et al., 2016; Ali and Yan, 2017b; Fotis et al., 2017). Our additional analysis (Table S8) confirms that functional identity of overstorey tree height strong positively linked with the whole-community aboveground biomass while functional evenness negatively related. This suggests again that the dominance of overstorey functionally-similar species led to increasing aboveground biomass, as a result of the mass ratio effect (Grime, 1998; Ali and Yan, 2017b). However, we also found that individual tree size variation in overstorey stratum increased whole-community aboveground biomass which is consistent to the niche differentiation processes, i.e., tree size variations within and among species promote the efficient utilization of resources and space (Ali and Yan, 2017a). This result is likely attributable to the fact that only a few dominant and functionally-similar big trees are able to efficiently use the available resources in order to occupy the overstorey stratum possibly due to the result of decades of environmental filtering (see Ali and Yan, 2017b, a). As such, strong influences of environmental filtering narrow down the functional trait diversity of overstorey trees that become dominant to drive aboveground biomass within a community (Keddy, 1992).

In the understorey, the mechanism seems to be very different: we found that high functional evenness of understorey species enhances aboveground biomass, suggesting that the distribution of basal area in understorey species is homogeneous across the multivariate trait space, as suggested by the niche complementarity hypothesis (Tilman, 1999; Zhang et al., 2012). Our results indicate that resource-use complementarity, the capability of co-occurring species having varieties of functional traits or conservative strategy for the efficient use of limited resources, manifests under resource-limiting environment, i.e., the understorey stratum of the studied subtropical forest (Hardin, 1960). Moreover, our additional analysis confirms that whole-community aboveground biomass was negatively related to the functional identity of resource-acquisitive or productivity-related traits (such as specific leaf area and leaf chemical contents) while positively related to the functional evenness. This finding suggests that the dominance of understorey functionally-dissimilar conservative species led to increasing aboveground biomass, which is indicative of the niche complementarity effect with conservative functional strategy (Prado-Junior et al., 2016; Ali and Yan, 2017b). It is plausible that light, water and soil nutrients are the major abiotic determinants for plant growth, recruitment and survival, and hence may, in turn, determine aboveground biomass through resource-use complementarity and competition among component species (Quesada et al., 2012; Jucker et al., 2014).

Light is limiting in the understorey as compared to the overstorey stratum of (sub-) tropical forests (Canham et al., 1990; Wright, 2002; Brenes-Arguedas et al., 2011). However, it is still less understood whether overstorey trees have a dominant role on the efficient utilization of water and nutrients through their large root systems, or for understorey trees that are characterized by a less extreme environment. Some studies point at the vulnerability of big trees for drought (Lindenmayer and Laurance, 2017) while understorey trees are protected against extreme drought (Qiu et al., 2012). This difference in knowledge on the effects of light *versus* those of nutrients and water also points to the relative ease of studying aboveground plant strategies and environmental conditions compared to the difficulty of studying belowground strategies and environmental conditions. We thus cannot exclude the effects of water and nutrients on our findings but suggest the differential effects of functional trait diversity of understorey and overstorey strata on aboveground biomass being likely driven by light, in line with previous research (Bartels and Chen, 2010; R uger et al., 2012; Ali and Yan, 2017b). Further research testing the influence of functional traits related to the uptake of water and soil nutrients across different forest strata will have to elucidate their effects on aboveground biomass and other functions in natural forests (but see Ali and Yan, 2017b, a).

Beyond the contrasting relationships between aboveground biomass and functional diversity across forest strata, overstorey stratum imposes competitive constraints on understorey because of their large stem volumes and functional dominance (Ali and Yan, 2017b; Zhang et al., 2017), hence altering space, light, water and soil nutrients in the surrounding environment (Gilliam, 2007; Mason et al., 2011). In our SEM analysis (Fig. 3), the big trees effect was strongly apparent by the negative direct effect of overstorey functional evenness on understorey functional evenness, and hence negative indirect effect on aboveground biomass via understorey functional evenness. We found that understorey functional evenness had a non-significant positive effect on aboveground biomass, which might be a result of the dominant role of overstorey stratum on available resources (Ali and Yan, 2017b; Zhang et al., 2017). As such, the big trees effect likely reduces the capability of understorey trees on the available resources (Hooper et al., 2005; Zhang et al., 2017), and hence a weak positive relationship between understorey functional evenness and aboveground biomass.

The direct negative relationship between aboveground biomass and soil nutrients indicate a high aboveground biomass on nutrient-poor soils in the studied forest. This study expected that soil nutrients would increase aboveground biomass across forest strata. However, we found the negative effects of soil nutrients on aboveground biomass which is consistent to several previous studies in natural (sub-) tropical forests (Poorter et al., 2015; Chiang et al., 2016; Prado-Junior et al., 2016; Ali and Yan, 2017b). This result may be indirectly attributable to species adaptations to the surrounding environment that determine species or functional trait diversity and composition, and hence may in turn influence aboveground biomass (see Prado-Junior et al., 2016; Ali and Yan, 2017b, a; van der Sande et al., 2017). For example, we have previously shown that the functional identity of overstorey tree height on the nutrient-rich soils whereas the conservative strategy of the understorey stratum on the nutrient-poor soils drive their corresponding aboveground biomass in a subtropical forest (Ali and Yan, 2017b). We have also previously shown that individual tree size inequality of overstorey stratum on nutrient-rich soils but overstorey Shannon's species diversity on nutrient-poor soils show complicated mechanisms for explaining variation in aboveground biomass across subtropical forest strata (Ali and Yan, 2017a). Interestingly, this study provides some clear evidence that high functional evenness of overstorey stratum is related to the nutrient-rich soils while the opposite is true for understorey stratum (Table S5), confirming again that overstorey trees are imposing competitive constraints on understorey trees (Ali and Yan, 2017b; Zhang et al., 2017). We anticipate that our study will encourage further studies on the direct and indirect effects of the soil nutrients,

light and water on the relationships between multiple metrics of biodiversity and aboveground biomass across forest strata in complex forest ecosystems.

We also hope that our study can encourage further studies on the direct and indirect effects of stand age, disturbance and macro-environmental conditions for the relationships between multiple metrics of biodiversity including stand structural complexity and each of the demographic processes of aboveground biomass in complex natural forests. For this, we make some recommendations, based on the limitations of our study. First, our plots are small (20 × 20 m) and part of one 5-ha forest-site, which may limit the variation in variables studied, so testing these findings across macro-environmental gradients is needed to further substantiate our results. Second, we recommend including a number of additional factors that might drive functional trait diversity and aboveground biomass that could not consider in this study, such as stand age, historical disturbance intensities and climatic water availability (Poorter et al., 2017). Third, it would be very interesting for future research to include demographic processes underlying change in aboveground biomass over time, and how these are driven by functional trait diversity of understorey and overstorey strata within a natural community (Rozenaal et al., 2017). Nevertheless, our results provide evidence for the niche complementarity in the understorey and functionally-similar big trees effect in the overstorey as main drivers for whole-community aboveground biomass in the studied forest, a result that informs improvement of models predicting carbon storage while conserving biodiversity across forest strata.

5. Concluding remarks

This study provides strong support for the niche complementarity effect in understorey stratum and functionally-similar big trees or niche overlap effect in overstorey stratum for driving whole-community aboveground biomass in the studied subtropical forest and other forest ecosystems in general. Given that we found contrasting mechanisms to explain aboveground biomass in a community, ecological models for explaining aboveground biomass can be improved by including separate effects of functional trait diversity of overstorey and understorey strata in natural forests. The strong environmental and competitive constraints of overstorey trees on functional trait diversity in understorey stratum suggest that pooling forest inventory and functional traits datasets of overstorey and understorey trees may mislead the underlying mechanisms for explaining the relationships between biodiversity and ecosystem function.

Data availability

The dataset used for analyses accompanies this paper as [supplementary file](#) (Appendix S2). More information about dataset is available upon request to the authors.

Statement of authorship

AA and ERY conducted research; AA compiled and analyzed the data; AA, ML, and ERY designed the study and wrote the paper.

Conflict of interest

The authors declare no conflict of interest.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.foreco.2018.05.015>.

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