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Research paper

The mediation roles of intraspecific and interspecific functional trait diversity for linking the response of aboveground biomass to species richness across forest strata in a subtropical forest

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ABSTRACT

Intraspecific functional trait diversity (FTD) has improved our understandings about the key mechanisms of species coexistence in plant communities. Yet, little is known about whether and how intraspecific and interspecific FTD mediate the response of aboveground biomass to species richness across forest strata (i.e. overstorey and understorey) and at whole-community in forests. To address this question, we tested the direct and indirect responses of aboveground biomass to species richness via intraspecific and interspecific FTD based on specific leaf area (FTD_{SLA}) and leaf dry matter content (FTD_{LDMC}) using structural equation modeling, in addition to the effects of soil nutrients, across 125 plots in a 5-ha subtropical forest in Eastern China. Results showed that intraspecific FTD mediates the response of aboveground biomass to species richness at overstorey and understorey strata, and whole-community level, while interspecific FTD did so at understorey strata only. At overstorey strata, 14% of the variation in aboveground biomass was accounted by the strong direct positive effect of species richness only. At understorey strata, soil nutrients had a strong negative direct effect followed by positive effects of species richness and FTD_{LDMC} on aboveground biomass with 44–45% of the variation in both intraspecific and interspecific FTD models. At whole community level, 14% of the variation in aboveground biomass was explained by the strong positive direct effect of species richness followed by negative direct effect of intraspecific FTD_{SLA}. Intraspecific and interspecific FTD_{LDMC} had positively mediated the response of aboveground biomass to species richness at understorey strata through niche differentiation. Intraspecific FTD had negligible mediation role, whereas interspecific FTD had no role, for linking the response of aboveground biomass to species richness at overstorey strata, indicating that only dominant species with a specific functional strategy may largely determine community trait space. Intraspecific FTD_{SLA} had negative relationship with aboveground biomass at the whole-community, probably due to the presence of a few large trees occupying larger niche space in a community. We conclude that intraspecific versus interspecific FTD plays a central role for linking the direct and indirect responses of aboveground biomass to species richness, but these relationships depend on the forest strata of a community.

1. Introduction

Substantial evidences exist for the positive relationship between species richness and aboveground biomass or productivity in forest ecosystems (Poorter et al., 2015), and such relationship is thus a potential ecological indicator for biodiversity conservation and carbon storage (Chisholm et al., 2013; Poorter et al., 2015; Zhang et al., 2016). However, increasing species richness may also lead to niche overlap and species redundancy (functionally similar species that make use of the same resources) instead of niche complementarity (Prado-Junior et al., 2016; Walker, 1992). Therefore, the positive relationship between species richness and aboveground biomass does not always hold

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true in forest ecosystems (Szwagrzyk and Gazda, 2007; Vilà et al., 2003). The direction of this relationship depends on the resource-use complementarity of co-occurring individuals within and between or among species, and functional traits can be used as indicators for the ecological mechanisms (e.g., Paquette and Messier, 2011; Vilà et al., 2007). However, in the past empirical studies, mean values of the functional traits have been generally used for relating functional trait diversity (FTD) with aboveground biomass or productivity in forest ecosystems. Intraspecific FTD was considered to be negligible for explaining variation in aboveground biomass (Ali et al., 2017; Conti and Díaz, 2013; Yuan et al., 2016) or productivity (Finegan et al., 2015; Prado-Junior et al., 2016). It is insufficient to use only interspecific FTD to represent total FTD of a forest community (de Bello et al., 2011; Mao et al., 2017). For instance, considering mean trait values per species can underestimates the ability of a species to endure the presence of others in a community, and ultimately underestimates the degree of niche differentiation and facilitation among species (e.g. Violle et al., 2012).

Intraspecific FTD has been recognized as a critical driver for maintaining individuals within species, co-occurring species dynamics, total FTD and functioning of communities (e.g. Chesson, 2000; Chu et al., 2009; Clark, 2010; Kichenin et al., 2013; Siefert et al., 2015). In fact, some plant species are tolerant and perform well for a diverse array of environmental heterogeneity by adjusting its phenotypic plasticity (Via et al., 1995), hence maintaining high level of intraspecific FTD (Clark, 2010; Kichenin et al., 2013; Siefert et al., 2015). At the global scale, intraspecific trait variability can explain about 25% of the total trait variation on average within communities (Siefert and Ritchie, 2016). In a given community, species richness maintains total FTD that directly influences ecosystem function (e.g. Clark, 2010; Flynn et al., 2011; Siefert et al., 2015). As such, both intraspecific and interspecific FTD may evoke or mediate the effects of species richness on aboveground biomass (Fig. 1). Interspecific FTD is the primary mechanism underlying the effect of species richness on the community level productivity or aboveground biomass (Loreau, 2010). At the same time, intraspecific FTD allows individual plants to adjust in response to environmental fluctuation (Clark, 2010; Ravenscroft et al., 2014; Spasojevic et al., 2016) and modifies their traits in response to the activity of their closest neighbors (Le Bagousse-Pinguet et al., 2015; Uriarte et al., 2010; Violle et al., 2012), thus modulating the stabilizing effect of species diversity on the aboveground biomass of coexisting species.

Natural forests are always structurally and functionally complex due to the life-history and resource allocation strategies of different tree species (Rüger et al., 2012; Wright, 2002). To consider the functional strategies and trade-offs underlying different life-history strategies (Wright et al., 2004; Zhao et al., 2017), it is therefore essential to gain insights into the relationship between species richness and aboveground biomass across forest strata (i.e. overstorey and understorey). Species compositions and thus functional strategies generally differ across overstorey and understorey strata (Ali and Yan, 2017a). In addition, understorey strata account for the majority of species richness but less quantities of aboveground biomass, whereas overstorey strata maintain few dominant species but large quantities of aboveground biomass due to their large wood volumes in subtropical forests (Ali and Yan, 2017b). As such, environmental conditions that influence plant performance vary with forest strata, and important resources such as light is often limiting in the understorey while abundant in overstorey strata of forests (e.g., Brenes-Arguedas et al., 2011; Wright, 2002). In this context, the mechanisms behind the relationship between species richness and aboveground biomass may be forest strata-specific.

The niche complementarity hypothesis predicts that communities with a variety of species (Tilman, 1999) or functional traits (Díaz et al., 2011) are therefore able to use available resources more efficiently, thus enhancing the magnitude of ecosystem functions in natural forests (Zhang et al., 2012a). As shown by the niche-based model, the functional similarity or dissimilarity within and among coexisting species or functional groups indicates how the available resources are distributed among species within the community (de Bello et al., 2011; Mao et al., 2017; Mason et al., 2011; Tilman, 1997). In a given forest, an increase of species richness may contribute to aboveground biomass through both the niche overlap of functionally similar species, and the niche complementarity across functionally dissimilar species (Prado-Junior et al., 2016; Walker, 1992). Indeed, the niche overlap effect may be more important in productive environment of the overstorey due to the presence of a few large tree species, while niche complementarity effect may be a main driver of aboveground biomass in the light-stressful understorey strata as a result of a larger number of small tree species. As such, we have previously reported that high aboveground biomass was potentially driven by functional identity of tree height through making use of plentiful soil nutrients at overstorey strata, whereas by conservative strategy at understorey strata through enduring nutrient-poor soils (Ali and Yan, 2017a).

Intraspecific FTD, due to the predominantly uneven abundances of dominant species, may largely determine community trait space and the ability of species to acquire resources (Johnson et al., 2015), and consequently influencing aboveground biomass (Li et al., 2017). As such, traits of dominant species have been shown to produce high aboveground biomass at community level through opposing strategies in different (sub-) tropical forests (Ali et al., 2017; Finegan et al., 2015; Lin et al., 2016; Prado-Junior et al., 2016). For instance, high specific leaf area (SLA) is positively related with relative growth rate, photosynthetic efficiency and leaf net carbon assimilation rate, i.e. acquisitive strategy of a plant, while high leaf dry matter content (LDMC) is associated with low leaf water and nutrient retention, i.e. conservative strategy of a plant (Finegan et al., 2015; Poorter and Markesteijn, 2008; Reich, 2014; Wright et al., 2010). Environmentally and taxonomically driven changes of some key traits such as SLA and LDMC may very well scale up to forest strata, community and ecosystem levels. In this case, the trait(s) weighted by the species' relative basal area or abundance will improve the scaling of individual responses to community and ecosystem functions (Ali et al., 2017; de Bello et al., 2011; Mao et al., 2017; Prado-Junior et al., 2016). Previous studies have shown that the few productive species dominating at the canopy contribute to most of the aboveground biomass in forests (Balvanera et al., 2005; Lohbeck

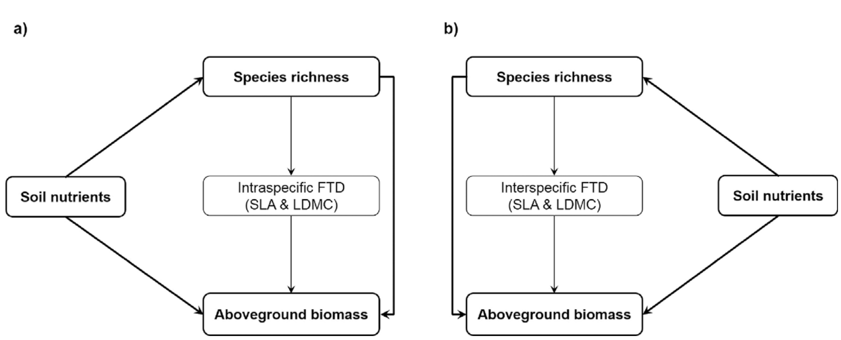

Fig. 1. Conceptual model showing how functional trait diversity mediates the response of aboveground biomass to species richness, in addition to the effects of soil nutrients. Conceptual model was constructed based on two theoretical frameworks, including (a) intraspecific functional trait diversity and (b) interspecific functional trait diversity, for each of the overstorey and understorey strata, and whole-community. Functional trait diversity is characterized by the variation in functional trait (e.g. SLA and LDMC) using Rao's quadratic entropy.

et al., 2016). High aboveground biomass or productivity can be built up by few dominant species with functional similarity through the niche overlap (species redundancy) or intraspecific FTD, rather than interspecific FTD (e.g., Prado-Junior et al., 2016). In this context, we addressed whether intraspecific and/or interspecific FTD mediate the response of aboveground biomass to species richness across forest strata and at whole-community in a subtropical forest (Fig. 1).

We present biophysical data including functional traits (SLA and LDMC) weighted by species' relative basal area for the quantification of intraspecific and interspecific FTD, species identity, soil nutrients and aboveground biomass from 125 plots inside a 5-ha natural subtropical forest in Eastern China. In order to unravel the mediation role of intraspecific and interspecific FTD for the response of aboveground biomass to species richness, we construct two separate theoretical frameworks based on conceptual model for each of overstorey and understorey strata, and whole-community level in a subtropical forest (Fig. 1). We hypothesized that intraspecific and interspecific FTD mediate the response of aboveground biomass to species richness in understorey strata through niche complementarity, whereas only intraspecific FTD would mediate this response in overstorey strata or whole-community due to the presence of a few large trees occupying larger niche space in a community. This hypothesis leads to three key predictions: 1) positive direct relationship between species richness and aboveground biomass at each of forest strata and whole-community level; 2) intraspecific and interspecific FTD will strongly affect aboveground biomass in understorey strata; and 3) intraspecific rather than interspecific FTD will strongly affect aboveground biomass in overstorey strata or whole-community. We tested the proposed hypothesis and predictions after accounting for the main effects of soil nutrients on species richness and aboveground biomass because soil nutrients may strongly influence species adaptation and aboveground biomass in (sub-) tropical forests (Ali and Yan, 2017a; Prado-Junior 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 (Ali and Yan, 2017b; Yan et al., 2013; Zhang et al., 2012b). The studied 5-ha forest plot is located in the center of the Park, and is divided into 125 (20 × 20 m) subplots. More details about the study area and forest plots are available in our previous studies (Ali and Yan, 2017a,b).

2.2. Available data

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).

In this study, we used two key functional traits across all individuals of 108 species; SLA and LDMC. Leaf traits measurements were obtained in the summer (i.e., June to August) of 2010–2013, when trees had fully developed leaves. We measured SLA and LDMC for each of the 20,253 individuals in the plots following Cornelissen et al. (2003). The detail description about the measurement of plant functional traits is provided in our previous study (Ali and Yan, 2017a).

To take into account for the effects of soil properties and nutrients on the relationships between FTD and aboveground biomass, the original dataset of soil physicochemical properties for each sampling plot within a 5-ha forest plot were used from the study of Zhang et al. (2012b). Soil physicochemical properties 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 properties and to avoid the strong correlations among them (see Table A1 for correlations), we ran principal component analyses (PCA) based on the soil physicochemical properties. In all statistical analyses, we used PC2 which basically represents soil nutrients gradients (see Table A2).

2.3. Quantification of intraspecific and interspecific functional trait 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. 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 17,004 stems belonging to 103 species, 65 genera and 37 families in the understorey strata across 125 plots in a 5-ha subtropical forest (Ali and Yan, 2017a,b).

For calculation of intra- and interspecific FTD of overstorey (75), understorey (103), and whole-community species (108 species in total), we used two functional traits that are important for plant growth and survival (Poorter and Markesteijn, 2008; Wright et al., 2010), and hence for standing aboveground biomass, biomass productivity and carbon storage (Finegan et al., 2015; Prado-Junior et al., 2016). We used five measures of diversity that were quantified for the overstorey and understory strata separately: species richness, intra- and interspecific FTD (single trait) based on SLA and LDMC. This resulted in ten diversity measures per plot for forest strata level analyses, while five measures per plot for whole-community level analyses.

We used Rao's quadratic entropy approach for the partitioning of total FTD into between species and within species components for each plot (de Bello et al., 2011). This approach is similar to the partitioning of total regional species diversity into between communities (β-diversity) and within communities (α-diversity). The species' relative basal area (relative to the whole-community or understorey/overstorey basal area) was used to weight the traits of species within each plot, because basal area is a better indicator of plant performance than abundance (Prado-Junior et al., 2016).

The intraspecific FTD at the plot-level (whole community, understorey or overstorey) is represented by the average trait dissimilarity between each pair of individuals within a species weighted by the relative basal area of that same species and averaged for all the species within the plot. It thus reflects the community-weighted mean intraspecific trait variation. The interspecific FTD at the plot-level (whole community, understorey or overstorey) is represented by the average trait dissimilarity between each pair of species weighted by their relative basal area within plot. An example R function used in this study for partitioning of the total FTD into inter- and intraspecific FTD is available in de Bello et al. (2011). The calculations on the Rao diversity indices were performed using the *ade4* and *cati* packages (Dray, 2016; Taudiere and Violle, 2015).

2.4. Estimation of aboveground biomass

We calculated aboveground biomass for each tree with DBH ≥ 5 cm

Table 1
Model selection of good-fit structural equation model (SEM) for aboveground biomass (AGB). Models were accepted, rejected and saturated based on χ^2 test. Only accepted models were considered in this study (see Table 2; and Figs. 2 and 3).

Ecosystem functions	Hypothesized model	df	Model fit statistics summary						Model remarks	SEM
			CFI	GFI	SRMR	AIC	R^2	χ^2 (P-value)		
Overstorey AGB	No FTD mediation model	0	1.00	1.00	0.000	1104.72	0.14	0.00 (0)	Saturated	Not shown
	Intraspecific FTD model	2	0.97	0.98	0.057	1771.62	0.14	5.15 (0.076)	Accepted	Fig. 2a
	Interspecific FTD model	2	0.90	0.97	0.077	1793.17	0.19	10.95 (0.004)	Rejected	Not shown
Understorey AGB	No FTD mediation model	0	1.00	1.00	0.000	1079.34	0.40	0.00 (0)	Saturated	Not shown
	Intraspecific FTD model	2	1.00	0.99	0.038	1772.41	0.44	1.71 (0.426)	Accepted	Fig. 2b
	Interspecific FTD model	2	0.99	0.99	0.045	1650.86	0.45	2.91 (0.233)	Accepted	Fig. 3
Whole-community AGB	No FTD mediation model	0	1.00	1.00	0.000	1124.13	0.11	0.00 (0)	Saturated	Not shown
	Intraspecific FTD model	2	0.99	0.99	0.035	1823.23	0.14	2.30 (0.317)	Accepted	Fig. 2c
	Interspecific FTD model	2	0.90	0.97	0.076	1801.00	0.14	8.87 (0.012)	Rejected	Not shown

Abbreviations: FTD, functional trait diversity; 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.
Note: df is based on the number of 'knowns' minus the number of free parameters in the model, not on the sample size.

(AGB*t*) using a global allometric equation (Chave et al., 2014), which is based on tree DBH, site-specific environment stress factor (E) and species' wood density (ρ).

$$AGBt = \exp\{-1.803 - 0.976(E) + 0.976 \times \ln(\rho) + 2.673 \times \ln(DBH) - 0.0299 \times (\ln(DBH))^2 \tag{1}$$

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

We estimated aboveground biomass of shrubs and small trees (AGB*s*) with DBH < 5 cm using a general multi-species allometric Eq. (2) developed locally for small trees (Ali et al., 2015), which is similarly based on tree DBH and species' wood density (ρ).

$$AGBs = 1.450 \times \exp\{-4.97 + 2.20 \times \ln(DBH) + 3.06(\rho)\} \tag{2}$$

2.5. Statistical analyses

All numerical variables including aboveground biomass, species richness, intraspecific and interspecific FTD indices 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). We first tested a structural equation model (SEM) for the relationship between species richness and aboveground biomass without including FTD (intraspecific and interspecific) as a mediator, in addition to the effects of soil nutrients at each of the overstorey and understorey strata, and whole-community in a natural subtropical forest (Fig. 1). To test our proposed hypothesis and predictions, we further constructed two SEMs based on known theoretical multivariate causes of FTD and aboveground biomass, i.e., intraspecific FTD model and interspecific FTD model, at each of the overstorey and understorey strata, and whole-community level, after accounting for the effects of species richness on FTD and aboveground biomass (Fig. 1). The direct effects of soil nutrients were only considered on species richness and aboveground biomass, but not on FTD indices because we were only interested whether and how intraspecific and interspecific FTD act as mediators for linking species richness with aboveground biomass. See conceptual model or SEM of Flynn et al. (2011) for known theoretical paths for linking species richness, FTD and aboveground biomass. 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). We critically used χ^2 test, representing the maximum likelihood estimation, to assess how well the hypothesized SEM fits the data (Ali and Yan, 2017b). The SEMs were implemented using the *lavaan* package (Rosseel, 2012).

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), accounting for subplots 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 each of the relationships between predictors and aboveground biomass. The goodness of fit of spatial and non-spatial GLS models was evaluated by the AIC, and we found that models without spatial autocorrelation always had the lower AIC values (Table A3), which is similar to the recent observations in forest ecosystems (Ali and Yan, 2017a, b; Chiang et al., 2016; Yuan et al., 2016).

For the interpretation of SEM results, 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 A4 and Figs. A1–A3, respectively. See Appendix B for the dataset used in the analyses. For all statistical and ecological analyses R 3.2.2 was used (R Development Core Team, 2015).

3. Results

3.1. Performance of intraspecific and interspecific FTD to aboveground biomass

According to the χ^2 test, the model without considered FTD as a mediator was saturated ($\chi^2 = 0.00$, $P = 0$) at each of the overstorey and understorey strata, and whole-community level (Table 1). Therefore, it was not possible to accept the goodness of fit for prediction of aboveground biomass. The intraspecific FTD model was well fit to the data at each of the overstorey ($\chi^2 = 5.15$, $P = 0.076$) and understorey strata ($\chi^2 = 1.71$, $P = 0.426$), as well as at the whole-community level ($\chi^2 = 2.30$, $P = 0.317$). The interspecific FTD model at understorey strata was also well fit to the data ($\chi^2 = 2.91$, $P = 0.233$) whereas model at each of the overstorey strata ($\chi^2 = 10.95$, $P = 0.004$) and whole-community level ($\chi^2 = 8.87$, $P = 0.012$) was rejected (Table 1). In conclusion, this result indicates that both intraspecific and interspecific FTD mediate the response of aboveground biomass to species richness at understorey strata, whereas only intraspecific FTD mediates the response of aboveground biomass to species richness at overstorey strata and whole-community level (Figs. 2 and 3).

3.2. Intraspecific FTD mediates the response of aboveground biomass to species richness at forest strata and whole-community level

With respect to the overstorey strata, the intraspecific FTD model explained 14, 20, 4, and 2% of variation in aboveground biomass, species richness, intraspecific FTD_{SLA}, and intraspecific FTD_{LDMC}, respectively (Fig. 2a). Species richness had the strongest positive direct effect on aboveground biomass ($\beta = 0.35$, $P < 0.001$), whereas intraspecific FTD_{SLA} ($\beta = 0.00$, $P = 0.997$), intraspecific FTD_{LDMC}

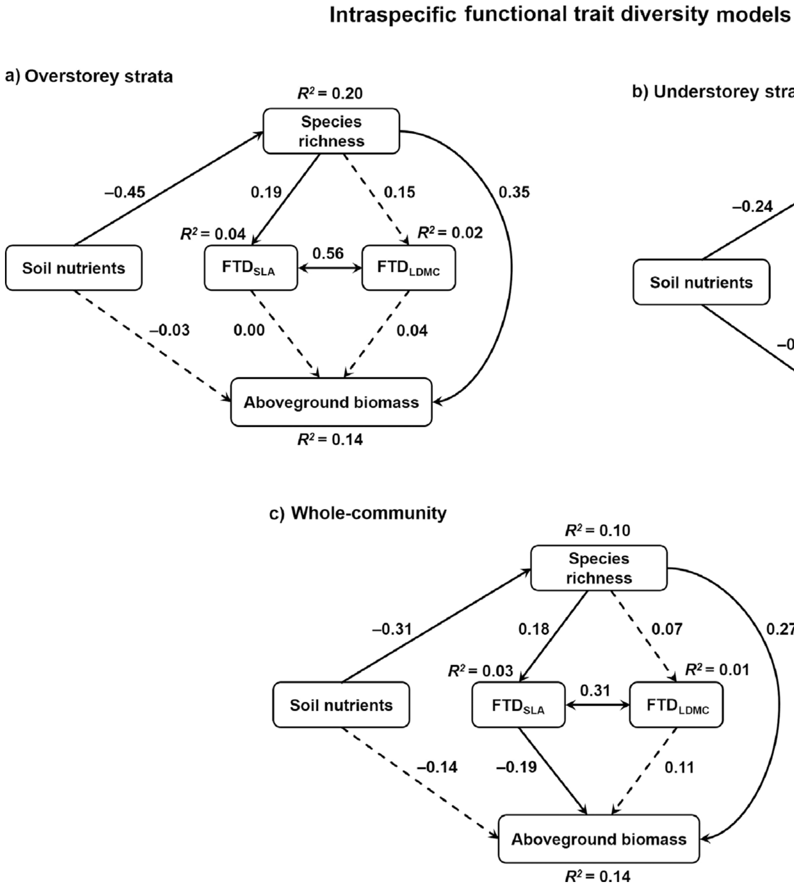

Fig. 2. The best-fit structural equation models of intraspecific functional trait diversity relating aboveground biomass to species richness, in addition to the effects of soil nutrients, at overstorey and understorey strata, and whole-community level. Solid arrows represent significant ($P < 0.05$) 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.

Table 2
The direct, indirect, and total standardized effects of soil nutrients, species richness and functional diversity (intra- and interspecific) 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 indicted in bold ($P < 0.05$).

Predictor	Pathway to aboveground biomass	*Intraspecific FTD models*						*Interspecific FTD model*	
		Overstorey strata model in Fig. 2a		Understorey strata model in Fig. 2b		Whole-community model in Fig. 2c		Understorey strata model in Fig. 3	
		Effect	*P*-value	Effect	*P*-value	Effect	*P*-value	Effect	*P*-value
Soil nutrients	Direct effect	−0.03	0.712	−0.51	< 0.001	−0.14	0.113	−0.52	**< 0.001**
	Indirect effect via species richness	−0.16	**0.002**	−0.07	**0.026**	−0.09	**0.018**	−0.04	0.107
	Total effect	−0.19	0.031	−0.57	**< 0.001**	−0.22	**0.009**	−0.56	**< 0.001**
Species richness	Direct effect	0.35	**< 0.001**	0.27	**< 0.001**	0.27	**0.002**	0.17	**0.045**
	Indirect effect via FD_{SLA}	0.00	0.997	−0.01	0.438	−0.03	0.138	−0.02	0.764
	Indirect effect via FD_{LDMC}	0.01	0.703	0.02	0.192	0.01	0.486	0.13	**0.023**
	Total effect	0.35	**< 0.001**	0.29	**< 0.001**	0.25	**0.005**	0.28	**< 0.001**
FTD_{SLA}	Direct effect	0.00	0.997	−0.06	0.402	−0.19	**0.035**	−0.03	0.764
FTD_{LDMC}	Direct effect	0.04	0.495	0.18	**0.014**	0.11	0.195	0.23	**0.017**

Abbreviations: FTDfunctional trait diversity; FTD_{SLA}functional trait diversity based on specific leaf area; FTD_{LDMC}functional trait diversity based on leaf dry matter content.

($\beta = 0.04$, $P = 0.495$) and soil nutrients ($\beta = -0.03$, $P = 0.712$) had negligible direct effects on aboveground biomass (Table 2). There was a significant positive direct effect of species richness on intraspecific FTD_{SLA} ($\beta = 0.19$, $P = 0.028$), but a non-significant positive direct effect on intraspecific FTD_{LDMC} ($\beta = 0.15$, $P = 0.097$; Fig. 2a).

When testing the role of intraspecific FTD at understorey strata, the model accounted for 44, 6, 3, and 2% of the variation in aboveground biomass, species richness, intraspecific FTD_{SLA}, and intraspecific FTD_{LDMC}, respectively (Fig. 2b). Soil nutrients had the strongest positive direct effect on aboveground biomass ($\beta = -0.51$, $P < 0.001$), followed by the positive direct effect of species richness had ($\beta = 0.27$, $P < 0.001$), positive direct effect of intraspecific FTD_{LDMC} ($\beta = 0.18$, $P = 0.014$), and a negligible direct effect of intraspecific FTD_{SLA} ($\beta = -0.06$, $P = 0.402$; Table 2). There was a significant positive direct effect of species richness on intraspecific FTD_{SLA} ($\beta = 0.18$, $P = 0.042$), but a non-significant positive direct effect on intraspecific

FTD_{LDMC} (β = 0.14, P = 0.125, Fig. 2b).

At whole-community level, the intraspecific FTD model accounted for 14, 10, 3, and 1% of the variation in aboveground biomass, species richness, intraspecific FTD_{SLA}, and intraspecific FTD_{LDMC}, respectively (Fig. 2c). Species richness had the strongest positive direct effect on aboveground biomass (β = 0.27, P = 0.002), followed by the negative direct effect of intraspecific FTD_{SLA} (β = −0.19, P = 0.035), non-significant negative direct effect of soil nutrients (β = −0.14, P = 0.113), and positive direct effect of intraspecific FTD_{LDMC} (β = 0.11, P = 0.195; Table 2). There was a significant positive direct effect of species richness on intraspecific FTD_{SLA} (β = 0.18, P = 0.038), but a non-significant positive direct effect on intraspecific FTD_{LDMC} (β = 0.07, P = 0.410; Fig. 2c).

In all intraspecific FTD models (Fig. 2), soil nutrients had the significant negative direct effect on species richness but the strength of the effect varies at overstorey (β = −0.45, P < 0.001), understorey (β = −0.24, P = 0.007) and whole-community (β = −0.31, P < 0.001). Soil nutrients had a significant indirect negative effect via species richness on aboveground biomass at overstorey (β = −0.16, P = 0.002), understorey (β = −0.07, P = 0.026) and whole-community (β = −0.09, P = 0.018; Table 2). There were negligible indirect effect of species richness on aboveground biomass via intraspecific FTD_{SLA} and intraspecific FTD_{LDMC} at forest strata and whole-community. The total (direct + indirect) effect of soil nutrients on aboveground biomass was quite similar at overstorey strata (β = −0.19, P = 0.031) and whole-community (β = −0.22, P = 0.009), but relatively high at understorey strata (β = −0.57, P < 0.001; Table 2). The total effect of species richness on aboveground biomass was quite similar at overstorey strata (β = 0.35, P < 0.001), understorey strata (β = 0.29, P < 0.001) and whole-community (β = 0.25, P = 0.005; Table 2).

3.3. Interspecific FTD mediates the response of aboveground biomass to species richness at understorey strata

At understorey strata, the interspecific FTD model accounted for 44, 6, 3, and 2% of the variation in aboveground biomass, species richness, interspecific FTD_{SLA}, and interspecific FTD_{LDMC}, respectively (Fig. 3). Soil nutrients had the strong negative direct effect on aboveground biomass (β = −0.52, P < 0.001), followed by the significant positive direct effect of species richness (β = 0.17, P = 0.045), positive direct effect of interspecific FTD_{LDMC} (β = 0.23, P = 0.017), and a negligible direct effect of interspecific FTD_{SLA} (β = −0.03, P = 0.764; Table 2). There was a significant positive direct effect of species richness on

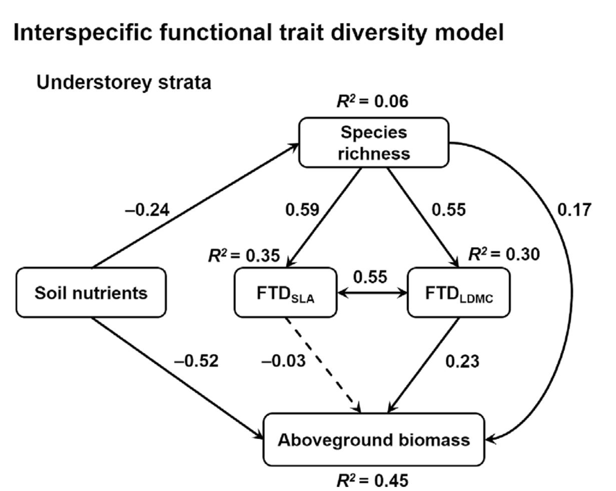

Fig. 3. The best-fit structural equation models of interspecific functional trait diversity relating aboveground biomass to species richness, in addition to the effects of soil nutrients, at understorey strata. General explanation is provided in Fig. 2.

interspecific FTD_{SLA} (β = 0.59, P < 0.00) and interspecific FTD_{LDMC} (β = 0.55, P < 0.034, Fig. 3). Soil nutrients had the significant negative direct effect on species richness (β = −0.24, P < 0.001), but a negligible indirect effect via species richness on aboveground biomass (β = −0.04, P = 0.107). Species richness had the significant positive indirect effect via interspecific FTD_{LDMC} (β = 0.13, P = 0.023), but a negligible indirect effect via interspecific FTD_{SLA} (β = −0.02, P = 0.764). The total effect of soil nutrients and species richness on understorey aboveground biomass was −0.56 (P < 0.001) and 0.28 (P < 0.001), respectively (Table 2).

4. Discussion

This study highlights the mediation role of intraspecific and interspecific FTD for linking the response of aboveground biomass to species richness, after accounting for the effects of soil nutrients, in a subtropical forest. In agreement with our hypothesis, this study showed that intraspecific and interspecific FTD mediate the response of aboveground biomass to species richness at understorey strata, whereas only intraspecific FTD did so at overstorey strata and whole-community level. The main novelty of this study is determining that high aboveground biomass in a subtropical forest is shaped by high intraspecific and interspecific FTD at understorey strata, whereas high intraspecific FTD has negligible or negative relationships with aboveground biomass at overstorey strata and whole-community, respectively.

At overstorey strata, the negligible mediation role of intraspecific FTD and no role of interspecific FTD for linking the response of aboveground biomass to species richness may be due to the intraspecific variation of few dominant species which largely determine community trait space and the ability to obtain resources. In line with the previous studies, these findings suggest that aboveground biomass or productivity likely depends to a great extent on the functional traits of the dominant species or functional groups within communities due to the mass ratio effect rather than niche complementarity effect (Ali and Yan, 2017a; Chiang et al., 2016; Conti and Díaz, 2013; Finegan et al., 2015). This is likely the result of decades of environmental filtering that trees need to pass through to be able to occupy the overstorey, combined with the fact that only a subset of the species, and hence individuals of those few species, are able to become tall enough to occupy the overstorey strata. Strong effects of environmental filtering will narrow down the range and diversity of functional strategies (hence low FTD) that becomes abundant to drive aboveground biomass (Keddy, 1992).

Interestingly, at the whole-community level, the strong negative association of intraspecific FTD_{SLA} with aboveground biomass implies the presence of few large trees having low intraspecific differentiation towards a more light acquisitive strategy within studied species in a community. Therefore, low intraspecific FTD_{SLA} tends to have high aboveground biomass at whole-community level. This result indicates intraspecific-level carbon gain but the presence of few large trees occupying larger niche space makes this relationship negative, and hence high functioning (Ali and Yan, 2017a; Johnson et al., 2015; Siefert et al., 2015). Alternately, this result may be attributable to complex vertical structures of the studied forest having a lot of unshaded leaves, which result mainly from the few dominant canopy species that are effective in light acquisition (Ali et al., 2017; Fotis et al., 2017).

At understorey strata, the strong positive associations of intraspecific and interspecific FTD_{LDMC} with aboveground biomass indicate the niche differentiation between and within species towards a more resource conservative strategy, supporting the niche complementarity hypothesis (Ali and Yan, 2017a; Díaz et al., 2011; Tilman, 1999). Our findings confirm that resource-use complementarity, the ability of functionally diverse co-occurring species or individuals within species to more efficiently utilize a pool of limiting resources, manifests under resource-limiting environments – in our case the understorey strata of a subtropical forest (Grime, 1973; Hardin, 1960). At structurally complex forests, overstorey trees have dominant effect over understorey trees by effectively intercept light to the understorey trees (Bartels and Chen, 2010; Lohbeck et al., 2016; Oberle et al., 2009). Consequently, few dominant overstorey trees with a high proportion of unshaded leaves within species have high aboveground biomass through low intraspecific niche differentiation towards light acquisitive strategy. This may be attributable to the greater effect of large woody trees on overall functioning of forest ecosystems, in contrast to that of small woody trees (Ali and Yan, 2017b; Liang et al., 2015). These results implies that expectations derived from intraspecific niche similarity at overstorey strata will scale up to the whole-community level due to the superior role of overstorey trees on understorey trees in terms of canopy properties and ecosystem function (Siefert et al., 2015). Further, this result indicates that in a complex subtropical forest, combining data across forest strata may swamp these relationships and that to better understand the mechanisms of intraspecific FTD – aboveground biomass it is worth to analyse the understorey and overstorey strata separately.

The contrasting relationships of aboveground biomass with intraspecific FTD_{SLA} and FTD_{LDMC} may be related to the plant's leaf economics spectrum (e.g., Garnier et al., 2004), at different forest strata as well as at whole-community. These results indicate that extensive intraspecific variation in leaf economic traits arising from plastic responses to light, nutrients and other environmental factors (Mao et al., 2017; Rozendaal et al., 2006), as well as genetic variability and ontogenetic variation (Mason et al., 2013; Siefert et al., 2015; Vasseur et al., 2012). Our findings that leaf economic traits consistently represent intraspecific FTD at different forest strata in the studied forest have important implications in the individual plant strategies, community assembly and ecosystem function (Reich, 2014; Siefert et al., 2015). For instance, this study showed that, on the one hand, exploitative plants characterized by high SLA and fast nutrient acquisition and turnover, thus being conducive to fast growth and high aboveground biomass at overstorey strata. On the other hand, conservative plants with high LDMC, nutrient-poor leaves and slower growth associated with slow nutrient and biomass turnover at understorey strata (Wright et al., 2004; Zhao et al., 2017).

The observed negative relationships of soil nutrients with species richness and aboveground biomass at forest strata and whole-community are not driven by a higher productivity with poor soils in the studied forests. However, this may be attributable to species adaptations to the local soil conditions through increasing longevity and stand biomass retention (Ali and Yan, 2017a, b; Poorter et al., 2015; Prado-Junior et al., 2016). As such, we have previously reported that nutrient-poor soils tend to be dominated by species with conservative strategy, whereas nutrient-rich soils tend to be dominated by species with acquisitive strategy in the studied forest (Ali and Yan, 2017a).

5. Concluding remarks

We conclude that the mediation role of intraspecific and interspecific FTD for the response of aboveground biomass to species richness along soil nutrients gradients depends on the forest strata of a community. For example, intraspecific and interspecific FTD mediate the response of aboveground biomass to species richness at understorey strata, whereas only intraspecific FTD mediates the response of aboveground biomass to species richness at whole-community and overstorey strata. Intraspecific and interspecific FTD_{LDMC} had strong direct positive effect on aboveground biomass at understorey strata representing niche differentiation. Intraspecific FTD_{SLA} had strong direct negative effect on aboveground biomass at whole-community level, probably due to the presence of a few large trees occupying larger niche space in a community. Intraspecific FTD had negligible mediation role, whereas interspecific FTD had no role, for linking the response of aboveground biomass to species richness at overstorey strata indicating that only dominant species may largely determine community trait space and the ability to obtain resources. Clearly, this study shows that intraspecific versus interspecific FTD plays a central role for linking the response of aboveground biomass to species richness. Lastly, this study suggests that trait variability within species need to be separately or explicitly considered in the theoretical development for linking biodiversity and ecosystem function across forest strata in a subtropical forest.

Statement of authorship

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

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2017.10.057.

References

Ali, A., Yan, E.-R., 2017a. Functional identity of overstorey tree height and understorey conservative traits drive aboveground biomass in a subtropical forest. Ecol. Indic. 83, 158–168.
Ali, A., Yan, E.-R., 2017b. The forest strata-dependent relationship between biodiversity and aboveground biomass within a subtropical forest. For. Ecol. Manage. 401, 125–134.
Ali, A., Xu, M.-S., Zhao, Y.-T., Zhang, Q.-Q., Zhou, L.-L., Yang, X.-D., Yan, E.-R., 2015. Allometric biomass equations for shrub and small tree species in subtropical China. Silva Fenn. 49, 1–10.
Ali, A., Yan, E.-R., Chang, S.X., Cheng, J.-Y., Liu, X.-Y., 2017. Community-weighted mean of leaf traits and divergence of wood traits predict aboveground biomass in secondary subtropical forests. Sci. Total Environ. 574, 654–662.
Balvanera, P., Kremen, C., Martínez-Ramos, M., 2005. Applying community structure analysis to ecosystem function: examples from pollination and carbon storage. Ecol. Appl. 15, 360–375.
Bartels, S.F., Chen, H.Y.H., 2010. Is understory plant species diversity driven by resource quantity or resource heterogeneity? Ecology 91, 1931–1938.
Brenes-Arguedas, T., Roddy, A.B., Coley, P.D., Kursar, T.A., 2011. Do differences in understory light contribute to species distributions along a tropical rainfall gradient? Oecologia 166, 443–456.
Chave, J., Rejou-Mechain, M., Burquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martinez-Yrizar, A., Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A., Nogueira, E.M., Ortiz-Malavassi, E., Pelissier, R., Ploton, P., Ryan, C.M., Saldarriaga, J.G., Vieilledent, G., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Glob. Change Biol. 20, 3177–3190.
Chesson, P., 2000. Mechanisms of maintenance of species diversity. Annu. Rev. Ecol. Syst. 31, 343–366.
Chiang, J.-M., Spasojevic, M.J., Muller-Landau, H.C., Sun, I.-F., Lin, Y., Su, S.-H., Chen, Z.-S., Chen, C.-T., Swenson, N.G., McEwan, R.W., 2016. Functional composition drives ecosystem function through multiple mechanisms in a broadleaved subtropical forest. Oecologia 182, 829–840.
Chisholm, R.A., Muller-Landau, H.C., Abdul Rahman, K., Bebber, D.P., Bin, Y., Bohlman, S.A., Bourg, N.A., Brinks, J., Bunyavejchewin, S., Butt, N., Cao, H., Cao, M., Cárdenas, D., Chang, L.-W., Chiang, J.-M., Chuyong, G., Condit, R., Dattaraja, H.S., Davies, S., Duque, A., Fletcher, C., Gunatilleke, N., Gunatilleke, S., Hao, Z., Harrison, R.D., Howe, R., Hsieh, C.-F., Hubbell, S.P., Itoh, A., Kenfack, D., Kiratiprayoon, S., Larson,

A.J., Lian, J., Lin, D., Liu, H., Lutz, J.A., Ma, K., Malhi, Y., McMahon, S., McShea, W., Meegaskumbura, M., Mohd Razman, S., Morecroft, M.D., Nytch, C.J., Oliveira, A., Parker, G.G., Pulla, S., Punchi-Manage, R., Romero-Saltos, H., Sang, W., Schurman, J., Su, S.-H., Sukumar, R., Sun, I.F., Suresh, H.S., Tan, S., Thomas, D., Thomas, S., Thompson, J., Valencia, R., Wolf, A., Yap, S., Ye, W., Yuan, Z., Zimmerman, J.K., 2013. Scale-dependent relationships between tree species richness and ecosystem function in forests. J. Ecol. 101, 1214–1224.

Chu, C.J., Weiner, J., Maestre, F.T., Xiao, S., Wang, Y.S., Li, Q., Yuan, J.L., Zhao, L.Q., Ren, Z.W., Wang, G., 2009. Positive interactions can increase size inequality in plant populations. J. Ecol. 97, 1401–1407.

Clark, J.S., 2010. Individuals and the variation needed for high species diversity in forest trees. Science 327, 1129–1132.

Conti, G., Díaz, S., 2013. Plant functional diversity and carbon storage – an empirical test in semi-arid forest ecosystems. J. Ecol. 101, 18–28.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Aust. J. Bot. 51, 335–380.

de Bello, F., Lavorel, S., Albert, C.H., Thuiller, W., Grigulis, K., Dolezal, J., Janeček, Š., Lepš, J., 2011. Quantifying the relevance of intraspecific trait variability for functional diversity. Methods Ecol. Evol. 2, 163–174.

Díaz, S., Quétier, F., Cáceres, D.M., Trainor, S.F., Pérez-Harguindeguy, N., Bret-Harte, M.S., Finegan, B., Peña-Claros, M., Poorter, L., 2011. Linking functional diversity and social actor strategies in a framework for interdisciplinary analysis of nature's benefits to society. Proc. Natl. Acad. Sci. 108, 895–902.

Dray, S., 2016. Analysis of Ecological Data: Exploratory and Euclidean Methods in Environmental Sciences. 1. 7–4 ed.

Finegan, B., Peña-Claros, M., Oliveira, A., Ascarrunz, N., Bret-Harte, M.S., Carreño-Rocabado, G., Casanoves, F., Díaz, S., Eguiguren Velepucha, P., Fernandez, F., Juan Carlos, L., Leda, L., Beatriz Salgado, N., Marcel, V., Lourens, P., 2015. Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. J. Ecol. 103, 191–201.

Flynn, D.F.B., Mirotchnick, N., Jain, M., Palmer, M.I., Naeem, S., 2011. Functional and phylogenetic diversity as predictors of biodiversity-ecosystem-function relationships. Ecology 92, 1573–1581.

Fotis, A.T., Murphy, S.J., Ricart, R.D., Krishnadas, M., Whitacre, J., Wenzel, J.W., Queenborough, S.A., Comita, L.S., 2017. Aboveground biomass is driven by mass-ratio effects and stand structural attributes in a temperate deciduous forest. J. Ecol. http://dx.doi.org/10.1111/1365-2745.12847.

Garnier, E., Cortez, J., Billes, G., Navas, M.L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., Toussaint, J.P., 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology 85, 2630–2637.

Grime, J.P., 1973. Competitive exclusion in herbaceous vegetation. Nature 242, 344–347.

Hardin, G., 1960. The competitive exclusion principle. Science 131, 1292–1297.

Johnson, L.C., Olsen, J.T., Tetreault, H., DeLaCruz, A., Bryant, J., Morgan, T.J., Knapp, M., Bello, N.M., Baer, S.G., Maricle, B.R., 2015. Intraspecific variation of a dominant grass and local adaptation in reciprocal garden communities along a US Great Plains' precipitation gradient: implications for grassland restoration with climate change. Evol. Appl. 8, 705–723.

Keddy, P.A., 1992. Assembly and response rules: two goals for predictive community ecology. J. Veg. Sci. 3, 157–164.

Kichenin, E., Wardle, D.A., Peltzer, D.A., Morse, C.W., Freschet, G.T., 2013. Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient. Funct. Ecol. 27, 1254–1261.

Le Bagousse-Pinguet, Y., Börger, L., Quero, J.-L., García-Gómez, M., Soriano, S., Maestre, F.T., Gross, N., 2015. Traits of neighbouring plants and space limitation determine intraspecific trait variability in semi-arid shrublands. J. Ecol. 103, 1647–1657.

Li, W., Zhao, J., Epstein, H.E., Jing, G., Cheng, J., Du, G., 2017. Community-level trait responses and intra-specific trait variability play important roles in driving community productivity in an alpine meadow on the Tibetan Plateau. J. Plant Ecol. 10, 592–600.

Liang, J., Zhou, M., Tobin, P.C., McGuire, A.D., Reich, P.B., 2015. Biodiversity influences plant productivity through niche–efficiency. Proc. Natl. Acad. Sci. 112, 5738–5743.

Lin, D., Anderson-Teixeira, K.J., Lai, J., Mi, X., Ren, H., Ma, K., 2016. Traits of dominant tree species predict local scale variation in forest aboveground and topsoil carbon stocks. Plant Soil 1–12.

Lohbeck, M., Bongers, F., Martinez-Ramos, M., Poorter, L., 2016. The importance of biodiversity and dominance for multiple ecosystem functions in a human-modified tropical landscape. Ecology 97, 2772–2779.

Loreau, M., 2010. Linking biodiversity and ecosystems: towards a unifying ecological theory. Phil. Trans. R. Soc. B : Biol. Sci. 365, 49–60.

Malaeb, Z.A., Summers, J.K., Pugesek, B.H., 2000. Using structural equation modeling to investigate relationships among ecological variables. Environ. Ecol. Stat. 7, 93–111.

Mao, W., Felton, A.J., Zhang, T., 2017. Linking changes to intraspecific trait diversity to community functional diversity and biomass in response to snow and nitrogen addition within an Inner Mongolian Grassland. Front. Plant Sci. 8, 339.

Mason, N.W.H., de Bello, F., Doležal, J., Lepš, J., 2011. Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities. J. Ecol. 99, 788–796.

Mason, C.M., McGaughey, S.E., Donovan, L.A., 2013. Ontogeny strongly and differentially alters leaf economic and other key traits in three diverse *Helianthus species*. J. Exp. Bot. 64, 4089–4099.

Oberle, B., Grace, J.B., Chase, J.M., 2009. Beneath the veil: plant growth form influences the strength of species richness-productivity relationships in forests. Glob. Ecol. Biogeogr. 18, 416–425.

Paquette, A., Messier, C., 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. Glob. Ecol. Biogeogr. 20, 170–180.

Pinheiro, J., Bates, D., 2016. nlme: Linear and Nonlinear Mixed Effects Models, R package version 3. 1–128 ed.

Poorter, L., Markesteijn, L., 2008. Seedling traits determine drought tolerance of tropical tree species. Biotropica 40, 321–331.

Poorter, L., van der Sande, M.T., Thompson, J., Arets, E.J.M.M., Alarcon, A., Alvarez-Sanchez, J., Ascarrunz, N., Balvanera, P., Barajas-Guzman, G., Boit, A., Bongers, F., Carvalho, F.A., Casanoves, F., Cornejo-Tenorio, G., Costa, F.R.C., de Castilho, C.V., Duivenvoorden, J., Dutrieux, L.P., Enquist, B.J., Fernandez-Mendez, F., Finegan, B., Gormley, L.H.L., Healey, J.R., Hoosbeek, M.R., Ibarra-Manriquez, G., Junqueira, A.B., Levis, C., Licona, J.C., Lisboa, L.S., Magnusson, W.E., Martinez-Ramos, M., Martinez-Yrizar, A., Martorano, L., Maskell, L.C., Mazzei, L., Meave, J.A., Mora, F., Munoz, R., Nytch, C., Pansonato, M.P., Parr, T., Paz, H., Perez-Garcia, E.A., Renteria, L.Y., Rodriguez-Velazquez, J., Rozendaal, D.M.A., Ruschel, A.R., Sakschewski, B., Salgado-Negret, B., Schietti, J., Simoes, M., Sinclair, F.L., Souza, P.F., Souza, F.C., Stropp, J., ter Steege, H., Swenson, N.G., Thonicke, K., Toledo, M., Uriarte, M., van der Hout, P., Walker, P., Zamora, N., Pena-Claros, M., 2015. Diversity enhances carbon storage in tropical forests. Glob. Ecol. Biogeogr. 24, 1314–1328.

Prado-Junior, J.A., Schiavini, I., Vale, V.S., Arantes, C.S., Sande, M.T., Lohbeck, M., Poorter, L., 2016. Conservative species drive biomass productivity in tropical dry forests. J. Ecol. 104, 817–827.

R Development Core Team, 2015. R Version 3.2.2. R Foundation for Statistical Computing, Vienna, Austria.

Rüger, N., Wirth, C., Wright, S.J., Condit, R., 2012. Functional traits explain light and size response of growth rates in tropical tree species. Ecology 93, 2626–2636.

Ravenscroft, C.H., Fridley, J.D., Grime, J.P., Cornelissen, H., 2014. Intraspecific functional differentiation suggests local adaptation to long-term climate change in a calcareous grassland. J. Ecol. 102, 65–73.

Reich, B.P., 2014. The world-wide 'fast-slow'plant economics spectrum: a traits manifesto. J. Ecol. 102, 275–301.

Rosseel, Y., 2012. Lavaan: an r package for structural equation modeling. J. Stat. Software 48, 1–36.

Rozendaal, D.M.A., Hurtado, V.H., Poorter, L., 2006. Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. Funct. Ecol. 20, 207–216.

Siefert, A., Ritchie, M.E., 2016. Intraspecific trait variation drives functional responses of old-field plant communities to nutrient enrichment. Oecologia 181, 245–255.

Siefert, A., Violle, C., Chalmandrier, L., Albert, C.H., Taudiere, A., Fajardo, A., Aarssen, L.W., Baraloto, C., Carlucci, M.B., Cianciaruso, M.V., Dantas, V.d.L., de Bello, F., Duarte, L.D.S., Fonseca, C.R., Freschet, G.T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., Jung, V., Kamiyama, C., Katabuchi, M., Kembel, S.W., Kichenin, E., Kraft, N.J.B., Lagerström, A., Bagousse-Pinguet, Y.L., Li, Y., Mason, N., Messier, J., Nakashizuka, T., Overton, J.M., Peltzer, D.A., Pérez-Ramos, I.M., Pillar, V.D., Prentice, H.C., Richardson, S., Sasaki, T., Schamp, B.S., Schöb, C., Shipley, B., Sundqvist, M., Sykes, M.T., Vandewalle, M., Wardle, D.A., 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. Ecol. Lett. 18, 1406–1419.

Spasojevic, M.J., Turner, B.L., Myers, J.A., Jones, R., 2016. When does intraspecific trait variation contribute to functional beta-diversity? J. Ecol. 104, 487–496.

Szwagrzyk, J., Gazda, A., 2007. Above-ground standing biomass and tree species diversity in natural stands of Central Europe. J. Veg. Sci. 18, 555–562.

Taudiere, A., Violle, C., 2015. Community Assembly by Traits: Individuals and Beyond. (0.99.1 ed).

Tilman, D., 1997. The influence of functional diversity and composition on ecosystem processes. Science 277, 1300–1302.

Tilman, D., 1999. The ecological consequences of changes in biodiversity: a search for general principles 101. Ecology 80, 1455–1474.

Uriarte, M., Swenson, N.G., Chazdon, R.L., Comita, L.S., John Kress, W., Erickson, D., Forero-Montaña, J., Zimmerman, J.K., Thompson, J., 2010. Trait similarity, shared ancestry and the structure of neighbourhood interactions in a subtropical wet forest: implications for community assembly. Ecol. Lett. 13, 1503–1514.

Vasseur, F., Violle, C., Enquist, B.J., Granier, C., Vile, D., 2012. A common genetic basis to the origin of the leaf economics spectrum and metabolic scaling allometry. Ecol. Lett. 15, 1149–1157.

Via, S., Gomulkiewicz, R., De Jong, G., Scheiner, S.M., Schlichting, C.D., Van Tienderen, P.H., 1995. Adaptive phenotypic plasticity: consensus and controversy. Trends Ecol. Evol. 10, 212–217.

Vilà, M., Vayreda, J., Gracia, C., Ibáñez, J.J., 2003. Does tree diversity increase wood production in pine forests? Oecologia 135, 299–303.

Vilà, M., Vayreda, J., Comas, L., Ibanez, J.J., Mata, T., Obon, B., 2007. Species richness and wood production: a positive association in Mediterranean forests. Ecol. Lett. 10, 241–250.

Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V., Messier, J., 2012. The return of the variance: intraspecific variability in community ecology. Trends Ecol. Evol. 27, 244–252.

Walker, B.H., 1992. Biodiversity and ecological redundancy. Conserv. Biol. 6, 18–23.

World Reference Base for Soil Resources, 2006. A Framework for International Classification, Correlation and Communication. Food and Agriculture Organization of the United Nations, Rome.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827.

Wright, S.J., Kitajima, K., Kraft, N.J., Reich, P.B., Wright, I.J., Bunker, D.E., Condit, R., Dalling, J.W., Davies, S.J., Díaz, S., 2010. Functional traits and the growth-mortality trade-off in tropical trees. Ecology 91, 3664–3674.
Wright, J.S., 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia 130, 1–14.
Yan, E.-R., Yang, X.-D., Chang, X.S., Wang, X.-H., 2013. Plant trait-species abundance relationships vary with environmental properties in subtropical forests in Eastern China. PLoS One 8, e61113.
Yuan, Z., Wang, S., Gazol, A., Mellard, J., Lin, F., Ye, J., Hao, Z., Wang, X., Loreau, M., 2016. Multiple metrics of diversity have different effects on temperate forest functioning over succession. Oecologia 182, 1175–1185.
Zhang, Y., Chen, H.Y.H., Reich, B.P., 2012a. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. J. Ecol. 100, 742–749.
Zhang, N., Wang, X.-H., Zheng, Z.-M., Ma, Z.-P., Yang, Q.-S., Fang, X.-F., Xie, Y.-B., 2012b. Spatial heterogeneity of soil properties and its relationships with terrain factors in broadleaved forest in Tiantong of Zhejiang Province, East China. Chin. J. Appl. Ecol. 23, 2361–2369.
Zhang, Y., Chen, H.Y.H., Taylor, A.R., 2016. Positive species diversity and above-ground biomass relationships are ubiquitous across forest strata despite interference from overstorey trees. Funct. Ecol. 31, 419–426.
Zhao, Y.-T., Ali, A., Yan, E.-R., 2017. The plant economics spectrum is structured by leaf habits and growth forms across subtropical species. Tree Physiol. 37, 173–185.
Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York.