

Functional evenness of wood traits and structural diversity mediate aboveground biomass positive response to species richness in mixed-species stands

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Abstract

Decades of research have helped establish the positive relationships between species richness and ecosystem biomass. However, species richness or related taxonomic metrics do not fully capture the functional differences between species, nor are they sufficient to reflect overall stand complexity. Further, the relative importance of structural diversity, functional trait dominance and diversity for stand biomass is still controversial, especially in multispecies stands with differential intra- and interspecific functional and structural patterns. In this study, we used plot level floristic and functional trait data in mixed-species plantations in West Africa, to examine the relationship between multiple diversity metrics and AGB. Multi-model inference and subset regression analyses were performed to identify the most important diversity metrics for AGB. Structural equation models were also used to evaluate both direct and indirect responses of AGB. Overall, 23 species were enumerated in the mixed species stands, plot level values ranging from 1 to 12 species. AGB was in average 15.5 Mg/plot, and varied from 9.3 to 23.1 Mg/plot. The relationship between taxonomic diversity and AGB varied with specific metric. Among taxonomic diversity metrics, only species richness correlated positively with AGB. Neither the single trait-functional diversity nor the functional dominance played a significant role in predicting AGB. In contrast, functional evenness and structural diversity showed positive effects on AGB, and mediated its positive response to species richness. This work reveals that functional evenness showed a significant advantage in predicting and mediating AGB response to species richness, when compared with structural diversity. It also suggests that niche complementarity plays a crucial role in enhancing AGB in mixed plantations, and operates through functional evenness and structural diversity. Maintaining high structural diversity and functional diversity would contribute to preserve biodiversity and enhance stand biomass stock in mixed species plantations.

Introduction

Mixed species plantations with high value species attract increased interest as they may provide a broader supply of ecological and socio-economic benefits (Felton et al., 2016; Gamfeldt et al., 2013; Heinrichs et al., 2019; Isbell et al., 2011). Mixed species stands have particularly been reported to provide higher biomass production (Erskine, Lamb, & Bristow, 2006) and to be more productive, stable and climate resistant than the average monocultures of the same species (Bauhus et al., 2017; H. Pretzsch et al., 2015; H Pretzsch et al., 2019).

As compared to monoculture, higher biomass production in mixed species stands can be attributed to several factors, including greater species diversity, greater stand structuring and canopy packing (H Pretzsch et al., 2019), facilitation and better resource utilization (Jactel et al., 2018; Hans Pretzsch, Forrester, & Bauhus, 2017). For instance, species rich stands may allow coexistence of functionally different species (species of different functional trait or attributes) that therefore efficiently access and utilize limiting resources,

thereby enhancing biomass production through efficient resource-use. It is further possible that in mixed species stands, certain species (e.g. nitrogen-fixing species) improve growing conditions for others, thereby enhancing overall production through facilitation (Erskine et al., 2006). This is consistent with the niche complementarity and facilitation mechanisms (Loreau & Hector, 2001), and have important implications for silviculture, as well managed mixed, more diverse and uneven-aged plantations would have higher net primary production than monoculture stand (Kelty, 1992, 2006). On the other hand, occurrence of dominant and highly productive tree species (with dominant traits) can positively influence biomass production, i.e. one or two species in mixed species plantation can largely explain increase in biomass production if they are dominant. This lends support to the sampling/selection effect hypothesis which posits that biomass production is enhanced through functional traits of the dominant species. Although the selection effects may seem more evident, because few larger trees often contain large portion of the stand aboveground biomass (Bastin et al., 2015; Fotis et al., 2018; Lin et al., 2016; S. Mensah, Veldtman, Du Toit, Kakaï, & Seifert, 2016; Sylvanus Mensah, Veldtman, & Seifert, 2017), studies have also lent support to both mechanisms, which are demonstrated to be non-mutually exclusive (Cavanaugh et al., 2014; Hooper, Chapin III, & Ewel, 2005; S. Mensah, du Toit, & Seifert, 2018; S. Mensah, Veldtman, Assogbadjo, Glèlè Kakaï, & Seifert, 2016; Ruiz-Benito et al., 2014; Ruiz-Jaen & Potvin, 2010; Wu et al., 2015), but can have different relative importance in different contexts (Fargione et al., 2007; Potvin & Gotelli, 2008), as a result of differences in functional traits among species, resource allocation and resource use efficiency (Huston, 1997; Tilman, Lheman, & Thomson, 1997). For instance in a recent study, we showed that both mechanisms operate through competitive exclusion imposed by dominant species (selection effects) and complementary use of resources by weak competitors (S. Mensah, du Toit, et al., 2018). Therefore both mechanisms may also prevail for mixed species stands, and understanding their relative contribution may inform about appropriate silvicultural options for their management.

Decades of research have helped establish positive relationships between species richness and ecosystem biomass or carbon storage, as the most dominant pattern. Across scales and biomes, several studies have reported positive effects of species diversity on stand biomass (Barrufol et al., 2013; Cheng, Zhang, Zhao, & von Gadow, 2018; Huang, Su, Li, Liu, & Lang, 2019; Liang et al., 2016; Liu et al., 2018; S. Mensah, Veldtman, Du Toit, et al., 2016; Paquette & Messier, 2011; Ruiz-Benito et al., 2014; Vilà et al., 2007), although neutral and negative patterns also exist (An-ning, Tian Zhen, & Jian Ping, 2008; Ruiz-Jaen & Potvin, 2011; Szwagrzyk & Gazda, 2007). While the positive relationship between species richness and biomass production can be used as a persuasive argument for the conservation of biodiversity and encourage more diverse plantations (Erskine et al., 2006), many previous studies have focused on species richness or related taxonomic indexes, which do not fully capture certain functional differences or similarities between species (Cardinale et al., 2006), nor are they sufficient to reflect the complexity of the stand community (Morin, Fahse, Scherer-Lorezen, & Bugmann, 2011). Much research is still needed across scales of the analysis (global, national or subnational), and in relation to the measure of biodiversity.

Apart from species richness or related taxonomic indices such as Shannon index, Pielou evenness and Simpson index, functional trait diversity (richness, evenness, dispersion and divergence), functional trait dominance or identity (community-weighted mean of a given functional trait) or structural diversity have been reported to predict stand aboveground biomass or productivity (Y. Li et al., 2019; Lin et al., 2016; S. Mensah, du Toit, et al., 2018; S. Mensah, Veldtman, Assogbadjo, et al., 2016; S. Mensah, Veldtman, Du Toit, et al., 2016; Prado-junior et al., 2016; Thom & Keeton, 2019; Wen et al., 2019; Zhang & Chen, 2015). Because species may differ in functional traits that drive differences in resource capture, rates of photosynthesis and biomass allocation (Falster, Duursma, & FitzJohn, 2018; Poorter et al., 2012), functional trait diversity, dominance or identity would better capture the degree of functional redundancy and niche overlap (Lasky et al., 2014; Prado-junior et al., 2016; Ruiz-Benito et al., 2014). Further, structural diversity (tree size variation and inequality) reflects how different species occupy different vertical and horizontal layers, and therefore may indicate the degree of complementarity (e.g. light-adapted and shade-tolerant species), competition and resource utilisation. Nevertheless, some recent studies showed controversy in the relationship between these structural and functional diversity/dominance metrics (Finegan et al., 2015; Lin et al., 2016; Prado-junior et

al., 2016; Xu et al., 2019). For instance, Lin et al. (2016), after accounting for topographic variables and tree stem density, found that functional dominance was the main driving factor for forest aboveground carbon, while functional diversity had negligible effects. The authors argued that this could have been due to the fact functional traits that relate strongly to plant complementary resource use were not included in the analysis. However, even after using five functional traits (maximum tree height; leaf carbon content; leaf nitrogen content; leaf area; and specific leaf area), Xu et al. (2019) reported that neither the functional nor the phylogenetic diversity showed a significant advantage in predicting aboveground biomass and biomass production when compared with species richness in old-growth temperate forests. Further, Fotis et al. (2018) recently reported limited effect of functional diversity on aboveground biomass in mixed mesophytic temperate forests of the eastern USA, whereas Szwagrzyk and Gazda (2007) found that negative effects of functional diversity on aboveground biomass in Central Europe. Consequently, the relative importance of functional dominance (selection effects), functional diversity and structural diversity (niche complementarity) for stand biomass is still controversial, and requires further investigation, especially in mixed species stands that harbor species occupying different positions across the vertical layer, possibly favoring a better use of resources (e.g., light) and reduced competition.

Combining information on taxonomic, functional, and structural diversity would provide additional insights into our understanding of mechanisms behind diversity-biomass relationships in mixed species stands. However, it is unclear how each particular metric would predict AGB, and whether some have significant advantage in mediating AGB response. Therefore, in this study, we used taxonomy-, structure-, and functional trait-based diversity to examine the relationships between AGB and multiple diversity metrics. First we sought to determine the most important taxonomic diversity measure among species richness, Shannon diversity, Pielou evenness and Simpson index, for predicting AGB. Second we tested for clear effects of multiple trait-functional diversity, single trait-functional diversity, functional dominance, and structural diversity on AGB. Finally, we retained the most important structure-, and functional trait-based diversity metrics, and tested for their mediation role in predicting AGB response to species richness.

Materials and methods

Study area and forest inventory

The present study was carried out in mixed species stands located in the Sudano-Guinean ecological transition zone in Republic of Benin. The transition zone is characterized by a unimodal rainfall regime (one rainy season and one dry season of unequal durations), with an annual rainfall of 1200 mm, and average daily temperature of 28°C (Adomou, 2005). There is little or no variation in the type of soil, which is mainly ferruginous. The plantations were established in the Bellefoungou Forest Reserve (9°46'40" - 9°49'00" N and 1°42'00" - 1°45'00" E), to restore the forest cover in degraded areas subject to high anthropogenic pressure. They were initially established using exotic species (*Tectona grandis* L., *Gmelina arborea* Roxb.), but did not receive silvicultural and management interventions, hence, evolved into mixed species stands with the occurrence of many other native species including *Vitellaria paradoxa* (Gaertn C. F.), *Isoberlinia doka* Craib & Stapf, *Pterocarpus erinaceus* Poir. Like most tropical sudanian vegetation, these stands exhibit a well-structured, multi-storey woody vegetation, consisting of sub-canopy, canopy and emergent tree species. The most dominant species in these stands is

T. grandis.

The dataset used in the analyses was collected from 30 inventory plots of 0.18 ha (Houeto et al., 2014; Salako et al., 2013), and consisted of floristic information (tree species names, density, and diameter at breast height – dbh and tree height) and functional trait data (maximum plant height and specific wood density). In each plot, all individual of dbh [?] 5 cm were measured for their dbh and tree height, and identified at species level. The number of primary branches at crown base level was also recorded for each individual to account for variability in the crown structure. Data on functional traits important to plant growth (maximum plant height and specific wood density) were obtained from field inventory and publicly available sources. The data on maximum plant height was obtained from the inventory data, while that of species wood density

was obtained from the Global Wood Density Database (Zanne et al., 2009). We used wood density and plant maximum height because they are known to relate with light capture, stem growth and plant investment in biomass. For instance, plant maximum height enhance light capture and facilitate higher growth, while wood density indicates whether a tree species favors a fast growth whereby conductive tissues are rapidly built in lower wood density species (Falster et al., 2018; Prado-Junior et al., 2016).

Quantification of aboveground biomass stock

We used the multispecies allometric biomass equation developed by (Chave et al., 2014) to calculate the aboveground biomass (AGB) for all individual trees present in the plots. The formula for the multispecies allometric biomass equation is: $AGB = 0.0673 \times (\rho \times DBH^2 \times Ht)^{0.976}$, where AGB is the aboveground tree biomass in kilograms, ρ the species-specific wood density ($g[?]cm^{-3}$), DBH the diameter at breast height (cm), and Ht the total height (m).

Quantification of taxonomic, functional and structural diversity metrics

We computed plot-level taxonomic, functional and structural diversity metrics. Taxonomic diversity was quantified using species richness, Shannon Index, Pielou Evenness and Simpson index. Species richness was defined at plot level, as the number of distinct species enumerated inside each plot.

To quantify functional trait-based diversity, we computed multiple- and single-trait diversity metrics and functional dominance. Multiple-trait diversity metrics include functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis) (Mouchet, Villéger, Mason, & Mouillot, 2010; Villéger, Mason, & Mouillot, 2008). They were calculated at plot level, using the relative abundance of each species in each plot and the values of functional traits. We quantified the single trait functional divergence (FDvar), as the variance of each trait value weighted by the species' relative density in each plot (Mason, Mouillot, Lee, & Wilson, 2005). For functional dominance, we calculated the plot-level community weight mean (CWM) for each functional trait based on the relative density of the species. We used CWM because it reflects functional shifts in mean trait values and species dominance in a community (S. Mensah, Veldtman, Assogbadjo, et al., 2016; Ricotta & Moretti, 2011). Both the multiple-trait functional diversity and dominance were calculated with "FD" package in R (Laliberté, Legendre, & Shipley, 2015). FDvar was calculated for each trait (i.e. wood density and plant maximum height) using the FDiversity software.

Structural diversity can be expressed with measures that relate to the horizontal and vertical extent as well as to the internal branching pattern of the trees. Thus, we focused on tree height and diameter differentiation across individual trees inside each plot, as well as on number of primary branches at crown base level, and assessed structural diversity as coefficient of variation (standard deviation to mean) of each of these three variables at plot level (S. Mensah, Pienaar, et al., 2018).

Statistical analyses

All statistical analyses were performed in the R statistical software package, version 3.3.2 (R Core Team, 2019). We used scatterplot to explore the bivariate relationship between four taxonomic diversity metrics (species richness, Shannon Index, Pielou Evenness and Simpson index) and AGB, and tested for their significant effects on AGB using separate simple linear models. To determine how multiple trait-functional diversity, single trait-functional diversity, functional dominance, and structural diversity influence AGB, we ran a multiple linear model incorporating all the 11 metrics. These metrics were functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis) for the multiple trait-functional diversity; functional divergence of wood density (FDvar WD) and of maximum plant height (FDvar Hmax) for single trait-functional diversity; community weight mean of wood density (CWM WD) and of maximum plant height (CWM Hmax) for functional dominance; and structural diversity [CV DBH: tree diameter variation; CV Ht: tree height variation; CV Nbp: variation of number of primary branches]. Due to this high number of independent variables and the likelihood of autocorrelation, a Multi-model Inference followed by a full averaging procedure was performed using the package "MuMIn" (Barton, 2018) to

determine the optimal best model, which was selected based on the Akaike Information Criterion (AICc). Between two subset models that are equally supported ($\Delta AICc < 2$), the most parsimonious was the one with more independent variables. In addition to the significance fits of the predictors retained in the finally selected models, we computed for all predictors their relative importance. For easier interpretation of the results, bivariate relationships were also constructed.

Finally, we used Structural Equation Modelling (SEM) to assess the direct and indirect response of AGB to diversity metrics. To simplify the analytical framework of the SEM, we only considered the independent variables that were retained in the previous selected models. These were species richness, functional evenness, coefficient of variation of tree diameter and of the number of branches. We tested the a-priori model that AGB increased with increasing species richness, as result of positive mediation of functional evenness, and structural diversity.

To determine the individual mediation role of functional evenness, coefficient of variation of tree diameter and number of branches, we fitted three separate SEMs, and a fourth integrative SEM incorporating both direct and indirect paths between species richness and AGB via functional evenness, coefficient of variation of tree diameter and number of branches. The SEMs were fitted using “lavaan” package (Rosseel, 2012) in the R statistical software. The goodness of fit of the SEM was assessed using the Chi square statistic, comparative fit index (cfi), and root mean square error of approximation (rmsea) (Grace & Bollen, 2005; S. Mensah, du Toit, et al., 2018; S. Mensah, Veldtman, Assogbadjo, et al., 2016).

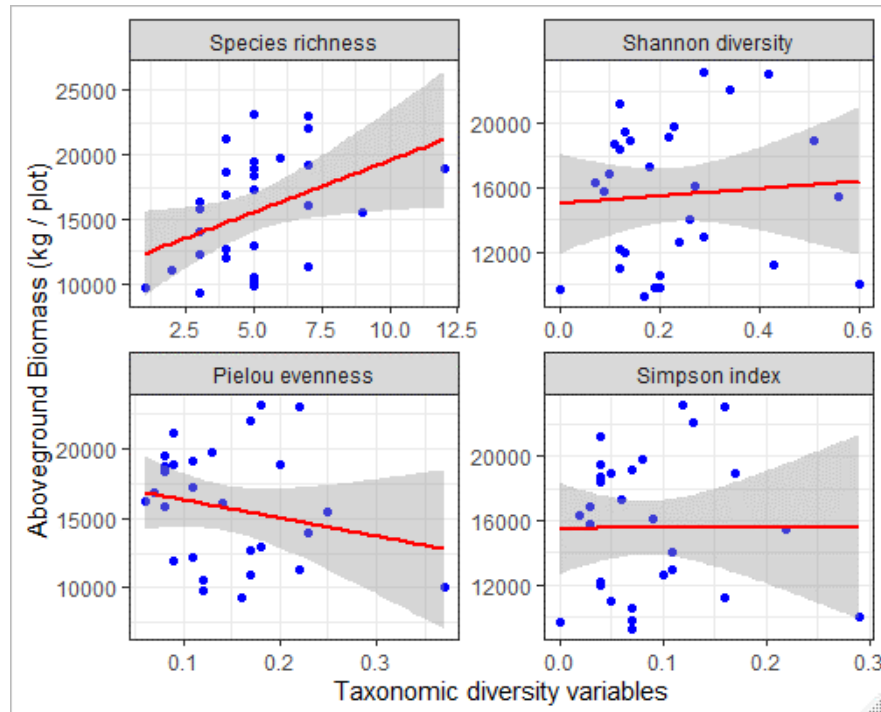


Fig. 1 Bivariate relationships of plot-level aboveground biomass with taxonomic diversity metrics

Results

Overall, 23 species were enumerated in the mixed species stands studied, with an average of 5 species per plot, and range value of 1 to 12 species. AGB was in average 15.5 Mg across all plots, and varied from 9.3 to 23.1 Mg per plot. The relationship between taxonomic diversity and AGB varied with specific metric. Among the four taxonomic diversity metrics, only species richness influenced positively AGB (Figure 1), and the effects were shown by significantly higher values of AGB in plot with more species ($r^2=0.16$; $p<0.05$;

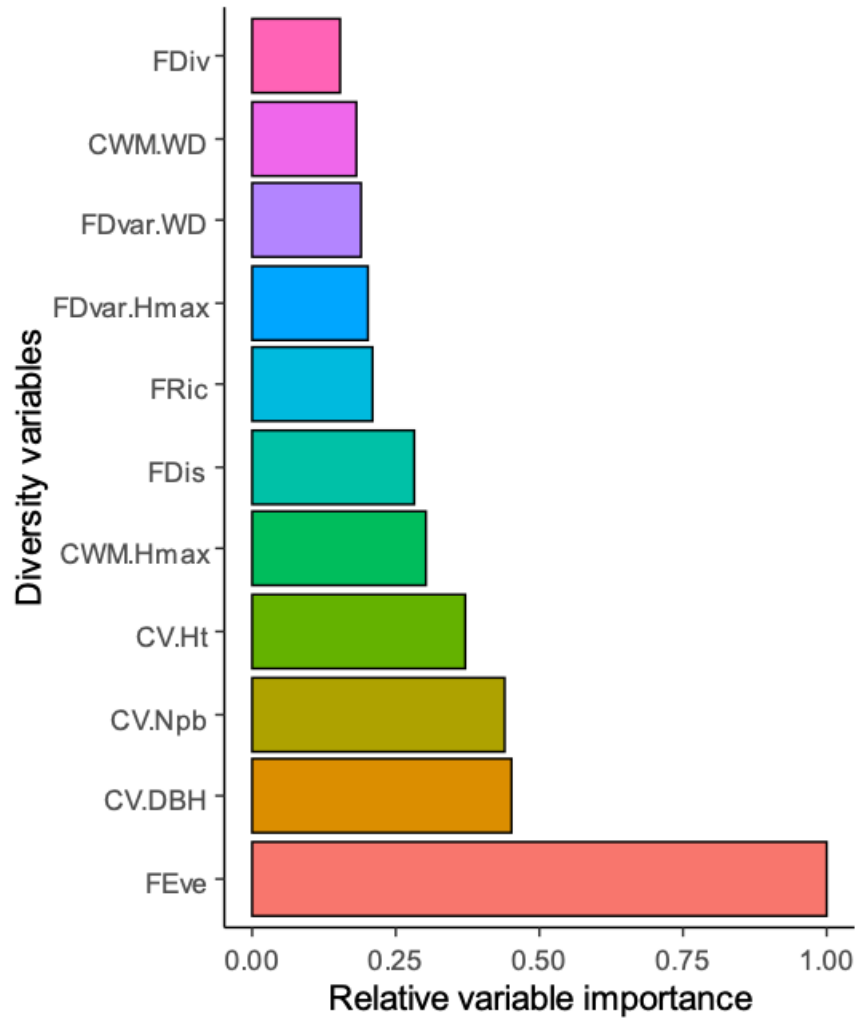


Fig. 3 Relative importance of structural diversity, functional dominance, multiple- and single-trait functional diversity metrics used as predictors in the multiple linear model. Statistical fit summaries are presented in Table 1

We analysed the direct and indirect response of AGB to diversity metrics by considering only independent important variables for AGB, as retained in the previous selected model. The outputs of the SEM testing for species richness effect on AGB via functional evenness and structural diversity revealed chi-square values ranging from 0.08 to 1.72 and $P > 0.05$ (Table 2), indicating good fit of the SEM to the data. The values of cfi (close to 1), and rmsea (< 0.16) also demonstrate good fits of the models (Table 2).

Table 2. Summary of fit statistics for the SEMs relating species richness, functional evenness and functional diversity metrics to AGB; cfi: comparative fit index; and rmsea: root mean square error of approximation

SEM	cfi	rmsea	df	Chi ²	<i>P</i>	Remarks
Fig.4a	1.000	0.000	1	0.083	0.774	Accepted
Fig.4b	0.994	0.155	1	1.724	0.189	Accepted
Fig.4c	1.000	0.000	1	0.193	0.661	Accepted
Fig.4d	1.000	0.014	1	1.005	0.316	Accepted

Chi²:Chi-square test ($P > 0.05$ indicates absence of significant discrepancy between the data and the model);
*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$

Species richness showed significant positive direct effect on FEve ($\beta = 0.53$; $P < 0.001$; Table 3), which also showed positive and significant effect ($\beta = 0.62$; $P < 0.001$; Table 3; Figure 4a) on AGB. Therefore, species richness, through FEve had a positive significant effect on AGB ($\beta = 0.53 \times 0.62 = 0.39$). Similarly, species richness, through structural diversity (CV DBH and CV Npb) showed positive significant effects on AGB (Table 3; Fig. 4b-c). However, when comparing the three SEMs, we found that the variation in AGB explained was greater for FEve ($r^2=0.39$) than for CV DBH ($r^2=0.20$) and CV Npb ($r^2=0.24$). Further, when we combined functional evenness, CV DBH and CV Npb in the integrative SEM, only FEve showed significant mediation role in linking species richness to AGB (Table 3; Fig. 4d).

Table 3. Results of the SEMs testing the direct and indirect effects of species richness on AGB via functional evenness and structural diversity. Fit statistics are presented in Figure 3

	SEMs	Est	SE	z	P
Testing mediation role of functional evenness	Testing mediation role of functional evenness				
	From species richness to functional evenness	0.53	0.12	4.26	<0.001
	From functional evenness to AGB	0.62	0.11	5.51	<0.001
Testing mediation role of CV DBH	Testing mediation role of CV DBH				
	From species richness to CV DBH	0.47	0.14	3.48	0.001
	From CV DBH to AGB	0.45	0.15	3.07	0.002
Testing mediation role of CV Npb	Testing mediation role of CV Npb				
	From species richness to CV Npb	0.71	0.08	8.97	<0.001
	From CV Npb to AGB	0.49	0.14	3.59	<0.001
Direct effect of species richness	Direct effect of species richness				
	From species richness to AGB	-0.16	0.22	-0.74	0.459
	From species richness to functional evenness	0.53	0.12	4.26	<0.001
	From species richness to CV DBH	0.46	0.14	3.30	0.001
	From species richness to CV Npb	0.71	0.08	8.84	<0.001
	From functional evenness to AGB	0.58	0.16	3.48	0.001
	From CV DBH to AGB	-0.03	0.19	-0.15	0.883
	From CV Npb to AGB	0.35	0.23	1.52	0.129

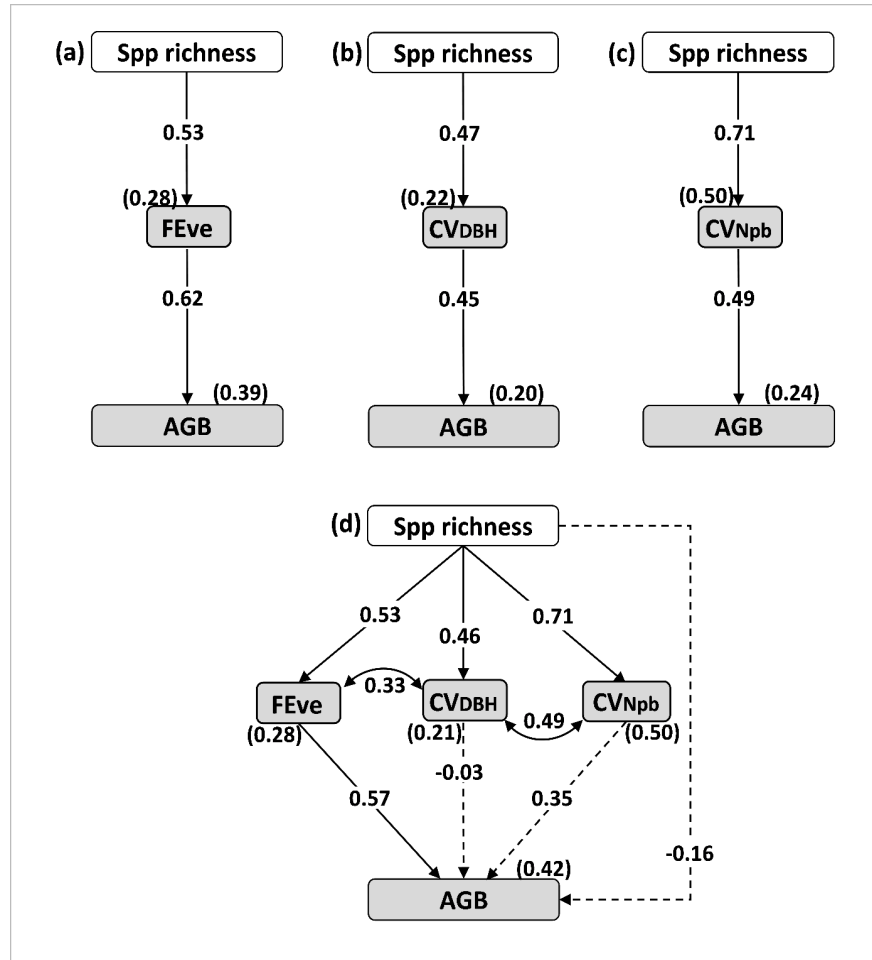


Fig. 4 Structural Equation Model-fit path summary relating AGB to species richness via functional evenness and structural diversity metrics (Significant paths ($P < 0.05$) are represented with solid arrows and non-significant paths ($P > 0.05$) by dashed arrows. The single-pointed arrows represent causal paths and double-pointed arrows the residual correlations. The values without parentheses are the standardized path coefficients. The values with parentheses are the coefficients of determination. CV DBH: tree diameter variation; CV Npb: variation of number of primary branches. Detailed statistics are shown in Tables 2-3.

Discussion

Increasing species richness promotes tree biomass stock in mixed species stands

Plot-level aboveground biomass increased with increasing species richness, as per our expectation and in line with several previous studies at local (Con et al., 2013; S. Li et al., 2018; Liu et al., 2018; S. Mensah, Veldtman, Assogbadjo, et al., 2016; Wang, Lei, Ma, Kneeshaw, & Peng, 2011), regional (Ouyang et al., 2019; Paquette & Messier, 2011; Ruiz-Benito et al., 2014) and global scales (Cavanaugh et al., 2014; Liang et al., 2016). None of other three taxonomic diversity metrics (Shannon diversity, Pielou evenness and Simpson index) explained variation of the biomass in these stands, suggesting that species richness was the only studied taxonomic diversity metric predictor of AGB. Increasing plot level species richness may drive difference in AGB through increasing stocking capacity (higher density), or co-existence of functionally different species increasing resource partitioning (Mittelbach et al., 2001; Waide et al., 1999), for example, several canopy strata optimising use of vertical growing space and light (S. Mensah, du Toit, et al., 2018; Morin et al., 2011;

Yachi & Loreau, 2007), in line with the niche complementarity hypothesis. These functionally different species may also enable plant–plant interactions such as facilitation, whereby some species could improve growing conditions (e.g. enhancing soil fertility through fixing nitrogen) for the productivity of other species (Erskine et al., 2006; S. Mensah, Veldtman, Assogbadjo, et al., 2016). However, increasing species richness may also enhance biomass production through highly performing dominant species; i.e. by increasing the likelihood of their presence in the ecosystem or by increasing the chances of having dominant species traits that naturally favored biomass production (Fotis et al., 2018; Lin et al., 2016; S. Mensah, Veldtman, Du Toit, et al., 2016; Wasof et al., 2018). Although our dataset reflect a local scale variation of species richness and AGB, it must be noted that the result adds to the general evidence that species richness has a positive effect on forest biomass.

Positive species richness effect on AGB manifested through niche complementarity

Recent studies have provided evidence for the need to explore beyond species richness, how stand biomass and carbon relates to functional trait and structure-based diversity (Conti & Díaz, 2013; Dimobe, Kuyah, Dabré, Ouédraogo, & Thiombiano, 2019; Finegan et al., 2015; Hao, Zhang, Zhao, & von Gadow, 2018; Lin et al., 2016; Prado-junior et al., 2016; Wang et al., 2011; Zhang & Chen, 2015). Others researchers also documented the importance of phylogenetic diversity (Lasky et al., 2014; Satdichanh et al., 2019; Wasof et al., 2018). In this study, we compared the relative importance (and mediation) of functional trait, structure and dominance metric in explaining species richness effects on biomass stock. Interestingly, none of the single-trait functional diversity (FDvar) and dominance (CWM) metrics explained AGB variation in our stands. Contrary to some previous studies (Conti & Díaz, 2013; Finegan et al., 2015; Fotis et al., 2018), our study showed that FDvar and CWM of wood density and plant maximum height in these mixed species stands did not influence AGB. Lin et al. (2016) showed that biomass carbon responds most strongly to CWM values of wood density and maximum tree height in subtropical evergreen broad-leaved forest in China. Similarly, Wasof et al. (2018) showed that biomass of the forest understorey was mainly related to CWM of plant traits (leaf area and plant height) in temperate deciduous forests in Northern France. Some of our previous studies also showed that CWM of traits correlate strongly with biomass and carbon stock (S. Mensah, du Toit, et al., 2018; S. Mensah, Veldtman, Assogbadjo, et al., 2016; Sylvanus Mensah, Salako, Glèlè Kakai, & Sinsin, 2020). Although not anticipated, the conflictual result is not surprising and might be due the complexity of these stands ecosystem structures, perhaps because of the low functional trait values (low level of functional diversity) of the dominant species.

Nevertheless, our analyses showed that among the multi-trait functional diversity indices, functional evenness had a significant and positive relationship with biomass, partly corroborating reports of positive relationship between multi-trait functional diversity metrics and AGB in forest stands (Dimobe et al., 2019; Hao et al., 2018; S. Mensah, Veldtman, Assogbadjo, et al., 2016; Rawat, Arunachalam, Arunachalam, Alatalo, & Pandey, 2019). Our finding is also in line with the general expectation that evenness should positively correlate with biomass production (Kirwan et al., 2007; Nijs & Roy, 2000; Wilsey & Potvin, 2000). Functional evenness reflects the evenness of species contribution to AGB (in this case) within the stand (Mason et al., 2005). As such, our result suggests that there is homogeneity in the distribution of the relative density (i.e., lower variance in the abundance of different species) across the multivariate trait space, reducing interspecific competition (Tilman, 1982). Because high values of functional evenness indicate effective resource utilization and development of productive communities (Kelemen et al., 2017) through niche complementarity and facilitative effects (Polley, Wilsey, & Derner, 2003; Polley, Wilsey, & Tischler, 2007), the positive functional evenness and AGB relationship (Figure 2) as well as the significant mediation role of functional evenness (Figure 4), as observed in this study are supportive of the niche complementarity, as a mechanism driving positive species richness effect on AGB in our mixed species stands.

Furthermore, the positive effects of structural diversity metrics on AGB stress the importance of niche complementarity hypothesis, as the main mechanism operating in these stands. Particularly, we found that CV DBH and CV Npb were the most important predictors of AGB, after functional evenness. These results indicate that structural diversity promotes AGB, as also pointed out in previous studies (Wang et al., 2011;

Yan, Zhang, Wang, Zhao, & Gadow, 2015). The structural diversity metrics as computed here (i.e. CV DBH, CV Ht and CV Npb) reflect the amount of both intra and interspecific vertical and horizontal tree size and crown variation within the plot, (Seidel et al., 2019; Wang et al., 2011), and thus are somewhat indicative of resources capture and use by species (Yachi & Loreau, 2007). For example, greater intra and interspecific vertical and horizontal tree size and crown variations would translate into forest vertical stratification and crown complementarity, which allow for greater light infiltration and promote complementary use of light by trees in the subcanopy, canopy and above canopy layer, leading to higher performance at stand level, as previously shown in multi-storey Afromontane natural forest in South Africa (S. Mensah, du Toit, et al., 2018). We thus argue that the positive effects of both CV DBH and CV Npb on AGB result from resource-use efficiency and complementarity due to high structural (tree size and crown) differentiation, supporting facilitation and niche differentiation or complementarity, as also shown in spruce-dominated forest stands in Canada (Wang et al., 2011).

Conclusion

Information on how species diversity influences biomass production are vital to support forest management and preserve biodiversity. In this study, we examined the relationships between AGB and multiple diversity metrics in mixed species stands. We found that (i) AGB was positively influenced by species richness; (ii) most important predictors of AGB were functional evenness and structural diversity; (iii) functional evenness and structural diversity mediate aboveground biomass positive response to species richness. Our research therefore underlines the importance of tree species richness as a primary driver of aboveground biomass. Functionally or morphologically different species have different specialized strategies to optimize resources uptake and use. Altogether, our results suggest that resource-use complementarity, the ability of different species with functional and structural (tree size and crown) differentiation to efficiently use the limited resources, is the main mechanism governing positive diversity-biomass relationship in mixed species stands. The study further suggests that maintaining high structural diversity and functional diversity would contribute to preserve biodiversity and enhance biomass stock.

References

- Adomou, A. (2005). *Vegetation patterns and environmental gradient in Benin: implications for biogeography and conservation*. Wageningen University.
- An-ning, S., Tian Zhen, J., & Jian Ping, G. (2008). Relationship between species richness and biomass on environmental gradient in natural forest communities on Mt. Xiaolongshan, northwest China. *Forestry Studies in China*, 10 (4), 212–219. <https://doi.org/10.1007/s11632-008-0041-7>
- Barrufol, M., Schmid, B., Bruelheide, H., Chi, X., Hector, A., Ma, K., ... Niklaus, P. A. (2013). Biodiversity promotes tree growth during succession in subtropical forest. *PLoS ONE*, 8 (11), 1–9. <https://doi.org/10.1371/journal.pone.0081246>
- Barton, K. (2018). MuMIn: Multi-Model Inference. R package version 1.42.1. Retrieved from <https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf>
- Bastin, J. F., Barbier, N., Réjou-Méchain, M., Fayolle, A., Gourlet-Fleury, S., Maniatis, D., ... Bogaert, J. (2015). Seeing Central African forests through their largest trees. *Scientific Reports*, 5. <https://doi.org/10.1038/srep13156>
- Bauhus, J., Forrester, D. I., Gardiner, B., Jactel, H., Vallejo, R., & Pretzsch, H. (2017). Ecological stability of mixed-species forests. In *Mixed-Species Forests: Ecology and Management* (pp. 337–382). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-662-54553-9_7
- Cardinale, B. J., Srivastava, D. S., Duffy, J. E., Wright, J. P., Downing, A. L., Sankaran, M., & Jouseau, C. (2006). Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, 443 (7114), 989–992. <https://doi.org/10.1038/nature05202>

- Cavanaugh, K. C., Gosnell, J. S., Davis, S. L., Ahumada, J., Boundja, P., Clark, D. B., ... Andelman, S. (2014). Carbon storage in tropical forests correlates with taxonomic diversity and functional dominance on a global scale. *Global Ecology and Biogeography* , 23 (5), 563–573. <https://doi.org/10.1111/geb.12143>
- Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., ... Vieilledent, G. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology* , 20 , 3177–3190. <https://doi.org/10.1111/gcb.12629>
- Cheng, Y., Zhang, C., Zhao, X., & von Gadow, K. (2018). Biomass-dominant species shape the productivity-diversity relationship in two temperate forests. *Annals of Forest Science* , 75 (4). <https://doi.org/10.1007/s13595-018-0780-0>
- Con, V. T., Thang, N. T., Ha, D. T. T., Khiem, C. C., Quy, T. H., Lam, V. T., ... Sato, T. (2013). Relationship between aboveground biomass and measures of structure and species diversity in tropical forests of Vietnam. *Forest Ecology and Management* , 310 , 213–218. <https://doi.org/10.1016/j.foreco.2013.08.034>
- Conti, G., & Díaz, S. (2013). Plant functional diversity and carbon storage - an empirical test in semi-arid forest ecosystems. *Journal of Ecology* , 101 (1), 18–28. <https://doi.org/10.1111/1365-2745.12012>
- Dimobe, K., Kuyah, S., Dabré, Z., Ouédraogo, A., & Thiombiano, A. (2019). Diversity-carbon stock relationship across vegetation types in W National park in Burkina Faso. *Forest Ecology and Management* , 438 (November 2018), 243–254. <https://doi.org/10.1016/j.foreco.2019.02.027>
- Ersikine, P. D., Lamb, D., & Bristow, M. (2006). Tree species diversity and ecosystem function: Can tropical multi-species plantations generate greater productivity? *Forest Ecology and Management* , 233 (2–3), 205–210. <https://doi.org/10.1016/j.foreco.2006.05.013>
- Falster, D. S., Duursma, R. A., & FitzJohn, R. G. (2018). How functional traits influence plant growth and shade tolerance across the life cycle. *Proceedings of the National Academy of Sciences of the United States of America* , 115 (29), E6789–E6798. <https://doi.org/10.1073/pnas.1714044115>
- Fargione, J., Tilman, D., Dybzinski, R., Lambers, J. H. R., Clark, C., Harpole, W. S., ... Loreau, M. (2007). From selection to complementarity: shifts in the causes of biodiversity-productivity relationships in a long-term biodiversity experiment. *Proceedings of the Royal Society B* , 274 , 871–876. <https://doi.org/10.1098/rspb.2006.0351>
- Felton, A., Nilsson, U., Sonesson, J., Felton, A. M., Roberge, J. M., Ranius, T., ... Wallertz, K. (2016). Replacing monocultures with mixed-species stands: Ecosystem service implications of two production forest alternatives in Sweden. *Ambio* , 45 , 124–139. <https://doi.org/10.1007/s13280-015-0749-2>
- Finegan, B., Peña-Claros, M., de Oliveira, A., Ascarrunz, N., Bret-Harte, M. S., Carreño-Rocabado, G., ... Poorter, L. (2015). Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. *Journal of Ecology* , 103 (1), 191–201. <https://doi.org/10.1111/1365-2745.12346>
- Fotis, A. T., Murphy, S. J., Ricart, R. D., Krishnadas, M., Whitacre, J., Wenzel, J. W., ... Comita, L. S. (2018). Above-ground biomass is driven by mass-ratio effects and stand structural attributes in a temperate deciduous forest. *Journal of Ecology* , 106 (2), 561–570. <https://doi.org/10.1111/1365-2745.12847>
- Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., ... Bengtsson, J. (2013). Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications* , 4 , 1340. <https://doi.org/10.1038/ncomms2328>
- Grace, J. B., & Bollen, K. A. (2005). Interpreting the results from multiple regression and structural equation models. *Bulletin of the Ecological Society of America* , 86 (October), 283–295. [https://doi.org/10.1890/0012-9623\(2007\)88\[50:UFCAFW\]2.0.CO;2](https://doi.org/10.1890/0012-9623(2007)88[50:UFCAFW]2.0.CO;2)

- Hao, M. H., Zhang, C., Zhao, X., & von Gadow, K. (2018). Functional and phylogenetic diversity determine woody productivity in a temperate forest. *Ecology and Evolution* , 8 (5), 2395–2406. <https://doi.org/10.1002/ece3.3857>
- Heinrichs, S., Ammer, C., Mund, M., Boch, S., Budde, S., Fischer, M., ... Schall, P. (2019). Landscape-scale mixtures of tree species are more effective than stand-scale mixtures for biodiversity of vascular plants, bryophytes and lichens. *Forests* , 10 (1). <https://doi.org/10.3390/f10010073>
- Hooper, D. U., Chapin III, F. S., & Ewel, J. J. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* , 75 (1), 3–35. <https://doi.org/10.1890/04-0922>
- Houeto, G., Glele Kakai, R., Salako, V., Fandohan, B., Assogbadjo, A. E., Sinsin, B., & Palm, R. (2014). Effect of inventory plot patterns in the floristic analysis of tropical woodland and dense forest. *African Journal of Ecology* , 52 (3), 257–264. <https://doi.org/10.1111/aje.12112>
- Huang, X., Su, J., Li, S., Liu, W., & Lang, X. (2019). Functional diversity drives ecosystem multifunctionality in a *Pinus yunnanensis* natural secondary forest. *Scientific Reports* , 9 (1), 6979. <https://doi.org/10.1038/s41598-019-43475-1>
- Huston, M. A. (1997). Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. *Oecologia* , 110 (4), 449–460. <https://doi.org/10.1007/s004420050180>
- Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W. S., Reich, P. B., ... Loreau, M. (2011). High plant diversity is needed to maintain ecosystem services. *Nature* , 477 (7363), 199–202. <https://doi.org/10.1038/nature10282>
- Jactel, H., Gritti, E. S., Drössler, L., Forrester, D. I., Mason, W. L., Morin, X., ... Castagneyrol, B. (2018). Positive biodiversity–productivity relationships in forests: Climate matters. *Biology Letters* , 14 (4), 20170747. <https://doi.org/10.1098/rsbl.2017.0747>
- Kelemen, A., Tóthmérész, B., Valkó, O., Migléc, T., Deák, B., & Török, P. (2017). New aspects of grassland recovery in old-fields revealed by trait-based analyses of perennial-crop-mediated succession. *Ecology and Evolution* , 7 (7), 2432–2440. <https://doi.org/10.1002/ece3.2869>
- Kelty, M. J. (1992). Comparative productivity of monocultures and mixed-species stands. In M. J. Kelty (Ed.), *The Ecology and Silviculture of Mixed-Species Forests* (pp. 125–141). Kluwer Academic Publishers. https://doi.org/10.1007/978-94-015-8052-6_8
- Kelty, Matthew J. (2006). The role of species mixtures in plantation forestry. *Forest Ecology and Management* , 233 (2–3), 195–204. <https://doi.org/10.1016/j.foreco.2006.05.011>
- Kirwan, L., Lüscher, A., Sebastià, M. T., Finn, J. A., Collins, R. P., Porqueddu, C., ... Connolly, J. (2007). Evenness drives consistent diversity effects in intensive grassland systems across 28 European sites. *Journal of Ecology* , 95 (3), 530–539. <https://doi.org/10.1111/j.1365-2745.2007.01225.x>
- Laliberté, E., Legendre, P., & Shipley, B. (2015). Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. R package.
- Lasky, J. R., Uriarte, M., Boukili, V. K., Erickson, D. L., John Kress, W., & Chazdon, R. L. (2014). The relationship between tree biodiversity and biomass dynamics changes with tropical forest succession. *Ecology Letters* , 17 , 1158–1167. <https://doi.org/10.1111/ele.12322>
- Li, S., Lang, X., Liu, W., Ou, G., Xu, H., & Su, J. (2018). The relationship between species richness and aboveground biomass in a primary *Pinus kesiya* forest of Yunnan, southwestern China. *PLoS ONE* , 13 (1). <https://doi.org/10.1371/journal.pone.0191140>
- Li, Y., Bao, W., Bongers, F., Chen, B., Chen, G., Guo, K., ... Ma, K. (2019). Drivers of tree carbon storage in subtropical forests. *Science of the Total Environment* , 654 (November), 684–693. <https://doi.org/10.1016/j.scitotenv.2018.11.024>

- Liang, J., Crowther, T. W., Picard, N., Wiser, S., Zhou, M., Alberti, G., ... Reich, P. B. (2016). Positive biodiversity-productivity relationship predominant in global forests. *Science* ,354 (6309). <https://doi.org/10.1126/science.aaf8957>
- 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 and Soil* ,409 (1–2), 435–446. <https://doi.org/10.1007/s11104-016-2976-0>
- Liu, X., Trogisch, S., He, J. S., Niklaus, P. A., Bruehlheide, H., Tang, Z., ... Ma, K. (2018). Tree species richness increases ecosystem carbon storage in subtropical forests. *Proceedings. Biological Sciences* , 285 (1885). <https://doi.org/10.1098/rspb.2018.1240>
- Loreau, M., & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature* ,412 (6842), 72–76. <https://doi.org/10.1038/35083573>
- Mason, N. W. H., Moullot, D., Lee, W. G., & Wilson, J. B. (2005). Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos* , 111 (1), 112–118. <https://doi.org/10.1111/j.0030-1299.2005.13886.x>
- Mensah, S., du Toit, B., & Seifert, T. (2018). Diversity–biomass relationship across forest layers: implications for niche complementarity and selection effects. *Oecologia* , 187 (3), 783–795. <https://doi.org/10.1007/s00442-018-4144-0>
- Mensah, S., Pienaar, O. L., Kunneke, A., du Toit, B., Seydack, A., Uhl, E., ... Seifert, T. (2018). Height – Diameter allometry in South Africa’s indigenous high forests: Assessing generic models performance and function forms. *Forest Ecology and Management* , 410 , 1–11. <https://doi.org/10.1016/j.foreco.2017.12.030>
- Mensah, S., Veldtman, R., Assogbadjo, A. E., Glèlè Kakaï, R., & Seifert, T. (2016). Tree species diversity promotes aboveground carbon storage through functional diversity and functional dominance. *Ecology and Evolution* , 6 (20), 7546–7557. <https://doi.org/10.1002/ece3.2525>
- Mensah, S., Veldtman, R., Du Toit, B., Kakaï, R. G., & Seifert, T. (2016). Aboveground biomass and carbon in a South African Mistbelt forest and the relationships with tree species diversity and forest structures. *Forests* , 7 (4). <https://doi.org/10.3390/f7040079>
- Mensah, Sylvanus, Salako, V. K., Glèlè Kakaï, R., & Sinsin, B. (2020). Multifunctionality is more responsive to trait diversity than dominance in natural forests. *Ecological In* , *In press* .
- Mensah, Sylvanus, Veldtman, R., & Seifert, T. (2017). Allometric models for height and aboveground biomass of dominant tree species in South African Mistbelt forests. *Southern Forests* , 79 (1), 19–30. <https://doi.org/10.2989/20702620.2016.1225187>
- Mittelbach, G. G., Steiner, C. F., Scheiner, S. M., Gross, K. L., Reynolds, H. L., Waide, R. B., ... Gough, L. (2001). What is the observed relationship between species richness and productivity? *Ecology* , 82 (9), 2381–2396. <https://doi.org/10.1890/03-8021>
- Morin, X., Fahse, L., Scherer-Lorenzen, M., & Bugmann, H. (2011). Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecology Letters* ,14 , 1211–1219. <https://doi.org/10.1111/j.1461-0248.2011.01691.x>
- Mouchet, M. A., Villéger, S., Mason, N. W. H., & Moullot, D. (2010). Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology* , 24 (4), 867–876. <https://doi.org/10.1111/j.1365-2435.2010.01695.x>
- Nijs, I., & Roy, J. (2000). How important are species richness, species evenness and interspecific differences to productivity? A mathematical model. *Oikos* , 88 (1), 57–66. <https://doi.org/10.1034/j.1600-0706.2000.880107.x>

- Ouyang, S., Xiang, W., Wang, X., Xiao, W., Chen, L., Li, S., ... Peng, C. (2019). Effects of stand age, richness and density on productivity in subtropical forests in China. *Journal of Ecology* , 107 , 2266–2277. <https://doi.org/10.1111/1365-2745.13194>
- Paquette, A., & Messier, C. (2011). The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography* , 20 (1), 170–180. <https://doi.org/10.1111/j.1466-8238.2010.00592.x>
- Polley, H. W., Wilsey, B. J., & Derner, J. D. (2003). Do species evenness and plant density influence the magnitude of selection and complementarity effects in annual plant species mixtures? *Ecology Letters* , 6 (3), 248–256. <https://doi.org/10.1046/j.1461-0248.2003.00422.x>
- Polley, H. W., Wilsey, B. J., & Tischler, C. R. (2007). Species abundances influence the net biodiversity effect in mixtures of two plant species. *Basic and Applied Ecology* , 8 (3), 209–218. <https://doi.org/10.1016/j.baae.2006.02.006>
- Poorter, H., Niklas, K. J., Reich, P. B., Oleksyn, J., Poot, P., & Mommer, L. (2012). Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytologist* , 193 (1), 30–50. <https://doi.org/10.1111/j.1469-8137.2011.03952.x>
- Potvin, C., & Gotelli, N. J. (2008). Biodiversity enhances individual performance but does not affect survivorship in tropical trees. *Ecology Letters* , 11 , 217–223. <https://doi.org/10.1111/j.1461-0248.2007.01148.x>
- Prado-junior, J. A., Schiavini, I., Vale, V. S., Arantes, C. S., Sande, M. T. Van Der, Lohbeck, M., & Poorter, L. (2016). Conservative species drive biomass productivity in tropical dry forests. *Journal of Ecology* , 104 , 817–827. <https://doi.org/10.1111/1365-2745.12543>
- Prado-Junior, J. A., Schiavini, I., Vale, V. S., Raymundo, D., Lopes, S. F., & Poorter, L. (2016). Functional traits shape size-dependent growth and mortality rates of dry forest tree species. *Journal of Plant Ecology* , 10 (6), 895–906. <https://doi.org/10.1093/jpe/rtw103>
- Pretzsch, H., del Río, M., Ammer, C., Avdagic, A., Barbeito, I., Bielak, K., ... Bravo-Oviedo, A. (2015). Growth and yield of mixed versus pure stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) analysed along a productivity gradient through Europe. *European Journal of Forest Research* , 134 (5), 927–947. <https://doi.org/10.1007/s10342-015-0900-4>
- Pretzsch, H., Steckel, M., Heym, M., Biber, P., Ammer, C., Ehbrecht, M., ... del Rio, M. (2019). Stand growth and structure of mixed - species and monospecific stands of Scots pine (*Pinus sylvestris* L.) and oak (*Q. robur* L., *Quercus petraea* (Matt.) Liebl.) analysed along a productivity gradient through Europe. *European Journal of Forest Research* . <https://doi.org/10.1007/s10342-019-01233-y>
- Pretzsch, Hans, Forrester, D. I., & Bauhus, J. (2017). *Mixed-species forests: Ecology and management* . *Mixed-Species Forests: Ecology and Management* . Springer Berlin Heidelberg. <https://doi.org/10.1007/978-3-662-54553-9>
- R Core Team. (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from <https://www.r-project.org/>.%0A
- Rawat, M., Arunachalam, K., Arunachalam, A., Alatalo, J., & Pandey, R. (2019). Associations of plant functional diversity with carbon accumulation in a temperate forest ecosystem in the Indian Himalayas. *Ecological Indicators* , 98 (November 2018), 861–868. <https://doi.org/10.1016/j.ecolind.2018.12.005>
- Ricotta, C., & Moretti, M. (2011). CWM and Rao's quadratic diversity: A unified framework for functional ecology. *Oecologia* , 167 (1), 181–188. <https://doi.org/10.1007/s00442-011-1965-5>
- Rosseel, Y. (2012). lavaan: An R package for structural equation modeling. *Journal of Statistical Software* , 48 , 1–36.
- Ruiz-Benito, P., Gomez-Aparicio, L., Paquette, A., Messier, C., Kattge, J., & Zavala, M. a. (2014). Diversity increases carbon storage and tree productivity in Spanish forests. *Global Ecology and Biogeography* , 23 (3),

311–322. <https://doi.org/10.1111/geb.12126>

Ruiz-Jaen, M. C., & Potvin, C. (2010). Tree diversity explains variation in ecosystem function in a neotropical forest in Panama. *Biotropica* , 42 (6), 638–646. <https://doi.org/10.1111/j.1744-7429.2010.00631.x>

Ruiz-Jaen, M. C., & Potvin, C. (2011). Can we predict carbon stocks in tropical ecosystems from tree diversity? Comparing species and functional diversity in a plantation and a natural forest. *New Phytologist* , 189 (4), 978–987. <https://doi.org/10.1111/j.1469-8137.2010.03501.x>

Salako, V. K., Glele Kakai, R. L., Assogbadjo, A. E., Fandohan, B., Houinato, M., & Palm, R. (2013). Efficiency of inventory plot patterns in quantitative analysis of vegetation: A case study of tropical woodland and dense forest in Benin. *Southern Forests* , 75 (3), 137–143. <https://doi.org/10.2989/20702620.2013.816232>

Satdichanh, M., Ma, H., Yan, K., Dossa, G. G. O., Winowiecki, L., Vagen, T. G., ... Harrison, R. D. (2019). Phylogenetic diversity correlated with above-ground biomass production during forest succession: Evidence from tropical forests in Southeast Asia. *Journal of Ecology* , 107 (3), 1419–1432. <https://doi.org/10.1111/1365-2745.13112>

Seidel, D., Ehbrecht, M., Dorji, Y., Jambay, J., Ammer, C., & Annighofer, P. (2019). Identifying architectural characteristics that determine tree structural complexity. *Trees - Structure and Function* , 33 (3), 911–919. <https://doi.org/10.1007/s00468-019-01827-4>

Szwagrzyk, J., & Gazda, A. (2007). Above-ground standing biomass and tree species diversity in natural stands of Central Europe. *Journal of Vegetation Science* , 18 , 555–562. [https://doi.org/10.1658/1100-9233\(2007\)18\[555:ASBATS\]2.0.CO;2](https://doi.org/10.1658/1100-9233(2007)18[555:ASBATS]2.0.CO;2)

Thom, D., & Keeton, W. S. (2019). Stand structure drives disparities in carbon storage in northern hardwood-conifer forests. *Forest Ecology and Management* , 442 (November 2018), 10–20. <https://doi.org/10.1016/j.foreco.2019.03.053>

Tilman, D. (1982). *Resource competition and community structure* . Princeton University Press.

Tilman, D., Lheman, C. L., & Thomson, K. T. (1997). Plant diversity and ecosystem productivity : Theoretical considerations. *Proceedings of the National Academy of Sciences* , 94 , 1857–1861.

Vila, M., Vayreda, J., Comas, L., Ibanez, J. J., Mata, T., & Obon, B. (2007). Species richness and wood production: a positive association in Mediterranean forests. *Ecology Letters* , 10 , 241–250. <https://doi.org/10.1111/j.1461-0248.2007.01016.x>

Villeger, S., Mason, N. W. H., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* , 89 (8), 2290–2301. <https://doi.org/10.1890/07-1206.1>

Waide, R. B., Willig, M. R., Steiner, C. F., Mittelbach, G., Gough, L., Dodson, S. I., ... Parmenter, R. (1999). The relationship between productivity and species richness. *Annual Review of Ecology and Systematics* , 30 , 257–300. <https://doi.org/10.1146/annurev.ecolsys.30.1.257>

Wang, W., Lei, X., Ma, Z., Kneeshaw, D. D., & Peng, C. (2011). Positive relationship between aboveground carbon stocks and structural diversity in spruce-dominated forest stands in New Brunswick, Canada. *Forest Science* , 57 (6), 506–515. <https://doi.org/10.1111/oik.01525>

Wasof, S., Lenoir, J., Hattab, T., Jamoneau, A., Gallet-Moron, E., Ampoorter, E., ... Decocq, G. (2018). Dominance of individual plant species is more important than diversity in explaining plant biomass in the forest understorey. *Journal of Vegetation Science* , 29 (3), 521–531. <https://doi.org/10.1111/jvs.12624>

Wen, Z., Zheng, H., Smith, J. R., Zhao, H., Liu, L., & Ouyang, Z. (2019). Functional diversity overrides community-weighted mean traits in linking land-use intensity to hydrological ecosystem services. *Science of the Total Environment* , 682 , 583–590. <https://doi.org/10.1016/j.scitotenv.2019.05.160>

- Wilsey, B. J., & Potvin, C. (2000). Biodiversity and ecosystem functioning: Importance of species evenness in an old field. *Ecology*, 81 (4), 887–892. [https://doi.org/10.1890/0012-9658\(2000\)081\[0887:BAEFIO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[0887:BAEFIO]2.0.CO;2)
- Wu, X., Wang, X., Tang, Z., Shen, Z., Zheng, C., Xia, X., & Fang, J. (2015). The relationship between species richness and biomass changes from boreal to subtropical forests in China. *Ecography*, 38 (6), 602–613. <https://doi.org/10.1111/ecog.00940>
- Xu, W., Luo, W., Zhang, C., Zhao, X., von Gadow, K., & Zhang, Z. (2019). Biodiversity-ecosystem functioning relationships of overstorey versus understorey trees in an old-growth temperate forest. *Annals of Forest Science*, 76 (3). <https://doi.org/10.1007/s13595-019-0845-8>
- Yachi, S., & Loreau, M. (2007). Does complementary resource use enhance ecosystem functioning? A model of light competition in plant communities. *Ecology Letters*, 10, 54–62. <https://doi.org/10.1111/j.1461-0248.2006.00994.x>
- Yan, Y., Zhang, C., Wang, Y., Zhao, X., & Gadow, K. Von. (2015). Drivers of seedling survival in a temperate forest and their relative importance at three stages of succession. *Ecology and Evolution*, 5 (19), 4287–4299. <https://doi.org/10.1002/ece3.1688>
- Zanne, A. E., Lopez-Gonzalez, G., Coomes, D. A., Ilic, J., Jansen, S., Lewis, S. L., ... Chave, J. (2009). Data from: Towards a worldwide wood economics spectrum. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.234>
- Zhang, Y., & Chen, H. Y. H. (2015). Individual size inequality links forest diversity and above-ground biomass. *Journal of Ecology*, 103, 1245–1252. <https://doi.org/10.1111/1365-2745.12425>

Figure Legend

Fig. 1 Bivariate relationships of plot-level aboveground biomass with taxonomic diversity metrics

Fig. 2 Bivariate relationships of aboveground biomass with multiple-trait functional diversity [Fric: functional richness; FEve: functional evenness; FDiv: functional divergence; FDis: functional dispersion], single-trait functional diversity [FDvar WD: functional divergence of Wood Density; FDvar Hmax: functional divergence of Plant maximum height]; functional dominance [CWM WD: community-weighted mean trait value of Wood Density; CWM Hmax: community-weighted mean trait value of Plant Maximum Height]; and structural diversity [CV DBH: tree diameter variation; CV Ht: tree height variation; CV Nbp: variation of number of primary branches]

Fig. 3 Relative importance of structural diversity, functional dominance, multiple- and single-trait functional diversity metrics used as predictors in the multiple linear model. Statistical fit summaries are presented in Table 1

Fig. 4 Structural Equation Model-fit path summary relating AGB to species richness via functional evenness and structural diversity metrics (Significant paths ($P < 0.05$) are represented with solid arrows and non-significant paths ($P > 0.05$) by dashed arrows. The single-pointed arrows represent causal paths and double-pointed arrows the residual correlations. The values without parentheses are the standardized path coefficients. The values with parentheses are the coefficients of determination. CV DBH: tree diameter variation; CV Nbp: variation of number of primary branches. Detailed statistics are shown in Tables 2-3.

Data Accessibility Statement

Upon acceptance, the data used in this study will be archived in a publicly accessible repository such as Dryad

Conflict of Interest: The authors declare that they have no conflict of interest.

Author Contribution

SM conceived the project and designed methodology; AA and RGK supervised the work; SM analysed the data and led the drafting of the manuscript, with advice and editorial contribution from AA and RGK. All authors contributed to the writing of the manuscript

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