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Context-dependency of tree species diversity, trait composition and stand structural attributes regulate temperate forest multifunctionality

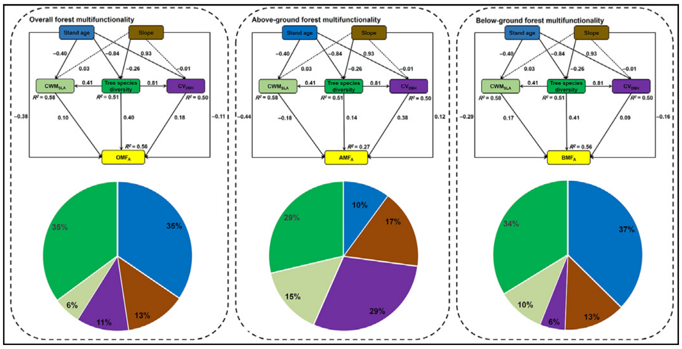
Anvar Sanaei [a], Arshad Ali [b,c], Zuoqiang Yuan [a,*], Shufang Liu [a], Fei Lin [a], Shuai Fang [a], Ji Ye [a], Zhanqing Hao [d], Michel Loreau [e], Edith Bai [f], Xugao Wang [a,*]

[a] *CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110164, China*
[b] *Department of Forest Resources Management, College of Forestry, Nanjing Forestry University, Nanjing 210037, Jiangsu, China*
[c] *Co-Innovation Center for Sustainable Forestry in Southern China, Nanjing Forestry University, Nanjing 210037, Jiangsu, China*
[d] *School of Ecology and Environment, Northernwest Polytechnical University, China*
[e] *Centre for Biodiversity Theory and Modelling, Theoretical and Experimental Ecology Station, CNRS and Paul Sabatier University, 09200 Moulis, France*
[f] *Key Laboratory of Geographical Processes and Ecological Security of Changbai Mountains, Ministry of Education, School of Geographical Sciences, Northeast Normal University, Changchun 130024, China*

HIGHLIGHTS

- Context-dependent forest diversity attributes are key to higher forest multifunctionality.
- Species diversity promoted forest multifunctionality, and most single forest functions.
- Below-ground single and multifunctionality were better explained by species diversity.
- Above-ground single and multifunctionality were better explained by stand structure.
- The niche complementarity and mass ratio effects could explain forest multifunctionality.

GRAPHICAL ABSTRACT



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ABSTRACT

High species diversity is generally thought to be a requirement for sustaining forest multifunctionality. However, the degree to which the relationship between species-, structural-, and trait-diversity of forests and multifunctionality depend on the context (such as stand age or abiotic conditions) is not well studied. Here, we hypothesized that context-dependency of tree species diversity, functional trait composition and stand structural attributes promote temperate forest multifunctionality including above- and below-ground multiple and single functions. To do so, we used repeated forest inventory data, from temperate mixed forests of northeast China, to quantify two above-ground (i.e. coarse woody productivity and wild edible plant biomass), five below-ground (i.e. soil organic carbon, total soil nitrogen, potassium, phosphorus and sulfur) functions, tree species diversity, individual tree size variation (CV$_{DBH}$) and functional trait composition of specific leaf area (CWM$_{SLA}$) as well as stand age and abiotic conditions. We found that tree species diversity increased forest multifunctionality and most of the single functions. Below-ground single and multifunctionality were better explained by tree species diversity. In contrast, above-ground single and multifunctionality were better explained by CV$_{DBH}$. However, CWM$_{SLA}$ was also an additional important driver for maintaining above- and below-ground forest multifunctionality through opposing plant functional strategies. Stand age markedly reduced forest multifunctionality, tree species diversity and CWM$_{SLA}$ but substantially increased CV$_{DBH}$. Below-ground forest

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* Corresponding authors.
E-mail addresses: zqyuan@iae.ac.cn (Z. Yuan), wangxg@iae.ac.cn (X. Wang).

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multifunctionality and tree species diversity decreased while above-ground forest multifunctionality increased on steep slopes. These results highlight that context-dependency of forest diversity attributes might regulate forest multifunctionality but may not have a consistent effect on above-ground and below-ground forest multifunctionality due to the fact that those functions were driven by varied functional strategies of different plant species. We argue that maximizing forest complexity could act as a viable strategy to maximizing forest multifunctionality, while also promoting biodiversity conservation to mitigate climate change effects.

1. Introduction

Ecosystem functions can be defined as the stocks (e.g. above-ground biomass) and the changes in stocks over time (e.g. above-ground biomass productivity) (Hooper et al., 2005), which can be specifically defined as forest functions in forest ecosystems (Ali, 2019; Lohbeck et al., 2016). However, ecosystem multifunctionality can be defined as the ability of an ecosystem to simultaneously provide multiple functions and services (Hector and Bagchi, 2007), which can be specifically called as forest multifunctionality in forest ecosystems (Schuldt et al., 2018; Yuan et al., 2020). It is generally well understood that several single forest functions or forest multifunctionality could change over time and space driven by both above- and below-ground biodiversity (Lohbeck et al., 2016; Schuldt et al., 2018; Yuan et al., 2020). However, forest diversity is rapidly declining due to climate change, deforestation and habitat fragmentation, with potentially large influences on forest multifunctionality (Grimm et al., 2013; Lohbeck et al., 2016). Through this understanding, the signs of global change due to higher levels of carbon dioxide and huge deforestation has seriously attracted the attention of ecologists to study forest multifunctionality in relation to forest diversity attributes in order to better understand the consequences underlying forests and global change (Lohbeck et al., 2016; Schuldt et al., 2018; van der Plas, 2019; Yuan et al., 2020).

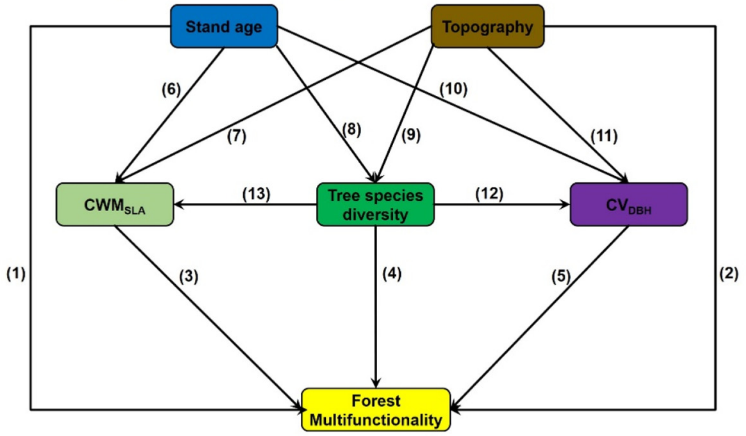
In the recent years, major concerns over detrimental effects of species diversity loss on ecosystem multifunctionality have led to extensive research on how biodiversity–ecosystem functioning relationships are modulated by environmental degradation (Hector and Bagchi, 2007; Mouillot et al., 2011). Through this time, biodiversity–ecosystem functioning research has extended from grasslands (i.e. a short-lived plant system) to forests (a long-lived plant system) (Gamfeldt et al., 2013; Ratcliffe et al., 2017; Schuldt et al., 2018; Yuan et al., 2020). It is increasingly acknowledged that individual forest ecosystem functions (e.g. aboveground biomass, litterfall productivity and soil organic carbon stock) depend on abiotic factors and tend to increase as stands age (Ali et al., 2016; Liu et al., 2018; Ouyang et al., 2019). Forest diversity inherently constitutes multiple attributes such as taxonomic diversity, functional trait diversity and composition, phylogenetic diversity, and stand structural diversity (e.g. individual tree size variation in terms of either tree diameter or height or both), which each can regulate forest functions (Prado-Junior et al., 2016; Yachi and Loreau, 2007). However, the multivariate relationships between different forest diversity attributes and forest functions remain debated probably due to the differential effects of stand age and abiotic factors on forest diversity attributes (Becknell and Powers, 2014; Lohbeck et al., 2015; Ouyang et al., 2019).

Plant species and trait diversity change over succession (Becknell and Powers, 2014; Castro-Izaguirre et al., 2016) because light availability and stand age are often negatively associated (Vickers and Palmer, 2000). Generally, this entails a shift from shade intolerant and resource acquisitive species (e.g. high community-weighted mean of specific leaf area) to shade tolerant and conservative species over successional stages (Becknell and Powers, 2014; Garnier et al., 2004; Subedi et al., 2019). As a result, old-growth stands exhibit lower levels of acquisitive traits, which in turn has implications for forest functioning (Subedi et al., 2019; Yuan et al., 2019). By contrast, the susceptibility of forests to age-related mortality increases, which in turn may lead to higher mortality and finally lower productivity in old-growth forests of *Pseudotsuga menziesii* compared to young-growth forests of *Pseudotsuga menziesii* in Pacific Northwest forests of USA (Acker et al., 2002). Although there is also contrasting evidence that old-growth forests are more productive (Glatthorn et al., 2017), higher tree mortality and litter production in old-growth forests could enhance soil organic matter which in turn may influence soil nutrients and soil carbon storage (Lange et al., 2015; Liu et al., 2018; Richards et al., 2010; Teixeira et al., 2020). Besides stand age, forest diversity attributes and functions depend highly on abiotic factors, particularly topography (Jucker et al., 2018). Topographical factors (e.g., elevation and slope) can regulate forest diversity attributes and functions directly and indirectly via changes in soil physiochemical properties as well as microclimatic conditions (Jucker et al., 2018; Yasuhiro et al., 2004). For example, a recent study reported that topographic slope through decreasing stand structural variability could also influence forest multifunctionality (Yuan et al., 2020).

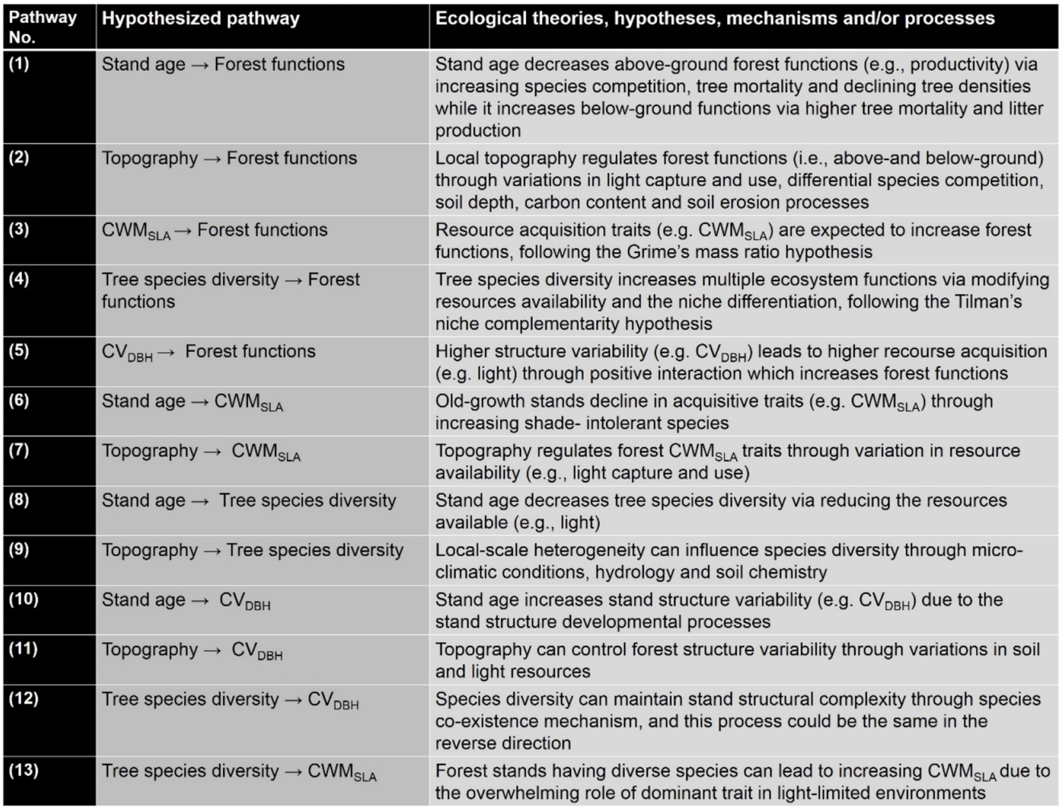
The resource-use complementarity among co-occurring species is often attributed to the positive relationships between forest diversity attributes and forest functions (Castro-Izaguirre et al., 2016; Huang et al., 2018). Species diversity, a key measure of forest diversity, has been recognized as the main biotic driver of forest multifunctionality (Gamfeldt et al., 2013). Specifically, multiple plant species could regulate several single functions, which in turn could contribute largely to forest multifunctionality (Allan et al., 2015; Yuan et al., 2020). However, due to the existing trade-off among several functions (Allan et al., 2015), all functions cannot reach maximum levels simultaneously (Cardinale et al., 2012). Therefore, higher species diversity has been proposed as a key driver of ecosystem multifunctionality (Gamfeldt et al., 2013; Hector and Bagchi, 2007; Isbell et al., 2011; Yan et al., 2020), as a result of the niche complementarity effect (Loreau et al., 2001; Tilman et al., 2001). In addition, plant species, through utilization of different or even identical resources across time and space, could coexist and subsequently ameliorate the environment for other species and thereby enhance ecosystem functions (Hooper et al., 2005). The stand structural diversity hypothesis posits that stand structural variation increases aboveground biomass directly and indirectly via species diversity over time (Ali et al., 2016), and recent studies also showed that stand structural diversity regulates above-ground carbon and also soil functions (Teixeira et al., 2020). This may be explained by the way stand structural variation increases the capture and use of light or other resources, which in turn could affect forest functioning through niche complementarity via plant-plant interaction, asymmetric competition for light, and absolute growth rate (Forrester, 2019; Yachi and Loreau, 2007). In fact, stand structural diversity could affect overall forest productivity (LaRue et al., 2019), and particularly the diversity and productivity of understory stratum via light capture and use (Ali et al., 2016), meanwhile influenced by plant diversity (Li et al., 2019), and hence, it reflects the habitat quality and forest functioning (LaRue et al., 2019). Apart from plant species and structural diversity, functional trait composition could also regulate ecosystem functions under the assumptions of the mass ratio hypothesis (Mouillot et al., 2011; Yuan et al., 2020), i.e., the traits of most dominant plant species determine ecosystem functions (Grime, 1998). However, these three sources of forest heterogeneity and complexity are rarely examined simultaneously in the context of forest multifunctionality.

This study aims at exploring the main driving factors and ecological mechanisms underlying the relationships between three dimensions of forest heterogeneity (tree species diversity, trait composition, and stand structural diversity) and forest multifunctionality including overall, above-ground and below-ground multifunctionality, as well as several important individual functions. To do this, we use seven forest functions which pertain to above- and below-ground functions and processes defined as overall forest multifunctionality because they are crucial drivers of forest functioning, biological productivity, as well as soil nutrient cycling or soil fertility (Fry et al., 2018; Isbell et al., 2011; Maestre et al., 2012). We hypothesize that context-dependency of tree species diversity, functional trait composition and stand structural attributes promote temperate forest multifunctionality including above- and below-ground multiple and single functions in a temperate mixed forest of Northeast China. We ask the following two research questions to address the proposed hypothesis based on the multiple paths in the conceptual model (see Fig. 1 for explanation). First, how do stand age and topography affect tree species diversity, functional trait composition, stand structural attributes and forest functioning. Second, what is the main influencing driver – tree species diversity, functional trait composition or stand structural diversity– of overall forest multifunctionality as well as above-ground and below-ground components. Our hypothesis leads to the following three main expectations: 1) context-dependency of individual tree size variation increases above-ground forest multifunctionality better than tree species diversity and trait composition, probably due to the fact that aboveground functions (e.g.

a) Conceptual model for hypothesized causal paths



b) Schematic illustration of ecological hypotheses/theories/mechanisms/paths



Pathway No.	Hypothesized pathway	Ecological theories, hypotheses, mechanisms and/or processes
(1)	Stand age → Forest functions	Stand age decreases above-ground forest functions (e.g., productivity) via increasing species competition, tree mortality and declining tree densities while it increases below-ground functions via higher tree mortality and litter production
(2)	Topography → Forest functions	Local topography regulates forest functions (i.e., above-and below-ground) through variations in light capture and use, differential species competition, soil depth, carbon content and soil erosion processes
(3)	CWM$_{SLA}$ → Forest functions	Resource acquisition traits (e.g. CWM$_{SLA}$) are expected to increase forest functions, following the Grime's mass ratio hypothesis
(4)	Tree species diversity → Forest functions	Tree species diversity increases multiple ecosystem functions via modifying resources availability and the niche differentiation, following the Tilman's niche complementarity hypothesis
(5)	CV$_{DBH}$ → Forest functions	Higher structure variability (e.g. CV$_{DBH}$) leads to higher recourse acquisition (e.g. light) through positive interaction which increases forest functions
(6)	Stand age → CWM$_{SLA}$	Old-growth stands decline in acquisitive traits (e.g. CWM$_{SLA}$) through increasing shade- intolerant species
(7)	Topography → CWM$_{SLA}$	Topography regulates forest CWM$_{SLA}$ traits through variation in resource availability (e.g., light capture and use)
(8)	Stand age → Tree species diversity	Stand age decreases tree species diversity via reducing the resources available (e.g., light)
(9)	Topography → Tree species diversity	Local-scale heterogeneity can influence species diversity through micro-climatic conditions, hydrology and soil chemistry
(10)	Stand age → CV$_{DBH}$	Stand age increases stand structure variability (e.g. CV$_{DBH}$) due to the stand structure developmental processes
(11)	Topography → CV$_{DBH}$	Topography can control forest structure variability through variations in soil and light resources
(12)	Tree species diversity → CV$_{DBH}$	Species diversity can maintain stand structural complexity through species co-existence mechanism, and this process could be the same in the reverse direction
(13)	Tree species diversity → CWM$_{SLA}$	Forest stands having diverse species can lead to increasing CWM$_{SLA}$ due to the overwhelming role of dominant trait in light-limited environments

Fig. 1. A conceptual model (a) and schematic illustration of ecological hypotheses/theories/mechanisms (b) to test the effects of tree species diversity, functional trait composition of specific leaf area (CWM$_{SLA}$), individual tree size variation (CV$_{DBH}$), topography and stand age on overall forest multifunctionality (combination of above-and below-ground functions), multi-threshold approach (i.e. 30%, 60%, and 90%), above-ground and below-ground multifunctionality, and each individual function. The numbering of each hypothesized path is explained in (b).

forest productivity and herb diversity) might be directly related to light capture and use through stand structural complexity (Ali et al., 2016; Yachi and Loreau, 2007); 2) context-dependency of tree species diversity increases below-ground forest multifunctionality better than functional trait composition and stand structural complexity, probably due to the fact that mixed species might contribute quality of litters to the soil which in turn regulate soil functions such as nutrients and carbon cycling (Lange et al., 2015; Richards et al., 2010); and 3) while we expect the stronger effect of tree species diversity on overall forest multifunctionality, context-dependency of functional trait composition and stand structural attributes may also matter.

2. Materials and methods

2.1. Study forests

Our study forests are located on Changbai Mountain in Northeast China (41°43′–42°26′ N to 127°42′–128°17′ E; Fig. S1). The elevation of the study area varies between 791 and 1435 m above sea level with a slope ranging from 0.15° to 22°. Mean annual rainfall and temperature are 700 mm and 2.8 °C, respectively. According to the FAO soil classification, the soil type of the area is classified as dark-brown soil (Yang, 1985). The studied area includes four types of mixed forests such as broad-leaved Korean pine mixed forest (BKF), larch forest (LF), poplar–birch forest (PBF) and spruce–fir forest (SFF). These forests harbour a rich diversity of plant and animal species (Shao et al., 1994) and hence are an ideal ecosystem for biodiversity – ecosystem functioning studies. The PBF forest resulted from natural succession following the burning or clear-cutting of the BKF forest, and represents the early successional stage of the BKF. The other two forest types (LF and SFF) are likewise the result of disturbance, though as a result of an eruption of Changbai Mountain's active volcano.

We studied four large and permanent forest dynamics plots (size varies from 4 to 4.8 ha) from the Chinese forest biodiversity monitoring network (http://www.cfbiodiv.org) (Table S1). We divided the studied plots according to the standard field protocol (Condit, 1998) into 419 subplots (20 m × 20 m) (Table S1). For woody species (diameter at breast height [DBH] ≥ 1), the data covered 52,569 individual plants in total belonging to 67 species, 38 genera and 21 families. For wild edible plant species (edible for human), the data covered 5512 individual plants in total which belonging to 12 species, 8 genera and 8 families.

2.2. Quantification of forest single functions and multifunctionality

We measured seven individual forest ecosystem functions which pertain to above- and below-ground functions and processes, including: (1) coarse woody productivity (CWP), (2) wild edible plant biomass, (3) soil organic carbon (SOC), (4) total soil nitrogen (TSN), (5) total soil phosphorus (TSP), (6) total soil potassium (TSK) and (7) total soil sulfur (TSS) (Table S2). We selected these variables (or functions) because they are highly associated (directly or indirectly) with forest functioning, biological productivity, as well as soil nutrient cycling or soil fertility, and hence altogether could act as a proxy of forest functioning because the capability of ecosystems to support services is highly dependent on these single functions (Fry et al., 2018; Isbell et al., 2011; Maestre et al., 2012; Yan et al., 2020).

The total aboveground biomass (AGB) of each individual tree (DBH ≥ 1 cm) was calculated using the local species-specific allometric equations through their corresponding DBH (Table S3) (Chen and Zhu, 1989; Li et al., 2010; Wang, 2006). We calculated the biomass growth (Mg ha^{-1} yr^{-1}) of each subplot by calculating the difference in biomass between two inventories (Table S1). Aboveground biomass recruitment (Mg ha^{-1} yr^{-1}) was calculated as the biomass by individuals recruited into DBH ≥ 1 cm between the two forest inventories. Finally, coarse woody productivity (Mg ha^{-1} yr^{-1}) was quantified by summing biomass growth and recruitment per subplot of recent two inventory intervals (Yuan et al., 2019). The names of wild edible plant species were assigned following Flora Reipublicae Popularis Sinicae (Hong and Blackmore, 2015), and then the mean AGB stock (Mg ha^{-1}) of those wild edible plants were calculated using multispecies allometric equation based on crown area (Li et al., 2010). More detailed information about forest study sites inventories could be found in Table S1.

For the quantification of soil functions, we collected a sample (at 0–10 cm depth) from the center of each 30 m × 30 m grid and also two additional samples were randomly picked up at 2, 5, or 15 m intervals. In total, we collected 192, 210, 192, and 210 soil samples for LF, KBF, SFF and PBF sites, respectively. After that, using spatial interpolation based on ordinary kriging we estimated the soil variables for each 20 m × 20 m subplot. Prior to the analysis of the soil samples, roots and litter were picked out and samples were sieved through a 2 mm mesh. The acidified dichromate ($K_2Cr_2O_7$–H_2SO_4) oxidation method was used to measure SOC (Lu, 1999), Kjeldahl and molybdate colorimetry methods were used to analyze TSN and TSP contents, respectively. The ammonium acetate method and a spectrometer were used for TSK and TSS was extracted via oxidation with Mg $(NO_3)_2$.

For the quantification of forest multifunctionality based on the seven above-mentioned functions, we used multiple approaches: overall averaging and multi-threshold (Byrnes et al., 2014), above-ground and below-ground forest multifunctionality, as well as individual forest functions. Prior to the averaging approach, standardized *Z*-scores (between 0 and 1) were calculated for all of seven selected functions and then seven standardized Z-scores variables were averaged to obtain averaged forest multifunctionality index (Maestre et al., 2012). We used a similar approach for the calculation of above-ground and below-ground forest multifunctionality indices based on two above-ground and five below-ground functions, respectively. For incorporating tradeoffs and also synergies between different used functions and also to overcome some limitations in averaged approach we conducted multi-threshold approach (i.e. 30%, 60%, and 90% of maximum observed functioning) (Byrnes et al., 2014). As suggested, the number of forest functions that go beyond a threshold was used for calculating threshold based forest multifunctionality (Byrnes et al., 2014). For simplicity, 30, 60 and 90 percentage of the maximum observed value of each function were calculated as the average of each function in each threshold level.

2.3. Quantification of stand age and forest diversity attributes

To examine the direct and indirect effects of stand age on forest diversity attributes and multifunctionality, we determined the stand age of each plot by coring five individuals for dominant or codominant trees per species which were located either within the plot or in the vicinity of the plot (Table S1). We then calculated stand age using the mean ring count from tree samples of species with the oldest age, used as a common approach for the estimation of stand age, hence, the four stands aged from 75 to 275 years (Table S1) (Wang et al., 1980).

We quantified three forest diversity attributes: tree species diversity, individual tree size variation, and functional trait composition. Species richness was determined by counting the number of species within each subplot, and after that Shannon's species diversity was calculated using the species richness and their relative basal area values using the *vegan* package in the statistical platform R (Oksanen et al., 2018). We followed a standard protocol for the calculation of specific leaf area (SLA) using field and lab data (Cornelissen et al., 2003). For quantifying SLA, we collected more than 10 undamaged leaves per species. The leaf area (LA) was scanned using a portable scanning/planimeter, and then the ratio between the one-sided area of a leaf and its dry mass calculated as SLA (Yuan et al., 2016). Further, we used the proportional basal area for a given species for weighting values to compute community weighted mean (CWM) of SLA in each subplot (Garnier et al., 2004) using the *FD* package in R (Laliberte and Legendre, 2010). In this study, we used CWM_{SLA} because several previous studies have suggested that CWM_{SLA} is a strong indicator of below-ground (e.g. soil phosphate, nitrate, respiration and organic matter) (Fry et al., 2018; Teixeira et al., 2020) and above-ground (e.g. productivity) forest functioning (Yuan et al., 2019). The coefficient of variation (CV in %) for individual trees DBHs within each subplot was used to quantify the stand structural variation (Ali et al., 2016; Forrester, 2019). We used individual tree size variation, as a proxy of stand structural diversity, because it reflects the habitat quality and forest functioning (LaRue et al., 2019) as light capture and use of the component species are highly dependent on stand tree size variation (Ali, 2019; Yachi and Loreau, 2007).

2.4. Statistical analyses

Structural equation modeling (SEM), as a powerful multi-variable statistical technique used widely in ecology, was used to test the covariances between hypothesized paths in the conceptual model (Fig. 1a) because it allows us to integrate multivariate relationships in a single hypothesized network (Grace et al., 2010). To account for spatial autocorrelation in averaged forest multifunctionality with predictors (Fig. 1) we performed generalized least-square (GLS) analysis with and without spatial autocorrelation using the *nlme* package in R (Pinheiro and Bates, 2016). Then we compared the Akaike Information Criterion (AIC) values between spatial and nonspatial GLS models. We did not find any spatial autocorrelation as AIC value was lower in nonspatial models (Table S4). The chi-square test statistic and associated *P*-value (i.e. $P > 0.05$ indicates accepted SEM) were used to evaluate the model fit to the data (Table S5) (Malaeb et al., 2000). We calculated the direct, indirect and total effects of predictors on response variable (s) via mediator(s). We assessed the relative contribution of stand age, topographic slope, tree species diversity, CV_{DBH} and CWM_{SLA} on forest multifunctionality using the ratio of the effect of a given predictor over the summation of effects of all predictors, and represented it as a percentage. In addition, in order to complement the results from SEMs, we conducted principal component analysis (PCA) to assess how predictor variables (forest diversity attributes and topographic slope) and also response variables (i.e., overall, above-ground and below-ground forest multifunctionality) were correlated with shifts in the forest stand age. The PCA was performed using *factoextra* package (Kassambara and Mundt, 2020).

We conducted pairwise Pearson correlations to assess how predictor variables and response variables were correlated with each other (Fig. S2). In order to complement the results from SEMs, we showed the bivariate relationships, using simple linear regression, based on the hypothesized paths in the conceptual model (Fig. S3). In order to avoid the collinearity issues and to get comparable standardized direct, indirect and total effects (i.e. varying between 0 and 1 in either positive or negative direction), all variables were natural-log transformed and then standardized (Zuur et al., 2009). The forest multifunctionality and SEM analysis were calculated using *multifunc* (Byrnes, 2014) and *lavaan* (Rosseel, 2012) packages in R, respectively. All analyses were implemented using R version 3.6.1 (R Development Core Team, 2019).

3. Results

The tested SEMs showed that stand age promoted CV_{DBH} but decreased tree species diversity and CWM_{SLA}. Moreover, only tree species diversity decreased with increasing topographic slope (Figs. 2 and 3). Tree species diversity directly promoted CV_{DBH} and CWM_{SLA} (Figs. 2 and 3). All SEMs indicated that stand age had significant negative effects on overall, above- and below-ground forest multifunctionality (Fig. 2). In addition, overall and below-ground forest multifunctionality were moderately decreased but above-ground forest multifunctionality was increased with topographic slope (Fig. 2). Below-ground forest multifunctionality was negatively driven by topographic slope, followed by a negligible positive effect of stand age (Fig. 2c). With respect to above-ground single functions, CWP was strongly negatively driven by stand age (Fig. 3a) whereas wild edible plant biomass was positively driven by topographic slope (Fig. 3b). Both stand age and topographic slope had significantly influenced below-ground single functions, even though the strength of the effect of stand age was greater than topographic slope (Fig. 3c-j). More specifically, stand age possessed a significantly direct positive effect on most of the individual below-ground functions (Fig. 3), whereas topographic slope had a negative effect on individual below-ground functions (Fig. 3).

Forest diversity attributes, including tree species diversity, CWM_{SLA} and CV_{DBH} significantly promoted overall forest multifunctionality (Fig. 2a). Above-ground forest multifunctionality was strongly promoted by CV_{DBH}, followed by a negative effect of CWM_{SLA} and a positive effect of tree species diversity (Fig. 2b), whereas below-ground forest multifunctionality was promoted by tree species diversity, CWM_{SLA} and CV_{DBH} (Fig. 2c). In addition, additional SEMs (Fig. S4) showed that 30% and 60% threshold-level forest multifunctionality also increased strongly with increasing species diversity, followed by positive direct effects of CWM_{SLA} and CV_{DBH} (Fig. S4a and b). In a partial contrast, 90% threshold-level forest multifunctionality increased strongly with increasing CV_{DBH} but declined directly with increasing CWM_{SLA}, whereas species diversity possessed nonsignificant direct effect (Fig. S4c). With respect to the individual above-ground functions, CWM_{SLA} declined but CV_{DBH} promoted CWP, whereas tree species diversity had negligible effect on CWP (Fig. 3a). As such, CV_{DBH} increased wild edible plant biomass, followed by a significant positive effect of tree species diversity but a negligible positive effect of CWM_{SLA} (Fig. 3b). Individual below-ground functions were positively driven by tree species diversity, followed by positive effect of CWM_{SLA} and negligible to positive direct effects of CV_{DBH} (Fig. 3c-j, Tables S7-S10).

Stand age had an indirect positive effect on overall forest multifunctionality via CV_{DBH}, but indirect negative effects via tree species diversity and CWM_{SLA} (Fig. 2d, e and f, Table S6). Tree species diversity had negatively mediated the responses of CV_{DBH} and CWM_{SLA} to stand age (Table S6). Moreover, there were negative indirect effects of topographic slope on overall forest multifunctionality, CWM_{SLA} and CV_{DBH} via tree species diversity (Fig. 2d, e and f, Table S6). In addition, tree species diversity contributed considerably to the overall forest multifunctionality relative to CV_{DBH} and CWM_{SLA} (Fig. 2g). However, CV_{DBH} contributed substantially to above-ground multifunctionality (Fig. 2h). Tree species diversity was equally important because of the indirect effects via CV_{DBH} and CWM_{SLA} (Fig. 2h), and as such tree species diversity also markedly contributed to below-ground multifunctionality (Fig. 2i).

In consistent with SEMs, forest diversity attributes and multifunctionality showed somehow clear trend across old-growth (245, 255 and 275 years) and young (75 years) forests along the first axis of PCA (Fig. 4). More specifically, the first axis of PCA showed that high tree species diversity, CWM_{SLA}, and forest multifunctionality indices had occupied the positive loadings, and hence indicated these variables decreased with increasing stand age (Fig. 4). However, high CV_{DBH} was found at old-growth forest along first axis of PCA, and hence indicated that stand structural complexity increased with increasing stand age. We also found that overall forest multifunctionality was related with tree species diversity, CWM_{SLA} and CV_{DBH} (Fig. 4a). Interestingly, above-ground forest multifunctionality was closely related with CV_{DBH} whereas below-ground forest multifunctionality was closely related to species diversity and CWM_{SLA} (Fig. 4b and c).

4. Discussion

In this study, we found that tree species diversity promoted forest functioning, including overall, above-and below-ground forest multifunctionality, and most individual forest functions (including wild edible plant biomass, soil organic carbon, total soil nitrogen, phosphorus and sulfur) probably due to the resource-use complementarity and reduced competition effects (Loreau and Hector, 2001; Tilman et al., 2001). Our results supported previous studies showing the

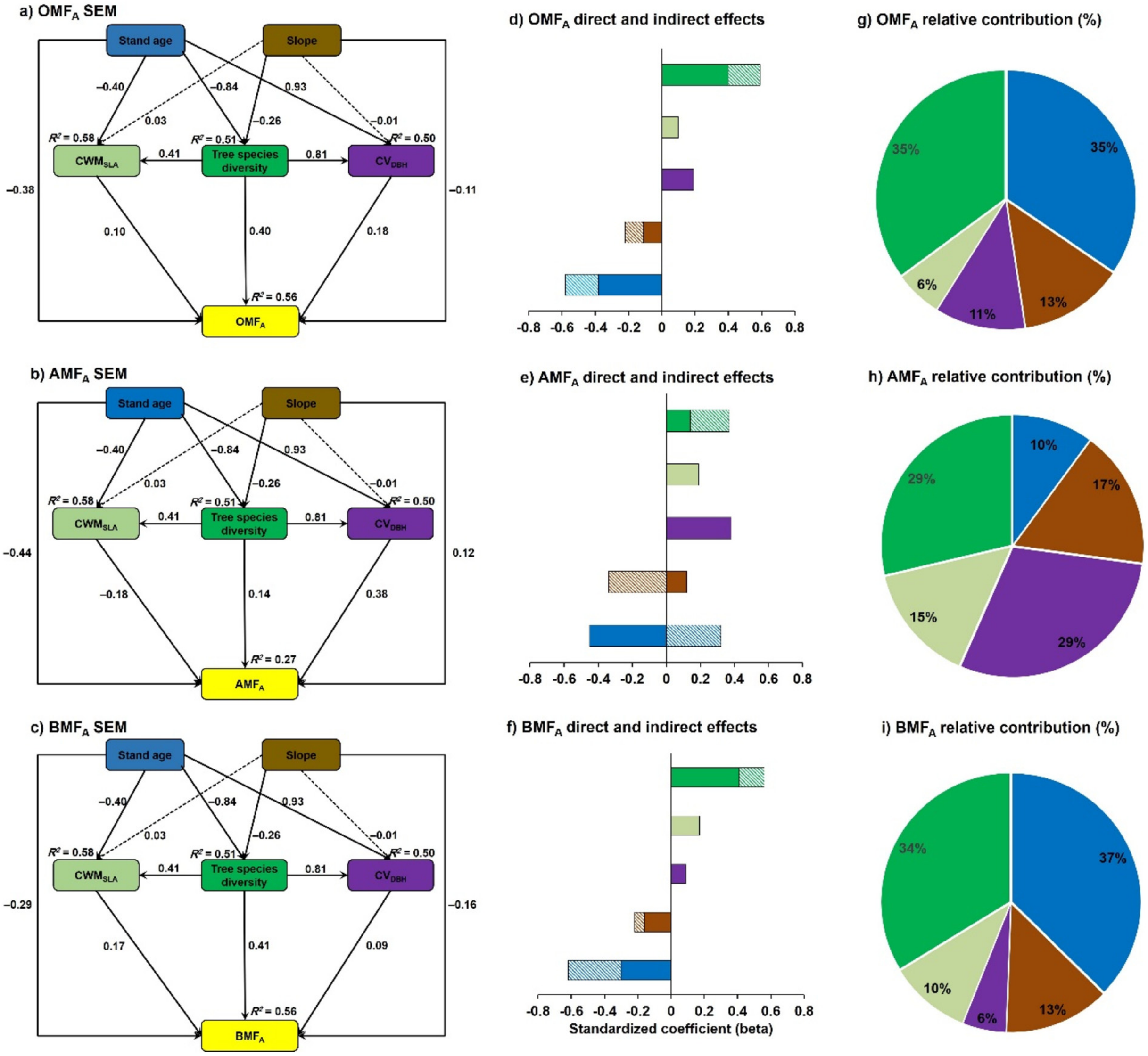


Fig. 2. Structural equation models (SEMs) linking tree species diversity, individual tree size variation (CV_{DBH}), functional trait composition of specific leaf area (CWM_{SLA}), slope and stand age for explaining forest multifunctionality (MF_A) at overall forest multifunctionality (OMF_A) and above-ground (AMF_A) and below-ground (BMF_A) forest multifunctionality. Solid arrows represent significant paths ($P < 0.05$) while dashed arrows represent nonsignificant paths ($P > 0.05$). Bar charts show direct and indirect effects (e-h), and pie-charts show relative contributions (i-l). The solid colour bars represent direct effects whereas striped bars represent indirect effects. Variables names are consistent with the colors provided in SEMs. Model-fit statistics for each SEM are given in Table S5.

positive contribution of plant species diversity to multifunctionality in forests (Gamfeldt et al., 2013; Schuldt et al., 2018) and grasslands (Hector and Bagchi, 2007; Isbell et al., 2011; Yan et al., 2020). However, the main novelty of our study is that tree species diversity promoted below-ground forest multifunctionality better than CV_{DBH} due to the varied functional trait composition of different plant species that contribute to soil nutrients via litterfall inputs in more diverse stands through top-down processes (Richards et al., 2010). Above-ground forest multifunctionality was mostly explained by CV_{DBH} probably due to the vertical stratification and crown plasticity which could diminish competitive interferences (Jucker et al., 2015). CWM_{SLA} declined above-ground forest multifunctionality but promoted below-ground forest multifunctionality, indicating the simultaneous role of conservative and acquisitive plant species in natural forests (Prado-Junior et al., 2016; Yuan et al., 2019) which is line with the mass ratio hypothesis (Grime, 1998). In sum, the significant effects of tree species diversity, CV_{DBH} and CWM_{SLA} on forest multifunctionality provide support to both the niche complementarity and mass ratio effects in the studied forest ecosystem, but tree species diversity exerted the strongest influence, and hence, providing strong support to the niche complementarity effect (Loreau et al., 2001; Tilman et al., 2001).

The strong contribution of tree species diversity to forest below-ground multifunctionality may be related to the greater litter production in mixed-species stands which could increase soil nutrients and as a result regulate soil functions (Lange et al., 2015; Richards et al., 2010). However, we also found the positive relationship between tree species diversity and CWM_{SLA}, indicating the dominant role of the acquisitive and light-demanding species, i.e., have higher efficiency for light acquisition (Yuan et al., 2019). So, the positive effect of CWM_{SLA} on below-ground forest multifunctionality might result from the higher litter productivity of acquisitive species (i.e. grow-fast and die-quickly), which could also contribute to soil nutrients (Kazakou et al., 2006; Reich, 2014). Moreover, the negative relationship between CWM_{SLA} and above-ground forest multifunctionality might be due to the higher metabolic rates of acquisitive species (Allan et al., 2015; Fry et al., 2018) which could lead to a grow-fast and die-quickly strategy (Reich, 2014) and hence lower forest productivity (Yuan et al., 2020). For example, the lack of a positive effect of tree species diversity but the presence of

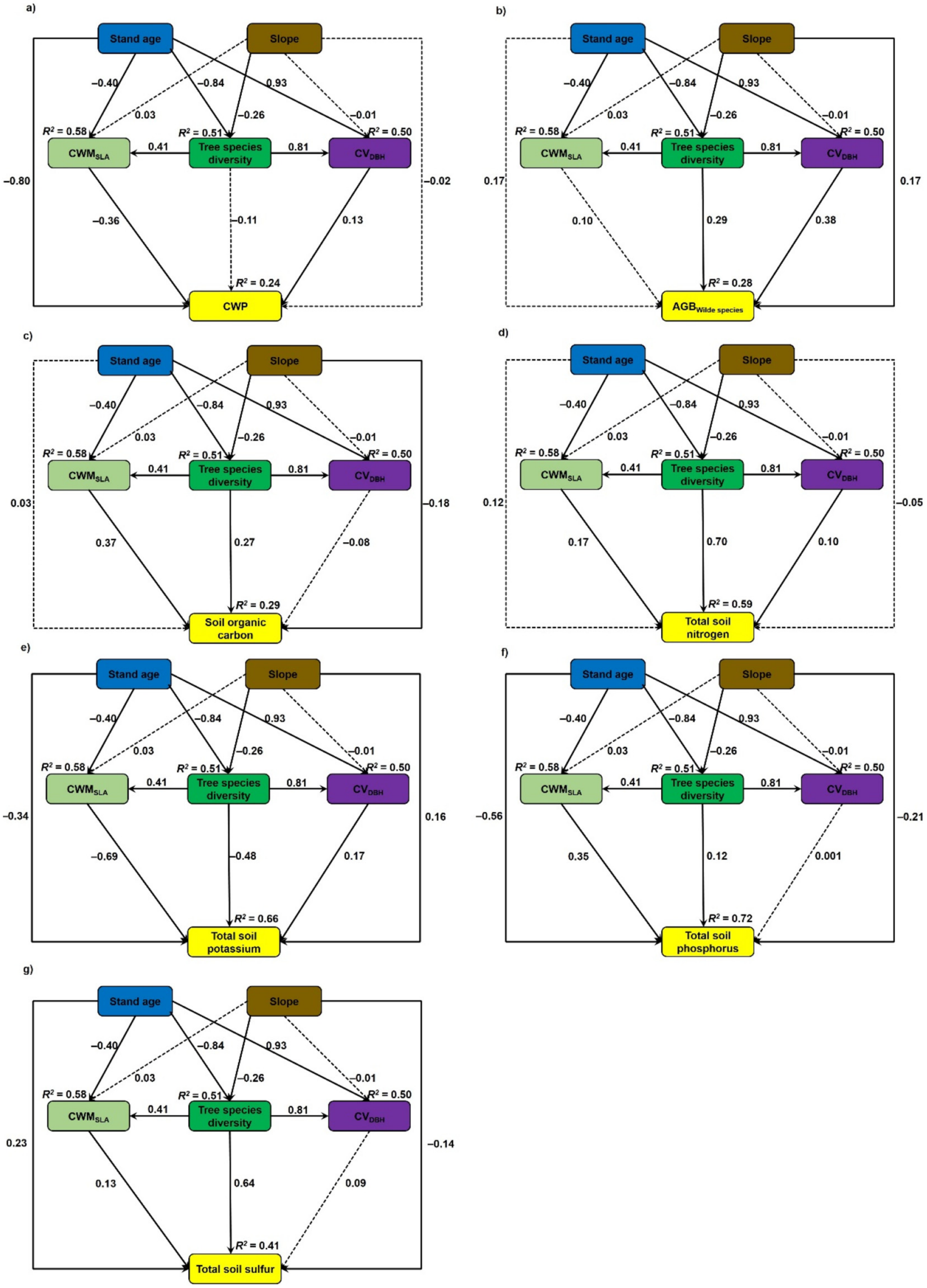


Fig. 3. Structural equation models linking tree species diversity, individual tree size variation (CV_{DBH}), functional trait composition of specific leaf area (CWM_{SLA}), slope and stand age for explaining each above-ground (a and b) and below-ground (c-g) single forest function. Solid arrows represent significant paths ($P < 0.05$) while dashed arrows represent nonsignificant paths ($P > 0.05$). Model-fit statistics for each SEM are given in Table S5.

a negative effect of CWM_{SLA} on CWP supports the conclusion that acquisitive species' functional strategy could decrease forest productivity (Jacob et al., 2010; Yuan et al., 2019). Moreover, the number of species that contribute to overall forest multifunctionality is higher than for individual functions (Gamfeldt et al., 2013; Hector and Bagchi, 2007; Isbell et al., 2011), and hence, higher tree species diversity is needed to maintain or maximize higher overall forest multifunctionality (Hector and Bagchi, 2007; Zavaleta et al., 2010).

Besides overall forest multifunctionality, the role of tree species diversity in maximizing above-ground functions (e.g., forest above-ground biomass, carbon storage and productivity) has been well recognized (Ali et al., 2016; Gamfeldt et al., 2013; Liu et al., 2018). For instance, different species having different niches are able to efficiently use available resources or facilitate their coexistence, and thus enhance forest functions (Loreau et al., 2001; Tilman et al., 2001).

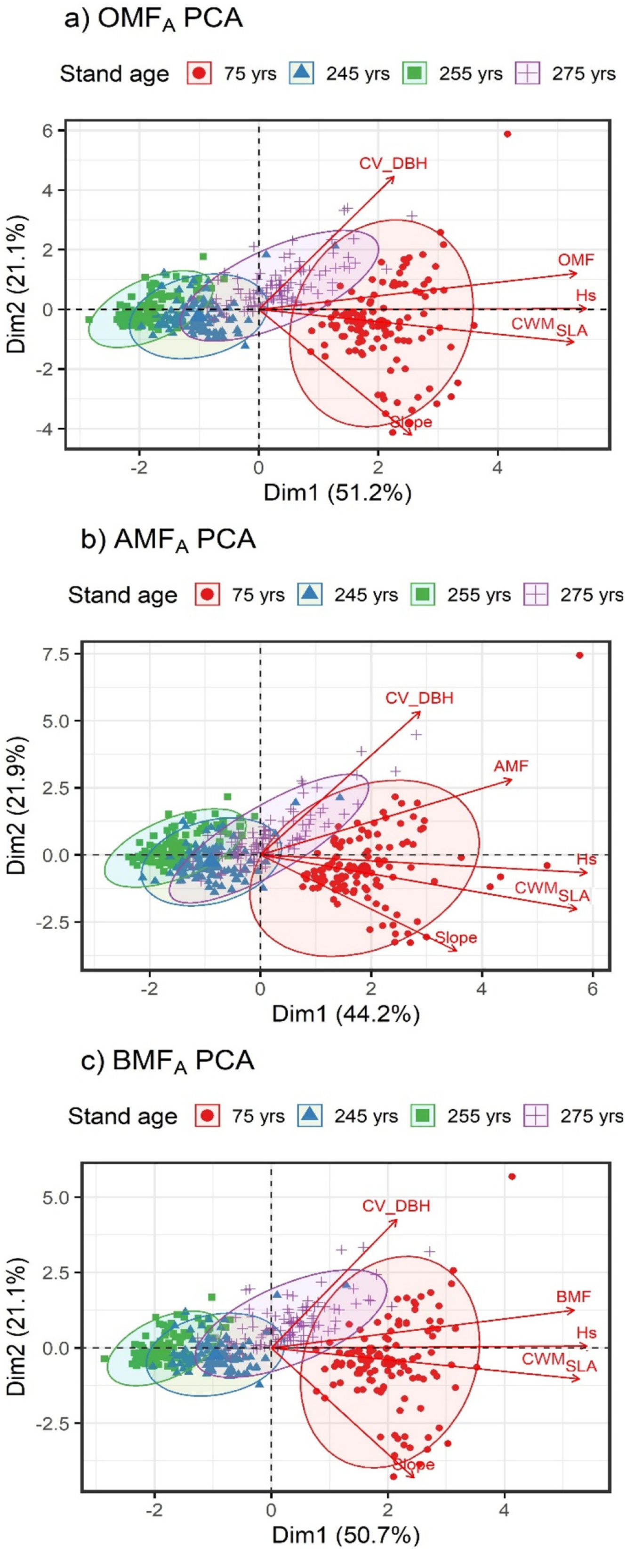


Fig. 4. Principle component analysis (PCA) of the relationships of tree species diversity, functional trait composition, individual tree size variation and topographic slope across four stand ages (75, 245, 255 and 275 years) with each of a) overall forest multifunctionality (OMF$_A$), b) above-ground forest multifunctionality (AMF$_A$) and c) below-ground forest multifunctionality (BMF$_A$). Abbreviations are: Hs, tree species diversity; CV_DBH, individual tree size variation and CWM$_{SLA}$, functional trait composition of specific leaf area.

Our results showed that CV_{DBH} increased forest multifunctionality in all models even though it only substantially increased above-ground functions. This finding is in agreement with previous studies that have found that CV_{DBH} is an important factor for positive diversity-forest functioning relationships (Ali et al., 2016; Forrester, 2019). This positive effect may reflect a greater ability of individuals to capture light and other resources in more diverse stands, which can coexist through niche differentiation, confirming the complementarity effects thereby increasing available niches and reducing the degree of asymmetric competition (Yachi and Loreau, 2007). Moreover, the higher contribution of CV_{DBH} to above-ground forest multifunctionality and also to individual above-ground functions might be due to the fact that above-ground functions are directly related to light capture and use through stand structural complexity leading to maximum crown occupancy (in both vertical and horizontal strata), unlike below-ground functions (Ali et al., 2016; Jucker et al., 2015; Yachi and Loreau, 2007).

Through PCA analysis, we found that young forest (PBF plot with 75 years), which contained high tree species diversity and CWM_{SLA}, was more productive in terms of forest multifunctionality than old-growth forests (LF, SFF and BKF plots with 245, 255 and 275 years, respectively) (Fig. 4). Numerus mechanisms might account for the negative influence of stand age on forest multifunctionality, such as increasing tree mortality, higher evaporation and greater respiration, and decreasing light and stand density in old-growth forests (Acker et al., 2002; Michaletz et al., 2014). By contrast, the higher mortality and also litterfall production in old-growth forests (Acker et al., 2002; Liu et al., 2018) in turn could enhance soil nutrients and also soil carbon storage (Liu et al., 2018) through plant dead materials. Moreover, the greater CWM_{SLA} in young leaves (forest recovered from clear-cutting) compared to old-growth forests might be attributed to a shift from shade-intolerant and resource acquisitive species (e.g. CWM_{SLA}) to shade-tolerant and conservative species (Becknell and Powers, 2014; Subedi et al., 2019), which in turn could decrease forest above-ground functions but may also increase below-ground functions through high turnover rates (Fry et al., 2018; Teixeira et al., 2020). In addition, higher CV_{DBH} in old-growth forests compared to young forest could be driven not only by the reduced competition and the capability of individuals for capturing light over time (Ali et al., 2016) but also by increasing complementarity effects over forest succession (Li et al., 2019). Above-ground and below-ground forest multifunctionality and associated individual functions were differently influenced by topographic slope, as such, above-ground functions increased while below-ground decreased. Topographic slopes differ in capturing light, temperature and moisture, for example, steep slopes have lower temperature and soil water content while possessing higher solar radiation (Galicia et al., 1999) and having shallower soils. Hence, these factors may result in declining below-ground functions and tree species diversity (Yuan et al., 2020).

In experimental systems (especially experimental grasslands), only species richness is typically manipulated, which only provides evidence to the importance of species richness in maintaining ecosystem multifunctionality through underlying ecological mechanisms (Hector and Bagchi, 2007; Isbell et al., 2011; Zavaleta et al., 2010). However, in natural complex ecosystems particularly in forests, it is important to evaluate the relative importance of species richness, functional traits and stand structural variation to ecosystem multifunctionality in order to improve forest management and biodiversity conservation (Lohbeck et al., 2016). Our results show that diversity in species, functional traits and structure are key to maintain higher forest multifunctionality. Although we only used two above-ground functions that quantify carbon stock or productivity in general, they are of particular importance for climate change mitigation (Liu et al., 2018; Lohbeck et al., 2016). Nevertheless, the above-ground functions we studied represent a small portion of functions compared with the numerous below-ground functions which might be correlated. Such biogeochemical functions represent ecosystem functions which have been globally recognized for maintaining ecosystem services and biodiversity conservation (Gamfeldt et al., 2013; Isbell et al., 2011; Lohbeck et al., 2016; Yan et al., 2020).

5. Conclusions

In this study, we provide some lines of evidence that context-dependency of forest diversity attributes are key to maintain higher overall forest multifunctionality. However, there were not consistent effects on above-ground and below-ground forest functioning. In brief, below-ground forest multifunctionality was more responsive to tree species diversity, whereas above-ground forest multifunctionality was more responsive to stand structural diversity. Therefore, testing the effects of multiple attributes of forest diversity on each of above-ground and below-ground forest multifunctionality may provide greater insights as compared to considering overall forest multifunctionality. We argue that complexity and heterogeneity in forests (variation in stand structure, species, and trait composition) are important if we are to optimize forest multifunctionality while promoting biodiversity conservation to mitigate climate change effects.

Data availability statement

Dataset and associated R codes used in the main results are available upon reasonable request to the corresponding author.

CRediT authorship contribution statement

Anvar Sanaei: Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing. **Arshad Ali:** Conceptualization, Methodology, Writing - review & editing. **Zuoqiang Yuan:** Conceptualization, Investigation, Methodology, Writing - review & editing. **Shufang Liu:** Investigation. **Fei Lin:** Investigation. **Shuai Fang:** Investigation. **Ji Ye:** Investigation. **Zhanqing Hao:** Conceptualization, Investigation, Supervision. **Michel Loreau:** Writing - review & editing. **Edith Bai:** Writing - review & editing. **Xugao Wang:** Conceptualization, Investigation, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.143724.

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