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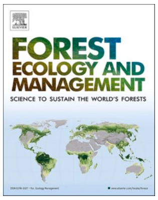

Tree species diversity enhances plant-soil interactions in a temperate forest in northeast China

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ABSTRACT

The plant-soil interactions may drive the diversity and functioning of forests, but we do not fully understand how interrelationships between plant and soil compartments are underlined by multiple ecological mechanisms. Here, we hypothesize that positive plant-soil interactions enhance biodiversity and functioning in a temperate forest. To do so, we tested the relationships between plant diversity (i.e., tree and herb species richness) and functions (i.e., coarse woody productivity and litterfall productivity), and soil diversity (i.e. bacterial, fungal and nematode) and functions (i.e. soil nutrient and carbon stock), and their interrelationships in a temperate forest in northeast China. The positive relationship between diversity and functioning was predominant within plant and soil compartments, and hence, provide support to the niche complementarity effect. As such, the positive interrelationships between the diversity of soil and plant compartments provide support to the positive plant-soil interactions. Tree species diversity was positively related with herb species diversity and coarse-woody productivity. Importantly, tree species diversity had pronounced positive effect on soil biodiversity resulting in increased soil carbon stocks, indicating that tree species diversity effect matters for linking positive interrelationships between plant and soil compartments of a temperate forest. This study shows that tree diversity effect is the main regulating biotic mechanism for linking the positive connections between plant and soil compartments of a temperate forest, and hence, the niche complementarity effect can enhance forest functioning through positive interactions on resource supply. We argue that linking the multiple key functions and diversity indices of forests can enhance our knowledge on the main influential factors and underlying ecological mechanisms.

1. Introduction

When we imagine a forest, most of us think of the various vegetation layers that make up the canopy and the understorey, but below the forest floor there exists a whole other hidden world that plays an equally important role in shaping biogeochemical cycling in forest ecosystems (Wardle et al., 2004; Bardgett and van der Putten, 2014; Cheng, 2020). These plant and soil compartments do not exist in isolation, but are instead interdependent (Wardle et al., 2004; Bardgett and van der Putten, 2014; Fujii et al., 2017) through multiple interconnected mechanisms (e.g., plant-soil interactions; van der Putten et al., 2013; Zhao et al., 2020). These interactions play a decisive role in driving and

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shaping forest structure, diversity and functions (Hooper et al., 2000; van der Putten et al., 2013). However, most studies exploring the relationships between biodiversity and ecosystem functioning in forests have ignored this interdependence between plant and soil compartments, choosing instead to focus on the effects of soil nutrients on plant diversity – functioning relationships (Chen et al., 2018; Zhou et al., 2019).

In hierarchically structured forest ecosystems, the plant compartment is composed of overstorey and understorey strata. It is generally well-understood that overstorey stratum can shape the diversity and functioning of the understorey stratum through regulating the available resources such as light and nutrients (Barbier et al., 2008; Ali and Yan, 2017; Chun et al., 2020). However, most studies on forest ecosystem had generally focused on overstorey stratum but had ignored the understorey diversity and functioning and their key contribution in nutrient cycling (but see Fujii et al., 2017). Moreover, both the overstorey and understorey strata intertwined with soil compartment as they are not inherently isolated but hierarchically connected (Gilliam, 2007). Indeed, plant species absorb nutrients from the soil and then subsequently return those to the soil through litterfall or roots, which attributed to the biogeochemical cycle (Attiwill and Adams, 1993). As such, it has been well documented that forest tree species attributes such as biomass, composition and diversity act as key determinants for soil biodiversity and functioning (Wardle et al., 2004), which are explained by the range of resources provided by leaf and roots (Bardgett and van der Putten, 2014). For example, tree and herb species diversity and their associated productivity could influence litterfall production and decomposition (Fujii et al., 2017) which not only increase soil nutrients but also foster soil microbial activity (Breulmann et al., 2012), consequently, leading to higher soil organic carbon (Lange et al., 2015; Zhou et al., 2019).

The soil compartment is a major reservoir of microorganisms (e.g., bacteria, and fungi) (Bardgett and van der Putten, 2014) which, in turn, drive ecosystem stability, and structure as well as functioning (Bardgett and van der Putten, 2014; Delgado-Baquerizo et al., 2017; Wagg et al., 2019). For example, it has been broadly shown that soil microbial diversity, particularly bacteria and fungi, could increase several soil processes such as litterfall decomposition, soil nutrient cycling and also plant productivity and diversity (Fierer et al., 2012; Jing et al., 2015; Delgado-Baquerizo et al., 2017). Specifically, soil microbial diversity through mineralizing soil organic matter could enhance soil nutrients (Van Der Heijden et al., 2008) and ultimately leading to increase soil carbon stock (Lange et al., 2015). Importantly, soil carbon stock as a balance between carbon inputs from plant biomass and also outputs via decomposition is a pivotal forest function which strongly affected by plant diversity and productivity (Zhou et al., 2019), biogeochemical cycles of soil nitrogen and phosphorus (Wieder et al., 2015), litterfall productivity (Zhou et al., 2019) as well as soil biodiversity (Lange et al., 2015) through multiple interconnected mechanisms. For instance, the positive interaction between soil organic carbon and nutrients (Lange et al., 2015) could foster soil microbial activity (Delgado-Baquerizo et al., 2017). Altogether, plant-induced changes in soil properties could certainly improve the availability of nutrients, and hence, as a consequent influence plant diversity and performance (van der Putten et al., 2013; Lange et al., 2014).

We have previously reported that stand structure, phylogenetic diversity and soil fungi diversity jointly regulated temperate forest multifunctionality (Yuan et al., 2020). In addition, we have also reported that the context-dependency of plant diversity attributes regulated above- and below-ground forest multifunctionality in relatively opposite directions probably due to the varied plant species' functional strategies (Sanaei et al., 2021). In the current study, we link coarse-woody productivity, litterfall production and soil organic carbon as main functions, rather than forest multifunctionality index (as explored in our previous studies), with tree species diversity, herb species diversity, soil bacterial diversity, soil fungal diversity, soil nematode diversity and soil properties through integrative modeling. Indeed, we selected these plant and soil functions because these functions determine the capability of forest ecosystems to provide goods and services, all of which are necessary in climate change mitigation and also soil biogeochemical processes (Trogisch et al., 2017). By doing so, we aim to explore the specific relationships within and between plant and soil compartments to better understand the main regulating factor for enhancing biodiversity and functioning of a temperate forest (Fig. 1). To address the aim of current study, we use forest inventory and field-based experimental dataset from a 25-ha temperate forest plot in Northeast China in order to test the following research questions, predictions and hypothesis. 1) What is the relationship between plant and soil compartments in terms of diversity and functions? We predict the positive diversity – function interrelationship between plant and soil compartments due to the niche partitioning. 2) What are the strength and magnitude of the relationships between diversity and function within each forest compartment? We predict that the strength and magnitude of the positive diversity – function relationship is more pronounced in the soil compartment than plant because soil diversity and functions are widely regarded as prominent factors for nutrient resources. 3) What is the main regaulting factor for linking the diversity and functions of plant and soil compartments? We predict that tree diversity can enhance the functions of plant and soil compartments, thereby changing the abiotic and biotic conditions of the forests. In sum, although plant and soil processes and their interactions play a key role in shaping the diversity and functioning of forests, we do not fully understand how interrelationships between plant and soil compartments are underlined by multiple ecological mechanisms, and hence, here we hypothesize that the positive plant-soil interactions through plant and soil complementarity resource use enhance biodiversity and functioning in a temperate forest.

2. Materials and methods

2.1. Study area and forest inventory data

This study was carried out in 25-ha in temperate mixed forest in the Changbai Mountain in Northeast China, which is one of the sites in the worldwide network monitoring forests (Fig. S1). The study area has a mean annual temperature of 2.8 °C and mean annual precipitation of 700 mm and the soil type is dark-brown (Yang, 1985). The elevation ranges from 792.9 to 809.4 m, and the slope ranges from 0.15° to 19.1°.

The 25-ha forest plot was established at 2004 and after that re-inventoried every five years, as so far, surveyed three times, respectively, 2004, 2009 and 2014 (Table S1). In the first inventory (2004), the individuals of woody species with stem diameter at breast height (DBH) $\geq$ 1 cm were recorded (59,138 individuals in total) and then were identified, belonging to 52 species, 32 genera and 18 families, which among them *Pinus koraiensis* was the dominant species, even though, *Tilia amurensis*, *Quercus mongolica, Fraxinus mandshurica* and *Acer mono* were also co-dominant (Yuan et al., 2012). We divided the 25-ha plot into 625 subplots (20 m × 20 m) following a standard protocol (Condit, 1998), even though, only 120 subplots were included in the present study (Fig. S1), where the average tree density was 2102.3 ± 350 (stems ha^{-1}) and the average aboveground biomass (AGB) was 254.7 ± 89 (Mg ha^{-1}).

2.2. Quantification of plant diversity and function

During field sampling, tree and herb species were identified within each subplot. For quantifying tree species richness, we counted woody species with DBH $\geq$ 1 cm. Herb species were identified following Flora Reipublicae Popularis Sinicae (Hong and Blackmore, 2015). In brief, a total of 102 herb species belonging to 40 families were identified (Li et al., 2008). Species richness for either tree and herb was calculated using the *vegan* package (Oksanen et al., 2015) in R (R Development Core Team, 2019), which represents the observed tree and herb species

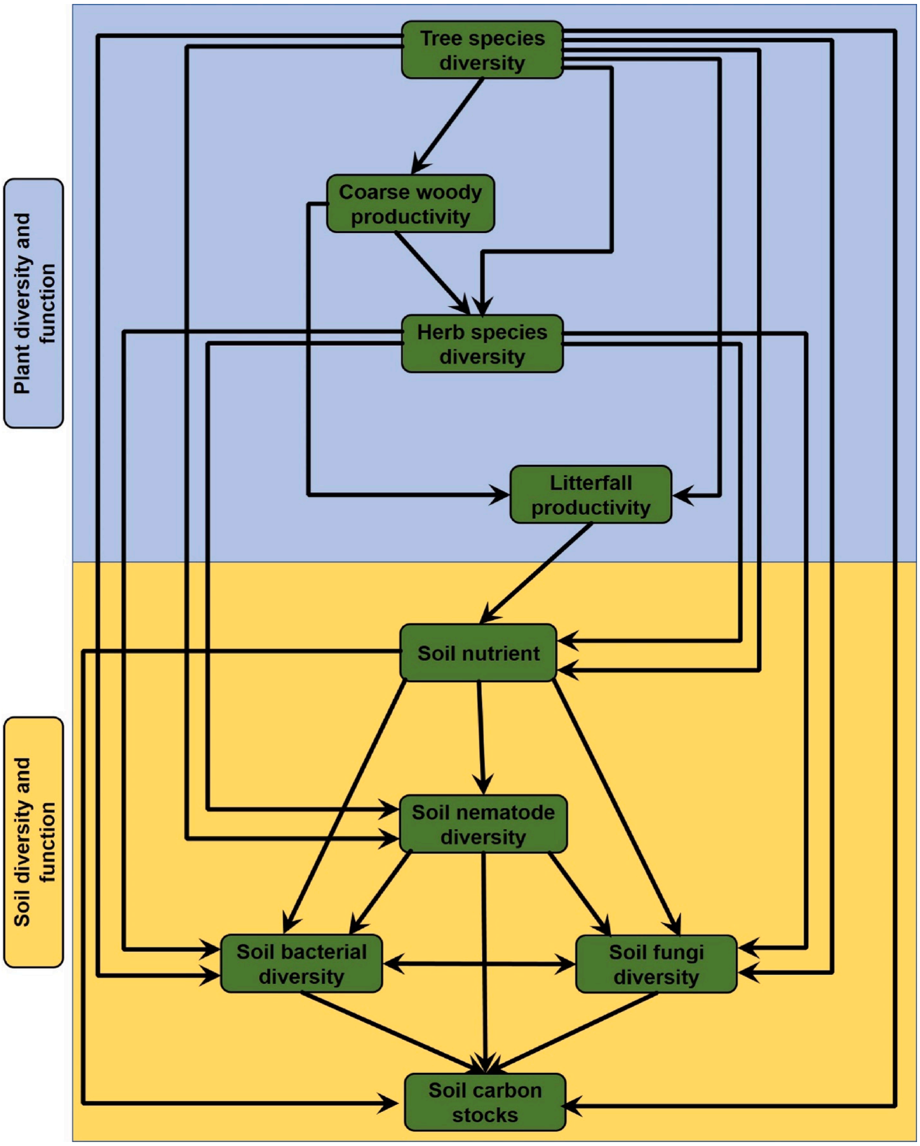


Fig. 1. A conceptual model to test the individual and integrative effects underpinning the interdependence relationships between diversity and functions within and between plant and soil compartments.

within each subplot, respectively.

We defined the above-ground function as coarse-woody productivity (CWP). To do so, we first calculated the total AGB of the individual tree with DBH $\geq$ 1 cm using the allometric equations through their corresponding DBH (Yuan et al., 2019). Then, the biomass growth (Mg ha^{-1} yr^{-1}) of each subplot was calculated by increased biomass from 2004 (the first inventory) to 2014 (the last inventory). Above-ground biomass recruitment (Mg ha^{-1} yr^{-1}) was calculated as the biomass by individuals recruited into DBH $\geq$ 1 cm between the two forest inventories. Lastly, we quantified CWP (Mg ha^{-1} yr^{-1}) by summing of biomass growth and recruitment per subplot from 2004 to 2014 (Yuan et al., 2019).

For quantifying the litterfall production, we firstly placed 150 traps in the centre of each selected 20 m × 20 m subplot with >31 m intervals in a regular pattern in 2005 (Li et al., 2012), and then, the litterfall collection was conducted in May 2006. All leaves, flowers, capsules, twigs and other reproductive structures collected in each trap were identified and recorded twice a month from May to December whereas once a month from January to April (Li et al., 2012; Wang et al., 2017). It should be mentioned that to eliminate the potential edge effects, quadrats located at the edge of 25-ha forest plot were not included, and hence, we selected 120 subplots. Lastly, the continuous litterfall productions monitoring data (the data from 2007 to 2017) were used for the quantification of the total litterfall production, where litterfall production inventories did not coincide with the CWP inventories.

2.3. *Quantification of soil diversity and function*

For quantifying soil diversity, and functions, we randomly selected two soil points within each subplot and then collected five soil cores from each soil point (0–10 cm depth) within each subplot in 2017, after that we mixed soil samples of each sampling point evenly and then transferred to the laboratory for further analysis. We divided each soil sample into two parts: one part for measuring soil microbial diversity (i.e., bacterial, and fungi) and nematode, and another part for measuring soil nutrients and soil organic carbon after picking out the roots and stones. For quantifying the structure of soil bacterial and fungi community an Illumina MiSeq platform (Illumina USA) was used following the manufacturer's instructions. The nematodes were extracted from 200 g of fresh soil using updated cotton-wool filter method (Townshend, 1963) then were assigned to four trophic groups (Yeates et al., 1993). The methods used for the soil diversity measurements were described in detail in Appendix B. The Shannon-Wiener diversity index was used for representing soil bacteria, fungi and nematode diversity within each subplot.

For quantifying soil nutrients, six soil nutrient variables including available and total nitrogen, available and total phosphorus, available and total potassium were measured. Kjeldahl and Olsen methods were used to analyze available nitrogen and phosphorus contents, respectively. Soil total phosphorus and nitrogen were measured by the colourimetry method. Ammonium acetate and neutral normal ammonium acetate (NH_4OAc) methods were used for total and available potassium, respectively. Prior to analysis, we performed a Principal Component Analysis (PCA) to reduce dependency and collinearity issue as well as to reduce the number of soil nutrient variables as suggested by previous studies (Ali and Yan, 2017; Yuan et al., 2020). As such, the first axis of PCA (PCA1) explained 54% of the total variation and the second axis of PCA (PCA2) explained 24% of the variation (Fig. S2). In all subsequent analyses, the first axis (PCA1) of the PCA was used to represent differences in soil nutrients among subplots.

We defined the soil function as the soil carbon stock. So that, for estimation soil carbon stock firstly, we measured organic carbon (g kg^{-1}) using the acidified dichromate ($K_2Cr_2O_7$–H_2SO_4) oxidation method (Lu, 1999) then soil carbon stock was calculated according to the equation (1):

$$SOCD = (1 - G_i) \times h \times D_i \times C_i/100 \quad (1)$$

Where, SOCD is the soil organic carbon density (kg m^{-2}), h is the soil depth (i.e. 10 cm), G_i is the fraction (%) of >2 mm sand in soil, D_i is the bulk density (g cm^{-3}), C_i is the value of organic carbon content (g kg^{-1}). A summary of descriptive statistics for all used variables is shown in Table S1.

2.4. Statistical analyses

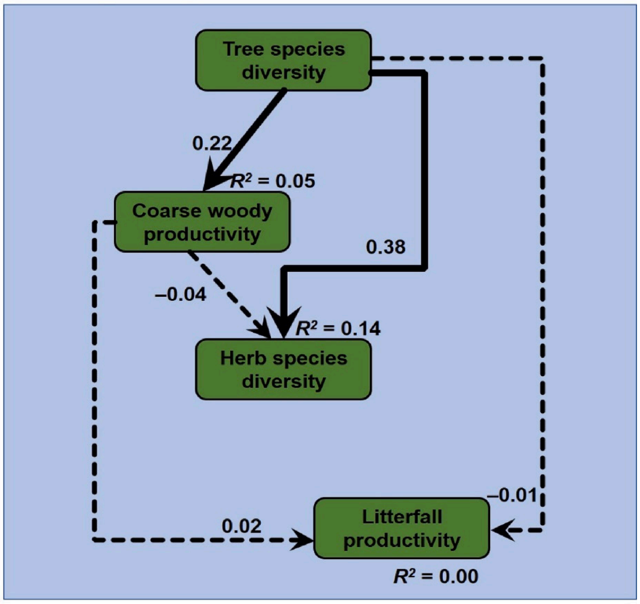
To test the confounding effects of spatial autocorrelation on the hypothesized causal paths we performed generalized least squares (GLS) analysis through original data (Pinheiro and Bates, 2016). The GLS analysis showed that there was no spatial autocorrelation as the higher Akaike Information Criterion values were found for the models with spherical autocorrelation (Table S2). Thus, we conducted structural equation modeling (SEM) analysis. Because SEM permits us to test the multiple hypotheses, mechanisms and theories in one model, so we used SEM for testing the potential interactions among plant and soil forest diversity and functioning of the proposed conceptual model in the temperate mixed forest (Fig. 1). For plant diversity we used tree species diversity and herb species diversity, whereas coarse woody productivity and litterfall productivity were used as plant functions. By incorporating soil bacteria, fungi and nematode diversity we defined soil diversity and for soil functions we used soil nutrients as well as soil carbon stocks. Firstly, we tested the diversity and ecosystem functioning relationship for each of plant and soil compartment separately. Secondly, we joined two separate plant and soil compartments by including all pathways in the SEM (Fig. 1). For quantifying the fit of the model as recommended we used Chi-square test statistic and associated *P*-value (i.e. $P > 0.05$ shows a good fitting model), standardized root mean square residual (SRMR) and comparative fit index (CFI) (Malaeb et al., 2000). As recommended a chi-square with a $P > 0.05$ representing that expected and observed covariance matrices are statistically indistinguishable, the RMSR < 0.05 and CFI > 0.95 were interpreted as showing the best model fit (Malaeb et al., 2000; Rosseel, 2012). In SEM analysis, variables that connected by a single link constitute direct effects, while directed pathways passing through a third variable along the causal path represent indirect effects, and finally the total effect equals the sum of all pathways (direct and indirect effects) connecting two variables (Grace, 2006). We simplified our initial model by removing some non-significant paths (Table S3). In order to preliminarily explore how predictor and response variables are related to each other, we used pairwise Pearson correlation (Fig. S3). Furthermore, using simple linear regression we fitted the bivariate relationships based on the postulated paths in the conceptual framework (Fig. S4). Before analysis, original data were log transformed and then standardized (Zuur et al., 2009). We fitted the SEMs using the *lavaan* package (Rosseel, 2012). All analyses were done in R 4.0.3 (R Development Core Team, 2019).

3. Results

3.1. Individual models of plant and soil compartments

The model-fit statistics showed that the individual plant and soil compartments SEMs were saturated ($\chi^2 = 0$). The SEM for plant compartment showed that tree species diversity was positively

a) Plant diversity and function



b) Soil diversity and function

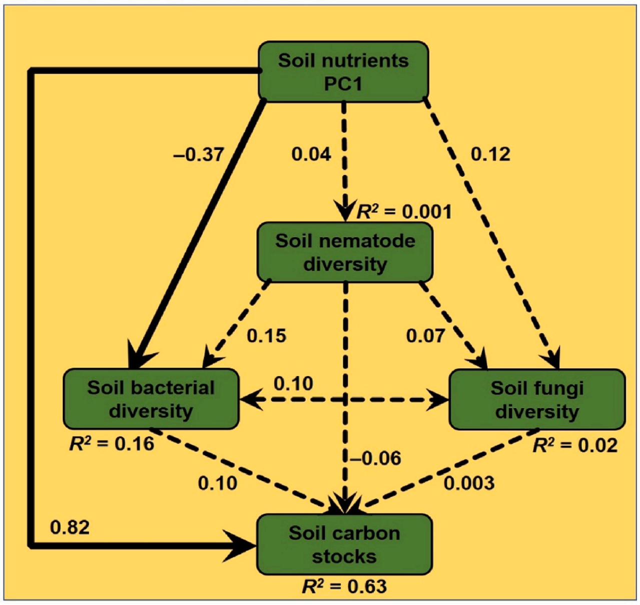


Fig. 2. Individual structural equation models (SEMs) of a) plant diversity and function and b) soil diversity and function. Because these SEMs are saturated, the goodness-of-fit cannot be given. Solid black arrows indicate significant paths ($P < 0.05$), while dashed arrows show the non-significant paths ($P > 0.05$).

associated with CWP and herb species richness (Fig. 2a). Moreover, there were negligible negative effects of tree species diversity and CWP on litterfall productivity (Fig. 2a). In the case of soil compartment, soil nutrients PC1 was positively correlated with soil carbon stock while negatively associated with bacterial diversity (Fig. 2b). Soil diversity attributes (i.e., bacterial, fungi and nematode) positively and insignificantly associated (Fig. 2b).

3.2. Integrative models of plant and soil compartments

The model-fit statistics showed that the data conformed well to the structural equation model ($\chi^2 = 8.01$; P-value $= 0.71$; CFI $= 1.00$). The integrative SEM for plant and soil compartments showed that tree species diversity, soil diversity (i.e., bacterial, fungal and nematode) and soil nutrients PC1 explained 65% of the variation in soil carbon stocks (Fig. 3). Importantly, there was a strong positive association between tree species diversity and soil diversity, particularly bacterial and nematode (Fig. 3). By contrast, herb species diversity and soil bacterial diversity were negatively and significantly correlated. Herb species diversity was positively and significantly correlated with nematode diversity while positively and insignificantly associated with fungi diversity (Fig. 3). Tree species diversity remarkably increased soil nutrients PC1 (Fig. 3). Moreover, tree species diversity and soil carbon stocks were significantly interrelated (Fig. 3). In addition, tree species diversity indirectly positively linked to soil carbon stocks via soil nutrients PC1 but indirectly negatively associated with bacterial diversity via soil nutrients PC1 (Table S4).

3.3. The strength and magnitude of diversity – ecosystem functioning relationships within and between forest compartments

The strength of the effects between forest diversity and functioning were stronger within the plant compartment than soil (Fig. 3). As such, the positive relationship between tree species diversity and functioning was predominant in the plant compartment (Fig. 3). In addition, in the soil compartment, soil bacterial and fungi diversity slightly increased soil carbon stocks but soil nematode diversity decreased, where bacterial, fungi and nematode diversity were positively and insignificantly

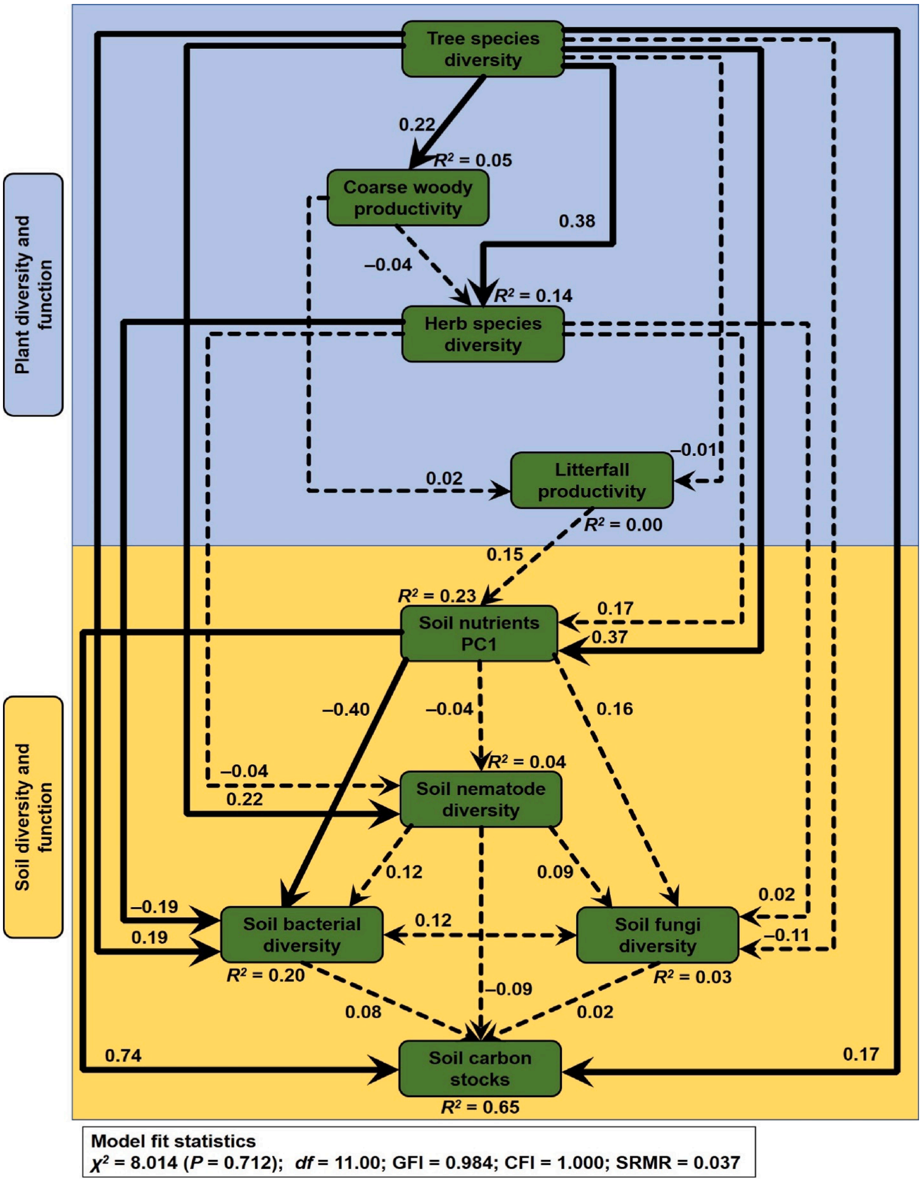


Fig. 3. Structural equation model (SEM) for testing the integrative forest diversity and functions relationships within and between plant and soil compartments. Solid black arrows indicate significant paths ($P < 0.05$), while dashed arrows show the non-significant paths ($P > 0.05$). Abbreviations: χ^2, chi-square; df, degree of freedom; GFI, goodness of fit index; CFI, comparative fit index; SRMR, standardized root mean square residual.

correlated (Fig. 3). In the soil compartment, soil nutrients PC1 were negatively and substantially correlated with soil bacterial diversity but this significant effect was absent on soil fungi and nematode diversity (Fig. 3). There was a negligible negative correlation between litterfall productivity with tree species diversity but non-significant positive correlation with CWP where tree and herb species diversity were positively and significantly correlated (Fig. 3). The significant bivariate diversity – functioning relationships within and between plant and soil compartments are presented in Fig. 4. In consistent with SEMs results tree species diversity, as the main regulating biotic factor for linking the positive connections between plant and soil compartments, significantly positively associated with CWP, herb species diversity, soil nutrient, nematode diversity and soil carbon stock (Fig. 4). Altogether, using both SEM analysis (i.e., individual and integrative models) and linear regression analyses (Figs. 2–4) we found that tree species diversity is positively associated with plant and soil diversity and functioning, and hence, showing the key role of tree species diversity in shaping forest diversity and functioning.

4. Discussion

We explore multiple diversity – ecosystem functioning relationships within and between plant and soil compartments through an integrative approach in a temperate forest. We found the positive diversity – function relationship within each compartment (i.e., plant and soil) and between two compartments, and hence, confirming plant and soil niche complementarity and partitioning effects (Loreau et al., 2001; Tilman et al., 2001; Silvertown, 2004). Importantly, the positive plant diversity – soil diversity relationship, resulted in increased soil carbon stocks, reinforces the fact that plant and soil diversity are mutually interrelated and have tightly bipartite interactions (Hooper et al., 2000; Wardle et al., 2004; van der Putten et al., 2013). Interestingly, in the soil compartment, soil carbon stock responded differently to soil diversity; for instance, soil organic carbon stock increased with bacterial and fungal diversity while decreased with nematode diversity, indicating differences in resource requirements of soil communities (Lange et al., 2014). In a nutshell, this study collectively reaffirms that plant-soil

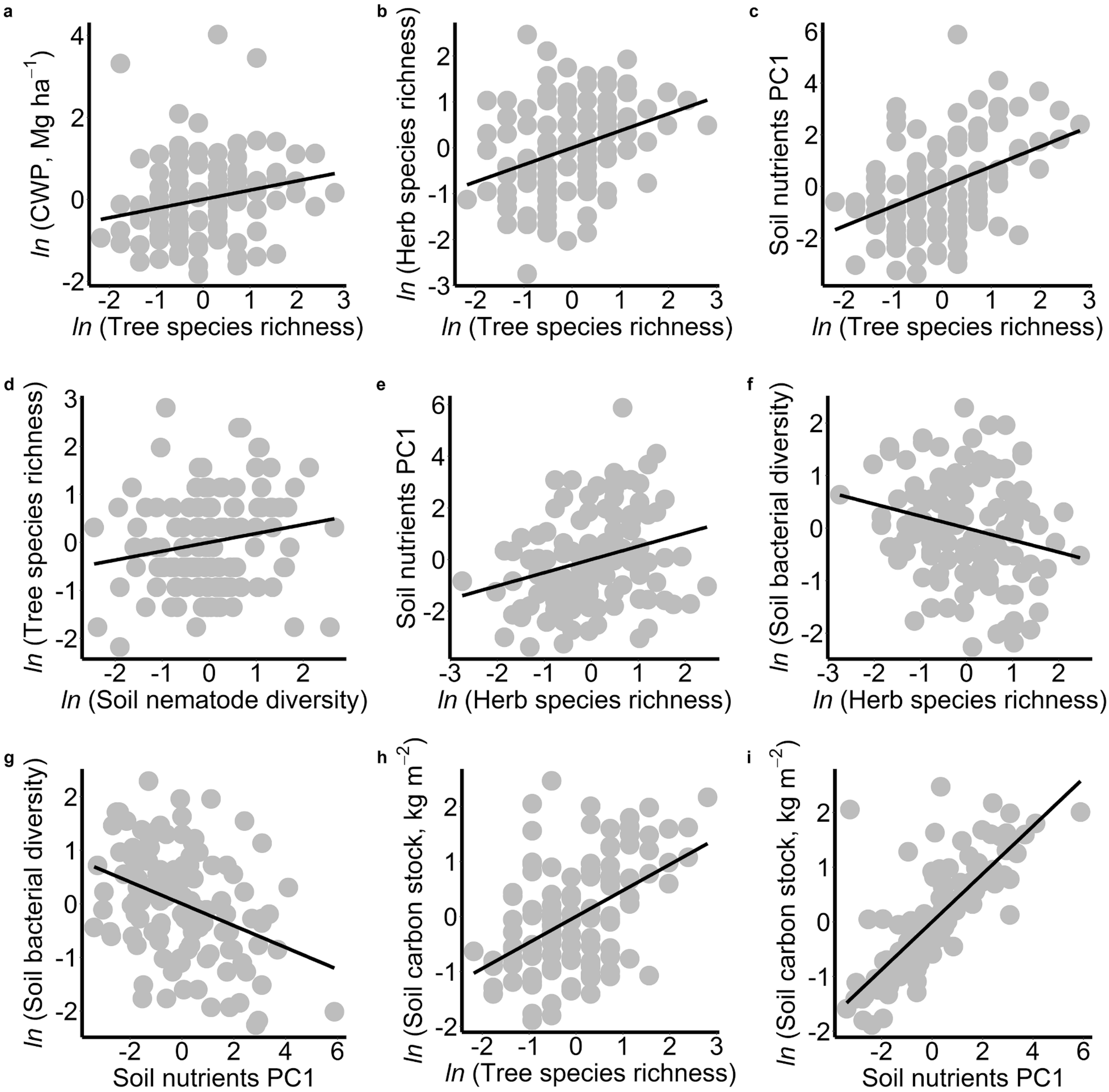


Fig. 4. The significant bivariate ($P < 0.05$) diversity – functions relationships within and between plant and soil compartments based on the hypothesized causal paths.

interactions act as an important ecological force for underlying interdependence diversity – function relationship within each compartment as well as the relationship between the diversity of soil and plant, because plant and soil compartments are intimately dependent on each other (Wardle et al., 2004; Bardgett and van der Putten, 2014), resulting in an increase the flow of energy between plant and soil compartments (Lange et al., 2014).

The results reveal that tree species diversity and soil organic carbon stock was positively associated. This result corroborates with previous study that confirmed the positive effect of tree species richness on forest carbon storage (Liu et al., 2018). It is generally well-understood that plant community attributes through returning biomass and litterfall productivity as well as by root carbon inputs can enhance soil carbon stock (Lange et al., 2015; Wieder et al., 2015; Zhou et al., 2019). More specifically, this evidence suggests that diverse stands, which supply varied litterfall with different decomposition rates and relevant root system activities, input the majority of organic matter into the soil (Liu et al., 2018), resulting in higher soil carbon stock through microorganism decomposition (Fierer et al., 2012; Jing et al., 2015; Delgado-Baquerizo et al., 2017). Interestingly, our results show that the community assembly mechanisms driving soil diversity (i.e., bacteria and nematode) patterns were different from herb species richness but similar to tree species richness. As such, the positive interrelationships between tree species diversity and both bacteria and nematode diversity may originate from a variety of food sources due to the varied biomass production, plant-dead material (or litterfall production) and roots which can increase soil microbial activity and soil nutrients (Facelli and Pickett, 1991; Scherber et al., 2010; Lange et al., 2015). Alternatively, soil microbial diversity could increase tree species diversity indirectly by decomposition and converting litterfall to the soil organic matter, thereby higher soil nutrient availability (Lange et al., 2014). We found that bacterial and nematode diversity, which were positively correlated with tree species diversity, were negatively associated with herb species richness, these contrasting responses indicate a niche differentiation of herbs and trees in forest ecosystems (Wang et al., 2016). Moreover, it is evident that tree species with longer root systems penetrate much deeper in soil than herbs (Scholes and Archer, 1997), therefore these differences could be a result of differential response to the soil microbes (Wang et al., 2016). In addition, since different soil microorganisms prefer the different quality of litterfall (e.g., high or low C:N ratio) (Lange et al., 2014), decomposition of herb litterfall may be favored by other soil microorganisms (for example fungi as we found here) which might result in the reduction of litterfall decomposability, and hence, reduction of nutrients availability for herbs.

We found that the higher levels of plant and soil functioning associated with greater plant and soil diversity. As such, tree species diversity positively increased CWP, resulting from the positive species interaction which underpins the role of niche complementarity effects, i.e., the efficient utilization of resources by component species within a community through niche differentiation and facilitation (Loreau and Hector, 2001; Loreau et al., 2001; Tilman et al., 2001; Hooper et al., 2005). More specifically, more diverse tree and herb layers produce the majority of leaf and subsequently litterfall (Huang et al., 2017). This leads to higher soil nutrients and soil water content (Facelli and Pickett, 1991; Fischer et al., 2019), and hence, resulting in a higher forest CWP (Liu et al., 2018). In parallel with above-mentioned results, we found that tree species diversity positively associated with herb species diversity, this finding may result from the reduction of interspecific competition in the understorey stratum through increasing resource heterogeneity by overstorey plant species (Vockenhuber et al., 2011), which leads to a higher diversity of understorey plant species (Gamfeldt et al., 2013). Similarly, along with this, the positive interaction among soil diversity (i.e., bacteria, fungi and nematode) may arise from some underlying mechanisms i.e., availability to new niches for colonization, increasing nutrient mineralization, and the emergence of novel behavioral prey refuges (Jiang et al., 2017).

Importantly, the variable effects of soil microbial diversity, including positive and negative effects, on soil carbon stock indicates the fact that soil microbes vary in the magnitude and direction of their influence on soil functions (Van Der Heijden et al., 2008) or may originate from differences in resource requirements of soil communities (Lange et al., 2014). Specifically, the positive association could be driven not only by decomposition of litterfall and turnover of the soil organic matter (Lange et al., 2015; Wilpiszeski et al., 2019) but also by increasing soil aggregation through soil microbial diversity which in turn could affect soil carbon storage by the degradation of soil microbial byproducts (Wilpiszeski et al., 2019). Through this understanding, the positive relationship between soil carbon stock and soil nutrient can be inferred by differences in litter input quantity and quality which consequently leading to higher soil organic matter (Wieder et al., 2015; Zhou et al., 2019), thereby biogeochemical cycles of some soil nutrient factors such as nitrogen and phosphorus (Wieder et al., 2015). Moreover, numerous mechanisms might account for the negative influence of soil nutrients on soil bacterial and nematode diversity such as limiting soil microbial diversity and activities (Olatunji et al., 2019) and also decreasing competitive fitness of microbes in nutrient-rich soils (Carrero-Colón et al., 2006).

5. Conclusions

This study showed the positive diversity – function relationship within plant and soil compartments, as such tree species diversity promoted CWP and soil carbon stocks and in the case of soil compartment soil diversity attributes enhanced soil carbon stocks, and hence, supporting the niche complementarity effects. Indeed, complementarity resource use between tree species might be the result of tree crown complementarity and root complementarity because more diverse stands diversify the available resource pool through higher canopy packing, varied root structure, root exudation and litter inputs. In addition, the positive association between tree species diversity and soil diversity attributes, particularly bacteria and nematode, is indeed due to the fact that plant and soil compartments are mutually interrelated through plant-induced changes which may lead to varying abiotic and biotic conditions of the forests. Tree species diversity had pronounced positive effects on soil biodiversity resulting in increased soil carbon stocks. Our findings contribute to the growing body of evidence that tree species diversity is the main regulating factor for higher forest biodiversity and functions, because higher tree diversity leads to creating more favorable conditions and niches for soil diversity and increases nutrient release, therefore, diverse stands support the rich set of forest functions.

6. Authors' Contributions

AS, ZY and XW conceived the idea; ZY, LF, JY, SF, ZH and XW conducted the study and collected the data. AS analysed the data. AS, ZY and AA drafted manuscript. ML, ASM, PBR, TJ, and XW revised, reviewed and commented on the drafts.

Authors declared that they do not have any conflict of interest.

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.foreco.2021.119160.

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