Received: 25 November 2019 | Accepted: 17 February 2020

DOI: 10.1111/1365-2745.13378

RESEARCH ARTICLE

Journal of Ecology BRITISH ECOLOGICAL SOCIETY

Above- and below-ground biodiversity jointly regulate temperate forest multifunctionality along a local-scale environmental gradient

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Funding information
National Natural Science Foundation of China, Grant/Award Number: 31730015, 31722010 and 41671050; Youth Innovation Promotion Association CAS, Grant/Award Number: 2017241; Strategic Priority Research Program of the Chinese Academy of Sciences, Grant/Award Number: XDB 31030000; Key Research Program of Frontier Sciences, Grant/Award Number: ZDBS-LY-DQC019; Nanjing Forestry University, Grant/Award Number: 163010230; UK NERC Independent Research Fellowship, Grant/Award Number: NE/S01537X/1; Fellowship 'Atracción de Talento Investigador', Grant/Award Number: 2016-T2/AMB-1665; TULIP Laboratory of Excellence, Grant/Award Number: ANR-10-LABX-41

Handling Editor: Eric Allan

Abstract

1. Tree diversity has been shown to promote a broad range of ecosystem functions in forests. However, how important these effects are in driving ecosystem multifunctionality in natural forests, relative to other drivers, such as below-ground biodiversity (e.g. soil microbial diversity), community-level functional traits and environmental conditions, remains poorly understood. Here, we hypothesize that tree species or phylogenetic diversity (PD), stand structure, functional traits and soil microbial diversity jointly regulate temperate forest multifunctionality (FM) along a local-scale environmental gradient.
2. Using repeated census data from a 25-ha old-growth temperate forest, we first quantified eight ecosystem functions and properties related to above- and below-ground nutrient cycling. We then used these to estimate ecosystem multifunctionality using both averaging and multiple threshold (50%, 75% and 95%) approaches. Finally, we used structural equation models to explore how different facets of tree (tree species, functional and PD) and soil (bacteria, fungi and nematode diversity) biodiversity influence ecosystem multifunctionality, as well as how these relationships are modulated by stand structural attributes and environmental conditions (topography and soil nutrients).
3. Forest multifunctionality was positively related to stand structural complexity but negatively related to acquisitive traits (i.e. community-weighted mean of specific leaf area). Plant PD had no significant direct effect on FM, but it had a significant

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indirect effect via increased stand structural complexity. The effect of soil microbial diversity on FM increased with increasing threshold levels of FM and outperformed tree diversity and environmental conditions at the highest threshold level (i.e. 95%). Forests on steep slopes had lower levels of ecosystem multifunctionality due to decreased stand structural complexity. Soil nutrients were responsible for regulating FM via plant trait composition and, to a lesser extent, via tree diversity, stand structure and soil microbial diversity.

4. *Synthesis*. Plant PD, stand structure and soil microbial diversity jointly regulated FM, and these effects were influenced by local-scale changes in environmental conditions. Soil microbial diversity was a key driver of highly multifunctional forests, whereas conservation of complex stand structure and conservative trait dominance could enhance mean values of multiple functions.

KEYWORDS

biodiversity–ecosystem functioning, dominant species, environmental conditions, functional traits, natural forest, soil microbes

1 | INTRODUCTION

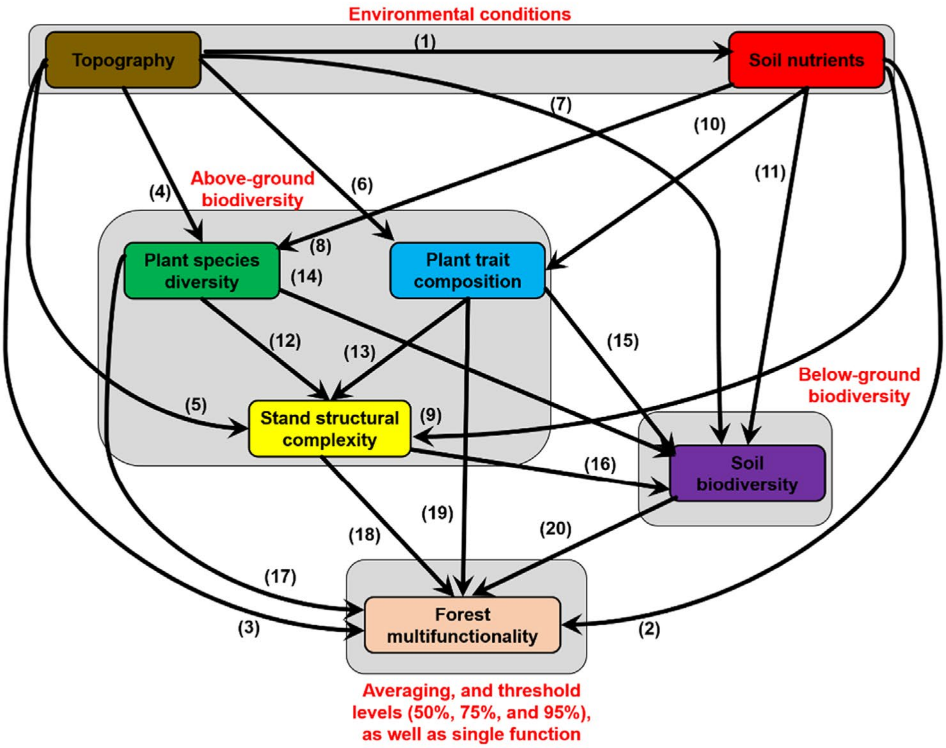
Forest ecosystem services that benefit human well-being depend on several forest functions that are in turn controlled by biodiversity in naturally assembled forest communities (Schuldt et al., 2018; van der Plas, 2019). However, in natural forests, biodiversity is a complex and multifaceted concept that includes both above-ground (e.g. tree species, structure, evolutionary and functional trait diversity and composition; Ali, 2019; Seibold, Cadotte, MacIvor, Thorn, & Müller, 2018; van der Plas, 2019) and below-ground biodiversity (e.g. soil macroscopic animals and microbial diversity such as bacteria, fungi and nematodes; Townshend, 1963; Wagg, Bender, Widmer, & Heijden, 2014). Existing studies have mainly focused on biodiversity within a single trophic group (Delgado-Baquerizo et al., 2016; Felipe-Lucia et al., 2018), neglecting the fact that ecosystem functioning depends strongly on complex interactions between trophic levels and between above- and below-ground biodiversity (Baeten et al., 2018; Schuldt et al., 2018; Soliveres et al., 2016). Further studies are needed to explore the relative effects of above- and below-ground biodiversity on forest multifunctionality (FM) while considering the direct and indirect effects of environmental conditions (see Figure 1a).

It is well-known that above-ground biodiversity (i.e. tree diversity) enhances both single ecosystem functions (Paquette & Messier, 2011; Poorter et al., 2015) and multiple ecosystem functions (i.e. multifunctionality) in forests (Felipe-Lucia et al., 2018; Gamfeldt et al., 2013). However, quantitative information on species traits and phylogeny might better predict ecosystem functions than species richness (Potter & Woodall, 2014), since communities with functionally dissimilar species ought to have greater resource-use complementarity and reduced competition (Petchey & Gaston, 2006; van der Plas, 2019). The net effect of species diversity on ecosystem functioning also depends on the selection effect (i.e. selection of particular functional traits or species; Loreau & Hector, 2001). In addition, stand structural complexity (e.g. individual tree size variation) sustains forest functioning through several underlying mechanisms such as plant–plant interactions (reviewed by Ali, 2019).

A growing body of studies has also begun to elucidate the role of below-ground biodiversity (e.g. soil microbial diversity) in maintaining ecosystem multifunctionality (Delgado-Baquerizo et al., 2016; Wagg et al., 2014). For example, soil microbial diversity and composition have been recognized as key biotic factors for regulating ecosystem multifunctionality in temperate grasslands (Wagg et al., 2014). Nevertheless, nutrient cycling can be maximized only if the effects of above- and below-ground biodiversity are complementary (Jing et al., 2015), otherwise, they may have opposing effects on ecosystem functions (Schuldt et al., 2018).

Biodiversity is not merely a predictor of various ecosystem functions but also responds to environmental changes in naturally assembled communities (Jing et al., 2015; Ratcliffe et al., 2017). Generally, topographic variables such as slope strongly affect soil chemistry, hydrology and microclimate at the local scale (Jucker et al., 2018). As such, topography and soil nutrients can directly shape local environmental conditions in which plants grow, which in turn influence the composition and distribution of soil microbes (Coomes, Kunstler, Canham, & Wright, 2009). For example, in alluvial valleys or nutrient-rich soils, forests are structured by strong competition for light, and hence, develop more structurally complex and dense canopies while also leading to higher productivity and turnover rates (Coomes et al., 2009; Prado-Junior et al., 2016). By contrast, interspecific competition tends to decline with lower resource availability (Paquette & Messier, 2011), which may favour conservative trait values

(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 (explanation to each pathway)
(1)	Topography → Soil nutrients	Topography is an important soil formation factor, and hence, complex topographical features such as slope and elevation at the local scale increase soil nutrients.
(2)	Soil nutrients → Forest functions	Fertile soils could directly relieve species from limited resources, leading to high forest functioning. High soil fertility could also promote tree competition, with high mortality and turnover rates.
(3)	Topography → Forest functions	Topographic heterogeneity at the local scale can govern forest functioning, e.g. forest productivity.
(4)	Topography → Plant species diversity	Local habitat specialization and heterogeneity can promote forest species diversity.
(5)	Topography → Stand structure	Topography controls the fine-scale variation in the structure and composition of forests.
(6)	Topography → Plant trait composition	
(7)	Topography → Soil biodiversity	Abiotic factors can determine the composition and distribution of soil microbial diversity in natural forests.
(8)	Soil nutrients → Plant species diversity	Soil resource availability can increase diversity because of niche creation, or the competitive advantage of certain species.
(9)	Soil nutrients → Stand structure	Forests on nutrient-rich soils can develop more structured and dense canopies.
(10)	Soil nutrients → Plant trait composition	Selection for specific functional traits due to habitat filtering.
(11)	Soil nutrients → Soil biodiversity	Abiotic factors can determine the composition and distribution of soil microbial diversity in natural forests.
(12)	Plant species diversity → Stand structure	Different tree species in mixed forests have contrasting growth patterns and dimensions that can lead to above-ground and below-ground stratification, the effects of tree species diversity may be partially attributable to structural diversity.
(13)	Plant trait composition → Stand structure	Eco-physiological and morphological tree characters (e.g. maximum height) can optimize canopy packing through vertical stratification and/or crown plasticity.
(14)	Plant species diversity → Soil biodiversity	Plant attributes (i.e. plant community attributes and functional traits) could determine the diversity of soil microbial communities in forest ecosystems.
(15)	Plant trait composition → Soil biodiversity	
(16)	Stand structure → Soil biodiversity	
(17)	Plant species diversity → Forest functions	Plant diversity promotes multiple functions via niche complementarity effects.
(18)	Stand structure → Forest functions	Stand structure acts as a mechanism in regulating ecosystem functioning via interactions among individuals in natural forests. Stand structure complexity and diversity can regulate the ecosystem functions (e.g. productivity) by increasing the global level of light availability and absorption in a forest stand.
(19)	Plant trait composition → Forest functions	According to the mass ratio hypothesis, trait values that intensify resource conservation (i.e. high CWM of wood density) are expected to be associated with low productivity, whereas trait values that intensify resource acquisition (i.e. high CWM of leaf nutrients) are expected to be related with high productivity.
(20)	Soil biodiversity → Forest functions	Soil biodiversity and soil community composition determine ecosystem multifunctionality.

FIGURE 1 A conceptual model (a) and schematic illustration of ecological hypotheses/theories/mechanisms (b) to test the effects of above- and below-ground biodiversity on forest multifunctionality, and single forest functions, along a local-scale environmental gradient in temperate forests. (a) The hypothesized causal relationships amongst environmental conditions (topography and soil nutrients), above-ground biodiversity (plant species diversity, functional trait composition, stand structural diversity), below-ground biodiversity (i.e. microbes) and forest multifunctionality (the main focus of the study) or forest single functions (for evidence). The numbering of each hypothesized path is explained in (b) as well as in the introduction. (b) Brief description of ecological hypotheses/theories/mechanisms in relation to hypothesized paths in (a) [Colour figure can be viewed at wileyonlinelibrary.com]

(e.g. low SLA and high wood density [WD]) and hence high carbon accumulation rates on infertile soils (Ali, Chen, You, & Yan, 2019; Prado-Junior et al., 2016).

In addition, it is important to evaluate how different ecosystem functions show synergies or trade-offs (Felipe-Lucia et al., 2018; Van der Plas et al., 2018), in order to better understand the underlying ecological mechanisms of diversity—multifunctionality relationships in forests (Figure 1). Plant species diversity often has a positive effect on a number of ecosystem functions while environmental conditions or dominant species may simultaneously reduce other ecosystem functions, thereby controlling the level of ecosystem multifunctionality (Gamfeldt et al., 2013). Inherent trade-offs exist between ecosystem functions depending on the identity and number of functions measured (Meyer et al., 2018). For example, wood biomass and non-timber forest products cannot be simultaneously increased in Swedish forests (Gamfeldt et al., 2013). In addition, ecosystem multifunctionality may be driven by different individual functions that respond strongly to diversity or environmental conditions or by all functions increasing together (Zirbel, Grman, Bassett, & Brudvig, 2019). Thus, identifying how different ecosystem functions respond to biodiversity and environmental conditions, as well as their relative contributions to multifunctionality, is critical to formulating sustainable management and conservation policies (Baeten et al., 2018; Felipe-Lucia et al., 2018; van der Plas, 2019).

In this context, we aim to better understand how plant attributes (i.e. species diversity, trait composition and stand structure) and below-ground biodiversity (i.e. soil microbial diversity) regulate temperate FM while accounting for multiple environmental (i.e. topography and soil nutrients) conditions (Figure 1a). To do so, we integrate the predictions from multiple theories/hypotheses into a single model (Figure 1b). Using structural equation modelling (SEM), we link FM, quantified based on eight key forest functions (i.e. above-ground carbon stock, soil carbon stock, coarse woody productivity, litterfall production, seed production, above-ground biomass of herb layer, litter and soil saturation moisture capacity), to above- and below-ground biodiversity as well as to environmental conditions in a 25-ha permanent temperate forest plot. Based on the conceptual model (Figure 1), we hypothesize that tree species or phylogenetic diversity (PD), stand structure, functional traits and soil microbial diversity jointly regulate temperate FM along a local-scale environmental gradient. This hypothesis leads to the following three predictions: (a) tree diversity has an independent positive effect on FM, as has been shown in other boreal and temperate forests (Gamfeldt et al., 2013; Van der Plas et al., 2016), as well as in grassland (Soliveres et al., 2016) and dryland ecosystems (Le Bagousse-Pinguet et al., 2019); (b) stand structural complexity better predicts FM than does tree species diversity and trait composition because individual tree size variation is crucial for maintaining whole-ecosystem biodiversity (Ali, 2019; Gough, Atkins, Fahey, & Hardiman, 2019); and (c) local environmental factors associated with soil nutrients and topography primarily influence FM indirectly by shaping stand structure and composition (Jucker et al., 2018; Paquette & Messier, 2011).

2 | MATERIALS AND METHODS

2.1 | Study site and 25-ha dynamic forest plot

The study area covers forest area from 41°41′49″ to 42°25′18″N in latitude, 127°42′55″ to 128°16′48″E in longitude on the Changbai National Natural Reserve in Northeast China. We conducted our sampling efforts on a 25-ha permanent temperate mixed forest plot within the core zone of this National Nature Reserve that has been protected from the clear-cutting. The 25-ha plot is formed by late successional stages of broad-leaved Korean pine mixed forest (approximately stand age of 300 years in the summer of 2004; Hao, Zhang, Song, Ye, & Li, 2007). The region has a mean annual precipitation of 700 mm and a mean annual temperature of 2.8°C (Yang, 1985). The soil is classified as dark brown forest soil (mollisol according to Soil Survey Staff, 1999), which formed in granite and basalt (Yang, 1985).

Our study plot is one of the sites of the worldwide network monitoring forests (CTFS-ForestGEO; http://www.forestgeo.si.edu). A total of 59,138 individual trees with a stem diameter at breast height (DBH) ≥1 cm were identified in the first inventory in 2004, belonging to 52 species, 32 genera and 18 families. The second and third inventories were conducted in 2009 and 2014 respectively. Following a standard field protocol (Condit, 1998), the 25-ha plot was divided into 625 subplots (20 × 20 m), in which three topographic variables were measured using a total station instrument: elevation (with values from 792.9 to 809.4 m), slope (with values from 0.15° to 19.1°) and terrain convexity (with values from −1.51 to 1.34 m).

2.2 | Quantification of FM

We quantified eight forest functions related to both above- and below-ground processes (Hölting, Beckmann, Volk, & Cord, 2019; Trogisch et al., 2017) to represent FM (Table S1 in Appendix A): (a) above-ground carbon stock, (b) coarse woody productivity, (c) litterfall production, (d) number of seeds, (e) above-ground biomass of herb layer, (f) soil organic carbon density, (g) litter saturation moisture capacity, and (h) soil saturation moisture capacity. For the estimation of above-ground carbon stock, we first estimated the above-ground biomass for each individual tree with DBH ≥ 1 cm using species-specific level allometric equations (Yuan et al., 2016). Then, we calculated biomass growth (Mg ha^{-1} year^{-1}) as the increment of individuals alive in the last and first inventories (van der Sande et al., 2017). Above-ground biomass recruitment (Mg ha^{-1} year^{-1}) was calculated as the biomass by individuals recruited into DBH ≥ 1 cm between the first and last forest inventories. By summing all biomass growth and recruitment per subplot and dividing it by the inventory length (in years), we obtained coarse woody productivity (Mg ha^{-1} $year^{-1}$; Yuan et al., 2018). Above-ground biomass stock (Mg/ha) was used as the averaged above-ground biomass for all trees alive in the first and last forest inventories. To quantify the litterfall production and the number of seeds (i.e. seed production), we placed 150 traps in the 25-ha plot at a spacing of >31 m, in the centre of each selected 20 × 20 m subplot, in a relatively regular pattern, in June 2005 (Figure S1 in Appendix B; Li, Hao, Bin, Zhang, & Wang, 2012). The continuous litterfall and seed production monitoring data from January 2007 to December 2017 were used to calculate FM. Around each trap, we also established three 1 × 1 m micro-quadrats in August and September 2006 to monitor long-term understorey herb diversity and dynamics (Zhang et al., 2009). Here, the above-ground biomass of the herb layer within each micro-quadrat in August 2014 was sampled, dried and calculated. The water holding capacity (WHC) of litters and soils were expressed as the maximum water retention ratio after litters and soils were immersed in water (Pramer & Schmidt, 1964). Please see detailed measurement approaches in Supporting Information, Appendix B.

Averaging and multiple threshold methods were used to calculate a FM index (Byrnes et al., 2014; Zirbel et al., 2019). For the averaging approach, we calculated *z*-scores (standardized deviates) for each forest function and averaged them as described by Maestre et al. (2012). For the threshold approach, FM was calculated as the number of forest functions that exceeded a threshold (i.e. the percentage of the highest measured value for every single function, where the highest was quantified as the mean of the five highest values (Byrnes et al., 2014). We used threshold values of 50%, 75% and 95% in order to represent different levels of FM (Zirbel et al., 2019).

2.3 | Measurements of soil physicochemical properties and soil microbes

In August 2017, we randomly selected two soil sampling sites at the midpoints between the central point and the four corners in the above-mentioned 150 subplots.

In each sampling site litter was collected to measure litter WHC. The dried twigs and herbs were first removed from the surface and three sampling points were then sampled with a sampler of 0.25 m^2 to collect the intact litter layer above the soil mineral horizons using a hand spade. Then, the soil bulk density and WHC were measured with stainless cylinders of volume 200 cm^3 within each sampling site. Lastly, five soil cores (3.8 cm diameter, 10 cm deep) at each sampling point were collected, pooled and brought to the laboratory with plastic zipper bags. Each soil sample was further divided into two parts after removing roots and stones and air-dried for 24 hr: one for soil nutrients analysis and the other for soil microbial diversity measurement (i.e. bacteria, fungi and nematodes). The raw values from the two sampling points were averaged to represent mean soil physicochemical properties and soil microbial diversity per subplot (see detailed measurements and calculations of soil nutrients, soil and litter water capacity analysis and soil microbial diversity in Supporting Information, Appendix B). To eliminate the potential edge effects, and because some quadrats could not be sampled due to some physical constraints (i.e. tree trunks or stumps), we selected a total of 120 quadrats for further soil analysis.

Eight soil nutrient variables including soil pH; organic matter content; available nitrogen, phosphorus and potassium; total nitrogen, phosphorus and potassium were measured, and then a principal component analysis (PCA) was performed to produce a reduced set of orthogonal variables. The first axis of the PCA (soil PCA1) explained 51.3% of the total variation and was negatively correlated with organic matter and total nitrogen, which represented a soil fertility gradient from fertile to infertile soils. The second axis of the PCA (soil PCA2) explained 18.6% of the variation and represented soil nutrient availability (Table S2 in Appendix A).

An Illumina Miseq platform (TIllumina USA) was used to determine the structure of soil bacterial and fungal community whereas nematodes were extracted from 200 g of fresh soil using an updated cotton-wool filter method (Liang et al., 2009; Townshend, 1963). For each sample, the first 100 nematodes encountered on the slides were identified to genus level at 100× magnification under an inverted microscope. A detailed measurement approach for soil microbial diversity is provided in Supporting Information, Appendix B.

2.4 | Quantification of tree diversity and soil microbial diversity indices

Tree diversity (i.e. taxonomic, phylogenetic and functional trait diversity), trait composition, stand structural attributes and soil biodiversity were used to represent multiple indices of the above-ground (i.e. plant) and below-ground (i.e. soil) parts of the studied forest. Taxonomic diversity was calculated as species richness while the Shannon–Wiener index of soil fungi (H_{Fungi}), bacteria ($H_{Bacteria}$) and nematodes ($H_{Nematodes}$) was computed within each subplot.

To calculate plant functional trait diversity, we selected and measured six plant functional traits which were closely related to life-history and niche partitioning strategies (Pérez-Harguindeguy et al., 2013): plant maximum tree height (MH), WD, leaf phosphorus content (LPC), leaf nitrogen content (LNC), SLA and leaf area (LA). MH reflects the species longevity and life-history strategy, with higher values indicating that trees can benefit from high light levels in the upper canopy and have the ability to grow quickly. High WD is related to shade-tolerance and could increase survival (i.e. reduce mortality) but decrease growth. LNC and LPC are important for photosynthesis and growth, whereas leaf physical traits such as LA and SLA indicate light interception ability and trade-offs between construction cost and longevity of plant tissues (Chave et al., 2009; Pérez-Harguindeguy et al., 2013).

We calculated the plant functional diversity of each subplot as functional dispersion (FDis), a measure of the mean distance in multidimensional trait space of individual trees to the centroid of all trees (Laliberte & Legendre, 2010). This index was chosen because it is suitable for species-poor communities with only a few species. FDis was calculated for the combination of all six traits based on abundance matrices within each subplot. The community-weighted mean (CWM) of each trait value (CWM_{MH}, CWM_{WD}, CWM_{LPC}, CWM_{LNC}, CWM_{LA} and CWM_{SLA}) was calculated as the weighted species' relative basal area within each subplot (Garnier et al., 2004). A detailed measurement approach for the mentioned functional traits is provided in Supporting Information, Appendix B.

To calculate plant PD, a phylogenetic supertree was constructed using Phylomatic (http://www.phylodiversity.net) which includes updated time-calibrated phylogeny of seed plants using multigene molecular and fossil data (Zanne et al., 2014). The most widely used measure of phylogenetic metric, Faith's PD index, was calculated, which is defined as the total length of all branch lengths separating taxa in a local community (Faith, 1992).

Stand structural attributes were quantified with the coefficient of variation for tree DBH (CV_{DBH}) within each subplot, as a proxy of tree size variation (reviewed by Ali, 2019). Stands with greater CV_{DBH} might have higher light acquisition and light-use efficiency because their leaves occupy a range of light environments and span a physiological spectrum (Gough et al., 2019).

The values of each of the PD, trait composition and stand structural complexity of the first and last forest inventories were averaged to obtain one value per subplot in order to represent the averaged plant diversity, trait composition and stand structural complexity of the community during the inventory periods (Yuan et al., 2019).

2.5 | Statistical analyses

Due to the experimental design of the study area (25-ha forest plot), we were initially interested in checking the spatial autocorrelation in the response variable (i.e. FM) among subplots. We tested spatial autocorrelation among subplots in averaged FM as well as each threshold level (i.e. 50%, 75% and 95%), using Moran's *I* test (Bivand et al., 2011). We did not find any strong spatial autocorrelation correlograms for any of the distance classes (Figure S1 in Appendix A).

To examine the effects of plant species diversity and soil microbial diversity indices, as well as plant trait composition, on FM, we performed four series of multiple linear regressions models, i.e. one for averaging and three for the threshold levels (i.e. 50%, 75% and 95%) of FM. To avoid multicollinearity problems, we excluded highly correlated predictors of FM (i.e. $r > 0.60$; see Table S3 in Appendix A). For example, species richness and PD were highly correlated ($r = 0.84$), and hence, we selected PD as the surrogate of plant species diversity in the following analyses, owing to its better relationship with other predictors as well as its better predictive power for FM compared with species richness (see Figure S2 in Appendix A). Using this approach, we included two plant diversity (phylogenetic and functional trait diversity), two plant trait composition (CWM_{WD} and CWM_{SLA}), one stand structure (CV_{DBH}) and three soil microbial diversity (Shannon's diversity of fungi, bacteria and nematodes) indices as predictors of FM in the four series of multiple linear regression models. Then, for each FM index, we performed all subsets regression analysis and selected the optimal model that had the lowest AICc (i.e. Akaike information criterion adjusted for small sample sizes). However, if the difference was <2 units, we obtained the standardized regression coefficient (β) of each FM predictor using a model averaging approach (Table S4 in Appendix A).

Based on our conceptual model (Figure 1a), we tested partially confirmatory SEMs with a fixed model structure for each multifunctionality index. In the SEMs, we used the diversity (e.g. PD, CWM_{SLA}, CV_{DBH} and H_{Fungi}) and environmental (topographic slope and soil PCA1) indices obtained from the previous optimal regression model. Model fit to the data was evaluated using a Chi-square test ($p > 0.05$ indicates that the model is accepted), Bentler's comparative fit index (CFI close to 1 indicates perfect model) and the standardized root mean square residual (SRMR <0.08 indicated the best model). We simplified the initial model by dropping non-significant paths in order to improve the model fit (Figure S3).

The indirect effect of each predictor was calculated through the interaction of the standardized direct effect of a given predictor on a mediator with a direct effect of a given mediator on the response variable. More specifically, the single indirect effect was calculated by multiplying the standardized direct effects of a given predictor on FM via mediator in one route, and then we summed the multiple indirect effects of a given predictor to quantify the total indirect effect. To quantify the relative contribution of different predictors to FM, we calculated the relative importance for each predictor of FM using the ratio between the beta coefficient of a given predictor and the sum of the absolute value of beta coefficients of all predictors (Yuan et al., 2019).

To evaluate the trade-offs (negative) or synergies (positive) amongst forest functions and their relationships with FM we calculated the Pearson correlations between pairs of single functions and with FM. In addition, we used the same SEM structure (as used for multifunctionality) for each individual function, because we were interested in evaluating whether and how the same predictors of FM influence individual functions, which might provide further explanation of the underlying mechanisms and theories associated to FM.

All analyses were conducted in R 3.4.3 (R Development Core Team, 2019). Plant species diversity and soil microbial diversity indices and trait composition were calculated using the VEGAN (Oksanen et al., 2015) and FD packages (Laliberte & Legendre, 2010). The calculations of FM, the model averaging procedure and SEM analyses were performed in MULTIFUNC (Byrnes, 2014), MuMIn

(Barton, 2016) and LAVAAN (Rosseel, 2012) packages respectively. Moran's *I* test was evaluated using the SPDEP package (Bivand et al., 2011).

3 | RESULTS

The best multiple linear regression models indicated that FM, at averaging and different threshold levels, was driven by different plant species diversity and soil microbial diversity indices (Figure 2). More specifically, stand structure complexity (i.e. CV_{DBH}) was positively related to all FM indices (Figure 2a–d). Plant PD was positively related to averaged FM (FM_A) only, whereas CWM_{SLA} was negatively related to FM_A and multifunctionality at two threshold levels (FM_{T50} and FM_{T75}; Figure 2a–c). Soil fungal diversity (H_{Fungi}) was positively related to FM_{T95} only, whereas soil bacterial diversity ($H_{Bacteria}$) and nematode diversity ($H_{Nematodes}$) were not significantly related to any level of FM (Figure 2), and hence, soil bacterial and nematode diversities were not included in SEMs analyses.

The SEMs indicated that the CV_{DBH} had significant direct positive effects (β = 0.20 to 0.24) on FM across all four models (Figure 3) whereas CWM_{SLA} (β = −0.18 to −0.31) had an effect only in a subset of them (Figure 3a–c), and they both had no significant indirect effect on four FM indices (Table S5). Although H_{Fungi} had a non-significant direct effect on FM_A, the direct effect and relative

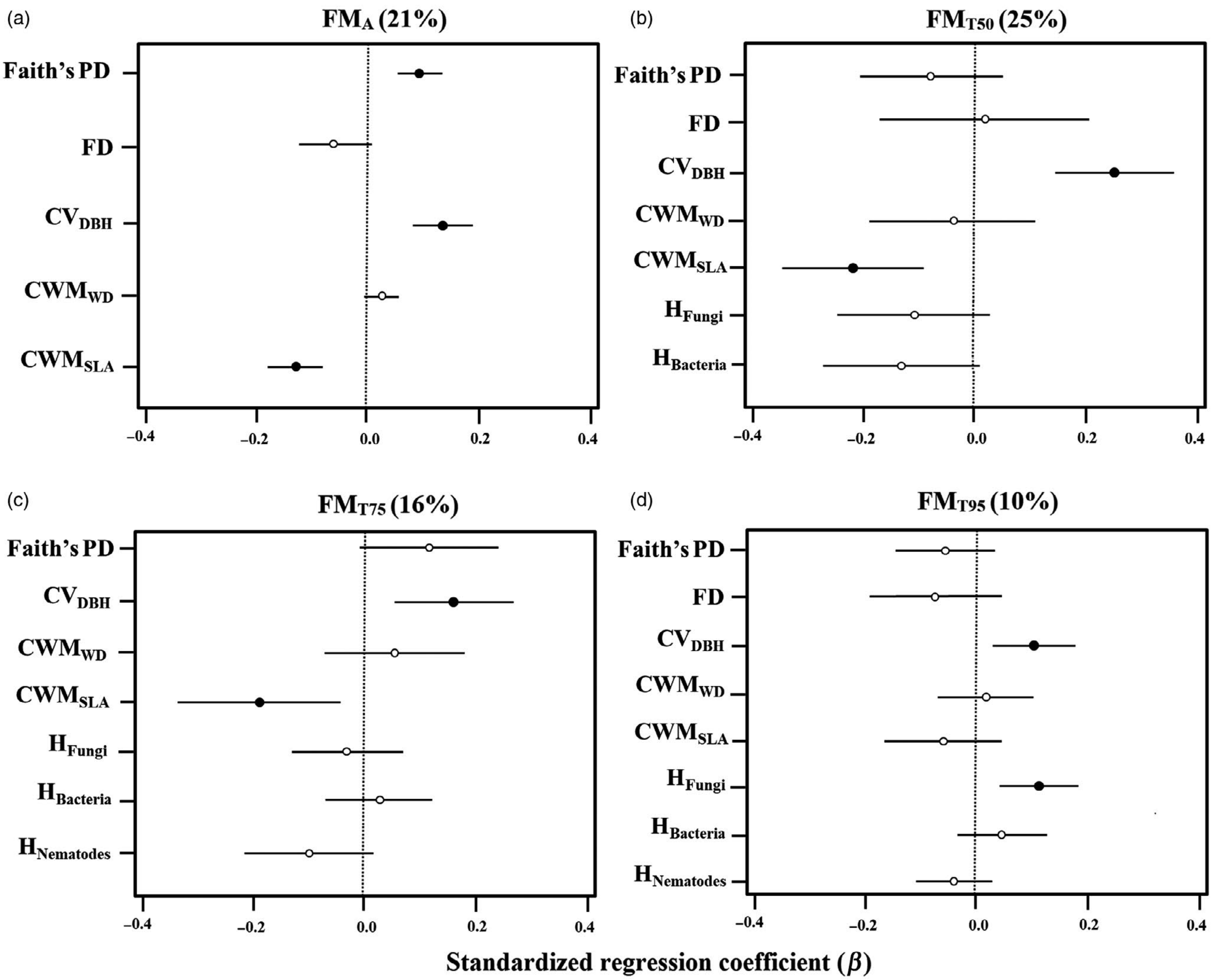


FIGURE 2 Standardized regression coefficients (β) for the explanatory effects included in the selected (a) averaged-based (FM_A), (b) 50% threshold-based (FM_{T50}), (c) 75% threshold-based (FM_{T75}), and (d) 95% threshold-based forest multifunctionality (FM_{T95}) models. Full-model R^2 is reported for each index in parentheses in the title of each panel for the selected model (see also Table S4 in Appendix A). Close circles indicate a significant effect on forest multifunctionality ($p < 0.05$) and lines indicate standard errors. CV_{DBH}, coefficient of variation of diameter at breast height; CWM_{SLA}, community-weighted mean of specific leaf area; CWM_{WD}, community-weighted mean of wood density; FD, functional trait dispersion diversity; $H_{Bacteria}$, the Shannon–Wiener index of bacteria; H_{Fungi}, the Shannon–Wiener index of fungi; $H_{Nematodes}$, the Shannon–Wiener index of nematodes; PD, Faith's phylogenetic diversity; Slope, topographic slope of subplot

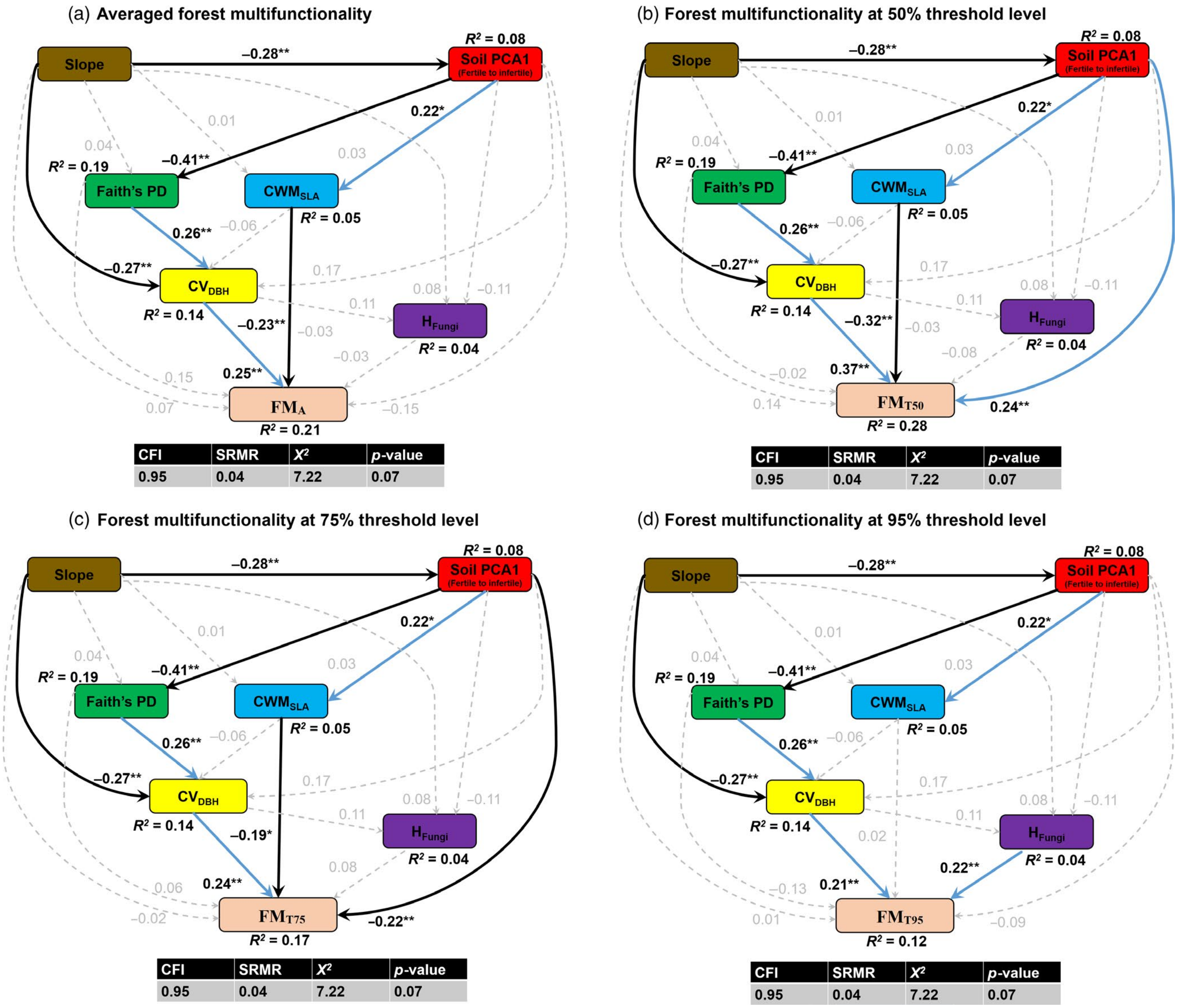


FIGURE 3 Structural equation models linking topography (slope), soil fertility (soil PCA1; fertile to infertile gradient), plant phylogenetic diversity (PD), stand structural complexity (CV_{DBH}), plant functional trait composition (community-weighted mean of specific leaf area; CWM_{SLA}) and soil fungal diversity (H_{Fungi}) with forest multifunctionality at averaged and threshold levels. Blue solid, black solid and grey dashed arrows represent significant positive, significant negative ($p < 0.05$) and non-significant effects. Values near arrows represent standardized coefficients (see Table S5 in Appendix A). For abbreviations, see Figure 2 [Colour figure can be viewed at wileyonlinelibrary.com]

contribution increased with the increasing thresholds levels of FM (Figures 3 and 4). The topographic slope had only indirect effects on FM in all models (Figure 3): a negative indirect effect through decreasing CV_{DBH} and a positive indirect effect through decreasing nutrient availability (soil PCA1). However, negative indirect effects of slope exceeded its positive indirect effect resulting in a net negative indirect effect (Table S5). Increased soil nutrients (i.e. low values of soil PCA1) had a significant opposing direct effect on FM_{T50} and FM_{T75} (Figure 3b,c), while it also had positive and negative effects on plant PD and CWM_{SLA} respectively (Figures 3 and 4). Plant PD did not have a direct effect on any of the four FM indices but it could indirectly promote FM by increasing stand structural complexity (CV_{DBH}). Collectively, the relative contribution of plant PD and soil H_{Fungi} on FM increased with increasing levels of threshold while slope and CWM_{SLA} had contrasting effects (Figure 4a).

With regard to the trade-offs between single functions, only above-ground biomass stock had a positive correlation with each of coarse woody productivity ($r = 0.53$) and soil WHC ($r = 0.35$), whereas all other correlations were relatively weak (ranging between 0.23 and −0.18 (Figure S4; Table S6 in Appendix A). Most of the single functions, particularly above-ground biomass stock and coarse woody productivity, were positively correlated with FM at averaged, and 50% and 75% threshold levels (Figure S4; Table S6). For evidence, we showed that environmental conditions, plant species diversity and soil microbial diversity were also important for driving single forest functions, even though the strength and magnitude of the individual effect varied depending on the function (Figure S5).

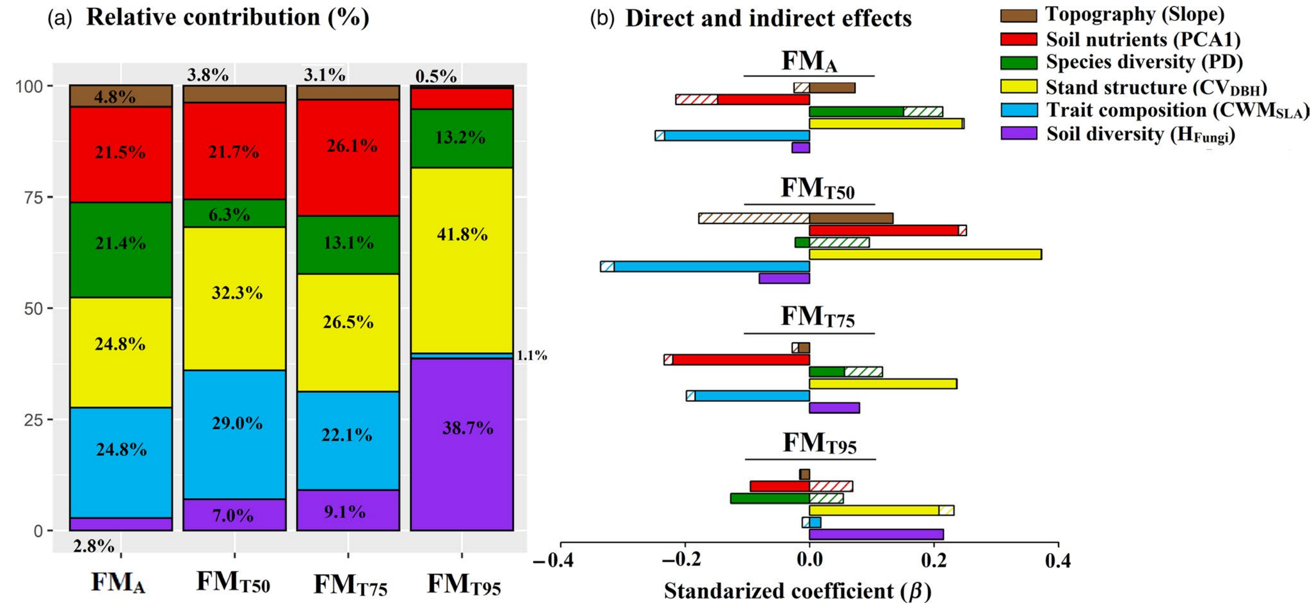


FIGURE 4 Relative contributions (a), and direct and indirect effects (b) of above-ground biodiversity, below-ground biodiversity and environmental conditions on forest multifunctionality at averaged, 50%, 75% and 95% threshold levels. The solid colour filled bar represents a direct effect whereas pattern colour filled bar represents an indirect effect. For explanation, see Figure 3 (see also Table S5 in Appendix A) [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

This study evaluates the importance of plant and soil microbial diversity to FM along a local environmental gradient (i.e. topography and soil nutrients) in an old-growth temperate forest. We provide observational evidence that communities with higher plant diversity, larger tree size variations and a lower SLA dominance are critical for sustaining FM. Interestingly, soil fungal diversity and stand structural complexity were important biotic factors for maintaining the highest level of FM. Our results showed the effects of different facets of forest diversity on FM, which is often underestimated in real-world ecosystems when multiple trophic groups, their associated biodiversity and the multiple ecosystem functions they perform are ignored (Schuldt et al., 2018; Seibold et al., 2018; van der Plas, 2019).

Phylogenetic diversity is often regarded as a predictor of ecosystem functioning based on the assumption that evolutionary diversification generates ecological differentiation (e.g. greater size variation), with distant relatives being more ecologically dissimilar than close relatives (Srivastava, Cadotte, MacDonald, Marushia, & Mirotchnick, 2012). For example, PD proved to be a more appropriate measure of biodiversity than species taxonomic diversity for predicting biomass accumulation across 79,324 forest plots in the United States (Potter & Woodall, 2014). Our study shows that stand structural complexity has a direct positive effect on FM, and PD an indirect positive effect via increasing stand structural complexity, as previously shown by several studies on single forest functions (Paquette & Messier, 2011; Poorter et al., 2015; Potter & Woodall, 2014). These results can be explained by the fact that diverse communities can build diverse and heterogeneous canopies and hence provide more ecosystem services than do species-poor stands, because of more efficient light capture and use across a range of light conditions (Gough et al., 2019). They further show that stand structural complexity had a significant positive effect on several ecosystem functions, including productivity, above-ground biomass and litter production. Stand structural complexity generally regulates or mediates the relationship between species diversity and forest functioning through several underlying ecological mechanisms across different forest biomes (Ali, 2019). For example, a higher stand structural complexity can promote greater packing of different tree canopy heights and thereby increase above-ground light capture and use at the community level (Yachi & Loreau, 2007). In addition, the negative relationship between topographic slope and stand structural complexity, and hence the indirect negative effect of topographic slope on FM via stand structural complexity, may be due to the fact that stands in benign conditions are influenced by strong competition for light, and hence, frequently develop taller, vertically stratified canopies (Jucker et al., 2018) that enhance ecosystem functioning through increased light capture efficiency (Gough et al., 2019).

Phylogenetic diversity, which was strongly correlated with species richness (r = 0.84), is an effective biotic attribute of plant diversity for predicting averaged FM, which confirmed the conclusion that plant diversity could increase FM (Felipe-Lucia et al., 2018; Gamfeldt et al., 2013). Tree diversity was also a stronger predictor of multifunctionality than microbial diversity was. However, the forest functions we selected may be more directly related to plant attributes such as the stand structure and trait composition than to soil microbial diversity (Ali et al., 2019; Prado-Junior et al., 2016; van der Sande et al., 2017; Yuan et al., 2019). As such, the strength and magnitude of the biodiversity effects are likely to be dependent on the identity of the ecosystem functions considered (Meyer et al., 2018). For example, some previous studies included functions reflecting nutrient capture and cycling (such as root decomposition rates, root biomass, potential nitrification and phosphorus retention) that are directly related to soil microbial activities (Delgado-Baquerizo et al., 2016; Jing et al., 2015; Soliveres et al., 2016). In this study, we mainly considered forest functions that are common proxies for provisioning and regulating services (Trogisch et al., 2017). For example, above-ground biomass is strongly linked to forest timber production. Seed and litterfall production are important forest functions that support the provision of food and fibre, sustain below-ground forest functioning and play key roles in the global carbon cycle (Hölting et al., 2019). The above-ground biomass of the herb layer is also strongly related to wild edible plant products and plants of cultural value, whereas seed production is the main indicator of forest regeneration ability (Li et al., 2012).

Our analysis also suggests that maintaining higher levels of ecosystem multifunctionality requires a higher soil fungal diversity (Mori et al., 2016), while other studies found that soil diversity also drove ecosystem multifunctionality at lower thresholds (Delgado-Baquerizo et al., 2016; Wagg et al., 2014). This discrepancy may be due to the fact that different functions might have different contributions to FM at different levels of multifunctionality. For example, wood productivity and above-ground carbon stock contributed more to multifunctionality at the 50% threshold level, but their relative importance became weaker at higher threshold levels. Soil fungal diversity can be more important than soil bacterial and nematode diversity for decomposing recalcitrant plant materials, and hence it could promote key ecological processes, such as nutrient cycling and litter decomposition, that connect above- and below-ground communities in terrestrial ecosystems (Delgado-Baquerizo et al., 2018). Also, fungi are known to be more tolerant to harsher condition than other soil microbes (Austin et al., 2004), and thus fungal diversity may have a large effect on temperate FM where soils remain frozen conditions during most time of the year. A wide range of soil fungi form intimate symbiotic associations with plants and can stimulate plant productivity by supplying plants with limiting nutrients (Van Der Heijden, Bardgett, & Straalen, 2008). In particular, mycorrhizal fungi generally enhance resource complementarity by providing resistance to disease and drought, as well as limiting nutrients that are otherwise inaccessible to plant roots (Van Der Heijden et al., 2008), which promotes higher levels of FM (Delgado-Baquerizo et al., 2016; Wagg et al., 2014).

The observed positive contribution of soil fungal diversity to FM rather than to single functions might be due to trade-offs between different forest functions (Byrnes et al., 2014; Zirbel et al., 2019). For example, a trade-off between above-ground biomass stock and soil carbon stock makes maximizing multiple functions simultaneously impossible (Van der Plas et al., 2018). It is important to clarify that some individual functions with positive correlations were driven by different aspects of biotic and abiotic factors, which implied the necessity of considering the role of independent and combined effects of both plant and soil microbial diversity, as well as underlying environmental conditions to maintain forest functioning (Schuldt et al., 2018; Soliveres et al., 2016). Thus, regarding the question of whether management of ecosystems for the protection of biodiversity is equivalent to managing FM, both the relationships among the specific functions measured and the dependence on biodiversity are important (Meyer et al., 2018). However, trade-offs among functions were rare in this temperate forest, which highlights the potential for 'win-win' forest management strategies to achieve multifunctional forests (Felipe-Lucia et al., 2018; Van der Plas et al., 2018).

One of the important findings of this study is that plant trait composition was an important driver of temperate FM due to the dominance of species with conservative trait values (i.e. low SLA), which is in agreement with previous studies that underlined the importance of functional identity (Prado-Junior et al., 2016; Yuan et al., 2019). However, communities dominated by conservative species are expected to have lower biomass productivity due to lower photosynthetic rates, stem hydraulic conductivity ecosystem functions, i.e. above-ground biomass, litter WHC and soil and litter production were strongly driven by low $\mathrm{CWM}_{\mathrm{SLA}}$. This result might be attributable to the fact that plant species could reduce cell elasticity, leaf water potential and continued plant growth and performance during the onset of the harsher environment (Klein, 2014). Species with low SLA also have a balanced hydraulic strategy to cope with freeze-thaw cycles since they transpire less water (Poorter & Bongers, 2006), and thus increase species performance and productivity in old-growth forests.

Moreover, we found that increased soil nutrients (i.e. lower values of soil PCA1) may relieve tree species from limited resources, and thus increase species diversity through niche creation (Dybzinski, Fargione, Zak, Fornara, & Tilman, 2008). On the other hand, however, fertile soils may allow more trees to pass the environmental filter, and hence, the selection of certain functional trait may be less important, thereby decreasing the dominant role of fast-growing acquisitive trees (Van der Sande et al., 2016), as indicated by our SEM (i.e. the significant soil nutrients $\rightarrow \mathrm{CWM}_{\mathrm{SLA}}$ path in our study).

5 | CONCLUSIONS

Our study shows the joint importance of plant species diversity and soil microbial diversity in regulating FM, as well as the importance of local environmental conditions in maintaining above- and below-ground biodiversity in natural forests. Soil microbial diversity was a key factor for promoting a higher level of FM. But conservative plant functional traits (i.e. low $\mathrm{CWM}_{\mathrm{SLA}}$) and complex stand structures (associated with a high species PD) also appeared to be important drivers of FM. Thus, both above- and below-ground biodiversity are critical to promote higher levels of ecosystem multifunctionality.

ACKNOWLEDGEMENTS

This work was funded by Strategic Priority Research Program (XDB 31030000) and the Key Research Program of Frontier

Sciences (ZDBS-LY-DQC019) of the Chinese Academy of Sciences, the National Natural Science Foundation of China (31730015, 31722010 and 41671050) and Youth Innovation Promotion Association CAS (2017241). A.A. is financially supported by the Metasequoia Faculty Research Startup Funding at Nanjing Forestry University (Grant No. 163010230). T.J. was supported by a UK NERC Independent Research Fellowship (Grant No. NE/S01537X/1). P.R.-B. was supported by the Fellowship 'Atracción de Talento Investigador' (Comunidad de Madrid, 2016-T2/AMB-1665). M.L. was supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41). The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

Z.Y. and X.W. designed the study; Z.Y., X.Z., H.L., Z.H. and X.W. collected and contributed data; Z.Y. and A.A. analysed the data and wrote the first draft, after which all the authors contributed greatly to the manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.b8gtht78m (Yuan, Hao, & Wang, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Yuan Z, Ali A, Ruiz-Benito P, et al. Above- and below-ground biodiversity jointly regulate temperate forest multifunctionality along a local-scale environmental gradient. *J Ecol*. 2020;108:2012–2024. https://doi.org/10.1111/1365-2745.13378