INTRODUCTION

Forests are highly diverse terrestrial ecosystems, offering many ecosystem services (ES; Maes et al., 2015). Besides the frequently mentioned supply of timber, energy, food and recreation (Miura et al., 2015), soil-related ES such as carbon sequestration, balancing gas emissions and maintaining biogeochemical cycles are often underestimated or even ignored (Miura et al., 2015).

Fungal guilds and soil functionality respond to tree community traits rather than to tree diversity in European forests

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Abstract
At the global scale, most forest research on biodiversity focuses on aboveground organisms. However, understanding the structural associations between aboveground and belowground communities provides relevant information about important functions linked to biogeochemical cycles. Microorganisms such as soil fungi are known to be closely coupled to the dominant tree vegetation, and we hypothesize that tree traits affect fungal guilds and soil functionality in multiple ways. By analysing fungal diversity of 64 plots from four European forest types using Illumina DNA sequencing, we show that soil fungal communities respond to tree community traits rather than to tree species diversity. To explain changes in fungal community structure and measured soil enzymatic activities, we used a trait-based ecological approach and community-weighted means of tree traits to define ‘fast’ (acquisitive) versus ‘slow’ (conservative) tree communities. We found specific tree trait effects on different soil fungal guilds and soil enzymatic activities: tree traits associated with litter and absorptive roots correlated with fungal, especially pathogen diversity, and influenced community composition of soil fungi. Relative abundance of the symbiotrophic and saprotrophic guilds mirrored the litter quality, while the root traits of fast tree communities enhanced symbiotrophic abundance. We found that forest types of higher latitudes, which are dominated by fast tree communities, correlated with high carbon-cycling enzymatic activities. In contrast, Mediterranean forests with slow tree communities showed high enzymatic activities related to nitrogen and phosphorous. Our findings highlight that tree trait effects of either ‘fast’ or ‘slow’ tree communities drive different fungal guilds and influence biogeochemical cycles.

KEYWORDS
enzyme activity, fungal diversity, fungal guilds, soil, tree traits, tree–fungi interactions
Tree species diversity loss is paralleled by a reduction in overall diversity and ES of forests (Ampoorter et al., 2020; van der Plas et al., 2016), including a decrease in microbial diversity and the turnover of soil biochemical cycles (Delgado-Baquerizo et al., 2016; Penone et al., 2019). As many ES delivered by forests depend on soil-inhabiting organisms (Delgado-Baquerizo et al., 2016), deciphering the interplay between aboveground tree diversity and belowground communities and their functional role is of paramount importance (Akira et al., 2016; Guerra et al., 2020; Miura et al., 2015).

Previously, it has been shown that forests with different levels of tree species richness such as monospecific versus multispecies stands exhibit differences in soil microbial communities, and this is commonly attributed to tree species composition and identity rather than tree diversity per se (Goldmann et al., 2015; Lejon et al., 2005; Perez-Izquierdo et al., 2017; Sun et al., 2016). The relevance of tree species composition and identity on soil microbial communities is coupled to tree traits, which are defined as morpho-physio-phenological characters that reflect growth, reproduction and survival of trees (Violle et al., 2007) and also, indirectly, forest soil characteristics (Bardgett et al., 2014). Thereby, multispecies forest systems are potentially superior to monospecific systems because they provide a higher number of ecological niches, which can further increase the number of associated soil microbial species with complementary traits, thus maximizing positive effects (Liu et al., 2018). As an example, distinct tree species influence soil biota differently due to the specific characteristics of their root exudates and quality of their root and leaf litter (Kardol & De Long, 2018). Therefore, considering tree traits helps to predict how tree composition influences soil biota and related processes, such as carbon, nitrogen and phosphorous cycles (Bardgett, 2017; Eisenhauer & Powell, 2017). However, the effects of tree traits on microbial communities and biogeochemical cycles are poorly understood, although such knowledge is a key to properly predict ecosystem effects of future climate change scenarios (Bardgett, 2017; Felipe-Lucia et al., 2018).

The main tree life strategies relate to the balance between active growth and maintaining survival under different environmental conditions (Grime, 1977; Reich, 2014; Wardle et al., 2004; Wright et al., 2004), and they are often paralleled by trait changes. Chen et al. (2016) described that tree species with thicker roots respond weakly or not at all to nutrient heterogeneity, whereby trees with thinner roots can selectively adjust root growth according to nutrient availability. Analogous to these findings, two potential pathways in nutrient-rich spaces are possible: trees forming arbuscular mycorrhiza vary in root proliferation, whereas the ectomycorrhizal trees adapt mycorrhizal hyphal proliferation searching for nutrient patches. Thereby, these variations were comprehended as a function of root diameter traits (Chen et al., 2016). The community-weighted mean (CWM) is a metric that summarizes the expression of a single trait within a given species assemblage (Garnier et al., 2004; Ricotta & Moretti, 2011). This metric is based on the ‘biomass ratio hypothesis’, postulating that traits of the most abundant species largely determine ecosystem processes (Grime, 1977). Thus, analyses of tree traits help to assess the relationships between tree performance, soil nutrient concentrations, litter decomposition rates and microbial communities (Fortunel et al., 2009; Garnier et al., 2004; de Vries et al., 2012).

Multiple traits can be integrated into a ‘plant economics spectrum’ (Wright et al., 2004). The ‘plant economics spectrum’ identifies plant life strategies that explain ‘how a species sustains a population operating in the presence of competing species, in varying landscapes and under diverse regimes of disturbance’ (Reich, 2014). Originally, this perspective of plant ecology and evolution was developed for leaf traits (Reich, 2014; Wright et al., 2004); however, plant economics spectra also exist for stems, roots and even decomposition processes (Cornwell et al., 2007; Freschet et al., 2012; Kong et al., 2015; McCormack et al., 2012; Osnas et al., 2013; Santiago, 2007). Plant traits influence soil microbial communities in line with the ‘plant economics spectrum’. Particular soil communities are linked to ‘fast’ tree traits that include processes related to the acquisition strategy of plants, such as fast biochemical cycling and high nutrient availability (Bardgett, 2017; Wardle et al., 2004; Figure 1). The corresponding plant-trait pool is commonly associated with nutrient-rich soils and includes fast-growing plant species with inexpensive tissue investment, fast turnover, high photosynthetic rates and fast foraging roots with a short lifespan (Wright et al., 2004).

The other end of the ‘plant economics spectrum’ is characterized by plants that exhibit a conservative life strategy. These plants are characterized by slow-growing species with high tissue investment, slow turnover rates, low photosynthetic rates and slow foraging roots with a long lifespan (Reich, 2014; Wright et al., 2004). This strategy is usually associated with nutrient-poor soils and slow biochemical cycling (Figure 1).

Plants adapted to fertile soils differ markedly in their ecophysiological traits from those adapted to infertile soils, which is further reflected in differences in their associated soil biota (Wardle et al., 2004). For instance, fertile soils promote bacteria-driven food webs, whereas food webs in infertile soils, such as those found in many forests, are fungus-dominated (Richard, 2017; Wardle et al., 2004). In forest soils, fungi represent a key component in terms of species richness and functionality (Blackwell, 2011; Hawksworth, 2001). Though there are many fungal lifestyles and interkingdom interactions, the commonly distinguished guilds encompass pathotrophs, saprotrophs, symbiotrophs, taxa capable of different lifestyles and a majority with yet unknown functional classification (Nguyen et al., 2016; Rai & Agarkar, 2016; Zellinger et al., 2016). Each of these guilds reacts differently to biotic and abiotic stimuli due to distinct nutrient acquisition strategies and can therefore be expected to also be affected by varying ecological factors (Schappe et al., 2020). Since trees are foundation species in forest ecosystems, their main traits directly affect symbiotrophic and pathotrophic fungal communities, and indirectly also saprotrophs through their dead organic matter input that regulates quantity and quality of substrates used by this functional group (Alberti et al., 2017; Purahong et al., 2017; Roy-Bolduc et al., 2016; Urbanová et al., 2015). Interactions amongst different fungal guilds...
modify soil carbon dynamics and nutrient availability through (a) priming effects, i.e. increasing decomposition rates, often linked to intensive carbon inputs (Yin et al., 2014), or (b) the Gadgil effect, i.e. the competition of saprotrophic and mycorrhizal fungi for limited organic resources (Fernandez & Kennedy, 2016).

Soil enzymes are mainly produced by microorganisms (Kuşcu & Ömer Karaöz, 2016). Thus, enzymatic activity is a good proxy for soil functionality, since it indicates the rate of important microorganism-mediated processes in soil such as soil C, N, P and S cycles (Adetunji et al., 2017; Baldrian, 2009). Enzymes can help to characterize the soil metabolic potential, soil fertility and soil quality in different ecosystems (Baldrian, 2009). This is especially useful in forest soils where the enzymatic activity is more stable compared with agriculture soils or grasslands (Błońska et al., 2017). This stability is mainly related to a higher accumulation of soil organic matter in forest soils (Adetunji et al., 2017; Błońska et al., 2017). Although many soil organisms are involved in decomposition and nutrient cycling processes, fungi are the most important decomposers in terrestrial ecosystems (Hättenschwiler et al., 2005; Paul, 2016; Zhou et al., 2007). This is related to the ability of fungi to decompose recalcitrant polymers. Cellulose decomposition for instance is ten times faster in the fungi-dominated litter of a Pinus abies forest than in bacteria-dominated soils (Štursová et al., 2012; Žifčáková et al., 2016). Accordingly, it is essential to address the influence of tree diversity on fungal communities and their enzymatic activities in soils to generally understand microbial processes in forest ecosystems.

This study aimed to assess the influence of CWM traits of leaves, litter and roots in tree communities on soil fungal communities using the framework of the ‘plant economics spectra’. Accordingly, we characterized the soil forest functionality by measuring enzyme activities and included them in our CWM trait analyses. We investigated 64 plots across four broad European forest types, comprising 13 main tree species across 33 different tree species assemblages, ranging from monospecific to multispecies forests. Through taxonomic profiling of fungal communities by Illumina amplicon sequencing and determination of
soil enzymatic activities, we aimed to establish links between fungal communities, their potential metabolic activities and the CWM of leaf, litter and root traits. This enabled us to test the following hypotheses: since tree composition is more important for fungal diversity than tree diversity, we hypothesized that (1) soil fungal diversity relates to tree trait diversity. Moreover, recognizing the relevance of the plant economics spectrum to understand plant species strategies, we expected that (2) tree species with fast-acquisitive strategies enhance fungal diversity. We estimated that (3) fungal community composition of saprotrophs responds positively to high-quality litter and that (4) fast root traits favour symbiotic communities. Due to interactions between tree roots and soil fungi, we expected further that (5) the enzyme activities are more strongly linked to root traits than to leaf or litter traits, and that (6) higher enzymatic activities are associated with fast tree communities.

2 | MATERIALS AND METHODS

2.1 | Site description and sampling design

The project SoilForEUROPE (https://websie.cefe.cnrs.fr/soilforeurope/) includes four study regions that are part of the comparative research platform FunDivEUROPE in European forests (Baeten et al., 2013). The regions follow a latitudinal gradient across different uneven-aged, mature European forest types: boreal forests (Finland, North Karelia, area 150 km × 150 km), hemiboreal, nemoral coniferous, mixed broadleaved–coniferous forests (Poland, Białowieża Primeval Forest, area 30 km × 40 km), mountainous beech forests (Romania, Valley of the river Râşca, Suceava, area 5 km × 5 km) and thermophilous, deciduous forests (Italy, Tuscany, area 50 km × 50 km). Among these regions, we focused on 64 plots (30 m × 30 m each, subdivided into nine 10 m × 10 m subplots; Figure S1), selected by stand evenness, tree age, tree density, tree species composition and soil type. These plots include tree monospecific and multispecies forests with three dominant trees species (Table S1). Between April and July 2017, we collected soil from the central subplot (subplot 1, Figure S1) and the four subplots in each plot corner (subplots 2–5, Figure S1). We adopted the tree-triangle approach by Vivanco and Austin (2008) to locate sampling spots within each subplot, which represent the influence of surrounding trees on a patch of soil. These spots were determined based on the dimensions of tree individuals, which we visually estimated based on diameter at breast height and crown area. These triangles consisted either of trees of the same species or of three different species. Samples were taken to cover the influence of roots from the three tree species, their potential metabolic activities and the CWM of leaf, litter and root traits. This enabled us to test the following hypotheses: since tree composition is more important for fungal diversity than tree diversity, we hypothesized that (1) soil fungal diversity relates to tree trait diversity. Moreover, recognizing the relevance of the plant economics spectrum to understand plant species strategies, we expected that (2) tree species with fast-acquisitive strategies enhance fungal diversity. We estimated that (3) fungal community composition of saprotrophs responds positively to high-quality litter and that (4) fast root traits favour symbiotic communities. Due to interactions between tree roots and soil fungi, we expected further that (5) the enzyme activities are more strongly linked to root traits than to leaf or litter traits, and that (6) higher enzymatic activities are associated with fast tree communities.

2.2 | Soil, environment and trait data

The FunDivEUROPE (https://data.botanik.uni-halle.de/fundiveurope/datasets) database holds several data sets related to the 64 plots of SoilForEUROPE (Table S1). Here, we used 1) locational variables: latitude, longitude, altitude, annual mean temperature and annual mean precipitation (Baeten et al., 2013); 2) edaphic variables: soil type, C stock, N stock, C/N ratio, bulk density, texture (% sand, % clay) and pH (summarized in Table S1) (Dawud et al., 2016; De Wandeler Hans, 2012); and 3) tree basal area and other tree variables (Table S2) were used in the package ‘FD’ (Laliberté & Legendre, 2010; Laliberté et al., 2014) for R (R Development Core Team, 2019) to generate CMWs for traits of leaves (dry matter content, nitrogen content and surface area), litter (cellulose content, lignin content, calcium content, nitrogen content, total polyphenol content and litter decomposition) (Baeten et al., 2013; De Wandeler et al., 2016; Garnier et al., 2004; Jucker & Bouriaud, 2014; Katge et al., 2020; Ratcliffe et al., 2013).

We included only traits of absorptive roots, because they represent the absorptive portion of the fine roots according to the functional classification of McCormack et al. (2015). We determined ectomycorrhizal colonization (Figure S2) by counting the root tips colonized by ectomycorrhizal fungi per cm² under the stereomicroscope. Absorptive roots were scanned with a flat-bed scanner (at 800 dpi). The software WinRHIZO (Regent Instruments, 2009) was used to analyse root length, root surface area, volume and diameter for each sample. Oven-dried samples (40°C, at least 72 h) were weighted with a precision scale to quantify specific root length (SRL) and root tissue density (RTD). Root length density was calculated as root length per fine-earth volume. Finally, total organic nitrogen concentration was determined by dry combustion (Elementar Vario El Cube; Elementar Analysensysteme GmbH).

CWMs were evaluated at the plot level by weighing the influence of individual species with their relative basal area (at 1.3 m stem height) of the target trees. Principal component analyses (PCA) were then performed separately for leaf, litter and root traits as well as for edaphic and locational variables (Figure S3). From each of the PCA computations, the first axis scores were used in all subsequent analyses.

2.3 | DNA extraction, amplification of ITS genes and Illumina sequencing

Total genomic DNA was extracted from 0.5 g of each subplot sample using a Power Soil™ DNA Isolation Kit (Qiagen Laboratories Inc.) following the manufacturer’s instructions. After pooling DNA at the plot level, the internal transcribed spacer (ITS) region 2, a widely used fungal marker (Nilsson et al., 2019; Schoch et al., 2012), was targeted for DNA amplification. For the PCR, we used a primer mix containing P5-5 N-ITS4 and P5-6 N-ITS4 together with P7-3 N-fITS7 and P7-4 N-fITS7 (Gardes & Bruns, 1993; Ihrmark et al., 2012; Leonhardt et al., 2019). Amplification of each sample was performed in triplicate using 7.50 μl of HiFi HotStart ReadyMix DNA Polymerase
2x (Kapa Biosystems) and 0.30 μl (10 μM) of each primer with 2 μl of template (10 ng/μl concentration to amplified) with a final volume of 15 μl. PCR conditions were as follows: 3 min at 95°C, followed by 30 cycles of 95°C for 30 s, 55°C for 30 s and 72°C for 60 s, with a final extension of 72°C for 7 min. Success of amplification of each reaction was verified by electrophoresis with ethidium bromide staining in a 1.5% agarose gel. Triplicate PCR products were pooled, and 25 μl amplicons were purified with AMPure XP beads (Beckman Coulter). Subsequently, the Illumina index and sequencing adapters were added by PCR using a Nextera XT Illumina Index Kit (Illumina), according to the manufacturer’s instructions. Library quantification was conducted with the Quant-iT PicoGreen dsDNA assay. Afterwards, samples were pooled to equal molarity. Fragment sizes and quality of pooled samples were evaluated using an Agilent High Sensitivity DNA assay measured with an Agilent 2100 Expert (Agilent Technologies), following the Illumina recommendations. Paired-end sequencing of 2 x 300 bp was performed with a MiSeq Reagent Kit v3 on an Illumina MiSeq System (Illumina Inc.) at the Department of Soil Ecology, UFZ—Helmholtz Centre for Environmental Research in Halle (Saale), Germany.

2.4 | Bioinformatics

Raw fungal sequences were extracted based on their unique barcodes. The bioinformatic workflow was mainly based on MOTHUR (Schloss et al., 2009; Schöps et al., 2018) (Figure S4 for rarefaction curves) and OBITools (Boyer et al., 2016) implemented in the pipeline DeltaMP (https://github.com/lentendu/DeltaMP/). Briefly, primers were detected allowing only five mismatches and cut-off, and sequences with at least 50 nt length were quality-filtered and trimmed to reach an average quality Phred score of 20. The paired-end reads were merged employing PandaSeq algorithm with a threshold of 0.6 and a minimum overlap of 20 nucleotides. The sequences were clustered into operational taxonomic units (OTUs) by 97% sequence identity using cd-hit-est (Fu et al., 2012). The taxonomy of the most abundant read per OTU was assigned according to the UNITE vi7 reference database using the Bayesian classifier (Nilsson et al., 2018). FUNGuild V1.0 tool was used to parse fungal taxonomy and establish ecological guilds (Nguyen et al., 2016). Using the information from FUNGuild, the ‘overall’ fungal communities were grouped into three main functional guilds—‘pathotroph’, ‘saprotroph’, ‘symbiotroph’ and ‘multiple trophic modes’, i.e. all OTUs that potentially switch between trophic modes during their life cycles, and ‘unassigned’, i.e. OTUs without sufficient taxonomic classification for functional description.

2.5 | Potential enzyme activity

Functionality in all soil samples was evaluated by measuring the enzymatic activity potentials of acid phosphatase (EC 3.1.3.2), N-acetylglucosaminidase (EC 3.2.1.50), xylosidase (EC 3.2.1.37), cellobiohydrolase (EC 3.2.1.91) and β-glucosidase (EC 3.2.1.21). The determination of the five hydrolytic enzyme activities was based on 4-methylumbelliferone (MUB)-coupled substrates (German et al., 2011; Sinsabaugh et al., 2003). We chose hydrolytic enzymes because they represent the main biogeochemical cycles and are a good proxy for microbial decomposition processes and nutrient availability for substrates such as cellulose, hemicellulose, chitin and phosphate (Allison et al., 2011; Baldrian, 2009). Approximately 0.3 g of fresh soil was dispersed into 50 ml of 50 mM Na acetate buffer (pH 5) through sonication for 5 min. The soil suspensions were added to the respective MUB-coupled substrates in a microtiter plate with eight technical replicates and incubated for 1 h at 25 ± 1°C in the dark. Shortly before measurement, NaOH was added to all wells to enhance fluorescence of MUB, which was excited at 360 nm and measured at 465 nm using a Tecan Infinite® F200 PRO plate reader (TECAN). Fluorescence values in the assay and control wells were corrected with autofluorescence values of the soil suspension and buffer, respectively. MUB standards (1.25 and 2.5 μM) dissolved in buffer and soil suspensions were used to calculate emission and quench coefficients. Enzyme activities (nmol x h⁻¹ x g dry soil⁻¹) were calculated according to German et al. (2011) and corrected for soil water content, which was determined with a Mettler Toledo HB43-S Halogen Moisture Analyzer (Mettler Toledo GmbH).

2.6 | Statistical analyses

Statistical analyses were performed using R software (R-v3.6.1, R Development Core Team, 2019 R-v3.6.1) and the packages phyloseq (v1.30.0) (McMurdie & Holmes, 2013) and vegan (v2.5.6) (Oksanen et al., 2017). Initially, our data was normalized by rarefying to the lowest number of sequences among the samples, in our case 32,466 reads per sample. We retained OTUs with at least two reads in more than 10% of the samples.

To determine the tree species richness effects on fungal diversity, we calculated the Shannon index (Shannon, 1948). To test whether fungal diversity was impacted by the forest diversity level (monospecific or multispecies) or forest type, we performed analysis of variance (ANOVA) after testing for normal distribution with the Shapiro test and Q–Q plots, followed by Tukey’s HSD post hoc test (Mendiburu, 2010). To evaluate whether the economics spectra favour fungal diversity, we used the computed PCAs that summarize CWM values of leaf, litter and root traits together with Pearson’s correlation analysis of the fungal Shannon diversity and the PCA1 axes from each spectrum of CWM traits. Likewise, linear mixed models (LMMs) using forest type as random effect were calculated.

To estimate the importance of forest type, tree community composition and tree species diversity effects on fungal community composition, we performed analyses of similarities (ANOSIM). Hence, we calculated the Bray–Curtis distances of the fungal community composition and visualized them by using nonmetric multidimensional scaling (NMDS). Moreover, the function ‘capscale’ was employed to perform distance-based redundancy analysis (db-RDA), using forest type as the main variation factor to diminish regional
effects. Variation partitioning was performed on the fungal community composition data to determine the variation explained by locational, edaphic and tree variables, and these were retained or removed on the basis of Vif values, using a value of 10 as threshold to evaluate collinearity (Hair et al., 1995). In addition, canonical analysis of principal coordinates (CAP) was used to explore the weight of

FIGURE 2  Pearson’s correlations between the Shannon diversity of different fungal guilds and the first PCA axes for CWM traits for leaves (a, b), litter (c, d) and absorptive roots (e, f); (a), (c) and (e) overall fungal community (blue line); (b), (d) and (f) overall community (blue line) and specific fungal guilds. Note the different scaling of the y-axes in the left and right columns of panels. Shaded areas represent the 95% confidence intervals for each prediction. Arrows below each panel indicate the continuum of the tree community trait composition. Leaf and absorptive root traits range from fast to slow tree community traits. Litter traits range from low quality to high quality. Aa—Abies alba, Ap—Acer pseudoplatanus, Bp—Betula pendula, Cb—Carpinus betulus, Cs—Castanea sativa, Fs—Fagus sylvatica, Oc—Ostrya carpinifolia, Pa—Picea abies, Ps—Pinus sylvestris, Qc—Quercus cerris, Qi—Quercus ilex, Qp—Quercus petraea, Qr—Quercus robur. Details on individual plots can be found in Table S1.
specific variables of the first PCA axes for CWM traits, and edaphic and locational variables on the fungal community composition. Significant differences in variance were evaluated using permutation multivariate analysis of variance (PERMANOVA).

To identify differential abundant fungal OTUs and their assigned ecological guilds along the spectra, the raw OTU data was used for robust differential abundance analyses of fungal communities performed with DESeq2 (v1.26.0) (Love et al., 2014), employing the Wald tests and the Benjamini–Hochberg (BH, aka ‘FDR’) adjustment. We estimated the main effects on PCA1 values from leaf, litter and absorptive roots traits as well as from locational and edaphic variables. Forest type was used in all models as a fixed factor, since it explained a large proportion of variance (i.e.: abundance – forest type + PCA1). Differences in differentially abundant OTUs among the fungal guilds for each tree community trait spectrum were evaluated by Fisher’s test, using the functions ‘pairwiseNominalIndependence’ and ‘cldList’ from the package rcompanion (v2.3.25) (Mangiafico, 2017) with a threshold of 0.05.

Finally, at the soil functionality level, to associate enzymes with the different spectra and tree community traits, the data from the five enzymes were centred around the mean and scaled to the standard deviation with the ‘scale’ function. Enzymatic activities were evaluated across leaf, litter and absorptive root spectra by linear correlation analyses. We used LMM of the R package glmmTMB (1.0.0) (Brooks et al., 2017), to determine the effect of abiotic, biotic factors, fungal guild’s diversity and their interactions on enzyme activity variability. We evaluated the effect of these variables on the first two PCA axes for the enzyme activities. Due to the particular positive responses of N-acetylglucosaminidase and phosphatase to the spectra, we additionally used these enzymes as response variables for the first PCA axes of leaf, litter and root trait spectra, as well as edaphic and locational variables using forest type as random factor, to assess the additional effects of tree traits to environmental and biotic diversity factors.

3 | RESULTS

3.1 | Relationships between fungal diversity, forest diversity and tree trait spectra

To determine the impact of tree species richness on fungal diversity, we compared the forest diversity levels among all study regions. We observed a higher fungal Shannon diversity in multispecies forests than in monospecific stands (ANOVA, F value = 4.34, df = 1, p = 0.041, Figure S5 (a)). Moreover, we found a significant impact of forest type (ANOVA, F value = 11.89, df = 3, p < 0.001, Figure S5 (b)), with the lowest and highest fungal diversity in thermophilous and hemiboreal forests, respectively, which differ in climatic and edaphic conditions (Table S1). Because our main interest was to unravel tree trait effects on fungal diversity, we performed PCA to summarize CWM trait values. The PCA showed that leaves and roots exhibiting conservative traits were associated with high values of CWM traits on the first PCA axis (Figure S3 (a) and (c)). In addition, high-quality litter correlated positively with high values of CWM traits on the first PCA axis (Figure S3 (b)). With this outcome, we focused on the relationships between the fungal Shannon diversity and the first PCA axis for CWM traits of leaves, litter and roots (Figure 2, Figure S6 separated by forest types). To compare tree traits and environmental factors, we used the first PCA axis of edaphic and locational variables to identify environmental effects using the same approach (Table S3. Figure S7 (a) and (b)).

The fungal Shannon diversities were similar for plots with the same tree composition (Figure 2 (a), (c) and (e)). While leaf traits did not show linear correlations (Figure 2 (a) and (b)), traits of litter (Figure 2 (c) and (d)) and roots (Figure 2 (e) and (f)) were correlated with the fungal Shannon diversities, though at different strengths for the individual fungal guilds. Positive correlations with litter traits indicated that the fungal Shannon diversity increased with higher litter quality (enriched with polyphenols and nitrogen; Figure 2 (c) and (d)). Tree communities with high root N concentrations and high specific root length also had higher fungal diversity (compare Figure 2 (e), (f) and Figure S3 (c)). Even though fast tree communities displayed a higher degree of mycorrhizal colonization (Figure S3), we observed no correlation between the Shannon diversity of symbiotrophic fungi and root traits (Figure 2 (f)).

3.2 | Relationships between tree community traits and fungal community composition and fungal guilds

Our study allowed us to explore the impacts of forest type, tree community composition and tree species diversity on the fungal community composition. The ANOSIM of fungal community
composition revealed a dominant influence of forest type ($r = 0.85$, $p < 0.001$) and also a significant impact of tree community composition ($r = 0.65$, $p < 0.001$). In contrast, tree species diversity (monospecific versus multispecies) did not affect fungal community composition ($r = 0.0076$, $p = 0.275$). Consistently, NMDS showed close clustering of fungal communities not only from the same forest type, but also from plots with the same tree identity within forest types (Figure S8). Likewise, db-RDA revealed that forest type and tree species composition explained 34% and 41% of the variance in fungal community, respectively. Tree diversity levels had no significant influence (< 1%). Variation partitioning revealed an explanatory value of the edaphic conditions of 8.5%, while locational variables explained 4.2%, and tree CWM traits, 1.9% of fungal variation in community structure (Figure 3). However, importance of those variables differed across the different forest types, that is tree traits explain 6%–16% of variance at regional scale, and for Hemiboreal forests, the tree traits were even better predictors than soil and location. Conversely, those effects were less pronounced in thermophilous deciduous forest (Table S4).

We were further interested, which specific variables influence the fungal community composition variations most. Therefore, we performed a CAP analysis, which included traits of leaves, litter and roots as well as edaphic and locational variables and explained 26% of the variance among fungal communities (Figure 4 (a)). The absorptive root traits showed a stronger correlation with fungal community composition than leaf and litter traits. Within the set of root parameters, particularly strong correlations with fungal community composition were found for parameters linked to root quality, that is RTD and nitrogen concentration (Figure 4 (a)). Our PERMANOVA showed that root ($R^2 = 0.37$), litter ($R^2 = 0.22$) and leaf ($R^2 = 0.19$) traits all significantly affected the fungal community composition (Figure 4 (a)). Leaf surface area was the trait explaining most of the variation within fungal communities from the leaf trait spectrum, whereas the contents of cellulose and lignin as well as nitrogen and calcium contents in litter also explained fungal variations (Figure 4 (a)). In addition, we compared the correlation of tree CWM traits associated with soil fungi to those exerted by locational and edaphic variables using the PCA1 values (Figure 4 (b)), as well as the individual variables (Figure S7 (c)) to illustrate that apparently not only environmental variables affect fungal communities. In general, CWM traits were correlated with locational and edaphic variables. Edaphic variables such as pH, carbon/nitrogen ratio and percentages of clay and sand showed a significant correlation with fungal community composition ($R^2 = 0.32$; Figure S7 (c)). Likewise, all locational variables showed a strong impact on fungal communities ($R^2 = 0.36$; Figure S7 (c)).

To explore the relationships between tree community traits and specific members of the fungal communities in soil, we identified the fungal OTUs exhibiting differential abundances along the leaf, litter and root trait spectra and linked them to their ecological guilds (Figure 5). The DESeq2 results showed that, from the total

![FIGURE 4](https://image-url)

**FIGURE 4** Canonical analyses of principal coordinates for fungal communities. Colours indicate the forest types. (a) Arrows represent correlative direction and strength of tree CWM traits for leaves, litter and absorptive roots, and (b) the first PCA axes of environmental (locational, edaphic) and biological (leaves, litter, roots) factors; leaf LDMC—dry matter content, leaf N—nitrogen content, leaf SLA—surface leaf area, litter, cellulose—cellulose content, litter lignin—lignin content, litter Ca—calcium content, litter N—nitrogen content, litter polyphenols—total polyphenol content, root Diam—diameter, root Myc—mycorrhizal colonization intensity, root N—nitrogen concentration, root RLD—length density, root RTD—tissue density, root SRL—specific root length.
of 8,661 fungal OTUs (Figure 5 (a)), the proportion of all fungal OTUs with differential abundances (1072 in total, Table S5) varied according to the different tree trait spectra: for the leaf spectrum around 2.8%, for the litter spectrum 5.3% and for the absorptive roots 4.3% of fungal OTUs, respectively (Figure 5 (b)). Interestingly, the symbiotrophic guild showed the largest proportion of differentially abundant OTUs for each of the spectra (Figure 5 (b)). For the litter spectrum, a high proportion of symbiotrophic OTUs was more abundant under low litter quality conditions, whereas saprotroph and unassigned OTUs were often more abundant in plots with higher litter quality (Figure 5 (d) and Table S5). Symbiotrophs were most responsive to tree root traits, and we observed the greatest enrichment of symbiotrophic OTUs in the soil of fast tree communities (Figure 5 (e)).

3.3 Relationships between the tree trait spectra and soil functionality

To evaluate the dependency of soil functionality on the tree community traits, soil enzymatic activities were correlated with the first PCA axes of leaf, litter and root CWM traits, respectively (Figure 6). We observed that xylosidase activity was significantly associated with leaf traits \((p = 0.019, r = 0.29, R^2 = 0.086)\) and that the activity was lower in soils with fast tree communities than in those with slow tree communities (Figure 6 (c)). The same pattern, even though not significant, was observed for N-acetylgalcosaminidase and phosphatase activities (Figure 6 (a) and (b)). In contrast, the leaf traits did not show significant relationships with C-cycling enzymes, cellobiohydrolase and \(β\)-glucosidase (Figure 6 (d) and (e)). In case of litter traits, the xylosidase activity was negatively correlated with the PCA1 \((p = 0.032, r = -0.26, R^2 = 0.072)\), i.e. plots with tree communities that show a high litter quality displayed a lower soil enzymatic activity (Figure 6 (h)). The other litter traits did not show significant linear correlations with the soil enzyme activities. However, the enzymes responded differently to the CWMs of absorptive root traits. While xylosidase activity was higher in fast tree communities, phosphatase, chitinase and \(β\)-glucosidase activities were higher in slow tree communities (Figure 6 (k–o)).

Finally, our results showed the highest phosphatase and N-acetylgalcosaminidase activities in thermophilous deciduous forests in Italy, the highest \(β\)-glucosidase and cellobiohydrolase were detected in mountainous beech forests in Romania, and the highest xylosidase activity was found in the hemiboreal forest in Poland (Figure 7 (a) and (b)). Moreover, the forest diversity did not show an effect on enzyme activity (Figure 7 (b)). An even stronger influence of forest type resulted in three main groups of enzymatic activity: hemiboreal forests contrasting to thermophilous deciduous forests...
or mountainous beech forests together with more sparsely plots from boreal forest (Figure 7 (b)). Our LMM (Figure 7 (c)) showed a high importance of the tree variables, specially litter quality and root traits on the first axis shown in Figure 7 (b), which explained almost 50% of the enzyme variation. The second axis of this PCA explained another 24% of the enzyme activity variation, and the

**FIGURE 6** Linear correlations of enzymatic activity of phosphatase, N-acetylglucosaminidase, xylosidase, β-glucosidase and cellobiohydrolase in relation to the CWM trait spectra of leaves (a–e), litter (f–j) and absorptive roots (k–o). Arrows indicate the continuum of the tree community trait composition. Leaf and absorptive root traits range from fast tree trait composition to slow tree trait composition. Litter traits range from low quality to high quality. For significant linear correlations, $p$-values as well as $r$ and $R^2$ values are given in the respective panels. Shaded areas represent the 95% confidence intervals for the predictions.
environmental variables appeared to be of significant importance (Figure 7 (c)). Individual fungal guild diversity had no significant impact on the enzymatic activities. However, several interactions of tree and environmental variables with fungal diversity were significantly influencing enzyme activities (Figure 7 (c)). Complementing the soil functionality, our study revealed that litter decomposition decreases with decreasing latitudinal gradient from boreal to thermophilous deciduous forests (Figure S9).

### 4 | DISCUSSION

#### 4.1 | Trait-based approach to understand tree–fungi interactions

It was previously shown that CWMs, supported by the 'biomass ratio hypothesis', facilitate the determination of the dominant tree traits shaping fungal communities in forest soils (Grime, 1977; Ricotta &
Moretti, 2011; de Vries et al., 2012). This trait-based approach appeared to be more informative than a simple correlation between tree identity or diversity and fungal diversities. Taxonomy-based views often have limited power for explaining assembly mechanisms of soil microbial communities and plant–soil feedbacks (Bardgett, 2017; Wardle et al., 2004). In our study, fungal community composition differed strongly between forest types and the divergences appeared to be rather driven by tree identity than by tree diversity, whereby root CWM traits showed the highest impact on the fungal community composition. At the functional level, the enzymes xylosidase, phosphatase and N-acetylglucosaminidase were especially affected by root CWM traits. The N and P enzymatic activities increase with decreasing latitude and rather conservative tree strategies. This complements recent works such as Buzzard et al. (2019), Sweeney et al. (2020) and Spitzer et al. (2020), who used trait-based ecology to explore plant–microbial interactions.

4.2 | Response of fungal guild diversities to tree economics spectra

In accordance with our first hypothesis, fungal diversity correlated with the tree community traits. Specifically, we found that the overall fungal diversity, as well as the diversity of specific fungal guilds, was mainly affected by traits of absorptive roots and leaf litter. Overall community diversity as well as symbiotroph and pathotroph diversities increased with high polyphenol and nitrogen contents in litter. Polyphenols have been found either to stimulate or to inhibit spore germination and hyphal growth (Hättenschwiler & Vitousek, 2000). Trees with high concentrations of polyphenols potentially trigger the diversity of pathotrophic and symbiotrophic fungi (Simon et al., 2018). In addition, higher diversity may be promoted by these tree species because of the low concentration of lignin in their litter, which facilitates nutrient release and allows growth of less-specialized soil fungi (Cotrufo et al., 2015; Paul, 2016). Previous studies indicated that niche partitioning through specialized resource use may be an important mechanism by which soil microbial diversity is maintained (Hanson et al., 2008; Vivelo & Bhatnagar, 2019). Moreover, lignin content significantly affects the overall biomass, fungal community structure and diversity, suggesting that high lignin content niches select for specific fungal taxa (Osono et al., 2003; Pioli et al., 2018; Talbot & Treseder, 2012). For example, just a few species of white-rot, brown-rot and soft-rot fungi dominate lignolytic structures compared with the high number of fungal species using more simple substrates in less lignolytic environments (Krishna & Mohan, 2017; Naranjo-Ortiz & Gabaldón, 2019).

With respect to the root trait spectrum, high specific fine-root length and high root nitrogen concentrations, as found for example in monocultures of Carpinus betulus and Quercus robur, were associated with increased overall fungal diversity. Conversely, fungal diversity was lower in soils associated with trees that invest more resources in traits such as RTD, which increases the tree’s lifespan, for example Quercus cerris and Quercus ilex. This finding supports our second hypothesis that fast-acquisitive strategies enhance fungal diversity. These tree effects can be explained by short-lived fine-root systems, which produce more root litter than long-lived fine-root systems (McCormack & Guo, 2014). Hence, there is a higher substrate availability for fungi associated with trees with acquisitive traits, consequently saprotrophs and several fungi from the unassigned group grow on these substrates and therewith increase fungal diversity (Beidler & Pritchard, 2017). Likewise, these traits enable symbionts to establish interactions with fine roots (Beidler & Pritchard, 2017; Fernandez & Kennedy, 2016). Multispecies forest plots exhibited a range of expressed traits, and the fungal Shannon diversity varied with tree species composition. Following the ‘biomass ratio hypothesis’, the traits of the most abundant tree species should exert the largest influence on the fungal diversity in a mixed forest, which probably also hides the trait impact of less abundant trees. However, the less abundant trees may offer small but different ecological niches, which result in higher fungal diversity. Thus, the impacts of tree diversity levels on fungal diversity are mainly observed when comparing large gradients of tree species diversity (Weißbecker et al., 2019).

The effect of root traits was particularly evident for the diversity of pathogenic fungi. Roots with thinner and lower-quality tissues may be more susceptible to pathogenic infections, since specialized fungal cell structures such as appressoria may be more successful in readily penetrating the plant cuticle, boosting tissue colonization and causing host plant immunity depression followed by enhanced diseases (Zeilingher et al., 2016). The specificity of the pathogens towards tree species is mediated by the expression of defence traits, such as tissue quality, tissue density, phenol content or mycorrhizal associations (Nicole et al., 1992; Rishbeth, 1972). Consequently, closely related tree species with similar traits may host the same pathogens (Desprez-Loustau et al., 2016). Variations may be related to trade-offs between growth and tree defence trait expressions amongst tree species (Desprez-Loustau et al., 2016), with faster-growing plants and trees having a lower pathogen and herbivore tolerance due to the metabolic cost of resistance (Fine et al., 2006; Lind et al., 2013; Oliva et al., 2012). Therefore, the low investment in defence traits leads to a higher tree susceptibility and increases the number of potential pathogens.

We found no response of the saprotroph or symbiotroph Shannon diversity along the root spectrum. Fungal saprotrophs are able to produce multiple extracellular enzymes, allowing them to keep growing even in the presence of refractory structural compounds in the soil organic matter (Krishna & Mohan, 2017). This substrate-use plasticity maintains a high diversity of fungal saprotrophs across tree communities with differing traits. Remarkably, the diversity of symbiotrophic fungi was also not affected by the tree root traits, even though our study plots were exclusively composed of ectomycorrhizal trees except for Acer pseudoplatanus. Ectomycorrhizal fungi form a polyphyletic group with the capacity to forage heterogeneous and patchy soil resources while maintaining multiple tree associations (Buscot, 2015). These features may explain the stable fungal symbiotroph Shannon diversity along the
tree root trait spectrum. Alternatively, changes in the fungal symbiotroph diversity might be distinguishable in deeper soil layers or directly in specific plant compartments, comparable to the results on mycorrhizal colonization. Our study analysed the upper 10 cm soil layer because most significant changes in the soil take place there due to the accumulation of aboveground and belowground litter (Ana et al., 2015; Uri et al., 2012). However, the whole fungal community dynamics and interactions with tree traits range through several soil horizons (Ana et al., 2015). For a better understanding of ecological inferences, the need to study additional layers and explore particular fungal groups with additional approaches, such as co-occurrences networks, joint species distribution models or machine learning methods, is given. This would reveal detailed interactions of tree traits, fungal communities and their influence on biogeochemical cycles (Hao et al., 2020; Lembrechts et al., 2020; Toju et al., 2016). Therefore, this study offers a basic idea, how symbiotrophic diversity might be related to root traits. But more work is needed for particular fungal groups such as mycorrhizal, endophytes or lichens that reveal specific diversity changes under a ‘plant economics spectrum’ framework.

4.3 | Tree community traits and their effect on the fungal community structure

Our results confirm previously described impacts of geography and soil properties on the soil fungal communities (Perez-Izquierdo et al., 2017; Prober et al., 2015; Tedersoo et al., 2015; Urbanová et al., 2015). However, following the recommendations of previous studies (Buzzard et al., 2019; Prescott & Grayston, 2013; Tedersoo et al., 2014), we focused on the effects of tree community traits on soil fungi.

We found fungal OTUs with differential abundances according to leaf and particularly litter traits. The relationship between litter quality and the dominant fungal guilds in soils explains community shifts, since litter quality changes due to decomposition: with a progression from complex to more simple structures, loss of easily attainable carbon and the accumulation of recalcitrant compounds (Krisha & Mohan, 2017; Purahong et al., 2016; Vivelo & Bhatnagar, 2019). Moreover, the decomposition of litter can result in a high proportion of basic cations, such as Ca\(^{2+}\) and Mg\(^{2+}\), which alter the soil pH and nutrient availability (Lladó et al., 2018; Nordén, 1994), and hence affect fungal communities (Goldmann et al., 2015). Litter quality is the predominant driver for nutrient content and availability in soils (Freschet et al., 2012). Consequently, and in accordance with other studies (Sterkenburg et al., 2015; Wu et al., 2019), we found an enrichment of fungal unassigned and saprotrophic OTUs stimulated by high-quality litter, that is high nutrient input, which verifies our third hypothesis. In contrast, at low litter quality, when the nutrient input to the soil is restricted, we found an enrichment of fungal symbiotrophs. This effect can be attributed to the tree-mycorrhizal strategies to reach nutrients in low fertility soils: the mycorrhizal fungi supply plants with water and nutrients in exchange for photosynthates and this resource-use complementarity can stimulate several mycorrhizal types (Ferlian et al., 2018).

Regardless of the effects of aboveground tree traits, the highest impact on fungal communities was exerted by absorptive root traits according to CAP and PERMANOVA. We found the commonly reported trade-off between RTD and root nitrogen concentration, that regulates ectomycorrhizal root colonization intensity, and therefore tree strategies to forage nutrients in warm and cold regions, respectively (Chen et al., 2016, 2018; Defrenne et al., 2019). In relation to the root traits, our analyses indicated an enrichment of differentially abundant symbiotrophic fungal OTUs in soils of the fast tree communities, a result supporting our fourth hypothesis. These symbiotrophic taxa can support tree growth by improving nutrient acquisition, which is, moreover, often coupled with less necessity for carbon investment in root growth (Chen et al., 2016). Higher symbiotrophic abundance in fast tree communities is potentially linked to high root respiration and a large amount of exudate secretion (Bardgett et al., 2014; De Deyn et al., 2008; Phillips et al., 2011). The latter stimulates growth of fungal taxa, particularly that of symbiotrophs such as mycorrhizal fungi, which are commonly present in the soil as propagules, being a reservoir of potential tree partners (Buscot, 2015; Jones et al., 2004; Sun et al., 2017). By breaking down organic matter, symbiotrophs can promote the subsequent growth of other fungal guilds, which induces shifts within the whole fungal community (Bardgett et al., 2014; Fernandez & Kennedy, 2016; Weemstra et al., 2016).

4.4 | Enzymatic activities and fast/slow tree communities

We found stronger correlations between soil enzymatic activities and the root trait spectrum than with the leaf and litter traits. These findings support our fifth hypothesis regarding potential enzymatic activities related to root traits. However, our sixth hypothesis claiming that enzymatic activities are more related to fast tree communities held only true for xylodolase and was rejected for N- and P-related enzymes. The activity of soil enzymes depends on two complementary prerequisites: (a) producers encounter resource limitation and have to synthesize resource-releasing enzymes, and (b) suitable substrates for these specific enzymes are present in the soil (Allison et al., 2011). Slow tree communities are commonly associated with low nutrient supply rates and carbon accumulation (Bardgett, 2017; Fort et al., 2016). In addition, the root spectrum demonstrates that slow tree communities have root tissues of higher quality. Thus, slow root decomposition processes are probably linked to constant supplies of substrates for synthesizing enzymes in the presence of limited nutrients in soil (Aponte et al., 2013; McCormack & Iversen, 2019). Accordingly, tree communities with conservative root traits fulfill the enzyme production prerequisites to promote activities of \(\beta\)-glucosidase, and particularly phosphatase and N-acetylglucosaminidase.
Roots have a variety of strategies to capture nutrients from the soil. Roots exude compounds into the soils to stimulate the production of microbial extracellular enzymes, and the quantity of this exudation and the nutrient absorption ability are proportional to the root diameter (Lambers et al., 2006; Ma et al., 2018). Therefore, the divergence of soil enzymatic activity between fast and slow tree communities is based on root diameter and root fungal associations (Kong et al., 2015). Our results are in agreement with other studies which used large fine-root data sets and found that root diameter is negatively related to specific root length, such that the two parameters support contrasting mechanisms for belowground resource acquisition (Bergmann et al., 2020; McCormack & Iversen, 2019). A high specific root length (long and thin roots) promotes a high nutrient acquisition capacity by the tree itself. Thicker roots (i.e. large root diameter) exhibit higher exudation rates and consequently induce greater hyphal growth and other microbial activities that increase N and P availability under slow tree communities (Yin et al., 2014). Our comparative models including the first PCA axes for leaf, litter and absorptive root traits confirm the significant role of the root traits for P-releasing enzymatic activity and fungal diversity. Moreover, the models indicate that leaf and litter traits are closely related to N-releasing enzymes (Table S6). These findings underline the importance of plant–fungi interactions as crucial factors, influencing nutrient cycling in different forest systems and under different environmental conditions (Kong et al., 2019).

4.5 Soil functionality affected by trees and fungal guilds

We found that litter quality and absorptive root traits affect the fungal diversity, community composition and soil activity. Thus, tree species from boreal and hemiboreal forest adapted to cold regions, tended to display absorptive traits with low litter quality and stimulated higher soil fungal diversity. These forest types showed a more abundant symbiotrophic fungal community and in addition exhibited a high level of xylodase activity. The thermophilous deciduous forest presented opposing traits, with less fungal diversity, an enriched saprotrophic community and high enzyme activities for N and P. As an intermediate point, the mountainous beech forest had a broad range of tree trait species and strong activity on cellulose compounds. Moreover, in the mountainous forests, the tree species distribution, microbial communities and soil activities were affected by the mountain elevation gradient.

It has been suggested that interguild fungal interactions can control C cycling, and that N and water availability are key factors determining these interactions (Fernandez & Kennedy, 2016). The most important interactions are between ectomycorrhizal and saprotrophic fungi, which can have positive and negative impacts, for example ‘priming’ and ‘Gadgil’ effects, respectively (Fernandez & Kennedy, 2016; Yin et al., 2014). Likewise, the magnitude and direction of these fungal interactions appear to be context-dependent (Fernandez & Kennedy, 2016). Our results under contrasting tree traits may represent the described effects. For instance, a deficiency of N that can induce interguild competitions explaining the low decomposition rates in thermophilous deciduous forest (Bending, 2003; Fernandez & Kennedy, 2016). In contrast, in the northern forest types that are dominated by fast tree species, carbon appeared to be the relevant factor. Subsequently, different fungal interactions led to different litter decomposition rates, which affect the organic layer formation and hence the soil carbon pools (Uri et al., 2012).

Despite the differences between multispecies and monospecific forests regarding fungal communities, the potential enzymatic activities of both systems did not change significantly. These results can be associated with functional redundancy (Louca et al., 2018). However, the higher fungal diversity in multispecies forest can be coupled to high fine root belowground species complementarity, and this high belowground complexity is characterized by great resilience and resistance against environmental disturbances maintaining soil functionality (Brassard et al., 2013; Wagg et al., 2019). Our LMM showed that the litter traits, soil and locational variables were significant variables to explain either first or second axes of the enzyme variability. However, just the absorptive roots explain the both main axes of the enzyme variability, confirming again our fifth hypothesis that root traits are more strongly linked to enzyme activities than to leaf or litter traits. Moreover, we identified that fungal diversity can interact with root traits to affect soil functionality, which may reflect the relationships between fungal communities and tree traits to maintain ES. These findings confirm the idea that the tree species influence soil carbon pools (Vesterdal et al., 2013) and nutrient cycling by affecting microbial diversity and composition (Bardgett et al., 2014; Urbanová et al., 2015).

5 CONCLUSIONS

We showed that fungal diversity is related to tree community traits rather than to tree diversity levels. We confirmed the positive effect of mixed forest for fungal diversity and established tree identity as main factor influencing fungal communities, because their leaf, litter and root traits determine a trade-off of earnings between quantity and quality. Our findings highlight the tree effect of either ‘fast’ or ‘slow’ communities driving different fungal guilds and influence N and P biogeochemical cycles. This information facilitates an understanding of forest functionality and helps decipher aboveground and belowground interactions in forests. However, we could sample only two levels of tree species richness in this study and considered only the top soil; hence, future research is needed to address active communities and explore different soil layers and plant compartments.

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SUPPORTING INFORMATION

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

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