








RESEARCH ARTICLE

Tree and mycorrhizal fungal diversity drive intraspecific and intraindividual trait variation in temperate forests: Evidence from a tree diversity experiment

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Funding information

Deutsche Forschungsgemeinschaft, Grant/Award Number: 319936945/GRK2324, FZT 118, 202548816, Ei 862/29-1 and Ei 862/31-1; University of Chinese Academy of Science (UCAS)

Handling Editor: Alicia Montesinos-Navarro

Abstract

1. The study of tree species coexistence is crucial to understand the assembly of forest communities. In this context, trees adjust their traits in response to the interactions with other trees and, specifically, as a result of the competition for resources. Further, mycorrhizal fungal diversity and associations are important drivers of ecosystem functioning in forests, but their role as drivers of intraspecific trait variation has been disregarded. Here, we studied intraspecific trait variation of trees in response to tree and mycorrhizal fungal diversity.
2. We sampled 3200 leaves from 640 trees belonging to 10 native, deciduous species in a tree diversity experiment in Central Germany. This experiment relies on the combination of gradients of tree richness and mycorrhizal associations. To handle large amounts of leaf samples, we acquired leaf-level spectral data and used deep learning to predict values for five leaf traits from the leaf economics spectrum (LES): specific leaf area, leaf dry matter content, carbon to nitrogen ratio, carbon content and phosphorus content. For every tree, we calculated the mean value for every trait and two multi-trait functional indices (functional richness and functional dispersion) based on values for individual leaves. Finally, we used sequencing-based data to assess the richness of mycorrhizal fungi associated with the trees.
3. We found that tree and mycorrhizal fungi richness had an effect on different leaf functional traits. Specifically, tree richness positively affected specific leaf area and, additionally, had a negative effect on the functional indices, which revealed that the phenotypic diversity within the tree crown decreased with tree species

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richness. In addition, leaf carbon to nitrogen ratio decreased with increasing arbuscular mycorrhizal fungal richness in both arbuscular and ectomycorrhizal tree species. Finally, we did not find differences between arbuscular and ectomycorrhizal trees regarding their location within the LES.

4. Our results suggest that trees modify their strategy in response to local tree diversity, not only by shifting trait values but also by shifting the variability intraindividually. In addition, higher mycorrhizal fungal diversity does not seem to lead to higher complementarity, but instead, tree and mycorrhizal fungi affect different aspects of leaf traits.

KEYWORDS

arbuscular mycorrhiza, ectomycorrhiza, intraindividual trait variation, intraspecific trait variation, leaf economics spectrum, plant–plant interactions

1 | INTRODUCTION

Biotic interactions shape species diversity in local communities through processes of competition and facilitation among others (Brännström et al., 2012; Chesson, 2000; Ricklefs, 2010). Referring to classical coexistence theories, each species is characterized by a particular niche framed by abiotic and biotic factors, where it avoids to be outcompeted by other local species (Grinnell, 1917). As plants need a common base of resources, this suggests that competition is the main type of plant–plant interaction (Hughesdon, 1927; Wright et al., 2014), and similarities in the resource uptake pathways of plants lead to a strong niche overlap and consequently higher competition for resources (Adler et al., 2018). However, such explanations for plant species coexistence have been criticized for being too simplistic (Escudero & Valladares, 2016), and there is growing demand to consider the variation within species when studying plant–plant interactions (Valladares et al., 2015). The reason behind is that species are not static entities, but instead are flexible, and plants adjust their functional traits (i.e. morphological, physiological or phenological characteristics that influence growth, reproduction or survival; Violle et al., 2007) via: (1) genetic adaptation (Baron et al., 2015) and (2) phenotypic plasticity, that is the ability of genotypes to express alternative phenotypic syndromes (Jump & Peñuelas, 2005; Stotz et al., 2022; Valladares et al., 2007). By adapting and shifting functional traits, individuals are able to reduce competition for limiting resources (Burns & Strauss, 2012; Roscher et al., 2018).

Differences in resource-use strategies are reflected by the expression of dissimilar functional traits (Suding et al., 2003). Across all functional traits in plants, leaf traits can be reliable proxies for resource-use strategies as summarized by the leaf economics spectrum (LES; Wright et al., 2004). The LES reflects a trade-off between a leaf's lifespan and its maximum photosynthetic rate (Diaz et al., 2016; Wright et al., 2004). In general, leaves with high values for traits related to photosynthetic activity, like high specific leaf area and high nitrogen concentration, are typically associated with higher resource acquisition, faster growth rates, and a lower investment

in leaf construction and protective tissues. Therefore, the LES describes the resource-use strategy of plants which range from an acquisitive, growth-related strategy to a long-lived, conservative strategy (Pietsch et al., 2014; Poorter et al., 2009; Reich et al., 1997, 1999; Scheepens et al., 2010). Although the LES originally described differences between species, there is evidence that the gradient of the LES also occurs within species at the individual level (classically referenced as intraspecific trait variation; Fajardo & Siefert, 2018; Niinemets, 2015). It even reflects the diversity of alternative phenotypic syndromes within the same plant (Intraindividual trait variation; Herrera, 2017), and it can therefore be assumed that plants adjust their LES traits in order to mediate biotic interactions. This is especially true in the case of trees because, as a result of their longevity, it is crucial for them to adjust to local conditions within their lifespan instead of adapting through generation turnover like short-lived plants as forbs and grasses (Trogisch et al., 2017). As an increasing number of species in a community typically results in higher complementarity in the use of resources (Barry et al., 2019), trees in rich communities tend to show higher values for acquisitive-related traits compared to those in monospecific communities (Davrinche & Haider, 2021; Deschamps et al., 2023; Felix et al., 2023). Further, recent studies suggest that the extent of within-individual trait variation could help to cope with micro-environmental conditions (March-Salas et al., 2021; Møller et al., 2022) but also with biotic interactions. Therefore, trees in monospecific communities have been suggested to display highly different leaf traits within their crown, probably to avoid competition with interacting conspecific neighbours (Proß et al., 2021).

Apart from plant–plant interactions, organisms from other trophic levels which are directly interacting with trees may act as drivers of leaf trait expression and variation (Tedersoo et al., 2020). Among the different plant interactions with other guilds, mycorrhizal associations, which improve soil nutrient uptake, may be among the most important ones (Kaschuk et al., 2009; Smith & Smith, 2011). Due to the variety of different nutrient uptake processes, the diversity of mycorrhizal associations seems to increase resource

niche partitioning between plants (Bever et al., 2010; Hazard & Johnson, 2018; Klironomos et al., 2000; Wagg et al., 2015). Among all the different mycorrhizal types, there are two which are dominant, especially in trees: (1) arbuscular mycorrhizal fungi (intracellular symbioses dominated by Glomeromycota; AMF), which is the most abundant mycorrhizal type occurring in ca. 74% of angiosperm species (Trappe, 1987), and (2) ectomycorrhizal fungi (intercellular symbioses; EMF), which is a common type among temperate tree species. In the case of AMF, several studies suggested that more diverse AMF communities can improve nutrient uptake by providing plants access to different resource pools (Horsch et al., 2023; Jansa et al., 2005; Wagg et al., 2015) and, besides the fewer studies carried out, similar results have been found for EMF communities (Leake, 2001).

Even though trees can interact with different types of mycorrhizal fungi simultaneously (Heklau et al., 2021, 2023), species have a preferred type of mycorrhizal partner (Brundrett & Tedersoo, 2018) and, thus, they are classified depending on the mycorrhizal host types as arbuscular mycorrhizal (AM) or ectomycorrhizal (EM) trees. In addition, due to evolutionary differences between host plant species as well as differences in the strategy of the mycorrhizal fungal types, AM and EM trees show strong differences in their resource-use strategy (Shi et al., 2020). Specifically, AM trees typically employ a more acquisitive strategy in terms of economic traits (Averill et al., 2019). Further, AM trees tend to show a greater extent of intraspecific variation in traits from the LES compared to EM trees (Shi et al., 2020), even though there are exceptions in the case of some EM trees (Niinemets, 2015). Therefore, this suggests that AM and EM trees could show dissimilarities in their response to plant and mycorrhizal fungal diversity described above, and it is expected that AM trees show higher intraspecific variation in response to the diversity of species (of both trees and fungi) compared to EM trees.

Tree diversity experiments manipulate the number of species while standardizing confounding factors like varying tree density or abiotic conditions (Bruehlheide et al., 2014). Therefore, they are useful set-ups to examine intraspecific changes of functional traits in trees in response to species richness. To explore the effect of tree species richness, mycorrhizal fungal richness and mycorrhizal types on LES traits, we studied the trait values and intraindividual trait diversity from ca. 640 trees representing 10 native deciduous tree species, five of them known to be primarily associated with arbuscular mycorrhizal fungi and the other five with ectomycorrhizal fungi, in the MyDiv tree diversity experiment located in Central Germany (Ferlian et al., 2018). In contrast to other tree diversity experiments, here a treatment of species richness is combined with different plot compositions of tree species differing in their host mycorrhizal type (either AM or EM). We hypothesized that (1) as nutrient partitioning is expected to be enhanced by the richness of species (both tree and fungal), trees increase the mean values of acquisitive-related traits in response to tree and mycorrhizal fungal richness, and (2) intraindividual trait diversity is highest in monocultures to accomplish niche differentiation between individual trees and decreases with increasing tree and mycorrhizal fungal richness. Due to the nature

of AM plants, which seem to be more responsive with respect to intraspecific trait-environment responses, (3) these responses to tree and mycorrhizal fungal richness are expected to be stronger in AM than EM tree species.

2 | MATERIALS AND METHODS

2.1 | Study site

This study was conducted in the MyDiv experiment, which is a biodiversity–ecosystem functioning (BEF) experiment located at the Bad Lauchstädt Experimental Research Station of the Helmholtz Centre for Environmental Research–UFZ in Saxony-Anhalt, Germany (51°23' N, 11°53' E; Figure 1a). The climate is temperate with a mean annual temperature of 8.8°C (monthly mean temperatures ranging from 0.8°C in January to 17.3°C in July) and mean annual precipitation of 484 mm (data obtained from Altermann et al., 2005 and <https://www.worldclim.org/>). The soil type is described as haplic Chernozem, which is very fertile and characterized by a stable aggregate structure, high water-retention and base saturation as well as high bioturbation rates (Altermann et al., 2005). The experiment was established in 2015 and is comprised by 80 plots (Figure 1b). It includes a set of 10 native deciduous angiosperm tree species, with five species each being primarily associated with arbuscular mycorrhizal fungi (AM; *Acer pseudoplatanus* L., *Aesculus hippocastanum* L., *Fraxinus excelsior* L., *Prunus avium* L. and *Sorbus aucuparia* L.) or with ectomycorrhizal fungi (EM; *Betula pendula* Roth., *Carpinus betulus* L., *Fagus sylvatica* L., *Quercus petraea* Liebl., *Tilia platyphyllos* Scop.) (Table S1; Ferlian et al., 2018). The design is based on the combination of different numbers of tree species and trees of the same or different host mycorrhizal types. Tree species were planted following a tree species richness gradient from monospecific plots (one species) over two-species mixtures up to four-species mixtures (Ferlian et al., 2018). The two- and four-species mixtures comprised only AM- or only EM-associated tree species or a balanced combination of AM- and EM-associated species (Figure 1). Every level of tree richness and mixture of mycorrhizal host types was replicated 10 times, thus allowing to have a comprehensive set of possible combinations (see Ferlian et al., 2018 for details). In every plot, 140 trees were planted at a distance of 1 m in a regular grid to mix species to the greatest extent possible (Figure 1c). In order to avoid edge effects, every plot has a 1.5 m buffer area consisting of the outermost tree rows and a core area of 8 × 8 m. A plastic cover was placed on the ground to prevent the growth of understory vegetation.

2.2 | Field sampling

As an extension of the tree-species pair design described in Trogisch et al. (2021) to study interactions among two directly neighbouring trees, sampling followed the tree-species quadrats design, which aims to study the interaction between four trees (hereafter,

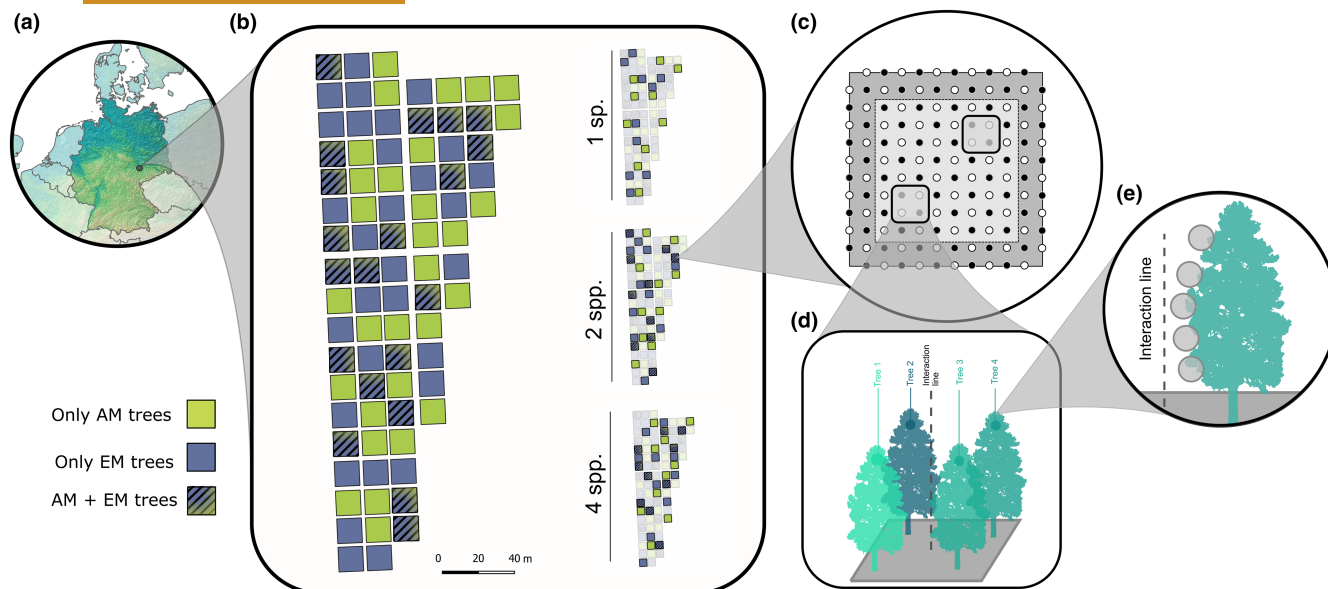


FIGURE 1 Location of (a) the MyDiv experiment in Germany, (b) plots in the experiment (adapted from Ferlian et al., 2018), (c, d) design of the tree species quadrats and (e) description of leaf sampling. As shown in (c), two tree species quadrats (TSQ) per plot were sampled in the inner part of the plots (light grey background) in order to avoid edge effects. Leaves from each individual within a TSQ were collected from the side pointing towards the focal line where trees interact (d, e). Five leaves were sampled from different heights of the tree, ranging from the lowest part of the crown to the top of the canopy.

referenced as tree-species quadrat, TSQ; Figure 1d). In every plot, two TSQs were sampled, which resulted in 160 sampled TSQs containing a total of 640 sampled trees.

Sampling took place from mid to late August 2021. From each tree, we collected leaves along the interaction line between the TSQ partners, that is the focal point where the joint interaction of the four individuals is expected to be maximal (Figure 1d). In order to cover the trait variation of the whole tree individual, we sampled at five different heights. At each height, we cut one fully developed leaf free from mechanical or pathogen damage. This resulted in a total of 3200 collected leaves. Immediately after collection, leaves were conserved in sealable plastic bags with a moistened tissue. The samples were transported in an isothermal bag equipped with cooling bags to prevent desiccation. In the laboratory, the samples were temporarily stored at 6–8°C. In addition to this sampling (hereafter, referred to as 'regular' sampling), we collected a so-called calibration set that we used to train models for leaf trait prediction based on spectroscopy. This independent calibration set included leaf samples from 20 trees of each of the 10 species, resulting in a total of 200 sampled individuals. The leaves were collected at random heights and orientations within the tree crown across all species richness and mycorrhizal host type combinations. To ensure sufficient material for the laboratory analyses, a different number of leaves per tree was sampled, according to the size of the species-specific leaves (see Table S1).

2.3 | Laboratory analyses

For the samples of the calibration set, we determined five morphological and chemical leaf traits, representing different dimensions

of plant growth strategy and being key components of the LES (Reich, 2014; Wright et al., 2004; Figure 2): specific leaf area (SLA; leaf area/leaf dry mass; Kazakou et al., 2006; Niinemets & Kull, 1994; Reich et al., 1992; Reich et al., 1997; Reich et al., 1999), leaf dry matter content (LDMC; leaf dry mass/leaf fresh mass; Niinemets, 1999; Niinemets, 2001; Poorter et al., 2009; Poorter & Bergkotte, 1992; Westoby et al., 2002), carbon to nitrogen ratio (C:N; Niinemets et al., 2007; Pérez-Harguindeguy et al., 2003), carbon content (C) and phosphorus content (P; Hevia et al., 1999; Raaijmakers et al., 1995; Tuohy et al., 1991). Leaf trait selection was based on previous analyses on the identification of independent and orthogonal sources of leaf trait variation (Figure S1) and the ability to obtain high-quality leaf trait predictions (see Section 2.5). Immediately after sampling, the fresh leaves of the calibration samples were weighed and scanned with a resolution of 300 dpi. The leaf area of the scans was analysed with the WinFOLIA software (Regent Instruments, Quebec, Canada). To determine the dry weight, we dried the leaves for 72 h at 60°C and weighed them again. Resulting from the leaf dry mass and the leaf fresh mass, both LDMC and SLA were calculated. Then, we grounded the dried leaves into a homogenous powder. To determine the P content, we used a spectrophotometric assay with the acid molybdate technique. We analysed C and N contents with an elemental analyser (Vario EL Cube, Elementar, Langensfeld, Germany) and calculated the C:N ratio.

2.4 | Near-infrared reflectance spectroscopy

Current chemical analyses on single leaves are usually limited due to the lack of sufficient material from individual leaves. Thus, we

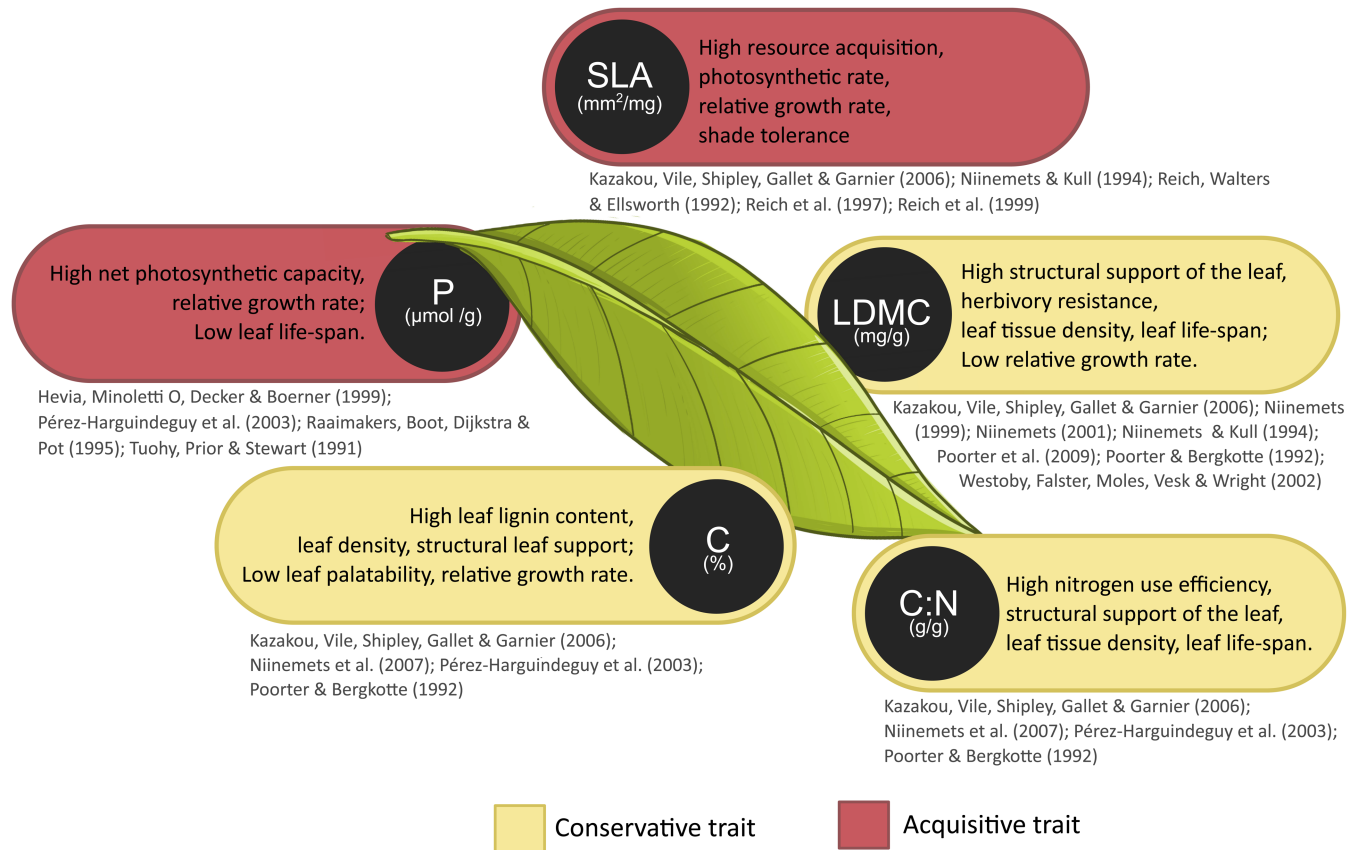


FIGURE 2 Leaf traits included in our study, ecological function of each trait and literature describing them. Yellow and red colour indicate that a trait is indicator of a conservative or an acquisitive strategy, respectively (according to the leaf economics spectrum LES; Wright et al., 2004).

used visible–near infrared spectrometry (Vis-NIRS), a technique of massive-phenotyping, to predict individual leaf trait values based on calibration models (Escudero et al., 2021; Foley et al., 1998). As reflectance depends on the size, density and shape of leaf tissues and their chemical compounds (Asner et al., 2014; Costa et al., 2018; Serbin et al., 2014), Vis-NIRS can be used for estimating morphological traits and leaf nutrients. For all leaves (regular and calibration samples), we acquired reflectance spectra with a portable Vis-NIRS device (ASD “FieldSpec4” Wide-Res Field Spectroradiometer, Malvern Panalytical Ltd, Almelo, Netherlands) in the laboratory immediately after collection. Reflectance was measured across the full range of the solar radiation spectrum (250–2500nm), by taking three repeated measures on the adaxial side of each leaf while avoiding main veins. The equipment was optimized regularly with a calibration white panel (Spectralon, Labsphere, Durham, New Hampshire, USA). For each measurement, 10 spectra were averaged internally to reduce noise. Outlier removal of spectral data was performed by using the Local Outlier Factor (LOF) method (Breunig et al., 2000) as in Li et al. (2023) and, additionally, a visual inspection of the spectra was performed (see Figure S2a).

2.5 | Leaf traits prediction

Leaf traits prediction and consecutive statistical analyses were conducted in the R environment with R version 4.1.3 (R Core

Team, 2021). As deep learning has recently emerged as a promising tool in trait-based ecology (Perry et al., 2022; Vasseur et al., 2022), we used a convolutional neural network (CNN) approach for leaf trait prediction based on the spectral data. First, input spectra were augmented from 2501 to 12,906 features by using transformations based on a combination of standard normal variates and Savitzky–Golay derivatives (Figure S3; Passos & Mishra, 2021). Samples within the calibration set were split into a training and a test set which accounted for a proportion of 70% and 30%, respectively. Then, a CNN composed of one convolutional layer followed by three dense layers was fitted to train the samples for every trait (see Figure S3). In order to avoid overfitting, batch normalization was applied after the convolutional layer (Vasseur et al., 2022). Hyperparameter tuning for every CNN was performed independently for every trait, by adjusting the number of filters, their size for the convolutional layers, and the number of nodes in the dense layers (see Table S2). For model optimization, an Adam algorithm and a loss function based on the mean squared error were used (Passos & Mishra, 2022). CNNs were trained using a Keras framework and a TensorFlow backend as implemented in the ‘Keras’ package (Kalinowski, 2023). We tested the predictive ability of the CNNs by assessing the coefficient of determination for the predicted and measured values in the test set (R^2_{test}) and in the whole calibration set (R^2_{model}). As technical problems occurred during the laboratory analysis of leaf phosphorus concentration, we only had a reduced number of calibration samples

for this trait. Therefore, to ensure the training of the CNN for this trait, we used additional and comparable samples from four deciduous species (*Fagus sylvatica*, *Fraxinus excelsior*, *Quercus robur*, *Tilia cordata*) collected by Proß et al. (2023) in the nearby Kreinitz experiment. This addition of samples aimed to represent the broadest trait space possible, in order to better reflect possible variation in our samples, as recommended in Burnett et al. (2021). Mean R^2_{model} of the trained CNNs for each trait was 0.83 ± 0.10 (mean \pm standard deviation), with a maximum R^2_{model} for SLA (0.94) and minimum for phosphorus (0.71; see Figure S4). Eventually, these trained CNNs were used for predicting trait values of leaves from the regular set of samples. After leaf trait prediction, we excluded ca. 175 predicted trait values for every trait as they were lying outside a 95% confidence interval around the predicted values' distribution (Figure S2b).

2.6 | Mycorrhizal fungal richness

In order to quantify mycorrhiza fungal richness associated to the trees, we used the metrics of arbuscular mycorrhizal and ectomycorrhizal fungi abundance measured in Ferlian et al. (2021; see Figure S5). To assess AMF and EMF richness, 200 root samples, one per plot and tree species, were taken in November 2019. In total, Ferlian et al. (2021) collected root samples from all species in all plots (excluding 12 samples that could not be assigned reliably to the correct tree species and, therefore, were excluded). They collected rootlets for every sampled tree and harvested those rootlets with 10 EM root tips in the case of EM trees or 10 lateral roots in the case of AM trees. Fungal species were identified by using Illumina sequencing (see Ferlian et al. (2021) for details). Based on these data, for every tree occurring in a plot, we calculated rarefied richness of AMF and EMF (hereafter, referenced as AMF and EMF richness) as implemented in the 'vegan' package. AMF and EMF reads per sample were rarefied to the minimum number of reads in every mycorrhizal type (Figure S5). Additionally, to avoid potential collinearity between predictors in further analyses, AMF and EMF richness were rescaled between 0 and 1 for every tree species, with 0 being the minimum richness of a specific fungal type (AMF or EMF) associated to a specific tree species, and 1 the highest richness of the same fungal type associated to the tree species.

2.7 | Statistical analyses

In order to identify the main sources of trait variation, differences between mycorrhizal types, and to better understand changes in trait variation in further analyses, we first performed a principal component analyses of the predicted traits in every leaf. We used the `prcomp` function from the 'stats' package.

To characterize changes in the resource-use strategy of individual trees, we calculated the mean value of every trait in every tree. We tested the interacting effect of species richness, mycorrhizal fungal richness (AMF richness and EMF richness), and host type (either

AM or EM trees) on mean trait values per tree by performing linear mixed-effects models. The models included the mean trait value as response variable, and the interaction effect of the \log_2 -transformed species richness with both AMF and EMF richness and with the host type (AM or EM tree species) as fixed effects. Tree species identity as well as TSQ nested in plot, in turn nested in species composition were added as crossed random effects. We first fitted a "beyond optimal" model, which included all the fixed effects. By including subsets of the predictors, all possible models that varied in their fixed effects (including the intercept only model) were fitted using a maximum likelihood estimator. For all these models, the Akaike information criterion corrected for small sample sizes (hereafter referenced as AICc) was calculated. We selected all models with ΔAICc lower than 2 as competing models holding similar information, and followed the principle of parsimony to prioritize the simplest model with the smallest number of predictors among all competing models (Burnham & Anderson, 2004; Richards et al., 2011). Finally, we assessed the significance of factors by comparing models with and without each factor selected in each model using a likelihood ratio test (Zuur et al., 2009). We used diagnostic plots of the residuals to study the assumptions of normality, homoscedasticity and linearity in our models: residuals versus fitted values plots, histograms of the residuals, and Q-Q plots for the deviance of the residuals (Figure S7). In order to avoid biases in the estimation of mean trait values, for every trait, only trees for which there was information available for the five leaves were considered for the analyses. Therefore, the final number of trees ranged between 499 and 521, depending on the trait considered (Table S3).

In order to assess the trait diversity for each tree, we used two functional indices which reveal complementary indices in the functional hypervolume: (1) functional richness (FRic) and (2) functional dispersion (FDis). FRic aims at detecting reductions of the niche space occupied by individuals (Botta-Dukát & Czúcz, 2016; Cornwell et al., 2006), while FDis describes whether the distribution of leaves in a trait space of a tree is clustered or dispersed (Laliberté & Legendre, 2010). To calculate these indices, we first obtained a leaf-by-leaf trait distance matrix per tree by using Euclidean distance and, next, for every tree we computed both indices through a principal coordinate analysis (PCoA) based on this distance matrix. In order to test the interacting effect of species richness, AMF richness, EMF richness and host mycorrhizal type (either AM or EM trees) on the functional indices, we followed the same approach as described above for the mean trait values. We also checked the normality, linearity and homoscedasticity of the residuals by using diagnostic plots (Figure S8). Again, to avoid biases in the assessment of the functional indices, for the analyses we only used trees for which there were less than four missing values across all leaves and traits.

3 | RESULTS

The first three axes of the PCA explained more than 80% of the total variation in our dataset (35% explained by the first axis, 25%

explained by the second axis, and 21% explained by the third axis; see Figure 3). The first axis was strongly related to LDMC, leaf C, and SLA (with loadings 0.66, 0.54, and -0.46 , respectively). The second axis was mainly related to leaf C:N, followed by SLA and leaf C (with loadings 0.70, -0.54 , and -0.42 respectively). Finally, the third axis of the PCA was related to leaf P and C:N (with loadings 0.82 and -0.47 , respectively). In this PCA, AM and EM trees were clearly separated along the second axis, with AM trees displaying higher values for leaf C:N. In contrast, the two groups were not divided along the first and third PCA axes.

Changes in mean values were found for SLA, C:N and C in the simplest models (Figure 4), although the drivers of these changes were different in every case (Figure S9a, c, d; Table S4). In the case of SLA, there was a significant effect of tree richness ($p=0.01$; Table 1), suggesting that there was an increase in mean SLA with tree richness (Figure 4a). The simplest model for C:N suggests that AMF richness had a significant negative effect on mean C:N ($p=0.04$; Figure 4b). In addition, we found that AM trees had higher values of C:N compared to EM trees ($p<0.01$). Accordingly, the results for C revealed that EM trees displayed higher values of this trait compared to AM trees ($p=0.02$; Figure 4c). Finally, among our results we did not find any effect of our predictors on mean LDMC and P in the simplest models.

For both functional indices, we found an effect of species richness (Figure S10; Table S5) with a significant decrease in different properties of the hypervolume along the tree richness gradient ($p<0.01$ and $p=0.04$ for FRic and FDis, respectively; Figure 5).

4 | DISCUSSION

By using five traits of the LES from 485 to 514 tree individuals, depending on the trait, in a tree diversity experiment in Central Germany, we investigated how mean trait values and intraindividual trait diversity of AM and EM trees vary in response to the interacting effect of tree and mycorrhizal fungal richness. We found a consistent decrease of trait diversity within the canopy with increasing tree richness, whereas tree richness only had an effect on trees' mean SLA. Moreover, a key result was that aboveground traits, such as C:N, can also be affected by soil fungal richness.

Assuming that niche differentiation is determined by both tree richness and mycorrhizal fungal richness, we expected that both components interacted in driving intraspecific responses in our experiment. However, we found that tree and mycorrhiza diversity acted on different leaf traits. First, effects of tree richness on the growth strategy of trees were observed for SLA, which is related to the photosynthetic rate of the tree and, therefore, is one of the main proxies for a fast growth strategy (Reich et al., 1997; Wright et al., 2004). The increase of SLA in response to plant diversity has been described before and seems to respond to the complementarity in the use of resources (Felix et al., 2023). Thus, the decrease in competition for resources in mixtures would allow trees to show a more acquisitive strategy. Despite the lack of significant effects for other traits, we observed negative trends of LDMC in response to tree diversity (see Figure S9b), which also seem to be aligned with the changes from a conservative to an acquisitive strategy as a result of

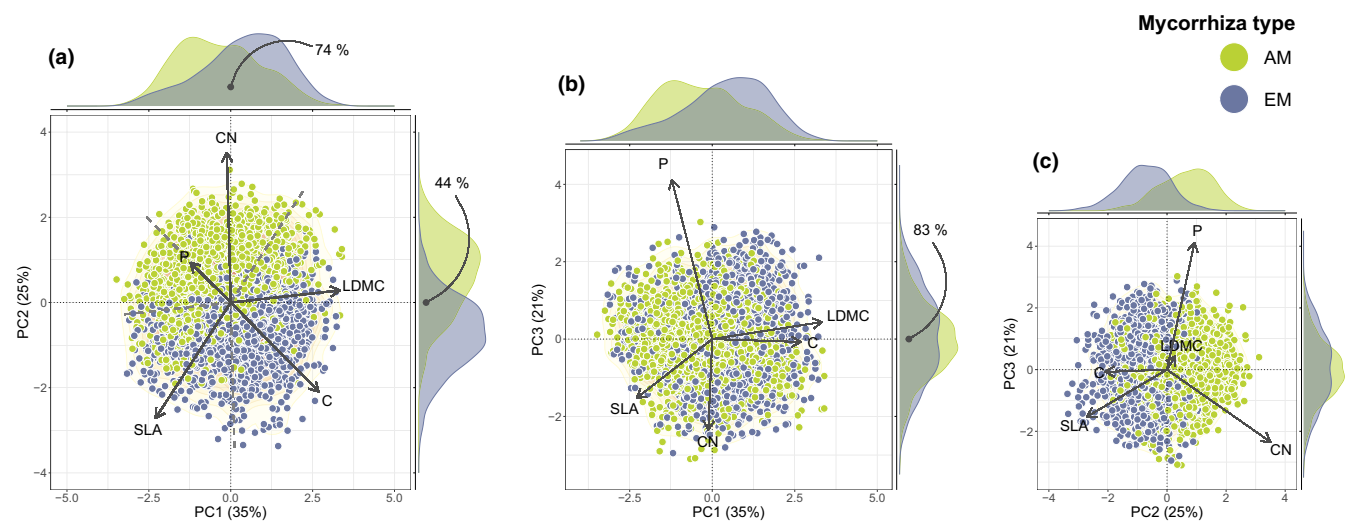


FIGURE 3 Main axes of a principal component analyses (PCA) for five leaf functional traits, including plots for (a) the first against the second component, (b) the first against the third component and (c) the second against the third component. Based on the loadings of every PCA axis, the first axis represents the variation in growth strategy, the second the variation in nitrogen content and the third one the variation in P content. The size of every plot is proportional to the portion of the variance explained by every combination of two axes (60% for the first and the second component, 55% for the first and the third component, and 45% for the second and the third component). The colour of the symbols represents the host mycorrhizal type (green: AM trees, blue: EM trees). Density plots for the distribution of the two mycorrhizal types in the main axes of the PCA are included in the margins of the PCA plots with the percentage of shared area between density distributions indicated on them.

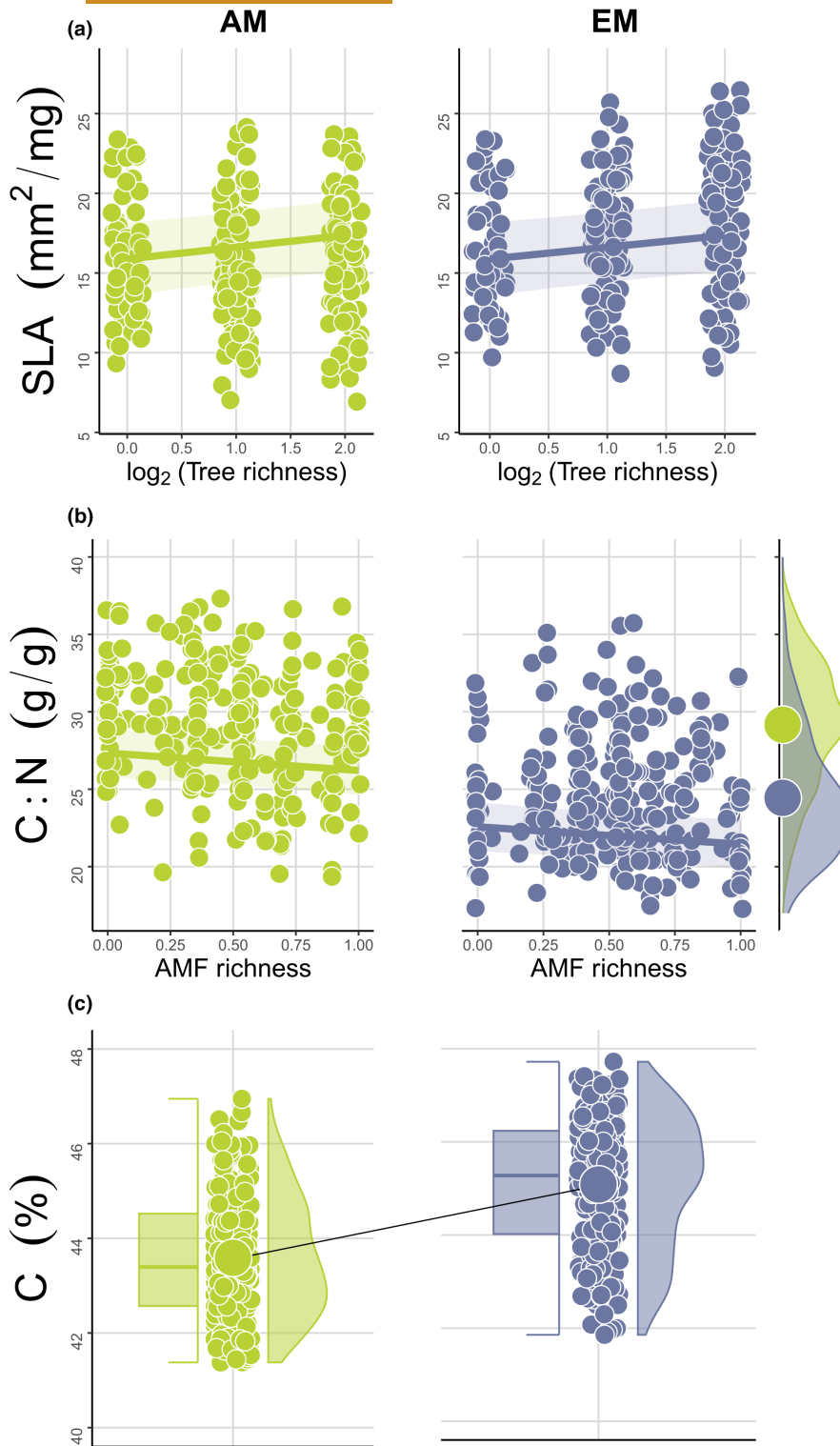


FIGURE 4 Main effects obtained in the simplest models for the mean values of (a) SLA, (b) C:N and (c) C content for AM and EM trees (in green and blue, respectively). Shaded areas in (a) and (b) represent the confidence intervals at 95%. Density plot (b) and raincloud plot in (c) indicate differences between AM and EM trees in terms of C:N and C, respectively. Large dots in (b) and (c) indicate the mean values of AM (green) and EM (blue) trees.

increasing complementarity in mixtures (Davrinche & Haider, 2021). Also, in the specific case of trees, SLA is strongly dependent on the availability of the light within the canopies. Therefore, a higher canopy stratification can lead trees to maximize photosynthesis in light-limited environments by decreasing leaf toughness and increasing SLA (Roberts & Paul, 2006; Williams et al., 2020). Indeed, in the case of our experimental site, the higher levels tree diversity are associated to a higher stratification that may contribute to explain the changes

in SLA observed here (Ray et al., 2023). In addition, the decrease of C:N in response to AMF richness could be related to a better supply of nitrogen to the tree when the richness of these fungi is high as suggested by Powell and Rillig (2018). As AMF are efficient in nutrient uptake in dry soils (Querejeta et al., 2003) this effect could be especially noticeable in our study site where the precipitation is rather low (mean annual precipitation of 484 mm). However, this remains speculative as we are lacking empirical evidence regarding the improvement

TABLE 1 Summary of the simplest linear mixed models. Estimates (standard errors) and significance assessed with likelihood-ratio tests are shown. The acronyms correspond to the different predictors (TR = tree richness; AMF = AMF richness; EMF = EMF richness; and MT = host mycorrhizal type), and interactions between predictors are indicated by "X".

TR	AMF	EMF	MT	TR X AMF	TR X EMF	TR X MT	AMF X EMF	AMF X MT	EMF X MT	TR X AMF X EMF	TR X AMF X MT	TR X EMF X MT	AMF X EMF X MT	TR X AMF X EMF X MT	R ² c	
Functional traits																
SLA	0.279 (0.4)														0.02	0.71
LDMC															0.00	0.80
C:N	-4.762 (1.353)*														0.27	0.66
C															0.18	0.77
P															0.00	0.69
Functional indices																
FD _{is}	-0.002 (0.001)**														0.02	0.03
	-0.003 (0.001)*														0.01	0.07

Note: R²m, marginal R²; R²c, conditional R².

*p < 0.05. **p < 0.01.

of soil nitrogen uptake by AMF in our experimental site. Further, it is remarkable that this pattern for C:N was encountered both for AM and EM tree species, which suggests that, despite the higher host-specificity of AMF in our study site (Ferlian et al., 2021), EM trees are not only linked to AMF through dual mycorrhization (see Figure S12; Heklau et al., 2021; Teste et al., 2019), but may also benefit from AMF richness. For instance, the dual mycorrhization of EM trees might be especially beneficial during dry periods (Querejeta et al., 2009), which might explain the advantage of these trees during droughts shown in Sachsenmaier et al. (2024) for our study site. Last, EMF richness did not have any significant effect on the traits studied, which suggest that even though EMF diversity can affect the uptake of nutrients (Khokon & Meier, 2023), this does not necessarily have an effect on the leaf strategy of the tree. All these changes in leaf functional traits, even though seem to be rather small and not significant for all traits, could have an effect on ecosystem functioning. First, while our approach of leaf trait prediction allows processing large sample sizes, it might underestimate the responses of leaf traits. Indeed, this may be the case of C and P, for which the higher impreciseness of the prediction (R² test is 0.65 and 0.66, respectively) might fail to detect a correlation with the predictors (Burnett et al., 2021). Further, intraspecific shifts in leaf traits, as the ones detected for SLA and N, may have an effect on different facets of ecosystem functioning (e.g. leaf herbivory, light capture) even if the variation within species is small compared to the variability found among them (Chacón-Labela et al., 2023; Williams et al., 2020). That is why, the effects of intraspecific trait variation on ecosystem functioning deserve further attention to better understand diversity effects in forests.

Recent studies have shown that the ability of plants to display different trait syndromes in repeated organs of the same individual may have important ecological and evolutionary implications (Herrera, 2017; Sobral, 2023; Sobral & Sampedro, 2022). Indeed, our approach, which suggests that for evaluating the growth strategy of trees not only shifts in mean trait values should be considered but also the changes in the phenotypic variability of leaves within the canopy (Escribano-Rocafort et al., 2017; Proß et al., 2021), reveals that the intraindividual diversity of leaf traits changes as a result of tree-tree interactions. Also, these changes in intraindividual diversity rarely act on single traits, but occur in different dimensions of the trait space (see Figure S11). Our results suggest that higher intraindividual diversity could be of great importance in monospecific communities where only intraspecific interactions are present. As an explanation for this, we propose that intraindividual trait diversity may help to reduce niche overlap between conspecific neighbours that directly interact (Castro Sánchez-Bermejo et al., 2023). Additionally, in the case of species-rich communities and as an extension of the framework proposed for intraspecific trait variation (Helsen et al., 2017), the reduced intraindividual trait diversity may contribute to niche packing (i.e. high phenotypic similarity between conspecifics from the same population; Violle et al., 2012), which is an adaptative strategy to reduce niche overlap between heterospecific neighbours. Even though we suggest that our results explain the importance of intraindividual trait variation for avoiding niche

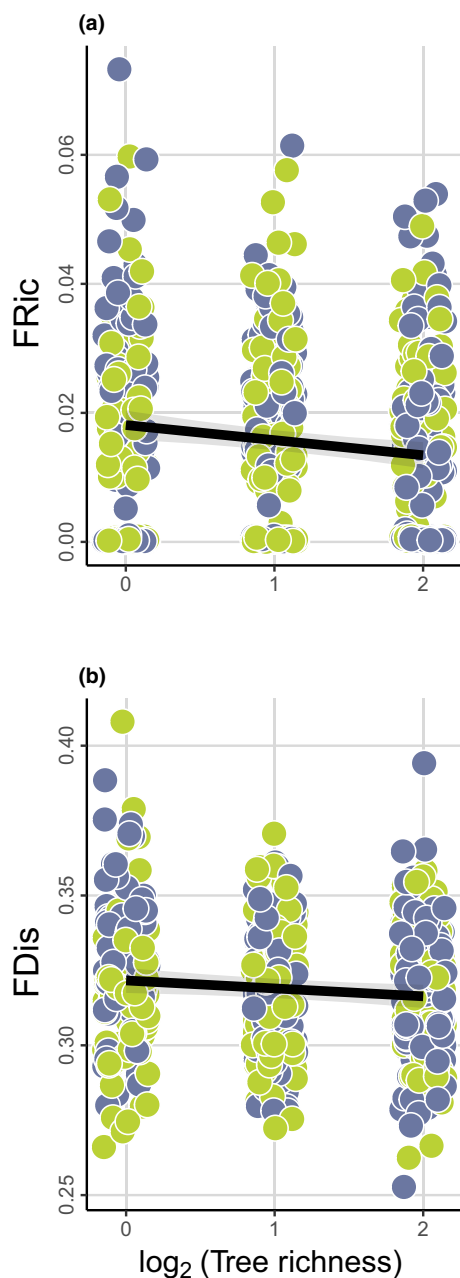


FIGURE 5 Main effects obtained in the simplest models for (a) functional richness (FRic) and (b) functional dispersion (FDIs) of individual trees. Grey areas represent the confidence intervals at 95% and symbols the observed values for the two host mycorrhizal types (green: AM trees, blue: EM trees).

overlap, we should also consider two complementary hypotheses to explain our results, which are: (1) intraindividual trait diversity in leaves may improve plant performance in intraspecific interactions by, for example, improving light capture (Møller et al., 2022), and (2) intraindividual trait diversity could be a mechanism to cope with unpredictability of the environment (March-Salas et al., 2021) in monospecific communities, as these tend to show less environmental stability (Mori et al., 2017).

Previous literature supports that AM and EM tree species differ in their strategy for resource acquisition and suggest that AM trees

have a fast and acquisitive strategy, while EM trees show a slow conservative strategy (Deng et al., 2023; Shi et al., 2020; Tedersoo et al., 2020; Tedersoo & Bahram, 2019). Specifically, it has been suggested that the higher acquisitiveness of AM trees could rely on the better mobilization and use of nutrients in their inorganic form (Averill et al., 2019; Phillips et al., 2013). Nevertheless, our results provide limited support to such general assumptions, and only for leaf C content, we found a significant difference which suggests that EM species invested more in leaf support. Rather, among the species included in the experiment, it seems that growth strategies are species-specific within the host mycorrhizal types, and there are AM trees with more acquisitive strategies (e.g. *Fraxinus excelsior*; see Figure S13), while others have a conservative strategy (e.g. *Sorbus aucuparia*). The same applies to EM species (*Tilia platyphyllos*, as an example, has an acquisitive strategy, while *Fagus sylvatica* has a more conservative strategy). Instead, as reflected by the PCA, host mycorrhizal types seem to mainly differ in C:N. Thus, EM trees seem to be more efficient in capturing nitrogen (Fellbaum et al., 2012; Tedersoo & Bahram, 2019), which explains the higher nitrogen content in the leaves resulting in the lower C:N ratio in EM as compared to AM trees (see Figure S14). While the main differences found between AM and EM trees suggest differences in N uptake, our results give only limited support to the differences in leaf P. However, we had expected differences in leaf P between the two host mycorrhizal types, because AM trees are described as efficient P capturers as a result of the symbiosis with AMF (Rosling et al., 2016). A possible explanation for the absence of this relationship in our study might be the soil type at the MyDiv experimental site, which was a nutrient-rich Chernozem, and the former land use, which was intensive agricultural use with high P fertilizer application (Ferlian et al., 2018). Finally, contrary to other studies on AM and EM trees, our experimental design did not include any gymnosperm species, which are EM trees in most cases (Averill et al., 2019) and show a conservative strategy in their leaf strategy (Díaz et al., 2016). Thus, our study suggests that the common belief in ecology of EM trees being more conservative than AM trees is not necessarily true, and, in the case of the temperate forests of central Europe, the higher conservativeness of EM trees could arise from the differences between gymnosperms and angiosperms instead of the mycorrhizal type.

5 | CONCLUSIONS

Our work has novel implications to understand the assembly of forests and, specifically, how trees modify their resource-use strategy in response to biotic interactions, not only by shifting their trait values, but also the diversity of phenotypic syndromes within individual trees. In addition, we found little empirical support for our hypotheses, which related trees' resource-use strategy to the interactive effect of tree and mycorrhizal fungal richness via complementarity in the use of resources (Barry et al., 2019). In contrast, our study shows that tree and mycorrhizal diversity act on different traits and, therefore, suggest that tree diversity is not enough to explain all

intraspecific responses in forests but better knowledge on the tree-mycorrhiza interactions is needed to more comprehensively understand how trees respond to biotic interactions.

AUTHOR CONTRIBUTIONS

PCS-B and SH conceived the idea and designed methodology; TM collected the leaf trait data with assistance from PCS-B and SH; KG and OF collected the mycorrhizal diversity data; PCS-B analysed the data with assistance from SH and HB; PCS-B led the writing of the manuscript. All authors contributed critically to the draft and gave final approval for publication.

ACKNOWLEDGEMENTS

We are grateful for the funding by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation)—319936945/GRK2324—and the University of Chinese Academy of Science (UCAS) to the International Research Training Group TreeDi. We acknowledge the support of the TreeDi coordinator and TreeDi members. NE was additionally supported by DFG grants (Ei 862/29-1, and Ei 862/31-1). We gratefully acknowledge the support by the German Centre for Integrative Biodiversity Research (iDiv) funded by the German Research Foundation (DFG-FZT 118, 202548816). We thank Michael Köhler for assistance in leaf sampling. We thank Beatrix Schnabel, Melanie Günther, Cynthia Albracht and Anna Heintz-Buschart for technical assistance in sample processing, Illumina sequencing and subsequent downstream processing of the retrieved sequencing data. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Code and data for the data analysis of this study are available at the Zenodo repository: <https://zenodo.org/doi/10.5281/zenodo.10654726>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Principal component analyses and correlations between nine leaf functional traits.

Figure S2. Data cleaning process for the spectral and predicted trait data.

Figure S3. Analytical framework used to generate convolutional neural networks (CNNs) to predict leaf traits from spectral data based on the calibration set.

Figure S4. Correlation between predicted and measured traits values to test the quality of convolutional neural networks (CNNs) to predict leaf traits from spectral data.

Figure S5. Violin plots for AMF richness and EMF richness in the different mycorrhiza treatments in the MyDiv experiment.

Figure S6. Rarefaction of arbuscular mycorrhizal fungal (AMF) and ectomycorrhizal fungal (EMF) richness.

Figure S7. Diagnostic plots for assumptions of normality, homoscedasticity and linearity in the linear mixed-effects models for the mean values of traits.

Figure S8. Diagnostic plots for assumptions of normality, homoscedasticity and linearity in the linear mixed-effects models for functional richness (FRic) and functional dispersion (FDis).

Figure S9. Competing models for the drivers of the mean value of SLA, LDMC, C:N, C, and P.

Figure S10. Competing models for the drivers of indices of intraindividual trait diversity.

Figure S11. Results for the drivers of the variance of SLA, LDMC, C:N, C and P.

Figure S12. Boxplots for the AMF and EMF richness associated with every tree species.

Figure S13. Two main axes of a principal component analyses (PCA) for five leaf functional traits for 10 tree species.

Figure S14. Results for the drivers of the mean of nitrogen leaf content.

Table S1. Tree species in the MyDiv experiment and their mycorrhizal type.

Table S2. Layers and hyperparameters used for building a convolutional neural network for every trait.

Table S3. Species included in our study and number of individuals for every trait and functional indices (FDis and FRic) included in the analyses.

Table S4. Model selection for the analyses of the drivers of the mean value for five functional traits.

Table S5. Model selection for the analyses of the drivers of the multi-trait functional indices.

How to cite this article: Castro Sánchez-Bermejo, P., Monjau, T., Goldmann, K., Ferlian, O., Eisenhauer, N., Bruelheide, H., Ma, Z., & Haider, S. (2024). Tree and mycorrhizal fungal diversity drive intraspecific and intraindividual trait variation in temperate forests: Evidence from a tree diversity experiment. *Functional Ecology*, 38, 1089–1103. <https://doi.org/10.1111/1365-2435.14549>