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Tree species mixing causes a shift in fine-root soil exploitation strategies across European forests

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Abstract

1. Mixed-species forests have often been shown to enhance above-ground ecosystem properties and processes. Despite the significance of fine roots for tree and ecosystem functioning, the role of tree species diversity for below-ground processes driven by fine roots remains largely unknown. Previously, an underyielding of fine-root biomass (FRB) in tree mixtures across four major European forest types has been reported. To explain this phenomenon, we tested here the effect of tree species mixing on fine-root traits related to soil exploitation efficiency, including biotic feedbacks from ectomycorrhizal fungi (EcM), and assessed the role of root trait dissimilarity.
2. We analysed morphological and chemical traits as well as ectomycorrhizal colonisation intensity of absorptive fine roots (i.e. first three most distal orders) in soil samples from 315 mixed and mono-specific tree neighbourhoods in mainly mature, semi-natural forest stands across Europe. Additionally, we quantified mycorrhizal abundance and diversity in soil samples from the same stands.
3. At the community level, fine roots in tree mixtures were characterised by higher specific root lengths and root nitrogen concentrations, lower diameters and root tissue densities indicating a *faster* resource acquisition strategy compared to mono-specific stands. The higher root EcM colonisation intensity and soil EcM diversity in mixtures compared to mono-specific stands may further provide evidence for positive biotic feedbacks. Moreover, the diversity of fine-root traits influenced FRB, as mixtures characterised by a higher trait dissimilarity were linked to a lower reduction in FRB. At the level of phylogenetic groups, thin-rooted angiosperm species showed stronger responses to mixing than thick-rooted gymnosperms, especially in terms of root morphology and EcM colonisation, indicating different strategies of response to tree mixing.
4. Our results indicate that a lower FRB can reflect a shift in soil resource acquisition strategies, rather than a lower performance of trees in mixtures. They show that several non-exclusive mechanisms can simultaneously explain negative net

effects of mixing on FRB. This study sheds new light on the importance of using integrative approaches including both above- and below-ground biomass and traits to study diversity effects on plant productivity.

KEYWORDS

absorptive fine roots, biodiversity–ecosystem functioning, functional dispersion, fungal diversity, SoilForEUROPE, species identity effects, trait dissimilarity, tree species richness

1 | INTRODUCTION

Mixed-species forests can positively affect above-ground ecosystem properties and processes (reviewed by Scherer-Lorenzen, 2014). For example, tree species mixtures can be more productive (Ammer, 2019) and more resistant and resilient towards environmental changes compared to their mono-specific counterparts (Jactel et al., 2017). Therefore, and especially in view of global change, many current forest management strategies focus on the promotion of mixed-species forests (Bauhus et al., 2017).

While above-ground overyielding of biomass in mixtures has frequently been observed (e.g. Zhang et al., 2012), evidence for below-ground mixing effects on fine-root biomass (FRB) is inconclusive (Finér et al., 2017; Ma & Chen, 2016). Yet, the commonly observed above-ground overyielding suggests that below-ground resource capture is likely sustained or even enhanced in mixtures (e.g. Archambault et al., 2019). Forrester et al. (2006) observed that mixing *Eucalyptus globulus* with *Acacia mearnsii* did not change the total below-ground carbon (C) allocation compared to monocultures, but strongly increased above-ground productivity, suggesting that in mixtures plant C was invested more efficiently below-ground to provide trees with soil resources. Similarly, in a young tree diversity experiment, simultaneous underyielding of FRB and above-ground overyielding in mixtures suggested a more efficient below-ground resource acquisition (Archambault et al., 2019). While FRB may be indicative of the potential to capture soil resources, it cannot be used as indicator of below-ground productivity or the carbon allocation to below-ground organs and processes.

Three types of mechanisms, that is, resource partitioning, abiotic facilitation and positive biotic feedbacks may enhance soil resource uptake by fine roots in mixtures (Barry et al., 2019). A well-studied example of plant association that involves all three mechanisms relates to the symbiotic nitrogen (N) fixation in trees, which may result in (a) resource partitioning by leaving more soil N available for non-fixing species (Forrester et al., 2006), (b) abiotic facilitation of non-N-fixing plants owing to increase in soil N availability through N-fixation and (c) biotic feedbacks through transfer via mycorrhizal networks (Munroe & Isaac, 2014). As this example shows, these underlying mechanisms often occur simultaneously, contribute to the same net effect and are thereby difficult to separate from each other (Forrester & Bauhus, 2016).

A greater overall resource capture in mixtures may be achieved by spatial, temporal and/or chemical resource partitioning or a combination thereof (Barry et al., 2019). A higher trait dissimilarity can conceptually be linked to a greater niche differentiation (De Bello et al., 2010). Hence, the quantification of trait diversity using trait-based diversity indices (Laliberté & Legendre, 2010) may be useful for assessing underlying mechanisms of diversity effects. Positive relationships of such trait-based indices with standing biomass or productivity of fine roots were reported (Mahaut et al., 2020; Sun et al., 2017) while other studies did not observe such effects (Bakker et al., 2019; Zeng et al., 2020).

Abiotic facilitation can increase soil resource availability when plant–plant interactions increase the plant-available resource pool (Barry et al., 2019). Examples include N-fixation, positive litter interaction effects accelerating nutrient cycling (Hättenschwiler, 2005) or hydraulic redistribution (Prieto et al., 2012).

Positive biotic feedbacks can increase fine-root resource acquisition in mixtures (Barry et al., 2019). This may be the case when interactions with symbiotic fungi in mixtures enhance soil nutrient exploitation of plants (Boddy, 1993; Read & Perez-Moreno, 2003). An example for such a biotic feedback is the nutrient and water transfer between tree species in mixtures through a common mycorrhizal network (Simard et al., 2015). Not only the abundance (e.g. fungal hyphae mass) but also the diversity of mycorrhizae may enhance nutrient uptake of plants through complementary fungal nutrient exploitation strategies (Agerer, 2001; Wagg et al., 2011). Yet, evidence on the response of root-EcM interactions to changing tree diversity levels is still scarce and inconsistent (Salahuddin et al., 2018; Weißbecker et al., 2018).

Tree species interactions may also enhance below-ground resource-uptake efficiency, that is, resource capture per C invested. In this case, species' interactions above-ground may cause a greater below-ground resource-uptake efficiency as a result of shifts in C allocation pattern from below- to above-ground biomass (Poorter et al., 2012). A reduction in herbivory and pathogen pressure in mixtures could also result in less C requirement for defence structures such as tougher tissue (de Kroon et al., 2012; Jactel & Brockerhoff, 2007).

These examples show that instead of only measuring FRB, the quantification of other fine-root traits related to soil resource exploitation efficiency (i.e. C invested in roots per unit of resource acquired) and capacity (i.e. potential resource uptake by roots, independent of C cost) could improve our understanding of overall diversity–productivity relationships. In addition, mycorrhizal symbionts, which often crucially support fine roots in soil resource capture (Brundrett, 2009), are also rarely considered (Laliberté, 2017).

Overall, there is growing evidence for a global trade-off in root strategies along a *resource acquisition and resource conservation* gradient, hereafter referred to as *acquisition conservation* gradient, ranging from roots with high root tissue density (RTD) that show a *slow* resource return on investment but are long-lived and well-protected, to *fast* roots with a high N content and high metabolic rate for fast resource return on investment but a short life span (Bergmann et al., 2020). A high root N concentration is generally indicative of high root metabolic activity (Reich et al., 2008) and may positively relate to specific root-uptake activities (e.g. Legay et al., 2020). Also, a low RTD, reflecting low construction cost (Chen et al., 2018), may indicate a higher efficiency in conditions where the risk of root loss from herbivory and/or pathogens is not high. The strategy of plants for efficient resource uptake and conservation is further defined by the *fungal collaboration* gradient—a trade-off between roots that efficiently acquire soil resources by themselves (high specific root length, SRL—*do-it-yourself* strategy), and those with typically higher fine-root diameter that rely on mycorrhizal colonisation (*outsourcing* strategy; Bergmann et al., 2020). Indeed, a higher SRL of fine roots generally translates into a larger volume of soil under the influence of roots and therefore a higher soil resource uptake per biomass invested (Freschet et al., 2020). Nonetheless, mycorrhizal hyphae may be as efficient in resource acquisition as fine roots (Chen et al., 2018), or even more efficient under conditions of low resource availability (Lambers et al., 2008). Therefore, both a higher mycorrhizal colonisation intensity and a high SRL may be linked to a high resource acquisition efficiency. Overall, evidence for such changes in resource-uptake strategies of fine-root systems in response to tree species mixing is strongly limited. To our knowledge, only morphological root trait adaptations including an increased SRL in mixtures have been observed (e.g. Bolte & Villanueva, 2006; Bu et al., 2017; Salahuddin et al., 2018).

Phylogenetics may determine variations in fine-root traits and thus resource acquisition strategies more than environmental conditions (Comas & Eissenstat, 2009; Valverde-Barrantes et al., 2017). Hence, it has been suggested to group species based on their root diameter and mycorrhizal type, because these two traits may strongly reflect the species' resource acquisition strategies (Chen et al., 2018). For example, we know that gymnosperm and angiosperm species differ considerably in their fine-root traits and represent contrasting soil exploitation strategies (Bauhus & Messier, 1999; Guo et al., 2008). Owing to their evolutionary background, thin-rooted angiosperms are thought to follow a more *acquisitive* strategy characterised by faster root proliferation in contrast to thick-rooted gymnosperms that generally harbour a more *conservative* acquisition strategy by forming roots that are longer-lived and rely more on mycorrhizal fungi for soil exploitation and nutrient acquisition (Liu et al., 2015; Ma et al., 2018). Evidence has also been gathered for contrasting fine-root trait plasticity of thick-versus thin-rooted species in response to changes in environmental conditions, with thin-, but not thick-rooted species enhancing root proliferation, thereby showing a higher plasticity (Bauhus & Messier, 1999; Chen et al., 2016, 2018; Wang et al., 2019). This suggests that gymnosperm and angiosperm tree fine roots may also respond differently to tree species mixing. Only a few studies have dealt with this question, as species-specific fine-root data in mixtures are difficult to obtain (Bolte & Villanueva, 2006; Salahuddin et al., 2018). More generally, it has also been suggested that plastic responses in mixtures may be more pronounced for absorptive roots (the three most distal root orders) than for higher-order roots (Salahuddin et al., 2018), suggesting that separating fine roots by root orders or functions is an important approach to identify species interactions (McCormack et al., 2015).

Previously, underyielding of standing FRB was observed in four European forest types (Wambsganss et al., 2021) despite evidence for predominantly positive above-ground diversity–productivity effects in these ecosystems (Jucker et al., 2016; Ratcliffe et al., 2017). An increased occupation of soil volume by fine roots in the most nutrient-rich soil depth in mixtures, as indicated by an increased root length density (RLD), suggested an enhanced below-ground resource-uptake efficiency and complementary use of space and resources in these mixed forest stands (Wambsganss et al., 2021). Here, our objective was to further investigate these below-ground adaptations in mixtures by analysing fine-root traits related to soil exploitation efficiency. We further aimed at assessing the effect of tree species mixing on the intensity of the relationship between trees and their mycorrhizal symbionts. We also intended to investigate the role of diversity of root trait values, as a proxy for resource partitioning mechanisms. Moreover, we wanted to shed light on differences in tree mixing effects driven by two phylogenetic groups with contrasting traits, namely thin-rooted angiosperm versus thick-rooted gymnosperm species.

Our hypotheses were as follows:

1. In tree mixtures, reductions in standing FRB are generally associated with changes in root traits linked to:
    a. a higher fine-root resource acquisition efficiency (i.e. higher root N concentrations and lower RTD) and higher length of roots deployed in soil (i.e. higher RLD), resulting in a faster/greater soil volume exploitation per unit of C invested in roots, and/or
    b. facilitation in resource acquisition by mycorrhizal fungi (positive biotic feedbacks), particularly higher root mycorrhizal colonisation and changes in traits related to the hosting of mycorrhizae (i.e. lower SRL and higher root diameter) and/or
    c. a higher functional fine-root trait dissimilarity and hence complementary resource acquisition strategies among tree species.
2. Fine-root morphology (SRL, RTD, diameter) and total fine-root length investment (RLD) respond more strongly to interspecific interactions in thin-rooted angiosperms than in thick-rooted gymnosperms, which rely more on adaptations through mycorrhizal associations.

2 | MATERIALS AND METHODS

2.1 | Study design

The study sites were selected from the pan-European FunDivEurope forest-plot network, representing a tree species richness gradient from mono-specific to high-diversity stands in each forest type (Baeten et al., 2013). The 30 m × 30 m plots in mostly mature uneven-aged forests were chosen according to predefined criteria comprising evenness, tree age, density, species composition and environmental factors (e.g. soil type). The comparative study design aimed at keeping abiotic and biotic variables as constant as possible while allowing for gradients in tree species diversity. Here, we used 63 plots (30 mono-specific, 33 mixtures) across four sites representing major European forest types including boreal (Finland), hemiboreal (Poland), mountainous beech (Romania) and thermophilous deciduous forest (Italy; Table S1). The plots consisted of one or three tree species from a pool of three to five indigenous species that were representative of the local tree community. At each plot, we chose five subplots, that is, tree neighbourhoods (*triplets*) for soil sampling following Vivanco and Austin (2008). These *triplets* consisted of three healthy, dominant or co-dominant tree individuals of a single species and three different species in the mono-specific stands and mixtures, respectively. Further criteria for the selection of the *triplets* were approximately equal diameters at breast height (DBH) and crown sizes of the three tree individuals and a homogeneous distribution of the *triplets* across the plot (Wambsganss et al., 2021). We then selected soil sampling locations based on the visually estimated dimensions of *triplet* trees (DBH and crown dimensions) to capture a point of approximately equal influence of all three trees. Sampling points were hence moved closer towards trees of smaller dimensions and further away from trees with larger dimensions to ensure equal influences.

2.2 | Root sampling and processing

In spring 2017, one soil core per subplot was extracted to a depth of 30 cm with a split-tube sampler (Eijkelkamp, inner diameter 5.3 cm). Soil cores were divided into three depth layers, that is, 0–10, 10–20 and 20–30 cm. Samples were frozen (−20°C) until processing. Soil samples were washed under tap water and live tree fine roots (≤2 mm in diameter) were separated from understorey (herbaceous) and dead tree fine roots. Rocks and coarse roots (both >2 mm in diameter) were kept for fine-earth volume estimations. Live tree fine roots were further sorted by species using reference samples and divided into absorptive and transport fine roots (McCormack et al., 2015). This was done based on root orders, that is, absorptive roots consisting of the first three most distal root orders (beginning from tips) and transport roots consisting of higher root orders. The functional classification approach was preferred over the traditional approach, that is, classifying fine roots as roots with a diameter ≤2 mm, because recent studies have shown that root functions and plasticity significantly differ with root orders (Freschet & Roumet, 2017; Laliberté, 2017; McCormack et al., 2015).

2.3 | Root traits

For each subplot sample, root traits (Table S2) were measured on live absorptive fine roots for each species and soil depth separately (except for the three *Quercus* species in Italy, which could not be reliably distinguished and were therefore pooled, hereafter referred to as *Quercus spec*). Root tips colonised by EcM were visually identified and counted on representative subsamples based on the presence or absence of a fungal sheath for the 12 species known to be associated with EcM (*Acer pseudoplatanus* was associated with arbuscular mycorrhizae). Thereafter, roots were scanned in water with a flat-bed scanner (resolution 800 dpi) and scans analysed with the software WinRhizo (Regents Instruments, Québec, Canada, 2009) to obtain root length, area, volume and diameter. Root volume and (average) diameter values were corrected by recalculating them from the sum of all diameter classes' averages (Freschet et al., 2020). Subsequently, all samples were dried (72 hr, 40°C) and weighed. For C and N analysis, root samples of the first depth layer (0–10 cm) were pooled at the plot level. Different root species and functional root types (absorptive vs. transport roots) were kept separately. Then, samples were milled to determine total organic C and N concentrations by dry combustion (Elementar Vario El Cube). Overall trait values of absorptive fine roots were calculated as cumulative values, that is, pooled across the three depth layers (with the exception of chemical traits, which were only available for the first depth layer) and species, as we focussed on overall mixing effects rather than species-specific effects.

2.4 | Diversity and biomass of fungi

Data on overall mycorrhizae and EcM subgroups are based on soil samples taken adjacent to the root sampling spots (0–10 cm soil depth). Molecular data of fungal diversity were obtained by standard total genomic DNA extraction. Sample processing, laboratory analysis and bioinformatics procedures were done according to Prada-Salcedo, Goldmann, et al. (2021). We amplified fungal ITS2, using the primers P5-5N-ITS4 and P5-6N-ITS4 together with P7-3N-fITS7 and P7-4N-fITS7 (Gardes & Bruns, 1993; Ihrmark et al., 2012; Leonhardt et al., 2019) and produced libraries using the Nextera XT Illumina index Kit (Illumina), based on the manufacturer's instructions. Subsequently, samples were sequenced with the MiSeq Reagent kit v3 on Illumina MiSeq system (Illumina Inc.). After bioinformatic analysis, the FUNGuild V1.0 tool was used to analyse fungal taxonomy and ecological guilds (Nguyen et al., 2016). Subsequently, we identified and classified fungal groups and determined fungal richness and diversity using the package PHYLOSEQ (McMurdie & Holmes, 2013) in R (R Core Team, 2018). Soil total fungal biomass and specifically mycorrhizal biomass were determined by phospholipid fatty acid analysis method described by Prada-Salcedo, Wambsganss, et al. (2021) and Pei et al. (2017). After lipids extraction, GC–MS analysis and peak areas conversion to nmol g soil^{-1}, the biomass was calculated accordantly to fungal biomarkers 18:2ω6,9c, 18:1ω9 and 16:1ω5c.

2.5 | Plasticity index

To assess the intraspecific trait plasticity of angiosperms and gymnosperms in mixed relative to mono-specific stands, a plasticity index (PI; Freschet et al., 2018) was calculated as the percentage of mean deviation from the mean mono-specific trait value:

$$\mathrm{PI}\,(\%) = \frac{\mathrm{Trait}_{\mathrm{mix}} - \mathrm{Trait}_{\mathrm{mono}}}{\mathrm{Trait}_{\mathrm{mono}}} \times 100, \tag{1}$$

where $\mathrm{Trait}_{\mathrm{mono}}$ is the mean trait value of a species in its mono-specific stand; $\mathrm{Trait}_{\mathrm{mix}}$ is the mean trait value of a species in the mixture.

2.6 | Diversity effects

Diversity effects were calculated for the cumulative biomass of absorptive roots following the additive partitioning method (Loreau & Hector, 2001).

The complementarity effect (CE) was calculated as:

$$\mathrm{CE} = N \times \mathrm{mean}\left(\Delta \mathrm{RY}_i\right) \times \mathrm{mean}\left(M_i\right), \tag{2}$$

where N is the number of species (here $N = 3$), $\Delta \mathrm{RY}_i$ is the difference between the observed and expected relative (R) yield, that is, FRB, of species i in mixture, M_i is the FRB in the mono-specific stand of species i.

The net diversity effect (NE) was calculated as:

$$\Delta Y = Y_{\mathrm{O}} - Y_{\mathrm{E}}, \tag{3}$$

where ΔY, that is, the net effect, is the deviation from total expected FRB in the mixture.

Y_{O} is the total observed FRB in mixture and Y_{E} is the expected FRB based on the observed average FRB values of the component species in mono-specific stands (i.e. the sum of all three species' FRB in mono-specific stands divided by 3).

If ΔY equals 0, effects of the component species are additive. If ΔY deviates from 0, effects are non-additive (i.e. negative if <0, positive if >0).

2.7 | Functional trait diversity

We quantified functional trait diversity as functional dispersion (FDis), an index considering multidimensional trait space and independent of species richness (Laliberté & Legendre, 2010), using the function *dbFD* of the FD package in R (Laliberté et al., 2014) and considering the following five traits measured on absorptive roots: SRL, RTD, RLD, EcM colonisation intensity and root N concentration. Since we used only quantitative traits, the FDis calculations were based on the Euclidean distance (Laliberté & Legendre, 2010). We used plot-specific species trait values for these calculations to reflect intraspecific trait plasticity. We excluded samples from *triplets* composed of the three different *Quercus* species (Italy), owing to the lack of species-specific data. The considered traits were selected due to their important role for the plant economics spectrum (Freschet et al., 2010; Reich, 2014) and to avoid redundancy. Species abundance data were derived from the biomass proportions of the individual species' absorptive fine roots (Zeng et al., 2020).

2.8 | Statistical analyses

All statistical analyses were performed using R version 3.5.1. (R Core Team, 2018), with significance levels set at $p = 0.05$.

To avoid model overfitting, a principal component analysis (PCA) was computed summarising absorptive root traits (SRL, RTD, root diameter, RLD and EcM colonisation intensity) that were available at the *triplet* level. As root chemical traits could only be measured at the plot level, we computed a second PCA for the plot-level data including chemical traits.

The first two axes of the *triplet*-level PCA were considered most important as they retained eigenvalues of >1 and described 64% of the total variation (Table S3). Hence, they were used as predictor variables in some of the models (see below). We also tested the third and fourth PC axes in some of the models; however, as these models did not yield significant results (not reported), we focus only on the first two axes. Moreover, bivariate correlations between absorptive root trait pairs that were expected to be significant based on the PCA biplots were checked using simple linear regression analyses to corroborate the interpretation of the PC axes.

Linear mixed-effects models (LMMs) were used for testing the hypotheses and accounting for the nested study design (package LME4, Bates et al., 2015). Random slopes and intercepts and plot nested within site were used as random effect structure for all models, except for site-level models and models based on plot-level data, where only site was used as random effect. Model assumptions were checked using the package DHARMA (Hartig, 2019). In case of violations of model assumptions, response variables were transformed (package BESTNORMALIZE, Peterson, 2017).

To assess the effect of tree mixing on the individual root traits (hypothesis 1), we tested each trait (SRL, RTD, RLD, diameter, mycorrhizal colonisation, root N) separately in response to tree species richness across sites. We further modelled each of the first two *triplet* root PCs separately in response to tree species richness. In addition, a redundancy analysis (RDA) including site as conditional factor (package VEGAN, Oksanen et al., 2013) was performed to affirm our focus on the first two PC axes (Figure S1). To check whether the traits were related to standing FRB and diversity effects on FRB models testing FRB as well as each diversity effect (NE and CE) separately were computed in response to the *triplet* root PCs. To specifically test hypothesis 1b (biotic feedbacks), we checked whether diversity effects and overall FRB were related to mycorrhizal biomass and diversity. To test hypothesis

1c (trait dissimilarity), NE and CE were modelled in response to functional dispersion of absorptive fine-root traits (representing functional trait diversity), respectively. To test how trait values differed between mixtures and mono-specific stands for angiosperms and gymnosperms, respectively (hypothesis 2), we separated the data for the two phylogenetic groups and then modelled each trait for each group separately across sites and for individual sites. We further modelled FRB of both gymnosperms and angiosperms separately in response to total mycorrhizal biomass and diversity as well as the diversity of EcM. In addition, to specifically test for differences in responses of gymnosperms and angiosperms to tree species mixing, we computed models testing each trait in response to the interaction between phylogenetic type and tree species richness using the whole dataset.

3 | RESULTS

3.1 | Fine-root trait coordination

The *triplet*-level PCA on absorptive root traits showed that variation of the fine-root trait data was coordinated along two main axes (Figure 1): PC1 described 42.4% of variation in root traits and indicated a gradient from high-SRL, low tissue density and low-diameter roots (negative values) to low-SRL and high-diameter roots (positive values). PC2 explained 21.4% of the variation and described a separate dimension indicating the reliance of trees on EcM colonisation intensity, which appeared to some extent be opposed to developing high RLD.

The *plot*-level PCA on absorptive root traits, which additionally included chemical root traits only available at the plot level, further showed two axes along which the fine-root trait data were coordinated (Figure S2): PC1, which described 48.3% of the variation, represented a trade-off between RTD and N concentrations, from high-RTD roots low in N concentrations (positive values) to low-RTD roots that are high in N concentrations (negative values). PC2 described 19.7% of the variation and indicated a trade-off between SRL and root diameter, similar to *triplet* PC1.

Bivariate trait pair analyses showed negative relationships between SRL and root diameter, SRL and RTD, EcM colonisation intensity and RLD as well as root N concentrations and RTD (Figure S3).

3.2 | Tree mixing effects on fine-root traits

Across all four forest types, tree mixing had a negative effect on *triplet* PC1 (Figure 1; Table 1). Moreover, tree mixing was

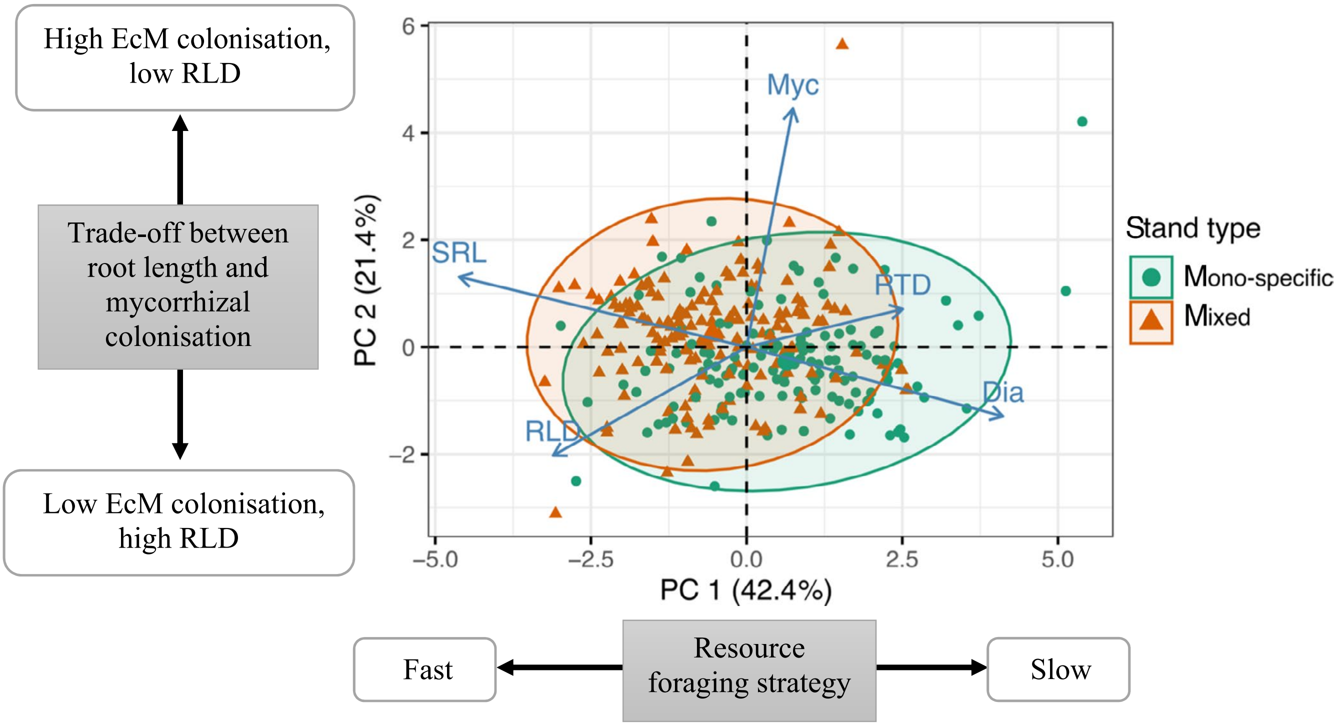

FIGURE 1 Biplot of the principal component analysis (PCA) using traits of absorptive roots at the *triplet* level (for the plot-level PCA including root N, see Figure S2). PC1 represents a resource foraging strategy gradient independent of mycorrhizal colonisation intensity (thus clearly distinct from a collaboration gradient), from high-SRL, low tissue density, low-diameter roots, that are characterised by fast foraging to low-SRL, high-diameter roots, which can be related to slow foraging. PC2 represents the reliance of trees on EcM colonisation intensity, which was negatively related with RLD (Figure S3), that is, negative values indicating a high RLD and low EcM colonisation intensity, and positive values representing a high EcM colonisation intensity and low RLD

TABLE 1 Relationships between tree species richness, *triplet* gymnosperm proportion (% basal area) with *triplet*-level root principal components (PC) 1 and 2, respectively, tested using linear mixed-effect models (from which marginal and conditional R^2 values were derived). Red and green shade indicate positive and negative slopes, respectively

	Absorptive root PC1			Absorptive root PC2		
Predictors (fixed effects)	**Estimate**	***t*-value**	***p***	**Estimate**	***t*-value**	***p***
Tree species richness	−1.04	−4.76	<0.001	0.45	2.88	**<0.01**
Triplet gymnosperm %	0.62	5.30	**<0.001**	−0.04	−0.42	0.68
mR^2	0.31			0.05		
cR^2	0.68			0.39		

Bold values indicate significant effects ($p < 0.05$).

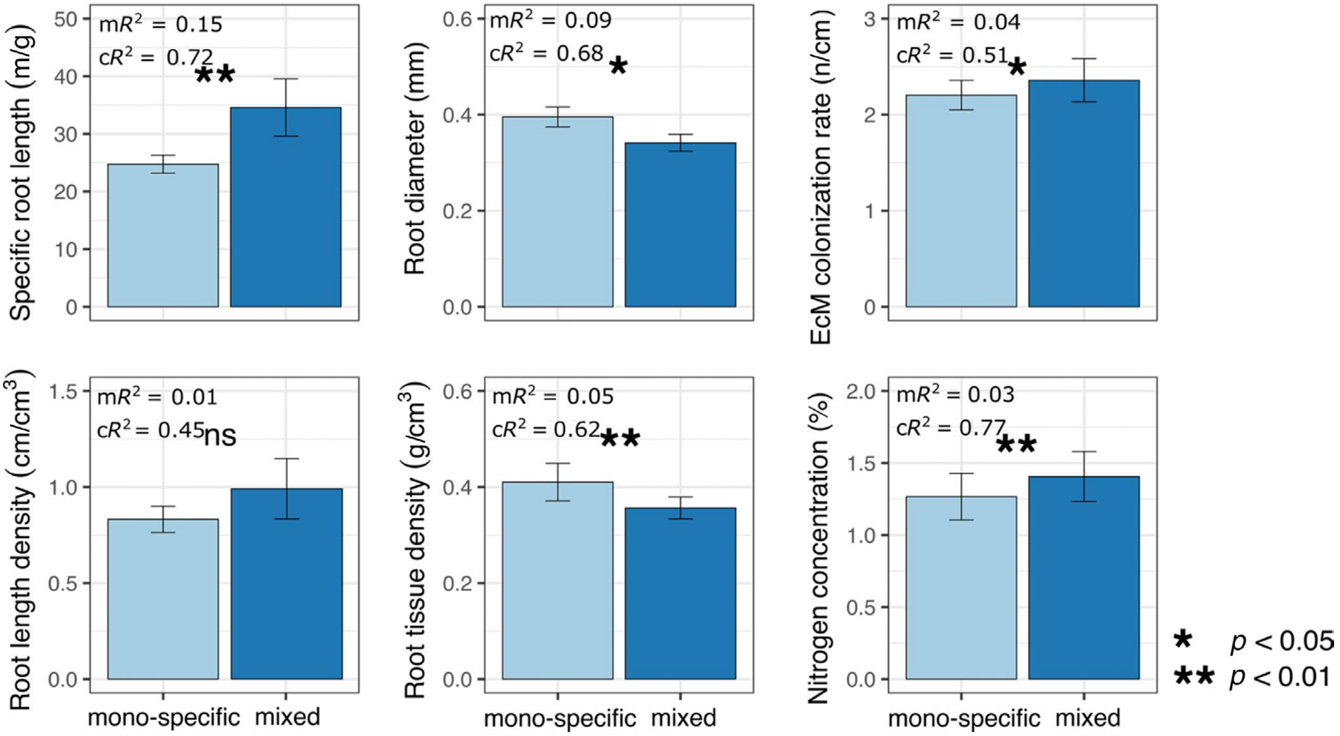

FIGURE 2 Mean cumulative traits of absorptive fine roots (±*SE*) by tree species richness across sites. Asterisks indicate significant differences between mixtures and pure stands tested with linear mixed-effect models (from which marginal and conditional R^2 values were derived)

positively related to *triplet* PC2, indicating a higher EcM colonisation and lower RLD in mixtures compared to mono-specific stands (Figure 1; Table 1). Root PC1 was further positively related to gymnosperm proportion in the tree *triplet*, whereas root PC2 was not, suggesting that the higher the gymnosperm proportion in *triplets*, the greater the community root diameter and RTD.

When analysing the traits individually, across all sites, community SRL, EcM colonisation intensity as well as root N concentrations were significantly higher while root diameter and RTD were significantly lower in mixtures compared to mono-specific stands (LMM, Figure 2). RLD did not significantly differ between mixtures and mono-specific stands.

Across sites, biomass of absorptive fine roots pooled across soil depths was positively related to *triplet* root PC1 and negatively related to *triplet* root PC2 (Figure 3).

3.3 | Role of mycorrhizae

Across sites, total mycorrhizal as well as EcM Shannon diversity were significantly higher in mixtures than in mono-specific stands, whereas total mycorrhizal biomass did not significantly differ between the two stand types (Figure 4; Table S4).

3.4 | Role of root trait dissimilarity

Across all four sites, functional trait diversity of absorptive roots in mixtures, reflected by the functional dispersion index, FDis, was positively related to both NE and CE in terms of biomass of absorptive fine roots (Figure 5). Furthermore, FDis was positively related to gymnosperm tree proportion in mixtures (Figure 6) and

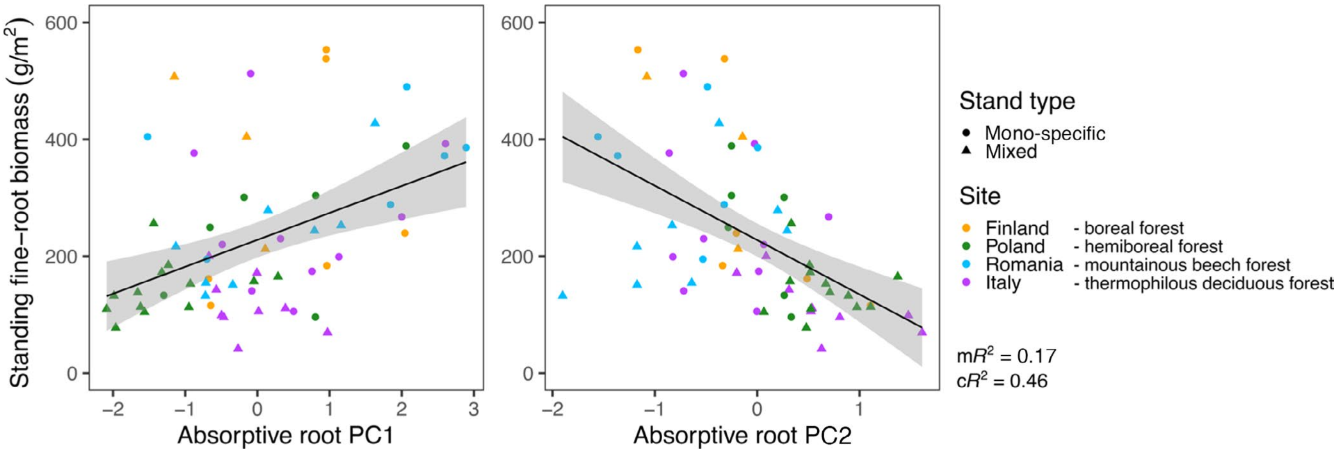

FIGURE 3 Relationship of biomass of absorptive fine roots with *triplet*-level root principal components (PC) 1 and 2. Significance was tested using linear mixed-effect models including both PCs as fixed effects in one model (from which marginal and conditional R^2 values were derived). The solid lines represent linear regressions for the two variables of interest, including a 95% confidence interval (shaded grey area)

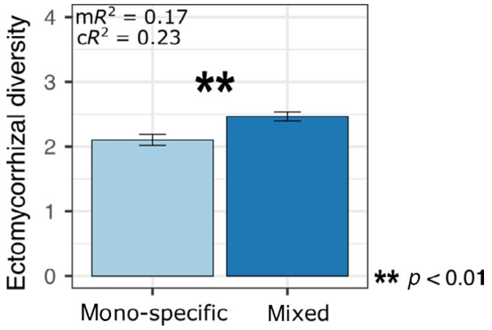

FIGURE 4 Mean ectomycorrhizal Shannon diversity (±*SE*) in soil samples (0–10 cm soil depth) in mixtures and pure stands across all four sites. Asterisks indicate significant differences between the two stand types tested with linear mixed-effect models (from which marginal and conditional R^2 values were derived)

also to total mycorrhizal as well as EcM diversity (LMM, $p < 0.01$; Table S5).

3.5 | The influence of phylogeny on fine-root traits

Mean trait values of absorptive roots varied considerably among species (Table S6) and clear differences between gymnosperms and angiosperms became apparent (Table 2). At all sites where both gymnosperms and angiosperms were sampled, absorptive roots in gymnosperms were characterised by larger average diameters, lower SRL and SRA compared to angiosperm roots. In hemiboreal (Poland) and mountainous beech forests (Romania), angiosperms had significantly higher RLDs compared to gymnosperms. In boreal forests (Finland), EcM colonisation intensity was significantly higher in angiosperm (i.e. *Betula pendula*) than gymnosperm species, whereas gymnosperms had a higher infection rate than angiosperms in hemiboreal forests. Angiosperm roots in hemiboreal forests also had significantly higher N concentrations (and lower root C/N ratio) than gymnosperms roots.

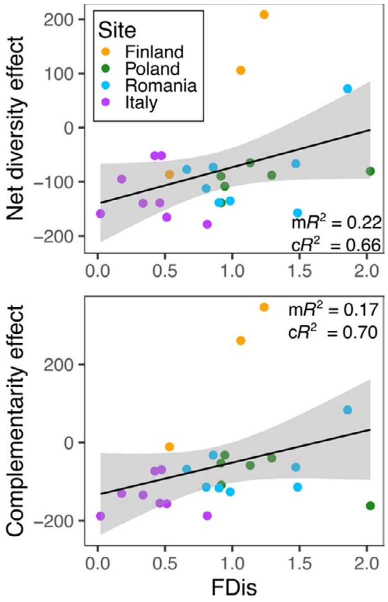

FIGURE 5 Relationship between functional dispersion of traits of absorptive roots (FDis) with mean net diversity and complementarity effects in terms of absorptive standing fine-root biomass (g/m^2). R^2 (marginal and conditional) values were derived from linear mixed-effect models. The solid lines represent linear regressions for the two variables of interest, including a 95% confidence interval (shaded grey area)

Angiosperms and gymnosperms showed differences in intraspecific trait plasticity (Figure 7; Table S7). Across sites, angiosperms had a significantly higher SRL, EcM colonisation intensity, root N and lower average root diameters and RTD in mixtures compared to mono-specific stands. For gymnosperms, trait values did not differ between the two stand types except for a higher SRL in mixtures than in mono-specific stands. Both total RLD of gymnosperms and angiosperms did also not significantly differ between mixed and mono-specific stands. Moreover, gymnosperm FRB was negatively

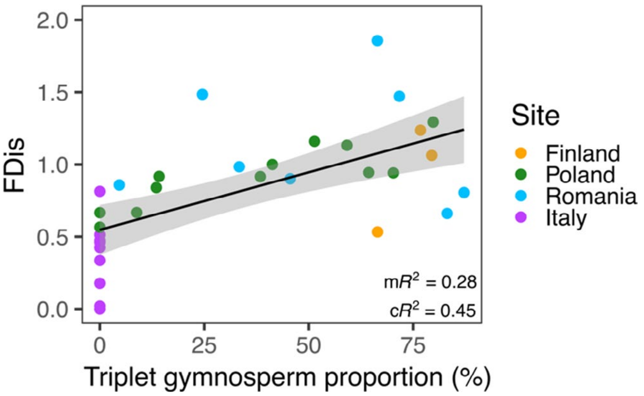

FIGURE 6 Relationship of *triplet* gymnosperm proportion with functional dispersion (FDis) of traits of absorptive roots in mixtures. R^2 (marginal and conditional) values were derived from linear mixed-effect models. The solid line represents a simple linear regression including a 95% confidence interval (shaded grey area)

related to total mycorrhizal biomass (LMM, $p = 0.04$) and tended to be negatively related to total mycorrhizal diversity ($p = 0.09$), whereas angiosperm FRB was neither significantly related to mycorrhizal diversity nor biomass (both $p > 0.05$; Table S5).

4 | DISCUSSION

Here, we demonstrated that the overall reduction in biomass of absorptive fine roots in mixtures across four major European forest types reported in a previous study (Wambsganss et al., 2021) is associated with morphological and chemical adaptations of fine-root traits. These changes in root trait values suggest a shift towards a *faster* foraging strategy of fine roots in mixtures. The higher root EcM colonisation intensity and the higher diversity of EcM in soils in mixtures further indicate positive biotic feedbacks. Our analyses also showed that these mixing effects depended on interspecific functional root trait dissimilarity as well as the diversity of EcM pointing to complementary soil resource acquisition strategies. We observed the strongest fine-root biomass reduction in mixtures with the lowest root trait dissimilarity while such effects were nearly non-existent in stands with higher root trait dissimilarity. Since root trait dissimilarity was strongly positively related to gymnosperm proportion in the mixture, this result can be explained by the generally stronger response of angiosperm than gymnosperm species to tree mixing observed here.

4.1 | Soil exploitation strategy

Supporting hypothesis 1a, tree mixing significantly affected fine-root traits, including higher root N concentrations and lower RTD (Figure 2). Mixtures were also characterised by higher SRL and lower root diameter compared to mono-specific stands. Contrasting our hypothesis, the length of roots deployed across the three soil layers (RLD) was not significantly higher in mixtures, despite an increased RLD observed in the topsoil only (Wambsganss et al., 2021). Our results strengthen previous findings of increasing SRL owing to interspecific interactions in forests (Bolte & Villanueva, 2006; Bu et al., 2017; Germon et al., 2018; Salahuddin et al., 2018) and suggests that other morphological root changes also occur simultaneously.

In accordance with recent studies (Bergmann et al., 2020; Ding et al., 2020; Erktan et al., 2018; Wang et al., 2018), a large share of the variation in our data was arranged along two axes (Figure 1; Figure S2), suggesting a trade-off between SRL and diameter—the *fungal collaboration* gradient—as well as a trade-off between RTD and root N—the *resource acquisition-conservation* gradient. The differences between morphological and chemical traits in mixtures compared to mono-specific stands could also be interpreted as a shift towards a more *do-it-yourself* strategy and concurrently a *fast/acquisitive* rather than a *slow/conservative* resource uptake (Bergmann et al., 2020). The positive relationship between total standing FRB and a root foraging strategy favouring thicker and shorter roots suggests that these trait adaptations may be linked to the negative net diversity effects on FRB reported for these mixtures (Wambsganss et al., 2021). Yet, the EcM colonisation intensity appeared to be independent of the SRL-diameter trade-off represented by our PCAs. Instead, it was coordinated along an independent, second dimension (Figure 1) indicating a potential trade-off with RLD (discussed in the next section). This suggests that in contrast to the fungal *collaboration* gradient (Bergmann et al., 2020), the trade-off between SRL and diameter shown by both of our PCAs should rather be interpreted as a gradient in root foraging strategies independent of EcM associations, as proposed by Ding et al. (2020). It is noteworthy that this trend may result from our focus on EcM species. Whereas positive relationships between fine-root diameter and mycorrhizal colonisation have been found relatively consistently for AM species (e.g. Kong et al., 2014; Ma et al., 2018; McCormack & Iversen, 2019), there is no such clear picture for EcM species (e.g. Ding et al., 2020; Kong et al., 2014; McCormack & Iversen, 2019). One possible explanation lies in the increased potential for EcM colonisation of thinner roots with many root tips (i.e. increased root branching intensity; Ding et al., 2020). Therefore, it cannot be excluded that the framework proposed by Bergmann et al. (2020), where mycorrhizal colonisation intensity aligns with fine-root diameter, may not adequately account for the trade-off in root morphology observed among EcM species.

A high SRL is often used as an indicator for a higher soil exploitation efficiency, that is, less C required per root length deployed and thus soil volume explored (Eissenstat, 1991). Yet, a higher foraging efficiency and fast strategy do not necessarily relate to a reduction in below-ground C investments, as high-SRL roots are often characterised by a shorter life span (McCormack et al., 2012; Weemstra et al., 2020). Similarly, a lower overall RTD implies a reduction in root construction costs but also reduces root structural defence capacity possibly resulting in a shorter life span (Eissenstat et al., 2000, 2015). The increased root N concentrations are also associated with increased root respiration rates (Reich et al., 2008) and a lower root life span (Bergmann et al., 2020; McCormack et al., 2012). Therefore, the shift in fine-root trait values from a less efficient resource

TABLE 2 Mean trait values (±*SE*) of absorptive fine roots (pooled across the entire soil profile, except for chemical traits) by phylogenetic group, richness and site. Bold letters indicate significant differences between angiosperm and gymnosperm trait values across both richness levels

				SRL	SRA	RTD	RLD	Dia	Myc	C/N	N
				Specific root length	Specific root area	Root tissue density	Root length density	Root diameter	EcM colonisation intensity	Root C/N conc.	Root N conc.
Site	Phylogenetic group	Tree species richness	*N*	m/g	cm^2/g	g/cm^3	cm/cm^3	mm	n/cm		%
Boreal forest (Finland)	*Angiosperm*	1	2	**38.9 ± 1.2**	**371 ± 7**	0.36 ± 0	0.31 ± 0.04	**0.31 ± 0.01**	**3.03 ± 0.23**	43.5 ± 1.92	1.1 ± 0.02
		3	3	**48.3 ± 3**	**440 ± 13**	0.32 ± 0.02	0.44 ± 0.07	**0.32 ± 0.03**	**2.63 ± 0.28**	38.6 ± 2.78	1.28 ± 0.09
	Gymnosperm	1	4	**16.9 ± 1.4**	**230 ± 15**	0.46 ± 0.08	0.28 ± 0.07	**0.44 ± 0.01**	**2.16 ± 0.14**	51.4 ± 3.63	0.94 ± 0.07
		3	3	**20.5 ± 0.6**	**271 ± 6**	0.36 ± 0.02	0.46 ± 0.16	**0.43 ± 0.01**	**2.24 ± 0.27**	40.5 ± 1	1.16 ± 0.02
Hemiboreal forest (Poland)	*Angiosperm*	1	3	**38.2 ± 6.4**	**378 ± 46**	0.34 ± 0.03	**0.34 ± 0.05**	**0.33 ± 0.02**	**2.32 ± 0.37**	**29.3 ± 3.68**	**1.63 ± 0.15**
		3	13	**60.1 ± 2.9**	**507 ± 17**	0.32 ± 0.01	**0.47 ± 0.06**	**0.28 ± 0.01**	**2.86 ± 0.15**	**22.8 ± 0.45**	**1.99 ± 0.04**
	Gymnosperm	1	3	**20.4 ± 3.7**	**277 ± 27**	0.32 ± 0.01	**0.16 ± 0.02**	**0.46 ± 0.05**	**2.53 ± 0.23**	**27.4 ± 2.51**	**1.69 ± 0.14**
		3	11	**26.8 ± 1.7**	**341 ± 13**	0.34 ± 0.04	**0.13 ± 0.02**	**0.42 ± 0.01**	**3.99 ± 0.65**	**26.0 ± 0.75**	**1.73 ± 0.04**
Mountainous beech forest (Romania)	*Angiosperm*	1	4	**33.4 ± 2**	**341 ± 11**	0.37 ± 0.02	**0.49 ± 0.12**	**0.34 ± 0.02**	1.39 ± 0.24	30.8 ± 1.84	**1.51 ± 0.11**
		3	8	**38.4 ± 1.5**	**376 ± 13**	0.4 ± 0.04	**0.61 ± 0.14**	**0.32 ± 0.01**	3.52 ± 0.34	29.5 ± 1.21	**1.49 ± 0.05**
	Gymnosperm	1	4	**11 ± 1.1**	**188 ± 11**	0.37 ± 0.02	**0.18 ± 0.03**	**0.56 ± 0.02**	2.51 ± 0.35	32.4 ± 2.62	**1.35 ± 0.1**
		3	8	**13.2 ± 0.8**	**214 ± 9**	0.39 ± 0.04	**0.16 ± 0.04**	**0.54 ± 0.01**	2.46 ± 0.21	31.9 ± 1.09	**1.33 ± 0.05**
Mediterranean thermophilous forest (Italy)	*Angiosperm*	1	10	23.2 ± 2.5	240 ± 18	0.54 ± 0.04	0.23 ± 0.05	0.35 ± 0.01	1.79 ± 0.16	47.7 ± 3.42	1.03 ± 0.06
		3	18	34.8 ± 1.9	330 ± 13	0.43 ± 0.02	0.19 ± 0.03	0.31 ± 0.01	2.6 ± 0.21	42.8 ± 1.61	1.11 ± 0.03

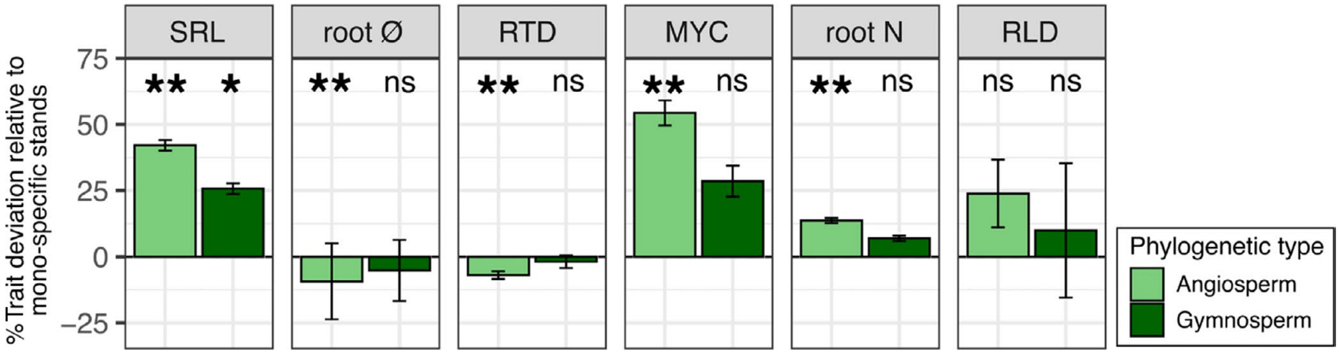

FIGURE 7 Plasticity index (±*SE*) for traits of absorptive fine roots of angiosperms and gymnosperms across sites. Asterisks indicate significant intraspecific trait deviation between mono-specific and mixed stands tested with linear mixed-effect models (**$p < 0.01$; *$p < 0.05$; ns $p > 0.1$). Abbreviations of the fine-root traits are shown in Table 2

foraging and *slow* strategy in mono-specific stands to more efficient foraging and *faster* strategy in mixtures may have maintained (or even increased) the capacity of trees to acquire nutrients. Yet, the decrease in FRB cannot be directly translated into lower C investments into nutrient acquisition without additional information on respiration and turnover rates of fine roots (Weemstra et al., 2020).

The shift in fine-root traits with species mixing may be explained in several ways. First, the generally thinner and longer roots in mixtures may be explained by shifts in C allocation patterns from below- to above-ground biomass (Poorter et al., 2012), which is then counterbalanced by shifts in root morphology (Freschet et al., 2015; Weemstra et al., 2020) and root traits related to soil resource uptake (Freschet et al., 2018). The observed above-ground overyielding of wood production across the pan-European plot network which this study is part of (Jucker et al., 2014) suggests that this mechanism might have occurred here. Concurrently, the potentially higher soil nutrient availability in mixtures at these plots (L. Gillespie et al., unpublished data) also indicates a higher community-level resource-use efficiency, for example, faster cycling and lower losses of nutrients (Richards et al., 2010), reducing below-ground C investment.

Second, since plastic reactions of fine roots in response to changes in water and nutrient availability are well documented (Hodge, 2004), the morphological and chemical adaptations in mixtures could also be linked to alterations of soil resource availability and distribution. Higher P contents and smaller C/N ratios of the forest floor in mixtures at our sites (L. Gillespie et al., unpublished data) suggest enhanced nutrient availability. Indeed, increasing root N concentrations and decreasing RTD with increasing soil nutrient availability have been observed for tree roots along broad environmental gradients (Ding et al., 2020; Ostonen et al., 2017) and increased P availability was shown to increase SRL and decrease RTD (Li et al., 2019). However, contrasting observations were also made (e.g. Freschet et al., 2018).

Third, the spatial distribution of soil resources may also partly explain our observations. A weak but positive tree diversity effect on abundance and diversity of earthworms was observed across the FunDivEUROPE plots (Ganault et al., 2021; De Wandeler et al., 2018), indicating an increased bioturbation and redistribution of soil nutrients in mixtures (Meysman et al., 2006; Patoine et al., 2020). As a response, trees could have formed higher-SRL roots to enhance their chance of encountering nutrient-rich spots (Chen et al., 2016). A higher concentration of nutrients in earthworm burrows (Cameron et al., 2014) could have generally led to the development of fewer roots in search for nutrients. Alternatively, fine-root turnover could have increased and standing FRB decreased, as earthworms may also consume living fine roots (Cortez & Bouche, 1992).

4.2 | Positive biotic feedbacks

The overall higher root EcM colonisation intensity and diversity in soil samples in mixtures compared to pure stands (Figures 2 and 4) corroborate our hypothesis 1b regarding positive biotic feedbacks. However, as traits related to the hosting of mycorrhizae (i.e. higher SRL and lower root diameter) did not change as expected with an increased EcM colonisation, our hypothesis is only partially supported.

Tree diversity can increase mycorrhizal diversity (Hanif et al., 2019; Kernaghan et al., 2003; Tedersoo et al., 2016), possibly owing to a greater host diversity, a greater diversity of organic inputs (Hättenschwiler et al., 2005) or more favourable micro-climatic conditions (e.g. higher soil moisture; Joly et al., 2017). Here, the higher EcM diversity in mixtures could be linked to higher EcM colonisation intensity of absorptive fine roots, as a higher diversity of EcM may also increase the potential of root tip infection (Bzdyk et al., 2019). A higher diversity of mycorrhizal fungi indicates complementary fungal nutrient exploitation strategies (Agerer, 2001; Kernaghan, 2005) and thus enhanced nutrient supply to their hosts through positive biotic feedbacks. Morphological root trait dissimilarity among tree species may also be related to different EcM associations and EcM hyphal proliferation strategies and hence complementarity in resource uptake (Cheng et al., 2016). Positive biotic feedbacks from EcM increasing soil resource uptake by trees may also explain the apparent reduction of C allocated in FRB but do not necessarily imply a lower overall below-ground C investment, as C transfer to mycorrhizae can be substantial (Eissenstat, 1992).

The increased EcM colonisation intensity in mixtures found here contradicts two related studies, reporting the opposite effect (Salahuddin et al., 2018; Yan et al., 2019). The shift towards a more *do-it-yourself* strategy in mixtures seems to contrast the higher EcM colonisation rate, as high-SRL roots are assumed to invest less C in mycorrhizal partners (Bergmann et al., 2020; McCormack & Iversen, 2019). The presence of the fungal sheath surrounding root tips should theoretically increase RTD (Reich, 2014), further contradicting the shift towards a *faster* fine-root resource acquisition. Yet, a trade-off between mycorrhizal colonisation rate and root diameter (or SRL) has mainly been observed for AM species, whereas such evidence for EcM species is scarce (Kong et al., 2014; McCormack & Iversen, 2019). A recent study even reported a negative relationship between root diameter and mycorrhizal colonisation rate in EcM conifer species (Ding et al., 2020) and the authors speculated that the higher root branching intensity of thinner roots led to an increased EcM infection probability. Still, the concomitant increase in mycorrhizal colonisation intensity and SRL or decrease in diameter and tissue density are unlikely to occur in combination on the same tree species and may rather be explained by a substantial increase in these trait values on distinct tree species (Table S6).

As mentioned in the previous section, the shifts in root EcM colonisation intensity appeared to be decoupled from shifts in root diameter and SRL but instead are negatively related with RLD (Figure 1; Figure S3). It has previously been observed that EcM tree species enhanced their nutrient foraging by investing in mycorrhizal fungal hyphae production rather than in root length (Chen et al., 2016). Hence, increasing EcM foraging precision could indicate another response of trees to changes in soil nutrient availability in mixtures.

4.3 | Complementary acquisition strategies

The average fine-root trait values varied considerably among tree species and in particular between angiosperms and gymnosperms (Table 2), which is in agreement with other studies (e.g. Bauhus & Messier, 1999; Salahuddin et al., 2018; Tobner et al., 2013), and suggests different soil exploitation strategies.

The buffered decrease in FRB with increasing fine-root trait diversity (Figure 5) indicates that in addition to the other mechanisms discussed before, resource partitioning among species in mixtures may also play a role, corroborating hypothesis 1c.

In general, a higher trait diversity may relate to a greater niche differentiation and thus a more complete or more efficient resource uptake (Barry et al., 2019). A higher functional diversity of absorptive fine roots may indicate complementary soil resource acquisition strategies among different tree species, possibly resulting in competitive reduction. The positive correlation between fine-root trait diversity and total soil mycorrhizal diversity, as well as EcM Shannon diversity (Table S5), further indicates that the dissimilarity in fine-root traits may also be related to diversity in mycorrhizal resource exploitation strategies (Agerer, 2001; Cheng et al., 2016).

Fine-root trait diversity was further positively related to the gymnosperm proportion in tree triplets across sites (Figure 6), where the gymnosperm-dominated mixtures had the highest trait diversity. Owing to their evolutionary background, trait differences within angiosperms are usually greater than within gymnosperms. Here, the mixtures with the highest gymnosperm proportion still included one angiosperm species, positively influencing the dissimilarity in fine-root trait values. Consequently, the gymnosperm-dominated mixtures were characterised by more neutral net diversity effects on standing FRB (Wambsganss et al., 2021). In contrast, low trait diversity in the angiosperm mixtures may indicate similar uptake strategies and more intense competition for soil resources among species. Our results could suggest that tree species with similar fine-root resource acquisition strategies adjusted these in mixture (as described above) to avoid competition (Hodge, 2004), resulting in the negative net diversity effects on standing FRB. In addition, these adaptations in angiosperm-dominated mixtures may have also been caused by changes in soil nutrient distributions in these stands, where decomposition rates (Joly et al., 2017) and earthworm abundance (De Wandeler et al., 2018) increased with deciduous leaf litter proportion. Yet, it has to be kept in mind that due to the imbalanced study design (i.e. stands with the highest angiosperm proportion occurring in Italy and the stands with the lowest angiosperm proportion occurring in Finland), we cannot clearly disentangle site effects from phylogenetic identity effects in this study.

4.4 | The influence of phylogeny on the response of fine-root traits to mixing

In accordance with our second hypothesis, thin-rooted angiosperms changed root morphology more strongly in response to tree mixing (increased SRL, decreased RTD and diameter) than thick-rooted gymnosperms (Figure 7). Neither gymnosperm nor angiosperm species deployed significantly higher root lengths in mixed compared to mono-specific stands. Thus, only qualitative root traits (i.e. how roots are built) changed in response to tree mixing, except for RLD in the topsoil (Wambsganss et al., 2021).

These responses were also reflected at the community level, where a higher mixture proportion of gymnosperms was related to a *slower* root foraging strategy and a higher angiosperm proportion to a *faster* root foraging strategy (Table 1).

In contrast to gymnosperms, angiosperms may have adapted their fine-root soil exploitation strategy in mixtures to optimise resource acquisition (Chen et al., 2016, 2018; Cheng et al., 2016)—a response likely attributable to their evolutionary background (Ma et al., 2018; Wang et al., 2019). This greater plasticity of angiosperm roots was observed under the relatively small range of conditions the trees experienced between mixed and mono-specific stands at our study sites. This pattern may change under a greater range of environmental conditions, as great morphological plasticity has also been shown for gymnosperm roots along broader environmental gradients (e.g. Zadworny et al., 2016).

In contrast to the assumedly lower dependence on mycorrhizae of thin angiosperm roots, our results indicate that they were characterised by a strong increase in EcM colonisation intensity in mixtures compared to mono-specific stands (Figure 7). Yet, gymnosperm FRB was overall negatively related to total mycorrhizal biomass and diversity, whereas angiosperm FRB was not (Table S5). This suggests a trade-off between C investment in FRB versus investment in mycorrhizae for gymnosperms, supporting their commonly reported greater dependence on mycorrhizae for soil exploitation (Ma et al., 2018). In contrast, the less clear balance between FRB and EcM colonisation intensity of angiosperms may suggest that angiosperms employ more different ways to increase their nutrient-uptake capacity (e.g. specific root uptake rate, Miller & Cramer, 2005; root hair length and density, Forde & Lorenzo, 2001).

5 | CONCLUSIONS

This study demonstrates that in tree species mixtures several potential non-exclusive and partially contradicting underlying mechanisms may simultaneously contribute to a lower below-ground biomass. Consequently, an underyielding of fine-root biomass in tree species mixtures does not necessarily reflect negative below-ground species interactions and a lower performance of mixtures. Here, integrating the role of mycorrhizal symbionts and further fine-root traits related to fine-root soil exploitation was key to shed light on these typically overlooked underlying patterns of biodiversity effects on plant biomass production.

Future tree diversity studies could further disentangle different divers of net diversity effects on fine-root biomass by considering gradients of abiotic (i.e. soil resource availability) and biotic properties (i.e. mycorrhizal symbionts).

We conclude that below-ground biomass by itself is not a suitable variable to represent tree community performance. Hence, we strongly recommend using integrative approaches that incorporate a range of traits and C costs of above- and below-ground plant compartments to shed light on the underlying mechanisms of tree diversity effects on ecosystem functioning.

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AUTHORS' CONTRIBUTIONS

All authors contributed to the design of the study; J.W. and L.D.P.-S. carried out data collection and performed the analysis; J.W. drafted the manuscript. All authors discussed and interpreted the results and contributed to writing of the manuscript.

DATA AVAILABILITY STATEMENT

The datasets used for this study are archived on a data portal associated with the FunDivEUROPE and SoilForEUROPE projects and available after a 1-year embargo (root biomass data: https://data.botanik.uni-halle.de/fundiveurope/datasets/518; root functional trait data: https://data.botanik.uni-halle.de/fundiveurope/datasets/521; plot-level C, N data: https://data.botanik.uni-halle.de/fundiveurope/datasets/520; Soil fungal biomass and diversity data: https://data.botanik.uni-halle.de/fundiveurope/datasets/522).

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SUPPORTING INFORMATION

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

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