Mycorrhizal type and tree diversity affect foliar elemental pools and stoichiometry

Elisabeth Bönisch[1,2] (iD), Evgenia Blagodatskaya[3] (iD), Rodolfo Dirzo[4,5] (iD), Olga Ferlian[1,2] (iD), Andreas Fichtner[6] (iD), Yuanyuan Huang[1,2] (iD), Samuel J. Leonard[4,5] (iD), Fernando T. Maestre[7] (iD), Goddert von Oheimb[8] (iD), Tama Ray[1,8,9] (iD) and Nico Eisenhauer[1,2] (iD)

[1]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstr. 4, 04103, Leipzig, Germany; [2]Institute of Biology, Leipzig University, Puschstr. 4, 04103, Leipzig, Germany; [3]Soil Ecology Department, Helmholtz-Centre for Environmental Research (UFZ), Theodor-Lieser-Str. 11, 06120, Halle, Germany; [4]Department of Biology, Stanford University, Stanford, CA 94305, USA; [5]Department of Earth Systems Science, Stanford University, Stanford, CA 94305, USA; [6]Institute of Ecology, Leuphana University of Lüneburg, Universitätsallee 1, 21335, Lüneburg, Germany; [7]Environmental Sciences and Engineering, Biological and Environmental Science and Engineering Division, King Abdullah University of Science and Technology, Thuwal, 23955-6900, Kingdom of Saudi Arabia; [8]Institute of General Ecology and Environmental Protection, TU Dresden University of Technology, Pienner Straße 7, 01737, Tharandt, Germany; [9]Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, 06108, Halle (Saale), Germany

Author for correspondence:
Elisabeth Bönisch
Email: *elisabeth.boenisch@idiv.de*

Summary

- Species-specific differences in nutrient acquisition strategies allow for complementary use of resources among plants in mixtures, which may be further shaped by mycorrhizal associations. However, empirical evidence of this potential role of mycorrhizae is scarce, particularly for tree communities.
- We investigated the impact of tree species richness and mycorrhizal types, arbuscular mycorrhizal fungi (AM) and ectomycorrhizal fungi (EM), on above- and belowground carbon (C), nitrogen (N), and phosphorus (P) dynamics.
- Soil and soil microbial biomass elemental dynamics showed weak responses to tree species richness and none to mycorrhizal type. However, foliar elemental concentrations, stoichiometry, and pools were significantly affected by both treatments. Tree species richness increased foliar C and P pools but not N pools. Additive partitioning analyses showed that net biodiversity effects of foliar C, N, P pools in EM tree communities were driven by selection effects, but in mixtures of both mycorrhizal types by complementarity effects. Furthermore, increased tree species richness reduced soil nitrate availability, over 2 yr.
- Our results indicate that positive effects of tree diversity on aboveground nutrient storage are mediated by complementary mycorrhizal strategies and highlight the importance of using mixtures composed of tree species with different types of mycorrhizae to achieve more multi-functional afforestation.

Introduction

The positive relationship between biodiversity and ecosystem functioning in terrestrial ecosystems (e.g. Cardinale *et al.*, 2007; Morin *et al.*, 2011; Huang *et al.*, 2018) largely depends on plant nutrient availability, uptake, and their spatio-temporal dynamics (Barry *et al.*, 2019). Theory predicts that these effects are substantially driven by dissimilarities in plant resource acquisition traits (i.e. different rooting systems; Dornbush & Wilsey, 2010) and resource use strategies (i.e. conservative vs acquisitive; Diaz *et al.*, 2004; Barry *et al.*, 2019). Diverse species assemblages occupy a greater number of resource niches, which reduces competition for limiting nutrients (Loreau & Hector, 2001; Hooper *et al.*, 2005; Ferlian *et al.*, 2018a). The complementary use of resources is expected to enhance resource use and net primary productivity of a community (Tilman, 1980).

Besides physiological differences between species supporting resource use complementarity (Barry *et al.*, 2019), plants associate with important symbiotic partners – mycorrhizal fungi (van der Heijden *et al.*, 1998). Mycorrhizal fungi support their plant hosts directly by supplying them with water, mineral nutrients, and protecting them against pathogens (Smith & Read, 2008), and indirectly by improving biogeochemical soil properties such as soil structure and pH (Rillig & Mummey, 2006). In return, plants provide fungi with carbohydrates and lipids (Luginbuehl *et al.*, 2017). Trees predominantly associate with either arbuscular mycorrhizal (AM) or ectomycorrhizal (EM) fungi. These two mycorrhizal types feature contrasting resource acquisition strategies (Read, 1991; Bonfante & Genre, 2010; Ferlian *et al.*, 2021). Caused by their limited saprotrophic abilities, AM fungi primarily provide inorganic phosphorus and nitrogen to plants (Smith & Smith, 2011). Their inorganic nutrient economy is

characterized by resource acquisitive traits, such as fast biochemical cycling, rapid growth of the host plant, fast decomposition, and high mineralization rates, which often leads to nutrient-rich soils, foliage, and litter (Phillips *et al.*, 2013; Powell & Rillig, 2018; Deng *et al.*, 2023). Ectomycorrhizal fungi show a slow organic nutrient economy, enhancing the availability and uptake of organic nutrients, mainly organic nitrogen (van der Heijden *et al.*, 1998), to plants by directly promoting the decomposition of organic matter through the exudation of extracellular enzymes (Diaz *et al.*, 2004; Lambers *et al.*, 2009; Phillips *et al.*, 2013). This favors a competitive condition between EM and free-living decomposers in soil, slowing down decomposition of plant litter, thereby promoting carbon accumulation in soils (Orwin *et al.*, 2011; Averill & Hawkes, 2016). This conservative resource use strategy is characterized by slow growth and slow foraging roots of host plants, poor-quality foliage and litter (Cornelissen *et al.*, 2001; Midgley & Phillips, 2014; Averill & Hawkes, 2016; Eskelinen, 2020). Thus, the presence of two distinct mycorrhizal types in a community, characterized by dissimilar resource uptake strategies and traits, is expected to enhance resource complementarity (Cheng *et al.*, 2016) among their associated plant hosts and alter above- and belowground elemental concentrations and pools (Ferlian *et al.*, 2018a,b; Eisenhauer *et al.*, 2022).

While resource complementarity plays a significant role in space, via the occupation of different nutrient niches in soil by roots, mycorrhizal hyphae, and other microbial communities, nutrient availability is also highly dynamic in time (Eisenhauer *et al.*, 2022). Availability of nutrients is strongly affected by seasonal changes in environmental factors, such as temperature, precipitation, and soil moisture (Niklaus *et al.*, 2001; Scherer-Lorenzen *et al.*, 2003; Oelmann *et al.*, 2007). This is caused by the dependency of soil microbial activity on suitable climatic conditions (Kuzyakov & Blagodatskaya, 2015; Baldrian, 2017). Therefore, mycorrhizal fungi exhibit a distinct seasonality (Keller & Phillips, 2018), which may further affect their ability to supply their hosts with nutrients. Moreover, both mycorrhizal strategies may complement each other over time and therefore enhance total nutrient uptake. However, direct effects of mycorrhizal types and tree species richness on the seasonal availability of nutrients have not been studied yet. Knowledge of spatial and temporal nutrient dynamics may improve our understanding of the underlying mechanism driving positive biodiversity effects on ecosystem functioning.

Here, we aim to shed light on the patterns of above- and belowground nutrient dynamics mediated by mycorrhizal type and tree species richness. The research was conducted within the tree diversity experiment, MyDiv, which manipulates both tree species richness and mycorrhizal strategy (Ferlian *et al.*, 2018b).

We characterized carbon (C), nitrogen (N), and phosphorus (P) concentrations and respective pools and ratios in the soil, soil microbial biomass, and foliage, and the temporal availability of the nutrients nitrate (NO_3–N), ammonium (NH_4–N), and phosphate (PO_4–P) in the soil, for 2 yr. To evaluate whether positive biodiversity effects on foliar elemental pools (net biodiversity effect, NE) were caused by the complementarity of species (complementarity effect, CE) or by higher performance of single species within diverse communities (selection effect, SE), the additive partitioning method of Loreau & Hector (2001) was applied. Accordingly, we tested the following hypotheses:

H1: Both species-rich and tree communities with mixed mycorrhizal types (AM + EM) will enhance aboveground nutrient storage and tree productivity, resulting in higher carbon (C), nitrogen (N), and phosphorus (P) concentrations and pools in foliage and soil microbial biomass and, as result, reduced concentrations and pools in soil.

H2: We expect the quality of foliage and soil microbial biomass to increase with tree species richness (i.e. lower C : N, C : P, and N : P ratios). As a result, the respective elemental ratios increase in the soil.

H3: Communities with high tree species richness and mixed mycorrhizal strategies will enhance resource exploitation from soils and therefore show lower concentrations of plant-available soil nutrients. These effects will be more pronounced during the growing season and under favorable climatic conditions (e.g. periods of increased soil moisture).

H4: We expect positive effects of high tree species richness and mixed mycorrhizal types (AM + EM) on aboveground elemental pools to be explained by higher complementarity (complementarity effect, CE) between tree species and mycorrhizal types.

Materials and Methods

Study site and experimental design

MyDiv is a long-term tree diversity experiment, located at the Bad Lauchstädt Experimental Research Station southwest of Halle (51°23′N, 11°53′E), Saxony-Anhalt, Germany. The experiment is run by the German Center of Biodiversity Research (iDiv), Halle-Jena-Leipzig and Helmholtz Center for Environmental Research (UFZ) The MyDiv was established in March 2015 on former arable land characterized by nutrient- and humus-rich Chernozem soil (Ferlian *et al.*, 2018b). The experimental site consists of 80 plots, which are divided into two blocks according to a gradient in abiotic parameters. Each of the 11 m × 11 m plots is divided into a buffer zone and a core zone (64 m²) and covered by a tarp to prevent weed growth that introduce other mycorrhizal types. Per plot, 140 two-year-old tree saplings were planted with 1m distance from each other (64 trees in the core zone). The species pool contains 10 deciduous tree species, five of which associate predominantly with AM and five with EM fungi (Table 1). The selected tree species are native to Germany, adapted to the site conditions, and are of either economical or recreational relevance (Ferlian *et al.*, 2018b). Further, only one species per genus was selected to have representative species spread widely across the angiosperm phylogeny (Ferlian *et al.*, 2018b). Based on these selection criteria, we could not avoid that four of the five EM species belong to the order Fagales. The experiment combines three levels of tree species richness (monocultures, two- and four-species mixtures) with three levels of mycorrhizal association types, either AM, EM, or a mixture of both (details on experimental design in Supporting Information

Table 1 Overview of tree species used in the MyDiv experiment with their respective mycorrhizal association.

Species	Family	Mycorrhizal association
Acer pseudoplatanus L.	Sapindaceae	AM
Aesculus hippocastanum L.	Sapindaceae	AM
Fraxinus excelsior L.	Oleaceae	AM
Prunus avium L.	Rosaceae	AM
Sorbus aucuparia L.	Rosaceae	AM
Betula pendula Roth	Betulaceae	EM
Carpinus betulus L.	Betulaceae	EM
Fagus sylvatica L.	Fagaceae	EM
Quercus petraea (Matt.) Liebl.	Fagaceae	EM
Tilia platyphyllos Scop.	Malvaceae	EM

For details, see Ferlian *et al.* (2018b). AM, arbuscular mycorrhizal fungi; EM, ectomycorrhizal fungi.

Table S1). The design does not contain any mixtures of three vs one tree species per mycorrhizal type. The treatments of the experiment were confirmed by DNA-sequencing. Further, AM trees showed substantially higher mycorrhization rates by arbuscular mycorrhizal fungi than by ectomycorrhizal fungi, whereas the opposite pattern was found for EM trees (table S1 in Ferlian *et al.*, 2021).

Data collection

Soil physico-chemical measurements Soil samples for the measurement of soil bulk density ($g\,cm^{-3}$) were collected with a 5-cm--diameter soil corer to a depth of 5 cm in May 2021. The samples were air-dried and weighted. The bulk density was then calculated as the dry weight of soil divided by its core volume. Soil samples for the analyses of soil pH, soil total C, N, and P concentrations ($g\,kg^{-1}$) were taken with 5-cm soil corers to 10-cm soil depth in October 2021. This approach is in line with common soil biodiversity and function monitoring approaches (e.g. Guerra *et al.*, 2021a,b) and is based on the biological activity of plants and animals, which is highest in the first 5–10 cm of the soil and decreases with deeper layers (e.g. Stone *et al.*, 2014; Weldmichael *et al.*, 2020). Four soil cores were pooled to one composite sample per plot, whereby all tree species were equally represented as neighbors. Plant material and stones were removed by sieving (2-mm mesh). For pH measurements, soil samples were solved in 25 ml of CaCl$_2$-solution ($0.01\,mol\,l^{-1}$), stirred, left for 1 h, stirred again, and measured with the probe (data and results on soil pH and bulk density can be found in Fig. S1; Tables S2, S3).

For analysis of soil total C, N, and P, samples were dried at 60°C and ground to fine powder with a ball mill (MM400; Retsch, Haan, Germany). For C and N analysis, samples were dried for another 24 h, and transferred into tin capsules. Analyses were conducted using an elemental analyzer (VarioMax; Elementar Analysensysteme GmbH, Langenselbold, Germany). The analysis of P was conducted by dissolving an aliquot of 500 mg ground soil using microwave digestion at 200°C for 30 min (5 ml HNO$_3$ and 0.5 ml H$_2$O$_2$ to avoid production of nitric oxides; Multiwave, Anton Paar GmbH, Graz, Austria). Measurements were carried out with an inductively coupled plasma optical emission spectrometer (wavelength: 177.5 nm; limit of determination: $0.13\,mg\,l^{-1}$; Arcos, Spectro Analytical Instruments GmbH, Kleve, Germany).

Soil microbial C, N, and P measurements For the analysis of soil microbial C, N, P concentrations ($\mu g\,g^{-1}$), pooled soil samples (same as for soil C, N, and P analyses) were kept at 4°C and analyzed within 3 d after sampling by chloroform–fumigation–extraction (CFE) method using 0.05 M K$_2$SO$_4$ extracts and a conversion factor (Kp) of 0.45 for C and 0.54 for N (Brookes *et al.*, 1985; Wu *et al.*, 1990). Microbial P concentration was determined by direct fumigation and anion exchange membrane techniques (Yevdokimov *et al.*, 2016) with the conversion factor 0.40 (Brookes *et al.*, 1985). We tested a different conversion factor according to the soil properties (Bilyera *et al.*, 2018); however, Kp values for P did not differ significantly from 0.40 for the soils used in our study.

Time series of available soil N and P To assess the intra- and inter-annual variation, as well as seasonal differences in soil nitrate (NO$_3$–N), ammonium (NH$_4$–N), and phosphate (PO$_4$–P), we inserted ionic exchange membranes (IEM) each month. Ionic exchange membranes are a valid method to measure *in situ* nutrient availability ($\mu g\,cm^{-2}\,d^{-1}$) for plants in soil. Experimental studies show that ion concentrations obtained by IEMs correlate with plant uptake of such ions (Ziadi *et al.*, 1999; Qian & Schoenau, 2002; Durán *et al.*, 2013). For 2 yr (April 2019–March 2021), cationic and anionic IEMs were inserted into the soil at 10 cm depth and replicated five times in a transect of 1 m per plot each month. After incubation for 1 month, the IEMs were dried at room temperature and cleaned. Further processing of the samples was conducted according to Rodríguez *et al.* (2009) and Durán *et al.* (2013). To assess daily concentrations of plant-available nutrients, the measured nutrient concentrations were divided by the days of incubation.

Foliar C, N, and P measurement For the analysis of foliar C, N, and P concentrations ($g\,kg^{-1}$), fresh leaves of all tree species were sampled in July 2021. Nine leaves from three different tree individuals per plot and tree species were sampled at a tree height of *c.* 2.5 m. The leaves were dried at 40°C in the drying oven for 24 h and ground with a ball mill (MM 400; Retsch). For C and N analyses, samples were transferred into tin capsules and analyzed using an elemental analyzer (Vario EL cube; Elementar Analysensysteme GmbH). The analysis of foliar P was conducted the same way as for the soil samples.

Environmental data Environmental data (soil moisture (%) and soil temperature (°C) in 10 cm depth; air temperature (°C), air humidity (%)) were measured with three weather stations (mean value used) at the MyDiv experimental site (Meteorological data of Bad Lauchstädt, Helmholtz Centre for Environmental Research (UFZ)). Therefore, only site-specific data were available in 2021, but no plot-specific data.

Calculations

Soil, soil microbial, and foliar pools   For each plot, soil nutrient pools (kg ha^{-1}) and soil microbial biomass nutrient pools (g m^{-2}) were calculated as the products of total C, N, and P and soil bulk density (g cm^{-3}) and sampling depth (10 cm). Community foliar elemental pools (per plot) were derived by multiplying foliar elemental concentrations (g kg^{-1}) with an index that captures the spatial structural complexity of biomass distribution within a stand (Stand Structural Complexity Index, SSCI; Ehbrecht *et al.*, 2017) (Fig. S2), since data on individual leaf biomass or Leaf Area Index (LAI) were not available (note that SSCI does not have any units, thus it can also not be given for foliar elemental pools). The SSCI was calculated based on terrestrial laser scanning data, which were collected in September 2021 at the study site (Ray *et al.*, 2023a). Here, we use the SSCI as a proxy for LAI assuming that structurally more complex stands are associated with greater spatial complementarity in canopy space, and thus greater light interception (Ray *et al.*, 2023a). For example, differences in branching intensity and branch density lead to greater crown complementarity (Hildebrand *et al.*, 2021), which in turn should result in a higher leaf foliage production of structurally more complex stands.

Biodiversity effects of foliar elemental pools   Net biodiversity effects (NE), selection effects (SE), and complementarity effects (CE) for the elemental pools were calculated using the additive partitioning method of Loreau & Hector (2001). To calculate the relative yield of each tree species, we used species-specific foliar elemental pools that were estimated from the community pools, as no species-specific foliar biomass data were available. For this, the proportion (%) of species-specific wood volume (m^3, V_i) to the community wood volume was determined (Fig. S3). This proportion was used to derive the species-specific elemental pools from community elemental pools (Eqn 1; Fig. S4).

$$V_i = (\pi D_i^2/4) H_i f \qquad \text{Eqn 1}$$

where D_i represents the stem diameter (m) for each tree i measured 5-cm above ground and H_i is the tree height (m). To account for the deviation of the tree volume from the volume of a cylinder f is added as a cylindrical form factor of 0.5 (Ray *et al.*, 2023a). Dead trees (2.6% according to the tree inventory data from 2021) were not considered in the analysis.

Statistical analyses

Linear mixed-effects models (Type I Sum of Squares) were used to assess the impact of tree species richness (numerical with three levels – one, two, four), mycorrhizal type (factorial, three levels: AM, EM, AM + EM), and their interacting effect on elemental concentrations, elemental ratios, elemental pools, and biodiversity effects (net biodiversity effects, selection effects, complementarity effects). Block (factorial, two levels) was used as a random effect. Further, effects of tree species richness and mycorrhizal type on soil pH and soil bulk density were tested. To test for effects between groups (e.g. AM vs EM; AM + EM vs AM; AM + EM vs EM), Tukey's honestly significant difference (HSD) tests were conducted. The relationship between response variables (C, N, P concentrations, ratios, and pools of soil, soil microbial biomass, and foliage) and tree species richness as a single explanatory variable for each group (AM, EM, AM + EM) was tested with simple linear regression analysis (Tables S4–S6). Effects of phylogenetic relatedness of tree species were tested adding an additional explanatory variable (factorial, two levels – Fagales vs non-Fagales) to the linear mixed-effects model. The strength of treatment effects on the response variables was measured as relative change in response variables C, N, P concentrations, ratios, and pools (Tables S7–S12).

To improve the normality of residuals, biodiversity effects were square-root-transformed with sign reconstruction (sign(y) = |y|) (Loreau & Hector, 2001). To test whether biodiversity effects were significantly > 0, we used one-tailed *t*-tests. Significantly larger biodiversity effects indicate overperformance in two- and four-species tree communities relative to monocultures.

For the analysis of the time series dataset on plant-available nutrients, we included the temporal trend to estimate the parameters of the models using Bayesian statistics. Models were fitted using R-Integrated Nested Laplace Approximation (R-INLA), with tree species richness, mycorrhizal type, season, and soil moisture, as well as their interactions as fixed effects, and block, plot, and year as random effects. To account for the temporal trend, a Random walk model of order 1 (RW1) trend was added. For model comparison, DIC values were used and insignificant interaction terms removed. The final model is given in the Table S13.

All statistical analyses were performed in R (v.4.3; R Development Core Team, http://www.R-project.org) using the packages NLME (v.3.1-164; Pinheiro & Bates, 2000) and EMMEANS (v.1.8.6; Lenth *et al.*, 2024) for mixed-effects model analysis and Tukey's HSD tests, respectively. For the additive partitioning method (calculation of biodiversity effects), we used the function *addpart* from the package PDIV (Niklaus, 2022). For the Bayesian-based time series analysis, R-INLA (v.22.12.16) was used (Zuur *et al.*, 2017).

Results

Elemental concentrations and ratios of foliage, bulk soil, and soil microbial biomass

Overall, effects of tree species richness and mycorrhizal type were most pronounced for the elemental ratios and concentrations of tree foliage (Figs 1a–c, 2). By contrast, no effects of either treatment were observed in bulk soil (Fig. 1d–f; Table S14b), and they were rarely present in soil microbial biomass (Fig. 1g–i; Table S14c). Soil microbial biomass N ($P = 0.039$) and P concentrations ($P = 0.018$) were significantly affected by tree species richness and increased by *c.* 3% and 15% in four-species tree stands compared with monocultures, respectively, while C concentration ($P = 0.093$) was only marginally affected. Mycorrhizal
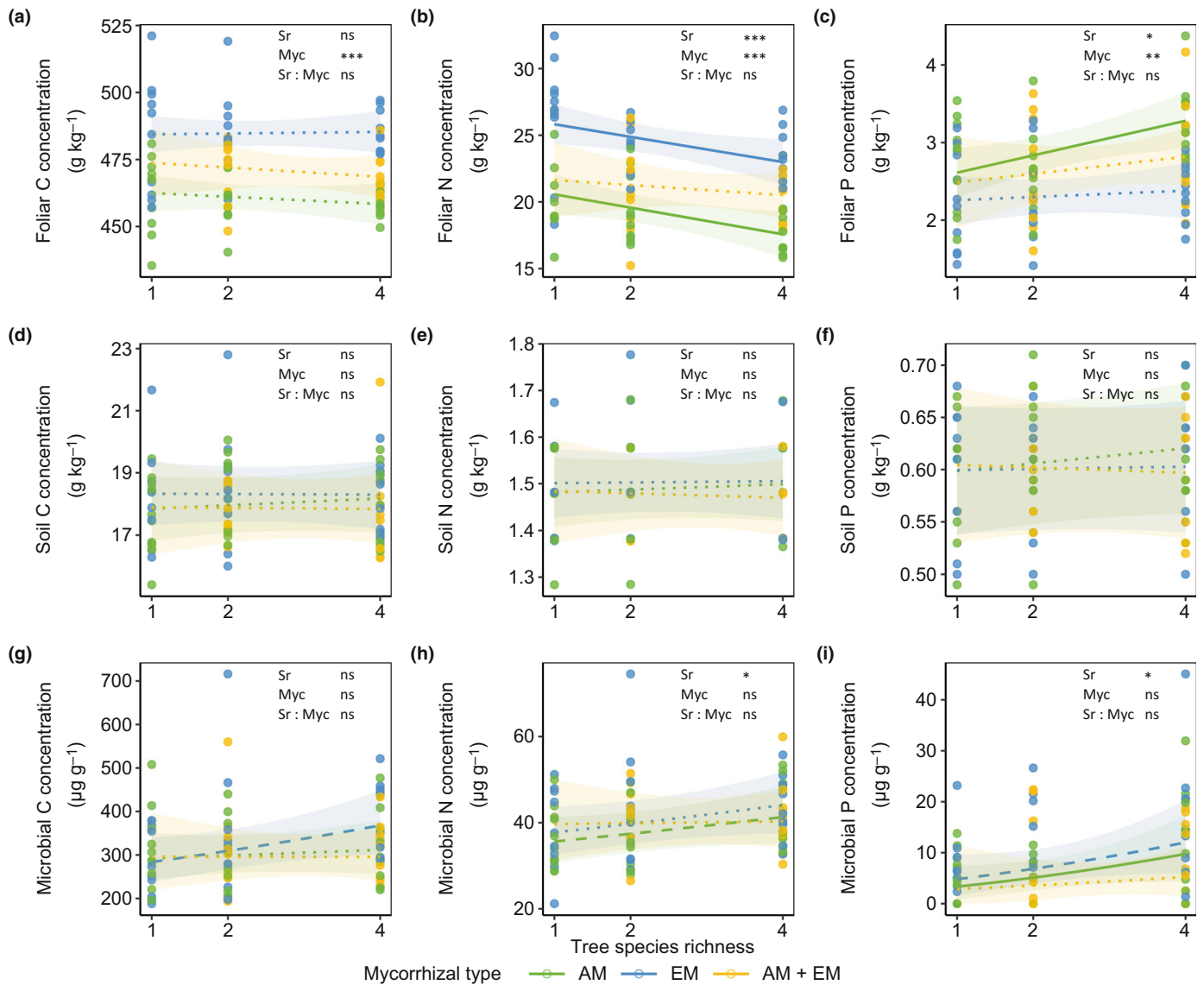
Fig. 1 Carbon (C), nitrogen (N), and phosphorus (P) concentrations in (a–c) foliage, (d–f) soil, and (g–i) microbial biomass in soil as a function of tree species richness (one, two, four; Sr) for communities containing arbuscular mycorrhizal tree species (AM), ectomycorrhizal tree species (EM), or both (AM + EM) tree species (Myc). Each dot represents a tree community, and colors indicate different Mycorrhizal types. Regression lines are based on mixed-effects models (predicted means). Solid lines indicate statistically significant relationships ($P < 0.05$), dashed lines marginally significant relationships ($0.1 > P > 0.05$), and dotted lines non-significant relationships ($P > 0.1$). Shaded areas indicate the 95% confidence interval of the prediction. Statistical significance of main effects is indicated in each panel (not significant (ns), $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$).

strategies did not affect soil microbial biomass. Consequently, elemental ratios (C : N, C : P, N : P) of bulk soil and soil microbial biomass were not significantly affected by species richness or mycorrhizal type (Fig. S5; Table S15b,c).

In tree foliage, tree species richness had contrasting effects on concentrations of N and P: while N concentrations decreased significantly with tree species richness ($P < 0.001$) by c. 13% in four-species communities compared with monocultures, P concentrations significantly increased ($P = 0.017$) by 14% in four-species stands compared with monocultures (Fig. 1a–c; Table S14a). C concentrations remained constant along the tree diversity gradient. Mycorrhizal type significantly affected C,

N, and P concentrations ($P < 0.001$ respectively), whereby C and N concentrations were highest for EM tree stands (5% and 24% larger than AM tree stands, respectively), and P concentrations for AM tree communities (23% higher than EM tree stands; Tables S14a, S16a). Tree stands with mixed mycorrhizal types (AM + EM) showed additive effects with values between AM and EM communities (Fig. 1a–c). Further, we found no interaction effect of mycorrhizal type and tree species richness on elemental concentrations. Ratios of the foliar elemental concentrations of C, N, and P were significantly affected by tree species richness (C : N: $P = 0.004$, C : P: $P < 0.001$, N : P: $P = 0.041$) and mycorrhizal type (C : N: $P < 0.001$, C : P: $P = 0.015$, N : P:
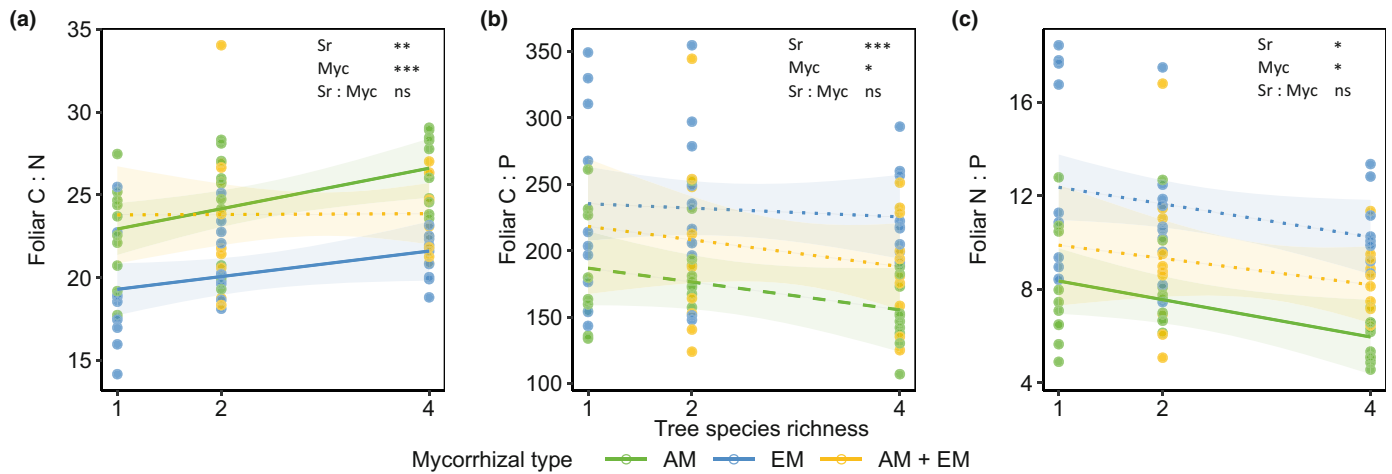
Fig. 2 Foliar elemental ratios (a) C : N, (b) C : P, and (c) N : P as a function of tree species richness (one, two, four; Sr) for communities containing arbuscular mycorrhizal tree species (AM), ectomycorrhizal tree species (EM), or both (AM + EM) tree species (Myc). Each dot represents a tree community, and colors indicate different mycorrhizal types. Regression lines are based on mixed-effects models (predicted means). Solid lines indicate statistically significant relationships ($P < 0.05$), dashed lines marginally significant relationships ($0.1 > P > 0.05$), and dotted lines non-significant relationships ($P > 0.1$). Shaded areas indicate the 95% confidence interval of the prediction. Statistical significance of main effects is indicated in each panel (not significant (ns), $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$).
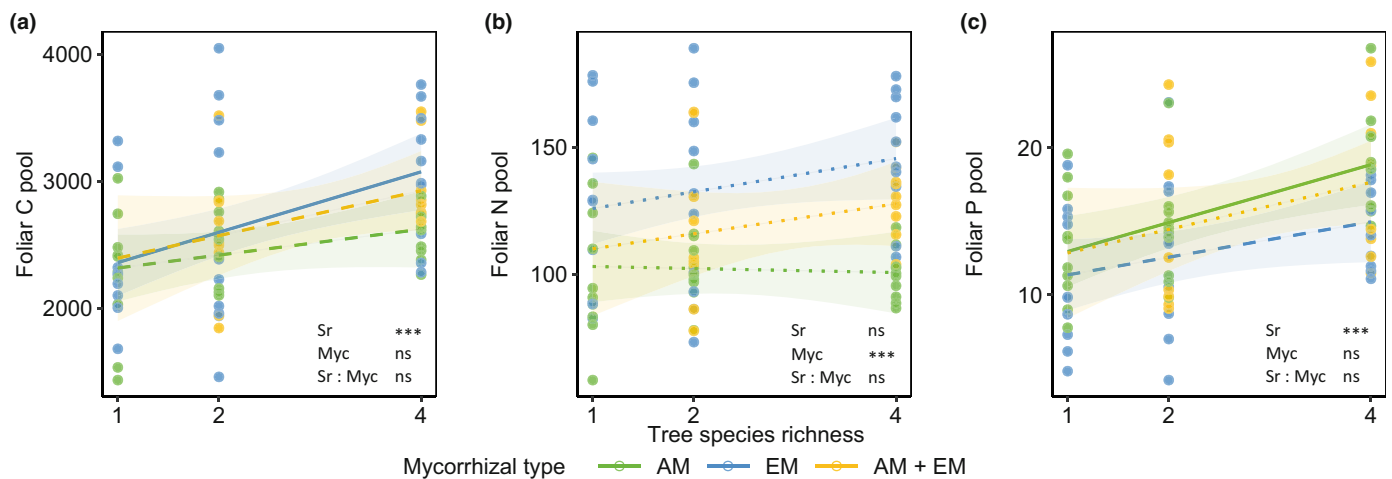

Fig. 3 Foliar (a) carbon (C), (b) nitrogen (N), and (c) phosphorus (P) pools as affected by tree species richness (one, two, four; Sr) for communities containing arbuscular mycorrhizal tree species (AM), ectomycorrhizal tree species (EM), or both tree species (AM + EM) (Myc). Elemental pools were calculated by multiplying the nutrient concentration (g kg^{-1}) with the Stand Structural Complexity Index, which is a proxy for leaf biomass per plot. Each dot represents a tree community, and colors indicate different mycorrhizal types. Regression lines are based on mixed-effects models (predicted means). Shaded areas indicate the 95% confidence interval of the prediction. Solid lines indicate statistically significant relationships ($P < 0.05$), dashed lines marginally significant relationships ($0.1 > P > 0.05$), and dotted lines non-significant relationships ($P > 0.1$). Statistical significance of main effects is indicated in each panel (not significant (ns), $P > 0.05$; ***, $P < 0.001$).

$P = 0.022$) (Fig. 2a–c; Table S15a). While C : N ratios of AM and EM tree communities increased with tree species richness by 15.3% (monocultures compared with four-species communities), ratios of C : P and N : P decreased by c. 9% and 22%, respectively. Ectomycorrhizal fungi tree communities showed 21% lower foliar C : N ratios than AM tree communities, while C : P and N : P ratios were c. 25% and 36% lower in AM tree stands than in EM tree stands (Table S17a). Foliar elemental ratios in mixed tree communities containing both mycorrhizal types showed an additive effect (Fig. 2).

Elemental pools of foliage, bulk soil, and soil microbial biomass

We only found significant effects of tree species richness and mycorrhizal type on elemental pools in the foliage of trees (Fig. 3; Table S18), but not on pools of bulk soil and soil microbial biomass (Fig. S6; Table S18). Tree species richness had an overall positive effect on pools of C ($P < 0.001$) and P ($P < 0.001$) in foliage, whereby the pool sizes increased by c. 25% and 41%, respectively, in four-species mixtures compared

with monocultures (Tables S18, S19). Foliar N pools were not significantly affected by tree species richness but by mycorrhizal type ($P < 0.001$; Fig. 3), with N pools in EM tree communities being 28% larger than N pools in AM tree communities (Table S19a). By contrast, P pools in foliage were 18% larger in AM than in EM tree communities. However, no significant main effect of mycorrhizal type on P and C pools was found (Table S18). For mixtures of the two mycorrhizal types, we consistently observed additive effects, similar to the elemental concentrations and ratios (Fig. 3). Significant interaction effects between the two treatments were not detected.

Seasonal availability of soil nitrate, ammonium, and phosphate

Our study reveals pronounced temporal fluctuations in the availability of nitrate, ammonium, and phosphate in the soil (Figs 4, S7–S9). Specifically, the highest concentrations of nitrate and ammonium were observed during spring (March–May; Table S20). Furthermore, we identified a significant interaction between soil moisture and season with respect to soil nitrate and ammonium levels (Figs 4, S10; Table S20). Seasonal effects on soil phosphate were not evident, but a significant positive effect of soil moisture on phosphate availability (Fig. S10; Table S20). Notably, when assessing these variations along the gradient of tree species richness and among different mycorrhizal types, we found significant effects only in the case of nitrate (Table S20). Nitrate availability in soil decreased with increasing tree species richness (Fig. 4). Regarding mycorrhizal types, nitrate availability displayed no consistent pattern, but we did observe interactions between mycorrhizal type and seasonal effects (Fig. 4; Table S20). In EM tree communities, soil nitrate availability peaked in early spring, surpassing the nitrate levels in AM tree communities, and declined notably during summer. In AM tree stands, the availability of nitrate reached its peak in May and stayed relatively stable throughout summer. The temporal pattern of further environmental variables can be found in Figs S11 and S12, not included in main analyses because of missing main effects.

Biodiversity effects of foliar elemental pools

Overall, we found significantly higher net biodiversity effects (sum of complementarity effects and selection effects) in four-species than two-species mixtures for foliar C ($P = 0.001$) and P ($P < 0.001$) pools, and marginally increased net biodiversity effects for foliar N pools ($P = 0.085$) (Tables 2, S21; Fig. 5). Notably, net biodiversity effects were significantly larger for all elemental pools in four-species communities (either AM, EM, or AM + EM stands) than those in monocultures (Tables 2, S21), except for N pools in AM tree stands. In addition, tree species richness significantly increased the selection effects for all elemental pools (C: $P < 0.001$, N: $P = 0.013$, P: $P < 0.001$) and complementarity effects for C pools ($P = 0.041$) and P pools ($P = 0.007$). For mycorrhizal types, we observed significantly different effects on selection effects and complementarity effects in

foliar C, N, and P pools, but not for net biodiversity effects. While in EM tree communities, net biodiversity effects of foliar C, N, and P pools were mainly driven by selection effects, complementarity effects had a significantly stronger impact on mixtures of both mycorrhizal types (AM + EM) (Fig. 5; Table S22). Regarding P pools, AM communities showed significantly greater complementarity effects than selection effects, whereas for EM communities, the opposite was observed (Table S22). In general, we found no significant interaction effects (Sr × Myc) on biodiversity effects for any of the elemental pools.

Discussion

Elemental concentrations, ratios, and pools in foliage are affected by tree species richness and mycorrhizal type

We found large effects of tree diversity on foliar elemental concentrations, ratios, and pools, but with contrasting consequences. Surprisingly, while tree diversity had a significantly negative effect on N concentrations in foliage, P concentrations and also pools increased with tree species richness. The formation of N pools, however, tended to be enhanced by tree species richness, outweighing the negative impact on N concentrations, which may be linked to higher biomass production of more diverse communities, as has been shown before both in the MyDiv experiment (Dietrich et al., 2022; Ray et al., 2023a) and in other tree diversity experiments (e.g. Huang et al., 2018) as well as observational studies (Liang et al., 2016; Duffy et al., 2017). The higher productivity in more species-rich stands is also supported by the significantly enhanced C pools within these communities, while C concentrations were not significantly affected. The missing effects on foliar C concentration and the decline in foliar N concentration with increasing tree species richness led to a decrease in foliage quality, reflected as increasing foliar C : N ratio. These findings were unexpected, as we assumed to find the opposite results (i.e. increased foliar elemental concentration and pools in tree foliage and accordingly higher foliage quality with higher tree diversity). Similar patterns were observed in a grassland study, where N and P decreased with plant diversity, while C concentration remained constant (Guiz et al., 2016, 2018; Dietrich et al., 2023). Explanations for these observations could also correspond to our findings, for example trees in mixtures might invest more nutrients into plant organs relevant for height growth instead into foliage biomass to remain competitive for other resources (e.g. light). The results may also imply that even though we found a negative effect of tree species richness on availability of nitrate in soil, suggesting an enhanced N uptake within these tree stands, this might be masked or diluted by an even greater increase in above- and belowground biomass production (Guiz et al., 2018). Having addressed that, we only observed this pattern for N but not for P. Foliar P concentrations, pools, and foliar quality (lower C : P, N : P) were all enhanced by higher tree species richness, in particular in AM tree communities. Significant AM fungi diversity effects on plant shoot P pools have been reported before for grassland communities (e.g. van der Heijden et al., 1998), and differential tree and
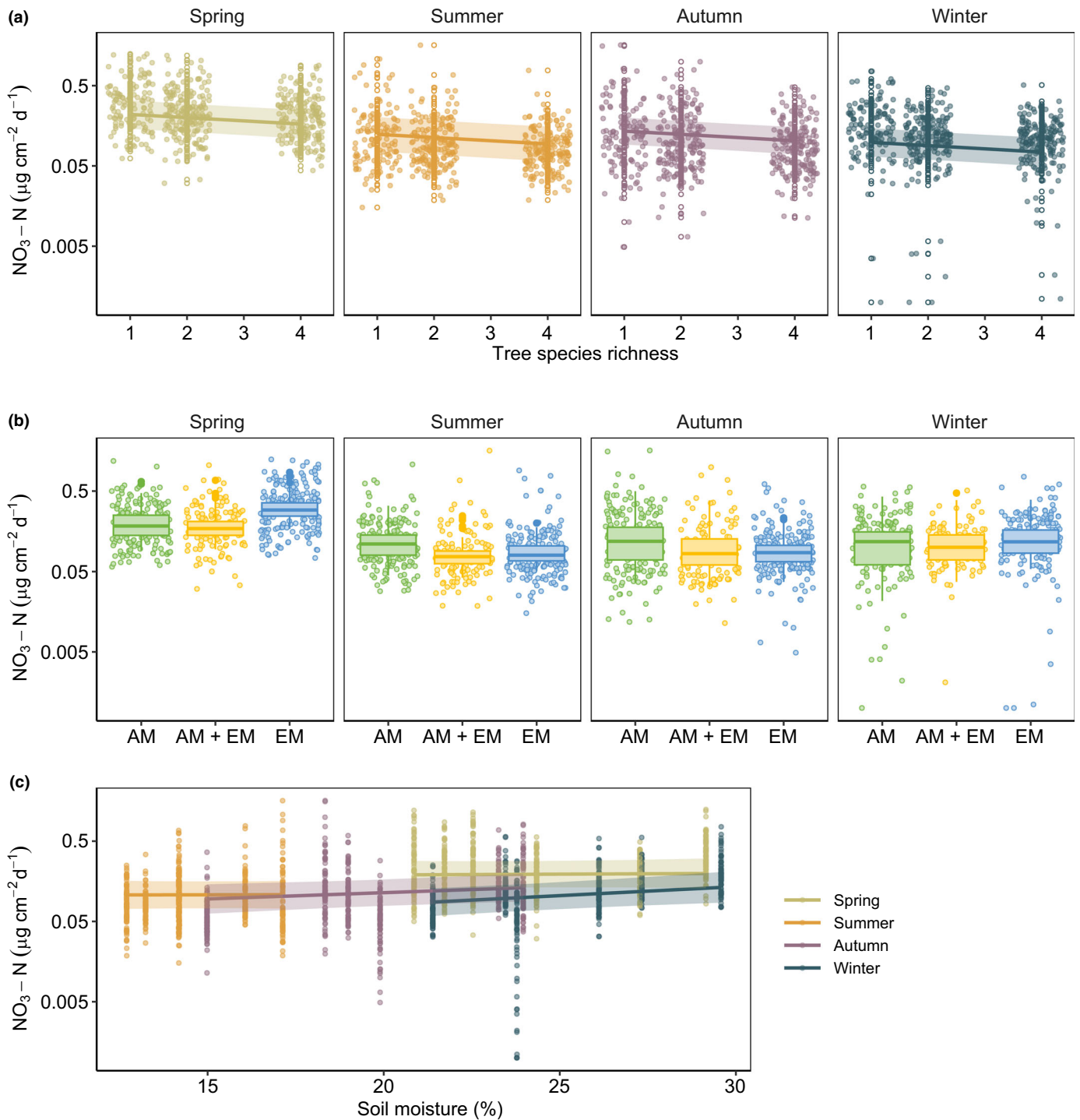
Fig. 4 Changes in seasonal availability of nitrate (NO$_3$–N) in soil as affected by (a) tree species richness (one, two, four; Sr), (b) mycorrhizal type (AM, EM, AM + EM; Myc), and (c) soil moisture (%). The data points depict the raw observations, regression lines and the shaded areas in panels (a) and (c), and boxplots in panel (b) denote 95% confidence intervals, which were derived from predictions generated by a random walk time series model using the Bayesian approach (see the Materials and Methods section). The boxplots show the median, the lower quartiles, and upper quartiles. The y-axis is log-scaled to convert the data into a more normally distributed form. Information on soil moisture was assessed on site via weather stations.

mycorrhizal diversity effects on foliar N and P concentrations might be due a rather high soil fertility (mostly soil N availability) at the experimental site (Ferlian *et al.*, 2018b). Therefore, our first hypothesis (increased aboveground elemental concentrations,

pools and quality of foliage with higher tree diversity) was partly confirmed.

All elemental concentrations, ratios, and pools in foliage were significantly or at least marginally affected by the mycorrhizal

Table 2 Summary of mixed-effects model analyses testing the effects of tree species richness (two, four; Sr), mycorrhizal type (AM, EM, AM + EM; Myc), and their interactions on net biodiversity effects, selection effects, and complementarity effects based on tree foliar (a) carbon (C) pool, (b) nitrogen (N) pool, and (c) phosphorus (P) pool ($n = 60$).

Source of variation	df	ddf	Net biodiversity effects		Selection effects		Complementarity effects	
			F	P	F	P	F	P
(a) C pool								
Tree species richness (Sr)	1	53	11.48	**0.001**	17.33	**< 0.001**	4.37	**0.041**
Mycorrhizal type (Myc)	2	53	0.58	0.561	4.54	**0.015**	4.11	**0.022**
Sr × Myc	2	53	1.24	0.296	2.68	*0.078*	1.08	0.348
(b) N pool								
Tree species richness (Sr)	1	53	3.08	*0.085*	6.61	**0.013**	0.01	0.939
Mycorrhizal type (Myc)	2	53	0.95	0.393	10.65	**< 0.001**	3.34	**0.043**
Sr × Myc	2	53	1.98	0.148	1.72	0.189	0.36	0.703
(c) P pool								
Tree species richness (Sr)	1	53	15.96	**< 0.001**	15.79	**< 0.001**	7.77	**0.007**
Mycorrhizal type (Myc)	2	53	0.41	0.675	13.62	**< 0.001**	6.06	**0.004**
Sr × Myc	2	53	0.99	0.375	0.53	0.592	2.32	0.108

Shown are the degrees of freedom (df), denominator degrees of freedom (ddf), F-values, and the statistical significance of the fixed effects (P-values). Significant effects ($P < 0.05$) are given in bold and marginally significant effects ($P < 0.1$) in italics. Species-specific elemental pools were derived from the community pools using species-specific wood volume (m³) (see the Materials and Methods section and Supporting Information Figs S2–S4).

type. Thus, we found greater C and N concentrations and increased N pools in EM tree stands than AM tree stands, while P concentrations and pools were significantly enhanced in the latter. Higher foliar C concentrations in EM trees can be explained by higher lignin concentrations in EM plants than in AM plants (Midgley *et al.*, 2015; Deng *et al.*, 2023). However, higher leaf N concentrations and the resulting lower foliar C : N ratios in EM trees compared with AM trees were unexpected, as several studies have demonstrated the nutrient conservative plant economic traits of EM plants, including lower N and P concentrations and respective lower foliage and litter quality, compared with nutrient acquisitive plant economic traits of AM plants comprising higher N and P concentrations as well as foliage and litter quality (Read, 1991; Smith & Read, 2008; Phillips *et al.*, 2013; Averill *et al.*, 2019). Further studies reported missing significant differences in nutritional status between both mycorrhizal type plants, in particular after consideration of phylogeny (Koele *et al.*, 2012). It is worth noting that four of the five EM tree species within the MyDiv experiment belong to a single order, Fagales. We therefore validated our analyses by accounting for phylogeny (Fagales vs non-Fagales species) in two statistical models (Table S23). In fact, initial significant differences between mycorrhizal types were missing for foliar C and P concentrations after accounting for phylogenetic groups (Fig. S13; Table S23; Model 1). However, for foliar N concentration, the mycorrhizal type effect was present before and after accounting for phylogeny (Fig. S14; Table S23; Model 2), likely because the N concentration of *Tilia platyphyllos*, the non-Fagales species, was similar to that of the other species within the EM group (Figs S15, S16). Therefore, some of our results may reflect the response of a particular lineage and consequently need to be treated cautiously. Additional research involving a larger group of phylogenetic lineages is therefore needed. Further, in tree stands with both mycorrhizal strategies, we found only additive effects but not an

expected elemental pool size that outperforms communities with one mycorrhizal type alone. This is consistent with findings of Dietrich *et al.* (2022), who could not observe any significant overyielding effects of tree productivity in communities of both mycorrhizal types. This contrasts our first hypothesis that optimized resource acquisition in mixed stands will lead to larger elemental pools in foliage (Ferlian *et al.*, 2018b; Eisenhauer *et al.*, 2022).

While aboveground tree diversity significantly modified foliar elemental concentrations, ratios, and pools, belowground elemental concentrations, ratios, and pools of soil nutrients and pools of soil microbes were not significantly affected. Only plant-available nitrate in soil showed a clear effect of tree species richness and mycorrhizal type, whereby the availability of nitrate decreased with increasing tree species richness, and effects of mycorrhizal type depended on the season. Overall, observed effects on soils were limited, which may result from the young age of the tree stands in the MyDiv experiment (7 yr since establishment in 2015 until time point of sampling for this study), given that plant diversity effects on ecosystem functioning have been shown to increase over time in grassland and forest biodiversity experiments (Guerrero-Ramírez *et al.*, 2017; Huang *et al.*, 2018). Changes in biogeochemical properties may require a longer period of time to become established (Oelmann *et al.*, 2011; Lange *et al.*, 2023). Further, land-use legacies from former agriculture might still persist, and thus, it is likely that the trajectory of the microbial soil community development is not significantly affected by tree species richness in such a short time (Fichtner *et al.*, 2014). Missing effects of tree species richness or mycorrhizal type on soil pH and soil bulk density (Fig. S1; Table S3) underpin this assumption. Furthermore, the plastic tarp, initially installed to prevent the growth of weeds that introduce other mycorrhizal types, may have inhibited some processes in nutrient cycling, such as accumulation of organic matter
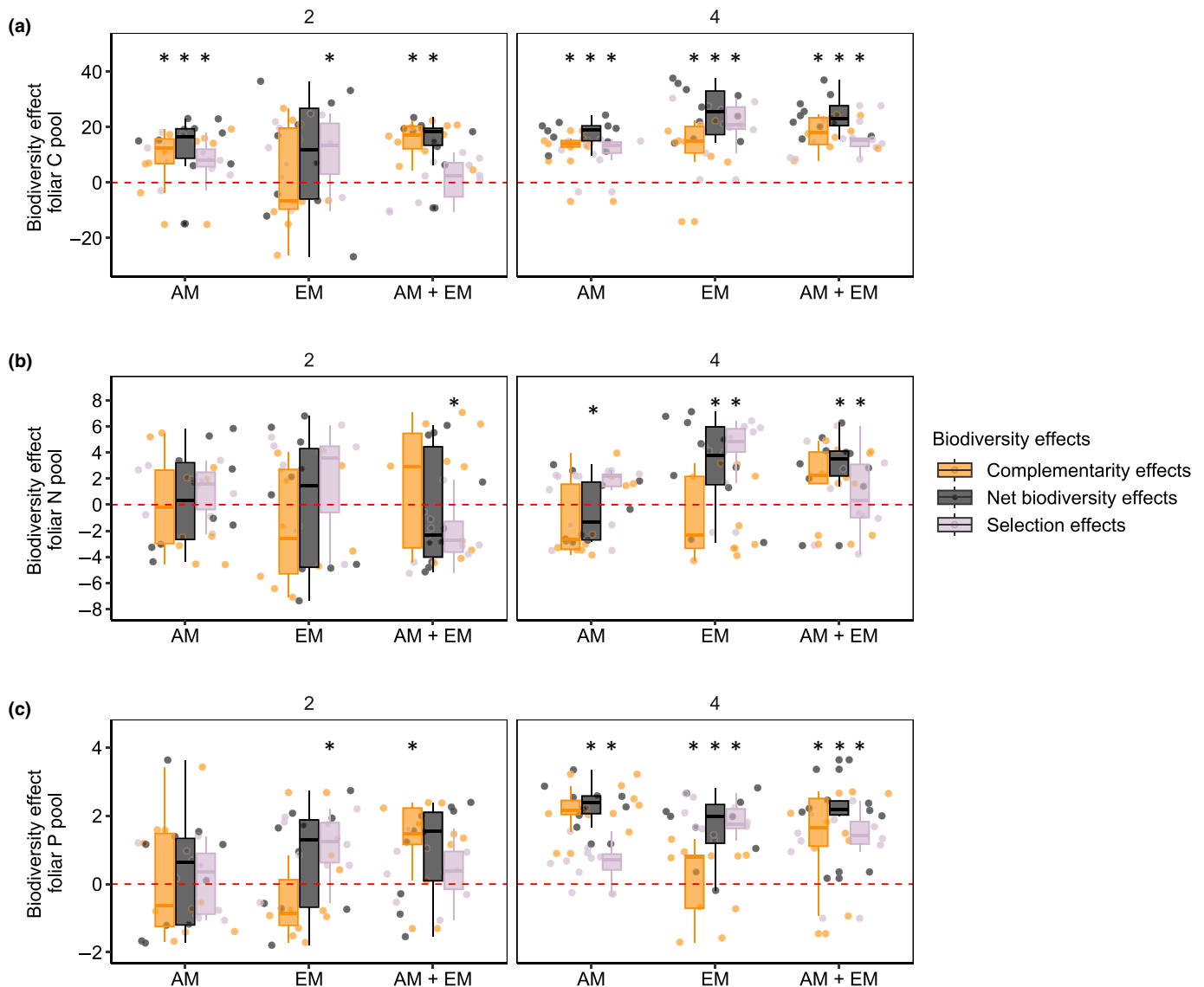
Fig. 5 Net biodiversity effects, complementarity effects, and selection effects for foliar (a) carbon (C) pool, (b) nitrogen (N) pool, and (c) phosphorus (P) pool as affected by tree species richness (two or four tree species) and mycorrhizal type (AM, EM, AM + EM). The boxplots show the median, the lower quartiles, and upper quartiles. Asterisks indicate whether the biodiversity effects were significantly > 0 (indicating overperformance of two- and four-species tree communities compared with monocultures determined by one-tailed *t*-tests; detailed results can be found in Supporting Information Table S21). Species-specific elemental pools in foliage were derived from total elemental pools using species-specific tree volume (see the Materials and Methods section). Values are square-root-transformed to meet the assumptions of analyses.

through litter fall and its direct interaction with soil organisms (Berg & McClaugherty, 2014). Plants usually modulate their belowground microbiome partly through the quality and composition of litter (Pollierer *et al.*, 2007; Prada-Salcedo *et al.*, 2022). Therefore, we may expect that species richness effects could be more pronounced in case of direct litter input. However, nutrient cycling can be affected by further processes, such as leaching of water-soluble compounds from litter, which plays a significant role in returning nutrients to the soil (Chapin *et al.*, 2011), the dynamics of root exudates, which were found to be influenced by diversity in tree experiments (Weinhold *et al.*, 2022), and further resource inputs (i.e. decomposing fine roots; McCormack *et al.*, 2015). Hence, it is anticipated that the tarp potentially

caused only modest impairments to these overall processes related to nutrient cycling. Furthermore, we were able to observe positive effects of tree diversity on N and P concentrations of soil microbial biomass. This finding may indicate that rhizodeposits play a critical role in tree effects on soil food webs (e.g. Pollierer *et al.*, 2007) as well as plant diversity effects on soil communities and functions (Lange *et al.*, 2015; Eisenhauer *et al.*, 2017). While tree diversity had an effect on soil microbial biomass, we could not find any effects of mycorrhizal type. This is in contrast to other tree diversity studies, which found effects of tree diversity or mycorrhizal associations on soil microbial community composition (Ferlian *et al.*, 2021; Singavarapu *et al.*, 2021). Further studies are required to test the relative importance of aboveground

vs belowground plant inputs in driving tree diversity and mycorrhizal type effects on ecosystem functioning.

Effects of mycorrhizal type on nitrate concentration vary with season and soil moisture

Along with the information on C, N, and P in bulk soil and soil microbial biomass, we assessed plant-available nutrients in soil to underpin soil-related analyses of resource use complementarity. Tree species richness showed consistent negative effects on soil nutrient availability, while mycorrhizal type effects varied with seasons. Consistent with our third hypothesis, we found that nitrate concentration decreased significantly with tree diversity. This effect was probably caused by greater utilization of soil nitrate due to complementary resource use strategies in more diverse tree populations (Ferlian et al., 2018a; Barry et al., 2019).

The effects of mycorrhizal type on nitrate concentration were strongly dependent on season, showing significantly higher levels of nitrate in EM communities in spring compared with summer and autumn, while nitrate concentrations in AM communities did not change significantly during these seasons. Soil phosphate and ammonium concentrations showed pronounced temporal dynamics but were less affected by the experimental treatments. In general, concentrations of ammonium and phosphate in soils were low, likely due to fast immobilization by plants and microorganisms and strong adsorption to soil- and organic colloids (Schachtman et al., 1998; Varma et al., 2017). These processes may potentially smooth the effects caused by tree species richness and mycorrhizal types. By contrast, nitrate as a negatively charged ion is not easily absorbed by clay particles in the soil and is therefore very mobile and susceptible to runoff and leaching (Riley et al., 2001).

The observed seasonality of nutrient availability is closely related to the activity of soil organisms and seasonal precipitation patterns, which are also subject to strong temporal fluctuations (Bardgett & van der Putten, 2014; Baldrian, 2017). Thereby, the seasonally dependent photosynthetic activity of plants and the allocation of photosynthates to the soil play major roles in resource provisioning to soil organisms (Baldrian, 2017). Weather conditions such as temperature, precipitation, and resulting soil moisture (Bardgett & van der Putten, 2014) are important predictors of the activity of soil biodiversity (Bonato Asato et al., 2023). In particular, soil water availability has strong effects on recovery and recurrence of soil microbial communities (Placella & Firestone, 2013). Fast responses were observed for nitrifying bacteria (Nitrobacter spp., Nitrospina spp., and Nitrospira) after rewetting of dry soil, followed by significant nitrogen mineralization (Placella & Firestone, 2013). This underlines our findings of high nitrate availability after summer droughts. In addition, studies on litter decay of AM and EM tree communities showed the influence of seasonally variable environmental factors (precipitation and temperature) on mycorrhizal activity (Keller & Phillips, 2018). The findings by Keller & Phillips (2018) may suggest for our observations a higher sensitivity of EM trees toward higher temperatures and moisture and thus, stronger nutrient release from elevated decay of litter.

Net biodiversity effects on tree stands of mixed mycorrhizal strategy are driven by complementarity

We found positive net biodiversity effects for C and P pools in foliage. For all elemental pools, net biodiversity effects, selection effects, and complementarity effects increased with tree species richness, except for N pools in AM tree stands. This shows that both complementarity effects and selection effects contributed to overall biodiversity effects on nutrient accumulation in foliage in young tree stands. Further, for all elemental pools in four-species communities (AM, EM, AM + EM), except N pools in AM tree stands, net biodiversity effects were significantly different from 0, indicating a higher performance of these communities compared with monocultures (Loreau & Hector, 2001). Similar effects have previously been observed for other ecosystem functions, such as biomass production in several forest studies (Huang et al., 2018; Dietrich et al., 2022). In the formation of elemental pools in EM tree stands, net biodiversity effects were mostly determined by positive selection effects, suggesting that the observed larger elemental pools are rather the result of the performance of individual dominant tree species (Scherer-Lorenzen et al., 2005; Morin et al., 2011; Dietrich et al., 2022). The observation of high selection effects in EM tree stands may be attributed to the pronounced nutrient uptake or biomass accumulation of Betula pendula, a fast-growing pioneer tree species (Stark et al., 2015), thus contributing a large part to the tree community nutrient pools (Figs S3, S4). However, from the analysis of foliar elemental concentrations, we found most of AM and EM species, including B. pendula, to show underperformance in foliar N concentration in four-species communities compared with monocultures (Fig. S17; Table S24; see also Fig. S16). This result is the opposite of what the significantly increased foliar N pools show. Therefore, we assume here that the increased pool sizes must be caused by enhanced biomass production (Figs S2–S4).

By contrast, we found that net biodiversity effects were more strongly driven by complementarity effects in mixed tree stands featuring both mycorrhizal types compared with EM tree communities. Comparing mixtures (AM + EM) with AM tree communities, we could not find any significantly stronger complementarity effect. Therefore, our findings suggest that mixed mycorrhizal strategies may enhance resource partitioning among associated plant hosts and alter aboveground nutrient dynamics in tree foliage, which is partly consistent with our fourth hypothesis (Cheng et al., 2016; Ferlian et al., 2018a,b; Eisenhauer et al., 2022).

Our study cannot fully explain underlying patterns of positive biodiversity effects, as a direct link between the aboveground and belowground elemental pools could not be established. Elemental assessment of foliage in summer was followed by analyses of soil elements in autumn, which may indicate some temporal mismatch between our measurements. As litter plays a very important role in the nutrient cycle, the investigation of the quantity and quality of litter and the derivation of nutrient resorption processes could provide additional insights. Future studies should also evaluate nutrient levels in roots (especially fine roots) and wood to enhance comprehension of nutrient distribution among plant organs and ecosystem components, particularly for a comprehensive assessment of how species richness affects elemental concentrations and

ratios. This could also be supported by assessments of leaf life spans and temporal changes in biomass, which both may play crucial roles in the overall storage and allocation of nutrients within trees. Our study lacks direct measurements of tree foliage biomass or leaf area index. However, we think that quantification of the SSCI is a precise proxy to account for these missing measurements (Hildebrand *et al.*, 2021).

Conclusion

In this study, we show that tree diversity enhances foliar P concentrations, pools, and quality (lower C : P, N : P), but decreases foliar N concentration. While C concentrations in foliage remained constant, C pools were enhanced with tree species richness. Further, tree species richness decreased the availability of soil nitrate, which may indicate higher nitrate uptake within these stands. Elemental concentrations and pool sizes in tree communities with both mycorrhizal strategies (AM + EM) did not exceed those of tree stands with EM or AM alone. However, the analysis of biodiversity effects suggests that resource use complementarity affects the resource uptake and aboveground nutrient storage in foliage more strongly in tree communities with both mycorrhizal types. Our findings thus highlight the importance of using forest species with diverse mycorrhizal strategies during, for example, restoration efforts for achieving a more complete use of available resources and thus to deliver more multifunctional forests.

Competing interests

None declared.

Author contributions

NE and OF designed and established the experiment. NE acquired the funds for this project. E Bönisch, SJL, RD, FTM, E Blagodatskaya, TR, AF and GO acquired and provided the data. E Bönisch analyzed the data and created the figures and wrote the manuscript. YH analyzed the time series data on plant-available nutrients. All authors significantly revised the manuscript and approved it for submission.

ORCID

Elisabeth Bönisch https://orcid.org/0000-0001-9386-880X
Evgenia Blagodatskaya https://orcid.org/0000-0002-8284-4017
Rodolfo Dirzo https://orcid.org/0000-0002-5751-9888
Nico Eisenhauer https://orcid.org/0000-0002-0371-6720
Olga Ferlian https://orcid.org/0000-0002-2536-7592
Andreas Fichtner https://orcid.org/0000-0003-0499-4893
Yuanyuan Huang https://orcid.org/0000-0002-6990-8864
Samuel J. Leonard https://orcid.org/0000-0002-1949-3664
Fernando T. Maestre https://orcid.org/0000-0002-7434-4856
Goddert von Oheimb https://orcid.org/0000-0001-7408-425X
Tama Ray https://orcid.org/0000-0001-9265-5431

Data availability

All data are available in the MyDiv data portal (https://mydivdata.idiv.de/; ID48, 65, 93, 94, 114, 116, 118, 158, 159). Data on soil pH are available at Ferlian *et al.* (2024c). Data on soil bulk density are available at Ferlian *et al.* (2024d). Data on plant-available nutrients in soil Ferlian *et al.* (2024b). Data on soil C and N are available at Ferlian *et al.* (2024a). Data on soil P are available at Ferlian & Eisenhauer (2024). Data on soil microbial C and N are available at Bönisch *et al.* (2024a). Data on soil microbial P are available at Bönisch *et al.* (2024b). Data on foliar C and N are available at Bönisch *et al.* (2024c). Data on foliar P are available at Bönisch *et al.* (2024d). SSCI data are available at Ray *et al.* (2023b). Tree inventory data are available at Quosh *et al.* (2023).

References

Averill C, Bhatnagar JM, Dietze MC, Pearse WD, Kivlin SN. 2019. Global imprint of mycorrhizal fungi on whole-plant nutrient economics. *Proceedings of the National Academy of Sciences, USA* **116**: 23163–23168.

Averill C, Hawkes CV. 2016. Ectomycorrhizal fungi slow soil carbon cycling. *Ecology Letters* **19**: 937–947.

Baldrian P. 2017. Microbial activity and the dynamics of ecosystem processes in forest soils. *Current Opinion in Microbiology* **37**: 128–134.

Bardgett RD, van der Putten WH. 2014. Belowground biodiversity and ecosystem functioning. *Nature* **515**: 505–511.

Barry KE, Mommer L, van Ruijven J, Wirth C, Wright AJ, Bai Y, Connolly J, De Deyn GB, de Kroon H, Isbell F et al. 2019. The future of complementarity: disentangling causes from consequences. *Trends in Ecology & Evolution* **34**: 167–180.

Berg B, McClaugherty C. 2014. Decomposition as a process: some main features. In: Berg B, McClaugherty C, eds. *Plant litter: decomposition, humus formation, carbon sequestration.* Berlin, Heidelberg, Germany: Springer, 11–34.

Bilyera N, Blagodatskaya E, Yevdokimov I, Kuzyakov Y. 2018. Towards a conversion factor for soil microbial phosphorus. *European Journal of Soil Biology* **87**: 1–8.

Bonato Asato AE, Wirth C, Eisenhauer N, Hines J. 2023. On the phenology of soil organisms: current knowledge and future steps. *Ecology and Evolution* 13: e10022.

Bonfante P, Genre A. 2010. Mechanisms underlying beneficial plant–fungus interactions in mycorrhizal symbiosis. *Nature Communications* 1: 48.

Bönisch E, Blagodatskaya E, Rose J, Ferlian O, Eisenhauer N. 2024a. Soil microbial carbon and nitrogen concentration in 2021 (Dataset). *MyDiv database.* doi: 10.25829/J0ET-KV83.

Bönisch E, Blagodatskaya E, Rose J, Ferlian O, Eisenhauer N. 2024b. Soil microbial phosphorus concentration in 2021 (Dataset). *MyDiv database.* doi: 10.25829/V1HX-J942.

Bönisch E, Leonard J, Ferlian O, Eisenhauer N. 2024c. Leaf carbon and nitrogen concentration in MyDiv plots in 2021 (Dataset). *MyDiv database.* doi: 10.25829/K2GN-T186.

Bönisch E, Leonard J, Ferlian O, Eisenhauer N. 2024d. Leaf phosphorus concentration in MyDiv plots in 2021 (Dataset). *MyDiv database.* doi: 10.25829/2PH8-WM80.

Brookes PC, Landman A, Pruden G, Jenkinson DS. 1985. Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. *Soil Biology and Biochemistry* 17: 837–842.

Cardinale BJ, Wright JP, Cadotte MW, Carroll IT, Hector A, Srivastava DS, Loreau M, Weis JJ. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences, USA* 104: 18123–18128.

Chapin FS, Matson PA, Vitousek PM. 2011. Nutrient cycling. In: Chapin FS, Matson PA, Vitousek PM, eds. *Principles of terrestrial ecosystem ecology.* New York, NY, USA: Springer, 259–296.

Cheng L, Chen W, Adams TS, Wei X, Li L, McCormack ML, DeForest JL, Koide RT, Eissenstat DM. 2016. Mycorrhizal fungi and roots are complementary in foraging within nutrient patches. *Ecology* 97: 2815–2823.

Cornelissen JHC, Callaghan TV, Alatalo JM, Michelsen A, Graglia E, Hartley AE, Hik DS, Hobbie SE, Press MC, Robinson CH et al. 2001. Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology* 89: 984–994.

Deng M, Hu S, Guo L, Jiang L, Huang Y, Schmid B, Liu C, Chang P, Li S, Liu X et al. 2023. Tree mycorrhizal association types control biodiversity-productivity relationship in a subtropical forest. *Science Advances* 9: eadd4468.

Diaz S, Hodgson JG, Thompson K, Cabido M, Cornelissen JHC, Jalili A, Montserrat-Martí G, Grime JP, Zarrinkamar F, Asri Y et al. 2004. The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science* 15: 295–304.

Dietrich P, Eisenhauer N, Roscher C. 2023. Linking plant diversity–productivity relationships to plant functional traits of dominant species and changes in soil properties in 15-year-old experimental grasslands. *Ecology and Evolution* 13: e9883.

Dietrich P, Ferlian O, Huang Y, Luo S, Quosh J, Eisenhauer N. 2022. Tree diversity effects on productivity depend on mycorrhizae and life strategies in a temperate forest experiment. *bioRxiv.* doi: 10.1101/2022.04.13.488178.

Dornbush ME, Wilsey BJ. 2010. Experimental manipulation of soil depth alters species richness and co-occurrence in restored tallgrass prairie. *Journal of Ecology* 98: 117–125.

Duffy JE, Godwin CM, Cardinale BJ. 2017. Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature* 549: 261–264.

Durán J, Delgado-Baquerizo M, Rodríguez A, Covelo F, Gallardo A. 2013. Ionic exchange membranes (IEMs): a good indicator of soil inorganic N production. *Soil Biology and Biochemistry* 57: 964–968.

Ehbrecht M, Schall P, Ammer C, Seidel D. 2017. Quantifying stand structural complexity and its relationship with forest management, tree species diversity and microclimate. *Agricultural and Forest Meteorology* 242: 1–9.

Eisenhauer N, Bonfante P, Buscot F, Cesarz S, Guerra C, Heintz-Buschart A, Hines J, Patoine G, Rillig M, Schmid B et al. 2022. Biotic interactions as mediators of context-dependent biodiversity-ecosystem functioning relationships. *Research Ideas and Outcomes* 8: e85873.

Eisenhauer N, Lanoue A, Strecker T, Scheu S, Steinauer K, Thakur MP, Mommer L. 2017. Root biomass and exudates link plant diversity with soil bacterial and fungal biomass. *Scientific Reports* 7: 44641.

Eskelinen A. 2020. Resource-enhancing global changes drive a whole-ecosystem shift to faster cycling but decrease diversity. *Ecology* 101: e03178.

Ferlian O, Biere A, Bonfante P, Buscot F, Eisenhauer N, Fernandez I, Hause B, Herrmann S, Krajinski-Barth F, Meier IC et al. 2018a. Growing research networks on mycorrhizae for mutual benefits. *Trends in Plant Science* 23: 975–984.

Ferlian O, Cesarz S, Craven D, Hines J, Barry KE, Bruelheide H, Buscot F, Haider S, Heklau H, Herrmann S et al. 2018b. Mycorrhiza in tree diversity–ecosystem function relationships: conceptual framework and experimental implementation. *Ecosphere* 9: e02226.

Ferlian O, Eisenhauer N. 2024. Soil phosphorus concentration in MyDiv plots in 2021 (Dataset). *MyDiv database.* doi: 10.25829/BQN6-BN54.

Ferlian O, Goldmann K, Eisenhauer N, Tarkka MT, Buscot F, Heintz-Buschart A. 2021. Distinct effects of host and neighbour tree identity on arbuscular and ectomycorrhizal fungi along a tree diversity gradient. *ISME Communications* 1: 1–10.

Ferlian O, Hilke I, Eisenhauer N. 2024a. Soil carbon and nitrogen in MyDiv plots in 2021 (Dataset). *MyDiv database.* doi: 10.25829/VY0G-B534.

Ferlian O, Maestre F, Eisenhauer N. 2024b. Monthly nitrogen and phosphorus availability in soil from 2019 to 2021 (Dataset). *MyDiv database.* doi: 10.25829/Z5KP-BV11.

Ferlian O, Quosh J, Eisenhauer N. 2024c. Soil pH in MyDiv plots in 2021 (Dataset). *MyDiv database.* doi: 10.25829/H3V9-Y564.

Ferlian O, Quosh J, Eisenhauer N. 2024d. Soil bulk density at different depths in MyDiv plots in 2021 (Dataset). *MyDiv database.* doi: 10.25829/W3AV-G565.

Fichtner A, von Oheimb G, Härdtle W, Wilken C, Gutknecht JLM. 2014. Effects of anthropogenic disturbances on soil microbial communities in oak forests persist for more than 100 years. *Soil Biology and Biochemistry* 70: 79–87.

Guerra CA, Bardgett RD, Caon L, Crowther TW, Delgado-Baquerizo M, Montanarella L, Navarro LM, Orgiazzi A, Singh BK, Tedersoo L et al. 2021a. Tracking, targeting, and conserving soil biodiversity. *Science* 371: 239–241.

Guerra CA, Wall D, Eisenhauer N. 2021b. Unearthing soil ecological observations: see supporting information as supplementary material. *Soil Organisms* 93: 79–81.

Guerrero-Ramírez NR, Craven D, Reich PB, Ewel JJ, Isbell F, Koricheva J, Parrotta JA, Auge H, Erickson HE, Forrester DI et al. 2017. Diversity-dependent temporal divergence of ecosystem functioning in experimental ecosystems. *Nature Ecology & Evolution* 1: 1639–1642.

Guiz J, Ebeling A, Eisenhauer N, Hacker N, Hertzog L, Oelmann Y, Roscher C, Wagg C, Hillebrand H. 2018. Interspecific competition alters leaf stoichiometry in 20 grassland species. *Oikos* 127: 903–914.

Guiz J, Hillebrand H, Borer ET, Abbas M, Ebeling A, Weigelt A, Oelmann Y, Fornara D, Wilcke W, Temperton VM et al. 2016. Long-term effects of plant diversity and composition on plant stoichiometry. *Oikos* 125: 613–621.

van der Heijden MGA, Klironomos JN, Ursic M, Moutoglis P, Streitwolf-Engel R, Boller T, Wiemken A, Sanders IR. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 396: 69–72.

Hildebrand M, Perles-Garcia MD, Kunz M, Härdtle W, von Oheimb G, Fichtner A. 2021. Tree-tree interactions and crown complementarity: the role of functional diversity and branch traits for canopy packing. *Basic and Applied Ecology* 50: 217–227.

Hooper DU, Chapin FS III, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75: 3–35.

Huang Y, Chen Y, Castro-Izaguirre N, Baruffol M, Brezzi M, Lang A, Li Y, Härdtle W, von Oheimb G, Yang X et al. 2018. Impacts of species richness on productivity in a large-scale subtropical forest experiment. *Science* 362: 80–83.

Keller AB, Phillips RP. 2018. Leaf litter decay rates differ between mycorrhizal groups in temperate, but not tropical, forests. *New Phytologist* 222: 556–564.

Koele N, Dickie IA, Oleksyn J, Richardson SJ, Reich PB. 2012. No globally consistent effect of ectomycorrhizal status on foliar traits. *New Phytologist* 196: 845–852.

Kuzyakov Y, Blagodatskaya E. 2015. Microbial hotspots and hot moments in soil: concept & review. *Soil Biology and Biochemistry* 83: 184–199.

Lambers H, Mougel C, Jaillard B, Hinsinger P. 2009. Plant–microbe–soil interactions in the rhizosphere: an evolutionary perspective. *Plant and Soil* 321: 83–115.

Lange M, Eisenhauer N, Chen H, Gleixner G. 2023. Increased soil carbon storage through plant diversity strengthens with time and extends into the subsoil. *Global Change Biology* 29: 2627–2639.

Lange M, Eisenhauer N, Sierra CA, Bessler H, Engels C, Griffiths RI, Mellado-Vázquez PG, Malik AA, Roy J, Scheu S *et al.* 2015. Plant diversity increases soil microbial activity and soil carbon storage. *Nature Communications* 6: 6707.

Lenth R, Singmann H, Love J, Buerkner P, Herve M. 2024. *Package "EMMEANS"*. R package v.1.8.9. [WWW document] URL http://cran.r-project.org/package=emmeans [accessed 18 January 2024].

Liang J, Crowther TW, Picard N, Wiser S, Zhou M, Alberti G, Schulze E-D, McGuire AD, Bozzato F, Pretzsch H *et al.* 2016. Positive biodiversity-productivity relationship predominant in global forests. *Science* 354: aaf8957.

Loreau M, Hector A. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412: 72–76.

Luginbuehl LH, Menard GN, Kurup S, Van Erp H, Radhakrishnan GV, Breakspear A, Oldroyd GED, Eastmond PJ. 2017. Fatty acids in arbuscular mycorrhizal fungi are synthesized by the host plant. *Science* 356: 1175–1178.

McCormack ML, Dickie IA, Eissenstat DM, Fahey TJ, Fernandez CW, Guo D, Helmisaari H-S, Hobbie EA, Iversen CM, Jackson RB *et al.* 2015. Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytologist* 207: 505–518.

Midgley MG, Brzostek E, Phillips RP. 2015. Decay rates of leaf litters from arbuscular mycorrhizal trees are more sensitive to soil effects than litters from ectomycorrhizal trees. *Journal of Ecology* 103: 1454–1463.

Midgley MG, Phillips RP. 2014. Mycorrhizal associations of dominant trees influence nitrate leaching responses to N deposition. *Biogeochemistry* 117: 241–253.

Morin X, Fahse L, Scherer-Lorenzen M, Bugmann H. 2011. Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecology Letters* 14: 1211–1219.

Niklaus PA. 2022. PDIV *package GitHub repository*. [WWW document] URL https://github.com/pascal-niklaus/pdiv [accessed 20 October 2023].

Niklaus PA, Leadley PW, Schmid B, Körner C. 2001. A long-term field study on biodiversity × elevated CO$_2$ interactions in grassland. *Ecological Monographs* 71: 341–356.

Oelmann Y, Richter AK, Roscher C, Rosenkranz S, Temperton VM, Weisser WW, Wilcke W. 2011. Does plant diversity influence phosphorus cycling in experimental grasslands? *Geoderma* 167–168: 178–187.

Oelmann Y, Wilcke W, Temperton VM, Buchmann N, Roscher C, Schumacher J, Schulze E-D, Weisser WW. 2007. Soil and plant nitrogen pools as related to plant diversity in an experimental grassland. *Soil Science Society of America Journal* 71: 720–729.

Orwin KH, Kirschbaum MUF, St John MG, Dickie IA. 2011. Organic nutrient uptake by mycorrhizal fungi enhances ecosystem carbon storage: a model-based assessment. *Ecology Letters* 14: 493–502.

Phillips RP, Brzostek E, Midgley MG. 2013. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon–nutrient couplings in temperate forests. *New Phytologist* 199: 41–51.

Pinheiro JC, Bates DM, eds. 2000. Theory and computational methods for linear mixed-effects models. In: *Statistics and computing. mixed-effects models in S and S-PLUS*. New York, NY, USA: Springer, 57–96.

Placella SA, Firestone MK. 2013. Transcriptional response of nitrifying communities to wetting of dry soil. *Applied and Environmental Microbiology* 79: 3294–3302.

Pollierer MM, Langel R, Körner C, Maraun M, Scheu S. 2007. The underestimated importance of belowground carbon input for forest soil animal food webs. *Ecology Letters* 10: 729–736.

Powell JR, Rillig MC. 2018. Biodiversity of arbuscular mycorrhizal fungi and ecosystem function. *New Phytologist* 220: 1059–1075.

Prada-Salcedo LD, Prada-Salcedo JP, Heintz-Buschart A, Buscot F, Goldmann K. 2022. Effects of tree composition and soil depth on structure and functionality of belowground microbial communities in temperate European forests. *Frontiers in Microbiology* 13: 920618.

Qian P, Schoenau JJ. 2002. Availability of nitrogen in solid manure amendments with different C:N ratios. *Canadian Journal of Soil Science* 82: 219–225.

Quosh J, Ferlian O, Becker D, Eisenhauer N. 2023. Tree inventory in MyDiv plots in 2021 (Dataset). *MyDiv database*. doi: 10.25829/R7N9-MH52.

Ray T, Delory BM, Beugnon R, Bruelheide H, Cesarz S, Eisenhauer N, Ferlian O, Quosh J, von Oheimb G, Fichtner A. 2023a. Tree diversity increases productivity through enhancing structural complexity across mycorrhizal types. *Science Advances* 9: eadi2362.

Ray T, Fichtner A, von Oheimb G. 2023b. Stand Structural Complexity Index (SSCI) from MyDiv plots in 2021 (Dataset). *MyDiv database*. doi: 10.25829/JQBA-YS79.

Read DJ. 1991. Mycorrhizas in ecosystems. *Experientia* 47: 376–391.

Riley WJ, Ortiz-Monasterio I, Matson PA. 2001. Nitrogen leaching and soil nitrate, nitrite, and ammonium levels under irrigated wheat in Northern Mexico. *Nutrient Cycling in Agroecosystems* 61: 223–236.

Rillig MC, Mummey DL. 2006. Mycorrhizas and soil structure. *New Phytologist* 171: 41–53.

Rodríguez A, Durán J, Fernández-Palacios JM, Gallardo A. 2009. Wildfire changes the spatial pattern of soil nutrient availability in *Pinus canariensis* forests. *Annals of Forest Science* 66: 210.

Schachtman DP, Reid RJ, Ayling SM. 1998. Phosphorus uptake by plants: from soil to cell. *Plant Physiology* 116: 447–453.

Scherer-Lorenzen M, Körner C, Schulze E-D, eds. 2005. *Forest diversity and function*. Berlin, Heidelberg, Germany: Springer-Verlag.

Scherer-Lorenzen M, Palmborg C, Prinz A, Schulze E-D. 2003. The role of plant diversity and composition for nitrate leaching in grasslands. *Ecology* 84: 1539–1552.

Singavarapu B, Beugnon R, Bruelheide H, Cesarz S, Du J, Eisenhauer N, Guo L-D, Nawaz A, Wang Y, Xue K *et al.* 2021. Tree mycorrhizal type and tree diversity shape the forest soil microbiota. *Environmental Microbiology* 24: 4236–4255.

Smith SE, Read D. 2008. Introduction. In: Smith SE, Read D, eds. *Mycorrhizal symbiosis, 3rd edn*. London, UK: Academic Press, 1–9.

Smith SE, Smith FA. 2011. Roles of arbuscular mycorrhizas in plant nutrition and growth: new paradigms from cellular to ecosystem scales. *Annual Review of Plant Biology* 62: 227–250.

Stark H, Nothdurft A, Block J, Bauhus J. 2015. Forest restoration with *Betula* ssp. and *Populus* ssp. nurse crops increases productivity and soil fertility. *Forest Ecology and Management* 339: 57–70.

Stone MM, DeForest JL, Plante AF. 2014. Changes in extracellular enzyme activity and microbial community structure with soil depth at the Luquillo Critical Zone Observatory. *Soil Biology and Biochemistry* 75: 237–247.

Tilman D. 1980. Resources: a graphical-mechanistic approach to competition and predation. *The American Naturalist* 116: 362–393.

Varma A, Prasad R, Tuteja N, eds. 2017. *Mycorrhiza – nutrient uptake, biocontrol, ecorestoration*. Cham, Switzerland: Springer.

Weinhold A, Döll S, Liu M, Schedl A, Pöschl Y, Xu X, Neumann S, van Dam NM. 2022. Tree species richness differentially affects the chemical composition of leaves, roots and root exudates in four subtropical tree species. *Journal of Ecology* 110: 97–116.

Weldmichael TG, Michéli E, Fodor H, Simon B. 2020. The influence of depth on soil chemical properties and microbial respiration in the upper soil horizons. *Eurasian Soil Science* 53: 780–786.

Wu J, Joergensen RG, Pommerening B, Chaussod R, Brookes PC. 1990. Measurement of soil microbial biomass C by fumigation-extraction – an automated procedure. *Soil Biology and Biochemistry* 22: 1167–1169.

Yevdokimov I, Larionova A, Blagodatskaya E. 2016. Microbial immobilisation of phosphorus in soils exposed to drying-rewetting and freeze-thawing cycles. *Biology and Fertility of Soils* 52: 685–696.

Ziadi N, Simard RR, Allard G, Lafond J. 1999. Field evaluation of anion exchange membranes as a N soil testing method for grasslands. *Canadian Journal of Soil Science* 79: 281–294.

Zuur AF, Ieno EN, Saveliev AA. 2017. *Beginner's guide to spatial, temporal, and spatial-temporal ecological data analysis with R-INLA.* Newburgh, UK: Highland Statistics.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Soil physico-chemical parameters (soil pH and soil bulk density) of tree communities.

Fig. S2 Wood volume and Stand Structural Complexity Index of tree communities.

Fig. S3 Total species-specific wood volume of tree communities.

Fig. S4 Total species-specific foliar elemental pools (C, N, P) of tree communities.

Fig. S5 Soil and soil microbial elemental ratios (C : N, C : P, N : P) of tree communities.

Fig. S6 Soil and soil microbial elemental pools (C, N, P) of tree communities.

Fig. S7 Temporal variability of nitrate availability in soil over the period of 2 yr.

Fig. S8 Temporal variability of ammonium availability in soil over the period of 2 yr.

Fig. S9 Temporal variability of phosphate availability in soil over the period of 2 yr.

Fig. S10 Seasonal availability of ammonium and phosphate as affected by soil moisture.

Fig. S11 Temporal variation of soil temperature over the period of 2 yr.

Fig. S12 Temporal variation of air temperature and air humidity over the period of 2 yr.

Fig. S13 Foliar C, N, and P concentrations between phylogenetic groups (Fagales, non-Fagales) before consideration of mycorrhizal types (AM, EM).

Fig. S14 Foliar C, N, and P concentrations between mycorrhizal types (AM, EM) before consideration of phylogenetic groups (Fagales, non-Fagales).

Fig. S15 Species-specific foliar elemental concentrations (C, N, P) of tree communities of AM or EM trees in monocultures.

Fig. S16 Species-specific foliar elemental concentrations (C, N, P) of tree communities of AM, EM, AM + EM trees with one, two, and four tree species.

Fig. S17 Relative performance of tree species-specific foliar elemental concentrations (C, N, P) in two- or four-species communities.

Table S1 Plot-specific information of the MyDiv experiment.

Table S2 Plot-specific data on soil pH and soil bulk density.

Table S3 Summary mixed-effects model analyses testing soil pH and soil bulk density.

Table S4 Summary simple linear regression analyses of elemental concentrations (C, N, P) in foliage, soil, and soil microbial biomass.

Table S5 Summary simple linear regression analyses of elemental ratios (C : N, C : P, N : P) in foliage, soil, and soil microbial biomass.

Table S6 Summary simple linear regression analyses of elemental pools (C, N, P) in foliage, soil, and soil microbial biomass.

Table S7 Relative changes in elemental concentrations (C, N, P) in foliage, soil, and soil microbial biomass between levels of tree species richness.

Table S8 Relative changes in elemental ratios (C : N, C : P, N : P) in foliage between levels of tree species richness.

Table S9 Relative changes in elemental pools (C, N, P) in foliage, soil, and soil microbial biomass between levels of tree species richness.

Table S10 Relative changes in elemental concentrations (C, N, P) in foliage, soil, and soil microbial biomass between levels of mycorrhizal type.

Table S11 Relative changes in elemental ratios (C : N, C : P, N : P) in foliage between levels of mycorrhizal type.

Table S12 Relative changes in elemental pools (C, N, P) in foliage, soil, and soil microbial biomass between levels of mycorrhizal type.

Table S13 Random Walk model for analyses of temporal trends in nutrient availability.

Table S14 Summary mixed-effects model analyses testing elemental concentrations (C, N, P) in foliage, soil, and soil microbial biomass.

Table S15 Summary mixed-effects model analyses testing elemental ratios (C : N, C : P, N : P) in foliage, soil, and soil microbial biomass.

Table S16 Summary Tukey's honestly significant difference analysis of elemental concentrations (C, N, P) in foliage, soil, and soil microbial biomass among mycorrhizal types.

Table S17 Summary Tukey's honestly significant difference analysis of elemental ratios (C : N, C : P, N : P) in foliage, soil, and soil microbial biomass among mycorrhizal types.

Table S18 Summary mixed-effects model analyses testing elemental pools (C, N, P) in foliage, soil, and soil microbial biomass.

Table S19 Summary Tukey's honestly significant difference analysis of elemental pools (C, N, P) in foliage, soil, and soil microbial biomass among mycorrhizal types.

Table S20 Summary of Random Walk model using Bayesian statistics testing the effects of tree species richness, mycorrhizal type, season, and soil moisture on nitrate, ammonium, and phosphate availability.

Table S21 Summary one-tailed *t*-test analyses testing whether biodiversity effects were significantly > 0 (monocultures).

Table S22 Summary Tukey's honestly significant difference analysis of biodiversity effects (net effects, selection effects, and complementarity effects) in foliage among mycorrhizal types.

Table S23 Summary mixed-effects model analyses testing the effects of phylogeny on elemental concentrations (C, N, P) in foliage.

Table S24 Summary of one-tailed *t*-test analyses testing whether species-specific elemental concentrations (C, N, P) in two- or four-species plots were significantly > 0.

Please note: Wiley is not responsible for the content or functionality of any Supporting Information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.