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RESEARCH ARTICLE

Effects of tree diversity and mycorrhizal type on the spatio-temporal variability of leaf litter production and quality in temperate forests

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Abstract

1. Forest ecosystem productivity is affected by tree species richness and may be further modulated by different mycorrhizal fungal types, for example, arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) fungi, which strongly affect soil processes. Productivity and soil processes are linked through leaf litterfall, a major pathway for carbon and nutrient input to soils.
2. Higher tree diversity and contrasting mycorrhizal strategies may enhance the variability and heterogeneity of litterfall quantity and quality, yet the combined effects of tree species richness and mycorrhizal type mixtures on the temporal dynamics and spatial distribution of litterfall remain underexplored.
3. We investigated leaf litterfall dynamics over 1 year in the 8-year-old MyDiv tree diversity experiment, spanning a gradient of tree species richness (one, two, four species) and mycorrhizal treatments (AM, EM, AM+EM). Monthly litterfall production and nutrient concentrations were measured, and annual wood production (i.e. wood biomass increment) was assessed to quantify aboveground biomass allocation to wood and litter.

Nico Eisenhauer and Rémy Beugnon jointly supervised this work.

4. Tree species richness did not affect annual production of wood or leaf litter. In contrast, annual wood production varied with mycorrhizal types, being highest in EM tree communities, whereas mycorrhizal type did not affect annual leaf litterfall. However, litterfall dynamics were influenced by both tree species richness and mycorrhizal type. Specifically, higher tree diversity extended the litterfall period and increased spatial variability (CV) of litterfall at the meter scale, while temporal variability remained unaffected. Phosphorus concentration in leaf litter differed among mycorrhizal types, with the highest values observed in AM communities. Species-rich stands exhibited lower C:P and N:P ratios in leaf litter and greater phosphorus fluxes. Contrary to expectations, mixed mycorrhizal communities did not produce more leaf litter than monotypic combinations (AM or EM tree species).
5. Synthesis: Our findings show that leaf litterfall dynamics are modified by tree species richness and mycorrhizal type. The increased spatial variability of litterfall at the meter scale and the extended litterfall period associated with higher tree species richness could create a wider range of resource niches for soil organisms in time and space. This may promote the diversity and activity of the decomposer community, ultimately strengthening overall forest nutrient cycling.

KEYWORDS
arbuscular mycorrhiza, ectomycorrhiza, elemental fluxes, litterfall, MyDiv, spatio-temporal dynamics, stoichiometry, tree diversity

1 | INTRODUCTION

In forest ecosystems, trees as primary producers directly affect the belowground system through the input of litter, thereby linking above- and belowground nutrient and carbon (C) dynamics. The quantity and quality of leaf litterfall play crucial roles in determining soil fertility, regulating numerous soil processes and affecting soil organisms (Beugnon et al., 2023; Castillo-Figueroa & Posada, 2025; Meier et al., 2005; Reich et al., 2005). Litter is an important source of nutrients for plants, and additionally of C for heterotrophic soil organisms (Beugnon et al., 2023; Reich et al., 2005).

Tree species richness has been shown to enhance forest productivity by increasing wood and leaf litter biomass production (Dietrich et al., 2022; Huang et al., 2017; Huang, Chen, et al., 2018; Huang, Ma, et al., 2018). Additionally, higher tree species richness was also found to be associated with improved litter quality, such as reduced C:N ratios (Beugnon et al., 2023; Huang et al., 2017; Wilcke et al., 2023). These positive effects of tree species richness on ecosystem functioning—including wood biomass and litterfall production—are largely attributed to niche complementarity. By combining species that exploit different resource niches (e.g. nutrients, water, light and space), competition for limiting resources is reduced, leading to more efficient resource uptake and storage, and ultimately greater primary productivity (Barry et al., 2019; Hildebrand et al., 2021; Levine & HilleRisLambers, 2009; Loreau & Hector, 2001; Luo et al., 2018). For instance, increased tree species richness has been shown to enhance wood biomass production (Dietrich et al., 2022) via enhanced structural complexity of the crown, allowing for complementary use of light and canopy space among trees (Kunz et al., 2019; Perles-Garcia et al., 2021; Ray et al., 2023).

The mycorrhizal association of trees is an important facet of functional tree diversity, but is rarely explicitly included in the analysis of tree diversity effects on ecosystem functioning. In temperate forests, most tree species form associations with one of two major types of mycorrhizal fungi: arbuscular mycorrhizal (AM) or ectomycorrhizal (EM) fungi, which have a notable influence on tree nutrition, leaf traits and leaf litter quality (Phillips et al., 2013). Trees associated with AM fungi are typically characterized by resource-acquisitive traits, leading to fast biochemical cycling, the rapid growth of the host plant and the production of high-quality foliage and litter (i.e. high N and P concentrations and low C:N, C:P, N:P ratios compared to EM trees; Phillips et al., 2013; Bardgett, 2017; Powell & Rillig, 2018; Averill et al., 2019). In contrast, trees associated with EM fungi tend to follow a resource-conservative strategy, with slower growth rates and lower-quality foliage and litter (Averill et al., 2019; Bardgett, 2017; Deng et al., 2023; Midgley & Phillips, 2014; Phillips et al., 2013).

AM and EM fungi have different evolutionary histories, leading to morphological and physiological differences and consequently divergent strategies for resource acquisition (Phillips et al., 2013). EM fungi are known to colonize the organic soil layer more extensively than AM fungi. In addition to their ability to access mineral-associated nutrients, particularly nitrogen (N), EM fungi may also

acquire organically bound nutrients by exuding enzymes that degrade soil organic matter, thereby gaining relatively greater access to organic N sources compared to AM fungi (Deng et al., 2023; Tedersoo & Bahram, 2019). In contrast, AM fungi primarily absorb nutrients in inorganic form, especially phosphate and, to a lesser extent, nitrogen, which they obtain from adsorption sites on soil mineral surfaces (Hodge & Storer, 2015; Jilling et al., 2018; Smith et al., 2015; Smith & Read, 2010). These contrasting strategies of AM and EM fungi may be functionally complementary if they occur simultaneously in tree species-rich communities.

As a result, litter quality is shaped not only by tree species identity (Pietsch et al., 2014; Wardle et al., 2004) but also by the type of associated mycorrhizal fungi (Phillips et al., 2013), with important implications for decomposition and biogeochemical cycling (Averill et al., 2014; Averill & Hawkes, 2016; Prescott & Vesterdal, 2021). Global forest inventories (Luo et al., 2023) and tree diversity experiments (Luo et al., 2024) have shown that mixing mycorrhizal types can enhance wood productivity, and it is very likely that leaf biomass and leaf litterfall are also increased, although we are not aware of any explicit measurements of leaf litterfall in response to varying mycorrhizal types.

Beyond potential effects on leaf litter production and quality, tree species richness and different mycorrhizal types may also modify spatial and temporal variation in litterfall dynamics. Temporal patterns of litterfall have been widely studied (Leff et al., 2012; Shen et al., 2019; Staelens et al., 2011; Zhang et al., 2014), revealing a range of phenological patterns, from unimodal dynamics, characterized by a major peak in autumn, common in temperate regions and primarily driven by declining temperature and light intensity that reduce photosynthetic activity (Taiz & Zeiger, 2002; Zhang et al., 2014), to bimodal or irregular patterns, observed in tropical and subtropical forests where multiple peaks occur throughout the year (Liu et al., 2024; Souza et al., 2019). Previous studies have largely focused on seasonal litterfall patterns (e.g. Zhang et al., 2014), implications for C and nutrient cycling (e.g. Neumann et al., 2018) or biodiversity effects (e.g. Beugnon et al., 2023).

Tree species vary in their litterfall rates and peaks, depending on leaf-lifespan and time of leaf abscission (Chabot & Hicks, 1982). This can be affected by environmental parameters, such as nutrient availability or drought (Reich et al., 1992). Further, most deciduous trees are summer green, retaining their leaves for less than a year (Chabot & Hicks, 1982). However, some temperate species, including the genera *Quercus* L., *Fagus* L., as well as *Carpinus* L., exhibit marcescence—the retention of foliage throughout the dormant season until the new growing season (Angst et al., 2025). This trait is likely linked to phylogeny rather than the environment (Mudrák et al., 2023). In the MyDiv experiment, four out of five EM tree species (*Betula pendula* Roth, *Carpinus betulus* L., *Fagus sylvatica* L., *Quercus petraea* (Matt.) Liebl., see Table S1) belong to the single order, Fagales, with *Carpinus*, *Fagus* and *Quercus* typically exhibiting marcescence (Bönisch et al., 2024; Koele et al., 2012). In contrast, the AM tree species lack marcescent characteristics and generally shed their leaves in autumn. These functional differences suggest potential for temporal complementarity in litter input and nutrient return to soil in diverse tree stands. Supporting this, observations from a subtropical forest indicate that more diverse tree communities exhibit more constant litter inputs year-round, likely due to complementary temporal dynamics of litterfall among tree species (Huang et al., 2017; Huang, Ma, et al., 2018). More continuous resource and nutrient inputs, along with a longer-persisting litter layer, are likely to stabilize the soil microclimate (Kemppinen et al., 2024) and ecosystem functioning (Wan et al., 2024). In particular, even small inputs of litter can result in cascading effects on soil biota and ecosystem processes (i.e. priming effect; Blagodatskaya & Kuzyakov, 2008; Klinges et al., 2024).

Likewise, litter deposition is typically spatially restricted to the vicinity of the litter-producing tree (Barnes et al., 2011; Beugnon et al., 2025; Chandler et al., 2008) and is therefore largely determined by tree species identity, age, height, canopy width and leaf functional traits (Binkley, 1986; Jonard et al., 2006; Orndorff & Lang, 1981; Staelens et al., 2004). For instance, leaf size may influence the dispersal distance of litter, with larger leaves, such as oak or maple leaves, being transported farther from the source tree (Barnes et al., 2011; Bigelow & Canham, 2015; Chandler et al., 2008; Ferrari & Sugita, 1996). Moreover, tree species composition and richness have been shown to increase the spatial heterogeneity of litter inputs at meter scales (Beugnon et al., 2025; Chandler et al., 2008), which is a relevant scale for detritivore meso- and macrofauna (Beugnon et al., 2025; Gholami et al., 2016; Ojala & Huhta, 2001). Such heterogeneity can create diverse nutrient niches for plants and soil organisms and introduce a wider range of organic substrates to decomposer communities, thereby influencing soil organism diversity and activity (Hättenschwiler et al., 2005; Joly et al., 2017; Reich et al., 2005; Uriarte et al., 2015). These processes may ultimately accelerate decomposition rates in species-rich forests (Beugnon et al., 2023). However, the combined influence of tree species richness and mycorrhizal types on litter quantity and quality across space and time, and the potential for such diversity to enhance spatio-temporal complementarity in litter inputs, remain poorly understood.

Here, we studied the effects of tree species richness and mycorrhizal types on aboveground productivity—wood and leaf litter biomass—and the spatio-temporal dynamics of leaf litterfall within young deciduous tree stands using a temperate biodiversity-ecosystem functioning (BEF) experiment (MyDiv). We quantified annual wood production (i.e. wood biomass increment) and the spatio-temporal dynamics of leaf litterfall quantity and quality based monthly measurements conducted over an entire year. Spatial variability in litterfall was quantified within each plot using the coefficient of variation (CV) per month and year.

Positive biodiversity–productivity relationships in forests are frequently reported and have also been observed in the MyDiv experiment (Dietrich et al., 2022). Accordingly, we hypothesized that species-rich tree communities would exhibit increased annual productivity (measured here as wood biomass increment and leaf litterfall) (H1). While previous studies have shown that mixing mycorrhizal types can enhance aboveground tree productivity (Luo et al., 2023, 2024), previous results from the MyDiv experiment

indicate that tree communities composed of exclusively AM trees showed higher productivity than communities composed of trees from both mycorrhizal types (AM+EM) or of only EM trees (Dietrich et al., 2022). Therefore, we hypothesized the highest wood biomass increment and leaf litterfall in AM tree communities, intermediate productivity in tree communities of both mycorrhizal types and lowest productivity in pure EM tree communities; regardless of tree species richness (H2). Owing to the diversity of leaf traits and associated litterfall patterns among tree species, as well as to temporal complementarity between the litterfall periods of AM and EM trees, we expected an extended and more variable litterfall over time in species-rich communities containing both mycorrhizal types (H3). Based on these differences, we also hypothesized that combining higher tree species richness with trees associated with both mycorrhizal types would enhance spatial variation in litter production (H4). Finally, based on the previously documented higher leaf litter quality produced by AM trees compared to EM trees and the general trend of improved foliage and litter quality with increasing tree diversity (Bönisch et al., 2024; Huang et al., 2017), we expected leaf litterfall quality to increase with the abundance of AM trees and in species-rich communities (H5).

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

This study was conducted at the MyDiv tree diversity experiment, located at the Bad Lauchstädt Experimental Research Station of the Helmholtz Centre for Environmental Research–UFZ, southwest of Halle, Saxony-Anhalt, Germany (51°23′ N, 11°53′ E). The site lies at an elevation of 114–116 m a.s.l. and is characterized by a temperate oceanic climate, with a mean annual temperature of 8.8°C and an average annual precipitation of 484 mm. The soil is a highly fertile Haplic Chernozem, rich in nutrients and organic matter (Altermann et al., 2005; Ferlian et al., 2018). Several soil properties, including elemental concentrations, show a gradient along the north–south axis of the site, which is accounted for by the block design (C_{inorg}: 0.26%–0.03%, C_{org}: 2.37%–1.63%, N_{tot}: 0.21%–0.14%, P_{tot}: 690–400 mg/kg, sand: 6.7%–5.2%; Ferlian et al., 2018).

The MyDiv experiment, established in 2015, manipulates tree species richness and mycorrhizal types. The site had previously been used for agriculture until 2012 and managed as grassland for 2 years prior to establishment. The experimental site consists of 80 randomly arranged plots, divided into two blocks according to a gradient in abiotic soil properties (Ferlian et al., 2018). Ten deciduous angiosperm tree species that are native to Germany were selected. Half of the species are primarily associated with AM fungi, while the other half is primarily associated with EM fungi (EM; Table S1). In March 2015, 140 two-year-old saplings were planted per plot either as monocultures, two species or four-species communities, such as tree stands consisting of AM trees, EM trees or as mixture of both (AM+EM; Figure 1a). The tree saplings were not inoculated with mycorrhizal fungi prior to planting, as natural colonization was expected to occur at the site. The effectiveness of the mycorrhizal treatment was later confirmed through morphological assessments of root colonization and DNA sequencing of root-associated fungal communities. For this purpose, roots were sampled two (Heklau et al., 2021) and four (Ferlian et al., 2021) years after planting and analysed for both morphological colonization (i.e. percentage of AM fungal structures; frequency of EM root tips) and molecular fungal community composition (i.e. OTU richness and community structure). AM trees showed substantially higher colonization rates by AM fungi than by EM fungi, whereas the opposite pattern was found for EM trees (Ferlian et al., 2021; Heklau et al., 2021). For instance, the frequency of AM colonization was the lowest in *Q. petraea* and the highest in *Fraxinus excelsior*. These two species also showed the lowest and highest intensities of AM colonization, respectively (Heklau et al., 2021). Each plot measures 121 m^2 (11 × 11 m) and includes a 1.5 m buffer zone formed by the outermost rows of trees, surrounding a central core area of 8 × 8 m. To minimize edge effects, all samples and measurements are taken exclusively within this core area. Trees were planted in a regular non-randomized pattern with 1 m spacing between individuals (Figure 1; Ferlian et al., 2018: appendix 1; Figure S4). The non-random planting scheme of the trees was specifically chosen to maximize interspecific interactions. Further, this design allows to explore intra-plot variability. In 2023, trees had a mean height of 5.2 m and a mean diameter at breast height (DBH) of 4.1 cm (see Table S2 for species-specific values).

2.2 | Measurements of annual wood production

To calculate wood production, we determined the increment in wood biomass ($kg{\cdot}ha^{-1}{\cdot}year^{-1}$) as the difference in wood biomass ($kg{\cdot}ha^{-1}$) in 2022 and 2023. For this, basal diameter (root collar diameter [RCD]) and tree height (H) were measured for all 64 trees within the core area of each plot in December or January of both years. Wood biomass for individual trees was estimated using the following allometric equation, which incorporates species-specific wood densities ρ ($g{\cdot}cm^{-3}$). Note that wood densities were not derived from sampled individuals at the MyDiv experiment but were obtained from Forrester et al. (2017) (Table S3) (Kershaw, 2016).

$$AGB = 0.42 \times RCD \times RCD \times H \times \rho$$

Tree biomass (kg) was then summed per plot, averaged per m^2 by dividing by the number of measured trees (up to 64) and extrapolated to biomass per hectare ($kg{\cdot}ha^{-1}$). The vitality of the trees was assessed for the same year of litterfall assessment (2023). Trees were classified as dead when the phloem was clearly dead (brown instead of green) or the whole tree was missing (e.g. by trees falling over). Out of the 5120 trees planted in the core areas of the plots, 502 individuals died between 2015 and 2023, corresponding to a mortality rate of approximately 10%. Proportions of dead trees per tree species or per treatment can be found in Table S4.

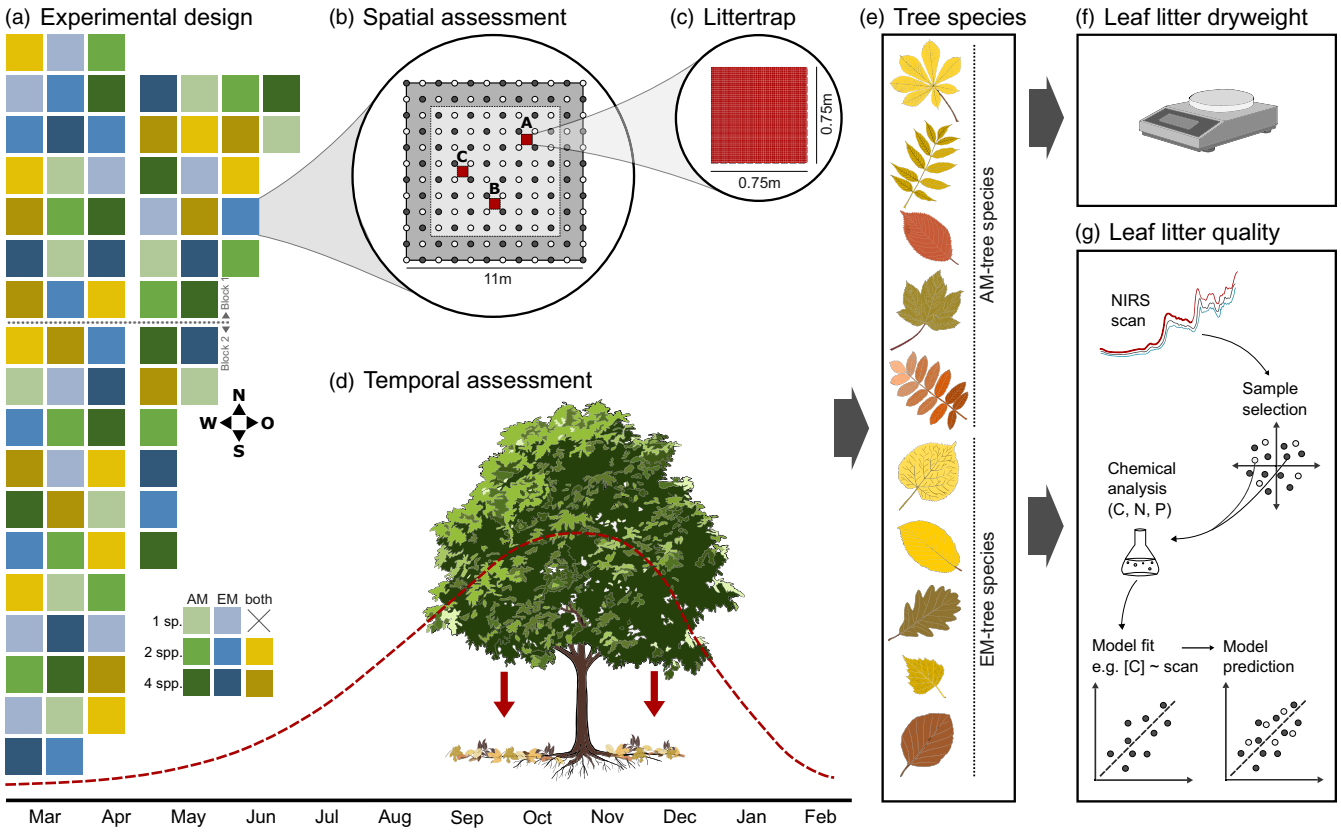

FIGURE 1 Conceptual figure of the study site and experimental design showing the MyDiv experimental design with colours indicating either communities of arbuscular mycorrhizal (AM) trees (green), ectomycorrhizal (EM) trees (blue) or mixtures of both (AM+EM; yellow) in monocultures, two species and four species communities (a). In each plot (b), three litter traps (c) were installed to assess spatial and temporal litterfall each month for 12 months (d) at species level (e). Trap- and species-specific leaf litter dry weight was measured (f) and elemental concentrations (C, N, P) were measured on a subset and predicted using near-infrared reflectance spectroscopy (NIRS) (g).

2.3 | Leaf litterfall assessment

To assess how tree species richness and mycorrhizal associations affect the spatio-temporal dynamics of leaf litterfall, we installed three litterfall traps per plot for 1 year (1 March 2023 to 4 March 2024; Figure S1). The traps were consistently placed at the same location within each plot, unless we identified dead trees (Figure 1b, see Table S5 for exceptions). The distances between traps were as follows: A–B and A–C: 3.16 m; B–C: 1.41 m.

Each litter trap was constructed with a synthetic 2 × 2-mm mesh within a 0.75 × 0.75-m plastic frame and installed at a tree height of 1.5 m, allowing for rapid drainage of precipitation and slowing down of the decomposition process (Figure 1c). To reduce the risk of litter falling out of the traps, nets were weighed down with rounded gravel stones. Owing to the randomized plot design of the MyDiv experiment and the collection of leaf litter exclusively within the core area of each plot (surrounded by a tree buffer zone; Figure 1b), we expected cross-plot litterfall (i.e. leaf litter originating from neighbouring plots and non-target species) to be minimal. In addition, the design ensured that conspecific tree species were rarely located adjacent to one another. Biomass values of cross-plot leaf litterfall for each treatment are provided in Table S6 and Figures S2 and S3. On average, ~27% of leaf litter collected in AM plots and ~8% in EM plots originated from neighbouring (non-target) species. In AM stands, the large amounts of cross-plot litterfall were primarily observed in monocultures and declined with increasing species richness.

The litter traps were emptied at the beginning of each month, starting in April 2023 and ending in March 2024 (Figure 1d, see Table S7 for sampling schedule). Leaf litter was collected separately from each trap, separated from other litter components, such as fruits or twigs, and sorted by species (resulting in a maximum possible number of samples of 600 per month, assuming that each species per plot sheds at least a small amount of litter; Figure 1e). Amounts of other litter components (e.g. twigs or branches, fruits) were not quantified. The species-specific samples for each trap were dried at 60°C for 48 h, and leaf litter dry weight was measured (kg·ha^{-1}).

2.4 | Leaf litter biomass indices

Monthly litterfall (kg·ha^{-1}) was calculated by averaging the total biomass of the three traps per month and tree stand. Cumulative and annual litterfall were calculated by summing monthly litterfall per tree stand. The metric 'number of months of litterfall' captures the total duration of the litterfall period by including all months in which

litterfall dry weight exceeded 0 g. Figure S4 and Table S8 additionally report results obtained using higher thresholds (0.5, 1 g) of litterfall dry weight. Temporal variability was calculated as the CV among months (CV = standard deviation/mean) in a given tree stand. Spatial variability was assessed at the monthly and annual level as the CV between the traps in a tree stand (i.e. with a spatial resolution of 1.41–3.16 m among the litter traps).

2.5 | Elemental analyses

2.5.1 | Sample preparation

To rapidly and cost-effectively determine C, N and P concentration in the large number of collected leaf litter samples, three near infrared (NIR) calibrations were developed to predict the three macronutrients in the samples from their NIR spectrum. For this, the collected litter samples were first shredded coarsely. Since the subsequent procedures would require a significant amount of material, only samples cumulating more than 1 g of litter were considered for processing. Subsequently, stratified sampling based on seasonal variability was applied to split the obtained sample set into two subsets while ensuring both contained months from all seasons without duplication (Subset 1: March, May, July, September, November and February; Subset 2: April, June, August, October, December and January). Afterwards, about 1 g of each sample was compressed into a pellet (MS25-EG, EuroLabo, Vertou, France) and prepared for spectral acquisition.

2.5.2 | Acquisition of NIR spectral data

NIR spectra of the samples were acquired by analysing the prepared pellets, in diffuse reflectance and with an optical resolution of 32 cm^{-1}, using the 4000–10,000 cm^{-1} NIRFlex N-500 benchtop FT-NIR spectrometer (Büchi, Flawil, Switzerland), which was equipped with a vial add-on that allows for automated measurements of six pellets per run (Figure S5). Once the acquisition was completed, a single csv file containing all acquired spectra was exported from the software.

2.5.3 | Calibration set selection for lab nutrient analyses

To determine the subset of samples for reference analysis, a workflow consisting of (1) applying principal components analysis (PCA) on the raw spectra of subset 1 (Figure S6), (2) applying a K-means clustering algorithm on the first three dimensions of the PCA to determine homogeneous clusters throughout the three dimensions (Mouselimis et al., 2024; Figures S7–S9) and (3) taking the centroid of the clusters obtained. The PCA was constructed using standardized variables. In each cluster, 50 samples were randomly selected (selection process is described in detail in Figures S5–S12). A total of 148 samples from subset 1 were selected for reference analysis using wet-chemistry methods.

2.5.4 | Reference analysis

To determine C and N concentrations in the selected samples, shredded material was finely ground using a ball mill (MM2000, Retsch, Haan, Germany) and approximately 3.5 g of the powder was weighed into tin capsules that were subsequently analysed on a Flash Smart NC Soil elemental analyzer (Thermo Scientific™, Waltham, MA, USA). After obtaining C, N and P values for the selected samples, they were organized in a csv file and used as targets in the calibration's development process. To measure P concentrations, the samples were ground with a Cyclotech 1093 Sample Mill (Foss Tecator, Hoganas, Sweden). For P analyses, the Phosphomolybdate Blue Colorimetric Method was used (Chapin et al., 1986). In short, 80 mg of material were treated with 8 mL concentrated nitric acid (HNO_3-65%) and 2 mL of hydrogen peroxide (H_2O_2-30%) in Teflon tubes and heated in a microwave oven to 170°C under pressure. After cooling, the digested samples were diluted in a 50 mL volumetric flask with demineralized water, 100 µL of the diluted solution was mixed with 80 µL of NaOH (2 mol·L^{-1}), 20 µL of sodium molybdate (14 g·L^{-1}) and 20 µL of ascorbic acid (20 g·L^{-1}). Blue intensity is measured at 880 nm, and it is directly proportional to the concentration of phosphorus in the sample.

2.5.5 | Development of calibrations

To develop C, N and P calibrations, the Kennard–Stone algorithm (Kennard & Stone, 1969) was used to split the data into training and testing sets, with 70% of the data being used for the development of calibration models and 30% for their evaluation (Gholamy et al., 2018). For each nutrient, a workflow was applied that involved processing spectra using a Savitzky–Golay (SG)-filter (Savitzky & Golay, 1964), either alone or in combination with a standard normal variate transformation (Barnes et al., 1989), followed by predictive model creation using Python (v3.12.7). The prediction performance of the predictive models was evaluated based on the value of the *R*-squared (R^2), root mean squared (RMSE), residual prediction deviation (RPD) and ratio of performance to interquartile distance (RPIQ). For C, spectra were converted from reflectance to absorbance and differentiated (window size = 7, polynomial order = 1, differentiation order = 1), then a Partial Least Squares Regression (PLSR) model with six latent variables (LV) was created. The model achieved R^2, RMSE, RPD, and RPIQ values of 0.87 (unitless), 0.60 mg·g^{-1}, 2.76 (unitless) and 3.51 (unitless), respectively. For N, a PLSR model with six LV was created

using normalized and differentiated (window size = 5, polynomial order = 1, differentiation order = 1) spectra. The model achieved R^2, RMSE, RPD and RPIQ values of 0.93 (unitless), 0.12 mg·g^{-1}, 3.81 (unitless), 3.99 (unitless), respectively. For P, the spectra were smoothed (window size = 9, polynomial order = 2, differentiation order = 0) and a locally-weighted partial least squares regression (LW-PLSR) model (Lesnoff et al., 2020) was created using the 4576–5664 cm^{-1} region. The model achieved R^2, RMSE, RPD and RPIQ values of 0.72 (unitless), 0.71 mg·g^{-1}, 1.89 (unitless) and 2.21 (unitless), respectively.

Our NIRS models allowed us to achieve significant improvement in the predictability in comparison to previous studies using comparable methods (Davrinche & Haider, 2021). In addition, we performed sensitivity analyses to test the consequences of potentially emerging errors from these predictions on model outputs. The analyses showed no major effect of the prediction error on the elemental concentration and fluxes (Figures S13 and S14).

2.6 | Leaf litter chemistry

Predicted C, N and P concentrations were used to calculate C:N, C:P and N:P ratios and to determine elemental fluxes. The species-specific elemental fluxes were calculated as the product of C, N and P concentrations in leaf litter with species-specific leaf litterfall biomass per year (kg·ha^{-1}·year^{-1}, averaged across three traps per plot). For cumulative and annual C, N and P fluxes, the monthly fluxes were summed across the sampling period.

2.7 | Statistical analyses

All statistical analyses were performed in R (v.4.3; R Development Core Team, http://www.R-project.org). Linear mixed-effects models (Type I Sum of Squares) were used to assess the influence of treatments on response variables (function *lme* from package *nlme* v.3.1-164; Pinheiro & Bates, 2000). The use of Type I Sum of Squares models is justified due to the unbalanced design of the MyDiv experiment (specifically, the absence of monocultures in AM+EM tree stands) and to reduce the inflation of interaction effects, which could otherwise obscure the main effects of tree species richness and mycorrhizal type. Fixed effects included tree species richness (continuous, three levels: one, two, four; log2-transformed), mycorrhizal type (categorical, three levels: AM, EM, AM+EM) and their interaction effect. To account for repeated measures and replicated monocultures across blocks, species composition (categorical, 60 levels) was included as a random effect. Block was not included as a random effect since it did not show significant influence on response variables. For analyses of monthly effects, a correlation structure (first-order autoregressive covariance structure, corCAR1) was included in the models to account for temporal autocorrelation.

3 | RESULTS

3.1 | Annual and monthly wood and leaf litter production

Annual biomass production (i.e. sum of wood biomass increment and leaf litter production), and annual wood biomass increment as well as annual leaf litter production were not significantly affected by tree species richness (Figure 2a–c; Table S9a–c). However, mycorrhizal type significantly affected annual biomass production and wood biomass increment, with EM tree communities showing the highest productivity ($p < 0.001$; Figure 2a,b; Tables S9a,b and S10). On average, total productivity in EM communities was approximately 23% (25% for wood productivity) higher than in mixed (AM+EM) communities and 54% (71% for wood productivity) higher than in AM communities (Table S11). In contrast, annual litterfall was not influenced by mycorrhizal type (Figure 2c; Table S9c).

However, leaf litterfall exhibited pronounced variation throughout the year, following a unimodal pattern with a peak in autumn (October to November; Figure 2d; Tables S12 and S13). The effect of tree species richness on monthly litterfall was significant in June ($p = 0.010$) and in October ($p = 0.025$), with lower litterfall observed in more diverse tree communities during spring and early summer, while litterfall was higher in diverse communities in autumn. For example, in October leaf litterfall was around 20% higher in four-species communities compared to monocultures (Table S13). Further, the influence of mycorrhizal type on leaf litterfall also varied seasonally. The strongest differences between mycorrhizal types occurred in autumn, winter and spring (October–January $p \leq 0.001$; February–March $p \leq 0.01$, April $p = 0.018$), and a smaller but significant difference was observed in summer (August $p = 0.028$). Trees of either mycorrhizal type shed most of their leaves in autumn (September to November). Over time, the dominant contributor to litterfall shifted: AM trees produced the majority of leaf litter from August to November (e.g. in October AM tree stands produced 119% more leaf litter than EM tree communities; Table S14), whereas EM trees produced most from November to April (e.g. in November EM tree communities lost around 52% more leaf litter compared to AM trees; Table S14). Overall, we found no strong interaction effect between tree species richness and mycorrhizal type on leaf litter production, except for a marginal effect detected in October ($p = 0.080$).

Cumulative litter production significantly decreased with increasing tree species richness during the summer months (June to August; Figure 2e; Table S12), while no significant effects of species richness were observed in the following months.

In contrast, mycorrhizal type showed a different temporal pattern on cumulative litterfall. From March to June, EM tree communities showed significantly higher cumulative litter production than AM tree communities. In October, this pattern reversed, with AM tree stands showing the highest litter production ($p < 0.001$). Mixtures of both mycorrhizal types (AM+EM) showed intermediate levels of litterfall in October, which declined to the lowest levels among the

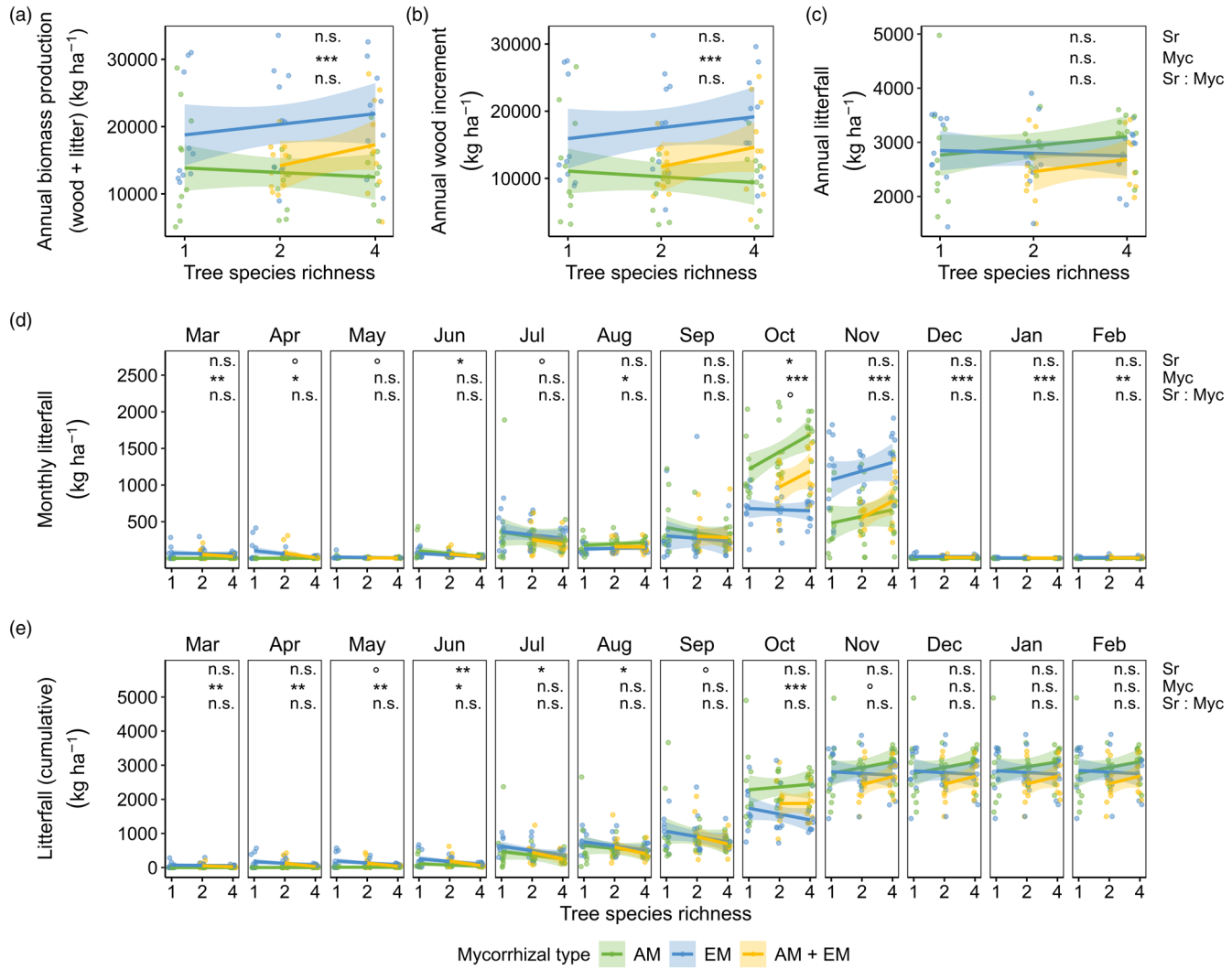

FIGURE 2 (a) Annual aboveground biomass production (wood biomass increment and leaf litter) (kg·ha^{-1}), (b) annual wood increment (2022–2023; kg·ha^{-1}·year^{-1}), (c) annual leaf litterfall (kg·ha^{-1}), (d) monthly and (e) cumulative litterfall (kg·ha^{-1}) as a function of tree species richness (one, two, four; 'Sr') for communities containing arbuscular mycorrhizal tree species (AM), ectomycorrhizal tree species (EM) or both (AM+EM, 'Myc'). Each dot represents a tree community, and colours indicate different mycorrhizal types. Shaded areas indicate the 95% confidence interval. Statistical significance of main and interaction effects is indicated in each panel (not significant, n.s.; $p > 0.05$; °$p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$).

mycorrhizal treatments in the subsequent months. A marginal effect of mycorrhizal type was observed in November, but no significant differences were detected thereafter (Figure 2e).

3.2 | Spatio-temporal variability in leaf litterfall

Annual temporal variability in leaf litterfall was not significantly affected by tree species richness but showed significant differences for the mycorrhizal treatments ($p = 0.008$), with AM tree communities showing the greatest temporal variability in litterfall, around 11% higher relative to EM or AM+EM tree stands, respectively (Figure 3a; Tables S15–S17). We found tree species richness to significantly increase the duration of litterfall ($p = 0.010$; Figure 3b; Table S16b), with around 11 months of litterfall on average in four-species communities. Mycorrhizal type significantly affected the total litterfall duration as well, being the longest in EM tree stands and the shortest in AM tree communities (Tables S17–S19).

In contrast to annual temporal variability, annual spatial variability of litterfall was increased significantly with tree species richness by approximately 63% in four-species tree stands compared to monocultures ($p < 0.001$; Figure 3c; Tables S16c, S17c, S20 and S21c). This was also observed for every month during the litterfall assessment (Figure 3d; Tables S22 and S23). Further, mycorrhizal type showed a significant effect on annual spatial variability in litterfall ($p < 0.001$; Figure 3c; Tables S16 and S17), while monthly analyses showed varying effects (Figure 3d; Table S23). From October to March, spatial variability of litterfall was greater in AM tree communities than EM tree communities, while the opposite was observed in July. No significant interaction effect of

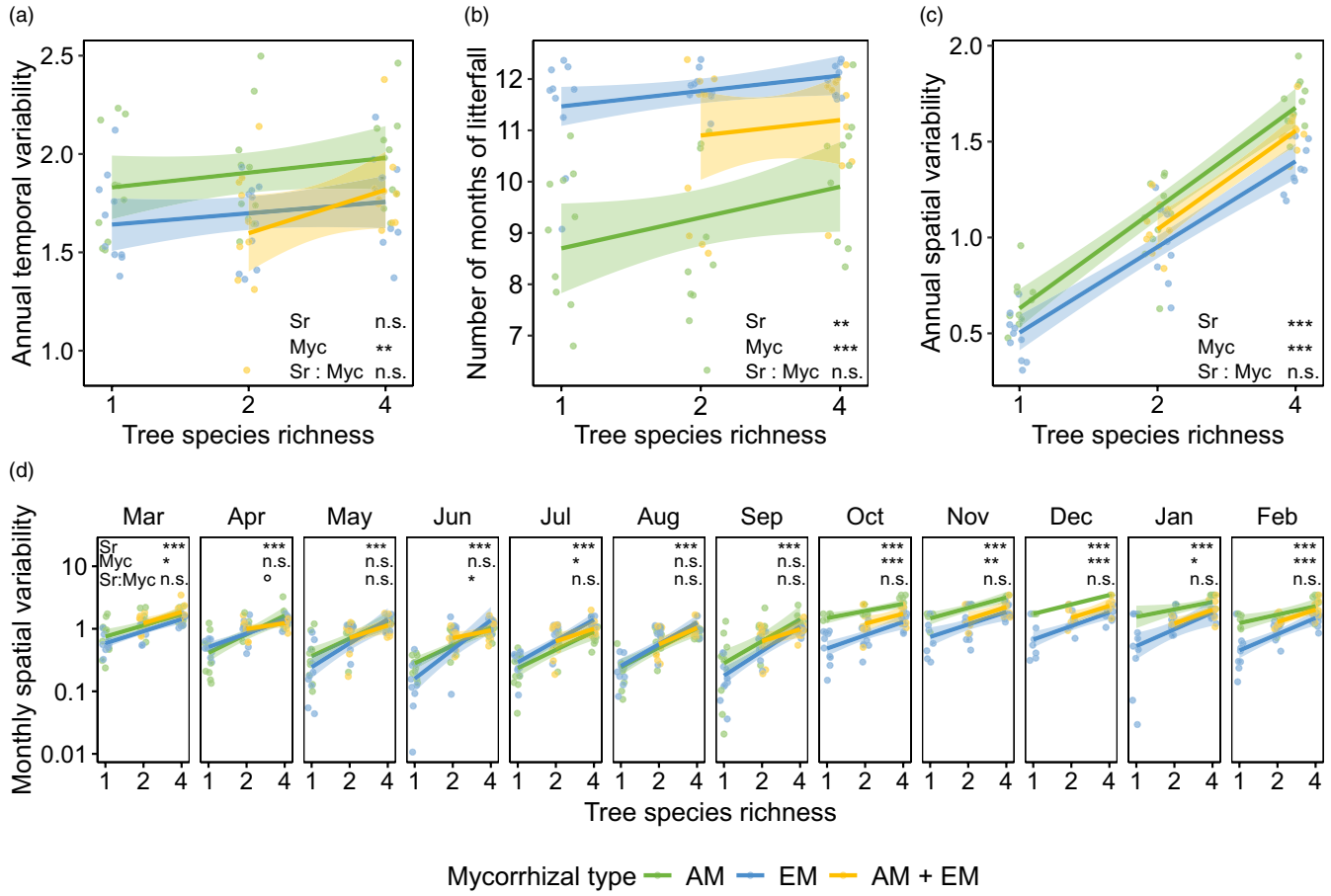

FIGURE 3 (a) Annual temporal variability of litterfall (CV = SD/mean), (b) number of litterfall months, (c) annual spatial variability (CV) of litterfall and (d) monthly spatial variability (CV) of litterfall as a function of tree species richness (one, two, four; 'Sr') for communities containing arbuscular mycorrhizal tree species (AM), ectomycorrhizal tree species (EM) or both (AM+EM, 'Myc'). Each dot represents a tree community, and colours indicate different mycorrhizal types. Shaded areas indicate the 95% confidence interval. Statistical significance of main effects is indicated in each panel (not significant, n.s.; $p > 0.05$; °$p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$).

tree species richness and mycorrhizal types could be observed for either of the annual response variables; only monthly analyses of litterfall spatial variability revealed a significant interaction effect in June ($p = 0.029$; Figure 3d). Here, mycorrhizal mixtures (AM+EM) showed decreased spatial variability in litterfall with increased tree species richness.

3.3 | Annual leaf litterfall quality and nutrient fluxes

The annual concentrations of C, N and P in leaf litter were not significantly influenced by tree species richness (Figure 4a–c; Table S24a), although P concentrations showed a marginal increase with higher species richness ($p = 0.077$). Mycorrhizal type had no effect on N concentration in leaf litter, but significantly influenced C and P concentrations, albeit in opposite directions: leaf litter from AM tree communities had about 31% higher P concentrations compared to EM tree stands, whereas C concentrations were highest in litter of EM trees ($p = 0.001$ and $p < 0.001$, respectively; Tables S24a–S26a). However, the relative differences in C concentrations in either tree community were small, ranging from approximately 1%–4% (Table S27a). For both C and P concentration in leaf litter, tree stands with both mycorrhizal types (AM+EM) exhibited intermediate values relative to communities with either AM or EM tree species. In contrast, N concentrations were lowest in mixed communities compared to either AM or EM tree stands.

The total fluxes of C and N (calculated as litter biomass × elemental concentration per year) remained unaffected by either tree species richness or mycorrhizal type (Figure 4d,e; Table S24b). However, P fluxes were significantly affected by both factors. Tree species richness enhanced litter P fluxes, with four-species stands exhibiting approximately 19% larger P fluxes compared to monocultures ($p = 0.007$; Table S27b). Moreover, mycorrhizal type had a significant effect ($p < 0.001$), with AM tree communities producing substantially larger P fluxes than EM (~33% larger) or mixed tree communities (~26% larger; Figure 4f; Table S26b).

Similar to the absence of tree species richness effects on C and N concentrations in leaf litter, C:N ratios also did not differ significantly between tree communities with varying species diversity

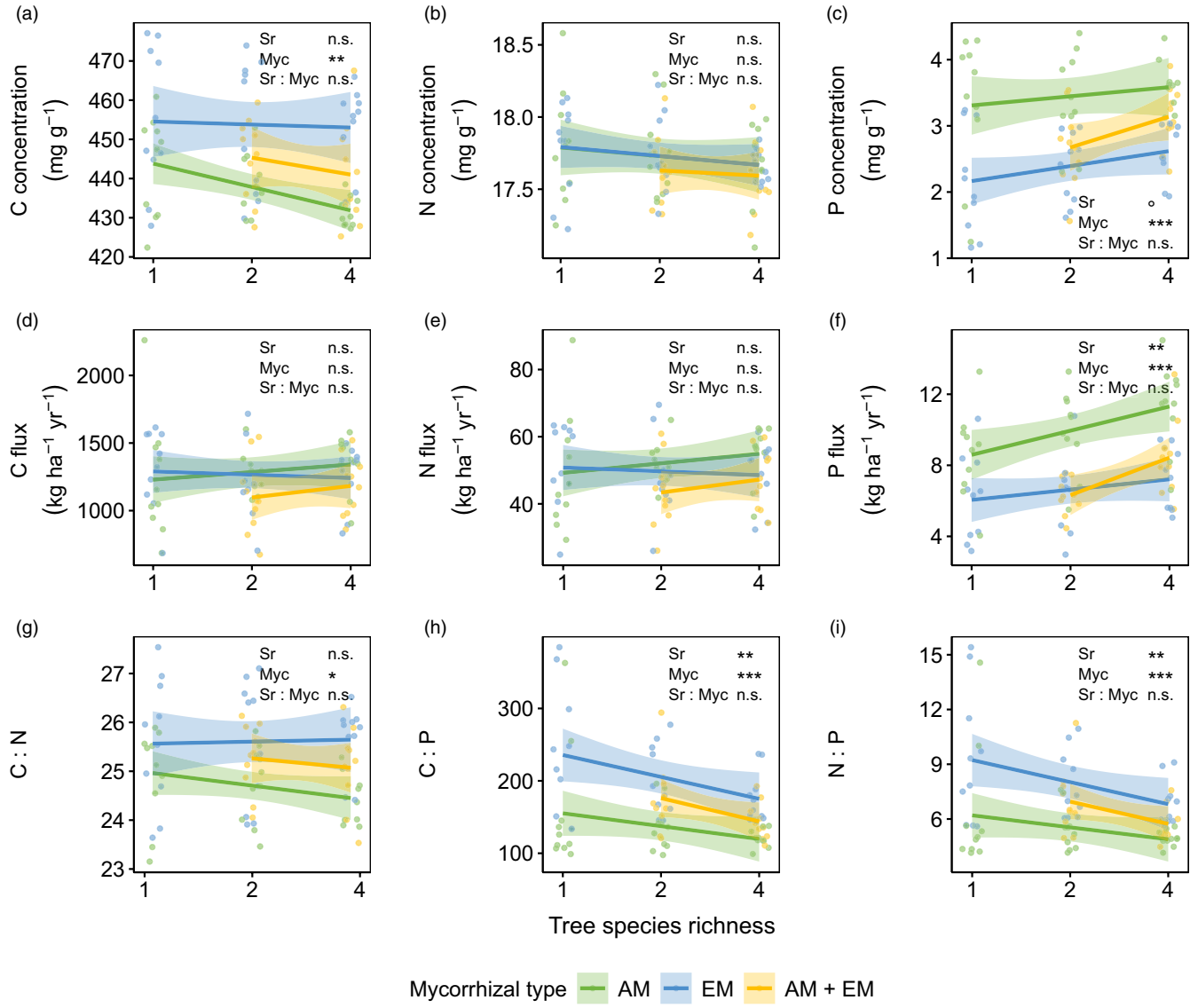

FIGURE 4 (a–c) C, N, P concentrations (mg·g^{-1}), (d–f) C, N, P fluxes (kg·ha^{-1}·year^{-1}) and (g–i) stoichiometry (C:N, N:P, C:P ratio) of annual leaf litterfall as a function of tree species richness (one, two, four; 'Sr') for communities containing only arbuscular mycorrhizal tree species (AM), only ectomycorrhizal tree species (EM) or both (AM+EM, 'Myc'). Each dot represents a tree community, and colours indicate different mycorrhizal types. Shaded areas indicate the 95% confidence interval. Statistical significance of main effects is indicated in each panel (not significant, n.s.; $p > 0.05$;°$p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$).

(Figure 4g; Table S24c). In contrast, driven by higher P concentrations, C:P and N:P ratios were significantly reduced by increasing tree species richness (both $p = 0.009$; Figure 4h,i; Table S24c). Leaf litter from four-species communities exhibited C:P and N:P ratios that were approximately 33% and 34% lower, respectively, compared to those from monocultures (Table S27c). In addition, mycorrhizal type had a pronounced effect on leaf litter quality across all measured ratios, with AM tree communities exhibiting the highest litter quality (lowest C:N, C:P and N:P ratios), while EM tree communities had the lowest litter quality (C:N: $p = 0.013$; C:P and N:P: $p < 0.001$). Specifically, C:P and N:P ratios in AM litter were approximately 50% and 45% lower compared to leaf litter of EM trees, respectively (Table S26c). Litter from tree communities with both mycorrhizal types (AM+EM) displayed intermediate elemental ratios, falling between those of the single mycorrhizal-type communities.

3.4 | Elemental fluxes over time (cumulative) of leaf litter

Despite the overall non-significant effect of tree species richness on the total annual C and N fluxes in litterfall (see above), both litterfall C and N fluxes increased differently over time depending on tree species richness (Figure 5; Table S28). A higher amount of C and N in leaf litterfall was measured in single tree species stands compared to four-species stands during the summer months of June, July and August (Figure 5a,b). A similar pattern was observed for

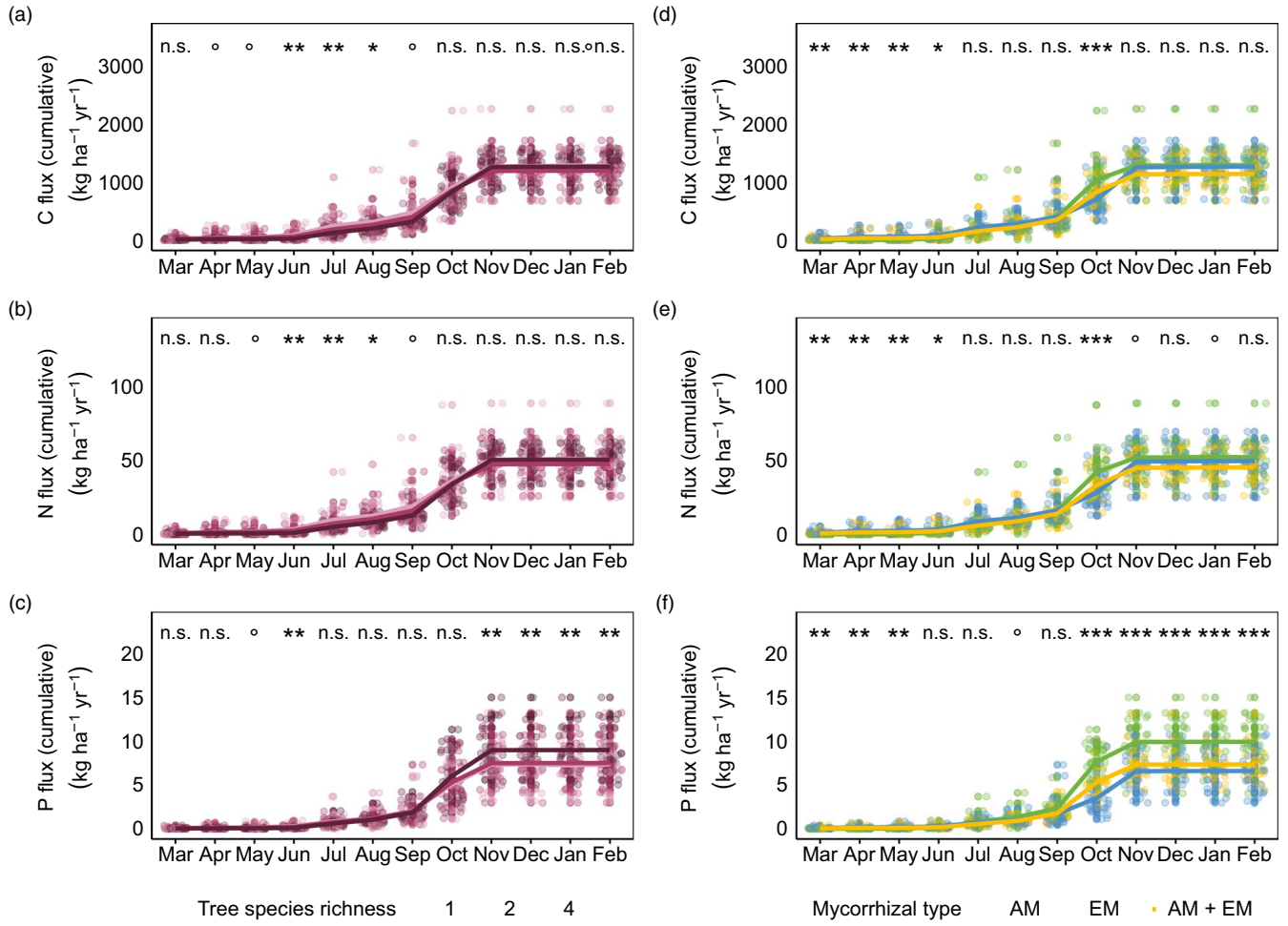

FIGURE 5 The cumulative amount of C, N and P flux (kg·ha^{-1}·year^{-1}) in leaf litterfall as a function of tree species richness (one, two, four) (a–c) for communities containing only arbuscular mycorrhizal tree species (AM), only ectomycorrhizal tree species (EM) or both (AM+EM) (d–f). Shaded areas indicate the 95% confidence interval. Statistical significance of main effects is indicated for each month by asterisks (not significant, n.s.; $p > 0.05$;°$p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$).

the amount of P in leaf litterfall during June (Figure 5c). In contrast, during the winter months from November to February, higher tree species richness significantly increased the cumulative P fluxes in leaf litter (Figure 5c).

Amounts of leaf litter C, N and P fluxes were significantly influenced by mycorrhizal type during spring and early summer (March–June for C and N; March–May for P), with EM tree communities exhibiting the largest fluxes (Figure 5d–f). This pattern shifted notably in the peak litterfall month of October, when AM tree stands showed the highest cumulative C, N and P fluxes, followed by mixed (AM+EM) communities and EM stands with the lowest values. For C and N, this shift was not sustained beyond October (Figure 5d,e). However, cumulative P fluxes remained significantly affected by mycorrhizal type in the subsequent winter months (November–February; Figure 5f). The amount of elemental fluxes (C, N and P fluxes) was driven by differences in the amount of litterfall (Figure 2d) and in changes in elemental concentrations (Figures S15 and S16; Table S28).

4 | DISCUSSION

In this study, we investigated how tree species richness and mycorrhizal types (AM, EM or both) affect aboveground productivity and the spatio-temporal variation in the quantity and quality of leaf litterfall production using a temperate tree diversity experiment. Overall, annual aboveground production of wood biomass and leaf litterfall were not affected by tree species richness (H1). In contrast, total aboveground production and wood production, but not litterfall, were significantly affected by mycorrhizal type, with EM tree communities showing the highest productivity (H2). The period of litterfall was extended in species-rich stands, particularly in those composed exclusively of EM species (H3). Moreover, tree species richness enhanced the spatial, but not the temporal variability in leaf litterfall, with the highest spatial variability observed in AM tree communities (H4). Contrary to C and N concentrations in leaf litter, P concentration in leaf litter was affected by tree species richness and mycorrhizal type, leading to

altered stoichiometry. Notably, EM trees consistently produced the lowest quality litter and AM trees the highest quality litter. Accordingly, annual and monthly leaf litter P fluxes (cumulated) were higher with increasing tree species richness and also in AM tree communities compared to EM tree communities or mixtures of the two mycorrhizal types (H5). Taken together, these findings highlight that tree species richness enhances the duration of litterfall and its spatial variability. In addition, EM trees mainly enhance aboveground wood productivity, while the presence of AM trees improves leaf litter quality. However, the combined presence of high species richness and mixed mycorrhizal types did not result in the highest values for any productivity or litter quality metric, which does not support our expectation of a complementarity effect. Indeed, we found no interacting effects between species richness and mycorrhizal type in any of the tested variables, despite an interaction of spatial variability of litterfall in June.

4.1 | No tree species richness effect on biomass (wood and litter) production

Contrary to our first hypothesis (H1), we did not observe increased annual production of wood (wood biomass increment) or leaf litter with higher tree species richness. Previous studies at the MyDiv experiment reported positive effects of tree species richness on annual wood production (Dietrich et al., 2022), which was explained by enhanced structural complexity of tree stands (Ray et al., 2023). These previous results align with global patterns showing positive biodiversity–productivity relationships for wood productivity in forest ecosystems (Huang, Chen, et al., 2018; Shovon et al., 2022). While wood biomass in a single year (e.g. 2023; Figure S17) reflected this trend, the wood biomass increment from 2022 to 2023 was enhanced but not statistically significant. Dietrich et al. (2022) found a significant positive effect of tree species richness on wood biomass increment over 5 years at MyDiv, however, the strength of this effect varied by year. Such interannual variation may be linked to past drought events, as suggested by a previous MyDiv study (drought years 2018–2020; Sachsenmaier et al., 2024, 2025), potentially explaining the lack of a significant increment in our study, given that 2022 was also a drought year (Bevacqua et al., 2024) (see Figure S18 for precipitation data from 2018 to 2024).

As with annual wood production, we did not observe a significant increase in annual leaf litterfall with higher tree species richness. While greater diversity was suggested to explain enhanced litterfall in tropical and subtropical forests (Beugnon et al., 2023; Huang et al., 2017; Huang, Ma, et al., 2018; Wilcke et al., 2023), early results of a tropical forest BEF experiment with limited species gradients (1–6 species) reported no such effects (Scherer-Lorenzen et al., 2007). However, a long-term study at the same tropical site showed that increased diversity enhanced tree productivity and, consequently, litter C fluxes 16 years after establishment (Schnabel, Guillemot, et al., 2025), suggesting that diversity effects on litterfall may only emerge over time.

4.2 | Production of wood biomass but not litter biomass affected by mycorrhizal type

In contrast to tree diversity, mycorrhizal type strongly influenced annual wood biomass increment, with 71% higher productivity in EM communities relative to AM communities. This increase in wood biomass primarily drove the significant mycorrhizal effects on total annual biomass production (around 54% higher productivity in EM vs. AM tree stands). In comparison, leaf litter production remained unaffected by mycorrhizal type. This is in contrast to our hypothesis (H2) and previous findings suggesting higher productivity in AM-associated trees due to their fast-growth strategies (Averill et al., 2018; Cornelissen et al., 2001; Deng et al., 2023; Ferlian et al., 2018; Phillips et al., 2013). In early successional stages, AM trees often grow rapidly, particularly at nutrient-rich sites (Phillips et al., 2013). However, several EM species used in the MyDiv experiment - *Q. petraea*, *F. sylvatica* and *B. pendula* -are known to be dominant canopy-forming species due to positive conspecific density dependence (Bennett et al., 2017; Jiang et al., 2021; Mao et al., 2024), which may contribute to their increased productivity relative to AM trees. Dietrich et al. (2022) noted temporal shifts in the wood productivity patterns within the MyDiv experiment over 6 years until 2020: productivity decreased over time in AM tree communities, remained stable in AM+EM mixtures and increased in EM tree communities. Our results suggest that this trend had continued, leading to a convergence and eventual reversal in productivity dominance between AM and EM tree communities by 2022.

We found no significant effect of mixing mycorrhizal types (AM+EM) on total annual leaf litterfall (Figure 2c), nor a strong effect of mycorrhizal types alone, which aligns with findings from another temperate forest study (Rosling et al., 2016). However, monthly litterfall dynamics were more variable, with a changing relative contribution of leaf litter by AM and EM tree species to the total litterfall through time. Given the unimodal pattern of litterfall in temperate regions, treatment effects (tree species richness and mycorrhizal type) may be temporally diluted. This is particularly evident as a closer examination of monthly litterfall patterns reveals significant positive effects of tree species richness during the peak litterfall season in October. Overall, our results do not support complementarity effects of mixed mycorrhizal types, but we cannot exclude the possibility that they may become apparent when the forests grow older.

4.3 | Prolonged period of leaf litterfall in EM tree stands but not AM+EM tree communities

The temporal dynamics of litterfall changed in response to tree species richness and mycorrhizal type, with a significant increase in litter production with increasing tree species richness in October during the peak litterfall season. The timing of leaf litterfall depends on biotic conditions, such as forest type and structure, species composition, plant diversity and density, herbivory, as well as plant species-specific traits (Chabot & Hicks, 1982;

Chapman et al., 2003; Chen et al., 2018; de Queiroz et al., 2019; Reich et al., 1992; Zhang et al., 2024). In addition, abiotic factors, such as seasonal patterns, nutrient and water availability, and climate also play a role (de Queiroz et al., 2019; Liu et al., 2024). Further, plant traits such as leaf lifespan and marcescence determine litterfall. In the case of our MyDiv study, marcescence occurs only in EM-associated tree species. As a result, we observed the most extended and stable litterfall period (~11.5 months) in EM communities (Figure 3b), with significantly greater litter production in the 6 months of November to April compared to AM stands (Figure 2b). In contrast, litterfall in AM tree stands peaked in October with more than twice the amount of leaf litter compared to EM tree stands, coinciding with a strong positive effect of tree species richness. AM communities also produced significantly more litter in August, largely due to early defoliation of chestnut trees (*Aesculus hippocastanum*) in AM and mixed stands, triggered by chestnut moth (*Cameraria ohridella*) infestation (Figure S19; Thalmann et al., 2003; Thomas et al., 2019).

The observed temporal variation and extension of the litterfall period were shaped not only by tree species richness and mycorrhizal type but also likely by species identity, as several EM-associated species exhibited pronounced marcescence. Altogether, our findings suggest that complementary phenology among co-occurring species, shaped by abiotic and biotic conditions as well as species traits, prolonged the leaf litterfall period and increased its spatial variability in species-rich communities and EM-dominated stands. This may lead to prolonged input of organic material into soils. This, in turn, may extend the resource availability for decomposers, the decomposition period and the subsequent release of nutrients to soil organisms and plant roots (Angst et al., 2024, 2025; Hättenschwiler et al., 2005). Prolonged nutrient availability may benefit plants and soil biota by ensuring a more continuous resource supply, potentially enhancing overall ecosystem productivity while also reducing nutrient leaching due to enhanced nutrient exploitation from soils (Barry et al., 2019; Oelmann et al., 2021; Schwarz et al., 2016).

4.4 | Spatial variability of litterfall was enhanced by tree species richness

Besides the temporal dynamics of litterfall, we further observed significant annual and monthly spatial variation in litterfall within the tree communities (Figure 3b,d). At the local scale, spatial variation in leaf litterfall is influenced by tree architecture, size and leaf functional traits (e.g. leaf size), all of which are determined by species identity. Most leaf litter is deposited within 5 m of the source trees, resulting in fine-scale spatial heterogeneity in litter inputs (Beugnon et al., 2025; Chandler et al., 2008; Uriarte et al., 2015; Xu et al., 2024). We found that spatial variability in litterfall increased markedly—by approximately 63% annually and also significantly on a monthly scale—with higher tree species richness (Figure 3c). Tree diversity increased the heterogeneity of litter input to the soil, thus potentially providing additional nutrient niches to plants and soil organisms and additionally increasing variation in organic material and its availability to the decomposer community (Beugnon et al., 2023; Uriarte et al., 2015). Consistent with our findings, simulation-based results suggest that greater tree diversity leads to a more heterogeneously distributed litterfall (Beugnon et al., 2025), which in turn may enhance litter decomposition as well as N and C cycling (Beugnon et al., 2023). Yet, these relationships are greatly influenced by the spatial distribution of tree species within the forest stand. Additionally, a study in a subtropical forest showed that increased tree diversity led to enhanced temperature buffering through higher canopy density and structural complexity, suggesting improved ecosystem functioning, including decomposition and linked C and nutrient cycling (Schnabel, Beugnon, et al., 2025; Schnabel, Guillemot, et al., 2025). In contrast, a study in a tropical forest found that the effect of micro-environmental variation, although high at fine scales, declines over time, with litter quality remaining the primary driver of decomposition processes (Castillo-Figueroa, 2025). However, this study did not consider species diversity, which limits inferences regarding diversity-related effects (Beugnon et al., 2024; Castillo-Figueroa, 2025; Joly et al., 2023). Improving our understanding of species-specific litterfall and species interactions in affecting the temporal and spatial distribution of litterfall is needed to better predict forest nutrient and carbon cycling (Beugnon et al., 2023; Trogisch et al., 2021; Yu et al., 2024).

4.5 | Leaf litter P fluxes and litter quality (C:P and N:P) enhanced by tree species richness

Nutrient and C concentrations, their ratios and respective elemental fluxes are key indicators to estimate drivers and limitations of forest productivity (Hobbie, 2015; Whittaker et al., 1979). While previous studies have shown positive effects of tree diversity on litter elemental concentrations and quality (Huang et al., 2017), we found no significant effects of tree species richness on C and N concentrations in leaf litter, and only a slight non-significant increase in P concentrations (Figure 4a–c). Consequently, C:N ratios remained unaffected by tree species richness, contrasting Huang et al. (2017) who reported improved litter quality (lower C:N) in tropical forests with higher diversity. However, we observed significantly narrowing C:P and N:P ratios with increasing tree species richness, mostly driven by the slight increase in P concentrations. Combined with a trend for higher litter biomass with increasing tree species richness, this led to significantly larger litter P fluxes in more diverse tree communities. This mirrors findings from a BEF grassland study, where plant species richness had no effect on foliar P concentrations but did increase plant biomass, ultimately increasing biomass P fluxes (Oelmann et al., 2021). While that study linked the pattern to tighter C-P coupling driven by higher biomass and C input, our results suggest a different mechanism. In our case, tree species richness did not significantly affect litter biomass, C concentrations or C fluxes. Instead, the increase in P fluxes appears to result from slightly elevated P concentrations, possibly indicating more efficient

soil P foraging by root systems and associated mycorrhizae in productive, species-rich communities - particularly those dominated by AM-associated tree species (van der Heijden et al., 2015). This is plausible given that the N-rich Chernozem soil at the MyDiv site has been identified as potentially P-limited (Altermann et al., 2005; Ferlian et al., 2018), which could allow trees to increase P acquisition at the stand level in more species-rich communities.

The type of mycorrhizal association significantly influenced the concentration of C and P in leaf litter. Thereby, AM trees showed significantly higher P concentrations in their litter relative to EM trees (Figure 4f), which is in accordance with the specific role of AM fungi in desorbing phosphate from soil mineral surfaces thus enhancing plant inorganic P uptake (Averill et al., 2019; Phillips et al., 2013). In contrast, leaf litter C concentrations tended to be higher in EM trees, though not significantly. Both trends have also been observed in fresh leaves from the MyDiv experiment (Bönisch et al., 2024; Castro Sánchez-Bermejo et al., 2024). While mycorrhizal types showed no effect on N concentration in leaf litter (Figure 4e) a previous study within the MyDiv experiment reported significantly higher N concentrations in fresh foliage from EM tree species relative to AM tree species (Bönisch et al., 2024). Both results contrast a global study reporting significantly higher N concentration in green and senescent tissue (Averill et al., 2019). This may have occurred possibly due to more efficient N resorption in EM trees compared to AM trees (Zhang et al., 2018). Leaf litter nutrient concentrations are influenced by nutrient resorption before and during senescence as well as by leaching (e.g. from rainfall) (Castillo-Figueroa et al., 2025; Guo et al., 2024; Joly et al., 2016; van den Brink et al., 2023). In this context, functional traits and species identity have been found to play a major role in resorption processes and subsequent decomposition rates (Castillo-Figueroa et al., 2025). Thus, also mycorrhizal type-specific processes of nutrient uptake and allocation may further shape the nutrient concentration in green foliage and leaf litter (Averill et al., 2019; Zhang et al., 2018). The pattern of possibly higher N resorption in EM trees within the MyDiv experiment aligns with a global study reporting on pronounced N resorption in temperate forests (McGroddy et al., 2004; Zhang et al., 2018).

These findings support our broader conclusion that species-rich AM tree communities may produce higher-quality litter that promotes a positive feedback loop with the soil microbial community. The resulting increase in nutrient-rich organic material may enhance microbial activity, litter decomposition and P mineralization, thereby increasing plant-available P. This effect was demonstrated by Bönisch et al. (2024), who found significantly elevated soil microbial P in species-rich tree stands. Overall, these findings highlight the strong relationship between plant diversity, soil P availability and ecosystem functioning (Wu et al., 2019). The spatial and temporal patterns of leaf litterfall are closely linked to soil nutrient availability. In mixed-species forests with contrasting mycorrhizal types, extended and asynchronous litterfall can help synchronize nutrient release with plant demand, supporting more efficient nutrient cycling (Staelens et al., 2004; Uriarte et al., 2015).

4.6 | Tree species richness enhances monthly cumulative P fluxes

The effects of tree species richness and mycorrhizal type cumulative leaf litter C, N and P fluxes varied across months and differed markedly between elements. Higher species richness was associated with lower amounts of C and N in litterfall during summer (June–August) and with reduced amounts of P in litterfall in June, but significantly increased quantities of litter P from November to February (Figure 5a–c). This divergence between cumulative C and N fluxes compared to P fluxes was reflected in the effects of mycorrhizal types. While EM tree communities exhibited significantly higher cumulative C, N and P fluxes in spring and early summer (March–June for C and N; March–May for P), the pattern shifted in October—the peak period of litterfall—when AM tree communities showed the highest cumulative elemental fluxes. Notably, only cumulative P fluxes remained elevated in AM communities through the winter months (November–February) (Figure 5d–f). Monocultures produced more litter from April to July (Figure 2e,f), primarily composed of green (non-senescent) leaves, except in EM species like *C. betulus*, *F. sylvatica* and *Q. petraea*, whose litter was ~90% brown, even during spring and summer due to their marcescence characteristics. Green litter typically contains higher nutrient concentrations than senescent litter (Zhang et al., 2014, 2018), likely explaining the significantly higher N concentrations in monocultures during these months (Figure S15), and consequently greater N fluxes (Figure S16). In contrast, species-rich mixtures likely contained a greater proportion of brown litter, contributing to overall lower N concentrations.

While monthly cumulative C and N fluxes showed similar monthly patterns (as did their concentrations and fluxes; Figures S15 and S16), cumulative P fluxes responded distinctly to experimental treatments. Tree species richness had a stronger effect on P concentrations than on C and N. In particular, AM tree litter contained significantly more P than EM litter, resulting in larger amounts of P-rich litter. This supports earlier findings that AM-associated species produce nutrient-rich litter (Phillips et al., 2013), and contrasts with a study reporting limited P cycling differences between AM and EM trees in temperate forest (Rosling et al., 2016).

Our results suggest that P return to soils via litterfall and decomposition may be enhanced in species-rich and AM-dominated communities. Phillips et al. (2013), whose framework underpins the rationale of the MyDiv experiment, proposed that AM and EM fungi differ in their nutrient acquisition strategies—AM fungi target inorganic P, while EM fungi access organic P—leading to distinct P cycling patterns. Supporting this, we found that although differences were not consistent year-round, AM tree communities produced more leaf litter during peak litterfall in October and had higher P concentrations in that litter. Combined, these led to significantly greater P fluxes than in EM communities. This contrasts with other temperate forest studies, where AM trees mainly affected belowground traits but not litter quality or quantity (Rosling et al., 2016), and where no differences in senescent leaf P concentrations between AM and EM species were found (Averill et al., 2019).

While our findings highlight clear aboveground differences, we did not assess belowground dynamics during litterfall, limiting our understanding of full-system P cycling. However, earlier work from the MyDiv experiment (Bönisch et al., 2024) reported no significant differences in soil total P, phosphate concentrations or microbial biomass P between mycorrhizal types.

5 | CONCLUSION AND OUTLOOK

An overarching hypothesis of the MyDiv experiment is that combining high tree species richness with functionally distinct mycorrhizal types (AM+EM) would enhance resource partitioning and increase community productivity. However, our findings, although limited to 1 year, do not support this hypothesis in terms of litter production or elemental traits. Instead, higher productivity and improved nutrient cycling were associated with either increased tree species richness or single mycorrhizal communities (AM or EM), without additional benefits from combining both mycorrhizal types. This contrasts with previous studies reporting synergistic effects of mixed mycorrhizal associations on forest ecosystem functioning (Liu et al., 2024; Luo et al., 2023, 2024). Potentially, early successional stages of the tree communities and or soil legacies from former agricultural land use (Fichtner et al., 2014) and the inherently nutrient-rich Chernozem soil may have inhibited joint effects of the two mycorrhizal types on leaf-litterfall quantity and quality at the stage of the experiment presented in this study. Contrary to expectations, tree species mixing—rather than mycorrhizal type mixing—extended the litterfall period and increased spatial variability in litter accumulation. This was likely driven by complementary phenology among co-occurring species, enhancing the temporal and spatial availability of organic matter and nutrients to primary producers and soil organisms, thereby supporting key ecosystem functions. Importantly, increased tree diversity also enhanced P concentrations and cumulative P fluxes in leaf litter, particularly in AM-dominated communities, highlighting the role of AM fungi in promoting P availability.

Further, litter quality also depends on additional chemical traits such as lignin:N ratios and phenolic compounds, which were not assessed in this study. Future research should explore how tree species identity and mycorrhizal type affect nutrient resorption and decomposition processes (Cleveland et al., 2013; Reed et al., 2012), ultimately shaping litter quality and nutrient cycling. In addition, both nutrient resorption and subsequent decomposition modify nutrient concentrations in litter over time (Wang et al., 2020). Several studies therefore recommend using the lignin mass fraction or relatively immobile elements such as Ca to standardize nutrient concentration data in litter (Schreeg et al., 2013; Wang et al., 2020; Yanai et al., 2012; Zhou et al., 2021). Future studies should account for this to obtain a more comprehensive and accurate understanding of temporal changes in nutrient concentrations in leaf litter.

Finally, our results provide first insights into intra-plot spatial variability of litterfall. An interesting avenue for future research is to expand this approach to assess inter-plot variability across spatial scales and to examine how biodiversity effects on litter inputs and related ecosystem functions emerge and interact under more heterogeneous spatial arrangements and landscape contexts.

AUTHOR CONTRIBUTIONS

Elisabeth Bönisch: Conceptualization, data curation, formal analysis, investigation, methodology, project administration, visualization, writing—original draft, writing—review and editing. **Benjamin M. Delory**: Investigation, writing—review and editing. **Šárka Angst**: Investigation, writing—review and editing. **Gerrit Angst**: Investigation, writing—review and editing. **Abderrahim Diane**: Formal analysis, validation. **Peter Dietrich**: Methodology, writing—review and editing. **Olga Ferlian**: Writing—review and editing. **Andreas Fichtner**: Investigation, writing—review and editing. **Rahel Gormanns**: Investigation, writing—review and editing. **Claudia R. Guimarães-Steinicke**: Methodology, writing—review and editing. **Stephan Hättenschwiler**: Funding acquisition, methodology, resources, writing—review and editing. **Julius Quosh**: Methodology, resources. **Tama Ray**: Writing—review and editing. **Anika Walter**: Investigation, methodology. **Nico Eisenhauer**: Conceptualization, funding acquisition, investigation, methodology, resources, supervision, writing—review and editing. **Rémy Beugnon**: Conceptualization, formal analysis, investigation, methodology, project administration, validation, supervision, visualization, writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

Benjamin M. Delory is an associate editor of *Journal of Ecology*, but took no part in the peer review and decision-making processes for this paper. The authors declare no further conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data underlying this study have been archived in the MyDiv data repository and are openly available at the following DOI URLs: leaf litterfall biomass and wood biomass increment at https://doi.org/10.25829/SAHC-C606 (Bönisch, Beugnon, Gormanns, & Eisenhauer, 2026), leaf litterfall C, N and P at https://doi.org/10.25829/PH0D-S656 (Bönisch, Beugnon, Walter, et al., 2026). R codes used in this study are available at the Zenodo repository at the following DOI URL: https://doi.org/10.5281/zenodo.19159916 (Bönisch & Beugnon, 2026).

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SUPPORTING INFORMATION

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

Table S1. Overview of tree species used in the MyDiv experiment with their respective mycorrhizal association (AM, arbuscular mycorrhizal fungi; EM, ectomycorrhizal fungi).

Table S2. Tree species-specific height (mean and maximum) and diameter at breast height (DBH; mean and maximum).

Table S3. Tree species-specific wood densities (*p*) used to calculate wood biomass were taken from Forrester et al. (2017).

Table S4. Overview of dead trees (including missing trees) within the core area of the plots in 2023 per species and per treatment: total number of trees, number of dead trees and relative number of dead trees.

Table S5. Coordinates of trap locations per plot in the MyDiv experiment.

Table S6. Total cross-plot leaf litterfall (i.e. leaf litter originating from neighbouring plots and non-target species; %, based on leaf litter dry mass) as affected by tree species richness (one, two, four; Sr) for communities containing only arbuscular mycorrhizal tree species (AM), only ectomycorrhizal tree species (EM) or both (AM+EM; Myc).

Table S7. Sampling schedule of leaf litter in the MyDiv experiment.

Table S8. Summary of mixed-effects model analyses (Type-1 Sum of Squares) testing the effects of tree species richness (one, two, four; Sr; log-transformed), mycorrhizal type (AM, EM, AM+EM; Myc) and their interactions on the number of months of litterfall in which leaf litterfall exceeded a minimum threshold of (a) 0 g, (b) 0.5 g and (c) 1 g ($n = 80$).

Table S9. Summary of mixed-effects model analyses (Type-1 Sum of Squares) testing the effects of tree species richness (one, two, four; Sr; log-transformed), mycorrhizal type (AM, EM, AM+EM; Myc) and their interactions on (a) total annual biomass (wood biomass increment and leaf litterfall), (b) annual wood biomass (increment) and (c) annual leaf litter biomass ($n = 80$).

Table S10. Summary of Tukey HSD analysis testing the difference in biomass production between mycorrhizal types (AM, EM, AM+EM; Myc) for (a) total annual biomass (wood biomass increment + leaf litter biomass) and (b) annual wood biomass (increment).

Table S11. Relative changes (%) in (a) annual biomass production (wood biomass increment + leaf litter biomass) and (b) annual wood production (wood biomass increment), showing the strength of the effects of mycorrhizal type (AM, EM, AM+EM, Myc).

Table S12. Summary of mixed-effects model analyses (Type-1 Sum of Squares) testing the effects of month (1–12), tree species richness (one, two, four; Sr), mycorrhizal type (AM, EM, AM+EM; Myc) and their interactions on (a) monthly leaf litter biomass and (b) cumulative litterfall ($n = 960$).

Table S13. Relative changes (%) in monthly leaf litterfall showing the strength of the effects of tree species richness (one, two, four; Sr).

Table S14. Summary of Tukey HSD analysis testing the difference in monthly leaf litterfall between mycorrhizal types (AM, EM, AM+EM; Myc) and relative changes in monthly leaf litterfall showing the strength of the effects of mycorrhizal type. NAs indicate missing main effect of mycorrhizal type.

Table S15. Summary of mixed-effects model analyses (Type-1 Sum of Squares) testing the effects of tree species richness (one, two, four; Sr), mycorrhizal type (AM, EM, AM+EM; Myc) and their interactions on annual temporal variability of litterfall ($n = 80$).

Table S16. Summary of Tukey HSD analysis testing the difference in (a) annual temporal variability, (b) number of months (litterfall duration in months) and (c) annual spatial variability of leaf litterfall between mycorrhizal types (AM, EM, AM+EM; Myc).

Table S17. Relative changes (%) in (a) annual temporal variability, (b) number of months and (c) annual spatial variability of leaf litterfall showing the strength of the effects of mycorrhizal type (AM, EM, AM+EM, Myc).

Table S18. Summary of mixed-effects model analyses (Type-1 Sum of Squares) testing the effects of tree species richness (one, two, four; Sr), mycorrhizal type (AM, EM, AM+EM; Myc) and their interactions on litterfall duration in month (number of months of litterfall in which leaf litterfall exceeded a minimum threshold of (a) 0 g) ($n = 80$).

Table S19. Average of litterfall months per level of tree species richness (one, two, four) and mycorrhizal type (AM, EM, AM+EM).

Table S20. Summary of mixed-effects model analyses (Type-1 Sum of Squares) testing the effects of tree species richness (one, two, four; Sr), mycorrhizal type (AM, EM, AM+EM; Myc) and their interactions on annual spatial variability of litterfall ($n = 80$).

Table S21. Relative changes (%) in (a) annual temporal variability, (b) number of months and (c) annual spatial variability of leaf litterfall showing the strength of the effects of tree species richness (one, two, four; Sr).

Table S22. Summary of mixed-effects model analyses (Type-1 Sum of Squares) testing the effects of month (1–12), tree species richness (one, two, four; Sr), mycorrhizal type (AM, EM, AM+EM; Myc) and their interactions on monthly spatial variability of litterfall ($n = 853$).

Table S23. Summary of Tukey HSD analysis testing the difference in monthly spatial variability in leaf litterfall between mycorrhizal types (AM, EM, AM+EM; Myc) and relative changes in monthly spatial variability in litterfall showing the strength of the effects of mycorrhizal type.

Table S24. Summary of mixed-effects model analyses (Type-1 Sum of Squares) testing the effects of tree species richness (one, two, four; Sr), mycorrhizal type (AM, EM, AM+EM; Myc) and their interactions on (a) annual C, N and P concentrations of leaf litter, (b)

annual C, N and P fluxes of leaf litter and stoichiometric ratios (C:N, C:P, N:P) ($n = 80$).

Table S25. Summary of Tukey HSD analysis testing the difference in (a) elemental concentrations (carbon [C], nitrogen [N], phosphorus [P]), (b) elemental fluxes and (c) stoichiometry of leaf litter between mycorrhizal types (AM, EM, AM+EM; Myc).

Table S26. Relative changes (%) in (a) elemental concentrations (carbon [C], nitrogen [N], phosphorus [P]), (b) elemental fluxes and (c) stoichiometry of leaf litter showing the strength of the effects of mycorrhizal type (AM, EM, AM+EM, Myc).

Table S27. Relative changes (%) in (a) elemental concentrations (carbon [C], nitrogen [N], phosphorus [P]), (b) elemental fluxes and (c) stoichiometry of leaf litter showing the strength of the effects of tree species richness (one, two, four; Sr).

Table S28. Monthly carbon (C), nitrogen (N), and phosphorus (P) concentrations, fluxes and stoichiometry.

Figure S1. Litter trap design (0.75 × 0.75 cm plastic frame with plastic mesh, attached at each corner of the frame to one neighbouring tree, mesh weighed with stones) (a) and placement within each plot of the MyDiv experiment (b).

Figure S2. Cross-plot leaf litterfall (i.e. leaf litter originating from neighbouring plots and non-target species; % of total leaf litterfall based on leaf litter dry mass) as affected by tree species richness (one, two, four) for communities containing only arbuscular mycorrhizal tree species (AM), only ectomycorrhizal tree species (EM) or both (AM+EM).

Figure S3. Total leaf litterfall dry mass ($g \cdot m^{-2}$) from March 2023 to February 2024 per tree species, including cross-plot leaf litterfall (i.e. leaf litter originating from neighbouring plots and non-target species).

Figure S4. The number of months of litterfall in which leaf litterfall exceeded a minimum threshold of (a) 0 g, (b) 0.5 g and (c) 1 g, as a function of tree species richness (one, two, four) for communities containing only arbuscular mycorrhizal tree species (AM), only ectomycorrhizal tree species (EM) or both (AM+EM).

Figure S5. NIRS measurements across the samples of subset 1 (months: February, April, June, August, October, December), coloured by sample.

Figure S6. Eigenvalues across the principal components analysis (PCA) dimensions.

Figure S7. Wavelength and loadings across the principal components analysis (PCA) dimensions.

Figure S8. Individuals - Sample distribution across the three principal components analysis (PCA) axes.

Figure S9. Cluster distribution across the principal components analysis (PCA) axes.

Figure S10. Random selection of the 100-sample subset.

Figure S11. Random selection of the 250-sample subset.

Figure S12. Proportion of the samples across the main treatments (tree species: Ac, *Acer pseudoplatanus* L.; Ae, *Aesculus hippocastanum* L.; Fr, *Fraxinus excelsior* L.; Pr, *Prunus avium* L.; So, *Sorbus aucuparia* L.; Be, *Betula pendula* Roth, Ca, *Carpinus betulus* L.; Fa, *Fagus sylvatica* L.; Qu, *Quercus petraea* (Matt.) Liebl.; Ti, *Tilia platyphyllos* Scop.; tree species richness (1, 2, 4) for communities containing only arbuscular mycorrhizal tree species [AM], only ectomycorrhizal tree species [EM] or both [AM+EM]).

Figure S13. Propagated error of near-infrared reflectance spectroscopy (NIRS) predictions of C, N and P concentrations (a–c; $mg \cdot g^{-1}$), fluxes (d–f; $kg \cdot ha^{-1} \cdot year^{-1}$) and ratios (g–i) per plot (1–80).

Figure S14. Propagated error of NIRS (near-infrared reflectance spectroscopy) predictions of C, N and P concentrations (a–c; $mg \cdot g^{-1}$), fluxes (d–f; $kg \cdot ha^{-1} \cdot year^{-1}$) and ratios (g–i) on the main models (compare to Figure 4): C, N, P concentrations and fluxes of annual leaf litterfall as a function of tree species richness (one, two, four; 'Sr') for communities containing only arbuscular mycorrhizal tree species (AM), only ectomycorrhizal tree species (EM) or both (AM+EM, 'Myc').

Figure S15. C, N and P concentrations ($mg \cdot g^{-1}$) of annual leaf litterfall as a function of tree species richness (one, two, four) (a–c) for communities containing only arbuscular mycorrhizal tree species (AM), only ectomycorrhizal tree species (EM) or both (AM+EM) (d–f).

Figure S16. C, N and P fluxes ($kg \cdot ha^{-1}$) of annual leaf litterfall as a function of tree species richness (one, two, four) (a–c) for communities containing only arbuscular mycorrhizal tree species (AM), only ectomycorrhizal tree species (EM) or both (AM+EM) (d–f).

Figure S17. Wood biomass ($kg \cdot ha^{-1}$) as a function of tree species richness (one, two, four) for communities containing only arbuscular mycorrhizal tree species (AM), only ectomycorrhizal tree species (EM) or both (AM+EM) until 2022 and 2023.

Figure S18. Monthly (a) and annual (b) total precipitation [mm] in Bad Lauchstädt (Saxony Anhalt, Germany) from 2018 to 2024.

Figure S19. Leaf litter biomass per tree species ($g \cdot m^{-2}$) in tree communities of varying tree species richness (one, two, four; Sr) and different mycorrhizal types (arbuscular mycorrhizal fungi [AM], ectomycorrhizal fungi [EM], mixtures [AM+EM]).

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