












## RESEARCH ARTICLE

# Tree diversity and mycorrhizal type co-determine multitrophic ecosystem functions

Huimin Yi<sup>1,2</sup>  | Nico Eisenhauer<sup>1,2</sup>  | Jan Christoph Austen<sup>1,2</sup>  | Roberto Rebollo<sup>3</sup>  |  
Tama Ray<sup>1,4,5</sup>  | Elisabeth Bönisch<sup>1,2</sup>  | Goddert von Oheimb<sup>5</sup>  | Andreas Fichtner<sup>6</sup>  |  
Andreas Schuldt<sup>7</sup>  | Guillaume Patoine<sup>1,2</sup>  | Olga Ferlian<sup>1,2</sup> 

<sup>1</sup>German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany; <sup>2</sup>Institute of Biology, Leipzig University, Leipzig, Germany; <sup>3</sup>Department of Environmental Systems Science, ETH Zürich, Zurich, Switzerland; <sup>4</sup>Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany; <sup>5</sup>Institute of General Ecology and Environmental Protection, Technische Universität Dresden, Tharandt, Germany; <sup>6</sup>Institute of Ecology, Leuphana University of Lüneburg, Lüneburg, Germany and <sup>7</sup>Forest Nature Conservation, University of Göttingen, Göttingen, Germany

## Correspondence

Huimin Yi

Email: [huimin.yi@idiv.de](mailto:huimin.yi@idiv.de)

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## Abstract

1. The relationship between biodiversity and multitrophic ecosystem functions (BEF) remains poorly studied in forests. There have been inconsistent reports regarding the significance of tree diversity effects on ecosystem functions, which may be better understood by considering critical biotic interactions of trees.
2. This study investigates the role of tree-mycorrhizal associations that may shape forest BEF relationships across multiple ecosystem functions. We used a field experiment (MyDiv) that comprises 10 deciduous tree species associated with either arbuscular mycorrhizal (AM) or ectomycorrhizal (EcM) fungi to create gradients in species richness (1, 2, 4 species) and different mycorrhizal communities (only AM-species [AM fungi associated tree species] or EcM-species [EcM fungi associated tree species], or a combination of both). We investigated the effects of tree species richness and mycorrhizal types on crucial multitrophic ecosystem functions (foliage damage, predation [using artificial caterpillars] and soil fauna feeding activity [~0–10 cm]) and assessed how these effects were mediated by stand characteristics.
3. Overall, we found that tree species richness and mycorrhizal types strongly affected multitrophic ecosystem functions. Compared to monocultures, 4-species mixtures with both mycorrhizal types experienced significantly lower foliage damage. The mixtures of EcM-species supported significantly higher predation (i.e. a greater proportion of artificial caterpillars being attacked), and this effect strengthened with tree species richness. The effects of tree species richness on soil fauna feeding activity were negative across all mycorrhizal types in the lower soil layer. Moreover, we showed that tree diversity effects were mediated by

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above-ground tree biomass, vertical structural complexity and leaf quality, with the dominating mechanisms largely depending on the mycorrhizal types.

4. *Synthesis*. Tree species richness affected multitrophic ecosystem functioning by (1) directly decreasing the proportion of foliage damage in the communities with both mycorrhizal types, where AM-species benefited from mixing with EcM-species, and (2) increasing predation rates via changes in the vertical structural complexity in mixtures of EcM-species. Our results highlight the importance of considering mycorrhizal types for managing well-functioning mixed-species forests and contribute to broadening the mechanistic understanding of the context-dependent BEF relationships in forests.

#### KEYWORDS

biodiversity-ecosystem functioning, biotic interactions, herbivory, mycorrhizal type, MyDiv, predation, soil fauna feeding activity, stand characteristics

## 1 | INTRODUCTION

Biodiversity loss has received increasing attention in recent decades, and a growing volume of research demonstrates the positive relationship between biodiversity and ecosystem functions (BEF), with a focus on grassland and agroecosystems but more recently also in forest ecosystems (Cardinale et al., 2007; Huang et al., 2018; Lefcheck et al., 2015; Tiemann et al., 2015; Weisser et al., 2017). However, biodiversity effects in forests showed more variability amongst studies: even for the same ecosystem function, for example herbivory and top-down control by predators, past research reported contrasting effects of tree species richness (Grossman et al., 2018; Hantsch et al., 2014; Jactel & Brockerhoff, 2007; Schuldt et al., 2010; Staab & Schuldt, 2020; Vehviläinen et al., 2007). Beyond tree species richness, several additional factors, such as multitrophic interactions, structural complexity and functional traits, may drive the BEF relationships but have been poorly studied, particularly in forests with trees as structurally complex organisms (Ampoorter et al., 2020; Felipe-Lucia et al., 2018; Finke & Denno, 2002; Hines et al., 2015; Muiruri et al., 2016; Schuldt et al., 2018).

A diverse forest potentially enhances tree biomass compared to monocultures (Dietrich et al., 2023; Huang et al., 2018; Williams et al., 2017), increases available food resources for generalist herbivores (Schuldt et al., 2010) and likely promotes the activity of decomposers (Beugnon et al., 2021; Eisenhauer et al., 2017; Lange et al., 2015). Consequently, higher prey density leads to higher predator density (Lindeman, 1942; Schuldt et al., 2019), causing positive bottom-up effects of plant diversity on higher trophic levels (Eisenhauer et al., 2013; Scherber et al., 2010). The higher tree species richness could favour generalist herbivores by optimizing nutrient uptake (i.e. *nutrient complementation hypothesis*; Bernays et al., 1994; Unsicker et al., 2008) but may decrease the population of specialists by diluting food resources (i.e. *resource concentration hypothesis*; Muiruri et al., 2019; Root, 1973). In general, most herbivores favour leaves of 'high quality' with higher nutrient

concentrations (nitrogen (N) and phosphorus (P)) and low carbon-to-nitrogen (C/N) ratios as well as low levels of secondary metabolites contributing to plant defence (Coley, 1983; Mundim et al., 2009; War et al., 2012). The tissue quality is also prone to change with species mixture (Chen & Chen, 2021; Ferlian et al., 2021). Additionally, the quality of leaf litter is also well-known to shape below-ground community composition and functioning (Gottschall et al., 2022; Kurokawa & Nakashizuka, 2008). Thus, as tree species richness affects biomass production (Huang et al., 2018) and nutrient quality (Chen & Chen, 2021), this is likely to have cascading effects on multiple trophic levels simultaneously (Schuldt et al., 2018).

A higher stand structural complexity in diverse forests (e.g. by mixing tree species with a broad spectrum of growth rates) attributes to higher diversity in both crown architecture and tree size, resulting in higher efficiency of canopy packing and a greater connectedness of canopies (Ehbrecht et al., 2021; Fahey et al., 2019). In diverse forests, non-host trees create chemical and physical barriers for herbivores or pathogens, particularly for oligophagous species, and decrease their host accessibility (i.e. *associational resistance*; Barbosa et al., 2009; Castagnérol et al., 2013; Guyot et al., 2019; Jactel et al., 2001; Jactel & Brockerhoff, 2007). Furthermore, the trees in diverse forests could profit from a higher vertical structural complexity that likely promotes top-down control via increasing the detectability and accessibility of prey, particularly to predatory birds (Groner & Ayal, 2001; Juchheim et al., 2020; Muiruri et al., 2016; Yang et al., 2018). Nevertheless, a greater connectedness of canopies in more diverse forests may aid the spilling-over of generalist herbivores/pathogens to neighbouring trees (i.e. *associational susceptibility*; Grossman et al., 2019; Jactel et al., 2017; Vehviläinen et al., 2007; White & Whitham, 2000). At the same time, a higher structural complexity will enhance the spatiotemporal stability of forest microclimates, for example, soil surface temperature, and further increase soil ecosystem functions (Gottschall et al., 2022; Richards & Coley, 2007). These results suggest that the structural complexity

of forest stands may be a significant mediator of tree diversity effects on multitrophic communities (Schuldt et al., 2019) and ecosystem functions.

Most tree species associate with mycorrhizal fungi, enhancing water and nutrient uptake, and protecting them against antagonists in exchange for photosynthetic C (Smith & Read, 2010; Tedersoo et al., 2020). The mycorrhizal association type, for example, arbuscular mycorrhizal (AM) or ectomycorrhizal (EcM) fungi (Steidinger et al., 2019), is one of the crucial functional traits affecting ecosystem processes (Bennett et al., 2017; Heděnc et al., 2020; Phillips et al., 2013; van der Heijden et al., 2015). More specifically, when compared to AM-species (i.e. tree species associating with AM fungi), EcM-species (associating with EcM fungi) allocate more photosynthetic C to the symbiotic fungi, resulting in less investment in above-ground tree biomass (Dietrich et al., 2023; Hobbie & Hobbie, 2008; Jakobsen & Rosendahl, 1990; van der Heijden et al., 2015). On average, AM-species produce higher-quality leaf litter, facilitating higher decomposition rates and elevated rates of C and nutrient mineralization (Phillips et al., 2013), but probably suffer more from herbivory damage and pathogen infection, in contrast to EcM-species (Bennett et al., 2017; Laliberté et al., 2015; Tao et al., 2016). Besides effects on the life strategies of the host, the two types of mycorrhizal fungi largely shape the soil microbial communities (Heděnc et al., 2020; Singavarapu et al., 2022) as well as higher trophic groups in the soil food web (Peng et al., 2022). Taken together, mycorrhizal types are likely to co-determine forest BEF relationships, as indicated by recent work (Deng et al., 2023; Dietrich et al., 2023; Luo et al., 2023; Yan et al., 2022). Due to the cascading effects across trophic levels (Eisenhauer et al., 2013; Schuldt et al., 2018), mycorrhizal association types can potentially shape the relationship between tree diversity and multitrophic ecosystem functions; however, empirical evidence is lacking thus far.

AM-species and EcM-species are systematically different, which allows them to complement each other via resource partitioning in essential processes like nutrient uptake and spatial resource use, both below-ground and above-ground (Chen et al., 2016; Eisenhauer et al., 2022; Ferlian et al., 2018; Luo et al., 2023; Tedersoo et al., 2020; Yu et al., 2021). For example, EcM-species supposedly favour a more conservative nutrient-use strategy than AM-species (Averill et al., 2019) and tend to produce less biomass during the sapling stage (Dietrich et al., 2023). This likely allows for height variation, complementing each other through the partitioning of canopy space (Ray, Delory, et al., 2023; Williams et al., 2017). In addition, Barry et al. (2019) and Yu et al. (2021) argued that the positive relationships between biodiversity and ecosystem functions can potentially be attributed to abiotic facilitation, meaning that plants benefit from their neighbours via changes in the abiotic environment, like microclimate (Wright et al., 2017) and soil conditions. For instance, EcM-species could acidify the soil by producing recalcitrant litter and releasing allelochemicals to protect roots against pathogens (Duchesne et al., 2011; Laliberté et al., 2015; Tedersoo et al., 2020; Tedersoo & Bahram, 2019), effects which

would benefit the neighbouring AM-species. Taken together, AM-species and EcM-species may facilitate each other's performance (Tedersoo et al., 2020) and further strengthen the BEF relationship, but research is lacking to confirm this assumption.

This study aims to investigate how mycorrhizal types and their diversity mediate the effects of tree species richness on multitrophic ecosystem functions. We made use of a six-year-old tree diversity experiment that manipulates mycorrhizal types and the species richness of trees. More specifically, the treatment of mycorrhizal type has three levels, only AM-species or EcM-species (1, 2 and 4 species), or even mixtures of both AM-species and EcM-species (2 and 4 species in total). The ecosystem functions targeted by this study include foliage damage (both herbivory and pathogen infection), predation, and decomposition (indicated by the feeding activity of soil fauna/detrivores). To further explore the mechanisms and potential mediators of the effects of tree species richness and mycorrhizal types on multitrophic ecosystem functions, we quantified tree biomass, vertical structural complexity within a stand, and leaf quality. We hypothesize that (1) polyculture plots generally provide higher levels of ecosystem functions (decreasing foliage damage, and increasing predation [top-down control of herbivores] and the feeding activity of soil fauna), but the effects of tree species richness are expected to differ between mycorrhizal types and are likely enhanced by mixing both mycorrhizal types; and (2) the effects of tree species richness on the target ecosystem functions will be mediated by tree biomass, vertical structural complexity and leaf quality, which in turn depend on the mycorrhizal types.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site and experiment design

This research was conducted at the tree diversity experiment MyDiv located at the Bad Lauchstädt Experimental Research Station of the Helmholtz Center for Environmental Research-UFZ, southwest of Halle (51°23'N, 11°53'E), Saxony-Anhalt, Germany. The site is around 114–116 m a.s.l., with an annual average temperature of 8.8°C and mean annual precipitation of 484 mm. The soil of the MyDiv site is very fertile and classified as Haplic Chernozem with a circumneutral pH of 6.6–7.4, and characterized by a thick humus horizon. For further information about the MyDiv site, see Ferlian et al. (2018).

The MyDiv experiment was established in March 2015 and manipulates tree species richness and mycorrhizal types (Ferlian et al., 2018). Ten deciduous angiosperm tree species commonly distributed in Germany were selected (Table S1). Half of the species predominantly associate with arbuscular mycorrhizae (AM-species), that is *Acer pseudoplatanus*, *Aesculus hippocastanum*, *Fraxinus excelsior*, *Prunus avium* and *Sorbus aucuparia*. The other five species predominantly associate with ecto-mycorrhizae (EcM-species), that is *Betula pendula*, *Carpinus betulus*, *Fagus sylvatica*, *Quercus petraea* and *Tilia platyphyllos*. The MyDiv experiment contains three levels

of tree species richness (1, 2, 4 species) and three levels of mycorrhizal types, with each plot comprising only AM-species (AM plot) or only EcM-species (EcM plot) with three richness levels, or both types (Mixed plot) with two richness levels (2 and 4 species). In total, the experiment includes eight combined treatments (3×AM plots+3×EcM plots+2×Mixed plots) each with 10 replicates, for a total of 80 plots of 11×11 m, distributed over two blocks that slightly differed in abiotic and biotic parameters measured before the MyDiv establishment (Ferlian et al., 2018). All trees were planted in a rectangular grid with a one-meter distance between trees (140 trees per plot). To avoid edge effects, data was collected from the core area, specifically central 8×8 m of each plot (Figure S1; a few dead trees were removed from the plots (Dietrich et al., 2023)). Plots are separated by grass paths (3 m wide) and water-permeable weed tarps covered the plots at the time of sampling to avoid weed interference.

## 2.2 | Foliage damage assessment

We recorded leaf damage by invertebrate herbivores and pathogens. In May 2021, three individuals for each tree species were randomly selected from the southeast quadrant of each plot to avoid conflicts with other measurements happening simultaneously (Figure S1). The damage of each tree was recorded on 15 recently expanded, green, full sun leaves on three branches (five leaves randomly selected from each branch), one located at breast height, and two slightly below and above breast height, respectively. If there were no suitable branches around breast height, the next accessible branches were chosen. For each leaf, we visually inspected whether leaves were damaged by invertebrate herbivores or pathogens. Further, based on the shape of the leaf damage, the guild that caused the damage was assigned to one of eight different feeding guilds (chewer, hole-feeder, miner, galler of the genus *Dasineura*, other galler, roller, sucking insect and skeletonizer) and two guilds of pathogenic fungi (rust and mildew) (Castagneyrol et al., 2013; Ferlian et al., 2021). For consistency reasons, the same researcher assessed leaf damage on all trees. For statistical analyses, we averaged the richness from all guilds present on each leaf as total foliage damage (Yi, Ferlian, et al., 2023a). Additionally, we analysed the proportion of damaged leaves due to chewers and hole-feeders (the two most dominant feeding guilds in this study).

## 2.3 | Predation rates

Predation in each plot was assessed using artificial caterpillars that enable the analysis of both predation rates and predator composition, for example, by differentiating bird and insect predation (Howe et al., 2009; Maas et al., 2015; Schwab et al., 2021). By using a clay extruder (Staedtler, Nürnberg, Germany), the caterpillars (length: 40 mm, diameter: 4 mm) were made of green, non-toxic and odourless plasticine (Becks Plastillin, Gomaringen, Germany) rolled around a 120 mm long piece of wire (diameter: 0.35 mm) used to secure the

caterpillars on the selected tree branch (Yang et al., 2018). We deployed 16 dummy caterpillars on eight trees within the core area of each plot for 2 weeks (from 14 to 30 June 2021), with at least two trees (non-neighbored) chosen for each species per plot (Figure S1). On each selected tree, two dummies were deployed at 25% and 50% of the mean tree height (averaging tree heights per plot by using MyDiv inventory data from December 2020). In the first and second weeks after exposure, the bite marks were identified (consistently by one researcher throughout the experiment), either caused by birds, insects or unspecified others (Low et al., 2014; Schwab et al., 2021). After the first record, we manually removed all bite marks or replaced the badly destroyed dummies with new ones for the second exposure. Photos were taken in case of doubt and later reviewed. For statistics, the proportion of attacked dummies (16 in total) per plot during the whole 2-week exposure period was regarded as the total predation rate (Yi, Ferlian, et al., 2023a). Specific bird and insect predation rates were calculated similarly.

## 2.4 | Soil fauna feeding activity

The bait-lamina test is a rapid and standardized approach to assessing the feeding activity of soil fauna (or soil invertebrates), revealing the decomposition of organic matter in the topsoil (Birkhofer et al., 2011; Hamel et al., 2007; Kratz, 1998). Bait-lamina strips are 16 cm long PVC strips with 16 holes (diameter: 2 mm) filled with a substrate made of cellulose (70%), bran flakes (27%) and activated carbon (3%) (Eisenhauer et al., 2014; Kratz, 1998). The substrate on the bait-lamina strips is mainly consumed by macrofauna like earthworms and mesofauna like Collembola and Enchytraeidae (Birkhofer et al., 2011). Due to the brief exposure period and the inhibitory effects of the activated carbon, it is believed that microorganisms have only a marginal effect on the decomposition rate of the strips (Eisenhauer et al., 2014; Helling et al., 1998). Soil fauna activity was assessed at the same time as above-ground animal activities to maximize comparability of data. Five strips per plot were placed vertically in a row (1 m) into the soil and exposed for 3 weeks (27 May–18 June 2021), with the bottom tip of the strip at a soil depth of 10 cm (Figure S1; Thakur et al., 2018). A row of five strips was randomly placed in the southeastern quadrant of each core area (Figure S1). Altogether, 400 strips (5×80 plots) were deployed in the MyDiv experiment. At the end of exposure time, we collected the bait laminas and recorded substrate consumption in the holes ('0' for fully consumed, '0.5' for partially consumed, and '1' for no consumption) (Sünnemann et al., 2021). The soil fauna feeding activity per plot was expressed as the proportion of removed substrate (fully or partially removed) to the total amount of strips per plot. For statistical analysis, the proportion of removed substrate of the upper eight bait holes indicated the soil fauna feeding activity in the upper soil layer (soil depth: ~0–5 cm), and that of the eight lower bait holes indicated the activity in the lower soil layer (soil depth: ~5–10 cm) (Yi, Ferlian, et al., 2023a). The removed proportion of 16 holes on a whole strip presented the activity in the total soil depth (~0–10 cm).

## 2.5 | Stand characteristics

The above-ground tree biomass, vertical structural complexity and leaf quality were selected as potential mediators to understand the mechanisms underlying the effects of tree species richness and mycorrhizal types (Dietrich et al., 2023; Ehbrecht et al., 2021; Huang et al., 2017, 2018; Phillips et al., 2013; Schuldt et al., 2019; Staab & Schuldt, 2020; see Supplementary Method 1 for details on the selection of mediators). We quantified tree wood volume as a proxy of above-ground tree biomass, because the biomass results attained from species-specific allometric equations are not reliable for young stands in MyDiv (Chave et al., 2014; Forrester et al., 2017; Figure S4; Table S6). To calculate the tree wood volume, we measured the stem diameter at 5 cm above the ground ( $d_0$ ) and the height (H) for all living trees in the core area in December 2020. Then, we estimated the wood volume for every living tree in the core area by

using  $[\pi \times \left(\frac{d_0}{2}\right)^2 \times H \times f]$ , where  $f$  is a cylindrical form factor of 0.5 (an average value for young broadleaved trees) to account for the deviation of the tree volume from the theoretical volume of a cylinder (Fichtner et al., 2018; Pretzsch, 2009; Ray, Delory, et al., 2023). We summed the volumes of all individual trees to determine the total wood volume per plot (in the following total stand volume) (Yi, Ferlian, et al., 2023b).

Furthermore, we quantified above-ground vertical structural complexity using the effective number of layers (ENL) determined by terrestrial laser scanning in the core area of each plot in September 2021 (Ray, Delory, et al., 2023; Ray, Fichtner, et al., 2023). ENL provides a holistic and reproducible description of the three-dimensional (3D) vertical stand structure, independent of human estimation (possible observer bias) and classic dendrometric parameters, for example, basal area, density, and height (Ehbrecht et al., 2016; Knuff et al., 2020). The algorithm of ENL considers the 3D space in voxels (3D pixel) with a 5 cm edge length for the entire area covered by the scan. We considered those voxels to be filled, if they contained at least one point from the laser scan. Then, the ratio ( $p_i$ ) between filled and available voxels is summarized in 25 cm thick layers. The final index value was calculated using the inverse Simpson index, as below, developed by (Ehbrecht et al., 2016):

$$\text{ENL} = \exp\left(-\sum_{i=1}^{N_{\text{top}}} p_i \times \ln p_i\right),$$

with  $N_{\text{top}}$  as the stand top height. A more evenly distributed layering along the vertical profile and/or increasing stand height result in higher values of the ENL.

To measure leaf C and N concentrations as a proxy of leaf quality, we sampled three leaves (without any damage from herbivores or pathogens) at 2.5 m height per tree and three individuals for each species per plot in July 2021 (Cadotte, 2017). Nine leaves for each species per plot were pooled into one sample. All samples were dried at 60°C to constant weight, and each sample was ground with a ball mill (MM 400, Retsch, Haan, Germany) to a homogeneous powder. Five milligrams from each sample were used to determine leaf total

C and total N concentrations with a CHNS elemental analyser (vario EL cube; Elementar Analysensysteme GmbH, Hanau, Germany). Averaging leaf C/N ratio of all species was used to define the leaf quality in every plot (Yi, Bönisch, et al., 2023).

## 2.6 | Statistical analysis

All of our statistical analyses were conducted in the software R, version 4.0.2 (R Core Team, 2023; Yi, 2023). We quantified the tree species richness effects (henceforth referred to as richness effects) by calculating effect sizes to test hypothesis (1). The effect sizes were expressed as log-ratios (lnRR) between measurements of the ecosystem function in polyculture and monoculture (Cardinale et al., 2007). Insect predation rates and soil fauna feeding activity in the lower soil layer contained zero values, resulting in undefined log ratios (Hedges et al., 1999; Lajeunesse, 2015). To mitigate this issue, we added 0.02 to all values for these variables, as it is close to the lowest values observed in both ecosystem functions, providing a conservative estimate of the log response ratio (Ballhorn et al., 2014; Viola et al., 2010). We first used a t-test to check whether the effect sizes differed from 0. Then, a two-way ANOVA was conducted to examine the effects of tree species richness, mycorrhizal type treatment, and their interaction on the effect sizes. Moreover, pairwise comparisons were performed (R package 'emmeans') to investigate the specific differences between levels of mycorrhizal type treatment within each level of tree species richness, as well as the differences between levels of tree species richness within each level of mycorrhizal type treatment. In addition, to confirm whether the results were still reliable after adding values, we also checked the richness effects on the rate of non-attacked dummies and the rates of non-decomposed holes in bait laminas as a reference. We further calculated the complementarity effects and selection effects using an additive partitioning method (Cappelli et al., 2022; Loreau & Hector, 2001; Nell et al., 2018) on total foliage damage and total predation, utilizing their species-specific data (rarely containing zero values), but not for the soil fauna activity, because only community-level, and not species-level, data were available.

Regarding hypothesis (2), we employed linear mixed effects models (R package 'lme4') and structural equation models (SEMs) (R package 'piecewiseSEM'). Before fitting the models, we checked the normality and homoscedasticity of the targeted ecosystem functions (Figure S2). Insect predation rates and soil fauna feeding activity in the lower soil layer were largely right-skewed due to zero inflation, and other ecosystem functions generally followed a normal distribution. To resolve these issues, we added 1/16 (16 dummies applied in each plot) to insect predation data and 0.5/40 (8 holes  $\times$  5 strips) to soil fauna activity in the lower soil layer, respectively, and the values were then log-transformed. For each ecosystem function, we fitted the standardized stand characteristics (to follow the normal distribution with mean of 0 and standard deviation of 1) and the mycorrhizal type treatment together as explanatory variables, as well as their interactions (fixed factors), using 'Block' as random factor. The 'lmerTest' package was employed to obtain  $p$ -values, and



marginal  $R^2$  (variation explained by fixed effects) was used to compare model performance. We calculated  $\Delta R^2$  to further understand how much variation in each ecosystem function can be explained by the stand characteristics, in addition to the mycorrhizal type treatment. Namely, it is the difference in the variation explained by stand characteristics and mycorrhizal type treatment together and the variation explained by mycorrhizal types alone.

Second, we conducted piecewise SEMs (or confirmatory path analysis) to systematically test hypothesis (2) by disentangling direct and indirect drivers of ecosystem functions. To test whether the mycorrhizal type treatment will shift the BEF relationships, we built one SEM for each mycorrhizal type ('Block' as random factor). The framework was based on an a priori hypothesis about causal relationships informed by pre-existing knowledge of the mechanisms driving biodiversity-multitrophic ecosystem function relationships (Figure S3). Tree species richness was shown to affect above-ground tree biomass (Gamfeldt et al., 2013; Huang et al., 2018), stand structural complexity (Ehbrecht et al., 2017; Perles-Garcia et al., 2021), and leaf quality (Chen & Chen, 2021; Huang et al., 2017; Lü et al., 2019). We included direct pathways from tree species richness to the three facets of stand characteristics. We further included direct pathways from those three facets to the ecosystem functions. In each SEM, we simultaneously included three ecosystem functions—total foliage damage, total predation rates, and total soil fauna feeding activity (~0–10cm)—as response variables. The correlations could also be addressed by adding covariation amongst functions. Each piecewise SEM was assessed by the global model fit via Fisher's C statistics ( $p > 0.05$ ). We assessed the independence of variables and included partial, nondirectional correlations if the improved models fit based on tests of directed separations ( $p \leq 0.10$  for violation of independence claims). We calculated standardized path coefficients, which allowed us to compare the strength of paths within and amongst models and of indirect pathways (calculated as the product of the coefficients along the path).

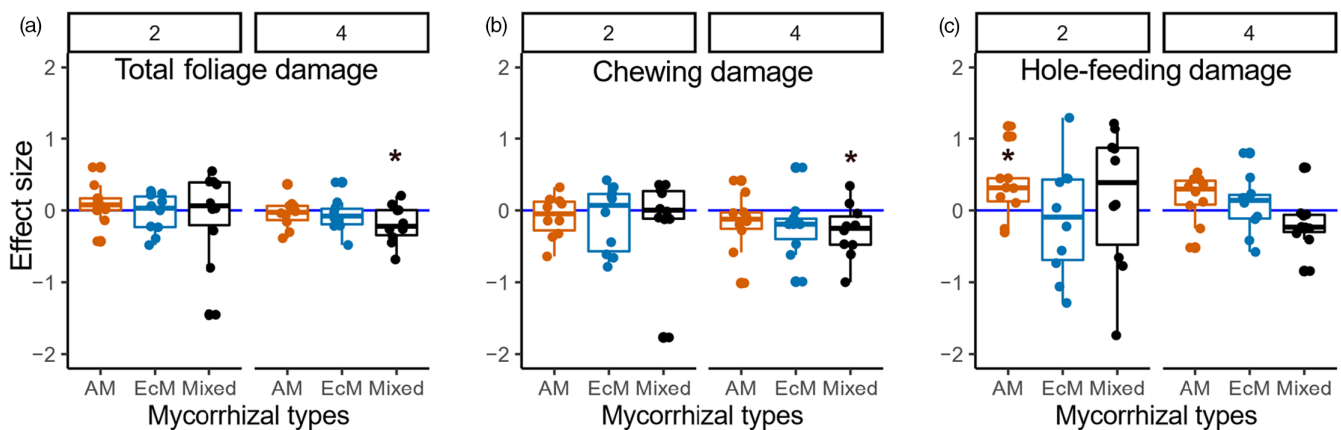
### 3 | RESULTS

#### 3.1 | Effects of tree species richness and mycorrhizal types on foliage damage

Overall, the treatment of mycorrhizal type significantly affected the status of foliage damage, and largely shaped the effects of tree species richness on the damage. The AM plots experienced significantly higher foliage damage, with a mean of  $0.823 \pm 0.086$  (95% confidence interval), than both Mixed plots (mean:  $0.608 \pm 0.104$ ;  $p < 0.001$ ) and EcM plots (mean:  $0.505 \pm 0.100$ ;  $p = 0.009$ ) (Table S2). More importantly, the effect sizes did not significantly differ from zero in any polyculture (2- or 4-species) of only AM-species or EcM-species (Figure 1; Table S3). Only when both mycorrhizal types were mixed, the effect sizes were significantly negative (for both total damage and chewing damage) (Figure 1a,b; Table S3). Regarding hole-feeding damage, the effect sizes in Mixed plots did not significantly differ from zero, but nine plots (out of 10) had negative values when the species richness level was four (Figure 1c; Table S3). Furthermore, with the additive partitioning method, in the 4-species polycultures of Mixed plots, both complementarity effects (positive;  $p = 0.025$ ) and selection effects (negative;  $p < 0.001$ ) were identified as significant; the same case was observed in EcM plots ( $p = 0.012$  &  $p = 0.001$ , respectively), but not in AM plots (Figure S6A,B).

#### 3.2 | Effects of tree species richness and mycorrhizal types on predation rates

The treatment of mycorrhizal type did not significantly influence the absolute rates of predation, but again shaped the effects of tree species richness on predation. The predation in all levels of mycorrhizal type treatment was not significantly different,



**FIGURE 1** The effect of tree species richness (2- and 4-species) on total foliage damage (a), chewing damage (b) and hole-feeding damage (c) in three levels of mycorrhizal type treatment. AM: plots only with AM-species, EcM: plots only with EcM-species, and Mixed: plots with even proportions of AM-species and EcM-species. The effect sizes (log-ratios— $\ln RR$ —between measurements of the function in polyculture and monoculture) that differ significantly from 0 (at  $p \leq 0.05$ ) are indicated by asterisks, (\*). Two-way ANOVA and pairwise comparisons did not show any significant difference amongst the effect sizes on three measurements of foliage damage across different levels of mycorrhizal type treatment and tree species richness.

and total predation rates ranged around  $0.413 \pm 0.036$  and were dominated by bird predation (mean:  $0.335 \pm 0.038$ ) (Table S2). However, when the tree species richness of EcM polycultures increased from two to four, the effect sizes significantly increased for both total predation ( $p=0.027$ ) and bird predation rates ( $p=0.007$ ; Figure 2a,b; Table S4). Consequently, in EcM plots, the effect sizes were significantly positive for both total and bird predation. The effect sizes in polycultures of AM-species did not significantly differ from zero, and even in 4-species communities, the effect sizes in AM plots were smaller than in EcM plots with marginal significance for total predation ( $p=0.089$ ) and being statistically significant for bird predation ( $p=0.023$ ; Figure 2a,b; Table S4). In Mixed plots, the effect sizes on total and bird predation were around 0, and the values were located between AM and EcM plots at the same level of tree species richness (Figure 2a,b; Table S4). As for the effects on insect predation, none of the effect sizes significantly deviated from zero, and the effect sizes in Mixed plots even marginally decreased from 2-species to 4-species mixtures ( $p=0.058$ ; Figure 2c; Table S4). Moreover, with the additional partitioning method, we observed marginally positive complementarity effects in 4-species polycultures of EcM ( $p=0.099$ ) and Mixed plots ( $p=0.102$ ), and significantly negative selection effects in AM plots (for both 2- and 4-species mixture,  $p=0.010$  &  $p<0.001$ , respectively) as well as in Mixed plots (only for 4-species mixture;  $p=0.031$ ; Figure S6C,D).

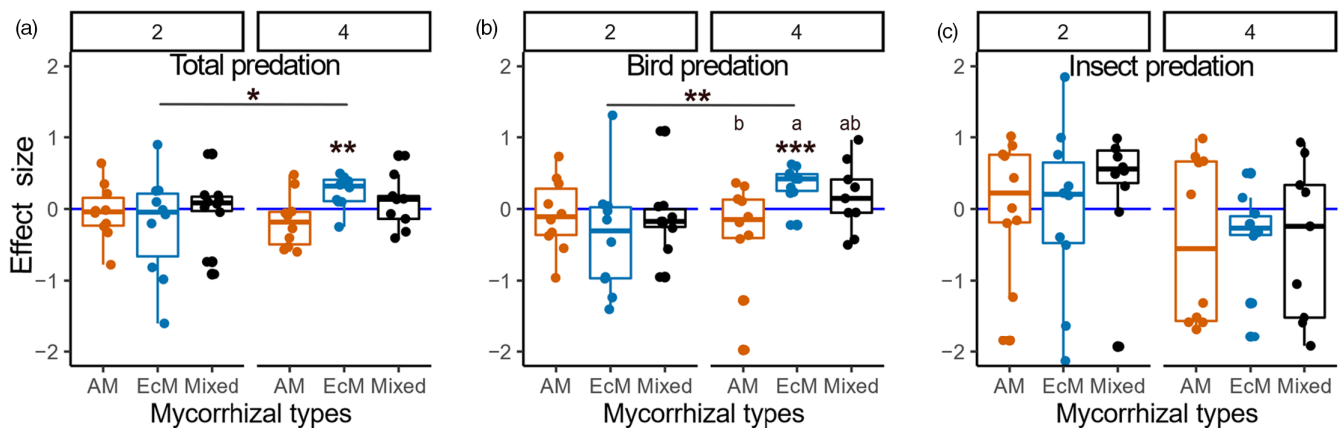
### 3.3 | Effects of tree species richness and mycorrhizal types on soil fauna feeding activity

The tree species richness and the treatment of mycorrhizal type did not significantly affect the absolute values of soil fauna feeding activities, but the richness effects varied between soil

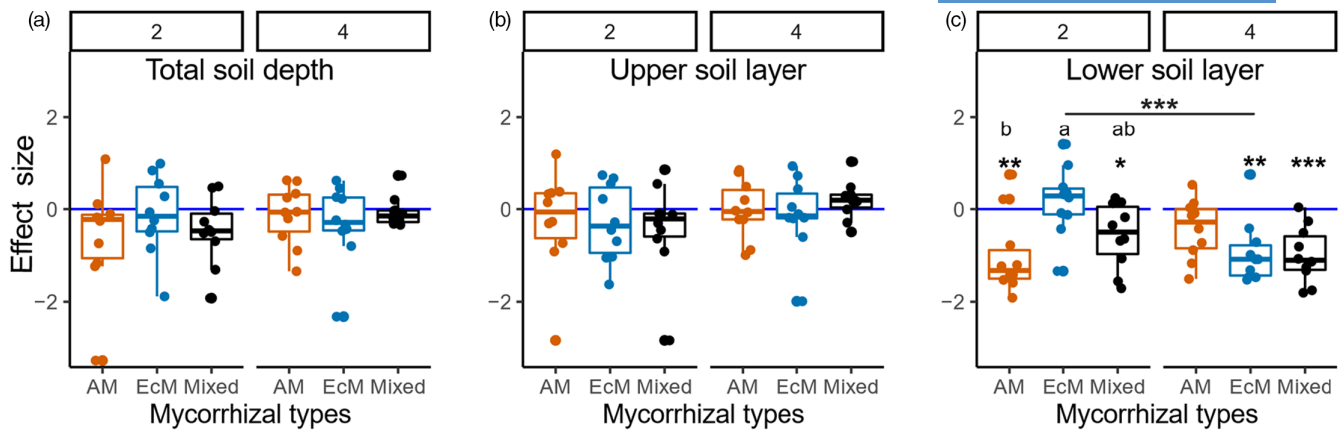
depths. In total soil depth (~0–10 cm), the average proportion of substrates in bait laminas consumed by soil fauna was around  $0.125 \pm 0.019$ , with a higher proportion of  $0.194 \pm 0.058$  consumed in the upper soil layer and a lower proportion in the lower soil layer (mean =  $0.056 \pm 0.016$ ) (Table S2). Regarding the richness effects, the effect sizes did not differ from zero in all mycorrhizal types and the two levels of species richness for the total feeding activity, as well as for the activity in the upper soil layer (Figure 3a,b). However, the effect sizes were significantly negative in polyculture (both 2- and 4-species) plots in the lower soil layer (Figure 3c; Table S5). Furthermore, the effect sizes for the feeding activity in the lower soil layer changed with tree species richness, which also depended on the treatment of mycorrhizal type. In EcM plots, the effect sizes significantly decreased from two to four tree species ( $p<0.001$ ); in Mixed plots, the negative richness effects strengthened with species richness (Figure 3c; Table S5).

### 3.4 | Effects of stand characteristics on ecosystem functions

The targeted ecosystem functions correlated with the three facets of stand characteristics, and the trends largely depended on the feeding guilds and the treatment of mycorrhizal type. The total foliage damage increased with total stand volume, but only in EcM plots ( $p=0.009$ ) and Mixed plots ( $p=0.053$ ) (Figure 4a; Table S8). At the same time, the total damage decreased with the leaf C/N ratio in EcM plots ( $p=0.003$ ; Figure 4c; Table S8). The trends of total damage were mainly driven by hole-feeding damage (Figure S7). The total predation rate significantly changed with ENL, but the direction in AM plots (decreasing;  $p=0.009$ ) was opposite to EcM plots (increasing;  $p=0.003$ ) (Figure 4e; Table S8). Still, the opposite trends were mainly attributed to the different

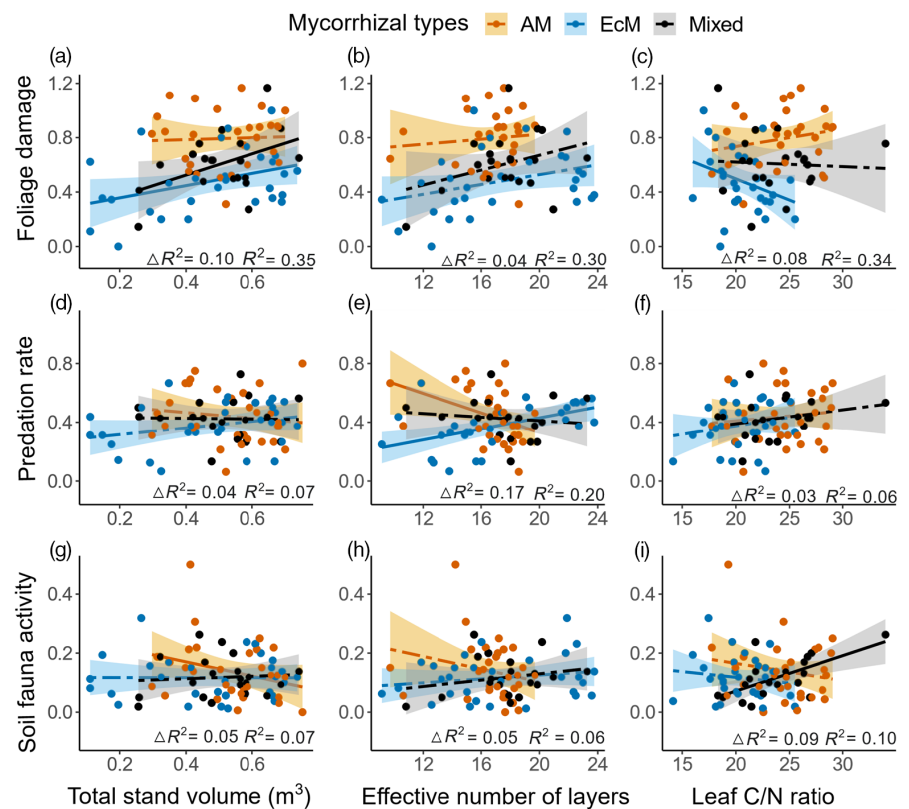


**FIGURE 2** The effect of tree species richness (2- and 4-species) on total predation rates (a), bird predation rates (b) and insect predation rates (c) in three levels of mycorrhizal type treatment. AM: plots only with AM-species, EcM: plots only with EcM-species, and Mixed: plots with equal proportions of both AM-species and EcM-species. The effect sizes (log-ratios—lnRR—between measurements of the function in polyculture and monoculture) that differ significantly from 0 are indicated by asterisks, \* $p \leq 0.05$ , \*\* $p \leq 0.01$ , and \*\*\* $p \leq 0.001$ . Different letters indicate significant differences amongst three levels of mycorrhizal type treatment with multiple comparison adjustments at  $p \leq 0.05$ , and the asterisks (\*\*) on a horizontal solid line indicate the significant difference in effect sizes between tree species richness.



**FIGURE 3** The effect of tree species richness (2- and 4-species) on soil fauna feeding activity in total soil depth (~0–10 cm) (a), the feeding activity in upper soil layer (b), and the feeding activity in lower soil layer (c) in three levels of mycorrhizal type treatment. AM: plots only with AM-species, EcM: plots only with EcM-species, and Mixed: plots with equal proportions of both AM-species and EcM-species. The effect sizes (log-ratios–InRR—between measurements of the function in polyculture and monoculture) significantly differing from 0 are indicated by asterisks, \* $p \leq 0.05$ , \*\* $p \leq 0.01$ , and \*\*\* $p \leq 0.001$ . Different letters indicate significant differences amongst three levels of mycorrhizal type treatment with multiple comparison adjustments at  $p \leq 0.05$ , and the asterisks “\*” on a horizontal solid line indicate the significant difference in effect sizes between tree species richness.

**FIGURE 4** Relationships between the multitrophic ecosystem functions and different facets of stand characteristics separated by mycorrhizal type treatment. Total foliage damage (a–c), total predation rate (d–f), and the soil fauna feeding activity in the total soil depth (~0–10 cm) (g–i) correlated with total stand volume, effective number of layers (ENL) and leaf C/N ratio, respectively. Significant correlations are indicated as solid lines and non-significant relationships as dashed lines, and the shaded area shows the 95% confidence interval.  $R^2$  indicates the variation in response variables (ecosystem functions) explained by both mycorrhizal types and the facets of stand characteristics, as well as their interactions.  $\Delta R^2$  indicates how much variation in each ecosystem function can be explained by the forest characteristics, in addition to the mycorrhizal type treatment.



responses of bird predation to ENL in AM plots (negative) and EcM plots (positive) (Figure S8). As for the soil fauna feeding activity, we found that the activity in the total soil depth decreased with total stand volume in AM plots ( $p = 0.038$ ) and increased with the leaf C/N ratio in Mixed plots ( $p = 0.019$ ) (Figure 4g,i; Table S8). The above-mentioned correlations were in line with the activity in the upper soil layer (Figure S9).

### 3.5 | Structural equation models on mediators of richness effects on ecosystem functions

Structural equation models (SEMs) showed that the tree species richness directly or indirectly determined the three multitrophic ecosystem functions, mediated by total stand volume (representing above-ground tree biomass), ENL (representing

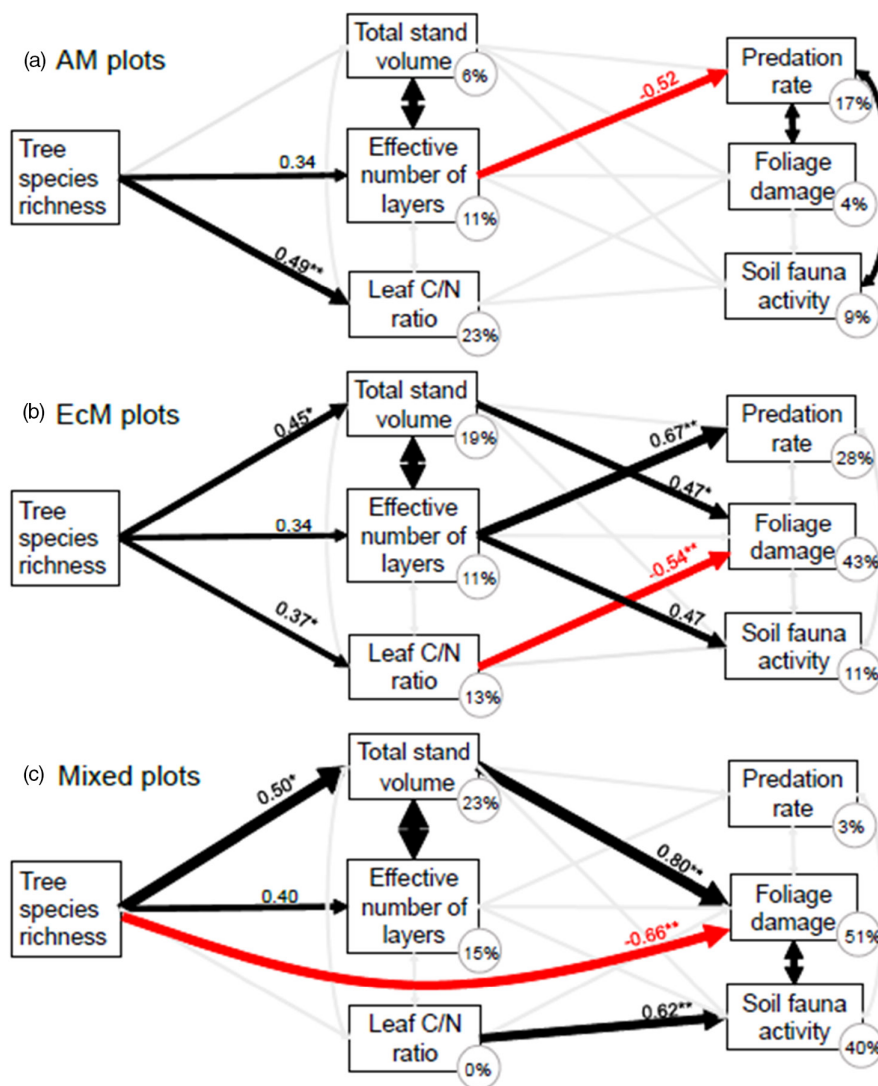


a stands' vertical structural complexity), and leaf C/N ratio (characterizing leaf quality) (Figure 5). More importantly, the mediating effects largely depended on the mycorrhizal types. In AM plots, tree species richness decreased the total predation by increasing ENL (Figure 5a; Table S9). The rest of the hypothesized paths between the mediators and the ecosystem functions in AM plots were nonsignificant. In EcM plots, tree species richness increased ENL that increased the predation rates and soil fauna feeding activity simultaneously (Figure 5b; Table S10). The total foliage damage significantly correlated with total stand volume (positively) and leaf C/N ratio (negatively), and both mediators increased with tree species richness in EcM plots. In Mixed plots, tree species richness increased only ENL and total stand volume, and only the latter positively correlated with foliage damage (Figure 5c; Table S11). However, the positive indirect effects of species richness ( $0.50 \times 0.80$ ) were weaker than the direct negative effects ( $-0.66$ ) on the foliage damage in Mixed plots. Moreover, foliage damage was significantly and positively correlated with the predation rates in AM plots, and

it correlated significantly with soil fauna feeding activity only in Mixed plots (positively) (Figure 5).

## 4 | DISCUSSION

Our study provides experimental evidence that mycorrhizal association is essential in shaping the relationship between tree species richness and multitrophic ecosystem functions. The results show that the expected tree species richness effects were only found in the tree communities comprising both mycorrhizal types, significantly decreasing foliage damage, and in the communities of ectomycorrhizal association, significantly increasing the predation rates, which is partially in line with our hypothesis (1). In contrast to this hypothesis, the effect of tree species richness on soil fauna feeding activity was significantly negative for the lower soil layer, but not for the upper soil layer and across the total soil depth ( $\sim 0$ – $10$  cm). Confirming our hypothesis (2), the treatment of mycorrhizal type largely shaped relationships between tree species richness and multitrophic ecosystem functions, by mediating the response to



**FIGURE 5** Structural equation models for the effects of tree species richness on three multitrophic ecosystem functions as mediated by stand characteristics (total stand volume, representing biomass effects; effective number of layers, representing vertical structural complexity effects; and leaf quality as represented by leaf C/N ratio) in three levels of mycorrhizal type treatment. Black arrows indicate significant and marginally significant positive ( $p \leq 0.10$ ) effects in the final models. Red arrows indicate significant and marginally significant negative ( $p \leq 0.10$ ) effects in the final model. Grey arrows indicate nonsignificant effects. Double-headed arrows show paths that were introduced as correlated errors. Standardized path coefficients are shown in red (negative) or black (positive) on top of the significant or marginally significant paths. Arrow width scales in relation to effect sizes. Global goodness of fit Fisher's  $C$  was 7.96 on 8 degrees of freedom in AM plots (a), 3.65 on 8 degrees of freedom in EcM plots (b), and 5.90 on 12 degrees of freedom in Mixed plots (c). For each endogenous variable (i.e. response variable), the part of variance explained (marginal  $R^2$ , in %) by fixed effects was added in the circles next to the variable box.

above-ground tree biomass, vertical structural complexity and leaf quality.

#### 4.1 | The effects of tree species richness and mycorrhizal types on multitrophic ecosystem functions

Tree species richness did not consistently promote the focal ecosystem functions. Rather, the richness effects largely depended on the treatment of mycorrhizal type and the feeding guilds. Only in the communities with both mycorrhizal types (Mixed plots), the richness effects were significantly negative, reducing foliage damage. In our study, mycorrhizal types diverged in the functional traits involved in defence and the recognition and exploitation by antagonists (Bennett & Bever, 2007; Bezemer & van Dam, 2005; Dreischhoff et al., 2020; Gehring & Bennett, 2009; Jung et al., 2012; Kaur et al., 2020; Strack et al., 2003; Tao et al., 2016). Thus, we speculate that in Mixed plots, EcM-species (on average less favoured by plant antagonists) could decrease the conspicuousness of AM-species to herbivores by creating physical and chemical barriers (i.e. *associational resistance*; Barbosa et al., 2009; Castagneyrol et al., 2014; Espelta et al., 2020; Jactel & Brockerhoff, 2007), potentially driving negative selection effects (Figure S6B; Cappelli et al., 2022). On the other hand, mixing AM-species and EcM-species did not promote predation rates; the richness effects on predation were only significantly positive in polycultures of EcM-species (increasing from 2- to 4-species). The promotion of predation did not necessarily link with tree species richness in all mycorrhizal types, which is in line with the inconsistent effects of tree species richness on predation shown by previous studies (Berezcki et al., 2015; Muiruri et al., 2016; Nell et al., 2018; Yang et al., 2018). The positive richness effects in EcM plots may have primarily resulted from complementarity effects (Figure S6C). Specifically, the broader spectrum of growth rates of species in EcM and Mixed plots (Dietrich et al., 2023) enabled an increase in canopy space partitioning with species richness, likely enhancing the detectability and accessibility of prey for birds. Nevertheless, the complementarity effects in Mixed plots may have been cancelled out by negative selection effects (Figure S6C,D). Still, our study suggests that to control tree antagonists, the type of mycorrhizal association is a promising characteristic for tree species selection in forestry.

Regarding the soil fauna feeding activity, richness effects were significantly negative in the lower soil layer, in all polyculture communities, but not in the total soil depth (~0–10 cm) or the upper soil layer. Our results of richness effects differ from those of Birkhofer et al. (2011) in grasslands across Germany, where legume and grass species richness increased the feeding activity because of elevated food resource availability. In our study, the contribution or impacts of above-ground food resources may have been reduced because of limited access to leaf litter by soil detritivores due to the weed tarp. However, Pollierer et al. (2007) and

Zhou et al. (2023) argued that in forests, roots play a more important role in supporting soil-dwelling fauna communities compared to leaf litter. Below-ground food resources, for example, adsorptive roots and rhizodeposits (Chen et al., 2016; Litton et al., 2007; Prada-Salcedo et al., 2021), may not differ so much in the upper soil layer between monoculture and polyculture communities. Furthermore, Bardgett et al. (2014) argued that the exploitation of nutrients and water from soil could increase with plant species richness. Indeed, recent results from the MyDiv experiment indicate that exploitation seems to be more efficient in EcM plots and Mixed plots, particularly for soil nitrate, during the vegetation period in 2020 (Bönisch et al., 2023). The relatively lower nutrient content and moisture in polyculture communities (Figure S14) potentially decreased soil fauna feeding activity in the lower soil layer (Sünnemann et al., 2021), and the negative richness effects even became stronger with the richness gradients in the EcM and Mixed plots (Figure 3c; Table S5). However, regarding the non-significant richness effects on soil fauna feeding activity across the total soil depth and upper soil layer, it is important to note that our study only encompassed three levels of tree species richness (1, 2, and 4), and the measurements were conducted over a 3-week period. Therefore, we should be cautious when generalizing these findings, as it is possible that a larger gradient of tree species richness and a longer monitoring duration may result in more pronounced richness effects on soil fauna feeding activity (Furey & Tilman, 2021; Yang et al., 2019).

#### 4.2 | Stand characteristics as mediators of ecosystem effects of tree species richness and mycorrhizal type

The total stand volume (representing above-ground tree biomass) and leaf C/N ratio (representing leaf quality) may explain why tree species richness effects on foliage damage only occurred in Mixed plots but not in AM or EcM plots. Firstly, tree species richness promoted the total stand volume, which may benefit generalist herbivores (e.g. chewers and hole-feeders) by increasing resource availability (Figure S5; Ali & Agrawal, 2012; Dietrich et al., 2023), thereby increasing the foliage damage, the relationship also observed by Schuldt et al. (2010). In Mixed plots, compared to the indirect effects (only mediated by total stand volume), tree species richness had rather strong negative direct effects on foliage damage. The direct effect suggests that, in future studies, we may need to consider additional mediators, for example, plant defence traits, chemical compounds and interspecific and/or intraspecific variations within stands (Des Roches et al., 2018; Mithöfer & Boland, 2012; Violle et al., 2012; Wang et al., 2020; Westerband et al., 2021), and quantify further nutrients, to explore whether the overall nutritional values of the diet for generalists was higher in the mixtures (i.e. *nutrient complementation hypothesis*; Bernays et al., 1994). On the other hand, it may be critical to explore species-specific effects, probably leading to the strong selection

effects (Figure S6B). For three AM-species (*A. pseudoplatanus*, *A. hippocastanum*, and *P. avium*) with elevated foliage damage in monocultures, damage significantly decreased by mixing with EcM-species (Figure S10), which likely contributed to the negative selection effects in Mixed plots. EcM-species also caused negative selection effects due to decreased damage for the species with higher monoculture damage (*B. pendula* and *T. platyphyllos*) and increased damage for the species with lower monoculture damage (*C. betulus* and *F. sylvatica*) (Cappelli et al., 2022), but simultaneously in both EcM and Mixed plots (Figure S10). Thus, we would argue that the significantly negative richness effects in Mixed plots may mainly be attributed to AM-species that benefited from being mixed with EcM-species rather than with other AM-species.

The vertical structural complexity, characterized by ENL and increasing with tree species richness, had contrasting effects: (1) it promoted predation rates in EcM plots, possibly explaining the significantly positive richness effects that strengthened with increasing tree species richness; (2) it decreased predation rates in AM plots, possibly explaining the significantly smaller richness effects compared to the EcM plots. In polycultures of EcM trees, the space close to the ground was efficiently occupied by slow-growing tree species (*F. sylvatica* and *Q. petraea*), and the top canopy was filled by the fast-growing species *B. pendula* (Figure S12.2). Consequently, canopies in the polyculture of EcM-species with a larger value of ENL were multi-layered but still open (Figure S13B) and increased the detectability of prey for insectivorous birds (Muiruri et al., 2016). In contrast, in AM plots, we found ENL only positively correlated with the mean of total stand volume but not with its standard deviation (Table S12); so, the larger numbers more likely indicate dense and thick-layered canopies (Figures S12.1 and S13A). The denser canopies in polycultures of AM-species in particular (Ray, Delory, et al., 2023) decreased the predation rates on *P. avium* and *S. aucuparia* (Figure S11; Nell & Mooney, 2019; Muiruri et al., 2016; Yang et al., 2018), likely resulting in the significantly negative selection effects (Figure S6D). The opposing responses of AM-species and EcM-species to ENL may explain (1) that the significant correlations did not occur in Mixed plots; (2) the positive complementarity effects (akin to EcM plots) and negative selection effects (resembling AM plots) simultaneously presented in Mixed plots (Figure S6C,D). In contrast to AM plots, species-specific responses to predation in Mixed plots were not statistically significant, likely due to limited sample sizes on each species. Future studies investigating the species-specific response to top-down control by predation, influenced by the diversity and mycorrhizal types of neighbouring trees, may benefit from increased per-species sample sizes within each plot. Nevertheless, the difference in vertical structural complexity between AM and EcM plots sheds light on the contrasting BEF relationships with regard to the top-down control of herbivores in forests. It also stresses the importance of considering three-dimensional vegetation structure to better understand the drivers of multitrophic communities (Schuldt et al., 2019) and ecosystem functions (Aikens et al., 2013; Muiruri et al., 2016; Williams et al., 2017).

Our results showed weak relationships between tree species richness and total soil fauna feeding activity (~0–10 cm) in all treatments of mycorrhizal types. Pollierer et al. (2021) and Birkhofer et al. (2011) suggested that the organic matter on bait laminas was mainly consumed by earthworms and collembolans. Their population was shown to be mainly driven by soil moisture and pH, as well as the nutrient content of the forest floor (Hopkin, 1997; Ilieva-Makulec et al., 2006; Schelfhout et al., 2017). However, we were only able to include above-ground variables as potential mechanisms in this study, and future studies should also consider changes in soil physicochemical conditions (Peng et al., 2022; Schelfhout et al., 2017), root traits (Prada-Salcedo et al., 2021; Wright et al., 2004), and nutrient-carbon trade between trees and mycorrhizae in our nitrogen-rich soil (Schwartz & Hoeksema, 1998).

Jointly analysing the different multitrophic ecosystem functions showed that their correlations differed across the mycorrhizal type treatments. Firstly, the significant correlations between foliage damage and predation rates (80% caused by birds) only occurred in AM plots but not in EcM or Mixed plots (Figure 5; Figure S15; Table S14). In AM plots with dense and thick-layered canopies (Figures S12.1 and S13A), birds might be limited in directly detecting prey in the dense canopy and might rather rely on leaf damage as a clue (Heinrich & Collins, 1983). Particularly when herbivory damage mainly was caused by generalists, they may not adopt strategies to minimize their apparent feeding damage on leaves (Stiegel et al., 2017) that attracted bird predators and drove the positive correlations. This speculation for AM plots may also serve to explain that foliage damage positively correlated with predation in monoculture plots with a homogenous stand structure (Figures S13 and S15; Table S13.1). Secondly, foliage damage positively correlated with soil fauna feeding activity only in Mixed plots but not in the plots with single mycorrhizal types (Figure 5). We speculate that the tree species in Mixed plots probably experienced less stress from competing for soil phosphorus (more limited than N at the MyDiv site; Ferlian et al., 2018) than in plots where all species were associated with the same mycorrhizal types and shared similar strategies to take up nutrients, particular for AM-species in AM plots (Altermann et al., 2005; Dietrich et al., 2023; Eisenhauer et al., 2022; Ferlian et al., 2018; Luo et al., 2023; Read, 1991; Yu et al., 2021). Under less stressed conditions, the tree species may benefit more from growing their adsorptive roots than trading with mycorrhizae (Schwartz & Hoeksema, 1998; Sterner & Elser, 2017). Likely, tree species in Mixed plots support higher rates of root proliferation as food sources for soil detritivores and higher above-ground biomass as a resource for herbivores. Noticeably, how EcM-species and AM-species respond to species richness and mycorrhizal types of their neighbours depends on the soil nutrition context, determining the intensity and nature of plant-mycorrhizal fungi symbiosis (Ma et al., 2023; Mao et al., 2019). Thus, the response of multitrophic ecosystem functions and their correlations to mycorrhizal types may vary in different environmental contexts. So, while our study showed that the mycorrhizal community indeed influenced the correlations between

multitrophic ecosystem functions, the relationships and underlying mechanisms need further exploration in the future.

### 4.3 | Conclusion and outlook

We conclude that mycorrhizal types play crucial roles in the relationship between tree diversity and multitrophic ecosystem functions. Furthermore, our study clearly indicates that (1) tree communities with both mycorrhizal types benefited from the difference between AM-species and EcM-species by decreasing the foliage damage; (2) AM-species and EcM-species differ in shaping the vertical structural complexity within a stand and further determine the efficiency of top-down control (predation rates) of herbivores. Additionally, we found evidence that mycorrhizal types may shape the correlations between multitrophic ecosystem functions. These findings suggest that future work should explore taxonomic groups at different trophic levels in more detail and quantify the biotic interactions amongst different groups, for example by determining energy fluxes in the food web (Barnes et al., 2018) and link above-below-ground food webs (Jochum & Eisenhauer, 2022). Energy flux analysis would allow investigating additional multitrophic ecosystem functions, such as below-ground herbivory and predation, in a common currency and facilitate multifunctionality analyses (Barnes et al., 2018). We note that we only assessed multitrophic ecosystem functions during peak animal activity time in this study, while future research may also explore their temporal dynamics across different seasons of the year (Bonato Asato et al., 2023; Sünemann et al., 2021; Thakur et al., 2018). Furthermore, our experimental sites represent typical temperate forest conditions characterized by a limited number of tree species; thus, for a more comprehensive and generalizable understanding, future research should explore how these findings of interacting effects of tree species richness and mycorrhizal type apply to other biomes with, for example warmer regions and larger tree species pools. We conclude that considering tree diversity and mycorrhizal associations is key to understanding multitrophic ecosystem functions, reconciling the previously observed contrasting relationships between biodiversity and ecosystem functions in forests, and designing multifunctional forests.

### AUTHOR CONTRIBUTIONS

Huimin Yi, Nico Eisenhauer and Olga Ferlian participated in designing this study. Jan Christoph Austen, Roberto Rebollo, Tama Ray, Elisabeth Bönisch, Goddert von Oheimb, Andreas Fichtner, collected and processed the data used in this study. For statistical analyses, Huimin Yi conducted all of the analysis in R with theoretical guidance from Nico Eisenhauer and Olga Ferlian; Andreas Schuldt and Guillaume Patoine provided very valuable suggestions for the analysis. Huimin Yi drafted the manuscript with substantial input from Olga Ferlian. Olga Ferlian is the coordinator of MyDiv and organized most of the data assessments. All authors read and approved the final manuscript.

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### CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

### PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14252>.

### DATA AVAILABILITY STATEMENT

All datasets are publicly available via MyDiv (<https://mydivdata.idiv.de>) with following DOIs: ID 120: multitrophic ecosystem functions: <https://doi.org/10.25829/H6M1-RW77> (Yi, Ferlian, et al., 2023a). ID 124: stand structural complexity; <https://doi.org/10.25829/58EF-HN10> (Ray, Fichtner, et al., 2023). ID 125: leaf nutrient quality; <https://doi.org/10.25829/MFDW-KW26> (Yi, Bönisch, et al., 2023). ID 126: total tree stand volume. <https://doi.org/10.25829/6QMG-QD35> (Yi, Ferlian, et al., 2023b). R script is publicly available at the following link: <https://doi.org/10.25829/M4CW-RX75> (Yi, 2023).

### ORCID

Huimin Yi  <https://orcid.org/0000-0003-1182-8092>

Nico Eisenhauer  <https://orcid.org/0000-0002-0371-6720>

Roberto Rebollo  <https://orcid.org/0000-0002-1129-0715>

Tama Ray  <https://orcid.org/0000-0001-9265-5431>

Elisabeth Bönisch  <https://orcid.org/0000-0001-9386-880X>

Goddert von Oheimb  <https://orcid.org/0000-0001-7408-425X>

Andreas Fichtner  <https://orcid.org/0000-0003-0499-4893>

Andreas Schuldt  <https://orcid.org/0000-0002-8761-0025>

Guillaume Patoine  <https://orcid.org/0000-0002-3748-6644>

Olga Ferlian  <https://orcid.org/0000-0002-2536-7592>



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## SUPPORTING INFORMATION

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

**Supplementary Method 1:** Selecting the mediating factors and their proxies.

**Figure S1:** Measurement design for the predation rates and the soil fauna feeding activity in core area of each plot.

**Figure S2:** Data distribution of foliage damage, predation rates, and soil fauna feeding activity in MyDiv.

**Figure S3:** Hypotheses driven framework of the direct and indirect drivers of multitrophic ecosystem functions in each level of mycorrhizal type treatment.

**Figure S4:** Relationships between three multitrophic ecosystem functions and different proxies for aboveground tree biomass in three levels of mycorrhizal type treatment.

**Figure S5:** Relationships between total stand volume (A), leaf C/N ratio (B) and effective number of layers (C) and tree species richness in three levels of mycorrhizal type treatment.

**Figure S6:** The complementarity effects and selection effects (2- and 4-species) on total foliage damage (A & B) and total predation rate (C & D) in three levels of mycorrhizal type treatment.

**Figure S7:** Relationships between the foliage damage and different facets of stand characteristics in three levels of mycorrhizal type treatment.

**Figure S8:** Relationships between the predation rate and different facets of stand characteristics in three levels of mycorrhizal type treatment.

**Figure S9:** Relationships between the soil fauna feeding activity and different facets of stand characteristics in three levels of mycorrhizal type treatment.

**Figure S10.1:** Relationship between total foliage damage of each species and tree species richness of each plot.

**Figure S10.2:** Effect sizes of tree species richness on total foliage damage of each species in three levels of mycorrhizal type treatment.

**Figure S11.1:** Relationship between total predation rate of each species and tree species richness of each plot.

**Figure S11.2:** Effect sizes of tree species richness on total predation rates of each species in three levels of mycorrhizal type treatment.

**Figure S12.1:** The distribution of basal diameter of AM-species in each AM-plot.

**Figure S12.2:** The distribution of basal diameter of EcM-species in each EcM-plot.

**Figure S12.3:** The distribution of basal diameter of AM-species and EcM-species in each Mixed-plot.

**Figure S13:** Examples of section images from laser scanner for AM-plots (A) and EcM-plots (B).

**Figure S14:** The comparison of soil water content amongst three levels of tree species richness.

**Figure S15:** Correlation matrices (with the method of 'spearman') among foliage damages, predation rates, and soil fauna feeding activity.

**Table S1:** The basic information for tree species in MyDiv (mean  $\pm$  SE).

**Table S2:** Summary for foliage damage, predation rate and soil fauna feeding activity (mean  $\pm$  SE) in MyDiv.

**Table S3:** Statistic summary for effect sizes on foliage damage (mean, 95% confidence interval, t-test, two-way ANOVA and pairwise comparison results).

**Table S4.1:** Statistic summary for effect sizes on predation rates (mean, 95% confidence interval, t-test, two-way ANOVA and pairwise comparison results).

**Table S4.2:** Statistic summary for effect sizes on the rate of non-attacked dummies by predators (mean, 95% confidence interval, t-test, two-way ANOVA and pairwise comparison results).

**Table S5.1:** Statistic summary for effect sizes on soil fauna feeding activity (mean, 95% confidence interval, t-test, two-way ANOVA and pairwise comparison results).

**Table S5.2:** Statistic summary for effect sizes on the rates of non-decomposed holes in bait laminas (mean, 95% confidence interval, t-test, two-way ANOVA and pairwise comparison results).

**Table S6.1:** Mixed effects models exploring bivariate relationship between nine multitrophic ecosystem functions and tree sizes (average tree diameter and basal area) and three levels of mycorrhizal type treatment in MyDiv.

**Table S6.2:** Mixed effects models exploring bivariate relationship between nine multitrophic ecosystem functions and tree sizes (total tree stand volume and total tree biomass) and three levels of mycorrhizal type treatment in MyDiv.



**Table S7:** Mixed effects models between three facets of stand characteristics and tree species richness within three levels of mycorrhizal type treatment in MyDiv.

**Table S8:** Mixed effects models exploring bivariate relationship between nine multitrophic ecosystem functions and three facets of stand characteristics and three levels of mycorrhizal type treatment in MyDiv.

**Table S9:** Summary for outputs from the structural equation model in AM plots.

**Table S10:** Summary for outputs from the structural equation model in EcM plots.

**Table S11:** Summary for outputs from the structural equation model in Mixed plots.

**Table S12:** Linear regression between effective number of layers and tree stand volume.

**Table S13.1:** Spearman rank correlation matrix for nine multitrophic ecosystem functions in monoculture plots.

**Table S13.2:** Spearman rank correlation matrix for nine multitrophic ecosystem functions in 2-species polyculture plots.

**Table S13.3:** Spearman rank correlation matrix for nine multitrophic ecosystem functions in 4-species polyculture plots.

**Table S14.1:** Spearman rank correlation matrix for nine multitrophic ecosystem functions in AM plots.

**Table S14.2:** Spearman rank correlation matrix for nine multitrophic ecosystem functions in EcM plots.

**Table S14.3:** Spearman rank correlation matrix for nine multitrophic ecosystem functions in Mixed plots.

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