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RESEARCH ARTICLE

Imprint of tree species mycorrhizal association on microbial-mediated enzyme activity and stoichiometry

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Abstract

1. Understanding the effects of tree species and their mycorrhizal association on soil processes is critical for predicting the ecosystem consequences of species shifts owing to global change and forest management decisions. While it is well established that forests dominated by different mycorrhizal types can vary in how they cycle carbon (C), nitrogen (N) and phosphorus (P), the degree to which these patterns are driven by microbial-mediated enzyme activity (EA) and ecoenzymatic stoichiometry (ES) remains elusive.
2. Here, we synthesized the effects of mycorrhizal association on seven soil enzymes involved in microbial C, N and P acquisition and ES using data from 56 peer-reviewed papers.
3. We found that relative to soil in ectomycorrhizal (EcM) trees, soil in arbuscular mycorrhizal (AM) trees exhibited greater activity of some C acquisition enzymes (e.g. beta-glucosidase; BG) and higher ecoenzymatic ratios of BG/NAG (N-acetyl-glucosaminidase) and BG/AP (acid phosphatase). These results supported that AM trees had rapid C and nutrient turnover rates, inorganic nutrient economics and high soil microbial C limitation. We also found evidence for an organic nutrient economy and greater soil microbial demand for nutrients in EcM trees compared to AM trees. In addition, the effect of mycorrhizal association on the activity of certain soil enzymes and enzymatic stoichiometry (i.e. BG and BG/NAG ratio) appeared to be associated with the differences in soil pH, phylogenetic group (i.e. conifers and broadleaves) and leaf habit (i.e. evergreen and deciduous) between AM and EcM trees.
4. The results from the global meta-analysis suggested that soil EA and ES appear to play critical roles in shaping the differences in the nutrient economy between AM

and EcM tree species, but leaf morphology and soil conditions should be considered in evaluations of soil processes in forests of different mycorrhizal associations. Given that most of the studies in the database were from the temperate and subtropical regions, further research in other biomes is needed to elucidate the underlying mechanisms driving the mycorrhizal effect at the global scale.

KEYWORDS
meta-analysis, microbial decomposition, nutrient economics, soil enzyme activity, substrate quality

1 | INTRODUCTION

The dominant mycorrhizal association (the relative abundance of trees associating with unique mycorrhizal groups) is often strongly linked to plant and microbial effects on soil biogeochemistry (C and nutrient cycling) in forests (Phillips et al., 2013; Read, 1991; Tedersoo & Bahram, 2019; van der Heijden et al., 2015). As such, understanding the relationships between tree mycorrhizal dominance and microbial-mediated soil processes will be critical for predicting ecosystem dynamics in the wake of global environmental changes (Bahram et al., 2020). Arbuscular mycorrhizal fungi (AM) and ectomycorrhizal fungi (EcM) are two dominant classes of mycorrhizal fungi that form symbioses with roots of certain trees—exchanging C for nutrients and water, and protecting trees against environmental stress (Brundrett & Tedersoo, 2018). Tree species associated with AM and EcM fungi differ in many nutrient use traits (e.g. foliar chemistry, resorption efficiency, litter quality, root and mycelium traits etc.), which in turn affect ecosystem C and nutrient cycling (Bahram et al., 2020; Phillips et al., 2013; Tedersoo & Bahram, 2019). Generally, AM tree species have higher litter quality, faster litter decomposition rates, lower forest floor C stocks and lower soil C/N ratios compared EcM tree species (Craig et al., 2018; Jo et al., 2019; Lin et al., 2017; Peng et al., 2020). The mycorrhizal-associated nutrient economy (MANE) framework suggested that AM trees are associated with an inorganic nutrient economy characterized by rapid nutrient cycling, whereas EcM trees are associated with an organic nutrient economy characterized by a slow turnover of plant-derived C and enhanced root–microbe couplings (Phillips et al., 2013). Differences in mycorrhizal types also coincide with marked differences in soil microbial growth rate, activity and microbiome structure and function (Bahram et al., 2020; Cheeke et al., 2017; Heděnec et al., 2020), which can alter the turnover and stocks of soil organic carbon (SOC) and nutrients (Lin et al., 2017). Still, the global patterns of AM-EcM differences in soil enzyme activity (EA) and ecoenzymatic stoichiometry (ES) and how the patterns of C and nutrient cycling are driven by EA and ES remain unclear.

Soil hydrolases and oxidases play important roles in microbial decomposition and stabilization of soil organic matter (SOM; Burns et al., 2013; Sinsabaugh, 2010). The commonly measured enzymatic activities (EAs), such as β-1,4-glucosidase (BG), β-1,4-N-acetylglucosaminidase (NAG) and acid (alkaline) phosphatase (AP), have been interpreted as microbial resource allocation to the acquisition of C, N and P respectively (Sinsabaugh et al., 2008; Sinsabaugh & Follstad Shah, 2012). Soil EAs might be affected by mycorrhizal types with different quantities and quality in substrates since microbes can trigger specific acquisition strategies (i.e. via their production of C vs. N acquisition enzymes) to cope with their resource limitation (Cheeke et al., 2017; Phillips et al., 2013). Therefore, the enzymatic composition is thought to capture the microbial carbon and nutrient economy (Moorhead et al., 2013; Sinsabaugh et al., 1993). Moreover, in the ecoenzymatic stoichiometry (ES) theory, the ratios of BG/(LAP+NAG), BG/AP and (LAP+NAG)/AP may indicate the relative microbial C versus N limitation, microbial C versus P limitation and microbial N versus P limitation respectively (Sinsabaugh et al., 2009; Sinsabaugh & Follstad Shah, 2012). The effects of mycorrhizal types on soil EAs and ES have been studied for decades, but no consistent pattern has been found across individual studies. For example, in a plantation study, Midgley and Sims (2020) reported that BG and oxidative EAs did not differ between AM and EcM plots, while NAG and AP activities were higher in EcM plots than AM plots. However, higher BG activity in AM forests than in EcM forests has also been reported (Midgley & Phillips, 2016; Ushio et al., 2010). The variation in reported EA units (e.g. reacted substrate per gram soil per hour or reacted substrate per gram C per hour) may have obscured the effect of mycorrhizal association on enzyme activity across studies (Midgley & Sims, 2020). In addition, the effects of mycorrhizal association on soil EAs and related processes may be context-dependent and may differ across biomes and along climate and soil gradients (Tedersoo & Bahram, 2019). In addition, the effects of mycorrhizal association on soil EAs and related processes may be context dependent and may differ across biomes and along climate and soil gradients (Tedersoo & Bahram, 2019). For instance, Steidinger et al. (2019) found that large-scale variation in the dominance of mycorrhizal associations changes along climate gradients, with greater AM tree dominance at low latitudes and greater ECM tree dominance at high latitudes. This suggests that climate condition is paramount for mediating mycorrhizal status and associated soil biogeochemistry. Therefore, quantitative estimation of mycorrhizal association effects on soil EA and ES at a larger scale is needed to unravel general patterns and inconsistencies. Lastly, given that trees might differ in both mycorrhizal type and phylogeny (i.e. broadleaves vs. conifers), it is also

critical to evaluate whether and how mycorrhizal type and phylogenetic group jointly affect EA and ES at the global scale.

Because of the increasing number of investigations of soil enzyme activity in the last decades, it has become possible to use a meta-analysis approach to synthesize how microbial-mediated EA and ES drive the C and nutrient cycling in tree species with different mycorrhizal associations at the global scale. In this study, we comprehensively reviewed previously published articles and conducted a quantitative synthesis to elucidate how soil EA and ES drive tree species mycorrhizal association on soil C and nutrient economies, and how the effects of tree species mycorrhizal association are modulated by soil physicochemical characteristics, geographical location, climate, leaf habit and phylogenetic group. Given that soils under AM trees generally have low C/nutrient ratios and higher nutrient availability (e.g. abundant in inorganic N; Smith & Smith, 2011; van der Heijden et al., 2015), we hypothesized that (H1) soil microbes in AM trees would be more C-limited than nutrient-limited as reflected by higher C acquiring EA and higher ratios of BG/NAG and BG/AP than in EcM trees. However, EcM trees were suggested to have organic nutrient economies due to high soil C/nutrient ratios and the high capability of ectomycorrhizal and saprotrophic fungi to utilize organic compounds in EcM trees (Phillips et al., 2013). Thus, we also hypothesized that (H2) soils under EcM trees would have higher microbial nutrient limitation with higher activities of N- and P-acquiring enzymes and oxidases and lower ratios of BG/NAG and BG/AP than in AM trees. In addition, we hypothesized that (H3) the mycorrhizal effects would be stronger in colder regions and more acid and nutrient-poor soils. Lastly, we hypothesized that (H4) the mycorrhizal effects would be affected by the differences/similarities in phylogenetic group and leaf habit between AM and EcM trees.

2 | MATERIALS AND METHODS

2.1 | Data collection and compilation

We searched for peer-reviewed journal articles on the topic of tree species and soil enzyme activity spanning 1970–2021 using the Web of Science (http://apps.webofknowledge.com/) and the China National Knowledge Infrastructure Database (CNKI; http://www.cnki.net/). The following terms were used in English and Chinese (for CNKI) for the search: (Mycorrhizal* OR "tree species" OR plantation* OR afforestation) AND (enzyme*). The gathered publications were further screened based on four criteria: (1) co-occurring AM and ECM forests must grow on the same site with similar edaphic and climatic conditions; (2) AM and ECM forests must be of the same age, and at least 10 years old; (3) field studies must have been conducted in monoculture stands (i.e. composed by a single tree species) or natural forests (coverage of dominant species >75% or the author clarified the dominant mycorrhizal types); and (4) at least one of the enzymes listed in Table 1 must be reported.

A total of 56 studies containing 286 paired observations were identified (Figure 1, Zheng et al., 2023). We first extracted the data of various soil enzymes, including BG, invertase (INV), NAG, urease (URE), AP, PPO and POD (Table 1) as they release C or nutrients from organic compounds. Data were directly obtained from tables or extracted from figures using GetData (version 2.25). We also contacted the corresponding authors, if the original enzyme data were not reported. The classification of mycorrhizal fungal types was based on the newly published database (Soudzilovskaia et al., 2020) and was confirmed by using the diagnosed database from previous studies (Brundrett & Tedersoo, 2019, 2020; Tedersoo & Brundrett, 2017). To determine deciduousness (i.e. evergreen or deciduous) and phylogeny (broadleaf or conifer) of each tree species, we extracted directly from the literature if available or searched the relevant database (i.e. *Flora Reipublicae Popularis Sinicae* and *The World Flora*) that reported such information. The enzymatic ratios BG/NAG, BG/AP and NAG/AP were calculated to indicate C/N, C/P and N/P demand of the microbes respectively. The enzymatic ratios were only calculated if the enzyme measurements were based on the same colorimetric substrates (e.g. *p*-nitrophenol [*p*NP]) or fluorescent substrates (i.e. 4-methylumbelliferone [MUB]). Apart from soil enzyme activity, soil physicochemical properties (e.g. soil pH, soil organic C and C/N) in the same layer were also collected. Furthermore, site-specific information has also been collected, including geophysical variables (latitude, longitude and altitude), climatic variables (mean annual temperature (MAT), mean annual precipitation (MAP)), Latin names of tree species, forest stand age and soil depth sampled for EA analysis. If the MAT and MAP were not directly provided from the papers, the site information (latitude and longitude) was employed to extract them from a global database (http://www.worldclim.org/).

TABLE 1 Soil enzymes included in the study.

Enzymes and abbreviations	Catalysed reaction	Indicator of microbial activity
β-1,4-glucosidase (BG)	Hydrolysis of cellobiose to glucose	C-acquisition
Invertase (INV)	Hydrolysis of sucrose to D-glucose and D-fructose	C-acquisition
β-1,4-N-acetyl-glucosaminidase (NAG)	Hydrolysis of chitin to acetyl glucosamine	N-acquisition
Urease (URE)	Hydrolysis of urea to CO_2 and NH_3	N-acquisition
Acid (alkaline) phosphatase (AP)	Hydrolysis of phosphate esters to inorganic phosphorus	P-acquisition
Polyphenol oxidase (PPO)	Depolymerization of lignin and phenolics	Complex compounds and SOM decomposition
Peroxidase (POD)	Depolymerization of lignin and phenolics	Complex compounds and SOM decomposition

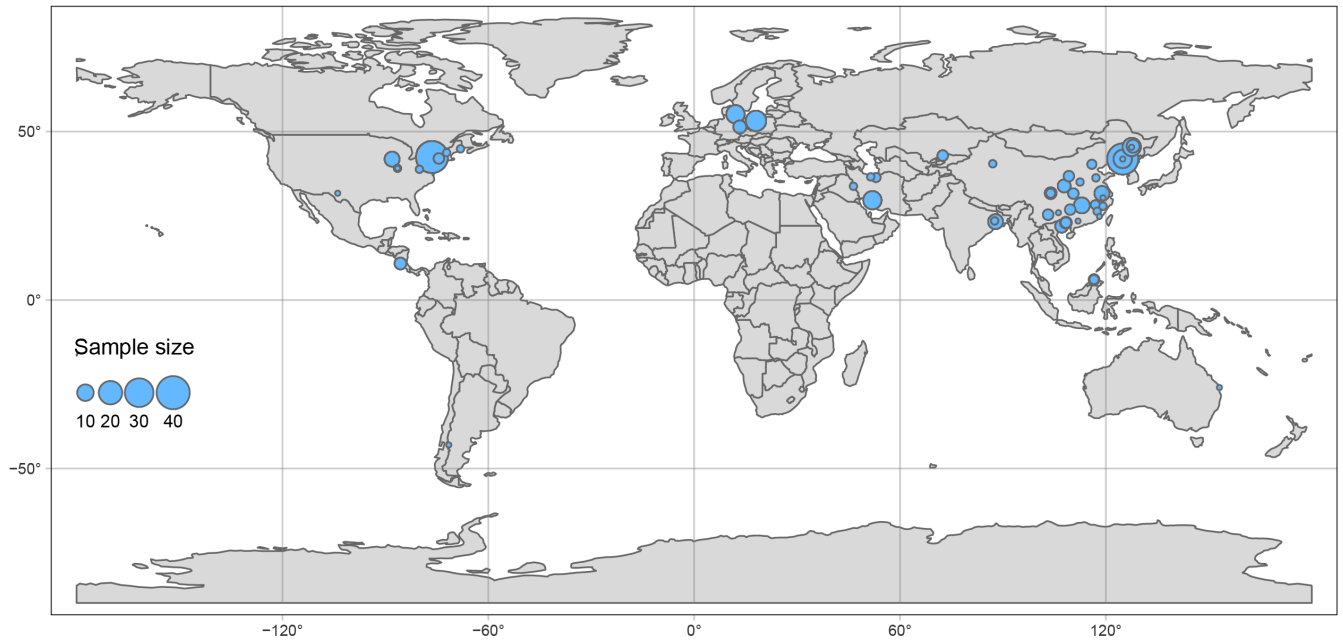

FIGURE 1 Map showing the location of the study sites from the compiled articles used in this meta-analysis. The number of pairwise observations from each site is represented by symbol size.

2.2 | Data analysis

We quantified the effect of mycorrhizal association on soil EA, ES and soil physicochemical properties by calculating the natural log of the adjusted response ratio (RR; Gurevitch et al., 2018; Hedges et al., 1999):

$$RR = \ln\left(\frac{\overline{X}_{AM}}{\overline{X}_{EcM}}\right), \quad (1)$$

where RR is the log transformed response ratio of the mean value of the chosen variable in the AM type group $(\overline{X}_{AM})$ to that in the EcM group $(\overline{X}_{EcM})$, which is an index of the effect of the mycorrhizal type on the target variable. Positive log response ratios indicated that AM trees had higher target variable values than EcM trees and vice versa. For the studies that had more than 1 AM or EcM tree species, we conducted meta-analyses using data from cross-paired plots within a study (e.g. 1 AM species and two ECM species in a common garden, would mean two effect sizes). Studies from common gardens and other forest sites were analysed together since stand type had no significant effects on the RR of soil EA and ES (Figure S1). The weighting factor (w) for each RR was calculated as Equation 2 (Adams et al., 1997; Bakbergenuly et al., 2020):

$$w = \frac{n_{AM} * n_{EcM}}{n_{AM} + n_{EcM}}, \quad (2)$$

where n_{AM} and n_{EcM} are the sample sizes in the AM and EcM plots respectively.

To conduct our meta-analyses, we initially ran intercept-only models to calculate the overall effect sizes (RR) with the 'lmer' function in the R package NLME. These intercept-only models fitted RR as the response variable and included 'study' as a random factor given that calculating effect sizes of all possible pairs from a single site may be non-independent. In addition, we conducted a conservative meta-analysis by using the mean values from sites with more than 1 AM or EcM tree species. The results of the conservative meta-analysis showed a consistent pattern as the results from the linear mixed model (Figure 2 and Figure S2A), which indicated that there was no issue of non-independence. Meta-regression models, which included fixed effects, were then run to explore the effects of geographic location, climate, soil depth and forest stand age, average soil pH and average soil C/N (in each AM-EcM comparison) on RR by fitting these variables as fixed factors (with the 'lmer' function). The effect of the phylogenetic group (i.e. coniferous vs. broadleaves) and leaf habit (i.e. deciduous vs. evergreen) in each AM-EcM comparison on RR of EA and ES was also tested. If the 95% CIs of RR did not overlap zero, the effects were considered to be significant at $\alpha = 0.05$ for mycorrhizal association. In addition, we tested whether the RR values of individual EA and ES were significantly related to soil physicochemical properties by regression and correlation analyses. All statistical analyses were performed in R (version 3.6.0; R Core Team, 2018).

3 | RESULTS

3.1 | Effects of mycorrhizal type on soil enzyme activity, ecoenzymatic stoichiometry and soil physicochemical property

AM forests had higher activity of BG and URE, and higher ratios of BG/NAG and BG/AP, but lower PPO activities than EcM forests (Figure 2a). There were no significant differences in activities of

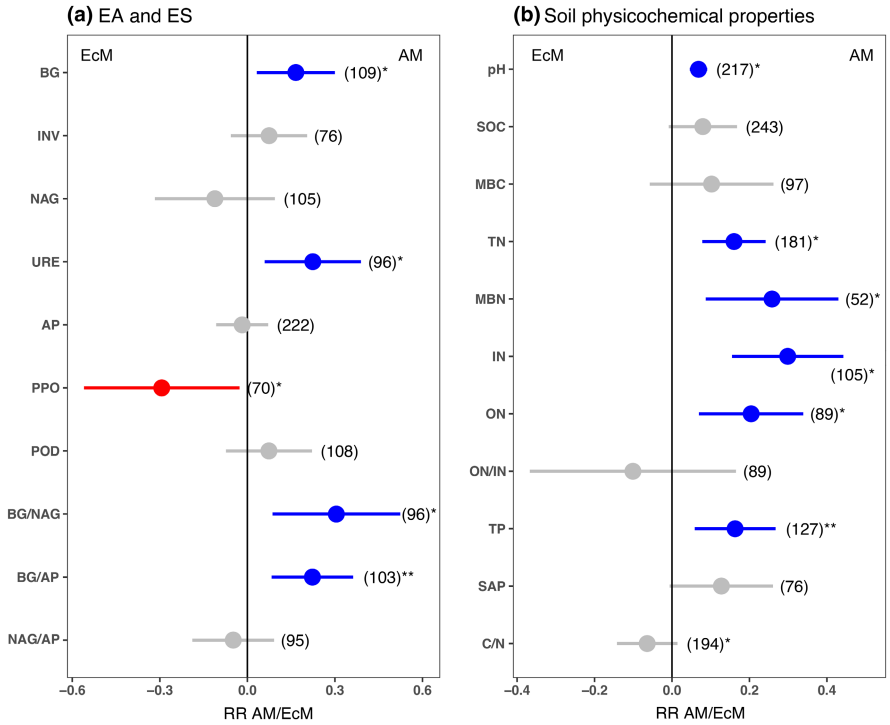

FIGURE 2 Mean and 95% CI of log response ratio (RR) of soil enzyme activity (EA) and enzymatic stoichiometry (ES) (a) and soil physicochemical properties (b). RR > 0 indicates higher values in AM trees than EcM trees (blue line/dot); RR < 0 indicated lower values in AM trees than EcM trees (red line/dot); the difference is considered non-significant if the CI overlaps with zero (grey line/dot). The numbers of pairs and significant levels are shown with the lines (*$p < 0.05$ and **$p < 0.01$). Enzyme abbreviations are given in Table 1. SOC, soil organic carbon; MBC, microbial biomass carbon; TN, total nitrogen; IN, inorganic nitrogen; ON, organic nitrogen; TP, total phosphorus; SAP, soil available phosphorus.

TABLE 2 The effects of geographic location, climate, sampled soil depth and forest stand age on the natural log response ratios (RR) of enzyme activity and stoichiometry generated from linear mixed models by adding each variable as the fixed effect and 'study' as a random effect.

		Altitude	Latitude	MAT	MAP	Soil depth		Stand age
Variables	***n***	***p***	***p***	***p***	***p***	***p***	***n***	***p***
BG	105	(−) 0.741	(+) 0.461	(−) 0.412	(−) 0.116	(−) 0.833	54	(+) 0.583
INV	76	(+) 0.801	(+) 0.235	(−) 0.468	(−) 0.06	(+) 0.549	36	(+) 0.256
NAG	100	(+) 0.848	(−) 0.63	(+) 0.659	(−) 0.963	(+) 0.186	48	(−) 0.399
URE	96	(−) 0.431	(+) **0.008**	(−) **0.013**	(−) **0.007**	(+) 0.532	44	(+) 0.782
AP	218	(+) 0.253	(−) 0.252	(+) 0.158	(+) 0.366	(−) 0.862	128	(−) 0.277
PPO	68	(−) 0.063	(+) **0.01**	(−) **0.009**	(−) **0.033**	(+) 0.24	40	(+) 0.212
POD	104	(+) 0.561	(−) 0.882	(−) 0.674	(+) 0.265	(−) 0.136	36	(−) 0.138
BG/NAG	91	(−) 0.498	(+) 0.724	(−) 0.821	(−) 0.408	(−) 0.066	48	(+) 0.183
BG/AP	99	(−) 0.141	(+) 0.267	(−) 0.337	(−) 0.08	(−) 0.618	48	(+) 0.631
NAG/AP	90	(−) 0.263	(+) 0.876	(−) 0.816	(−) 0.94	(+) 0.369	42	(−) 0.427

Note: Direction of the estimates (in parentheses) and *p*-values are shown, and values in bold indicate statistical significance ($p < 0.05$). Enzyme abbreviations are given in Table 1.

Abbreviations: MAP, mean annual precipitation; MAT, mean annual temperature.

INV, NAG, AP and POD between AM and EcM forests (Figure 2a). However, when EA was expressed per unit soil organic carbon (SOC), certain EA response ratios increased in significance while others lost significance. The SOC-specific EAs of NAG, AP and PPO were higher in EcM forests than in AM forests (Figure S1). For soil physicochemical properties, AM tree species had higher pH, SOC, TN, MBN, IN, ON and TP than EcM tree species (Figure 2b). In addition, the ON/IN and C/N ratios tended to be higher in EcM tree species than in AM tree species (Figure 2b).

3.2 | Moderating effect of environmental context

Meta-regressions revealed that the potential contextual moderator variables such as latitude, MAT and MAP only in a few cases were related to EA and ES. Latitude was positively related to the response ratio of URE and POD activity, while MAT and MAP were negatively related to the response ratio of URE and POD activity. The effects of mycorrhizal association on the activity of the remaining enzymes were not significantly mediated by the selected moderator variables (Table 2).

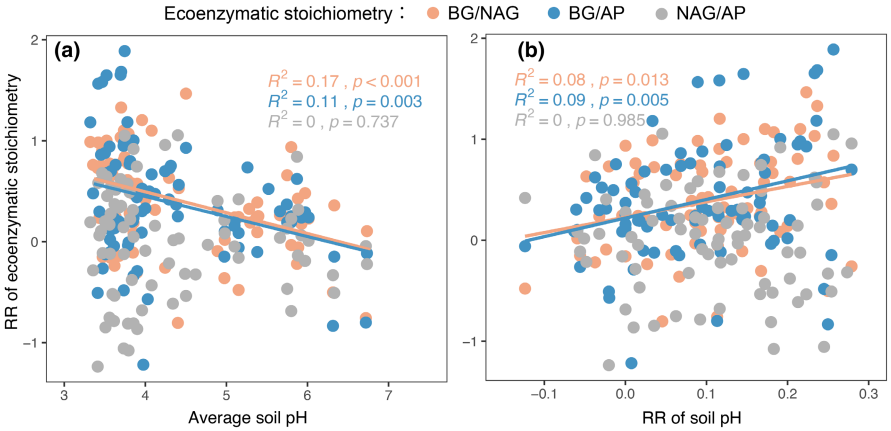

FIGURE 3 Relationships of response ratio (RR) of ecoenzymatic stoichiometry with average soil pH between AM and EcM trees (a) and with RR of soil pH (b). RR > 0 indicate higher values in AM trees than EcM trees.

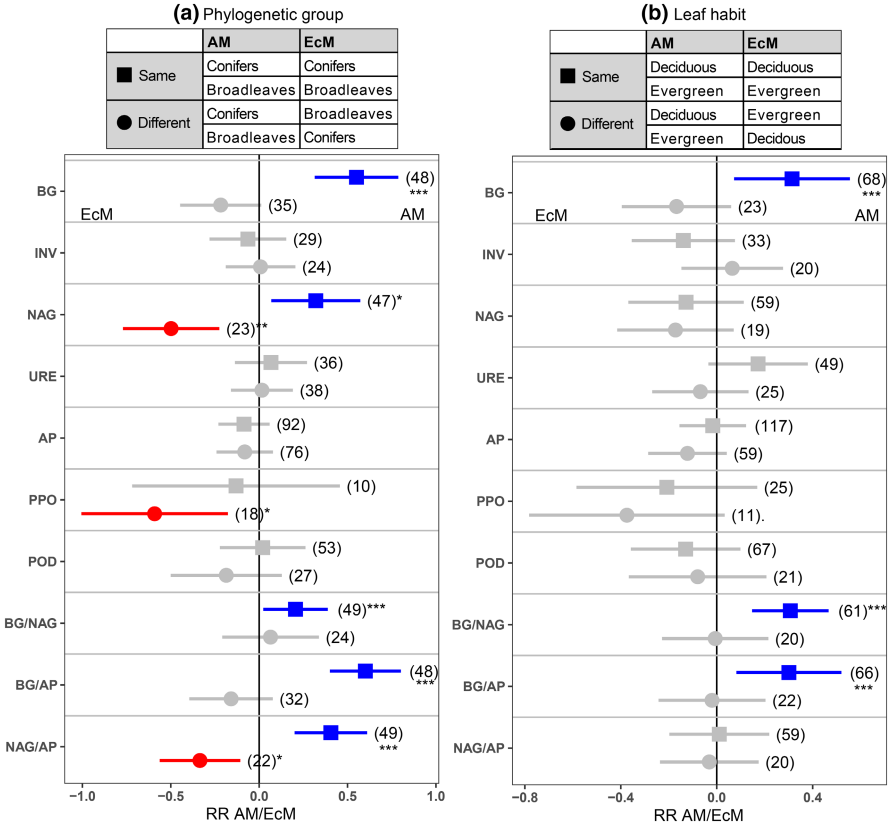

FIGURE 4 The effects of phylogenetic group (conifers/broadleaves) and leaf habit (deciduous/evergreen) of compared AM and EcM trees on the response ratios (RR) of enzyme activity and ecoenzymatic stoichiometry. Comparison of enzyme activity in AM and EcM trees within the same (squares) or across (circles) phylogenic group (a) and within (squares) or across (circles) the same leaf habits (b). The numbers of pairs and significant levels are shown with the lines (*p < 0.05, **p < 0.01 and ***p < 0.001). Enzyme abbreviations are given in Table 1.

The response ratios of BG/NAG and BG/AP ratios were negatively correlated with the average soil pH of AM and EcM forests (Figure 3a), indicating that the effects of mycorrhizal association on these ratios were stronger in more acid soils. However, the response ratios of BG/NAG and BG/AP were positively correlated with the response ratio of soil pH (Figure 3b). In addition, we found that the response ratio of EA correlated with the AM-ECM differences in soil pH, SOC, TN, IN and TP (Figure S3). These results suggested that differences in soil pH and substrate quality are important factors driving the mycorrhizal effect on EA and ES.

The effects of mycorrhizal association on BG activity and enzyme ratios BG/NAG and BG/AP tended to be stronger when the AM and EcM forests were compared within the same phylogenetic group (i.e. conifers or broadleaves) and within the same leaf habit (i.e. deciduous or evergreen). The positive response ratio for NAG and the NAG/AP ratio were observed when the AM and EcM forests were compared within the same phylogenetic group (i.e. conifers or broadleaves), while the negative response ratio for NAG and the NAG/AP ratio were observed when the AM and EcM forests were compared across the phylogenetic group (Figure 4).

4 | DISCUSSION

4.1 | Effect of mycorrhizal association on belowground carbon and nutrient economies

The various traits of tree species with different mycorrhizal associations have been reported to affect the strategies for plant nutrient acquisition (Phillips et al., 2013). This may in turn change microbial resource allocation to enzyme production involved in C and nutrient acquisition. The results supported our hypothesis (H1) that BG activity and ratios of BG/NAG and BG/AP were higher in AM soils than EcM soils. AM tree species can more quickly allocate C into the rhizosphere via root exudation compared to their EcM counterparts (Frey, 2019; Jeewani et al., 2021; Kaiser et al., 2015), which may stimulate microbial growth and BG activities in the soils of AM trees (Toljander et al., 2007). Indeed, in line with findings in the previous review, synthesis and observational studies (Craig et al., 2018; Lin et al., 2017; Peng et al., 2020; Prescott & Vesterdal, 2021), we found that AM soils had higher microbial biomass C and SOC than in EcM soils (Figure 2b), although forest floor under EcM trees can have higher C stocks than under AM trees. This could be due to EcM-saprotroph competition and recalcitrant foliar litter (Averill & Hawkes, 2016; Soudzilovskaia et al., 2015). Moreover, litter decomposition rates and soil fauna abundance beneath AM trees were higher than beneath EcM trees (Lin et al., 2017; Midgley et al., 2015; Peng et al., 2022), which in turn hastens C and nutrient turnover and supports a higher C accumulation in topsoil by facilitating mineral-associated organic matter formation under AM forest (Cotrufo et al., 2013; Lin et al., 2017; Zheng et al., 2022). According to the ecoenzymatic theory (Sinsabaugh & Follstad Shah, 2012), the higher ratios of BG/NAG and BG/AP in AM tree species (Figure 2a) suggest higher microbial C limitation in comparison with EcM tree species. This result was in line with the higher N and P contents in AM soil, while C/N ratios tended to be higher in EcM soils (Figure 2b). Lastly, our results showed that AM soils also had higher urease activity and inorganic nutrient concentrations than EcM soils, which also support the MANE framework that AM trees are dominated by an inorganic nutrient economy with higher nitrification rates and nitrate leaching than in EcM trees (Lin et al., 2017; Phillips et al., 2013). Thus, our findings supported that AM trees had rapid C and nutrient turnover rates, inorganic nutrient economies and high soil microbial C limitation.

We hypothesized (H2) that EcM soils would have greater activities of enzymes involved in nutrient acquisition owing to reports of more recalcitrant and nutrient-poor litter inputs in EcM tree species (Frey, 2019; Vesterdal et al., 2013). We found partial support for this hypothesis. SOC-specific NAG and AP activities were higher in EcM than AM soils (Figure S2B). This was consistent with a recent study reporting that EA involved in N and P acquisition positively correlated with the proportion of ECM trees in a natural gradient in AM versus EcM dominance (Cheeke et al., 2017). Moreover, EcM soils had lower BG/NAG and BG/AP ratios—both indicators of greater microbial N and P demand in EcM soils. Lastly, EcM soils also had greater PPO activities. Given that organic matter oxidized by PPO often contains N (e.g. protein–phenol complexes), this too may indicate greater microbial N demand in ECM soils. This result is also in accordance with lower soil pH and relatively higher soil C/N ratio and ON/IN ratio in EcM forests (Figure 2b), as more acid soil and recalcitrant and N-poor substrates in ECM tree species may favour fungal rather than bacterial growth and oxidative enzyme production (Heděnec et al., 2020; Rousk et al., 2009).

The idea of less microbial N and P demand in AM forests is often attributed to the inorganic nutrient economy with rapid nutrient cycling supported by high quality leaf litter, whereas EcM forests are associated with an organic nutrient economy characterized by slower turnover of plant-derived C, nutrient immobilization and enhanced root couplings (Phillips et al., 2013). Much of the N and P in forest soils is immobilized in SOM and this N and P must be depolymerized by soil extracellular enzymes before it can be utilized by microbes or plants (Schimel & Bennett, 2004). EcM soils have demonstrated greater enzymatic capabilities to mine SOM for N and P compared to AM forests in which AM fungi mainly scavenge for inorganic N and P forms (Phillips et al., 2013; Read & Perez-Moreno, 2003; Rosling et al., 2016). Moreover, saprotrophic fungi in EcM soils may be more N-limited than in AM soils due to the competition between ectomycorrhizal fungi and saprotrophic decomposers (Gadgil & Gadgil, 1975), which can stimulate fungi to produce more N-acquiring enzymes (e.g. NAG) in EcM soils. In addition, root exudation, especially of oxalate that stimulates the lignin-degrading enzyme activities, tended to be higher in EcM than in AM tree species (Yin et al., 2014). Indeed, our results indicated that microbes in EcM soils invest more resources to acquire nutrients (i.e. N and P) than in AM soils (Figure 2a and Figure S1). Therefore, our findings support the organic nutrient economy and high nutrient limitation in EcM tree species.

4.2 | Factors modulating AM-EcM enzyme differences

The effect of mycorrhizal associations may be confounded with tree phylogeny, leaf habit, edaphic and climatic conditions (Dickie et al., 2013, 2014). Here, we tested how the effect of mycorrhizal associations is related to tree phylogeny, leaf traits and edaphic and climatic conditions. The results showed positive relationships between the AM-ECM differences in pH and the corresponding AM-ECM differences in BG/NAG and BG/AP ratios, which suggest that differences in soil pH played an important role in driving mycorrhizal effects on soil EA and ES. Soil pH can affect enzyme activity by influencing the formation of the enzyme, and the ionization and solubility of substrates and co-factors (Tabatabai, 1994; Turner, 2010). Soils with low pH are generally considered relatively C and nutrient limited for microbial growth, which is probably related to high-density carboxyl and phenolic groups that dissociate to release H^+ ions (Adeleke et al., 2017). In particular, P is less biologically available in low pH soils (Carrino-Kyker et al., 2016), whereas aluminium is mobilized

below pH 5 and geochemically binds inorganic P (Goldberg et al., 2020). Indeed, we found that soil microorganisms produced more AP to acquire P in EcM forests characterized by lower soil pH and lower available P (Figure 2a and Figure S2B). Similarly, soil N availability has been shown to be regulated by soil pH. Consistent with previous studies (Midgley & Phillips, 2016; Phillips et al., 2013), EcM forests had lower soil pH and inorganic N concentrations (Figure 2b) but greater soil N acquiring enzyme activity than soil in AM forest (Figure 2a and Figure S2B). In addition, our results showed that the mycorrhizal effect on BG/NAG and BG/AP ratios tended to be less pronounced in sites with soils that have higher pH. Our results are in line with a study conducted in a high pH site (pH 6–8; Midgley & Sims, 2020), reporting that the activities of microbial C-acquiring enzymes (BG) showed no significant difference among soils in AM and EcM trees. At some high soil pH sites, ammonium concentration and nitrification rates in EcM soils were higher or showed no difference compared to AM soils (Chen et al., 2018; Craig et al., 2019), which suggests that mycorrhizal association has a less pronounced effect on nutrient cycling in high pH soils, where substrate and nutrient availability is high. The significant relationships between the AM-ECM differences in pH and SOC with the AM-ECM differences in enzyme activities (Figure S3) also provide compelling support that soil physicochemical properties (i.e. pH and SOC contents) are important factors regulating the mycorrhizal effects on enzyme activity. In short, mycorrhizal effects are modulated by soil and site conditions, and inherent soil pH may be a particularly important factor mediating C and nutrient cycling.

We found that the mycorrhizal effect on BG activity and the ratios of BG/NAG and BG/AP tended to be stronger within the same phylogenetic group (conifers or broadleaves) and same leaf habit (deciduous or evergreen), respectively, than across these tree species groups. This result suggests that the phylogenetic group and leaf habit affect the mycorrhizal effect on EA and ES, and that the effects of the phylogenetic group and leaf habit may overshadow the effect of mycorrhizal associations. Moreover, we found that NAG and PPO activities and the NAG/AP ratio were higher in EcM trees than in AM trees, when AM and EcM trees are compared across both phylogenetic groups, and in this case, it is impossible to tell if it is an effect of mycorrhizal association or phylogeny. Disentangling phylogenetic, leaf habit and mycorrhizal association effects is particularly difficult in soil biogeochemistry studies. The classification schemes (i.e. according to leaf morphology and mycorrhizal associations) can directly lead to differences in leaf and root chemical properties among tree species, which in turn result in differences in soil biogeochemistry. Compared to evergreen (or coniferous) forests, deciduous (or broadleaved) forests have lower N use efficiency and higher litter decomposition rates due to higher litter quality (e.g. lower litter lignin/N and C/N ratios) (Prescott & Vesterdal, 2021; Silver & Miya, 2001). In addition, soils under deciduous (or broadleaved) forests and evergreen (or coniferous) forests commonly differ in pH, C/N ratio and N cycling rates (Augusto et al., 2015; Vesterdal et al., 2008), which may mediate the mycorrhizal effect on soil enzyme activity as we discussed above. However, some coniferous trees are AM associated, which contradicts that most AM trees have higher soil pH and low C/N ratios. Midgley and Sims (2020) suggested that mycorrhizal association better predicts tree species effects on soil processes than leaf habit in temperate forest ecosystems. Another recent study conducted in a lower montane tropical forest showed that leaf litter decomposition rates cannot be predicted directly from litter mycorrhizal type because litter chemical quality and environmental conditions mediate the manifestation of slower decomposition in EcM stands (Seyfried et al., 2021). Nevertheless, our results suggest that mycorrhizal effect alone may not predict soil process precisely without considering leaf morphology traits due to phylogenetic autocorrelation.

Climate conditions could also be important factors, because they may shape mycorrhizal associations and photosynthetic allocation to above- and below-ground biomass through long-term adaptation of plant–microbe symbiosis to local climatic and edaphic conditions (Classen et al., 2015; Jo et al., 2019; Steidinger et al., 2019). For example, with decreasing MAT, the prevailing mycorrhizal association shifts from AM species to EcM species along with decreasing soil pH and nutrient mobility (Frey, 2019; Steidinger et al., 2019; Tedersoo & Bahram, 2019). The increasing mycorrhizal effect on URE and POD activity with decreasing MAT (Table 2) supports that low pH and poor nutrient conditions in colder biomes would strengthen the mycorrhizal differences in enzyme production as discussed above. Our results are also consistent with mycorrhizal groups showing significant effects on litter decay in temperate forests but not in subtropical and tropical forests (Keller & Phillips, 2019), which may be related to the differences in soil pH and nutrient availability between these ecosystems (Keller & Phillips, 2019; Zhang et al., 2018).

4.3 | Limitation and future research

Our findings outlined the differences in soil EA and ES between AM and EcM forests, which support the understanding of the cycling of soil C and nutrients under altered forest types. However, several critical uncertainties remain due to the restriction of data coverage and knowledge gaps regarding soil enzymes. First, most of the studies in the database were from the temperate zone, mainly because AM and EcM trees rarely co-occur in cold or tropical biomes. The mycorrhizal association effect on soil biogeochemical processes in other biomes such as western North America, Australia and South America (where there are many AM conifers) should be further investigated. Second, tree species with dual colonists like *Populus tremuloides* (which can associate with either AM or ECM) span climate gradients but are not included in the current study. Since tree species are held constant, studying ES in those species can reveal the degree to which the mycorrhizal fungi are driving the ES patterns. Third, more than 90% of studies were conducted in mineral soil, but for some tree species, a significant amount of biogeochemical processes occur on the forest floor. Lastly, different enzymatic activity measurement methods (e.g. fluorescence and colorimetry) were used across the studies, which prevented us from testing

the joint/shared effects of covariates by performing multivariate analysis. Further studies based on consistent methodology are thus needed to strengthen our understanding of the effects of mycorrhizal associations on soil EA and ES and soil biogeochemical processes in the future.

5 | CONCLUSIONS

This meta-analysis quantitatively synthesized the effect of mycorrhizal associations on common soil EA and ES based on field studies. Our results showed that activity of BG and URE, and enzyme ratios of BG/NAG and BG/AP were higher in AM trees than in EcM trees, which is likely because AM trees allocate more C to below-ground processes and have an inorganic nutrient economy. The SOC-specific EA of NAG, AP and PPO were higher in EcM trees than in AM trees, suggesting that microbes in EcM trees had higher enzymatic capability to take up nutrients immobilized in organic form. Our results showed that the mycorrhizal effect on BG/NAG and BG/AP ratios tended to be more pronounced in sites with low soil pH. In addition, the effect of mycorrhizal association on the activity of certain soil EA and ES (i.e. BG and BG/NAG ratio) appeared to be driven by the difference in soil pH, phylogenetic group (i.e. conifers and broadleaves) and leaf habit (i.e. evergreen and deciduous) between AM and EcM trees. These results indicate that mycorrhizal association alone cannot reliably predict soil biogeochemical processes without considering plant traits and soil conditions. Further research is needed to elucidate the underlying mechanisms driving the mycorrhizal effect and to obtain enough EA data in cold and tropical biomes, in AM conifers, and on the forest floor that could not be included in this study due to the paucity of data.

AUTHOR CONTRIBUTIONS

Haifeng Zheng and Lars Vesterdal and conceived the ideas and designed the methodology; Haifeng Zheng and Senhao Wang collected the data; Haifeng Zheng and Richard P. Phillips analysed the data; Haifeng Zheng, Johannes Rousk and Lars Vesterdal led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

Johannes Rousk is an Associate Editor of Functional Ecology, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository at https://doi.org/10.5061/dryad.r7sqv9shh (Zheng et al., 2023).

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REFERENCES

Adams, D. C., Gurevitch, J., & Rosenberg, M. S. (1997). Resampling tests for meta-analysis of ecological data. *Ecology*, *78*(4), 1277–1283.

Adeleke, R., Nwangburuka, C., & Oboirien, B. (2017). Origins, roles and fate of organic acids in soils: A review. *South African Journal of Botany*, *108*, 393–406.

Augusto, L., De Schrijver, A., Vesterdal, L., Smolander, A., Prescott, C., & Ranger, J. (2015). Influences of evergreen gymnosperm and deciduous angiosperm tree species on the functioning of temperate and boreal forests. *Biological Reviews*, *90*(2), 444–466.

Averill, C., & Hawkes, C. V. (2016). Ectomycorrhizal fungi slow soil carbon cycling. *Ecology Letters*, *19*(8), 937–947. https://doi.org/10.1111/ele.12631

Bahram, M., Netherway, T., Hildebrand, F., Pritsch, K., Drenkhan, R., Loit, K., Anslan, S., Bork, P., & Tedersoo, L. (2020). Plant nutrient-acquisition strategies drive topsoil microbiome structure and function. *The New Phytologist*, *227*(4), 1189–1199. https://doi.org/10.1111/nph.16598

Bakbergenuly, I., Hoaglin, D. C., & Kulinskaya, E. (2020). Methods for estimating between-study variance and overall effect in meta-analysis of odds ratios. *Research Synthesis Methods*, *11*(3), 426–442.

Brundrett, M., & Tedersoo, L. (2019). Misdiagnosis of mycorrhizas and inappropriate recycling of data can lead to false conclusions. *New Phytologist*, *221*(1), 18–24. https://doi.org/10.1111/nph.15440

Brundrett, M. C., & Tedersoo, L. (2018). Evolutionary history of mycorrhizal symbioses and global host plant diversity. *The New Phytologist*, *220*(4), 1108–1115. https://doi.org/10.1111/nph.14976

Brundrett, M. C., & Tedersoo, L. (2020). Resolving the mycorrhizal status of important northern hemisphere trees. *Plant and Soil*, *454*(1), 3–34. https://doi.org/10.1007/s11104-020-04627-9

Burns, R. G., DeForest, J. L., Marxsen, J., Sinsabaugh, R. L., Stromberger, M. E., Wallenstein, M. D., Weintraub, M. N., & Zoppini, A. (2013). Soil enzymes in a changing environment: Current knowledge and future directions. *Soil Biology and Biochemistry*, *58*, 216–234.

Carrino-Kyker, S. R., Kluber, L. A., Petersen, S. M., Coyle, K. P., Hewins, C. R., DeForest, J. L., Smemo, K. A., & Burke, D. J. (2016). Mycorrhizal fungal communities respond to experimental elevation of soil pH and P availability in temperate hardwood

forests. *FEMS Microbiology Ecology*, *92*(3), fiw024. https://doi.org/10.1093/femsec/fiw024

Cheeke, T. E., Phillips, R. P., Brzostek, E. R., Rosling, A., Bever, J. D., & Fransson, P. (2017). Dominant mycorrhizal association of trees alters carbon and nutrient cycling by selecting for microbial groups with distinct enzyme function. *The New Phytologist*, *214*(1), 432–442. https://doi.org/10.1111/nph.14343

Chen, X., Ding, Z., Tang, M., & Zhu, B. (2018). Greater variations of rhizosphere effects within mycorrhizal group than between mycorrhizal group in a temperate forest. *Soil Biology and Biochemistry*, *126*, 237–246. https://doi.org/10.1016/j.soilbio.2018.08.026

Classen, A. T., Sundqvist, M. K., Henning, J. A., Newman, G. S., Moore, J. A. M., Cregger, M. A., Moorhead, L. C., & Patterson, C. M. (2015). Direct and indirect effects of climate change on soil microbial and soil microbial-plant interactions: What lies ahead? *Ecosphere*, *6*(8), 1–21.

Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Denef, K., & Paul, E. (2013). The microbial E fficiency-matrix S tabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: Do labile plant inputs form stable soil organic matter? *Global Change Biology*, *19*(4), 988–995.

Craig, M. E., Lovko, N., Flory, S. L., Wright, J. P., & Phillips, R. P. (2019). Impacts of an invasive grass on soil organic matter pools vary across a tree-mycorrhizal gradient. *Biogeochemistry*, *144*(2), 149–164. https://doi.org/10.1007/s10533-019-00577-2

Craig, M. E., Turner, B. L., Liang, C., Clay, K., Johnson, D. J., & Phillips, R. P. (2018). Tree mycorrhizal type predicts within-site variability in the storage and distribution of soil organic matter. *Global Change Biology*, *24*(8), 3317–3330. https://doi.org/10.1111/gcb.14132

Dickie, I. A., Koele, N., Blum, J. D., Gleason, J. D., & McGlone, M. S. (2014). Mycorrhizas in changing ecosystems. *Botany*, *92*(2), 149–160.

Dickie, I. A., Martínez-García, L. B., Koele, N., Grelet, G.-A., Tylianakis, J. M., Peltzer, D. A., & Richardson, S. J. (2013). Mycorrhizas and mycorrhizal fungal communities throughout ecosystem development. *Plant and Soil*, *367*(1), 11–39.

Frey, S. D. (2019). Mycorrhizal fungi as mediators of soil organic matter dynamics. *Annual Review of Ecology, Evolution, and Systematics*, *50*(1), 237–259. https://doi.org/10.1146/annurev-ecolsys-110617-062331

Gadgil, P. D., & Gadgil, R. L. (1975). *Suppression of litter decomposition by mycorrhizal roots of Pinus radiata*. New Zealand Forest Service.

Goldberg, S., Davis, J. A., & Hem, J. D. (2020). The surface chemistry of aluminum oxides and hydroxides. In *The environmental chemistry of aluminum* (pp. 271–331). CRC Press.

Gurevitch, J., Koricheva, J., Nakagawa, S., & Stewart, G. (2018). Meta-analysis and the science of research synthesis. *Nature*, *555*(7695), 175–182. https://doi.org/10.1038/nature25753

Heděnec, P., Nilsson, L. O., Zheng, H., Gundersen, P., Schmidt, I. K., Rousk, J., & Vesterdal, L. (2020). Mycorrhizal association of common European tree species shapes biomass and metabolic activity of bacterial and fungal communities in soil. *Soil Biology and Biochemistry*, *149*, 107933. https://doi.org/10.1016/j.soilbio.2020.107933

Hedges, L. V., Gurevitch, J., & Curtis, P. S. (1999). The meta-analysis of response ratios in experimental ecology. *Ecology*, *80*(4), 1150–1156. https://doi.org/10.1890/0012-9658(1999)080[1150:TMAORR]2.0.CO;2

Jeewani, P. H., Luo, Y., Yu, G., Fu, Y., He, X., Van Zwieten, L., Liang, C., Kumar, A., He, Y., Kuzyakov, Y., Qin, H., Guggenberger, G., & Xu, J. (2021). Arbuscular mycorrhizal fungi and goethite promote carbon sequestration via hyphal-aggregate mineral interactions. *Soil Biology and Biochemistry*, *162*, 108417. https://doi.org/10.1016/j.soilbio.2021.108417

Jo, I., Fei, S., Oswalt, C. M., Domke, G. M., & Phillips, R. P. (2019). Shifts in dominant tree mycorrhizal associations in response to anthropogenic impacts. *Science Advances*, *5*(4), eaav6358.

Kaiser, C., Kilburn, M. R., Clode, P. L., Fuchslueger, L., Koranda, M., Cliff, J. B., Solaiman, Z. M., & Murphy, D. V. (2015). Exploring the transfer of recent plant photosynthates to soil microbes: Mycorrhizal pathway vs direct root exudation. *New Phytologist*, *205*(4), 1537–1551.

Keller, A. B., & Phillips, R. P. (2019). Leaf litter decay rates differ between mycorrhizal groups in temperate, but not tropical, forests. *New Phytologist*, *222*(1), 556–564.

Lin, G., McCormack, M. L., Ma, C., & Guo, D. (2017). Similar below-ground carbon cycling dynamics but contrasting modes of nitrogen cycling between arbuscular mycorrhizal and ectomycorrhizal forests. *The New Phytologist*, *213*(3), 1440–1451. https://doi.org/10.1111/nph.14206

Midgley, M. G., Brzostek, E., & Phillips, R. P. (2015). Decay rates of leaf litters from arbuscular mycorrhizal trees are more sensitive to soil effects than litters from ectomycorrhizal trees. *Journal of Ecology*, *103*(6), 1454–1463. https://doi.org/10.1111/1365-2745.12467

Midgley, M. G., & Phillips, R. P. (2016). Resource stoichiometry and the biogeochemical consequences of nitrogen deposition in a mixed deciduous forest. *Ecology*, *97*(12), 3369–3378.

Midgley, M. G., & Sims, R. S. (2020). Mycorrhizal association better predicts tree effects on soil than leaf habit. *Frontiers in Forests and Global Change*, *3*, 1–14. https://doi.org/10.3389/ffgc.2020.00074

Moorhead, D. L., Rinkes, Z. L., Sinsabaugh, R. L., & Weintraub, M. N. (2013). Dynamic relationships between microbial biomass, respiration, inorganic nutrients and enzyme activities: Informing enzyme-based decomposition models. *Frontiers in Microbiology*, *4*, 223. https://doi.org/10.3389/fmicb.2013.00223

Peng, Y., Holmstrup, M., Schmidt, I., Bachega, L., Schelfhout, S., Zheng, H., Heděnec, P., Yue, K., & Vesterdal, L. (2022). Tree species identity is the predominant modulator of the effects of soil fauna on leaf litter decomposition. *Forest Ecology and Management*, *520*, 120396. https://doi.org/10.1016/j.foreco.2022.120396

Peng, Y., Schmidt, I. K., Zheng, H., Heděnec, P., Bachega, L. R., Yue, K., Wu, F., & Vesterdal, L. (2020). Tree species effects on topsoil carbon stock and concentration are mediated by tree species type, mycorrhizal association, and N-fixing ability at the global scale. *Forest Ecology and Management*, *478*, 118510.

Phillips, R. P., Brzostek, E., & Midgley, M. G. (2013). The mycorrhizal-associated nutrient economy: A new framework for predicting carbon-nutrient couplings in temperate forests. *The New Phytologist*, *199*(1), 41–51. https://doi.org/10.1111/nph.12221

Prescott, C. E., & Vesterdal, L. (2021). Decomposition and transformations along the continuum from litter to soil organic matter in forest soils. *Forest Ecology and Management*, *498*, 119522. https://doi.org/10.1016/j.foreco.2021.119522

R Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org/

Read, D. J. (1991). Mycorrhizas in ecosystems. *Experientia*, *47*(4), 376–391.

Read, D. J., & Perez-Moreno, J. (2003). Mycorrhizas and nutrient cycling in ecosystems – A journey towards relevance? *New Phytologist*, *157*(3), 475–492. https://doi.org/10.1046/j.1469-8137.2003.00704.x

Rosling, A., Midgley, M. G., Cheeke, T., Urbina, H., Fransson, P., & Phillips, R. P. (2016). Phosphorus cycling in deciduous forest soil differs between stands dominated by ecto-and arbuscular mycorrhizal trees. *New Phytologist*, *209*(3), 1184–1195.

Rousk, J., Brookes, P. C., & Baath, E. (2009). Contrasting soil pH effects on fungal and bacterial growth suggest functional redundancy in carbon mineralization. *Applied and Environmental Microbiology*, *75*(6), 1589–1596. https://doi.org/10.1128/AEM.02775-08

Schimel, J. P., & Bennett, J. (2004). Nitrogen mineralization: Challenges of a changing paradigm. *Ecology*, *85*(3), 591–602.

Seyfried, G. S., Dalling, J. W., & Yang, W. H. (2021). Mycorrhizal type effects on leaf litter decomposition depend on litter quality and environmental context. *Biogeochemistry*, *155*, 1–18.

Silver, W. L., & Miya, R. K. (2001). Global patterns in root decomposition: Comparisons of climate and litter quality effects. *Oecologia*, *129*(3), 407–419.

Sinsabaugh, R. L. (2010). Phenol oxidase, peroxidase and organic matter dynamics of soil. *Soil Biology and Biochemistry*, *42*(3), 391–404. https://doi.org/10.1016/j.soilbio.2009.10.014

Sinsabaugh, R. L., Antibus, R. K., Linkins, A. E., McClaugherty, C. A., Rayburn, L., Repert, D., & Weiland, T. (1993). Wood decomposition: Nitrogen and phosphorus dynamics in relation to extracellular enzyme activity. *Ecology*, *74*(5), 1586–1593. https://doi.org/10.2307/1940086

Sinsabaugh, R. L., & Follstad Shah, J. J. (2012). Ecoenzymatic stoichiometry and ecological theory. *Annual Review of Ecology, Evolution, and Systematics*, *43*(1), 313–343. https://doi.org/10.1146/annurev-ecolsys-071112-124414

Sinsabaugh, R. L., Hill, B. H., & Follstad Shah, J. J. (2009). Ecoenzymatic stoichiometry of microbial organic nutrient acquisition in soil and sediment. *Nature*, *462*(7274), 795–798.

Sinsabaugh, R. L., Lauber, C. L., Weintraub, M. N., Ahmed, B., Allison, S. D., Crenshaw, C., Contosta, A. R., Cusack, D., Frey, S., Gallo, M. E., Gartner, T. B., Hobbie, S. E., Holland, K., Keeler, B. L., Powers, J. S., Stursova, M., Takacs-Vesbach, C., Waldrop, M. P., Wallenstein, M. D., … Zeglin, L. H. (2008). Stoichiometry of soil enzyme activity at global scale. *Ecology Letters*, *11*(11), 1252–1264. https://doi.org/10.1111/j.1461-0248.2008.01245.x

Smith, F. A., & Smith, S. E. (2011). What is the significance of the arbuscular mycorrhizal colonisation of many economically important crop plants? *Plant and Soil*, *348*(1), 63–79.

Soudzilovskaia, N. A., Vaessen, S., Barcelo, M., He, J., Rahimlou, S., Abarenkov, K., Brundrett, M. C., Gomes, S. I. F., Merckx, V., & Tedersoo, L. (2020). FungalRoot: Global online database of plant mycorrhizal associations. *New Phytologist*, *227*(3), 955–966.

Soudzilovskaia, N. A., van der Heijden, M. G. A., Cornelissen, J. H. C., Makarov, M. I., Onipchenko, V. G., Maslov, M. N., Akhmetzhanova, A. A., & van Bodegom, P. M. (2015). Quantitative assessment of the differential impacts of arbuscular and ectomycorrhiza on soil carbon cycling. *New Phytologist*, *208*(1), 280–293. https://doi.org/10.1111/nph.13447

Steidinger, B. S., Crowther, T. W., Liang, J., Van Nuland, M. E., Werner, G. D. A., Reich, P. B., Nabuurs, G. J., de-Miguel, S., Zhou, M., Picard, N., Herault, B., Zhao, X., Zhang, C., Routh, D., & Peay, K. G. (2019). Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. *Nature*, *569*(7756), Article 7756. https://doi.org/10.1038/s41586-019-1128-0

Tabatabai, M. A. (1994). Soil enzymes. *Methods of Soil Analysis: Part 2. Microbiological and Biochemical Properties*, *5*, 775–833.

Tedersoo, L., & Bahram, M. (2019). Mycorrhizal types differ in ecophysiology and alter plant nutrition and soil processes. *Biological Reviews of the Cambridge Philosophical Society*, *94*(5), 1857–1880. https://doi.org/10.1111/brv.12538

Tedersoo, L., & Brundrett, M. C. (2017). Evolution of ectomycorrhizal symbiosis in plants. In *Biogeography of mycorrhizal symbiosis* (pp. 407–467). Springer.

Toljander, J. F., Lindahl, B. D., Paul, L. R., Elfstrand, M., & Finlay, R. D. (2007). Influence of arbuscular mycorrhizal mycelial exudates on soil bacterial growth and community structure. *FEMS Microbiology Ecology*, *61*(2), 295–304.

Turner, B. L. (2010). Variation in pH optima of hydrolytic enzyme activities in tropical rain forest soils. *Applied and Environmental Microbiology*, *76*(19), 6485–6493.

Ushio, M., Kitayama, K., & Balser, T. C. (2010). Tree species-mediated spatial patchiness of the composition of microbial community and physicochemical properties in the topsoils of a tropical montane forest. *Soil Biology and Biochemistry*, *42*(9), 1588–1595.

van der Heijden, M. G. A., Martin, F. M., Selosse, M. A., & Sanders, I. R. (2015). Mycorrhizal ecology and evolution: The past, the present, and the future. *The New Phytologist*, *205*(4), 1406–1423. https://doi.org/10.1111/nph.13288

Vesterdal, L., Clarke, N., Sigurdsson, B. D., & Gundersen, P. (2013). Do tree species influence soil carbon stocks in temperate and boreal forests? *Forest Ecology and Management*, *309*, 4–18. https://doi.org/10.1016/j.foreco.2013.01.017

Vesterdal, L., Schmidt, I. K., Callesen, I., Nilsson, L. O., & Gundersen, P. (2008). Carbon and nitrogen in forest floor and mineral soil under six common European tree species. *Forest Ecology and Management*, *255*(1), 35–48. https://doi.org/10.1016/j.foreco.2007.08.015

Yin, H., Wheeler, E., & Phillips, R. P. (2014). Root-induced changes in nutrient cycling in forests depend on exudation rates. *Soil Biology and Biochemistry*, *78*, 213–221.

Zhang, H.-Y., Lü, X.-T., Hartmann, H., Keller, A., Han, X.-G., Trumbore, S., & Phillips, R. P. (2018). Foliar nutrient resorption differs between arbuscular mycorrhizal and ectomycorrhizal trees at local and global scales. *Global Ecology and Biogeography*, *27*(7), 875–885.

Zheng, H., Heděnec, P., Rousk, J., Schmidt, I., Peng, Y., & Vesterdal, L. (2022). Effects of common European tree species on soil microbial resource limitation, microbial communities and soil carbon. *Soil Biology and Biochemistry*, *172*, 108754. https://doi.org/10.1016/j.soilbio.2022.108754

Zheng, H., Phillips, R. P., Rousk, J., Yue, K., Schmidt, I. K., Peng, Y., Wang, S., & Vesterdal, L. (2023). Data from: Imprint of tree species mycorrhizal association on microbial-mediated enzyme activity and stoichiometry. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.r7sqv9shh

SUPPORTING INFORMATION

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

Table S1. Potential contextual moderator variables in the analyses.

Figure S1. Mean and 95% CI of log response ratio of specific enzyme activity and enzymatic stoichiometry in planted and natural forests.

Figure S2. Mean and 95% CI of log response ratio of specific enzyme activity and enzymatic stoichiometry based on a conservative meta-analysis and based on SOC-specific enzyme activity.

Figure S3. Heat map showing the correlations between response ratios of soil enzyme activity and response ratios for soil physicochemical properties.

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