A synthesis and meta-analysis on the role of mycorrhizal fungal traits for understanding forest tree functions

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ACKNOWLEDGEMENTS

The authors wish to thank Sandra Jacobi and Astrid Stilke of the Forestry and Timber Industry Library (Thünen Institute) for their excellent assistance in providing all non-digital publications. Ina C. Meier thanks the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) for financial support (Heisenberg program; grant no. ME 4156/5-1).

CONFLICT OF INTEREST

The authors declare no competing financial or other interest or relationship.

AUTHOR CONTRIBUTIONS

ICM conceived the ideas and designed methodology; AMK collected the data; AMK analysed the data; AMK and ICM led the writing of the manuscript, contributed critically to the drafts, and gave final approval for publication.

STATEMENT ON INCLUSION

Our study was a global review and was based on a meta-analysis of secondary data rather than primary data. As such, there was no local data collection.

DATA AVAILABILITY STATEMENT

All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. All data analyzed in the study will be made publicly available as data publication after the participating researchers had the opportunity to publish the results. The R script including all analyses and figure preparations is available from the corresponding author upon reasonable request.

DATA SOURCES

Our meta-analysis used data from multiple published resources which are provided in a separate Data Sources section.

ABSTRACT

1. Nearly all tree species associate with mycorrhizal fungi, which aid their hosts in soil resource acquisition and influence the nutrient economy of the ecosystem. Yet despite the fundamentality of this symbiotic interaction, our understanding how fungal traits relate to host traits is still in its infancy.
2. We compiled a unique mycorrhizal fungal trait database, which sets mycorrhizal fungal effect traits in relation to host function in three tree response trait categories (i) resource acquisition, (ii) plant productivity, and (iii) carbon (C) release.
3. Based on quantitative synthesis and meta-analysis, we demonstrate current strengths and gaps of knowledge with respect to tree species and spatial coverage, and fungal trait-tree function relationships. Most studies demonstrate a positive influence of traits in the effect trait categories 'fungal community assembly', 'host-symbiont interactions', and 'soil exploration' on traits in the response trait categories 'resource acquisition' and 'plant production'. According to meta-analysis, fungal community composition was more influential for resource uptake and plant productivity than taxon-specific effects. Traits in the category 'fungal community assembly' related negatively to root C exudation (with low certainty). The influences of 'mycorrhizal colonization' or 'soil exploration' effect traits on 'host C release' response traits remained unclear.
4. We conclude that the fungal effect trait category 'soil exploration' and the tree response trait category 'C release' remain major avenues for future research, which should advance from lab-measurements of soft traits and increasingly focus on mycorrhizal fungal traits with the widest importance in ecosystem functioning.

KEYWORDS

decomposition, meta-analysis, nutrient uptake, plant productivity, quantitative synthesis, root exudation, trait-based ecology, water uptake

1 | INTRODUCTION

The mycorrhizal symbiosis is of fundamental importance for carbon (C) and nutrient cycles in ecosystems since it facilitates soil resource acquisition of hosting plants in return for photosynthates for fungal symbionts. Approximately 80% of all higher plants can form such

symbiosis (M. C. Brundrett, 2009), which earned a reputation as key determinant of terrestrial ecosystem functioning. In terrestrial ecosystems, approximately 75% of all tree species associate with arbuscular mycorrhizal fungi (AMF), and most of the remainder with orchid mycorrhizal fungi (OMF), ectomycorrhizal fungi (ECMF), or ericoid mycorrhizal fungi (ERMF; M. Brundrett & Tedersoo, 2019). While only 2% of all tree species form the ECM association (Heijden et al., 2015), these tree species are widely distributed. As a consequence, ECMF communities are taxonomically more diverse (i.e., composed of more distantly related fungal species) than AMF communities and dominate tree stems (ca. 60%) in world's forests (Heijden et al., 2015; Steidinger et al., 2019). The nutrient economy of AM and ECM forest ecosystems differs fundamentally (Phillips et al., 2013), which is consequence of functional differences between fungi of these two major mycorrhizal association types. AMF affect the nutrient uptake capacity of the tree hosts from competition between root and hyphal uptake only indirectly (Cornelissen et al., 2001). AMF have a high own N demand (Hodge & Fitter, 2010), which AMF can satisfy by scavenging for inorganic nutrients released by saprotrophic microbes (Read & Perez-Moreno, 2003) inter alia from their own labile litter. By contrast, ECMF more directly control nutrient uptake of their host from the formation of a fungal sheath surrounding fine roots (Tedersoo & Bahram, 2019), which limits nutrient uptake to hyphal tips or non-mycorrhizal root tips, but also protects hosts against soil-borne pathogens. ECMF have well-developed saprotrophic capacities and can mine soils for complex N-bearing organic compounds including their own poor-quality litter (Read & Perez-Moreno, 2003).

The form and properties of root systems are highly plastic and diverse and respond to abiotic and biotic influences. Upon formation of the symbiosis with mycorrhizal fungi, trees respond with a change of their fine root properties and functions. When trees form association with AMF, they increase their root cortical area and root diameter to provide intraradical habitat for their symbionts (Bergmann et al., 2020). In the association with ECMF, the morphology and architecture of tree roots changes strongly. Trees form root systems with higher branching intensity, i.e., with more root tips per lower order root length, which offers colonization sites for ECM symbionts and serves precision foraging into resource-rich patches (Comas et al., 2014; Eissenstat et al., 2015; Liese et al., 2017). In addition, they rely on far-reaching rhizomorphs (when associated with ECM basidiomycetes) and many thin fungal hyphae for soil exploration and exploitation of soil micropores. Consequently, fungal mycelium can represent a huge source for C sequestration in ECM forest soils (Clemmensen et al., 2013; Tedersoo & Bahram, 2019). Yet despite the multitude of influences of mycorrhizal symbioses

on anatomical, morphological, architectural, and physiological root traits, and differences in hyphal traits, most investigations on tree-mycorrhizal fungal relationships focus on percentage of root tips or length colonized by mycorrhizal fungi to represent the reliance of trees on the symbiosis (Halbritter et al., 2020; Soudzilovskaia et al., 2015).

Plant functional traits are morpho-physio-phenological characteristics which impact fitness indirectly via their effects on growth, reproduction, and survival (Violle et al., 2007). Functional traits imply how the morphology and physiology of plants relate to their biotic and abiotic environment and its resources, and how these traits influence ecosystem functioning and the provision of ecosystem services (de Bello et al., 2010; Leuschner & Meier, 2018; Violle et al., 2007). Given the meaning and range of trait-based approaches, functional ecology experienced increasing attention in ecological and evolutionary research during the last two decades (Dawson et al., 2021) The compilation of trait data into large databases accelerated this development. Recently, the Fine-Root Ecology Database FRED has been developed for composing coarse and fine root traits (Iversen et al., 2017). There is also growing interest in the development of a comparable trait database for fungi e.g., on the fungal community composition [FUNGuild (Nguyen et al., 2016); GlobalFungi (Větrovský et al., 2020)], plant biomass responses to mycorrhizal fungal inoculation [MycoDB (Chaudhary et al., 2016)], fungal ecology [FUN^{FUN} (Zanne et al., 2019)], functional properties of fungi [FungalTraits (Põlme et al., 2020)], or on mycorrhizal associations [FungalRoot (Soudzilovskaia et al., 2020)].

Mycorrhizal traits can be influenced by both the plant host and the community of fungal symbionts associated, which can have considerable variation in morphological, physiological, and biochemical traits (Chaudhary et al., 2022; Hazard & Johnson, 2018). This bilateral influence on mycorrhizal traits complicates their analysis. More complex fungal communities are profitable to the host since they raise the chance of greater functional diversity among the associated mycorrhizal fungi (Baxter & Dighton, 2001; Diagne et al., 2013; Khokon et al., 2023; Köhler et al., 2018). For example, ECMF communities composed of fungal symbionts with diverse exploration types (distance of soil exploration from the host tree as based on morphological traits of colonized root tips and emanating hyphae; Agerer, 2001) have higher chance of spatial and functional complementarity among the emanating fungal mycelia. Fungal ecologists have used selected mycorrhizal fungal traits like mycorrhizal colonization to understand host and ecosystem functioning for decades (Agerer, 2001; Chaudhary et al., 2022; Fernandez & Kennedy, 2018; Lekberg & Helgason, 2018; Zanne et al., 2019), but a holistic

examination of mycorrhizal fungal effect traits for key tree functions or for mycorrhizal economics [*cf.* (Bergmann et al., 2020; Wright et al., 2004)] is still lacking. Here, we assembled global quantitative information on mycorrhizal fungal effect traits (i.e., traits of mycorrhizal fungi and mycorrhizal fungal communities) in relation to response functions of forest trees in the trait categories 'resource acquisition', 'plant productivity', and 'C release' (via root exudation and litter decomposition) by an extensive literature survey. Based on our expert knowledge, we recapitulated the underlying rationales and conceptualized potential relationships between fungal effect traits and key tree response traits. Finally, we used the assembled database for testing these conceptual models in a meta-analysis. We critically evaluated the current strengths and gaps in our knowledge on fungal symbiont-host tree trait relationships and highlight future research avenues that offer the potential for better understanding tree responses to limiting soil resources and soil C cycling in forest ecosystems.

2 | MATERIALS AND METHODS

2.1 | *The mycorrhizal fungal trait database*

We assembled information on mycorrhizal fungal effect traits used for understanding forest tree response functions from a systematic literature survey using the Web of Science (Clarivate Analytics, Philadelphia, PA, USA). We focused on six forest tree functions in the three trait categories (i) resource acquisition (N, P, and water uptake), (ii) plant productivity (merged both aboveground and belowground data), and (iii) plant C release (root exudation and litter decomposition), for which we employed the following search term: "(mycorrhiza* OR ectomycorrhiza*) AND (nitrogen OR phosphor* OR water OR produc* OR decompos* OR exud*) AND (tree*) NOT (grass*) NOT (herb*)". The survey included references between 1986 and 13 September 2022 (date of first study found and date at which the survey was performed, respectively) and covered nearly 2,900 published studies on mycorrhizal fungal traits of forest trees (Figure S1.1). Subsequently, we screened the initial literature list in accordance with the Preferred Reporting Items for Systematic Review and Meta-Analyses (PRISMA) guidelines [https://www.prisma-statement.org; (Moher et al., 2010)]. All non-English, duplicates and review articles (to avoid hidden duplicates) were excluded from the records. We checked all titles and abstracts for the eligibility criterion, i.e., relevant information on mycorrhizal fungal traits in relation to tree functioning. For the remaining articles, we also assessed whether the full text meets the eligibility criteria, e.g., only original and peer-reviewed

studies, woody plants as target species, absence of confounding treatment (Figure S1.1). As a result, a total of 464 studies entered the subsequent quantitative synthesis and meta-analysis. For each selected publication, we gathered information on the investigated tree species, tree function, tree organ, type of association (AM, ECM, or ERM) and mycorrhizal fungal traits, the study type (controlled experiment or field observation), the significance and type of the tree's functional response for a given mycorrhizal fungal trait (positive, negative, or neutral), the location of the study, and additional general information from the printer's imprint.

For meta-analysis, we further collected means, correlation coefficient (*r*), *F*-statistics, and *t*-statistics, sample size (*n*), standard deviation (*SD*), standard error (*SE*) or 95% confidence interval (*CI*) of our variable of interest, when reported. Unspecific error bars were recorded as SE. Studies were excluded if they provided only mean values without any associated descriptive statistics. Studies involving mycorrhizal associations often lack a defined control group, and therefore, AM associations were treated as the control, and ECM associations as the treatment. During data extraction, we also applied consistent decision rules to ensure comparability across experiments. Where multiple treatment levels were reported, we selected the treatment most representative of typical field conditions or least likely to introduce confounding stress, unless all levels were required for independent analysis. Data from figures were digitalized using the software WebPlotDigitizer 4.1 (https://automeris.io/). Finally, our dataset for meta-analysis consisted of 3,451 observations from 353 publications for the mycorrhizal traits, and 2488 observations from 177 publications for the mycorrhizal fungal taxon-specific dataset.

2.2 | *Replication statement*

Scale of inference	**Scale at which the factor of interest is applied**	**Number of replicates at the appropriate scale**
Tree species	Tree species	1-256 observations (Table 2) from 464 selected research articles (*cf.* PRISMA protocol; Figure S1.1)

2.3 | *Data-preprocessing*

When the study reported *SE*, the corresponding *SD* was computed as:

$$SD = SE\ x\ \sqrt{n}$$

where *n* is the sample size. If the study reported 95% confidence intervals (*CI*), the *SD* was computed as:

$$SD = \frac{\sqrt{n}\ x\ (upper\ CI - lower\ CI)}{2Z_{\alpha/2}}$$

where *n* is the sample size and $Z_{\alpha/2}$ represents the Z score for given level of significance (e.g., 1.96 at $\alpha = 0.05$).

When mean values were not directly available (e.g., data from boxplots), the first quartile (*Q1*), median (*Q2*), and third quartile (*Q3*) were recorded. Mean and Interquartile range (*IQR*) were calculated as:

$$Mean\ = \frac{Q1 + Q2 + Q3}{3}$$

$$IQR = Q3 - Q1$$

The *SD* was then estimated from the *IQR* using the following small-sample bias–corrected formula (Wan et al., 2014):

$$SD = \frac{IQR}{2\ \Phi^{-1}(\frac{0.75n - 0.125}{n + 0.25})}$$

where *n* is the sample size, Φ^{-1} is the inverse of the cumulative distribution function (quantile function) of the standard normal distribution and the denominator adjusts for finite-sample bias in quartile estimation.

2.4 | *Effect size and variance calculation*

To measure the effects sizes of mycorrhizal fungal traits on tree functioning, we calculated standardized mean differences (Hedges' *g*) and their variances using the *escalc()* function (*measure = "SMD"*) from the *metafor* package (*v4.8.0*) in R, when means, sample sizes (*n*), standard deviations (*SD*), or *t*-statistics were available for both control and treatment groups

(Viechtbauer, 2010). As *metafor* does not directly compute Hedges' g and variance from correlation coefficients (r) or F-statistics, we applied the following conversions:

When r was reported, Cohen's d was calculated as (Borenstein et al., 2009; Rosenthal, 1991):

$$d = \frac{2r}{\sqrt{1 - r^2}}$$

Cohen's d was then adjusted to Hedges' g using the small-sample correction factors (j):

$$j = 1 - \frac{3}{4N - 9}$$

where N is the total sample size. The effects size (Hedges' g) was calculated as:

$$g = d \; x \; j$$

The variance of r (Vr), Cohen's d (Vd) and Hedges' g (Vg) were calculated as:

$$Vr = \frac{(1 - r^2)^2}{N - 1}$$

$$Vd = \frac{\mathrm{Vr}}{(1 - r)^3}$$

$$Vg = Vd \; x \; j^2$$

When F-statistics, sample size (n) for the control (nc) and treatment (nt) groups were reported, Cohen's d was calculated as (Borenstein et al., 2009; Hedges & Olkin, 1985):

$$d = \sqrt{F \left(\frac{nc + nt}{nc \; nt}\right)}$$

Cohen's d was then adjusted to Hedges' g using the correction factors (j) (Hedges & Olkin, 1985):

$$j = 1 - \frac{3}{4df - 1}$$

$$df = nc + nt - 2$$

$$g = d \; x \; j$$

The variance of Cohen's d (Vd) and Hedges' g (Vg) was calculated as:

$$Vd = \frac{nc + nt}{nc \; nt} + \frac{d^2}{2\,(nc + nt)}$$

$$Vg = Vd\ x\ j^2$$

We calculated the effect size (Hedges' g) and variance for each observation associated with mycorrhizal fungal traits and tree functions. A positive Hedges' g value indicates positive effects of mycorrhizal traits on tree functioning, while a negative value indicates the opposite. Mean effect size considered to be significant when the *CI* range did not include zero (Borenstein et al., 2009).

To reduce the statistical dependence and avoid overrepresentation of studies reporting multiple outcomes (i.e., effect sizes) for the same trait-function combination, we aggregated the effect sizes and variance at the level of '*study x mycorrhizal trait (and taxon-specific) x tree function'*. For each unique combination, individual effect sizes were pooled using a fixed-effects model with inverse-variance weighting, implemented via the *rma.uni()* function in the *metafor* R package (Viechtbauer, 2010). We assessed the robustness of our aggregation approach by comparing fixed-effects and random effects pooling within a random subset of *study* × *mycorrhizal trait (and taxon-specific)* × *tree function*. Differences in pooled estimates were minimal (mean absolute difference = 0.27 and median ≈ 0 for mycorrhizal traits dataset; mean absolute difference = 0.685 and median ≈ 0 for mycorrhizal fungal taxon-specific dataset), supporting the use of fixed-effects models for within-study aggregation.

During the data cleaning, we removed seven extreme effect sizes ($|yi| > 10$), which were mainly attributed to combination of large mean values, very small *SD* and small sample size. Furthermore, effect sizes based on fewer than two observations and/or derived from a single article were further excluded from analyses to avoid small sample size effects (Borenstein et al., 2009). In total, 18 observations from 16 publications were removed at this stage. The same filtering criteria were applied when analyzing the influence of AM and ECM taxon-specific effects on tree functioning. The final dataset comprised 714 observations for mycorrhizal fungal traits and 487 observations for taxon-specific effect on tree functioning.

2.5 | *Visualization of the spatial distribution of data*

Data were visualized with R, version 4.2.2 (R development Core Team., 2020) using the 'ggplot2' package (Wickham, 2009). The publicly available global geographical dataset with information on longitudes, latitudes, and regions was imported in R using the function *map_data("world")* prior to creating the global map. The Antarctica region was removed from

the global map with the function *filter (region! = "Antarctica")* using the 'tidyverse' package (Wickham et al., 2019) since no study was published in the Antarctica region. Furthermore, our mycorrhizal trait dataset was merged with the global geographical dataset and sorted according to the city name using the function *left_join (by="region")* to create the global map. The different color gradients were used from the 'viridis' package (Garnier et al., 2021) to show the total number of studies on the global map.

2.6 | *Phylogenetic relatedness of the investigated tree species*

We generated a phylogenetic tree by constructing the backbone of tree using the function *phyl.maker()* from the 'V.Phylomaker' package (Jin & Qian, 2019), and visualized the tree using the function *ggtree()* from the 'ggtree' package (Yu et al., 2017). Furthermore, we annotated the phylogenetic tree using the functions *geom_text2()* to label the node numbers, *geom_tiplab2()* to align the tree species, and *geom_hilight() and geom_cladelabel()* to highlight the most dominant genera from the 'ggtree' package (Yu et al., 2017).

2.7 | *Publication-bias*

Publication bias was explored graphically with funnel plots of the Hedges' *g* against *SE*, and asymmetry of the funnel plot was subsequently assessed through Egger's regression test using *regtest()* function (Egger et al., 1997). However, Hedges' *g* plotted against *SE* can be susceptible to distortion, and leading to overestimation of the existence and extent of publication bias (Zwetsloot et al., 2017). Therefore, if asymmetry was identified, we further used the Rosenberg's fail-safe number (*fsn*) to further evaluate the potential impact of the unpublished articles on our conclusion (Rosenberg, 2005). A fail-safe number is considered robust if it is five times higher than the number of studies plus ten (Rosenthal, 1991). In addition, we also assessed the sensitivity of our results by performing a leave-one-out analysis using the *leave1out()* function within the R *metafor* package (Viechtbauer, 2010).

2.8 | *Data analyses*

For quantitative synthesis, in the first step, we identified significant positive or negative responses of mycorrhizal traits to tree functions as well as absent or non-significant relationships from the data provided in the main text, graphs and tables in the publication. In

the next step, we calculated the relative proportion of a specific response of a mycorrhizal trait to a tree function across all tree organs from each study separately. The response was defined as unambiguous positive or negative, when the relative proportion of the response was ≥60% of all responses, and as unclear, when the relative proportion of the response was ≤60%. We defined the certainty of the relationship between a mycorrhizal trait to a tree function as high, when ≥30 studies had the same result, and as intermediate and low certainty, when ≥10 and ≤10 studies, respectively, had the same result. We decreased the certainty level, when ≥10% of the studies were ambiguous.

For meta-analysis, the mean effect sizes were visualized using forest plot with the R *metafor* package (Viechtbauer, 2010). We used multivariate meta-analysis mixed effect models to test whether overall mycorrhizal traits/ taxon-specific effects on per tree function showed differences across studies. Heterogeneity of effect sizes was assessed through Cochran's Q statistics which indicates the presence or absence of heterogeneity across studies (Borenstein et al., 2009). Specifically, the Q_E test accounts for residual heterogeneity and the Q_M (i.e., omnibus test) accounts for heterogeneity explained by moderators (i.e., mycorrhizal fungal traits or taxa) included in the model. The significance of moderators was evaluated through *p*-values obtained from Q_M statistics. All the models were fitted with the *rma()* function of the *metafor* package in R (Viechtbauer, 2010).

3 | RESULTS

3.1 | *Global and tree species representation of the relationship between mycorrhizal fungal traits and host tree functions*

Most studies relating mycorrhizal fungal effect traits to forest tree response functions between the study years 1986 and 2022 were conducted on the European continent (125 studies) and in two countries of the Northern Hemisphere, which are dominated by the temperate climate zone (USA: 65 studies, China: 63 studies; Figure 1). These focal areas for mycorrhizal trait studies are followed by three countries dominated by tropical climate (i.e., Brazil, India, and Senegal), in which each 19 to 26 studies were conducted in the same time span. Only a few mycorrhizal trait studies were internationally published for three countries belonging to the largest countries of the world (Canada: 13 studies; Australia: 10 studies; Russia: 1 study). The grey color spots on the global map of studies relating mycorrhizal fungal effect traits to forest tree response

functions remain in large parts of hot-dry or tropical Africa, continental Central Asia, and in (sub) polar Greenland (Figure 1).

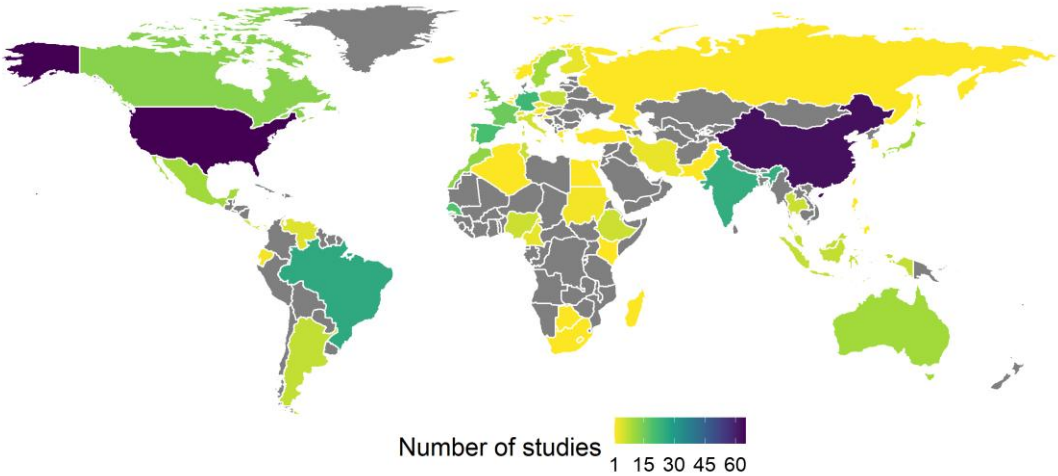


FIGURE 1 Global distribution of studies relating mycorrhizal fungal effect traits to forest tree functions between the study years 1986 and 2022 (*n* = 464 studies).

A total of 501 tree species were used across 464 publications to relate mycorrhizal fungal effect traits to forest tree response functions between the study years 1986 and 2022 (Figure 2). The most abundant tree species used in these publications was the economically important fruit tree olive (*Olea europaea* L.), which is followed in number by sugar maple (*Acer saccharum* Marshall), European beech (*Fagus sylvatica* L.), tulip tree (*Liriodendron tulipifera* L.), and Scots pine (*Pinus sylvestris* L.) (Table S1.1). More than 200 studies investigated trees from the Fabaceae family, which were represented by almost 100 tree species. Less studies were conducted in the pine and beech families, which were observed by fewer tree species (*c.* 150 and 110 studies, respectively; Pinaceae: 44 tree species; Fagaceae: 42 tree species). Yet in a comparison of the studied genera, *Pinus* (Pinaceae) and *Quercus* (Fagaceae) were the most widely used genera, followed by *Acer* and (with distance) *Betula* and *Fagus*. Among these dominantly investigated genera, the genus *Pinus* represents ECM trees of the evergreen leaf habit (Figure 2). Pine tree species are phylogenetically the most distant from the other genera which were dominantly investigated, since they were the only gymnosperms among these. Different successional status of deciduous ECM trees was represented by *Betula* (early successional), *Quercus* (mid successional), and *Fagus* (late successional), which are all Fagaceae and thus phylogenetically closely related. The genus *Acer* (Sapindaceae), which is located in the middle of the phylogenetic tree, was often used as representative of AM tree

species of mid/late successional status. The less often studied genera *Olea* and *Acacia* represent more special cases of an evergreen AM tree species (i.e., *Olea europaea*) and of evergreen AM/rhizobia tree species (*Acacia*), respectively. *Olea* is phylogenetically closely related to the genus *Fraxinus* (Oleaceae), which was used as representative of AM tree species of early/mid successional status.

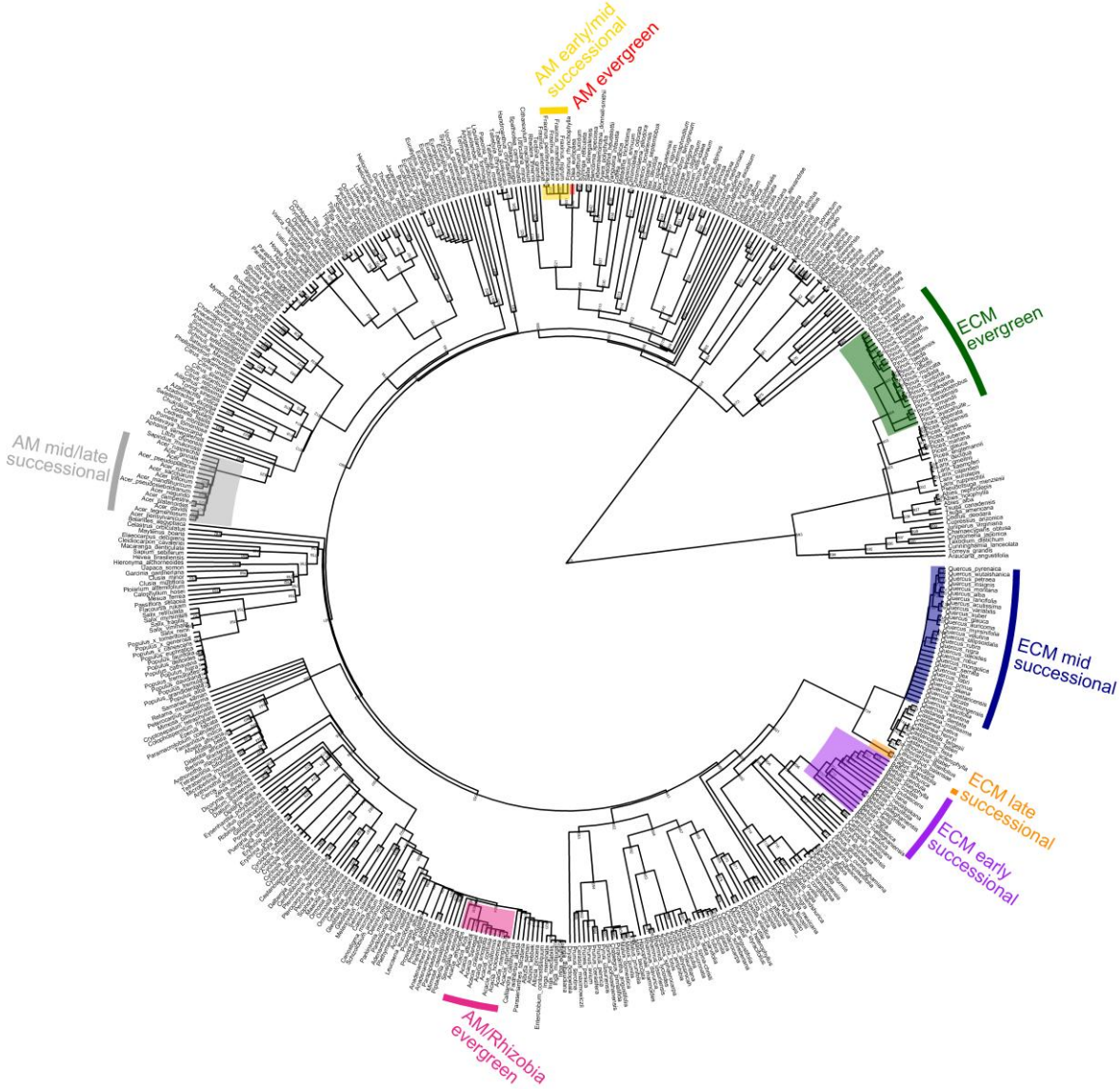


FIGURE 2 Phylogenetic tree for the tree species used to relate mycorrhizal fungal effect traits to forest tree functions (study years 1986-2022). The nodes with genera dominating the investigations are highlighted by different colors.

Color code in order of quantitative importance of tree genus usage: green = *Pinus*, blue = *Quercus*, grey = *Acer*, purple = *Betula*, orange = *Fagus*, pink = *Acacia*, yellow = *Fraxinus*, red = *Olea*. Mycorrhizal types: AM = arbuscular mycorrhiza, ECM = ectomycorrhiza.

Most of the mycorrhizal trait studies investigating ECM were conducted in Europe and the global north (39 and 89% of all studies, respectively), which were also dominating the absolute number of studies (423 of all 550 studies; Figure 3). Studies on AM traits were more evenly distributed, with many of them in Asia (33% of all studies). Most of the mycorrhizal trait studies in Africa and South America were on the AM symbiosis. Only few studies mostly in Europe investigated ERM traits (6 studies: ERM in comparison to ECM). Almost all studies comparing traits of the two major mycorrhizal association types originate from the northern hemisphere and there are many from North America (33 studies).

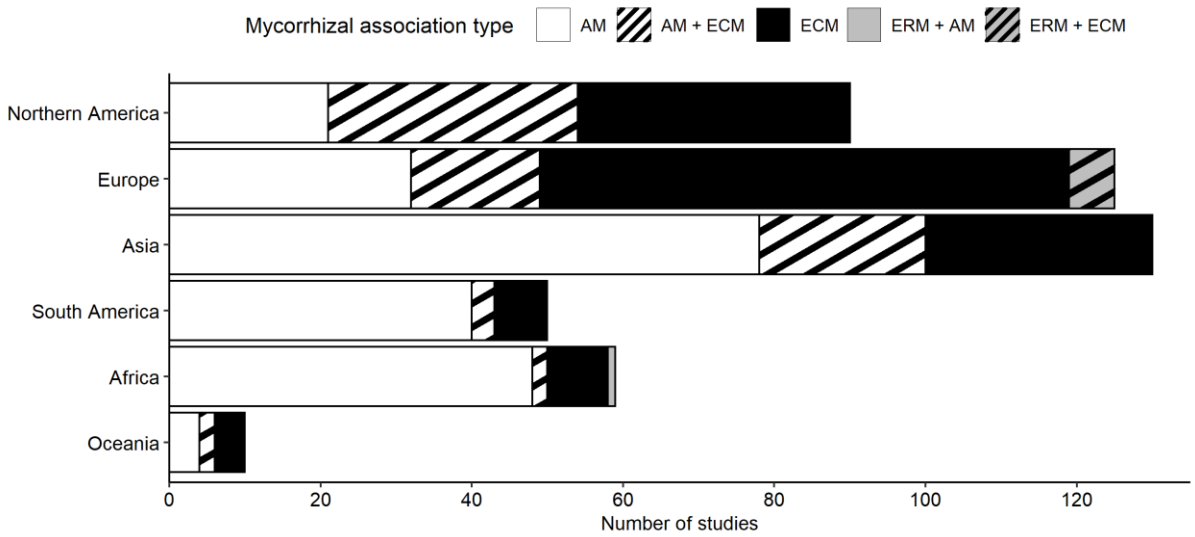


FIGURE 3 Continental distribution of distinct mycorrhizal association types studied to relate mycorrhizal fungal effect traits to forest tree functions (study years 1986-2022).

Mycorrhizal types: AM = arbuscular mycorrhiza, ECM = ectomycorrhiza, ERM = ericoid mycorrhiza.

3.2 | *Mycorrhizal fungal traits used for understanding forest tree functioning*

Our literature survey resulted in 17 mycorrhizal fungal effect traits in the categories (i) fungal community assembly, (ii) host-symbiont interaction, and (iii) soil exploration, which were analyzed for understanding six target forest tree response functions (Table 1). Most of all mycorrhizal trait studies focused on the influence of traits in the category ‘fungal community assembly’ on tree response functions (419 studies), predominantly by analyzing the effect of the genetic identity of mycorrhizal fungi, the fungal community composition, or the mycorrhizal fungal species richness. Almost 80% of all studies in the effect trait category

‘fungal community assembly’ were conducted under controlled experimental conditions, and only a fifth in natural field settings.

TABLE 1 Frequency of studied mycorrhizal fungal trait-forest tree function relationships in controlled experimental or natural field conditions (study years 1986-2022).

Mycorrhizal traits	Controlled experiment	Field observation	Total
Fungal community assembly			
Genetic identity	**225**	44	269
Community composition	**73**	28	101
Genetic richness	**32**	9	41
Genetic diversity	3	3	6
Genetic evenness	0	1	1
ECM functional genes	0	1	1
Host-symbiont interaction			
Mycorrhizal association type	18	**52**	70
Colonization intensity	24	23	47
ECM tree dominance	0	**11**	11
Common ECMF network	0	**4**	4
Hyphal proportion per plant	1	0	1
Soil exploration			
AMF spore density	**3**	2	5
AMF hyphal length	1	0	1
ECMF exploration type	0	**3**	3
ECM mycelial diameter	1	0	1
Hyphal foraging precision	1	0	1
ECM mycelium density	1	0	1

Numbers in bold indicate superior frequency of studies in either controlled experimental or natural field conditions.

The effect trait category ‘host-symbiont interaction’ was examined in fewer studies (n = 133 studies; Table 1). Among these more than 60% focused on the mycorrhizal association type and the ECM dominance as fungal effect traits, which were studied mostly in field observations. Only a third of the mycorrhizal trait studies in the effect trait category ‘host-symbiont interaction’ focused on the colonization intensity in either experimental or field

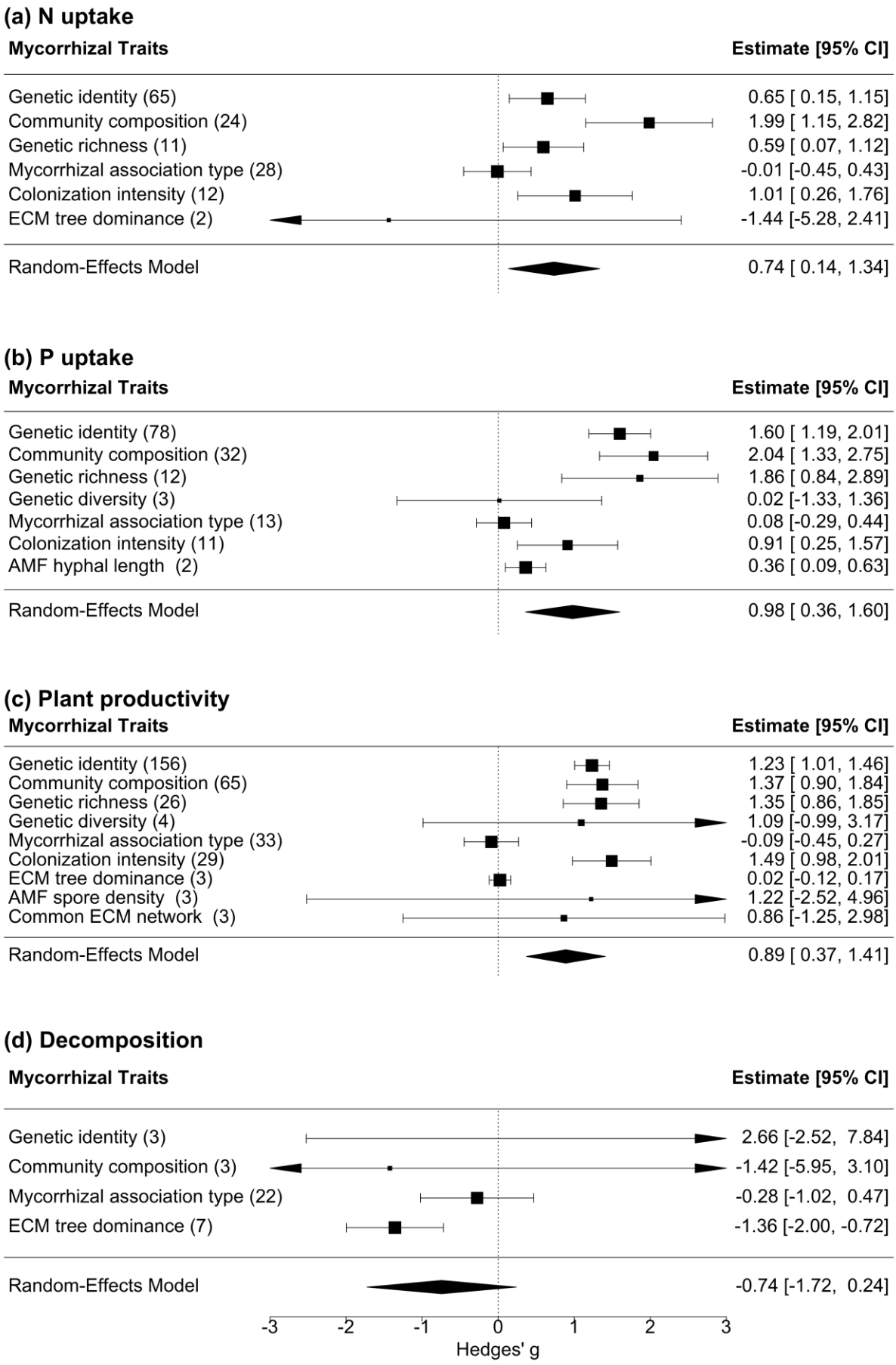
studies. The global front-runner in field observations of host-symbiont interactions was USA (Figure S1.2).

Less than 2% of all mycorrhizal trait studies focused on traits in the effect trait category 'soil exploration' by mycorrhizal hyphae (Table 1). Six experimental studies considered AMF spore density and hyphal length as influencing factor for understanding tree response functions and three field observations tested the effect of a specific ECMF exploration type. Among all investigations, only little attention was paid to the potentially important influence of fungal diversity measures, functional genes, and common mycorrhizal networks on host tree response functions.

3.3 | *Mycorrhizal fungal traits and taxon-specific effects on forest tree functioning*

Overall, mycorrhizal fungal traits had significant positive effects on N uptake (g = 0.74, 95% *CI* [0.14, 1.34], *QM* = 20.20, p = 0.001; Figure 4a), P uptake (g = 0.98, 95% *CI* [0.36, 1.60], *QM* = 16.50, p = 0.01; Figure 4b), and plant productivity (g = 0.89, 95% *CI* [0.37, 1.41], *QM* = 27.83, p = 0.001; Figure 4c). These positive responses were mainly driven by mycorrhizal fungal community composition, colonization intensity, genetic richness, and genetic identity (Figure 4a–c). In contrast, mycorrhizal association type and ECM tree dominance showed negligible effects on N uptake and productivity, and decomposition tended to decline under ECM tree dominance (g = –1.36, 95% *CI* [–2.00, –0.72]; Figure 4d).

At the taxon-specific level, both AM and ECM fungal species showed generally positive but statistically non-significant effects on N uptake (g = 0.70, 95% *CI* [0.18, 1.22], *QM* = 22.18, p = 0.33; Figure S1.3), P uptake (g = 1.51, 95% *CI* [1.16, 1.86], *QM* = 32.59, p = 0.30; Figure S1.4), and plant productivity (g = 1.13, 95% *CI* [0.90, 1.37], *QM* = 49.08, p = 0.39, Figure S1.5). Several AM taxa, including *Rhizophagus intraradices*, *R. irregularis*, *Funneliformis mosseae*, and *Glomus aggregatum*, as well as ECM taxa such as *Cenococcum geophilum*, *Hebeloma mesophaeum*, *Helvella lacunosa*, *Suillus grevillei*, and *Laccaria laccata*, exhibited consistently positive associations with nutrient uptake and productivity (Figure S1.3-5). These results indicate no systematic differences among AM and ECM taxa, but the overall pattern reveals broadly positive and variable taxon-specific responses, suggesting that both AM and ECM contribute to enhanced nutrient uptake and plant productivity through distinct but functionally convergent mechanisms.


(a) N uptake
Mycorrhizal Traits
Estimate [95% CI]
Genetic identity (65)
0.65 [0.15, 1.15]
Community composition (24)
1.99 [1.15, 2.82]
Genetic richness (11)
0.59 [0.07, 1.12]
Mycorrhizal association type (28)
-0.01 [-0.45, 0.43]
Colonization intensity (12)
1.01 [0.26, 1.76]
ECM tree dominance (2)
-1.44 [-5.28, 2.41]
Random-Effects Model
0.74 [0.14, 1.34]
(b) P uptake
Mycorrhizal Traits
Estimate [95% CI]
Genetic identity (78)
1.60 [1.19, 2.01]
Community composition (32)
2.04 [1.33, 2.75]
Genetic richness (12)
1.86 [0.84, 2.89]
Genetic diversity (3)
0.02 [-1.33, 1.36]
Mycorrhizal association type (13)
0.08 [-0.29, 0.44]
Colonization intensity (11)
0.91 [0.25, 1.57]
AMF hyphal length (2)
0.36 [0.09, 0.63]
Random-Effects Model
0.98 [0.36, 1.60]
(c) Plant productivity
Mycorrhizal Traits
Estimate [95% CI]
Genetic identity (156)
1.23 [1.01, 1.46]
Community composition (65)
1.37 [0.90, 1.84]
Genetic richness (26)
1.35 [0.86, 1.85]
Genetic diversity (4)
1.09 [-0.99, 3.17]
Mycorrhizal association type (33)
-0.09 [-0.45, 0.27]
Colonization intensity (29)
1.49 [0.98, 2.01]
ECM tree dominance (3)
0.02 [-0.12, 0.17]
AMF spore density (3)
1.22 [-2.52, 4.96]
Common ECM network (3)
0.86 [-1.25, 2.98]
Random-Effects Model
0.89 [0.37, 1.41]
(d) Decomposition
Mycorrhizal Traits
Estimate [95% CI]
Genetic identity (3)
2.66 [-2.52, 7.84]
Community composition (3)
-1.42 [-5.95, 3.10]
Mycorrhizal association type (22)
-0.28 [-1.02, 0.47]
ECM tree dominance (7)
-1.36 [-2.00, -0.72]
Random-Effects Model
-0.74 [-1.72, 0.24]
-3
-2
-1
0
1
2
3
Hedges' g

397

FIGURE 4 Mean effect sizes and 95% confidence intervals (CIs) for mycorrhizal traits and their influence on **(a)** plant nitrogen uptake, **(b)** phosphorus uptake, **(c)** plant productivity, and **(d)** decomposition. Random-effects model refers to overall effect size of mycorrhizal traits on tree functions. Number of the articles (*n*) for each mycorrhizal trait is shown in parentheses. The size of each square indicates the number of studies in relation to the overall mean calculation. Dotted vertical line shows Hedges' $g = 0$. When the CI does not include zero, the effect size is statistically significant.

3.4 | *Publication bias and sensitivity analysis*

No significant publication bias was detected for N uptake in relation to the effects of mycorrhizal fungal traits (Table S1.2; Figure S1.6; Egger's test: $p > 0.05$). While asymmetry of funnel plots was observed for other tree functions in relation to mycorrhizal fungal traits and taxon-specific effects (Figure S1.6; Figure S1.8), the Rosenberg fail-safe numbers were much larger than 5k + 10 for most tree functions, except water uptake and exudation, which were removed from the meta-analysis (Table S1.2). These results indicate that a large number of additional studies would be required to overturn the observed significant effect sizes for both datasets. In addition, exudation and decomposition variables were excluded from the taxon-specific dataset for meta-analysis due to insufficient data (Table S1.2). Our sensitivity analyses revealed that our results are unlikely to be driven by a single influential study (Figure S1.7; Figure S1.9).

3.5 | *Concept of fungal trait – tree functioning relationships*

With reference to the existing knowledge, we developed a conceptual framework of relationships between mycorrhizal fungal effect traits and key response functions of host trees (resource acquisition, plant production, and C release). This framework was separated for traits relating to the effect trait category 'fungal community assembly' (Figure 5a) and traits relating to the effect trait categories 'host-symbiont interaction' and 'soil exploration' (Figure 5b), respectively. Three widely assumed effect-response trait relationships represent the core of this conceptual framework: (i) More complex fungal communities with greater fungal species richness and/or species evenness and greater species diversity enhance host tree functioning with respect to soil resource acquisition and C release from root exudation and decomposition (Baxter & Dighton, 2001; Clemmensen et al., 2021; Diagne et al., 2013; Khokon et al., 2023;

Köhler et al., 2018). (ii) ECMF with distinct exploration types differ by their mycelium density and hyphal foraging precision (Agerer, 2001). Greater soil exploration by mycorrhizal hyphae (i.e. hyphal foraging precision at reduced mycelium density) increases resource acquisition and production of plants (Lilleskov et al., 2011, 2019). (iii) Mycorrhizal colonization of tree roots exerts a control on the root C release via exudation or decomposition (Argiroff et al., 2022; Fanin et al., 2022; Meier et al., 2013; Tedersoo & Bahram, 2019). We tested this conceptual framework against the published results on relationships between mycorrhizal fungal effect traits and key response functions of host trees.

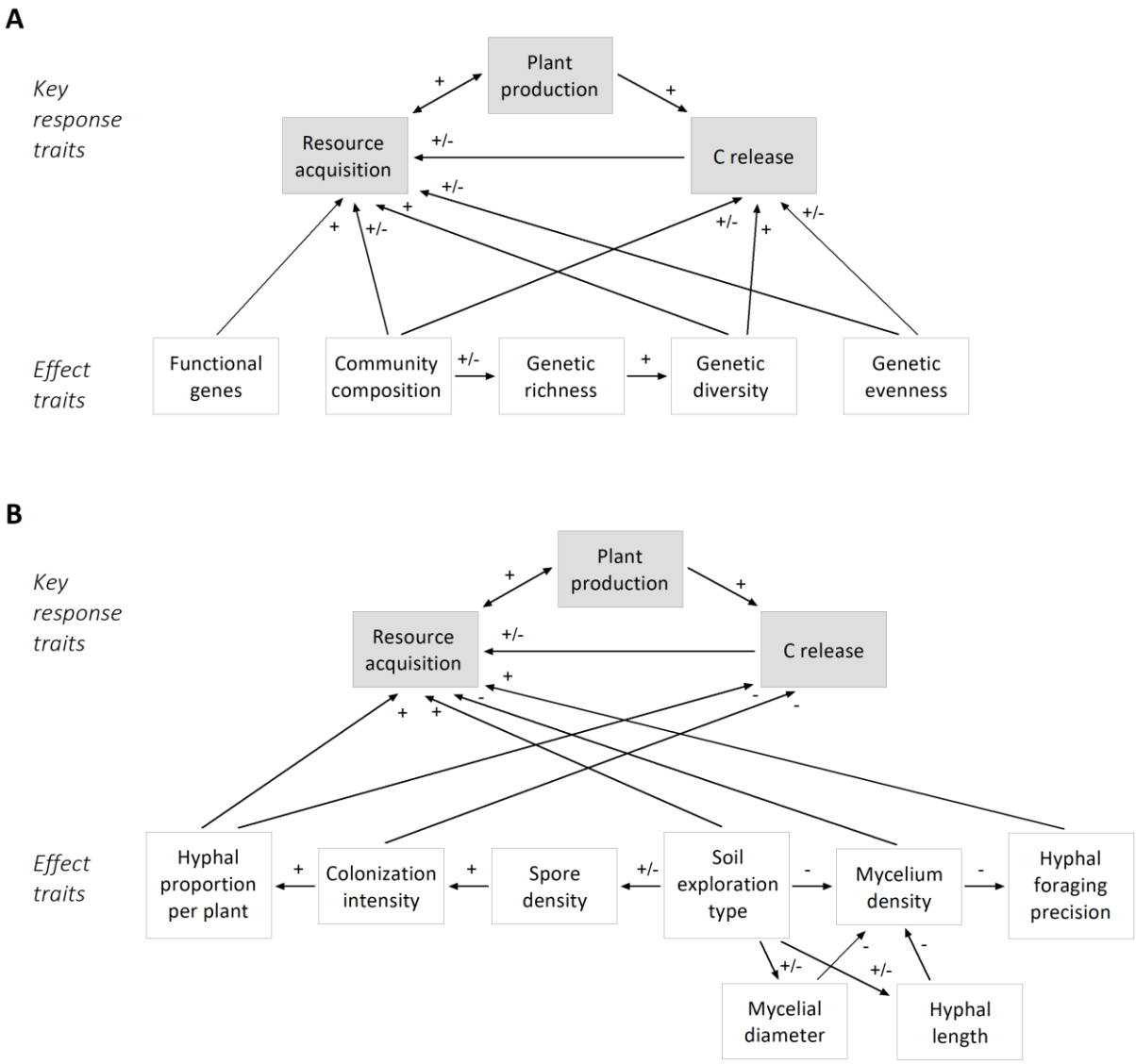


FIGURE 5 Conceptual models of plausible interactions between mycorrhizal fungal effect traits (**a**: fungal community assembly; **b**: host-symbiont interactions and soil exploration) and key response traits in forest trees.

'+' refer to positive effect and '-' to negative effect

The published results for mycorrhizal fungal trait–tree function relationships demonstrate an unambiguous positive influence of fungi of a specific genetic identity, specific community composition, and genetic richness on traits in the response trait categories ‘soil resource acquisition’ and ‘plant production’ (Table 2, 3; Figure 4). The few existing studies on fungal genetic diversity found a positive influence on plant production but an unclear influence on traits in the response trait category ‘soil resource acquisition’ (Table 2, Figure 4), which partially confirms our first assumption on trait relationships (Figure 5a). In contrast to our conceptual model, there is limited evidence (from few studies) for a negative effect of fungi of a specific genetic identity and specific community assembly on root exudation (Table 2, 3).

The fungal effect trait category ‘soil exploration’ remains an understudied domain of fungal trait–tree function relationships (Table 2). There is limited evidence for a positive effect of AMF spore density and AMF hyphal length on response traits in the categories ‘resource acquisition’ and ‘plant production’, but the influence of a specific ECMF exploration type is unclear. Each one study demonstrated a positive influence of hyphal foraging precision and a negative effect of ECM mycelium density on plant production, which is first confirmation of our second assumption on trait relationships (Figure 5b). The effect of traits in the effect trait category ‘soil exploration’ on C release via root exudation or litter decomposition remains utterly unknown due to absent investigation (Table 2, 3).

The influence of mycorrhizal colonization intensity on host C release from exudation and litter decomposition is unclear (Table 2), which renders a decision on our third assumption on trait relationships impossible (Figure 5b). However, the positive influence of a specific mycorrhizal association type on root exudation and litter decomposition in combination with the negative influence of ECM tree dominance on litter decomposition may give indirect hint on mycorrhizal control on response traits in the category ‘host C release’ (Table 2).

TABLE 2 Frequency of observations relating mycorrhizal fungal effect traits to forest tree functions (study years 1986-2022).

	Resource acquisition			Plant product.	C release		
Mycorrhizal trait	**P uptake**	**N uptake**	**H_2O uptake**		**Exudation**	**Decomp.**	**Rationale**
Fungal community assembly							
Genetic identity	146	116	38	256	2	2	Fungal species differ in their effect on host tree functions.
Community composition	55	38	12	89	1	2	Interspecific variation and the interaction of fungal species in a specific mycorrhizal community determines the fungal effect on host tree function.
Genetic richness	20	17	5	39	0	0	The number of fungal species in a community (determined by environmental factors that limit local species coexistence) increases the chance of functional diversity and complementary mutualistic associations - independent from fungal species abundance.
Genetic diversity	3	1	0	4	0	0	Fungal diversity can be mediated by species richness (local species coexistence) and turnover (species sorting). Fungal diversity in a mycorrhizal symbiosis increases the chance of functional diversity and segregation among individual fungal species and complementary mutualistic associations.
Genetic evenness	0	0	0	1	0	0	The evenness of the abundance of fungal species in a mycorrhizal niche space is a measure of functional evenness.
ECM functional genes		0	0	1	0		Genes which are energetically more active and specialized to nutrient resources are linked to fast tree production.
Host-symbiont interaction							
Mycorrhizal association type	13	31	1	40	4	24	Distinct mycorrhizal types have different enzymatic capacities and abilities to explore soil volumes and acquire resources to improve host functions.
Colonization intensity	11	14	0	32	2	4	The portion of root length or root tips colonized by mycorrhizal fungi indicates the degree by which mycorrhizal fungi influence tree functions.

ECM tree dominance	2	3	1	2	0	9	ECM-dominated forests have an organic nutrient economy with greater enzymatic capacities and ability to acquire limiting soil resources (*inter alia* organic N).
Common ECMF network	0	2	1	3	0	0	Common ECMF networks redistribute limiting resources along source-sink gradients from resource-rich hosts to connected resource-limited hosts, i.e., they decrease host functional diversity.
Hyphal proportion per plant	0	0	0	1	0	0	Hyphal proportion per plant is a measure of host C investment in emanating hyphae.
Soil exploration							
AMF spore density	2	1	0	5	0	0	The density of mycorrhizal propagules in soil indicates the spatial extent and probability of potential root colonization by symbionts with subsequent effects on host functions.
AMF hyphal length	1	1	0	1	0	0	Hyphal length is a measure of soil volume reached by fungal structures.
ECMF soil exploration type	0	1	0	2	0	0	Distinct ECMF exploration types differ in the extent and C cost of soil exploration by emanating hyphae.
ECM mycelial diameter	1	0	0	1	0	0	Mycelium diameter is a measure of explorable soil pores by fungal structures.
Hyphal foraging precision	0	0	0	1	0	0	Hyphal foraging precision enhances resource uptake from a heterogenous, patchy soil environment.
ECM mycelium density	0	0	0	1	0	0	Mycelium density is a measure of the range of soil exploitation by ECMF structures.

The color code refers to demonstrated positive (blue), negative (red), or unclear (orange) relationships between a mycorrhizal fungal effect trait and a host tree response function. White cells indicate absent or statistically non-significant observations. The color intensity ranges from high (dark color) to low (light color) certainty of the relationship according to number and unambiguousness of proofs (dark color ≥30 studies with the same result; intermediate color ≥10 studies with the same result; light color ≤10 studies with the same result. Decrease in color intensity with ≥10% ambiguous results).

TABLE 3 Summary of the relationships between categories of mycorrhizal fungal effect traits and categories of key response traits in forest trees (systematic literature review; *n* = 464 studies between 1986-2022).

Tree function / Fungal effect trait	Resource acquisition	Plant production	C release
Fungal community assembly	↗	↗	↘
Host-symbiont interaction	↗	↗	↔
Soil exploration	↗	↗	n.d.

Color code: blue = positive; red = negative; orange = unclear

Color intensity: dark color = high certainty; light color = low certainty

n.d. = no data

4 | DISCUSSION

Mycorrhization is essential for basic plant functions such as root C release and resource acquisition which fosters growth and fitness of plants. In the holobiont concept of plants, the interdependent interaction between the co-evolved host plants and root-associated endospheric fungi is treated as discrete ecological unit (Choi et al., 2021; Vandenkoornhuyse et al., 2015). While it is known that symbionts can co-construct host organs (Borges, 2017) and it has been hypothesized that genomic differences among mycorrhizal fungal guilds can reflect ecophysiological traits of plant holobionts (Tedersoo & Bahram, 2019), holobiont trait analyses, that is analyses of mycorrhizal fungal traits in relation to host plant traits, have not been widely implemented yet. Recently, an inclusive mycorrhizal trait framework has been developed that classifies traits according to function and location among the symbiotic partners (Chaudhary et al., 2022). Here, we relate fungal effect traits to host tree functions and synthesize the dependencies.

4.1 | *Important knowledge gaps in understanding holobiont functions of mycorrhizal trees*

Based on our quantitative synthesis, we identify critical knowledge gaps to understand the functioning of the mycorrhizal symbiosis in forest trees. These gaps originate from (i) temperate sampling bias and extremely limited knowledge from Afrotropical, dry-continental, and arctic tree or forest biomes, (ii) over-representation of five tree genera in trait analyses, of which three are phylogenetically closely related Fagaceae and only one genus (*Acer*) is widely used to study AM symbiosis of trees, (iii) under-representation of ecophysiological measurements of ERM and rare arbutoid mycorrhizas, and (iv) limited transfer of methods and studies to less controllable, natural field conditions with complex fungal communities and distant soil exploration by fungal hyphae. While the former three are probably merely result of a Eurocentric and economic-targeted sampling bias, solving the latter is more complex since not all methods are applicable in the field.

Despite pleas from more than three decades ago (Read, 1991), the majority of current studies on mycorrhizal functions uses inoculation with a limited number of easily culturable mycorrhizal fungal species to identify the influence of fungal genetic identity, diversity, or community composition on tree functioning (Bogar et al., 2022; Diagne et al., 2013; Thoen et al., 2020). Some studies stepped toward more natural conditions by growing host trees inoculated with a native pool of fungal species in the field (Siqueira et al., 1998), or by growing trees with natural fungal assemblages under controlled experimental conditions (De Grandcourt et al., 2004; Köhler et al., 2018; Meier et al., 2013). Only few studies investigated functions of trees associated with natural mycorrhizal fungal communities in the field (Anthony et al., 2022; Clemmensen et al., 2021; Khokon et al., 2023; Zavišić et al., 2018). Recently, mycorrhizal ecologists have been called on to revisit old and new tools for studying mechanistic functions of naturally complex fungal communities in the field (Lekberg & Helgason, 2018). Among the emerging new tools with potential for field application identified by these authors are the production of manipulated mycorrhizal assemblages by clustered regularly interspaced short palindromic repeats gene editing, -omics approaches (e.g., transcriptomics, proteomics, metabolomics) to study ecophysiological processes, and biomarker analyses (e.g., lab-on-a-chip microfluids, quantum dots) to trace function. In combination with these new tools, the more established imaging by mini-rhizotrons, when used for hyphal dynamics, and signature fatty acid analysis in combination with stable isotope labeling to determine plant C allocation to mycelia can be highly constructive (Lekberg & Helgason, 2018). For approaching the next level of mycorrhizal trait analyses in natural

ecosystems, such exploration of new tools in combination with more established methods should be at the center of our interest. Advanced measurements of understudied mycorrhizal traits will help to answer the question, whether we measure the right mycorrhizal traits, by helping to identify those functional traits of the holobiont which are critical for the mycorrhizal symbiosis. Critical mycorrhizal traits should preferably enter mycorrhizal trait databases on plant and fungal traits for a better understanding of the role of the mycorrhizal symbiosis in global ecosystem functioning.

4.2 | *ECMF exploration types can be vital for host tree functions*

In our quantitative synthesis, we identify soil exploration as an understudied but potentially important mycorrhizal fungal effect trait with great potential for understanding tree response functions. ECMF can be ecologically classified by the distance from the root surface, which their emanating hyphae radiate into soil, the presence and differentiation of their rhizomorphs, and the hydrophilicity of their hyphae (Agerer, 2001). These so-called exploration types represent different foraging strategies of ECMF and are connected to nutrient uptake, water transport rates, soil exploitation, soil organic matter formation and soil C cycling (Clemmensen et al., 2021; See et al., 2022). The morphology and chemistry of the extraradical mycelium can be used as vital ECMF traits, which are linked to functional variation among fungal taxa at the core of the mycorrhizal symbiosis (Agerer, 2001; Anthony et al., 2022; Lilleskov et al., 2011). Moreover, different ECM exploration types have different abilities to adapt against N pollution in the forest ecosystem (Lilleskov et al., 2011; Suz et al., 2021), which could play a pivotal role in maintaining ecosystem functionality under the threat of global change. Surprisingly few studies have directly related ECM exploration types to tree functioning so far. One study showed that the relative abundance of the medium-distance exploration type in the mycorrhizal fungal community affected tree N uptake (Pellitier et al., 2021). Another study demonstrated that the relative abundance of short and medium-distance exploration types increased seedling survival (Jalón et al., 2020). Other authors found that the relative abundance of medium and long distance exploration types decreased tree growth, possibly as a consequence of greater C requirement for mycelium production (Anthony et al., 2022). As an alternative to exploration types, soil exploration can be represented by hyphal morphology (e.g., hyphal length and diameter), hyphal foraging precision and density, and the dispersal of rejuvenation organs (spore density). Several studies showed that these fungal effect traits relate positively to nutrient uptake and plant productivity (Chen et al., 2016; Sastry et al., 2000; Schoen et al.,

2021). These promising results strengthen the potential importance of exploration type abundances for host tree functions, which requires further investigation.

4.3 | *Mycorrhizal fungal community effects on host tree functions*

Mycorrhizal fungal species can significantly differ in their effect on host tree function both intra- and interspecifically (Behm & Kiers, 2014; Johnson et al., 2012) and in dependency on the fungal community assemblage (Pena & Polle, 2014). Differential functional trait responses were found between different fungal isolates of the same species (Hortal et al., 2017; Plett et al., 2015) and between individual fungal hyphae of a single species (Fernandez & Kennedy, 2018). The number of fungal species in a mycorrhizal community, i.e., local species coexistence, increases the chance of functional diversity, segregation among individual fungal species, and complementary mutualistic associations (Khokon et al., 2023). Our quantitative synthesis showed that higher mycorrhizal fungal species richness enhances tree nutrient acquisition, water uptake, and plant productivity (Bompadre et al., 2013; Diagne et al., 2013; Köhler et al., 2018; Leberecht et al., 2016). Functional diversity in a mycorrhizal assemblage related positively to P uptake efficiency in young beech trees (Köhler et al., 2018), while an opposite relationship was observed in mature beech ecosystems (Zavišić et al., 2018). Different functional diversity effect are probably mediated by inclusion of highly productive or pathogen species in the fungal community [selection effect (Meier et al., 2013)]. A complementary approach can be the measurement of functional genetic features of mycorrhizal fungi and quantification of their expression level. Such combination of transcriptomics with ecophysiological measurements can be powerful for identifying functional genetic variation among fungi in their effect on resource acquisition (Hortal et al., 2017), tree growth (Anthony et al., 2022), and decomposition processes (Pellitier & Zak, 2018). Likewise, genetic evenness of fungal species in a community could be used as a measure of functional evenness, but this has rarely been conducted so far. However, it must be kept in mind that functional differences also exist among genes which are related to different trait categories. In a study in European forests, the proportion of energy and nutrient metabolism genes had a positive influence on tree growth, while organic N cycling genes had a negative effect (Anthony et al., 2022). Likewise, it remains unclear if genes with saprotrophic function are actively transcribed when ECM taxa form mycorrhiza and whether their number can predict extracellular enzyme activity (Pellitier & Zak, 2018). Instead, they can also encode for alternative plant-internal functions. Such

molecular crosstalk between trees and mycorrhizal fungi is only beginning to be revealed and much progress can be made here.

4.4 | *Mycorrhizal control of root and litter C release*

While mycorrhizal colonization of tree roots may exert a strong control on root C release via exudation or decomposition, we are only just at the beginning of quantifying this effect and understanding the underlying processes. It was shown that the two major mycorrhizal types (i.e., ECM and AM) are functionally distinct in litter quality, enzymatic capacity, and C cost to host plants (Phillips et al., 2013; Smith & Read, 2010). This is reflected in, first, greater C loss with root exudation in ECM tree species (Liese et al., 2018; H. Yin et al., 2014) depending on root morphology (Akatsuki & Makita, 2020), and in, second, slower litter decomposition rates in ECM ecosystems (Carteron et al., 2022; Jiang et al., 2021; L. Yin et al., 2021), but faster decomposition by ECMF (Carteron et al., 2022). Moreover, whether mycorrhizal colonization intensity *per se* exerts a control on root exudation and root litter decomposition remains contradictory (Argiroff et al., 2022; Meier et al., 2013; Trap et al., 2017). Furthermore, it has been debated whether common mycorrhizal network between roots of multiple plants are used to shuttle C from one plant to another, but the knowledge is presently still too sparse and unsettled to speculate on any control by the network on the root C release (Karst et al., 2023).

5 | CONCLUSION

Our holistic mycorrhizal trait attempt, which sets fungal effect traits in relationship to tree response traits, has unveiled several knowledge gaps originating from limited coverage of climate zones, tree species, and mycorrhizal types. Yet more critical than these sampling biases is the limited transfer of methods to the field, where mycorrhizal traits with the widest importance for ecosystem functioning could be studied. We are still to identify those mycorrhizal traits which are functional traits substantial to the symbiosis, which are not necessarily those that are the most often studied now. Rather, these mycorrhizal traits probably relate to soil exploration and exploitation and soil C transfer. An assessment of functionally relevant mycorrhizal effect traits requires broad quantification of traits from a diverse set of tree species, mycorrhizal types, and environments, and the establishment of causal relationships with host functions. Our conceptual framework provides a mechanistic basis for

identifying these trait-trait relationships and fungal effect traits with strongest influence on host tree functions.

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