A synthesis on the role of mycorrhizal fungal traits for understanding forest tree functions

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Summary

- Nearly all tree species associate with mycorrhizal fungi, which promote 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.
- We compiled a unique mycorrhizal fungal trait database, which sets fungal traits in relation to host functions of forest trees in the categories resource acquisition, plant productivity, and carbon (C) release.
- Based on 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 the fungal community assembly, host-symbiont interactions, and soil exploration on resource acquisition and plant production. By contrast, the fungal community assembly related negatively to root C exudation (with low certainty). The influence of mycorrhizal colonization or soil exploration on host C release remains unclear.
- 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 traits with the widest importance in ecosystem functioning.

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 (Brundrett, 2009), which justifiably earned reputation as key determinant of terrestrial ecosystem functioning. In terrestrial ecosystems, three-fourths of the 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; 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 in world's forests (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). They have a high own N demand (Hodge & Fitter, 2010), which they 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 (Soudzilovskaia *et al.*, 2015; Halbritter *et al.*, 2020).

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 (Violle *et al.*, 2007; De Bello *et al.*, 2010; Leuschner & Meier, 2018). 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 (Hazard & Johnson, 2018; Chaudhary *et al.*, 2022). This bilateral influence on mycorrhizal traits complicates their analysis. It is assumed that 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; Köhler *et al.*, 2018). ECMF communities are interpreted by the diversity of their exploration types, that is the distance of soil exploration from the host tree as based on morphological traits of colonized root tips and

emanating hyphae (Agerer, 2001). It is assumed that greater diversity of exploration types in the ECMF community raises the 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 since decades (Agerer, 2001; Fernandez & Kennedy, 2018; Lekberg & Helgason, 2018; Zanne *et al.*, 2019; Chaudhary *et al.*, 2022), but a holistic examination of decisive mycorrhizal fungal effect traits for key tree functions or for mycorrhizal economics (*cf.* Wright *et al.*, 2004; Bergmann *et al.*, 2020) is still lacking. Here, we assembled global quantitative information on mycorrhizal fungal traits in relation to forest tree functions in the 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 recapitulate the underlying rationales and conceptualize potential relationships between fungal effect traits and key tree response traits. Finally, we use the assembled database for testing these conceptual models in meta-analysis. We critically evaluate 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.

Materials and Methods

The mycorrhizal fungal trait database

We assembled information on mycorrhizal fungal traits used for understanding forest tree functions from a systematic literature survey in the Web of Science (Clarivate Analytics, Philadelphia, USA). We focused on six forest tree functions in the categories (i) resource acquisition (N, P, and water uptake), (ii) plant productivity (aboveground and belowground), 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 (Supporting Information Fig. **S1**). 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 criterion. As a result, a total of 464 studies entered the subsequent quantitative synthesis (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.

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.

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).

Data analyses

We identified significant positive or negative responses of mycorrhizal traits to tree functions as well as absent or non-significant relationships from our dataset. 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.

Results

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

Most studies relating mycorrhizal fungal traits to forest tree 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; Fig. **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 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). White spots on the global map of studies relating mycorrhizal fungal traits to forest tree functions remain in large parts of hot-dry or tropical Africa, continental Central Asia, and in (sub)polar Greenland.

A total of 501 tree species were used across 464 publications to relate mycorrhizal fungal traits to forest tree functions between the study years 1986 and 2022 (Fig. **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.) (Supporting Information Table **S1**). More than 200 studies investigated trees from the Fabaceae, 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 (Fig. **2**). Pine tree species are phylogenetic 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 both 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.

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; Fig. **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 here many from North America (33 studies).

Mycorrhizal fungal traits used for understanding forest tree functioning

Our literature survey resulted in 17 mycorrhizal fungal 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 functions (Table **1**). Most of all mycorrhizal trait studies focused on the influence of the fungal community assembly on tree functions (419 studies), predominantly by analyzing the genetic identity of mycorrhizal fungi, the fungal community composition, or the mycorrhizal fungal species richness. Almost 80% of all studies in the category fungal community assembly were conducted under controlled experimental conditions, and only a fifth in natural field settings.

The 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 on 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 (Supporting Information Fig. **S2**).

Less than 2% of all mycorrhizal trait studies focused on the category soil exploration by mycorrhizal hyphae (Table **1**). Six experimental studies considered AMF spore density and hyphal length as influencing factor for understanding tree 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 functions.

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 fungal community assembly (Fig. **4a**) and the host-symbiont interaction and soil exploration (Fig. **4b**), respectively. Three widely assumed 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; Diagne *et al.*, 2013; Köhler *et al.*, 2018; Clemmensen *et al.*, 2021). (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 (Meier *et al.*, 2013; Tedersoo & Bahram 2019; Argiroff *et al.*, 2022; Fanin *et al.*, 2022). We tested this conceptual framework against the published results on relationships between mycorrhizal fungal effect traits and key response functions of host trees.

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 soil resource acquisition and plant production (Table **2, 3**). The few existing studies on fungal genetic diversity found a positive influence on plant production but an unclear influence on soil resource acquisition (Table **2**), which partially confirms our first assumption on trait relationships (Fig. **4a**). 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 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 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 (limited) confirmation of our second assumption on trait relationships (Fig. **4b**). The effect of soil exploration on the 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 (Fig. **4b**). 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 host C release (Table **2**).

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 (Vandenkoornhuyse *et al.*, 2015; Choi *et al.*, 2021). 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 meta-analyze dependencies.

Important knowledge gaps in understanding holobiont functions of mycorrhizal trees

Based on our meta-analysis, we identify critical knowledge gaps to understand the functioning of the mycorrhizal symbiosis in forest trees. These gaps originate from (1) temperate sampling bias and extremely limited knowledge from Afrotropical, dry-continental, and arctic tree or forest biomes, (2) 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, (3) under-representation of ecophysiological measurements of ERM and rare arbutoid mycorrhizas, and (4) 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 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 (e.g., Diagne *et al.*, 2013; Thoen *et al.*, 2020; Bogar *et al.*, 2022). 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; Meier *et al.*, 2013; Köhler *et al.*, 2018). Only few studies investigated functions of trees associated with natural mycorrhizal fungal communities in the field (Zavišić *et al.*, 2018; Clemmensen *et al.*, 2021; Anthony *et al.*, 2022). 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.

ECMF exploration types can be vital for host tree functions

In our meta-analysis we identify soil exploration as understudied but potentially important mycorrhizal fungal trait with great potential for understanding tree response functions. ECMF can be ecological 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 and water transport rates and soil exploitation as well as to 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; Lilleskov *et al.*, 2011; Anthony *et al.*, 2022). 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 longer 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 traits relate positively to nutrient uptake and plant productivity (e.g., Sastry *et al.*, 2000; Chen *et al.*, 2016; Schoen *et al.*, 2021). These promising results strengthen the potential importance of exploration type abundances for host tree functions.

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 (Johnson *et al.*, 2012; Behm & Kiers, 2014) 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 (Plett *et al.*, 2015; Hortal *et al.*, 2017) 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. Our meta-analysis showed that higher mycorrhizal fungal species richness enhances tree nutrient acquisition, water uptake, and plant productivity (Bompadre *et al.*, 2013; Diagne *et al.*, 2013; Leberecht *et al.*, 2016; Köhler *et al.*, 2018). 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 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.

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 (Smith & Read, 2010; Phillips *et al.*, 2013). This is reflected in (i) greater C loss with root exudation in ECM tree species (Yin *et al.*, 2014; Liese *et al.*, 2018) depending on root morphology

(Akatsuki & Makita, 2020), and in (ii) slower litter decomposition rates in ECM ecosystems (Jiang *et al.*, 2021; Yin *et al.*, 2021; Carteron *et al.*, 2022), but faster decomposition by ECMF (Carteron *et al.*, 2022). Whether mycorrhizal colonization intensity *per se* exerts a control on root exudation and root litter decomposition remains contradictory, though (Meier *et al.*, 2013; Trap *et al.*, 2017; Argiroff *et al.*, 2022). 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).

Conclusion

Our holistic mycorrhizal trait attempt, which sets fungal traits in relationship to tree 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, they probably relate to soil exploration and exploitation and soil C transfer. An assessment of functionally relevant mycorrhizal 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 traits with strongest influence on tree functions.

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Author Contributions

ICM developed the initial idea. AMK generated the dataset for the meta-analysis and analyzed the data. AMK and ICM wrote, annotated, and approved the final version of the manuscript.

Data availability

The mycorrhizal fungal trait database that supports the finding of this study is available from the corresponding author upon reasonable request.

Competing interests

None declared.

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References

Agerer R. **2001**. Exploration types of ectomycorrhizae. *Mycorrhiza* **11**: 107–114.

Akatsuki M, Makita N. **2020**. Influence of fine root traits on *in situ* exudation rates in four conifers from different mycorrhizal associations. *Tree Physiology* **40**: 1071–1079.

Anthony MA, Crowther TW, van der Linde S, Suz LM, Bidartondo MI, Cox F, Schaub M, Rautio P, Ferretti M, Vesterdal L, *et al.* 2022. Forest tree growth is linked to mycorrhizal fungal composition and function across Europe. *The ISME Journal* **16**: 1327–1336.

Argiroff WA, Zak DR, Pellitier PT, Upchurch RA, Belke JP. **2022**. Decay by ectomycorrhizal fungi couples soil organic matter to nitrogen availability. *Ecology Letters* **25**: 391–404.

Baxter JW, Dighton J. **2001**. Ectomycorrhizal diversity alters growth and nutrient acquisition of grey birch (*Betula populifolia*) seedlings in host–symbiont culture conditions. *New Phytologist* **152**: 139–149.

Behm JE, Kiers ET. **2014**. A phenotypic plasticity framework for assessing intraspecific variation in arbuscular mycorrhizal fungal traits. *Journal of Ecology* **102**: 315–327.

Bergmann J, Weigelt A, van der Plas F, Laughlin DC, Kuyper TW, Guerrero-Ramirez N, Valverde-Barrantes OJ, Bruelheide H, Freschet GT, Iversen CM, *et al.* 2020. The fungal collaboration gradient dominates the root economics space in plants. *Science Advances* **6**: eaba375.

Bogar LM, Tavasieff OS, Raab TK, Peay KG. **2022**. Does resource exchange in ectomycorrhizal symbiosis vary with competitive context and nitrogen addition? *New Phytologist* **233**: 1331–1344.

Bompadre MJ, Rios De Molina MC, Colombo RP, Fernandez Bidondo L, Silvani VA, Pardo AG, Ocampo JA, Godeas AM. **2013**. Differential efficiency of two strains of the arbuscular mycorrhizal fungus *Rhizophagus irregularis* on olive (*Olea europaea*) plants under two water regimes. *Symbiosis* **61**: 105–112.

Borges RM. **2017**. Co-niche construction between hosts and symbionts: Ideas and evidence. *Journal of Genetics* **96**: 483–489.

Brundrett M. **2009**. Mycorrhizal associations and other means of nutrition of vascular plants: Understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. *Plant and Soil* **320**: 37–77.

Brundrett M, Tedersoo L. **2019**. Misdiagnosis of mycorrhizas and inappropriate recycling of data can lead to false conclusions. *New Phytologist* **221**: 18–24.

Carteron A, Cichonski F, Laliberté E. **2022**. Ectomycorrhizal stands accelerate decomposition to a greater extent than arbuscular mycorrhizal stands in a northern deciduous forest. *Ecosystems* **25**: 1234–1248.

Chaudhary VB, Rúa MA, Antoninka A, Bever JD, Cannon J, Craig A, Duchicela J, Frame A, Gardes M, Gehring C, *et al.* 2016. MycoDB, a global database of plant response to mycorrhizal fungi. *Scientific Data* **3**: 160028.

Chaudhary VB, Holland EP, Charman-Anderson S, Guzman A, Bell-Dereske L, Cheeke TE, Corrales A, Duchicela J, Egan C, Gupta MM, *et al.* 2022. What are mycorrhizal traits? *Trends in Ecology & Evolution* **37**: 573–581.

Chen W, Koide RT, Adams TS, DeForest JL, Cheng L, Eissenstat DM. **2016**. Root morphology and mycorrhizal symbioses together shape nutrient foraging strategies of temperate trees. *Proceedings of the National Academy of Sciences* **113**: 8741–8746.

Choi K, Khan R, Lee S-W. **2021**. Dissection of plant microbiota and plant-microbiome interactions. *Journal of Microbiology* **59**: 281-291.

Clemmensen KE, Bahr A, Ovaskainen O, Dahlberg A, Ekblad A, Wallander H, Stenlid J, Finlay RD, Wardle DA, Lindahl BD. **2013**. Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science* **339**: 1615–1618.

Clemmensen KE, Durling MB, Michelsen A, Hallin S, Finlay RD, Lindahl BD. **2021**. A tipping point in carbon storage when forest expands into tundra is related to mycorrhizal recycling of nitrogen. *Ecology Letters* **24**: 1193–1204.

Comas LH, Callahan HS, Midford PE. **2014**. Patterns in root traits of woody species hosting arbuscular and ectomycorrhizas: Implications for the evolution of belowground strategies. *Ecology and Evolution* **4**: 2979–2990.

Cornelissen JHC, Aerts R, Cerabolini B, Werger MJA, van der Heijden MGA. **2001**. Carbon cycling traits of plant species are linked with mycorrhizal strategy. *Oecologia* **129**: 611–619

Dawson SK, Carmona CP, González-Suárez M, Jönsson M, Chichorro F, Mallen-Cooper M, Melero Y, Moor H, Simaika JP, Duthie AB. **2021**. The traits of "trait ecologists": An analysis of the use of trait and functional trait terminology. *Ecology and Evolution* **11**: 16434–16445.

De Bello F, Lavorel S, Diaz S, Harrington R, Cornelissen JHC, Bardgett RD, Berg MP, Cipriotti P, Feld CK, Hering D, *et al.* 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation* **19**: 2873–2893.

De Grandcourt A, Epron D, Montpied P, Louisanna E, Béreau M, Garbaye J, Guehl J-M. **2004**. Contrasting responses to mycorrhizal inoculation and phosphorus availability in seedlings of two tropical rainforest tree species. *New Phytologist* **161**: 865–875.

Diagne N, Thioulouse J, Sanguin H, Prin Y, Krasova-Wade T, Sylla S, Galiana A, Baudoin E, Neyra M, Svistoonoff S, *et al.* 2013. Ectomycorrhizal diversity enhances growth and nitrogen fixation of *Acacia mangium* seedlings. *Soil Biology and Biochemistry* **57**: 468–476.

Eissenstat DM, Kucharski JM, Zadworny M, Adams TS, Koide RT. 2015. Linking root traits to nutrient foraging in arbuscular mycorrhizal trees in a temperate forest. *New Phytologist* **208**: 114–124.

Fanin N, Clemmensen KE, Lindahl BD, Farrell M, Nilsson MC, Gundale MJ, Kardol P, Wardle DA. **2022**. Ericoid shrubs shape fungal communities and suppress organic matter decomposition in boreal forests. *New Phytologist* **236**: 684-697.

Fernandez CW, Kennedy PG. **2018**. Melanization of mycorrhizal fungal necromass structures microbial decomposer communities. *Journal of Ecology* **106**: 468–479.

Garnier S, Ross N, Rudis B, Filipovic-Pierucci A, Galili T, Timelyportfolio, Greenwell B, Sievert C, Harris DJ, Sciaini M, *et al.* 2021. *Sjmgarnier/viridis: CRAN release v0.6.2 (v0.6.2CRAN).* Zenodo. URL https://doi.org/10.5281/zenodo.5579397.

Goodale CL. **2017**. Multiyear fate of a ^{15}N tracer in a mixed deciduous forest: Retention, redistribution, and differences by mycorrhizal association. *Global Change Biology* **23**: 867–880.

Halbritter AH, De Boeck HJ, Eycott AE, Robinson D, Vicca S, Berauer B, Christiansen CT, Estiarte M, Grünzweig JM, Gya R, *et al.* 2020. The handbook for standardised field and laboratory measurements in terrestrial climate-change experiments and observational studies (ClimEx). *Methods in Ecology and Evolution* **11**: 22–37.

Hazard C, Johnson D. **2018**. Does genotypic and species diversity of mycorrhizal plants and fungi affect ecosystem function? *New Phytologist* **220**: 1122–1128.

Heijden MGA van der, Martin FM, Selosse M-A, Sanders IR. **2015**. Mycorrhizal ecology and evolution: The past, the present, and the future. *New Phytologist* **205**: 1406–1423.

Hodge A, Fitter AH. 2010. Substantial nitrogen acquisition by arbuscular mycorrhizal fungi from organic material has implications for N cycling. Proceedings of the National Academy of Sciences **107**: 13754–13759.

Hortal S, Plett KL, Plett JM, Cresswell T, Johansen M, Pendall E, Anderson IC. **2017**. Role of plant–fungal nutrient trading and host control in determining the competitive success of ectomycorrhizal fungi. *The ISME Journal* **11**: 2666–2676.

Iversen CM, McCormack ML, Powell AS, Blackwood CB, Freschet GT, Kattge J, Roumet C, Stover DB, Soudzilovskaia NA, Valverde-Barrantes OJ, *et al.* 2017. A global fine-root ecology database to address below-ground challenges in plant ecology. *New Phytologist* **215**: 15–26.

Jalón LG de, Limousin J-M, Richard F, Gessler A, Peter M, Hättenschwiler S, Milcu A. **2020**. Microhabitat and ectomycorrhizal effects on the establishment, growth and survival of *Quercus ilex* L. seedlings under drought. *PLOS ONE* **15**: e0229807.

Jiang L, Wang H, Li S, Fu X, Dai X, Yan H, Kou L. **2021**. Mycorrhizal and environmental controls over root trait–decomposition linkage of woody trees. *New Phytologist* **229**: 284–295.

Jin Y, Qian H. **2019**. V.PhyloMaker: an R package that can generate very large phylogenies for vascular plants. *Ecography* **42**: 1353–1359.

Johnson D, Martin F, Cairney JWG, Anderson IC. **2012**. The importance of individuals: intraspecific diversity of mycorrhizal plants and fungi in ecosystems. *New Phytologist* **194**: 614–628.

Karst J, Jones MD, Hoeksema JD. **2023**. Positive citation bias and overinterpreted results lead to misinformation on common mycorrhizal networks in forests. *Nature Ecology & Evolution*, online early. doi: 10.1038/s41559-023-01986-1

Köhler J, Yang N, Pena R, Raghavan V, Polle A, Meier IC. **2018**. Ectomycorrhizal fungal diversity increases phosphorus uptake efficiency of European beech. *New Phytologist* **220**: 1200–1210.

Leberecht M, Tu J, Polle A. **2016**. Acid and calcareous soils affect nitrogen nutrition and organic nitrogen uptake by beech seedlings (*Fagus sylvatica* L.) under drought, and their ectomycorrhizal community structure. *Plant and Soil* **409**: 143–157.

Lekberg Y, Helgason T. **2018**. *In situ* mycorrhizal function – knowledge gaps and future directions. *New Phytologist* **220**: 957–962.

Leuschner C, Meier IC. **2018**. The ecology of Central European trees: Trait spectra, functional trade-offs, and ecological classification of adult trees. *Perspectives in Plant Ecology, Evolution and Systematics* **33**: 89–103.

Liese R, Alings K, Meier IC. **2017**. Root branching is a leading root trait of the plant economics spectrum in temperate trees. *Frontiers in Plant Science* **8**: 315.

Liese R, Lübbe T, Albers NW, Meier IC. **2018**. The mycorrhizal type governs root exudation and nitrogen uptake of temperate tree species. *Tree Physiology* **38**: 83–95.

Liese R, Leuschner C, Meier IC. **2019**. The effect of drought and season on root life span in temperate arbuscular mycorrhizal and ectomycorrhizal tree species. *Journal of Ecology* **107**: 2226–2239.

Lilleskov EA, Hobbie EA, Horton TR. **2011**. Conservation of ectomycorrhizal fungi: Exploring the linkages between functional and taxonomic responses to anthropogenic N deposition. *Fungal Ecology* **4**: 174–183.

Lilleskov EA, Kuyper TW, Bidartondo MI, Hobbie EA. **2019**. Atmospheric nitrogen deposition impacts on the structure and function of forest mycorrhizal communities: A review. *Environmental Pollution* **246**: 148–162.

Meier IC, Avis PG, Phillips RP. **2013**. Fungal communities influence root exudation rates in pine seedlings. *FEMS Microbiology Ecology* **83**: 585–595.

Moher D, Liberati A, Tetzlaff J, Altman DG. **2010**. Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. *International Journal of Surgery* **8**: 336–341.

Nguyen NH, Song Z, Bates ST, Branco S, Tedersoo L, Menke J, Schilling JS, Kennedy PG. **2016**. FUNGuild: An open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecology* **20**: 241–248.

Pellitier PT, Zak DR. **2018**. Ectomycorrhizal fungi and the enzymatic liberation of nitrogen from soil organic matter: why evolutionary history matters. *New Phytologist* **217**: 68–73.

Pellitier PT, Zak DR, Argiroff WA, Upchurch RA. **2021**. Coupled shifts in ectomycorrhizal communities and plant uptake of organic nitrogen along a soil gradient: An isotopic perspective. *Ecosystems* **24**: 1976–1990.

Pena R, Polle A. **2014**. Attributing functions to ectomycorrhizal fungal identities in assemblages for nitrogen acquisition under stress. *The ISME Journal* **8**: 321–330.

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

Plett JM, Kohler A, Khachane A, Keniry K, Plett KL, Martin F, Anderson IC. **2015**. The effect of elevated carbon dioxide on the interaction between *Eucalyptus grandis* and diverse isolates of *Pisolithus* sp. is associated with a complex shift in the root transcriptome. *New Phytologist* **206**: 1423–1436.

Põlme S, Abarenkov K, Henrik Nilsson R, Lindahl BD, Clemmensen KE, Kauserud H, Nguyen N, Kjøller R, Bates ST, Baldrian P, *et al.* 2020. FungalTraits: a user-friendly traits database of fungi and fungus-like stramenopiles. *Fungal Diversity* **105**: 1–16.

R Development Core Team. 2020. *R: The R Project for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. URL https://www.r-project.org/

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

Read DJ, Perez-Moreno J. **2003**. Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? *New Phytologist* **157**: 475–492.

Sastry MSR, Sharma AK, Johri BN. **2000**. Effect of an AM fungal consortium and *Pseudomonas* on the growth and nutrient uptake of *Eucalyptus* hybrid. *Mycorrhiza* **10**: 55–61.

Schoen C, Montibeler M, Costa MD, Antunes PM, Stürmer SL. **2021**. Inter and intra-specific variability in arbuscular mycorrhizal fungi affects hosts and soil health. *Symbiosis* **85**: 273–289.

See CR, Keller AB, Hobbie SE, Kennedy PG, Weber PK, Pett-Ridge J. 2022. Hyphae move matter and microbes to mineral microsites: Integrating the hyphosphere into conceptual models of soil organic matter stabilization. *Global Change Biology* **28**: 2527–2540.

Siqueira JO, Saggin-Júnior OJ, Flores-Aylas WW, Guimarães PTG. **1998**. Arbuscular mycorrhizal inoculation and superphosphate application influence plant development and yield of coffee in Brazil. *Mycorrhiza* **7**: 293–300.

Smith SE, Read DJ. **2010**. *Mycorrhizal Symbiosis*. New York, USA: Academic Press.

Soudzilovskaia NA, Douma JC, Akhmetzanova AA, van Bodegom PM, Cornwell WK, Moens EJ, Treseder KK, Tibbett M, Wang YP, Cornelissen JHC. **2015**. Global patterns of plant root colonization intensity by mycorrhizal fungi explained by climate and soil chemistry. *Global Ecology and Biogeography* **24**: 371–382.

Soudzilovskaia NA, Vaessen S, Barcelo M, He J, Rahimlou S, Abarenkov K, Brundrett MC, Gomes SIF, Merckx V, Tedersoo L. **2020**. FungalRoot: Global online database of plant mycorrhizal associations. *New Phytologist* **227**: 955–966.

Steidinger BS, Crowther TW, Liang J, Van Nuland ME, Werner GDA, Reich PB, Nabuurs GJ, de-Miguel S, Zhou M, Picard N, *et al.* 2019. Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. *Nature* **569**: 404–408.

Suz LM, Bidartondo MI, van der Linde S, Kuyper TW. **2021**. Ectomycorrhizas and tipping points in forest ecosystems. *New Phytologist* **231**: 1700–1707.

Tedersoo L, Bahram M. **2019**. Mycorrhizal types differ in ecophysiology and alter plant nutrition and soil processes. *Biological Reviews* **94**: 1857-1880.

Thoen E, Harder CB, Kauserud H, Botnen SS, Vik U, Taylor AFS, Menkis A, Skrede I. **2020**. *In vitro* evidence of root colonization suggests ecological versatility in the genus *Mycena*. *New Phytologist* **227**: 601–612.

Trap J, Akpa-Vinceslas M, Margerie P, Boudsocq S, Richard F, Decaëns T, Aubert M. **2017**. Slow decomposition of leaf litter from mature *Fagus sylvatica* trees promotes offspring nitrogen acquisition by interacting with ectomycorrhizal fungi. *Journal of Ecology* **105**: 528–539.

Vandenkoornhuyse P, Quaiser A, Duhamel M, Le Van A, Dufresne A. **2015**. The importance of the microbiome of the plant holobiont. *New Phytologist* **206**: 1196-1206.

Větrovský T, Morais D, Kohout P, Lepinay C, Algora C, Awokunle Hollá S, Bahnmann BD, Bílohnědá K, Brabcová V, D'Alò F, *et al.* (2020) GlobalFungi, a global database of fungal occurrences fromhigh-throughput-sequencing metabarcoding studies. *Scientific Data* **7**: 228.

Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. **2007**. Let the concept of trait be functional! *Oikos* **116**: 882–892.

Wickham H. **2009**. *ggplot2: Elegant Graphics for Data Analysis*. New York, USA: Springer.

Wickham H, Averick M, Bryan J, Chang W, McGowan LD, François R, Grolemund G, Hayes A, Henry L, Hester J, *et al.* 2019. Welcome to the tidyverse. *Journal of Open Source Software* **4**: 1686.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Barres J, Chapin T, Cornelissen JHC, Diemer M, *et al.* 2004. The worldwide leaf economics spectrum. *Nature* **428**: 821–827.

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

Yin L, Dijkstra FA, Phillips RP, Zhu B, Wang P, Cheng W. **2021**. Arbuscular mycorrhizal trees cause a higher carbon to nitrogen ratio of soil organic matter decomposition via rhizosphere priming than ectomycorrhizal trees. *Soil Biology and Biochemistry* **157**: 108246.

Yu G, Smith DK, Zhu H, Guan Y, Lam TT-Y. **2017**. ggtree: An R package for visualization and annotation of phylogenetic trees with their covariates and other associated data. *Methods in Ecology and Evolution* **8**: 28–36.

Zanne AE, Abarenkov K, Afkhami ME, Aguilar-Trigueros CA, Bates S, Bhatnagar JM, Busby PE, Christian N, Cornwell W, Crowther TW, *et al.* 2019. Fungal functional ecology: Bringing a trait-based approach to plant-associated fungi. *Biological Reviews* **95**: 409–433.

Zavišić A, Yang N, Marhan S, Kandeler E, Polle A. **2018**. Forest soil phosphorus resources and fertilization affect ectomycorrhizal community composition, beech P uptake efficiency, and photosynthesis. *Frontiers in Plant Science* **9**: 463.

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.

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

	Resource acquisition				C release		
Mycorrhizal trait	**P uptake**	**N uptake**	**H_2O uptake**	**Plant product.**	**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 trait and a host tree 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 key response traits in forest trees (systematic literature review; *n* = 464 studies between 1986-2022)

Tree function / Fungal 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

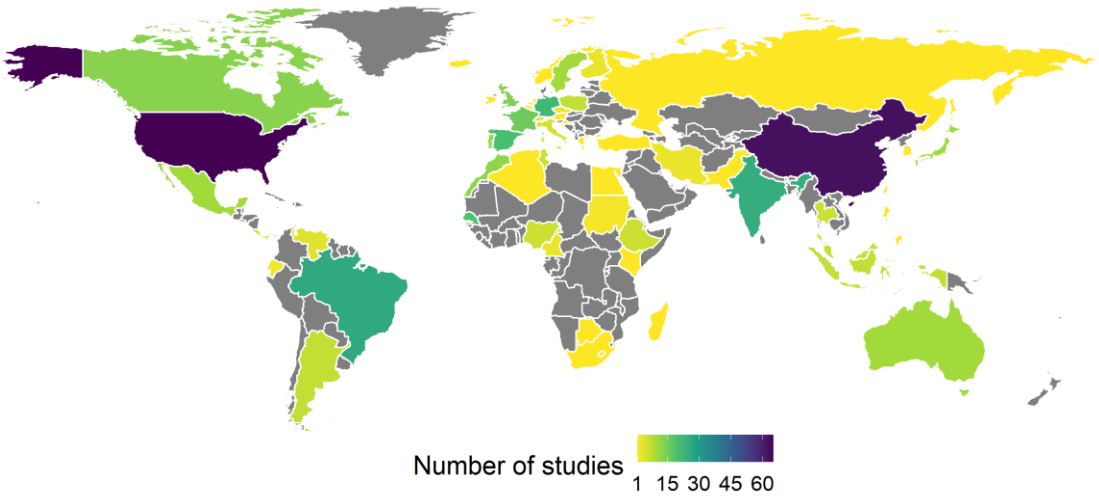

Fig. 1 Global distribution of studies relating mycorrhizal fungal traits to forest tree functions between the study years 1986 and 2022 (*n* = 464 studies).

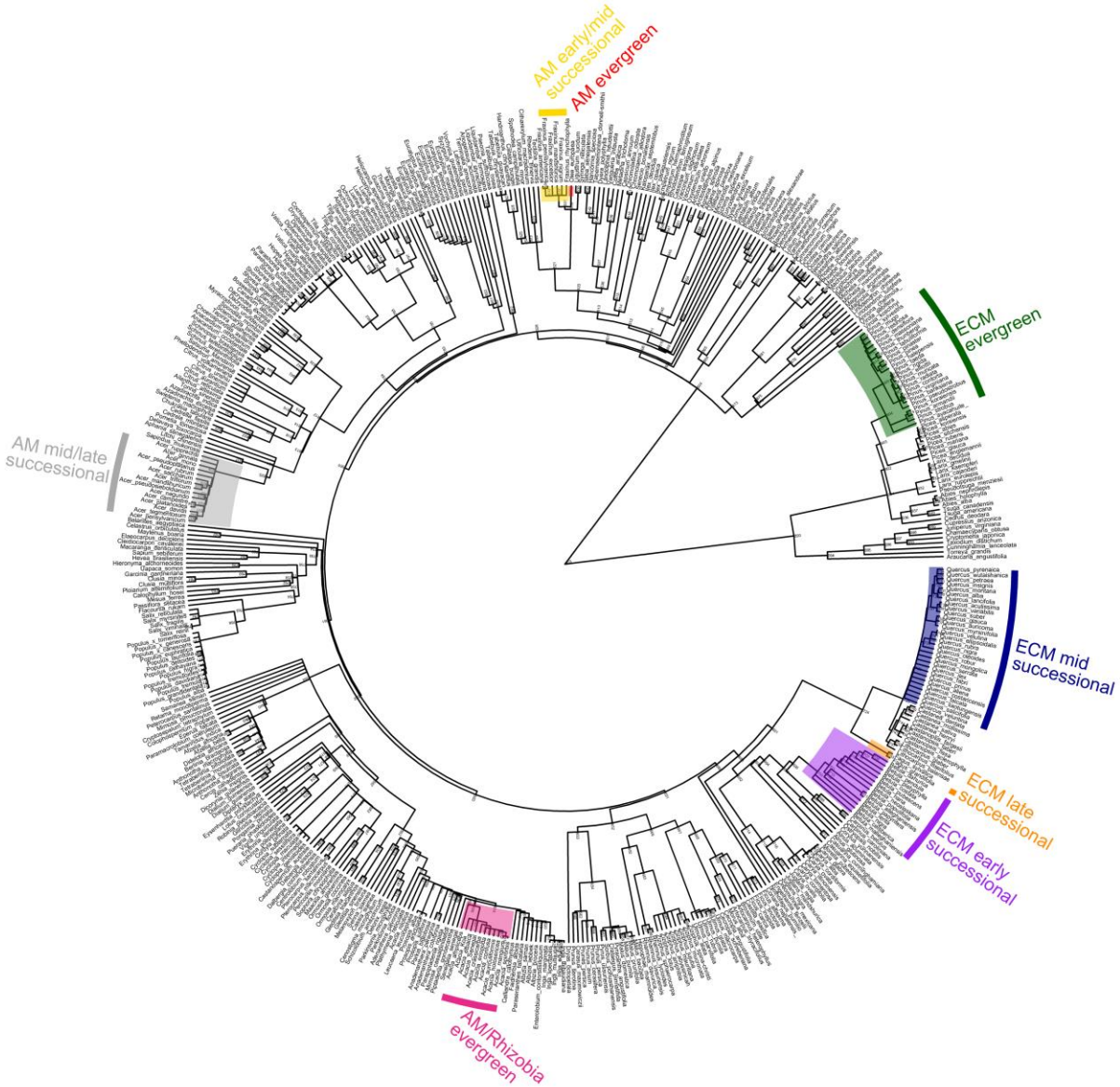

Fig. 2. Phylogenetic tree for the tree species used to relate mycorrhizal fungal traits to forest tree functions (study years 1986-2022). The nodes with genera dominating the investigations are highlighted by different colors.

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.

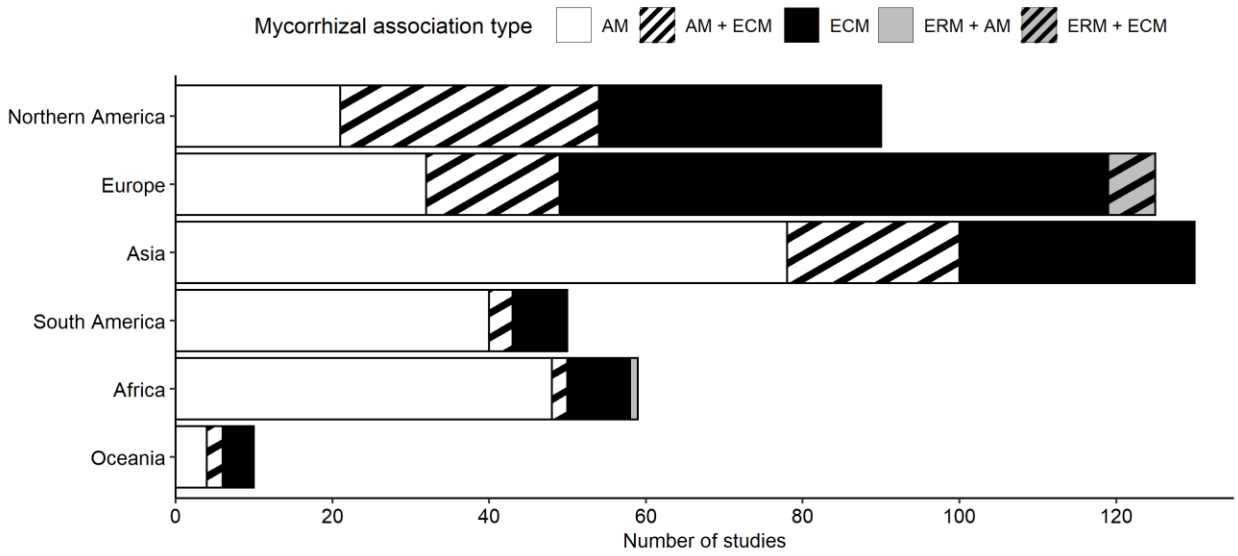

Fig. 3. Continental distribution of distinct mycorrhizal association types studied to relate mycorrhizal fungal traits to forest tree functions (study years 1986-2022).

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

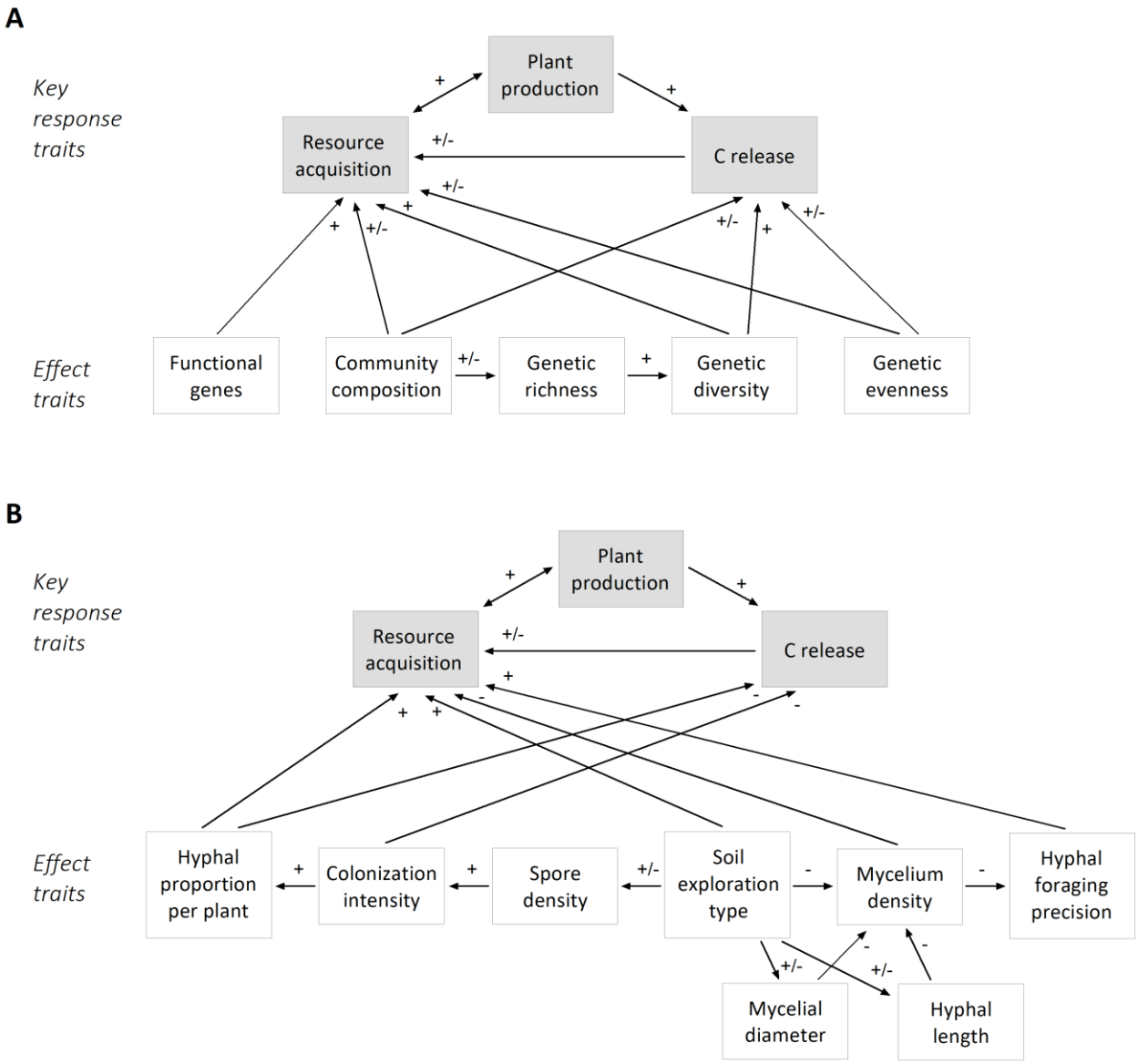

Fig. 4. Conceptual models of plausible interactions between mycorrhizal fungal effect traits (**a**: fungal community assembly; **b**: host-symbiont interactions and soil exploration) and key response traits in forest trees.

+ positive effect, - negative effect