Tansley review

The mycorrhizal symbiosis: research frontiers in genomics, ecology, and agricultural application

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Summary

Mycorrhizal symbioses between plants and fungi are vital for the soil structure, nutrient cycling, plant diversity, and ecosystem sustainability. More than 250 000 plant species are associated with mycorrhizal fungi. Recent advances in genomics and related approaches have revolutionized our understanding of the biology and ecology of mycorrhizal associations. The genomes of 250+ mycorrhizal fungi have been released and hundreds of genes that play pivotal roles in regulating symbiosis development and metabolism have been characterized. rDNA metabarcoding and metatranscriptomics provide novel insights into the ecological cues driving mycorrhizal communities and functions expressed by these associations, linking genes to ecological traits such as nutrient acquisition and soil organic matter decomposition. Here, we review genomic studies that have revealed genes involved in nutrient uptake and symbiosis development, and discuss adaptations that are fundamental to the evolution of mycorrhizal lifestyles. We also evaluated the ecosystem services provided by mycorrhizal networks and discuss how mycorrhizal symbioses hold promise for sustainable agriculture and forestry by enhancing nutrient acquisition and stress tolerance. Overall, unraveling the intricate dynamics of mycorrhizal symbioses is paramount for promoting ecological sustainability and addressing current pressing environmental concerns. This review ends with major frontiers for further research.

I. Introduction

It is widely acknowledged that mycorrhizal associations are prevalent in almost all terrestrial ecosystems, ranging from deserts and tropical forests to savannahs and arable land (Tedersoo *et al.*, 2014; van der Heijden *et al.*, 2015). Over 80% of land plants (>250 000 plant species) form symbiotic associations with mycorrhizal fungi (van der Heijden *et al.*, 2008, 2015; Tedersoo *et al.*, 2014). Based on their structure and function, four major types of mycorrhizal symbioses have been recognized: arbuscular mycorrhiza (AM), ectomycorrhiza (ECM), orchid mycorrhiza (ORM), and ericoid mycorrhiza (ERM; Fig. 1). Mycorrhizal fungi reside within the root cortex and rhizodermis. Fungal hyphae extend from the roots into the soil, actively exploring for limited nutrients essential for plant growth, such as nitrogen (N) and phosphorus (P), as well as a wide range of micro-elements (e.g. Fe, Cu, Zn, and Mn). Certain mycorrhizal fungi, including ECM and ERM, also acquire organically bound N and P. Mycorrhizal fungi receive carbon (C) compounds and vitamins from their host plants in return for these nutrients and other benefits (van der Heijden *et al.*, 2015; Martin *et al.*, 2017).

Mycorrhizal symbioses are of immense significance for biologists and ecologists because of their profound influence on plant and fungal growth, fitness, and diversity (van der Heijden *et al.*, 2015; Brundrett & Tedersoo, 2018). Moreover, these mutualistic relationships play a pivotal role in the N and P cycles within ecosystems (Saito & Ezawa, 2016; Nehls & Plassard, 2018; Pellitier & Zak, 2018). Numerous studies have demonstrated that AMF and ECM mycorrhizal symbionts can drain a substantial proportion of host C compounds, accounting for 5–30% of C flow. Globally, the flux of

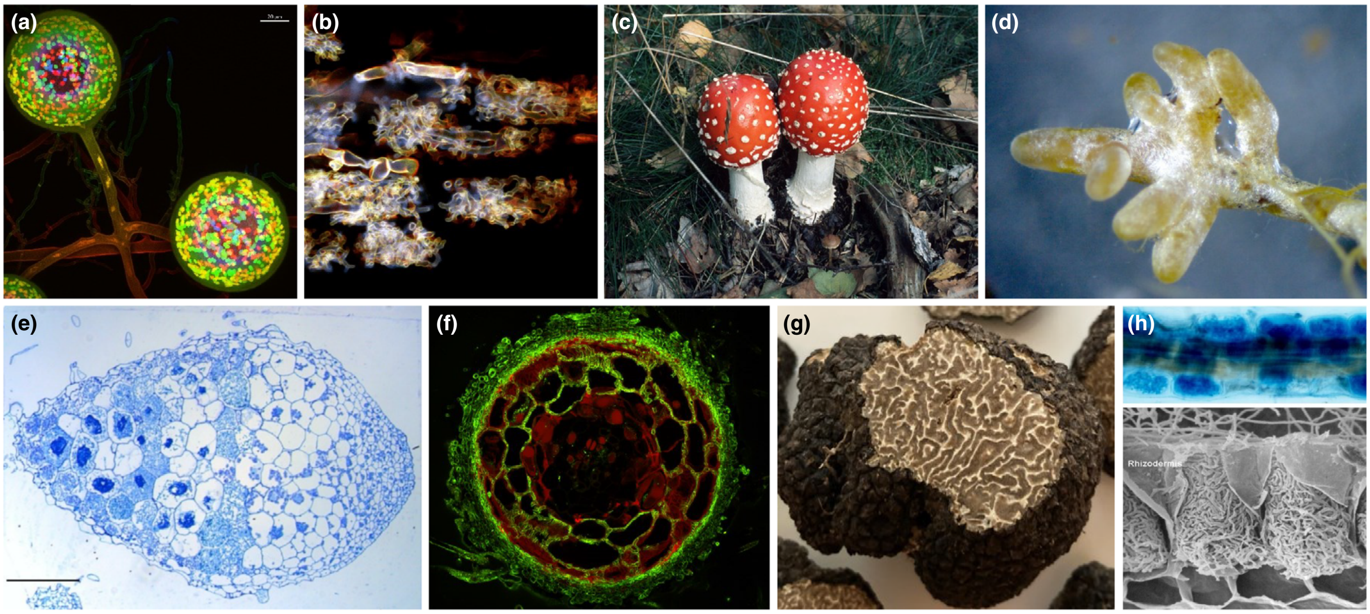

Fig. 1 Typical structures of various types of mycorrhizal symbioses. (a) Arbuscular mycorrhizal fungi (AMF) spores of *Rhizophagus irregularis* containing hundreds of stained nuclei; photo courtesy of Vasilis Kokkoris (Vrije Universeit, Amsterdam). Nuclei are visible due to staining with SYTO 13 Green Fluorescent nucleic acid dye. Each image is the result of *c.* 300 z stacks (0.35-μm intervals) visualized using confocal laser scanning microscopy. Bar, 20 μm. (b) AMF arbuscules in lettuce root cells colonized by an unknown species of native AMF. Hyphal threads were stained with WGA-Alexa Fluor 488, a chitin stain, and visualized using confocal laser scanning microscopy; photo courtesy of Jen McGaley and Uta Paszkowski (University of Cambridge). (c) Fruiting body of the ectomycorrhizal fly agaric *Amanita muscaria*; photo courtesy of Marcel van der Heijden. (d) Ectomycorrhizal roots formed between the ectomycorrhizal mate bolet *Xerocomellus pruinatus* and pine (×40 magnification); photo courtesy of Marc Buée (INRAE). (e) Protocorms of the germinating orchid *Serapias vomeracea* colonized by hyphae of the mycorrhizal fungus *Tulasnella calospora*. Only the plant cells in the basal part of the orchid protocorm (left) contain mycorrhizal fungal coils, whereas the apical part of the protocorm (right) with the plant apical meristem is not colonized. The dark blue structures in some of the colonized protocorm cells correspond to partially collapsed (and consumed) fungal coils that deliver carbon and nutrients to the orchid protocorm (Perotto & Balestrini, 2023). Bar, 250 μm. Photo courtesy of Silvia Perotto (Università di Torino). (f) Cross-section of a root of *Pinus sylvestris* colonized by the ectomycorrhizal fungus *Cenococcum geophilum*. All typical features of the ectomycorrhizal symbiosis are shown, including a loose external mantle, aggregated internal mantle, and Hartig net encasing epidermal and cortical root cells. Fungal hyphae are stained in green with WGA-Alexafluor 488, while root cells are stained in red by propidium iodide (Bar, 50 μm; photo courtesy of Maira de Freitas Pereira (INRAE)). (g) Ascocarp of the truffle *Tuber macrosporum*; photo courtesy of Janis Rogenmoser (University of Zurich). (h) Overview of root cells of *Erica carnea* colonized by hyphae of an ericoid mycorrhizal fungus stained in blue (top panel), and an electron micrograph showing *Pyrola minor* cells containing a large number of fungal hyphae forming pelotons; photo courtesy of Rosmarie Honegger (University of Zurich).

plant-fixed C entering the living mycelium is equivalent to *c.* 36% of annual CO_2 emissions from fossil fuels (Hawkins *et al.*, 2023). Therefore, it is important to investigate whether mycorrhizal fungi influence soil organic C formation, especially the more persistent mineral-associated organic C pool, which is thought to be important for long-term C sequestration (Clemmensen *et al.*, 2021; Hicks Pries *et al.*, 2023; Horsch *et al.*, 2023; Wu *et al.*, 2023). In the context of ongoing global change, it is also crucial to investigate the role of mycorrhizal associations in sustainable ecosystem functioning (Angulo *et al.*, 2022; Trivedi *et al.*, 2022; Wang *et al.*, 2022; Allsup *et al.*, 2023).

Over the past two decades, genomics, as a tool for analyzing the genetic information of organisms, has emerged as a fundamental approach for understanding the biology, evolution, and ecology of mycorrhizal symbioses. In addition to providing critical mechanistic insights, genetic information also identifies targets that can be prioritized for the application of mycorrhizal symbioses in agriculture and forestry. In this review, we discuss recent studies that illustrate the impact of genomics and related approaches (e.g. DNA metabarcoding and transcriptomics) on our understanding of mycorrhizal associations. First, we summarize the current knowledge on mycorrhizal fungal genomes and their implications for understanding the transition from saprotrophism to symbiosis across the fungal tree of life. Second, we examine how the genomes of mycorrhizal fungi and their host trees have been utilized to understand the molecular mechanisms underlying the establishment and function of symbiosis. These resources have facilitated the identification of the genes and pathways involved in symbiotic development, nutrient exchange, and stress tolerance. Third, we discuss how high-throughput metabarcoding tools have unraveled the remarkable biodiversity of soil fungi, revealing their distribution from small soil cores to the entire continent. In our discussion, we emphasize the significance of mycorrhizal networks in natural ecosystems and highlight their roles in providing various ecosystem services. We also briefly discuss the potential applications of mycorrhizal symbiosis in sustainable agriculture and ecosystem restoration, underscoring the importance of understanding the functional traits and ecological roles of mycorrhizal fungi. By synthesizing the latest research findings, this review aims to identify knowledge gaps and propose future directions for mycorrhizal research to address the global challenges in agriculture, forestry, and environmental sustainability.

II. Harnessing genomics to enhance our understanding of the development, evolution, and functioning of mycorrhizal symbioses

The Joint Genome Institute (JGI) MycoCosm database currently contains 2701 fungal genomes (as of November 2023), including 220+ mycorrhizal fungi, and the National Center for Biotechnology Information GenBank has annotations for 4770 genomes (as of November 2023), demonstrating the enormous progress made in the field (Martin *et al.*, 2011; Grigoriev *et al.*, 2014). The fungal species that have been sequenced are highly diverse and comprise major clades of Mycota. Among the genomes available in the MycoCosm database, 1693 belonged to Ascomycota, 696 to Basidiomycota, and 181 to Mucoromycota (including 13 to Glomeromycotina).

The release of the genomes of the ECM fungi *Laccaria bicolor* and *Tuber melanosporum* (Martin *et al.*, 2008, 2010) and the AM fungi *Rhizophagus irregularis* (Tisserant *et al.*, 2013) has opened up new avenues for geneticists to compare the mycorrhizal genomic blueprint with those of saprotrophic and pathogenic species, thereby advancing our understanding of mycorrhizal symbiont evolution. The current selection of sequenced mycorrhizal fungi is based on their ability to establish different mycorrhizal associations, their ecological significance, phylogenetic relationships, and practical considerations. This array of available genome sequences provides opportunities to investigate the evolutionary patterns and functional attributes of mycorrhizal symbioses across dozens of fungal families (Wolfe *et al.*, 2012; Kohler *et al.*, 2015; Peter *et al.*, 2016; Murat *et al.*, 2018; Miyauchi *et al.*, 2020; Marqués-Gálvez *et al.*, 2021; Lebreton *et al.*, 2022; Looney *et al.*, 2022; Kobayashi *et al.*, 2023; Plett *et al.*, 2023). For several families, such as Boletales, the data highlighted not only which areas of the genomes were similar between the different species but also when their sequences diverged on a scale of millions of years (Miyauchi *et al.*, 2020; Lofgren *et al.*, 2021; Wu *et al.*, 2022). The primary objectives of these genome-based studies were to (1) monitor the various independent lifestyle transitions from saprotrophism to mutualism in fungal lineages (e.g. Agaricales, Boletales, and Russulales), (2) establish connections between genome characteristics and important ecological traits, such as nutrient uptake and soil organic matter (SOM), and (3) identify gene sets involved in the development and functioning of mycorrhizal associations. In the following sections, we provide a summary of the key findings of these studies regarding the major types of mycorrhizal symbioses.

1. Arbuscular mycorrhizal fungi

Arbuscular mycorrhizal fungi (AMF) have captivated evolutionary biologists because of their ancient origins, which date back to *c.* 500 million years (Fig. 2; Simon *et al.*, 1993; Brundrett & Tedersoo, 2018). Their long evolutionary history and distinctive biological characteristics make them fascinating subjects of study. Ambiguity remained concerning the evolutionary history of Glomeromycota, either as sister to Mucoromycota and Mortierellomycota, or as sister to Dikarya (Ascomycota and Basidiomycota). Although it is generally thought that Mucoromycota comprises three subphyla, Glomeromycotina, Mortierellomycotina, and Mucoromycotina, and is sister to Dikarya (Spatafora *et al.*, 2016), it is worth noting that some authors have re-elevated Glomeromycotina to a phylum (Strassert & Monaghan, 2022).

Arbuscular mycorrhizal fungi possess coenocytic hyphae that contain thousands of nuclei and reproduce as large multinucleated spores (Fig. 1). To date, nuclear genome assemblies have been released from representative species of different AMF orders, from Glomerales to Diversisporales, and Archaeosporales. They have unusually large genomes: *c.* 150 Mb for *Rhizophagus* species to 784 Mb for *Gigaspora* species (Tisserant *et al.*, 2013; Kobayashi *et al.*, 2018; Morin *et al.*, 2019; Venice *et al.*, 2020), which are rich in repetitive sequences. The early diverging AMF *Paraglomus*

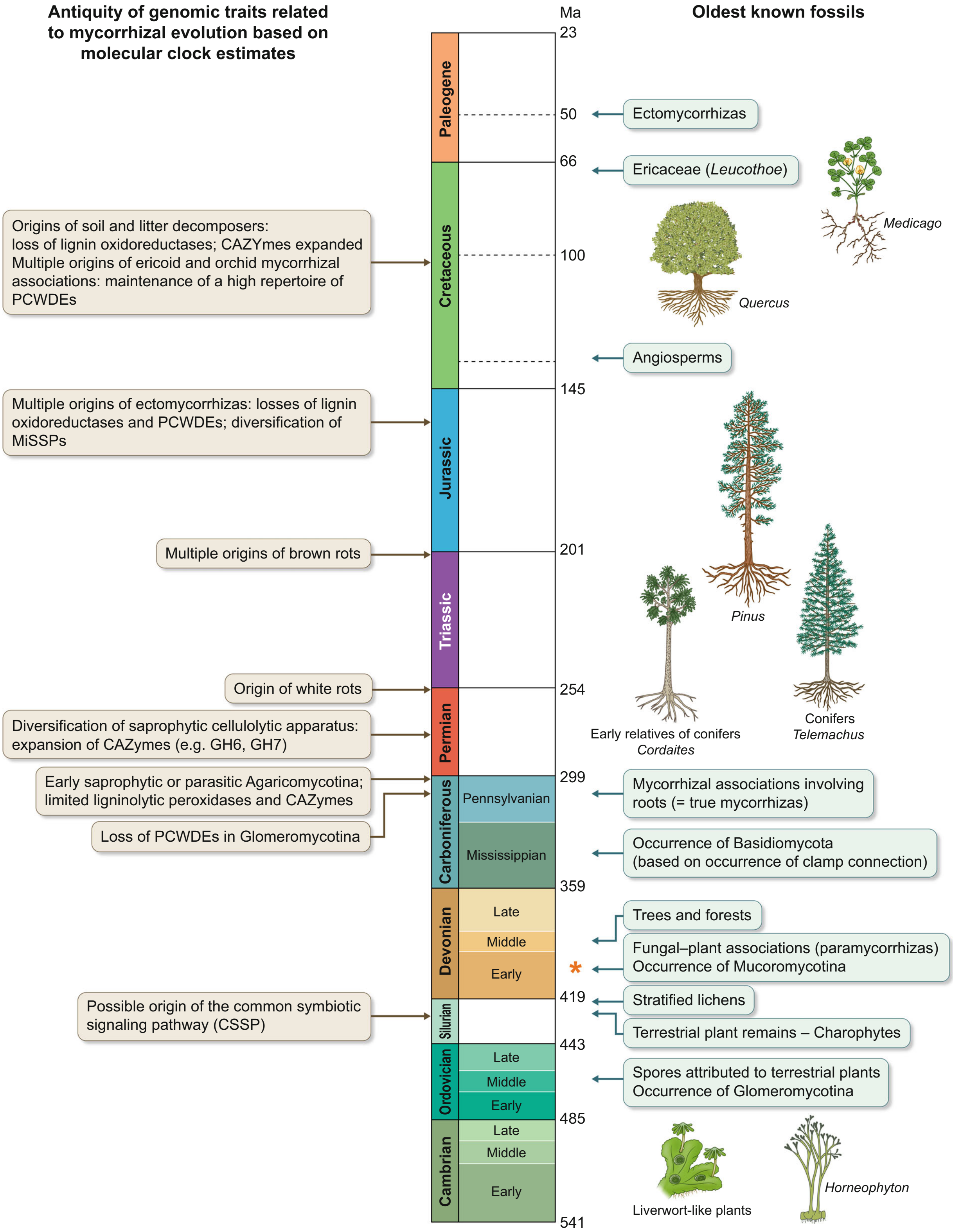

Fig. 2 Emergence of key symbiotic genomic traits related to mycorrhizal symbiosis evolution (left) based on molecular clock estimates along the geological time scale/geological epochs from the Cambrian to the Paleogene (middle) with oldest known fossils (right). The orange asterisk represents the formation of the Rhynie chert at 407 Ma. Illustrations of early land plants (liverwort-like plants, *Horneophyton*), early relatives of conifers (Cordaites), conifers (*Telemachus*, *Pinus*), and Angiosperms (*Quercus*, *Medicago*) are shown. CAZymes, carbohydrate-active enzymes; GH, glycosyl hydrolase; MiSSPs, mycorrhiza-induced small secreted proteins; PCWDEs, plant cell wall-degrading enzymes. Adapted from Strullu-Derrien *et al*. (2018).

occultum (Paraglomerales) possesses a much smaller genome size (39.6 Mb) and fewer genes and repeats than most AMF relatives (Malar *et al.*, 2022). Intriguingly, these early-branching AMF appear to be less beneficial in terms of stimulating plant growth than the more recently evolved AMF (Säle *et al.*, 2021). The genome of *Geosiphon pyriformis* (Archaeosporales), which establishes symbiosis with the N-fixing cyanobacterium *Nostoc punctiforme*, shares all hallmarks of obligate AMF biotrophy, suggesting that this fungus has an evolutionary history similar that to of AMF (Malar *et al.*, 2021). Genome and molecular biology analyses have revealed that AMF obligate biotrophy results from a loss of fatty acid biosynthesis but also entails the loss of genes encoding plant cell wall-degrading enzymes (PCWDEs), as well as genes involved in thiamine synthesis (Tisserant *et al.*, 2013; Reinhardt *et al.*, 2021). A breakthrough was the demonstration that host plants supply *R. irregularis* with large amounts of fatty acids (Kameoka & Gutjahr, 2022). The combination of Hi-C and HiFi PacBio sequencing identified two sets of homologous chromosomes among thousands of coexisting nuclei in AMF heterokaryons. These two sets of related genomes differ in content, gene expression, and epigenetic regulation, and the abundance of each set varies depending on the host plant and environmental conditions (Sperschneider *et al.*, 2023).

The notion that AMF are ancient asexual organisms has been challenged by genomic analysis (Ropars *et al.*, 2016). Genomic regions and nuclear organizations associated with sexual reproduction have been identified, including meiosis-specific genes, putative mating-type loci, and homokaryotic-dikaryotic life stages (Kokkoris *et al.*, 2021; Reinhardt *et al.*, 2021; Yildirir *et al.*, 2022).

Various Mucoromycotina fungi can establish AMF-like symbiotic associations with liverworts, hornworts, and other land plants. However, the genomes of these symbionts have not yet been sequenced. These so-called fine-root endophytes can enhance plant growth and nutrition (Hoysted *et al.*, 2023) and are often more abundant in agricultural fields than in native biomes (Albornoz *et al.*, 2022). Niche differentiation between the Mucoromycotinian and Glomeromycotinian AMF has been suggested (Mansfield *et al.*, 2023), pointing to their agronomic and ecological relevance, as they may have complementary functions in ecosystems. Genome sequencing of fine-root endophytes will highlight their evolution, biology, and ecology.

The development of symbiotic structures and metabolic activity in symbiotic tissues requires integrated coordination and communication between symbionts, leading to changes in gene expression and activation of signaling pathways. Conservation of the 'common symbiotic signaling pathway' (CSSP) among various angiosperm species is highly noteworthy (Fig. 2; Delaux *et al.*, 2015). This underscores the shared evolutionary origin of this ancient symbiotic signaling pathway. Phylogenomic studies have suggested that certain features of this pathway may have predated the evolution of the first terrestrial plants in the Middle to Late Ordovician and contributed to the establishment of the earliest AM associations with ancestral land plants (Delaux *et al.*, 2015). To date, only a few studies have measured fungal transcriptional responses to different environmental conditions (Grunwald *et al.*, 2009; Hohnjec *et al.*, 2005; Zeng *et al.*, 2018). Serrano *et al.* (2023) utilized both single-nucleus and spatial RNA sequencing techniques to explore the transcriptomes of AM symbiosis at the cellular and spatial resolution level. They identified cell type-specific responses to symbiosis, in agreement with previous studies using laser capture microdissection-based transcriptomic analyses (Gaude *et al.*, 2012; Hogekamp & Küster, 2013). These RNA profiling studies have identified a set of robust symbiosis-responsive genes, including many characterized marker genes that are critical to symbiosis, such as those involved in P metabolism (e.g. *MtPT4*) and those encoding effector-like proteins (Fig. 2). Although the identity and function of most transcripts differentially expressed by plants and fungi during symbiotic interactions have not yet been characterized, these studies provide valuable insights into the molecular mechanisms underlying AM symbiosis (see Lanfranco & Bonfante, 2023 for a review).

As effector-like small secreted proteins and small RNAs play a key role in plant–pathogen interactions, they have also been investigated in AM associations (Ledford *et al.*, 2023). Aparicio Chacón *et al.* (2023) identified a set of mycorrhiza-induced secreted effector-like proteins, some of which regulate the expression of host genes. Teulet *et al.* (2023) found proteins with structural similarity to known *Fusarium oxysporum* dual domain effectors. Of the hundreds of predicted effector proteins from the AM fungus *R. irregularis*, only five have been characterized to date: nucleus-localized secreted protein 7 (Kloppholz *et al.*, 2011), putative strigolactone-induced secreted protein 1 (Tsuzuki *et al.*, 2016), nucleus-localized crinkler effector 1 (Voß *et al.*, 2018), secreted LysM-containing effector RiSLM (Zeng *et al.*, 2020), and nuclear-localized effector 1 (Wang *et al.*, 2021).

There is limited information on how plant or fungal genetic variations affect plant transcriptional responses to fungi (Mateus *et al.*, 2019). The impact of AMF endobacteria and virome and hyphal-associated microbial communities on the regulation of gene expression and physiological capabilities of the association remain unclear and require further investigation (Lanfranco & Bonfante, 2023).

2. Ectomycorrhizal fungi

The transition from saprotrophism to ECM symbiosis is a key evolutionary event that has occurred multiple times during the evolution of Fungi (Tedersoo *et al.*, 2010; Strullu-Derrien *et al.*, 2018; Fig. 2). Although the exact mechanisms driving these transitions remain unclear, comparative genomic and phylogenomic studies have provided hypotheses and patterns for further investigations (Kohler *et al.*, 2015; Miyauchi *et al.*, 2020; Lebreton *et al.*, 2021). The transition to an ECM lifestyle likely occurred through a series of steps, starting with soil/litter saprotrophic fungi colonizing plant roots and gradually forming a mutualistic relationship with the host. Ecological factors such as easy access to soluble carbohydrates may have driven this transition. In nutrient-poor environments, the formation of mutualistic associations with plants allows ECM fungi to access soluble carbohydrates and vitamins, thereby expanding their ecological niche. The ability of ECM fungi to form symbiotic associations with a diverse range of tree species suggests adaptive radiation, specific symbiotic mechanisms, and niche specialization during their evolutionary history (Martin *et al.*, 2016, 2017; Sato, 2023; Fig. 2). ECM fungal lineages diverging in the Late Cretaceous might have had opportunities to co-evolve with ECM angiosperms (e.g. through the development of host recognition systems; Tang *et al.*, 2021; Lebreton *et al.*, 2022; Looney *et al.*, 2022) and repression of plant defenses (Plett *et al.*, 2011, 2014; Kang *et al.*, 2020), resulting in their expansion into novel niche spaces and subsequent rapid diversification (Martin *et al.*, 2016; Sato, 2023). The repeated evolution of the ECM lifestyle (and the absence of reversion to the ancestral state) and convergent evolution in hundreds of fungal lineages highlight its adaptive significance and underscore the selective pressures driving this evolutionary development (Wolfe *et al.*, 2012; Lebreton *et al.*, 2021).

Gene copy numbers of PCWDEs tend to show distinct patterns associated with specific ecological niches in fungi (Floudas *et al.*, 2012, 2020; Kohler *et al.*, 2015) because of their role in the degradation of plant cell wall material (Fig. 2). A drastic contraction in the gene families encoding PCWDEs is a hallmark of ECM and AM fungi (Fig. 3). Most lack ligninolytic class II peroxidases (PODs), invertases, endocellulases, cellobiohydrolases, and cellulose-binding motifs, which restrict their ability to degrade SOM and the plant cell walls of their hosts. As ancestral ECM lineages shifted toward symbiotic relationships, the need for these degradative enzymes diminished, resulting in their gradual loss over evolutionary time (Martin & Selosse, 2008; Wolfe *et al.*, 2012; Lebreton *et al.*, 2021). This makes mycorrhizal fungi dependent on their host plants for C. Nevertheless, many of the sequenced fungi have maintained a unique array of PCWDEs, including endoglucanases and oxidoreductases/laccases, suggesting that several ECM fungi possess diverse abilities to scavenge plant and microbial detritus (necromass) from soil and litter (Bödeker *et al.*, 2014; Veneault-Fourrey *et al.*, 2014; Op De Beeck *et al.*, 2018; Pellitier & Zak, 2018; Nicolás *et al.*, 2019; Floudas *et al.*, 2020; Maillard *et al.*, 2023). Fine-tuned regulation of these PCWDE genes is necessary to avoid triggering plant defense responses (Miyauchi *et al.*, 2020).

In Mucoromycota, Endogonales is an enigmatic group of fungi that establish ectomycorrhizal symbiosis and biotrophic associations with ferns, lycophytes, hornworts, and liverworts, as well as comprising of putative saprotrophs associated with decayed wood and leaf litter (Desirò *et al.*, 2017). To better understand the evolution of mycorrhizal symbioses and trophic ecology in Endogonales, the genomes of four collections of Endogonaceae, including three ECM collections and one putative saprotroph, were sequenced (Chang *et al.*, 2019). The genomes of ECM isolates exhibit typical characteristics of ECM fungi, including a restricted set of PCWDE genes. Furthermore, dating analysis suggested that Endogonaceae originated in the Permian–Triassic boundary, indicating that the mycorrhizal association between Endogonales and plants may have played a critical role in the colonization of land by plants.

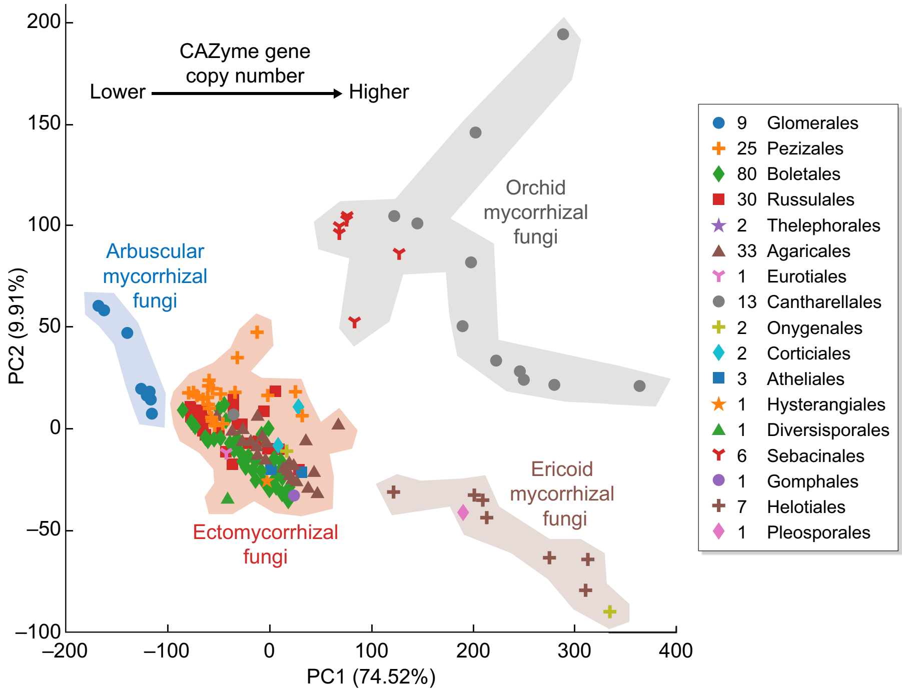

Fig. 3 Differential distribution of the gene copy numbers for CAZyme genes acting on microbial, fungal, and plant polysaccharides, and lignin derivatives in the genomes of 217 species of arbuscular mycorrhizal fungi, ectomycorrhizal fungi, orchid mycorrhizal fungi or ericoid mycorrhizal fungi with contrasting ecologies. Principal coordinate analysis of the total CAZyme gene copy numbers identified in arbuscular mycorrhizal fungi, ectomycorrhizal fungi, ericoid mycorrhizal fungi, and orchid mycorrhizal fungi. Each symbol corresponds to a genome of the mycorrhizal species available in the JGI MycoCosm database (mycocosm.jgi.doe.gov). The taxonomic order of the sequenced species is indicated by different colored symbols as shown in the legend (right panel). Note the divergent distributions in CAZyme gene sets in various mycorrhizal lifestyles with an increasing repertoire of CAZyme from arbuscular mycorrhizal fungi (lower) to ericoid mycorrhizal fungi (higher; from left to right). Principal component analysis (PCA) was performed using the MycoCosm PCA tool (mycocosm.jgi.doe.gov). CAZyme gene repertoires were obtained after semi-manual curation of protein sequences by the CAZy team (www.cazy.org) (Drula *et al.*, 2022).

The field of mycorrhizal genetics has strayed beyond mere genome comparison and gene discovery to the realm of systems biology, exploring the cellular and molecular bases of symbiosis. This evolution was driven by the availability of large-scale transcriptomic datasets (Plett *et al.*, 2014, 2019; Liao *et al.*, 2018; Bouffaud *et al.*, 2020; Ruytinx *et al.*, 2021). They have facilitated the identification of gene networks and hubs involved in key biological processes such as nutrient uptake, metabolism, and signaling in ECM symbiosis. Various ECM symbioses are characterized by the upregulation of genes from overlapping functional categories, such as information storage and processing, transport, and metabolism. However, each association expressed a distinct set of symbiosis-associated genes involved in redox reactions, nutrient transport, and metabolism. A significant number of these genes have orthologs in saprotrophic species, indicating that they are not unique to ECM fungi but are associated with essential core metabolic pathways (Lebreton *et al.*, 2022; Looney *et al.*, 2022; Wu *et al.*, 2022). Because of these alterations in gene expression, ectomycorrhizal interactions lead to changes in the levels of fungal and host plant metabolites, including marked shifts in the metabolism and transport of carbohydrates, amino acids, aromatic acids, organic acids, fatty acids, and water (Hortal *et al.*, 2017; Plett *et al.*, 2021, 2023; Tang *et al.*, 2021; Bogar, 2023; Stuart *et al.*, 2023).

Novel genes specific to the ECM lifestyle, such as those coding for mycorrhiza-induced small secreted proteins (Plett *et al.*, 2011, 2014; Plett & Martin, 2011; Pellegrin *et al.*, 2015) and small RNAs (Wong-Bajracharya *et al.*, 2022), have also emerged, enhancing the symbiotic capabilities of ECM fungi and controlling host plant immunity as well as the ingress of other microbes colonizing the host plant. Several genes that possibly mediate compatibility between plants and fungi have been identified (Lofgren *et al.*, 2021; Tang *et al.*, 2021; Lebreton *et al.*, 2022).

Identifying plant genes that contribute to and are required for ECM symbiosis is a daunting task, and a limited number of genes have been identified and characterized (Tagu *et al.*, 2005; Labbé *et al.*, 2019). Notably, Cope *et al.* (2019) have demonstrated that the ECM fungus *L. bicolor* releases lipochitooligosaccharides and uses the CSSP to colonize *Populus* roots. On the other hand, the conserved core CSSP genes appear to be missing in the ECM-forming Pinaceae lineage (Garcia *et al.*, 2015).

3. Orchid mycorrhizal fungi

With nearly 30 000 species, the orchid family offers valuable resources for studying plant evolution and environmental adaptation, and serves as an economically and culturally important ornamental plant in human society. Orchids appeared to have emerged *c.* 112 million years ago (Ma; Fig. 2). The subfamilies Orchidoideae and Epidendroideae diverged from each other at the end of the Cretaceous, and the tribes of the upper epidendroids diverged rapidly between 37.9 and 30.8 Ma (Givnish *et al.*, 2015; Zhang *et al.*, 2017). Orchids are renowned for their reliance on mycorrhizal fungi during germination, seedling establishment, and nutrient acquisition, particularly during the early stages of their life cycle. The protocorms of germinating orchids are fully dependent on colonization by mycorrhizal fungi for their establishment and growth (Perotto & Balestrini, 2023). Thus, orchids cannot survive without mycorrhizal fungi (Rasmussen & Rasmussen, 2014). In recent years, there has been a growing interest in the genomics of orchids and ORM fungi to unravel the genetic mechanisms underlying orchid-fungal interactions and the specificity of these symbiotic relationships (Chen *et al.*, 2022; Song *et al.*, 2022). The genomes of several orchid species (Cai *et al.*, 2015; Zhang *et al.*, 2016, 2017; Yang *et al.*, 2021; Jiang *et al.*, 2022; Li *et al.*, 2022) have been sequenced. Comparison of chromosome-scale genome assemblies of two closely related orchid species, the partially mycoheterotrophic *P. zijinensis* and the fully mycoheterotrophic *P. guangdongensis*, with genomes of autotrophic orchids, suggests that mycoheterotrophy is associated with increased substitution rates and gene loss in *P. guangdongensis*. Conversely, trehalase genes, which are responsible for converting trehalose to glucose, have expanded in most sequenced orchids, reflecting the reliance of orchid seeds, which lack endosperms, on trehalose obtained from ORM fungi during the protocorm stage. Furthermore, this study showed that mature plants of *P. guangdongensis*, unlike photosynthetic orchids, continue to express trehalase genes to exploit the trehalose released by its mycosymbionts.

Genome sequencing efforts have targeted specific ORM fungi to gain a deeper understanding of their genetic repertoires and symbiotic capabilities. The genomes of *Tulasnella calospora*, *Sebacina vermifera*, and *Ceratobasidium* spp. (Miyauchi *et al.*, 2020) have been published, and a dozen additional ORM fungi in Tulasnellaceae, Serendipitaceae, and Ceratobasidiaceae have been sequenced at the JGI. In contrast to ECM and AMF, ORM fungi possess a large set of PCWDEs that are expressed during their interactions (Balestrini *et al.*, 2014; Chen *et al.*, 2017, 2022; Ghirardo *et al.*, 2020; Fig. 3). Similar to ERM fungi, ORM species often have a higher set of PCWDEs than wood decayers and soil/litter decomposers (Miyauchi *et al.*, 2020), which supports their dual saprotrophic/symbiotic lifestyles. We hypothesized that the size of the PCWDE repertoire is reflective of the age of the mycorrhizal symbiosis along the saprotrophy to symbiosis continuum, with AMF symbiosis emerging in the Early Devonian (393–419 Ma), ECM symbiosis during the Jurassic (*c.* 200 Ma), and mycorrhizal associations with Ericaceae and orchid species up to the Cretaceous (*c.* 117 Ma; Strullu-Derrien *et al.*, 2018; Fig. 2). Continued efforts in genomics will further enhance our understanding of the complex interactions between orchids and their mycorrhizal partners, contributing to conservation efforts and orchid cultivation in horticulture and restoration practices.

4. Ericoid fungi

Ericoid mycorrhiza fungi form mutualistic symbioses with a wide range of Ericaceae plants, including heathers, blueberries, and rhododendrons, and play crucial roles in nutrient acquisition and stress tolerance in nutrient-poor and acidic soils. Genome sequencing has focused on several key ERM species, including the archetypal ERM fungi *Rhizoscyphus ericae* and *Oidiodendron maius* (Kohler *et al.*, 2015; Grelet *et al.*, 2016; Martino *et al.*, 2018). The availability of these genomes has provided insights into the genetic repertoire and functional attributes of ERM fungi. According to phylogenomic analysis, the most recent common ancestor of the sequenced ERM fungi, including *O. maius*, *M. bicolor*, *M. variabilis*, and *R. ericae*, was estimated to be *c.* 118 Ma (Martino *et al.*, 2018). Remarkably, this age coincides with the emergence of the Ericaceae family, which was estimated to have originated *c.* 117 Ma (Fig. 2; Schwery *et al.*, 2015). This suggests that ancestral ERM fungi and their plant partners have undergone simultaneous diversification, and the early establishment of this symbiosis may have initiated evolution of the Ericaceae family. This resembles theories that symbiotic associations between plants and early AM, such as fungi, enabled plants to colonize land at 450 Ma (Selosse & le Tacon, 1998). Unlike other types of mycorrhizal associations, ERM fungi demonstrate a relatively low dependence on plants because of their enhanced saprotrophic capabilities. Their extensive repertoire of degradative enzymes indicates that they may be facultative symbionts representing recently recruited lineages of soil-decomposer fungi, many of which are endophytes (Grelet *et al.*, 2016; Martino *et al.*, 2018). The sustained expression of PCWDEs in colonized roots likely aids in penetrating the thick outer cell walls of plants, allowing the establishment of intracellular structures within the epidermal root cells of ericaceous hosts (Martino *et al.*, 2018).

III. Mycorrhizal networks

Underground mycorrhizal networks are crucial for nutrient acquisition and transport by plants. They consist of interconnected hyphae that extend from the mycorrhizal roots to the surrounding soil, forming extraradical mycelial threads (Fig. 4). In natural soils, numerous intermingled mycorrhizal networks of varying sizes develop as each host plant is colonized by multiple fungal symbionts, up to several dozen per adult tree (Rog *et al.*, 2020). They play a vital role in efficiently prospecting soil, scavenging nutrients, transporting them to the host roots, and contributing to essential ecosystem services, including soil structure enhancement and water uptake (Table 1). Furthermore, mycorrhizal networks play a crucial role in C cycling and storage (Hawkins *et al.*, 2023; Table 1). The establishment and activity of these hyphal networks relies on a continuous supply of plant C compounds.

Within hyphal networks established by mycorrhizal fungi, a specific subset called common mycorrhizal networks (CMNs) is formed when the mycobiont establishes physical connections between the roots of two or more plant species. The transfer of sugars and other nutrients among interconnected plants, often involving saplings, through CMNs has been suggested in several studies (Finlay & Read, 1986; Arnebrant *et al.* 1993; Simard

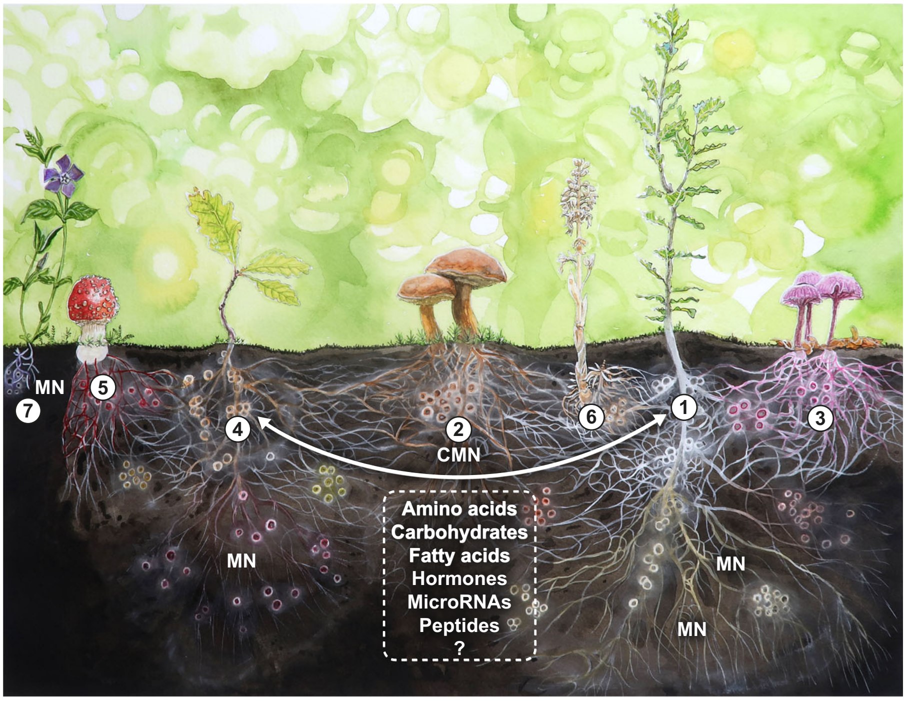

Fig. 4 View of the soil mycorrhizal community in a hypothetical forest dominated by oak species associated with different types of mycorrhizal fungi that form separate underground networks (MN) that may possibly be used to transport amino acids, carbohydrates, fatty acids, signaling microRNAs or peptides and hormones. An evergreen oak (*Quercus ilex*) (1) forms ectomycorrhizal roots and hyphal networks with *Xerocomellus chrysentheron* (red cracking bolete) (2) and *Laccaria amethystina* (amethyst deceiver) (3), whereas a sessile oak (*Quercus petrea*) (4) establishes ectomycorrhiza (ECM) and hyphal networks with *Xerocomellus chrysentheron* (2) and fly agaric (*Amanita muscaria*) (5). ECM rootlets are shown as colored dots on root systems. *X. chrysentheron* hyphal networks link *Q. ilex* and *Q. petrea* through a common mycorrhizal network (CMN). The nonphotosynthetic bird's nest orchid *Neottia nidus-avis* and its orchid mycorrhiza (ORM) fungal network (6) parasitize the evergreen oak mycorrhizal network. The lesser periwinkle (*Vinca minor*) is colonized by AMF, forming an independent mycorrhizal network (7). Different colors represent different mycorrhizal fungal networks, with ECM rootlets as dots of the same color. Note that other combinations are possible (e.g. boreal forests with ECM trees often harbor an understory of shrubs (e.g. *Vaccinium*) that form ericoid mycorrhiza (ERM) associations; Illustration courtesy of Florian Gadenne).

Table 1 Ecosystem services provide by mycorrhizal mycelia and networks.

Ecosystem service	Ecological importance	Selected references
Nutrient uptake and plant growth stimulation	Mycorrhizal fungi can promote plant growth and nutrient uptake. Up to 90% of plant P and N can be acquired by mycorrhizal fungi. Some plants are fully dependent on nutrients acquired by mycorrhizal fungi.	van der Heijden *et al*. (2008)
Belowground C storage and C cycling	Plants allocate 5–30% of their photoassimilates to mycorrhizal symbionts. Up to 13 Gt of CO_2 fixed by terrestrial plants is, at least temporarily, allocated to the underground mycelium of mycorrhizal fungi.	van der Heijden *et al*. (2008); Hawkins *et al*. (2023)
Soil structure formation and aggregation	Fungal hyphae and hyphal exudates enmesh soil particles together into larger aggregates and contribute substantially to the promotion of soil structure.	Jastrow *et al*. (1998)
Water uptake and reduction in nutrient leaching losses	Reduction in nutrient leaching by mycorrhizas. Water uptake by fungal hyphae. Evidence from natural systems is largely missing.	Ahonen-Jonnarth *et al*. (2003); Cavagnaro *et al*. (2015); Kakouridis *et al*. (2022)
Promotion of seedling establishment	CMN can quickly colonize the roots of emerging seedlings and can have strong effects on the success of seedling establishment. No effects or even negative effects are also regularly reported.	van der Heijden & Horton (2009)
Interplant C and nutrient transfer	High amounts of transfer have been observed in mycoheterotrophic plants and orchid protocorms. The ecological significance of transfer among green plants is debated and needs further study.	Simard *et al*. (1997); Klein *et al*. (2016); Henriksson *et al*. (2023); Karst *et al*. (2023); Merckx (2023)

et al., 1997; Wu *et al*., 2001; Klein *et al*., 2016; Selosse *et al*., 2016; Cahanovitc *et al*., 2022). However, the mechanisms underlying these transfers are complex, and it is challenging to discern the specific role of CMNs vs other pathways such as nutrient and signal movement through the soil solution (Babikova *et al*., 2013).

Many mycorrhizal fungi are generalists and have a broad host range, and several plants can be interconnected by hyphal networks. For instance, glasshouse experiments have provided evidence that *R. irregularis* is not host-specific, and that all mycorrhizal hosts within plant communities can possibly be interconnected by CMN formed by this symbiont (van der Heijden, 2004; Kivlin, 2020). In AMF, the fusion of hyphae through anastomosis and hyphal healing mechanisms has been observed *in vitro* (Giovannetti *et al*., 2001; de la Providencia *et al*., 2005). Hyphal fusion plays a crucial role in AMF networks, ensuring their interconnectedness and physical stability; however, the spatial distribution of these networks *in situ* is unknown.

In ECM fungi, genetic individuals (genets) can simultaneously colonize multiple trees (Beiler *et al*., 2010). DNA fingerprinting studies have identified large genets in several Boletales species (Fiore-Donno & Martin, 2001; Hirose *et al*., 2004; Beiler *et al*., 2010). Although these studies have provided evidence of very large genetic individuals (> 10 m), the extent of physiological integration or communication between different parts of these extensive mycelial networks remains largely speculative and requires further investigation. Most importantly, the size of ECM genets, including their subterranean mycelial networks (and CMNs), is expected to be considerably smaller. Most species investigated thus far have produced much smaller genets (< 1 m; Gryta *et al*., 2000; Grelet *et al*., 2010; Hortal *et al*., 2012; Murat *et al*., 2013). If genetic individuals are of small size, it is unlikely that hyphae produced by different fungal species originating from single mycorrhizal rootlets can connect distant neighboring plants. In addition, most ECM genets exist as autonomous entities because of the presence of vegetative incompatibility loci that prevent the fusion of individuals that differ genetically at the heterokaryon incompatibility (*het*) loci, that is, anastomosis between incompatible genotypes triggers cell death (Paoletti, 2016).

Consequently, the ecological significance of CMNs in nutrient cycling has been the subject of scrutiny and debate (Robinson & Fitter, 1999; Henriksson *et al*., 2023; Karst *et al*., 2023; Robinson *et al*., 2024). Therefore, there is an urgent need to identify the physiological and ecological roles of mycorrhizal networks (including CMNs) in natural ecosystems, and their relative importance in supporting plant growth and seedling establishment. Imaging tools for tracking and probing individual hyphae in intermingled mycelial networks in soils should be developed to test whether nuclei, transcripts, proteins, and metabolites can migrate from one plant individual to another via CMNs. Integrated approaches combining multi-locus genomic sequencing to assess the spatial distribution and size of genotypes, their activity by metatranscriptomics/metaproteomics, and the measurement of metabolic fluxes between different mycorrhizal plants in natural settings are currently being developed and will provide valuable information on the functioning of mycorrhizal networks.

IV. Mapping mycorrhizal diversity

In recent years, there has been strong focus on documenting underground biodiversity and creating global maps of various soil organisms. Efforts have been made to provide global maps of microbial biomass (Xu *et al*., 2013), earthworms (Phillips *et al*., 2019), protists (Oliverio *et al*., 2020), bacteria (Bahram *et al*., 2018; Delgado-Baquerizo *et al*., 2018), fungi (Tedersoo *et al*., 2014; Větrovský *et al*., 2020), and overall soil biota (Delgado-Baquerizo *et al*., 2020). In addition, global distribution maps of mycorrhizal plants, AM, and ECM fungi have been published (Öpik *et al*., 2010; Tedersoo *et al*., 2014; Davison *et al*., 2015; Soudzilovskaia *et al*., 2019; Fig. 5). However, global maps of ORC and ERM fungi, as well as 'mycorrhizal' Mucoromycota fine-root endophytes, are still lacking. Furthermore, maps documenting the world-wide distribution of mycorrhiza-associated microbes, such as mycorrhiza-helper bacteria, fungi, and protists, are required to fully understand the breadth of mycorrhizal systems (Frey-Klett *et al*., 2007; Emmett

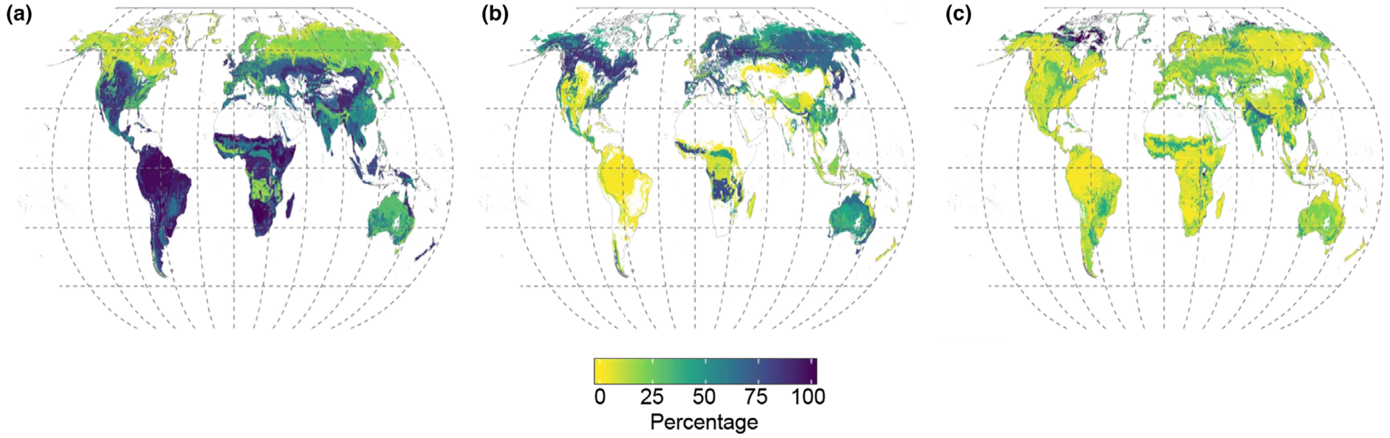

Fig. 5 Global map of the percentage of total aboveground plant biomass linked to the different mycorrhizal categories. (a) arbuscular mycorrhizal plants; (b) ectomycorrhizal plants; (c) nonmycorrhizal plants. Map resolution was 10 arcmin. Published by Soudzilovskaia *et al*. (2019).

et al., 2021; Yang *et al*., 2023; Zhang *et al*., 2023). Identifying the genetic diversity of these mycorrhiza-associated microorganisms and analyzing their spatiotemporal dynamics is crucial, as emerging studies have suggested their involvement in nutrient uptake facilitation and other services provided by mycorrhizal hyphae (Zhang *et al*., 2022; Li *et al*., 2023; Wang *et al*., 2023a,b). The ability of mycorrhizal fungi to acquire nutrients appears to be influenced by the composition of the bacteria associated with mycorrhizal hyphae. For instance, Zhang *et al*. (2023) demonstrated that common AM hyphal-associated bacteria promote plant growth and mycorrhizal formation. The concept of 'mycorrhiza suppressive soil' has been proposed for soils where microbial communities impede the nutrient uptake facilitated by mycorrhizal hyphae (Svenningsen *et al*., 2018). Variations in hyphae-associated microbial communities may contribute to the challenges encountered when replicating mycorrhizal experiments. Recent studies have demonstrated that protists feeding on hyphae-associated bacteria can affect mycorrhizal nutrient uptake, thereby highlighting the intricate nature of these multitrophic interactions (Rozmoš *et al*., 2022). Additionally, it has been suggested that AMF harbor an ancient lineage of mycoviruses (Ezawa *et al*., 2023), and a recent study suggested a recent and single infection of a large dsDNA viral genome in the genome of an AM fungal strain (Zhao *et al*., 2023). However, the role of viruses in regulating mycorrhizal function, including their effect on the genetic structure of the mycorrhizal mycobiome, remains poorly understood and requires further investigation. Overall, these studies emphasize the need to consider the 'holobiont' concept when trying to understand mycorrhizal functioning (Vandenkoornhuyse *et al*., 2015; Wang *et al*., 2023b).

V. Mycorrhizal symbiosis in ecosystems

1. Determining the relative importance of mycorrhizas

Numerous studies have emphasized the significance of mycorrhizal fungi in promoting plant growth and ecosystem functioning. However, there is a lack of research that clearly defines their relative importance compared with other essential microbial groups, including bacteria, endophytic and saprotrophic fungi, protists, archaea, viruses, and soil micro- and mesofauna, as well as their interactions. The relative importance of mycorrhizas for plant productivity and ecosystem performance depends on the ecosystem type (Fig. 6). We propose that mycorrhizal associations, including mycorrhizal helper bacteria, play a paramount role in forests, followed by grasslands and arable land (Fig. 6). This contention is supported by observations that ECM fungi are responsible for a substantial part of N acquisition in many forests, especially in nutrient-poor soils (Hobbie & Hobbie, 2006). Recent studies have revealed a strong correlation among tree productivity, ECM composition, and beta diversity (Anthony *et al*., 2022; S. Luo *et al*., 2023), further reinforcing this observation. However, it is crucial to acknowledge that the significance of mycorrhizal associations depends on nutrient availability, and their importance diminishes in nutrient-rich soils. The effects also depend on plant

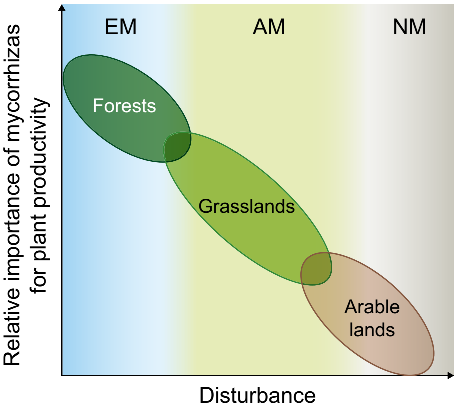

Fig. 6 Relative importance of mycorrhizal associations for plant productivity and ecosystem performance in different ecosystem types. forests, grasslands, and arable ecosystems. Different ecosystem types are dominated by different mycorrhizal associations. AM, arbuscular mycorrhizas; EM, ectomycorrhizas; NM, nonmycorrhizal.

species identity, as some plants, such as a wide range of members of Brassicaceae or Proteaceae, do not engage in associations with mycorrhizal fungi.

In grasslands, mycorrhizal associations exhibit greater variability. AMF, the dominant mycorrhizal fungi in grasslands, have an important impact on grassland functioning by altering competitive interactions among plant species, leading to either increased or decreased plant diversity (van der Heijden *et al.*, 1998; Hartnett *et al.*, 1999). However, the relative importance of mycorrhizas for biomass production in grasslands is lower, as biomass production often remains similar with or without mycorrhizas, signifying changes in plant species composition (van der Heijden *et al.*, 1998; Hartnett *et al.*, 1999). In arable and highly disturbed systems, mycorrhizal symbiosis is expected to have the lowest relative importance. These systems usually have a lower abundance or an absence of mycorrhizal associations, whereas fungal and bacterial pathogens are more abundant (Labouyrie *et al.*, 2023). Nonmycorrhizal and ruderal plant species often dominate these systems (Read, 1991). Nonetheless, it is crucial to acknowledge that co-occurring plant species within the same ecosystem may exhibit different mycorrhizal responsiveness, and that some plant species and crops in arable fields benefit from mycorrhizal symbiosis. Moreover, exceptions have been observed, such as plant species in extremely weathered and nutrient-poor soils in Australia, which have cluster roots and do not form associations with mycorrhizal fungi (Lambers *et al.*, 2008). Notably, nonmycorrhizal plants are not always restricted to low-nutrient soils; for example, Proteaceae are present throughout most of the Southern Hemisphere. In brief, the relative importance of mycorrhizal symbiosis in ecosystems fluctuates depending on the specific ecosystem type, nutrient availability, and plant species composition. It is important to acknowledge the current geographical bias in mycorrhizal research, which predominantly focuses on temperate and boreal regions and potentially overlooks the greater diversity of viable mycorrhizal and nonmycorrhizal strategies in subtropical and tropical ecosystems. Addressing this gap is essential for obtaining a more comprehensive understanding of mycorrhizal associations world-wide. Additionally, there is a trend toward overinterpreting data, which can hinder progress in certain research fields (Kuyper & Jansa, 2023).

2. Linking genes to ecological traits

The growing availability of mycorrhizal fungal genomes (Lebreton *et al.*, 2021) presents unprecedented opportunities to investigate the functional diversity of soil fungal communities. This can be achieved through expert and accurate annotation of environmental metabarcoding (Anthony *et al.*, 2022), metagenomics (Hagh-Doust *et al.*, 2023), and metatranscriptomic (Auer *et al.*, 2023; Zeng *et al.*, 2023) datasets. The latter approach has been used to examine gene expression in ECM root tips in natural environments, including the effects of anthropogenic N deposition on ECM tree metabolism (Liao *et al.*, 2018; Law *et al.*, 2022; Rivera Pérez *et al.*, 2022). Anthony *et al.* (2022) showed that tree growth was linked to the gene copy number of genes involved N uptake and assimilation in associated ECM symbionts. By combining high-throughput metabarcoding of fungal species residing in a specific experimental forest site with the sequencing of soil eukaryotic RNA extracts, the precise gene expression of each mycelial network extending beneath a tree species can be evaluated (Auer *et al.*, 2023; Zeng *et al.*, 2023). The use of metatranscriptomics will also help decipher the relative importance of each fungal species within the different soil biota in measuring genes involved in plant nutrition, C cycling, disease resistance, and stress adaptation.

VI. Mycorrhizal symbiosis and plant community dynamics

It is increasingly recognized that soil microbes, including mycorrhizal fungi, can mediate plant interactions and thus may contribute to biodiversity-productivity relationships, shaping plant communities (Klironomos, 2002; Van der Heijden *et al.*, 2008; Schnitzer *et al.*, 2011). Manipulative experiments targeting the abundance and presence of AMF and ECM have consistently demonstrated their profound effects on plant diversity and community structure (Liang *et al.*, 2019). Notably, the paucity of studies that manipulate other types of mycorrhizal symbioses, such as ERM and ORM, to investigate their effects on plant growth and establishment warrants further investigation and research attention. It is worth noting that the majority of studies in this field are relatively short-term, typically spanning < 1 yr. Therefore, there is a pressing need for long-term investigations to provide deeper insights into the role of mycorrhizal associations in plant communities. This necessity is particularly critical for perennial plant communities, which represent the predominant vegetation type on Earth, including grasslands, savannahs, and forests.

An increasing body of evidence from global surveys has highlighted the significance of mycorrhizal associations in shaping plant community structure, diversity, and productivity. Large-scale forest inventories have provided valuable insights into the role of mycorrhizal types in structuring forest ecosystems and tree diversity. Carteron *et al.* (2022), for instance, conducted an analysis of 82 000 forest plots across the United States and found that forests dominated by ECM fungi or AMF tend to exhibit lower tree diversity. By contrast, forests with a mixture of mycorrhizal strategies supported a higher number of tree species. More recently, Y. H. Luo *et al.* (2023), using the same database, demonstrated that mixed mycorrhizal plots displayed greater productivity than plots in which either AMF- or ECM-associated tree species were dominant. These findings suggest that the coexistence of both mycorrhizal types can complement each other and enhance ecosystem function. Additionally, the positive effects of mixed mycorrhizal strategies on forest productivity were more pronounced in plots with lower tree species richness (Y. H. Luo *et al.*, 2023). However, the mycorrhizal type of the dominant plant species also plays a crucial role in facilitating or suppressing subordinate or understory species. For example, a study conducted in the Great Smoky Mountains of the United States found a positive relationship between herb species richness and the number of AM tree species (Newman & Reddell, 1988). Deng *et al.* (2023) conducted a large-scale tree biodiversity experiment in China and observed that the relationship between tree species richness and productivity is dependent on the mycorrhizal type. Specifically, a positive relationship was observed between the richness of AM trees and productivity, whereas no such relationship was observed for ECM trees. By contrast, S. Luo *et al.* (2023) showed a positive relationship between mycorrhizal diversity and aboveground productivity in a subtropical evergreen broad-leaved forest ecosystem. Metatranscriptomics and metaproteomics approaches can help identify the mechanisms and key gene networks involved in mediating the observed biodiversity-ecosystem functioning relationships. Moreover, the presence or absence of mycorrhizal symbionts can facilitate or impair the establishment of invasive species (e.g. Pringle *et al.*, 2009; Dickie *et al.*, 2010).

VII. Mycorrhiza applications

There is considerable interest in enhancing agricultural sustainability and utilizing biological approaches to promote crop plant yield, as well as facilitate ecosystem restoration and sustainability. Mycorrhizal fungi have important potential as they are known to promote plant growth and provide protection against biotic and abiotic stresses in agriculture and forestry. A recent meta-analysis by Averill *et al.* (2022) indicated that restoring the native soil microbiome could lead to an average acceleration of 64% in plant biomass production across various ecosystems. However, the responsiveness of plants to mycorrhizal inoculation can be highly dependent on the experimental conditions, nutrient availability, and the specific plant species being studied (Lekberg & Koide, 2005; Hoeksema *et al.*, 2010; Chaudhary *et al.*, 2016). Too often, the literature presents an overly optimistic view of the importance of AMF in crop yield (for a discussion, see Ryan & Graham, 2018; Rillig *et al.*, 2019a,b). Additionally, results can vary based on plant genotypes (An *et al.*, 2010) and crop domestication status (Martín-Robles *et al.*, 2018). For example, a recent study comparing 99 wheat lines demonstrated a wide range of growth responses to inoculation, varying from 30% decrease to 80% increase in shoot biomass (Thirkell *et al.*, 2022). This highlights the importance of carefully considering the plant genotype, AMF species, genotypes, and likely nuclear organization (heterokaryons vs homokaryons) when attempting to promote agricultural yield through mycorrhizal inoculation.

Many studies evaluating plant growth responses to mycorrhizal inoculation have been conducted under highly controlled conditions in glasshouses, often using sterilized and nutrient-poor soils. Comparing the results of such studies to field conditions can be challenging. To make field inoculation practical and widely adopted, it is essential to conduct field inoculation trials and employ appropriate inoculation techniques that can easily be implemented by farmers or foresters. Mycorrhizal fungi can be coated onto seeds, applied as dressing or as 'fertilizer' grains, or sown together with (or below) seeds (Vosátka *et al.*, 2012; Oliveira *et al.*, 2019; Rocha et al., 2019). The addition of natural soils containing indigenous populations of mycorrhizal fungi (and other microbes) to neighboring sites or tree nurseries has also been advocated, as these inoculants may be better adapted to local conditions. Furthermore, field inoculation can change native AMF communities (Basiru & Hijri, 2022), and there are concerns regarding the potential unintended consequences of using a nonnative inoculum, which may pose a threat to soil and plant biodiversity and ecosystem functioning (Hart *et al.*, 2018). Before introducing an inoculant to the market, it is crucial to adhere to a range of basic quality criteria in order to assess inoculum viability and efficacy under controlled conditions (Salomon *et al.*, 2022). Additionally, tools need to be developed to enable farmers or foresters to predict under which conditions (crop type, crop genotype, soil type, nutrient availability, and weather conditions) inoculation is beneficial and economically viable. For example, a recent field inoculation study in 54 well-fertilized arable soils in Switzerland found that the success rate of AMF inoculation was best predicted by the presence of fungal pathogen genes in the soil, suggesting that inoculation can also help reduce biotic stress (Lutz *et al.*, 2023). Overall, mycorrhizal fungi have a great potential as biological agents for sustainable production. However, it is essential to elucidate the specific conditions under which inoculation is most effective. A combination of high-throughput rDNA metabarcoding, RNA sequencing, and metaproteomics would be a powerful approach to assess mycorrhizal inoculation success and to reveal whether field inoculation enhances specific ecosystem functions. For instance, the level of transcripts (or proteins) coding for nutrient transporters (or other functional traits that can be traced back to mycorrhizal fungi) can be linked to particular ecosystem functions, such as plant yield, nutrient content, SOM decomposition, or disease/stress resistance. Multi-omics approaches can also help to reveal the relative importance of mycorrhizal traits in comparison with other traits (e.g. nutrient uptake by plant roots or organic matter decomposition by nonmycorrhizal soil biota). Such studies will rely on a combination of traditional ecology/agronomy approaches (e.g. assessing plant yield, decomposition with litter or tea bags, disease suppression assays, hyphal compartments only accessible to fungal hyphae, or the inclusion of organic nutrient patches) and environmental genomics approaches. For instance, Liu *et al.* (2023) revealed that the application of pesticides is linked to genes responsible for N fixation, iron transport, and P metabolism, enabling the elucidation of how environmental stressors can influence soil functioning. However, the analytical methodology required to integrate ecology/agronomy approaches with genomics, transcriptomics, proteomics, metabolomics, and phenomics data remains nascent. Owing to their nature, -omics data are intrinsically highly variable and noisy, leading to several issues when trying to compare or reproduce them in natural settings. Integrating multi-omic data will likely rely on co-expression or co-abundance network approaches, such as those developed in random forest-based methods (Huynh-Thu *et al.*, 2010). In this approach, multiple types of -omics and ecological data can be integrated by identifying proteins and transcripts that shift their abundance in a coordinated manner across a range of experimental conditions (e.g. crop yield) or samples.

VIII. Future directions

By applying genomics and other -omics approaches to the study of mycorrhizal symbioses, we gained deeper insight into the molecular, physiological, and ecological processes underlying these mutualistic associations. This knowledge should be translated into practical applications that promote ecosystem functioning and conservation, contribute to the overall mitigation of climate change, and ensure sustainable arable land. Numerous long-term challenges remain in leveraging genomics and other -omics tools to deepen our understanding of mycorrhizal symbioses, including their evolution, development, function, and ecology (Table 1).

1. Expanding the repertoire of mycorrhizal genomes

The current collection of sequenced mycorrhizal genomes represents only a fraction (*c.* 0.4%) of the estimated 50 000 mycorrhizal fungal species identified. To capture the true genetic and functional diversity of this fungal guild, it is crucial to sequence additional genomes using novel sequencing initiatives, such as the JGI 10 000 Fungal Genomes project, Darwin Tree of Life, or Earth Microbiome. Exploring the genomes of mycorrhizal species from understudied ecosystems, such as the Arctic, montane, desert, and tropical biomes, could reveal specific gene sets associated with adaptation to these environments. Additionally, investigating the genomic blueprints of poorly explored early diverging mycorrhizal lineages, fine-root Mucoromycotina endophytes, bryophytes-associated mutualists, and mycorrhiza-like endophytic fungi can shed light on the functional capabilities and transition from saprotrophism to mutualism in these fungal groups.

2. Advancing our understanding of basic biological processes

Utilizing approaches such as multiplexed single-cell and 3D spatial gene expression analysis of mycorrhizal roots, transcriptomic-based co-expression analysis, proteomics, and protein–protein interaction studies can aid in linking genes to established biological processes and potentially predict evolutionary relationships as well as ecological adaptation (see Box 1). Approaches involving high-throughput protein-folding computations (e.g. AlphaFold; Jumper *et al.*, 2021) can help identify protein structures encoded by symbiosis-regulated genes with unknown functions, such as effector-like secreted proteins (Teulet *et al.*, 2023). Understanding the origin of these effector proteins is crucial, whether they evolved from saprotrophic ancestors or emerged anew to facilitate colonization within plant tissues. Addressing the signaling pathways and specific molecules involved in symbiotic development and the intricate molecular crosstalk between mycorrhizal partners are needed. Currently, the master genes that trigger the development of ectomycorrhizal symbiosis in both fungal and plant partners (if any) are unknown. Furthermore, it is important to investigate the factors underlying the varying host ranges of different mycorrhizal species (Lebreton *et al.*, 2021; Tang *et al.*, 2021). Why certain mycorrhizal fungal species can colonize a wide range of hosts, whereas others exhibit more restricted preferences, remains an intriguing aspect that requires further exploration.

3. Unearthing mycorrhizal diversity

Although progress has been made, especially in temperate and boreal ecosystems (Peay *et al.*, 2016), there are still vast regions of our planet that remain largely underexplored. A consensus has emerged that most of this diversity, both known and unknown, resides in the tropics. The mycobiome diversity in deserts and polar regions remains uncharacterized, but their populations are changing rapidly, driven by anthropogenic climate change (Baldrian *et al.*, 2023). We urge researchers to examine the biogeography of various mycorrhizal associations within these biomes. Other threats to soil habitats, such as microplastics, can also alter or even create new habitats for mycorrhizal fungi (Leifheit *et al.*, 2021). Owing to initiatives such as the Society for the Protection of Underground Networks, a better understanding of these mycorrhizal mycobiomes would allow us to improve predictions of anthropogenic impacts on microbiome composition, resilience, evolution, and productivity (Averill *et al.*, 2022; Baldrian *et al.*, 2023) (Box 1). The global inventory of mycorrhizal fungi, such as GlobalFungi (Větrovský *et al.*, 2020), must be accompanied by an atlas designed to explore microbial functions in space and time (to be described later). Given the increasing number of threats to the soil environment, there is an urgent need to characterize healthy soil microbiomes in ecosystems that are currently unaffected by environmental threats (if any). This provides a baseline for understanding how these microbial

Box 1. Topical questions in the genomics of mycorrhizal associations.

What are the genomic mechanisms underlying the specificity and recognition of plant hosts and mycorrhizal fungi and how do these mechanisms contribute to the establishment and maintenance of symbiosis?

How do idiosyncrasies in the gene repertoire of mycorrhizal fungi influence their ability to interact with different plant species, and what are the implications for plant diversity and ecosystem functioning?

How does genomics inform our understanding of the complex regulatory networks involved in mycorrhizal symbiosis, including the genes and pathways responsible for signaling, nutrient transport, and establishment of mutualism?

What is the genomic basis of the response of mycorrhizal fungi to environmental stressors, such as changes in soil pH, drought, pesticides, plastics, nutrient availability, and climate fluctuations, and how does this affect their symbiotic interactions with plants?

How can genomics contribute to the understanding of the evolution of mycorrhizal symbiosis and the genetic changes that have occurred over time, leading to a diverse range of mycorrhizal associations observed in nature?

What are genomics-based strategies for engineering or enhancing mycorrhizal symbiosis in crops to improve nutrient uptake efficiency, stress tolerance, and overall plant performance?

What is the role of epigenetic modifications in mediating plant-mycorrhizal fungus interactions, and how do epigenetic changes influence the outcomes of the symbiotic relationship?

Can comparative genomics shed light on the genetic basis of functional differences among various mycorrhizal fungal species and how can this knowledge be applied to optimize fungal partners for specific agricultural or ecological goals?

How can genomics, metatranscriptomics, and metaproteomics contribute to our understanding of the role of mycorrhizal fungi in carbon cycling, soil health, and overall ecosystem services and how might this knowledge inform environmental management strategies?

communities might respond to global changes. It would also help to identify tipping points that could permanently change the composition and function of the soil microbiome. For instance, large-scale inventories of European forests have shown that N deposition causes tipping points in mycorrhizal composition and functioning (van der Linde *et al.*, 2018). Although hundreds of studies have described the composition of the mycorrhizal mycobiome in various ecosystems, little is known about the connectivity between different components and mycorrhizal community shifts during succession and along the gradient of grassland-, shrub-, and tree-dominated zones.

4. Environmental genomics

Understanding the processes driving variations in natural microbial communities across space and time is a critical challenge for ecologists. With an increasing number of available fungal genomes from ecologically relevant species (see Section II), it is now possible to map anonymous DNA and RNA reads from soil and mycorrhizal roots to identify mycorrhizal species and their specific gene expression patterns, including targeting the mycorrhizal genes responsible for nutrient uptake, symbiosis development and signaling, and SOM decomposition. However, metagenomic approaches are still challenging for assembling entire fungal genomes from soil samples because they usually represent a very low proportion of soil DNA. Higher-throughput sequencing can help address the depth-of-coverage issue, but this can lead to other problems related to the high computational demands for large datasets. By contrast, using RNA profiling of soil hyphae and mycorrhizal root tips, we can now assess whether multiple symbiotic species can coexist on (or beneath) the same host tree by utilizing the same resources and performing identical ecological functions (i.e. exhibiting high functional similarity) or by utilizing different resources and providing distinct functions (i.e. exhibiting limited functional similarity; see Section V.2). Metatranscriptomics of soil fungal communities (Auer *et al.*, 2023; Zeng *et al.*, 2023) can be used to better understand the role of mycorrhizal networks, including CMN, because they can help identify whether different tree individuals within a plot are truly colonized by the same fungus, and whether the same sets of genes are expressed in different tree individuals. However, several challenges limit the widespread application of metatranscriptomics, including the lower stability of RNA compared with that of DNA, greater difficulty in extracting RNA, and difficulty in obtaining informative messenger RNA transcripts that provide insights into its functional role (Auer *et al.*, 2023). It is difficult to ascertain whether nuclei, transcripts, proteins, and metabolites can translocate from one plant to another through CMNs in natural settings. The absence of imaging tools that can trace and investigate individual hyphae within intermingled mycelial networks in soil presents a significant obstacle in understanding this phenomenon. Nevertheless, ongoing research is developing integrated methods that combine rDNA metabarcoding to evaluate the distribution of operational taxonomic units, estimate fungal genotype size through multi-locus eDNA population genomics, metatranscriptomics, metaproteomics, and measurement of metabolic fluxes between various components of forest or grassland plots. These integrated approaches will offer valuable insights into the functioning of fungal/plant communities. The adoption of this genome-to-ecosystem strategy will be crucial in unraveling the contributions of fungal guilds that thrive in the soil and roots within intricate terrestrial ecosystems (Box 1).

5. Promoting sustainable agriculture and forestry

Gaining insights into the genetic basis of beneficial traits in mycorrhizal fungal populations and communities is crucial for the development of strategies aimed at optimizing their use as biofertilizers or biocontrol agents, thereby reducing reliance on chemical inputs and promoting sustainable land management practices. To achieve sustainable agriculture and forestry, it is imperative to harness the potential of mycorrhizal symbioses and exploit the functional traits of the mycorrhizal inoculants. To successfully manage mycorrhizal fungal communities and promote ecologically sustainable agriculture or restoration initiatives, it is crucial to identify the range of fungal taxa present and the factors that influence their diversity and distribution at both regional and continental levels. DNA metabarcoding surveys can foster applications and predict under which conditions inoculation is beneficial for farmers and land managers (e.g. low abundance or diversity of mycorrhizal fungi) (Box 1). These genotyping approaches can also identify whether specific crop microbiomes are characteristic of well-performing (high-yield and high nutrient use efficiency) systems to distinguish them (functionally) from poorly performing (low-yield and large nutrient losses) systems. Moreover, such tools can be used to identify how mycorrhizal inoculation can alleviate biotic stress (e.g. high pathogen abundance). Furthermore, metatranscriptomics, metagenomics, and stable isotope probing may provide functional insights into and identify the role of mycorrhizal helper bacteria and other microbial consortia that contribute to plant growth. Mycorrhizal fungi can also facilitate the establishment and growth of plants in degraded habitats. However, it is necessary to investigate the specific conditions under which the application of mycorrhizal fungi is beneficial, the compatible host plants (or even genotypes), and whether specific taxa of mycorrhizal fungi can be applied alone or in microbial consortia, along with other microorganisms such as mycorrhiza-helper bacteria and protists, or using a complex field inoculum (Allsup *et al.*, 2023). Similar to the human microbiome, there is an important potential for microbiome engineering (Silverstein *et al.*, 2023). Many commercially available mycorrhizal products are either nonviable or ineffective (Salomon *et al.*, 2022), and it is often overlooked whether the fungi present in these commercial inoculants have been successfully established in the field. Therefore, it is essential to DNA barcode the inoculum, trace the establishment and survival of mycorrhizal fungal isolate(s) in the field, and determine the economic and ecological feasibility of their application.

6. Promoting C sequestration and climate resilience

Mycorrhizal symbioses have the potential to contribute to climate change mitigation by promoting C sequestration and cycling in soil

(Hawkins *et al*., 2023). Mycorrhizal networks contribute to *c*. 20–30% of the microbial biomass present in soils (Leake *et al*., 2004), representing substantial soil C storage. C fluxes through mycorrhizal mycelia are high, and C can be immobilized in both mycelia and secretions on both organic and mineral substrates for long periods (Finlay & Clemmensen, 2017). Metabarcoding surveys coupled with genomic/transcriptomic studies can help to identify fungal species and genetic traits associated with high C sequestration potential (Plett *et al*., 2021) (Box 1). A recent study demonstrated that mycorrhizal interactions might be a driver of alternative stable states and tipping points in tundra ecosystems. These regions are typically dominated by ERM associations that are associated with SOM accumulation and slow decomposition. However, tree encroachment can lead to an abrupt decrease in belowground SOM linked to the abundance of ECM trees that contribute to SOM decomposition while scavenging N (Clemmensen *et al*., 2021). In dry ecosystems, additional drought and reduced rainfall can reduce the abundance of ECM fungi, leading to increase abundance of saprotrophic fungi and enhanced SOM decomposition (Querejeta *et al*., 2021). Furthermore, mineral weathering in deeper soil horizons and mycelial biomass depends on SOM abundance and nutrient availability (Mahmood *et al*., 2023). These studies have shown that changes in mycorrhizal type and abundance may alter C sequestration and cycling. Other studies have demonstrated that mycorrhizal associations alleviate drought stress (Augé, 2001) and can enhance ecosystem resilience and drought resistance (Jia *et al*., 2021). Finally, several studies have shown that multiple stressors, including pesticides, reduce soil ecosystem functioning (Rillig *et al*., 2019a,b, 2023; Edlinger *et al*., 2022). Whether mycorrhizal fungi suffer from or provide resilience to multiple stressors requires further investigation.

IX. Conclusion

In conclusion, the integration of genomics and other -omics tools hold great promise for enhancing the utilization of mycorrhizal associations in sustainable ecosystem management. By unraveling the intricate dynamics of these symbiotic interactions, valuable insights that are crucial for promoting ecological sustainability and addressing pressing environmental concerns can be gained. This holistic approach, combining advanced genomic techniques with comprehensive global molecular diversity surveys, will undoubtedly contribute to the effective and responsible use of mycorrhizal fungi in ecosystem management in the future.

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Competing interests

None declared.

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