

## EDITORIAL

## Mycorrhizal Networks

# Mycorrhizal networks: Understanding hidden complexity

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## Abstract

1. The symbiotic relationship between mycorrhizal fungi and plants predates the origin of roots and has played a key role in shaping ecosystems for hundreds of millions of years. In associating with multiple plants simultaneously, mycorrhizal fungi can form complex below-ground networks that directly—and indirectly—influence plant communities, plant and soil resource dynamics, and broader ecosystem processes.
2. Research has provided increasing insight into the structure and function of these networks, including the movement and exchange of resources between symbionts, the mechanisms governing fungal and plant community assembly, and their potential applications in land management. As public interest in mycorrhizal networks has grown, so too have calls within the scientific community for greater clarity regarding their ecological functionality and broader significance.
3. This Special Focus brings together research that advances our understanding of these networks from multiple perspectives. Contributions explore the hierarchical complexity of fungal-plant associations, the ecological and functional implications of mycorrhizal selectivity, the resource exchange dynamics, and their relevance in applied contexts, such as agriculture.
4. By synthesising emerging evidence, this collection highlights key advances while also identifying unresolved questions and the future research directions necessary for disentangling the ecological roles of mycorrhizal networks.

## KEYWORDS

below-ground networks, community assembly, mycorrhizal fungi, mycorrhizal selectivity, plant communities, resource exchange

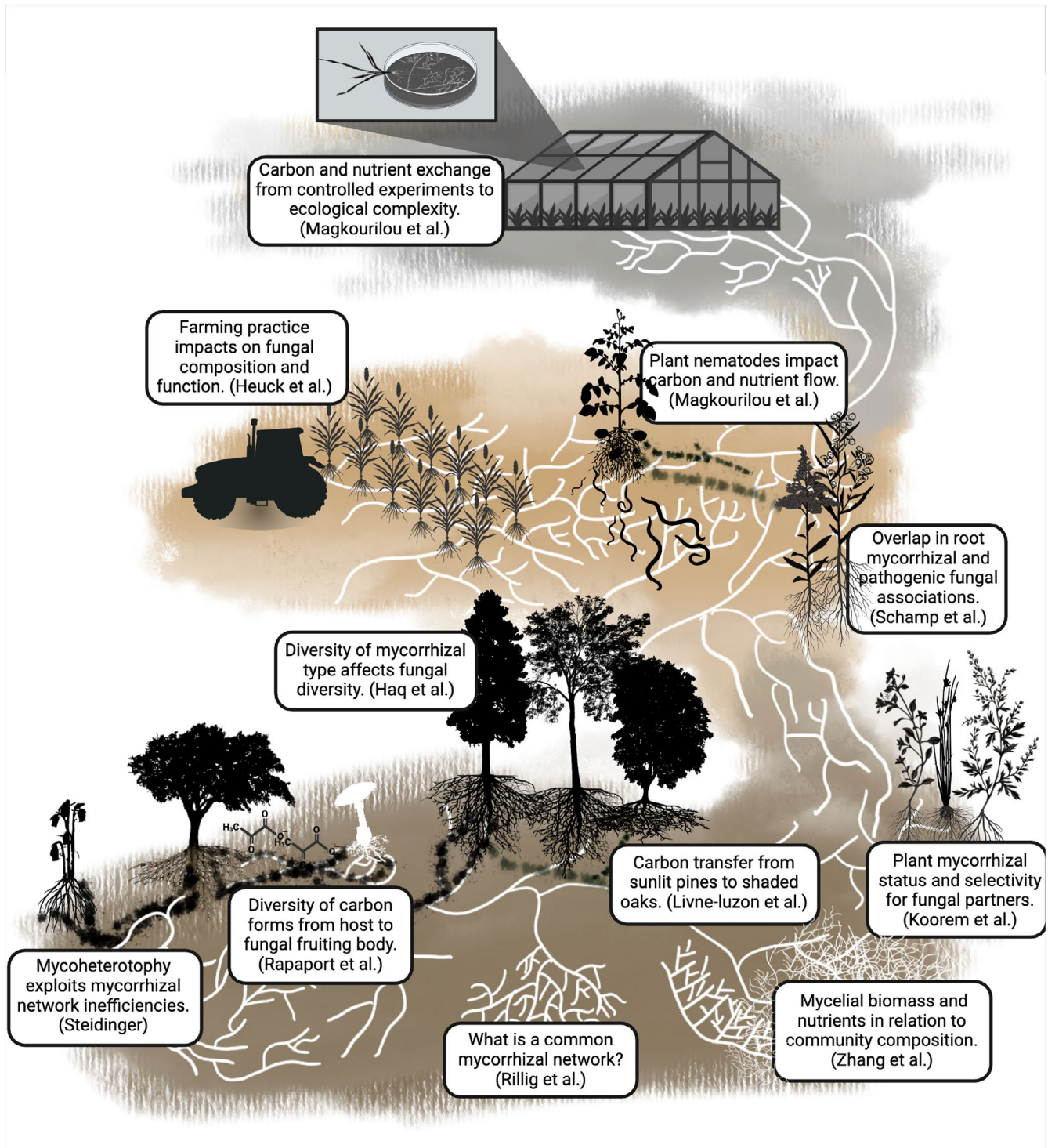
## 1 | INTRODUCTION

Ecology is the study of interactions in the natural world, and hence complexity is inherent. While some complex systems like pollination networks are conspicuous, others, like mycorrhizal networks, are hidden below-ground. By colonising multiple plant hosts simultaneously, mycorrhizal fungi can form physical links between plants within a community as well as interacting indirectly as discreet mycelial networks. Mycorrhizal symbioses are among the

most ubiquitous and important plant symbioses in the natural world (Smith & Read, 2008). Over several decades, there has been increasing understanding of the mechanisms underpinning these interactions between plants and fungi. As such, an ecological perspective on mycorrhizal networks should extend beyond single plant host–single fungal symbiont interactions (van der Heijden & Horton, 2009). Instead, it should aim to encompass the possibility of multiple simultaneous interactions between neighbouring fungi colonising neighbouring plants (Figure 1). Many species of mycorrhizal

fungi form extensive extraradical mycelia extending beyond the host root that can facilitate the exchange of resources among neighbouring host plants, potentially across communities, with critical implications for carbon and nutrient cycling (Wipf et al., 2019). In recent years, mycorrhizal networks have attracted much attention within the scientific community and beyond, to the extent that the

concept penetrated popular culture, including books (Simard, 2021), TV (Druyan, 2020), and even movies (Mills, 2021). Despite this, calls are now emerging from within the scientific community (Henriksson et al., 2023; Karst et al., 2023) asking for hard evidence concerning the existence of mycorrhizal networks, their functionality, and their broader ecological role(s).



**FIGURE 1** Illustrative overview of the papers published as part of the Special Focus on mycorrhizal networks, also covered in this Editorial. In this overview, papers are presented by context, either from controlled conditions (top); agricultural (middle); or ecological (bottom) context.

## 2 | ECOLOGICAL COMPLEXITY OF MYCORRHIZAL NETWORKS

Common mycorrhizal networks include a spectrum of interactions, from any linkage formed by the mycelium of a mycorrhizal fungus among two or more host plants, to the specific case where direct hyphal links with cytoplasmic continuity occur from plant to plant. While these have been strictly defined as continuous hyphal connections (Karst et al., 2023), advances in our understanding of mycorrhizal ecology emphasise the need for a broader framework to encompass the diversity of fungal-plant associations (Figure 1). In this context, the framework laid out by Rillig et al. (2025) provides a hierarchical reconceptualisation of the use of the term 'common mycorrhizal network'. The authors differentiate between 'common mycorrhizal networks with hyphal continuity', which emphasise the physical direct linkages, and broader 'common fungal networks' that include more diffuse associations without continuous hyphal structures. Such distinctions are critical to how we understand mycorrhizal fungi, their interactions with each other and their hosts, but also in directing and communicating future research inquiries to better understand their ecology. The Rillig et al. approach seeks to better capture the ecological and functional complexity of mycorrhizal networks, thereby better encouraging interdisciplinary exploration.

Another component of the great complexity of mycorrhizal networks is that their formation and diversity are influenced by multiple factors, including host plant diversity, fungal specificity, and environmental conditions. In this Special Focus, ul Haq et al. (2025) demonstrated how tree diversity and the mycorrhizal type—arbuscular mycorrhizal (AM) or ectomycorrhizal (EcM)—influence the fungal community composition, reinforcing the notion that mycorrhizal networks do not operate as homogenous entities but rather as a collection of dynamic and context-dependent interactions (Castro Sánchez-Bermejo et al., 2024). Their findings highlight the distinctions in nutrient acquisition strategies and ecological functions between AM fungi, characterised by low host specificity and an ability to scavenge inorganic nutrients, and EcM fungi that utilise organic nutrient sources and exhibit greater specificity. These distinctions contribute to the functional heterogeneity of mycorrhizal networks, which further underscores the need for us to adopt inclusive definitions for mycorrhizal networks (Rillig et al., 2025) as we seek to better understand their roles within ecosystems.

Despite the apparent generalism of AM fungi in their capacity to associate with a wide range of host plant taxa, studies show that plants can exhibit varying degrees of selectivity in their fungal associations (Sepp et al., 2019). Koorem et al. (2025) examine how plant mycorrhizal status (whether they are obligate, facultative or non-mycorrhizal) affects partner selection and the functional outcomes of the interactions. Their findings suggest that obligately mycorrhizal plant species are less selective in their fungal partners, contrasting with the greater selectivity observed in those plants that only sometimes associate with mycorrhizal fungi (facultatively mycorrhizal). This selectivity directly influences the composition of mycorrhizal communities and, in turn, can ultimately impact broader

ecosystem processes. This was further supported by the study of Schamp et al. (2025) who demonstrated that overlap in root fungal associations among plant species appears to be predictive of plant species richness and therefore the assembly of plant communities. Using vegetation plot data from an old-field plant community, plant species richness was found to be significantly higher in plots where plants were estimated to overlap more in AM fungi and significantly lower in plots where plant species were estimated to overlap more in pathogenic root fungi.

We also see how generalist and specialist strategies can shape diversity in the context of mixed mycorrhizal systems, where both AM and EcM fungi coexist, in ul Haq et al. (2025). Their findings suggest that mixed mycorrhizal systems can promote fungal diversity by supporting niches for generalist taxa while also maintaining the unique roles of specialists. Such supporting of diversity allows complementary resource use among fungal taxa, contributing to ecosystem stability. This underscores the value in understanding how selectivity, or specialisation, in mycorrhizal partnerships influences biodiversity and ecosystem functioning across plant communities.

## 3 | RESOURCE EXCHANGE AND MARKET DYNAMICS

A fundamental component of the role of mycorrhizal networks to ecosystems is their functioning in resource exchange. Mycorrhizal networks facilitate the bidirectional movement of nutrients, carbon and signalling molecules between plants and fungi, often described within a 'biological markets' theoretical framework (Noë & Kiers, 2018). It is within such 'markets' that plants and fungi 'negotiate' resource trades to maximise benefits. Experimental works have demonstrated that plants can preferentially allocate carbon to fungal partners that provide the most phosphorus (Bever et al., 2009), and that both fungus and plant can adjust the resources they supply the other, depending on what they receive in return (Kiers et al., 2011). New insights about the spatial heterogeneity of nutrients within the mycelial network emerge from the study of Zhang et al. (2025). The concentrations of [C], [N] and [P] were measured in AM hyphal in-growth bags, as well as in plant tissues in 2 × 2 m quadrats. Phosphorus is stored in the mycelium at levels equivalent to twentyfold those in plant tissue, in correlation with mycelium biomass. Yet, how do mycorrhizal markets operate in complex, natural systems where multiple factors, such as competition, environmental stressors and species-interactions, simultaneously influence resource availability? As mycorrhizal research advances, it becomes increasingly necessary to incorporate greater ecological complexity, while also striving to provide mechanistic insights (Read, 2003). How can researchers balance ecological realism with the need to control confounding variables?

The influence of biotic factors on mycorrhizal network functioning is evident in the experimental work of Magkourilou, Bell, et al. (2025), which explores how host infection by nematodes alters resource allocation among plants and AM fungi. Their findings

indicate that AM fungi preferentially allocate phosphorus to uninfected hosts over nematode-infected neighbouring plants, reinforcing the concept of partner selection, where fungal allocation is driven by expected returns. However, in multi-plant systems, infected hosts do not exhibit reduced carbon allocation to their fungal partners, complicating the classical market-based interpretation of mycorrhizal exchanges. A similar challenge to classical market assumptions is presented in the findings of Livne-Luzon et al. (2025), who investigated the context-dependent effects of below-ground carbon transfer. Their findings suggest that while shaded oak saplings receive carbon from sunlit pines, this transfer does not translate into direct growth benefits. This contradicts the expectation that carbon-sharing within mycorrhizal networks inherently enhances recipient performance.

Beyond the abundance of resources, the forms in which they are exchanged within mycorrhizal networks remain an underexplored yet key aspect of resource dynamics. Using a combination of isotopic labelling and metabolomic analysis, Rapaport et al. (2025) examined the diversity of carbon forms transferred within mycorrhizal networks, including amino acids, nucleotides and fatty acids being transferred between the roots and the fruiting bodies of ectomycorrhizal fungal partners *Tricholoma* and *Suillus*. The chemical diversity diverged between the two colonising fungal species, with >100 different molecules in *Tricholoma*, compared with 40 in *Suillus*, suggesting species-specific differences in chemical exchange. If different fungal taxa specialise in acquiring particular forms of carbon, could this shape plant-fungal compatibility and thus the stability of mycorrhizal networks under changing environmental conditions? The rapidity and diversity of these carbon transfers underscore the importance of considering resource quality, not just quantity, in determining the outcome of plant-fungal interactions.

Expanding this discourse, Steidinger (2025) introduces the 'mycorrhizal arbitrage' hypothesis, which proposes that mycoheterotrophy plants exploit putative 'inefficiencies' in biological markets to their advantage. Unlike the traditional understanding of the mutualistic interaction, these plants provide no carbon contributions to their fungal symbionts yet still extract resources, capitalising on variability in exchange rates across mycorrhizal networks. This hypothesis challenges conventional dichotomies of mutualism and parasitism, and raises broader questions around how such imbalances shape the evolution of mycorrhizal symbioses. To what extent could mycorrhizal markets be manipulated or exploited under various ecological conditions? The concept of mycorrhizal arbitrage gives us an interesting perspective on the potential flexibility, and vulnerabilities, of mycorrhizal-mediated exchanges.

#### 4 | APPLIED PERSPECTIVES AND AGRICULTURAL RELEVANCE

While intensely managed landscapes, such as those in modern agriculture, impose constraints on mycorrhizal networks, mycorrhizal fungi remain widespread and can exhibit high diversity across most

agricultural systems. Despite ongoing debate regarding the benefits and feasibility of managing mycorrhizal fungi to enhance agricultural productivity (Rillig et al., 2019; Ryan & Graham, 2018), growing evidence suggests that targeted shifts in management practices can promote beneficial fungal associations (Edlinger et al., 2022). Intensive agricultural systems face important challenges, such as soil degradation, nutrient balances and the need to reduce many chemical inputs. In this context, leveraging mycorrhizal networks represents an increasingly viable strategy for enhancing soil health and crop resilience. However, agricultural intensification has significantly disrupted mycorrhizal community structures (Banerjee et al., 2019), raising questions about how we can integrate mycorrhizal symbioses into modern farming practices.

Heuck et al. (2025) provide insights into how different management practices shape AM fungal communities. Their study found that organic agricultural systems tend to support higher fungal diversity compared with conventionally managed systems. Moreover, the communities harboured in these organic systems are more beneficial for crops than those from conventionally managed soils, yet this does not entirely exclude less beneficial fungal taxa. These findings highlight the opportunities to optimise agricultural management to select for the persistence and functional contributions of certain mycorrhizal fungi in managed soils.

Efforts to enhance soil mycorrhizal networks by managing fungal community composition may be limited if fungal selection is ultimately controlled by the host plant. Thus, beyond managing fungal community composition, effective management of mycorrhizal fungi requires a deeper understanding of plant-fungal selectivity and the implications for symbiotic functions, such as host plant nutrient uptake, soil diversity or plant. As the findings of Koorem et al. (2025) highlight, some plant hosts exhibit higher specificity in their associations, which the authors found was related to their relative reliance on the symbiosis. This suggests that understanding the selectivity of different crop species with putatively beneficial fungal taxa may be necessary before efforts go into implementing targeted management strategies (Frew et al., 2025). Therefore, could plant breeding programmes play a role in optimising mycorrhizal interactions, selecting crop lines that form associations with more beneficial fungal taxa? This may also be relevant to other efforts where managing mycorrhizal networks is particularly critical, such as in the conservation and restoration of forests and grasslands (Averill et al., 2022). Thus, it may be necessary to understand the specificity of hosts in the context of the resident fungal communities of a particular habitat before deciding which management approach to implement.

#### 5 | METHODOLOGICAL CONSIDERATIONS FOR MYCORRHIZAL NETWORK RESEARCH

Early research on mycorrhizal fungi relied heavily on simplified experimental systems, providing valuable insights but limiting ecological realism. Recent works have increasingly embraced more complex,

ecologically relevant approaches that better capture the variability of plant-fungal interactions. However, as Magkourilou, Durant, et al. (2025) highlight, incorporating greater ecological complexity into experimental designs presents significant challenges, including difficulties in isolating causal mechanisms and the need for long-term monitoring to assess persistence and functional impacts over time. The authors point to the persistent challenge in mycorrhizal research of scaling experimental findings from controlled conditions to natural ecosystems. While laboratory and greenhouse studies provide essential mechanistic insights, they fail to capture environmental heterogeneity and biotic interactions that shape mycorrhizal network dynamics in the field. Several studies within this Special Focus issue illustrate the importance of context-dependent factors in mycorrhizal network flows. For example, Livne-Luzon et al. (2025) demonstrate that below-ground carbon transfer within established plant communities does not always confer direct benefits to the recipient plants, or Magkourilou, Durant, et al. (2025) show that biotic stressors can alter fungal resource allocation, further emphasising how contextual factors can shape network function. We agree with Magkourilou, Bell, et al. (2025) that bridging this gap requires mycorrhizal ecologists to adopt multi-scale experimental designs that integrate controlled manipulations with larger-scale ecological observations. Only by combining these approaches can we achieve a more holistic and ecologically meaningful understanding of mycorrhizal networks across spatial and temporal scales.

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All authors contributed to writing and editing this editorial and gave approval for its submission.

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All authors are Associate Editors at *Functional Ecology* but took no part in the review process or decision-making process for this paper.

#### DATA AVAILABILITY STATEMENT

No data were used in the preparation of this Editorial.

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