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A mycorrhizal revolution

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It has long been postulated that symbiotic fungi facilitated plant migrations onto land through enhancing the scavenging of mineral nutrients and exchanging these for photosynthetically fixed organic carbon. Today, land plant–fungal symbioses are both widespread and diverse. Recent discoveries show that a variety of potential fungal associates were likely available to the earliest land plants, and that these early partnerships were probably affected by changing atmospheric CO_2 concentrations. Here, we evaluate current hypotheses and knowledge gaps regarding early plant–fungal partnerships in the context of newly discovered fungal mutualists of early and more recently evolved land plants and the rapidly changing views on the roles of plant–fungal symbioses in the evolution and ecology of the terrestrial biosphere.

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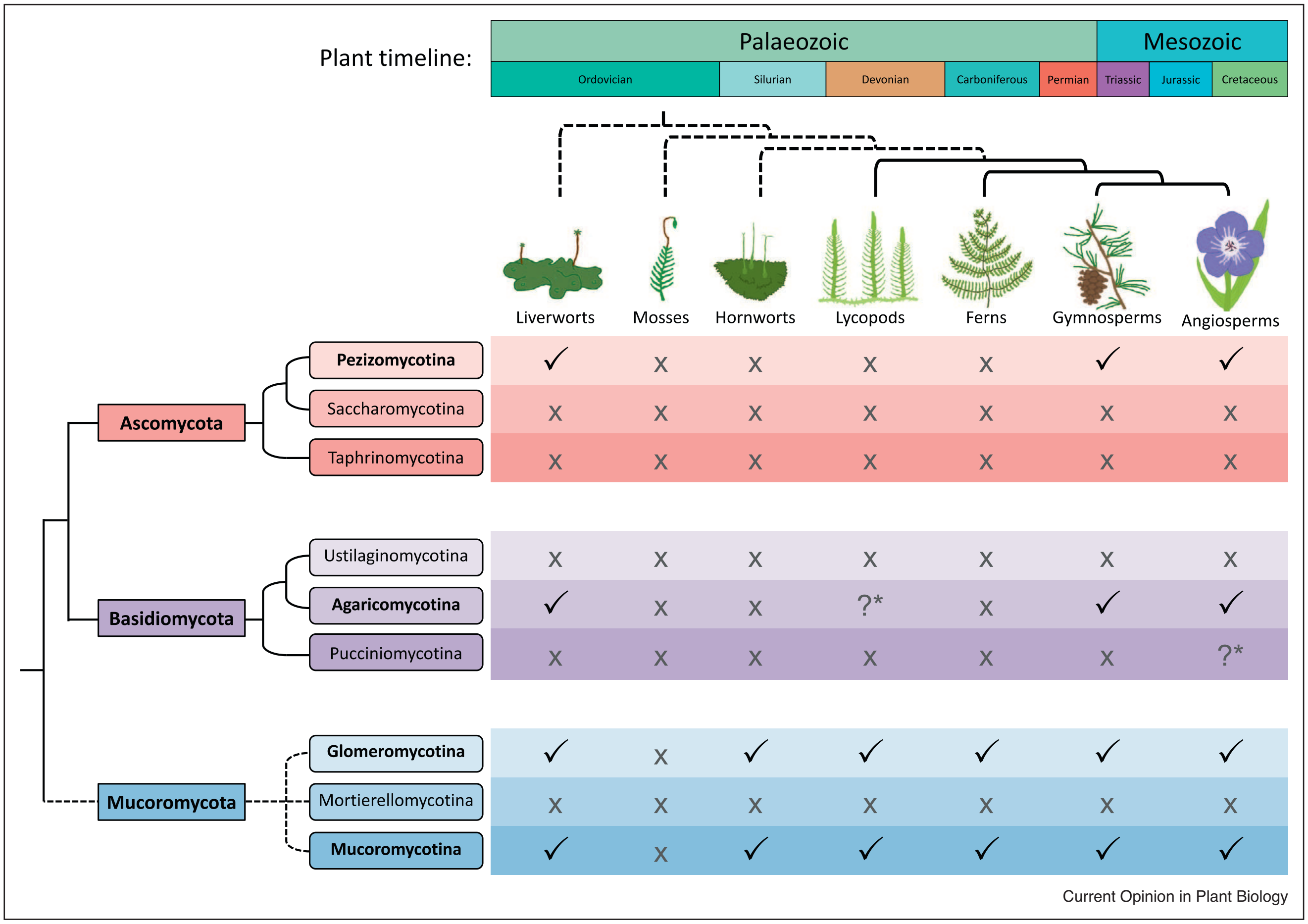
Introduction

Amongst the most important symbioses in nature after mitochondria and plastids are those between plants and soil-dwelling filamentous fungi. The vast majority of extant land plants, including most crops, form intimate symbioses with fungi in the phyla Mucoromycota, Ascomycota and Basidiomycota (Figure 1 [1•,2•]); these mutually beneficial partnerships are thought to have played a key role in plant terrestrialisation and diversification [3,4]. Such associations are termed 'mycorrhizas' (fungus-roots) in vascular plants, or 'mycorrhiza-like' in rootless non-vascular plants with intracellular fungal structures such as coils and/or arbuscules that are similar to those formed in rooted species [5]. In exchange for up to 20% of photosynthetically-fixed, organic carbon-based compounds (C) [6,7], mycorrhizal fungi may provide their plant partners with up to 80% of the nitrogen (N) and 100% of the phosphorus (P) required for plant growth and proliferation [8–12].

The first plants to colonise Earth's land surfaces in the Ordovician period (~475 Ma) were thought to have formed associations with arbuscular mycorrhizal Glomeromycotina fungi thereby gaining access to fungal-acquired mineral nutrients in return for plant carbohydrates [13] and/or lipids [14,15] in a manner similar to modern arbuscular mycorrhizal associations [7]. Thus, the first fungal symbionts may well have co-evolved with, and facilitated the transition of, rootless plants from water onto land [16,17] and subsequent terrestrial diversification [3,4]. This hypothesis has been strongly supported by cytological [18], molecular [19,20] and physiological evidence [4] alongside fossilised examples of early plants containing fungal structures bearing strong morphological similarity to modern mycorrhizas [21]. However, recent findings are now challenging the long-standing assumption that the symbionts of early land plants were solely Glomeromycotina fungi; instead they suggest that Mucoromycotina fungi have also played a major role [2•,22•].

Despite advances in our knowledge of non-vascular plant–fungal partnerships in liverworts and hornworts, there remains a significant gap regarding the occurrence, frequency, identity, appearance and function of Mucoromycotina associations in later-derived vascular plant lineages, including modern angiosperms, that have been of key significance in the development of Earth's terrestrial atmosphere and biota to the present day. More recently, an ascomycete fungus facilitating the growth of a non-mycorrhizal flowering plant under P-limited conditions was reported [23]; the study uncovers a previously unappreciated role of root fungal microbiota in nutrient cycling and highlights the diversity in plant–

Figure 1



		Liverworts	Mosses	Hornworts	Lycopods	Ferns	Gymnosperms	Angiosperms
Ascomycota	**Pezizomycotina**	✓	x	x	x	x	✓	✓
	Saccharomycotina	x	x	x	x	x	x	x
	Taphrinomycotina	x	x	x	x	x	x	x
Basidiomycota	Ustilaginomycotina	x	x	x	x	x	x	x
	Agaricomycotina	✓	x	x	?*	x	✓	✓
	Pucciniomycotina	x	x	x	x	x	x	?*
Mucoromycota	**Glomeromycotina**	✓	x	✓	✓	✓	✓	✓
	Mortierellomycotina	x	x	x	x	x	x	x
	Mucoromycotina	✓	x	✓	✓	✓	✓	✓

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The mycorrhizal status of the main land plant groups in relation to fungal phylogenetic diversity. Dashed lines indicate currently unresolved phylogenetic positions and asterisks signify uncertain mycorrhizal status with only one report of mycorrhizal formation in each case [57,38].

fungal nutritional interactions. Here we provide an overview of the recent leaps in understanding of the interactions between early land plants and symbiotic fungi in both the Glomeromycotina and Mucoromycotina [2•,24], with emphasis on the role, evolution and distribution of Mucoromycotina symbionts across the land plant tree of life.

Changing views on non-vascular plant symbioses with fungi

The symbioses between non-vascular plants and Mucoromycotina fungi have, in the last few years, received increasing attention. Unlike the strictly biotrophic and, to our current knowledge, asexual Glomeromycotina, e.g. the model mycorrhizal fungus *Rhizophagus irregularis*, Mucoromycotina encompasses saprotrophic, biotrophic, and putatively sexual lineages of fungi, including only poorly studied genera like *Endogone* and *Sphaerocreas* [25]. Until recently, the biology of the Endogonales was largely unknown [26•,27•]. In addition to endomycorrhizal associations, some members of *Endogone* can form ectomycorrhizal associations with trees [28,29], characterised by a root-covering mantle and intercellular penetration where hyphae form a network between cortical cells known as a Hartig net [7,30]. The remarkable versatility of these ancient and diverse fungi may be attributed to life history traits of the Endogonales, for example, facultative saprotrophy. However, more traits remain to be uncovered to understand further the evolutionary and ecological significance of these fungi.

The potential significance of Mucoromycotina fungi in land plant evolution was first recognised when *Endogone*-like fungi were found to associate with the likely earliest-diverging extant land plant lineage, Haplomitriopsida liverworts ([26•] Figure 1). This discovery generated the alternative hypothesis that a relict association with Mucoromycotina, apparently lost through land plant evolution, might have played a significant part in ancestral mycorrhizal-like symbioses [26•,31•]. This hypothesis was further supported by fossil evidence following re-examination of the Early Devonian Rhynie Chert plant *Horneophyton lignieri* [32]. In addition to

Glomeromycotina-like fungal structures in the aerial axes of *H. lignieri*, structures indicative of Mucoromycotina colonisation also appeared to be present within the plant's distinctive corm [32]. These fungal structures also showed similarities to symbiotic features in fossilised *Glomites rhyniensis* colonising *Nothia aphylla* [33]. These findings place Mucoromycotina as potential key players in the initial colonisation of Earth's landmasses [32]. However, structure does not always translate into function, particularly in fossils. A new cytological study showing intracellular colonisation of non-vascular plants with the broad-host range oomycete *Phytophthora palmivora* [34] suggests that branched haustoria-like structures and prolific intracellular hyphal growth could be interpreted as mycorrhizal-like if fossilised. Nonetheless, it is clear that fungal associations in early land plants were much more varied than previously assumed and likely included diverse mutualists and pathogens. Recent works show that in addition to the Halomitriopsida liverworts, many extant non-vascular plants such as complex and simple thalloid liverworts [35•], hornworts [31•], and early-diverging vascular plants [27•], harbour both Mucoromycotina and Glomeromycotina, sometimes simultaneously in the same host plant.

The earliest divergent lineage of liverworts, the Haplomitriopsida, form apparently exclusive partnerships with Endogonales [26•]. The first study on the cytology and functioning of liverworts with Mucoromycotina demonstrated a nutritional mutualism between partners, with plant-fixed carbon detected in the fungus and fungus-acquired nutrients (^{15}N and ^{33}P) in the plant [22•]. These findings clearly demonstrate that the nutritional role played by Mucoromycotina in Haplomitriopsida is analogous to that of Glomeromycotina in complex thalloid liverworts [18]. Additional experiments tested the carbon-for-nutrient exchange responses of liverwort-fungal associations against a simulated Palaeozoic decline in atmospheric CO_2 concentration, representative of the conditions experienced by early land plants [36]. In liverwort-Mucoromycotina symbioses, the amount of ^{33}P gained from the fungus by the plant, per unit of carbon delivered by the plant to the fungus, was either unaffected or even increased in response to declining CO_2, similarly to vascular plant-Glomeromycotina symbioses [4], but in direct contrast to observations in liverwort-Glomeromycotina associations [4]. Differences in CO_2 responsiveness between Mucoromycotina-plant and Glomeromycotina-plant symbioses, and between vascular-plant and non-vascular plant symbioses, likely provided physiological niches ensuring the persistence of both symbioses to the present [2•]. The subsequent discovery that some early diverging thalloid liverworts form simultaneous (dual) symbioses with nutritionally mutualistic Glomeromycotina and Mucoromycotina [26•] lent weight to this view, with the intriguing possibility that early plant–fungal symbioses were not only taxonomically and functionally diverse, but also potentially transient in nature, with plant and fungal partners shifting according to environmental conditions [2•].

Hornworts are an ancient plant phylum (300–400 Mya) that in some phylogenies are the sister group of the earliest vascular plants [37–39]. Molecular evidence of fungi in hornworts was limited [26•] until the extensive study by Desirò *et al.* [31•] revealed that these plants also have various symbiotic options. Hornworts were shown to form both single and dual associations with Glomeromycotina and/or Mucoromycotina, or to 'opt out' of symbioses altogether, suggesting the same may be true for other early-diverging plant lineages such as the liverworts and indeed, the first land colonists [26•,31•,40]. However, functional studies testing for nutritional mutualism between fungi and hornworts have yet to be performed.

Changing views on vascular plant symbioses with fungi

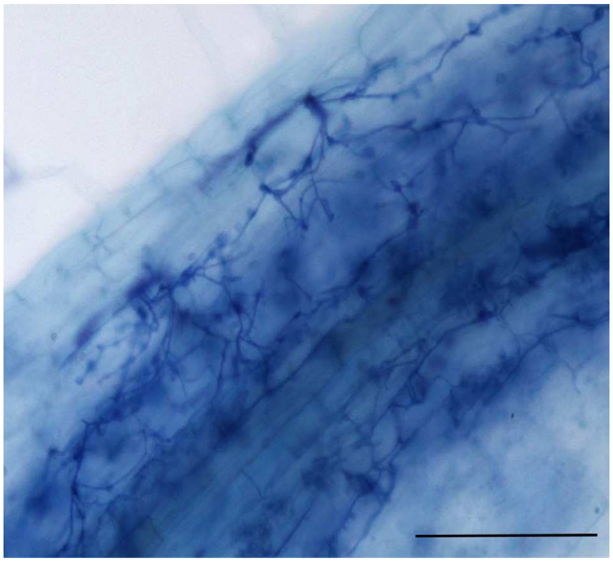
Research into early diverging vascular plant-Mucoromycotina symbiosis is in its infancy. Fungi have long been recognised to be present within lycopods [41,42], however, until recently their identity had been unclear [32,40,43]. Molecular analyses have now shown that Mucoromycotina associations, both single and in combination with Glomeromycotina, occur in this earliest diverging clade of extant vascular plants [27•], but, as with hornworts, there is still no functional evidence of mutualism in lycopod-fungal symbioses. In ferns, the most diverse early-diverging vascular plants, molecular, microscopical and physiological data have documented arbuscular mycorrhizas [1•,4,44]. Recent analysis of fern-fungal symbioses showed that although many ferns associate with Glomeromycotina, at least one — *Anogramma leptophylla* — can be colonised by Mucoromycotina and Glomeromycotina [27•]. So far, there is evidence of mutualistic nutrient exchange with Glomeromycotina for only two ferns, *Ophioglossum* and *Osmunda* [4,45].

The presence of Mucoromycotina in some early diverging vascular plants supports the idea that plants across the evolutionary tree are much more symbiotically versatile than hitherto assumed. However, with few exceptions, occurrence and knowledge of fungal associations across pteridophytes is based solely on light microscopy [44], a technique which may overlook Mucoromycotina co-colonisation [26•]. Cytological, molecular and physiological approaches are urgently needed to further understand the nature and functioning of these fungal partnerships in lycopods and ferns.

Fine root endophytes

Fungi known as fine root endophytes (*Glomus tenue*) colonise bryophytes and ferns [46–49] as well as the roots of vascular plants [50•]. Whilst their colonisation morphology is distinctive from that of the arbuscular

Figure 2



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Colonisation by fine root endophytes within the roots of *Lotus subbiflorus* (Fabaceae). Bar 100 μm.

Box 1 Outstanding questions

- How widespread are Glomeromycotina and Mucoromycotina in plant fossils?
- How is the colonisation and function of Mucoromycotina-plant symbioses controlled — by genetics, environment, or both?
- To what extent do fine root endophytes (FRE), other Mucoromycotina associations and Glomeromycotina associations overlap in nature?
- Why are FRE rarely observed without the presence of arbuscular mycorrhizal Glomeromycotina?
- Are Mucoromycotina associations with hornworts, lycopods, ferns and angiosperms mutualistic, both when present alone and when in dual symbiosis with Glomeromycotina?
- Do arbuscular mycorrhizal signals and colonisation pathways overlap with Mucoromycotina symbioses?

mycorrhizal fungi, the ability to produce arbuscules (Figure 2) led to their initial classification as *Glomus* within the arbuscular mycorrhizal fungi [50•]. However, recent research by Orchard *et al.* [51•] suggests that fine root endophytes are members of the Mucoromycotina, related to several Mucoromycotina identified from liverworts and lycopods by Field *et al.* [22•,35•] and Rimington *et al.* [27•,40]. This makes fine root endophytes the only known fungi to produce arbuscules outside of Glomeromycotina. A meta-analysis by Orchard *et al.* [50•] showed that fine root endophytes, which are likely a species group, are globally distributed across many ecosystems and colonise numerous vascular plant families [50•]. In Australia and New Zealand they are prevalent within the roots of crop and pasture species, where colonisation levels may be high and match those of arbuscular mycorrhizal fungi [50•]. Fine root endophytes have been associated both with disturbed or extreme environments and early successional plant establishment [46,50•,52–56] and may provide growth benefits to the host plant [50•,57], yet little is understood about the relationships between these fungi and plants. Even less is known of the evolutionary relationships between fine root endophytes and the arbuscular mycorrhizal fungi, for example, how they evolved to co-exist within plant species and even individual root segments [50•]. Putative fine root endophytes were recently identified in fossilised (permineralised) Permian specimens of root mantle from the tree fern *Psaronius* [58], raising questions about the evolutionary relationship between fine root endophytes and the arbuscular mycorrhial fungi, and when arbuscules first evolved. Developing methods to target and study fine root endophytes in a comparative context is imperative.

Future directions

The presence of symbioses with Glomeromycotina and Mucoromycotina in non-vascular and early vascular plants, in conjunction with evidence for Mucoromycotina nutritional mutualisms in early-diverging liverworts [26•,31•], strengthens the hypothesis that Mucoromycotina aided pioneering land plants. Genetic studies of plant–fungal symbioses [2•,24] are revealing extensive molecular and chemical crosstalk between the partners. To date, strigolactones from roots and lipochitooligosaccharides from fungi have been implicated in the establishment of arbuscular mycorrhizas [59,60•]. However, the molecular basis for the functioning of Mucoromycotina fungal partnerships, including those of fine root endophtyes, in non-vascular and vascular plants, has yet to be investigated (Box 1). Given that many model plants are not symbiotic (e.g. *Arabidopsis*, *Marchantia polymorpha*, *Physcomitrella*), molecular and functional analysis of targeted symbiotic liverworts, lycopods, ferns and angiosperms will go a long way toward elucidating the nature and dynamics of ancient and widespread Mucoromycotina symbioses, informing the interpretation of fossils [61], and our understanding of how lineages of fungi and plants co-evolved on land and transformed their environments.

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