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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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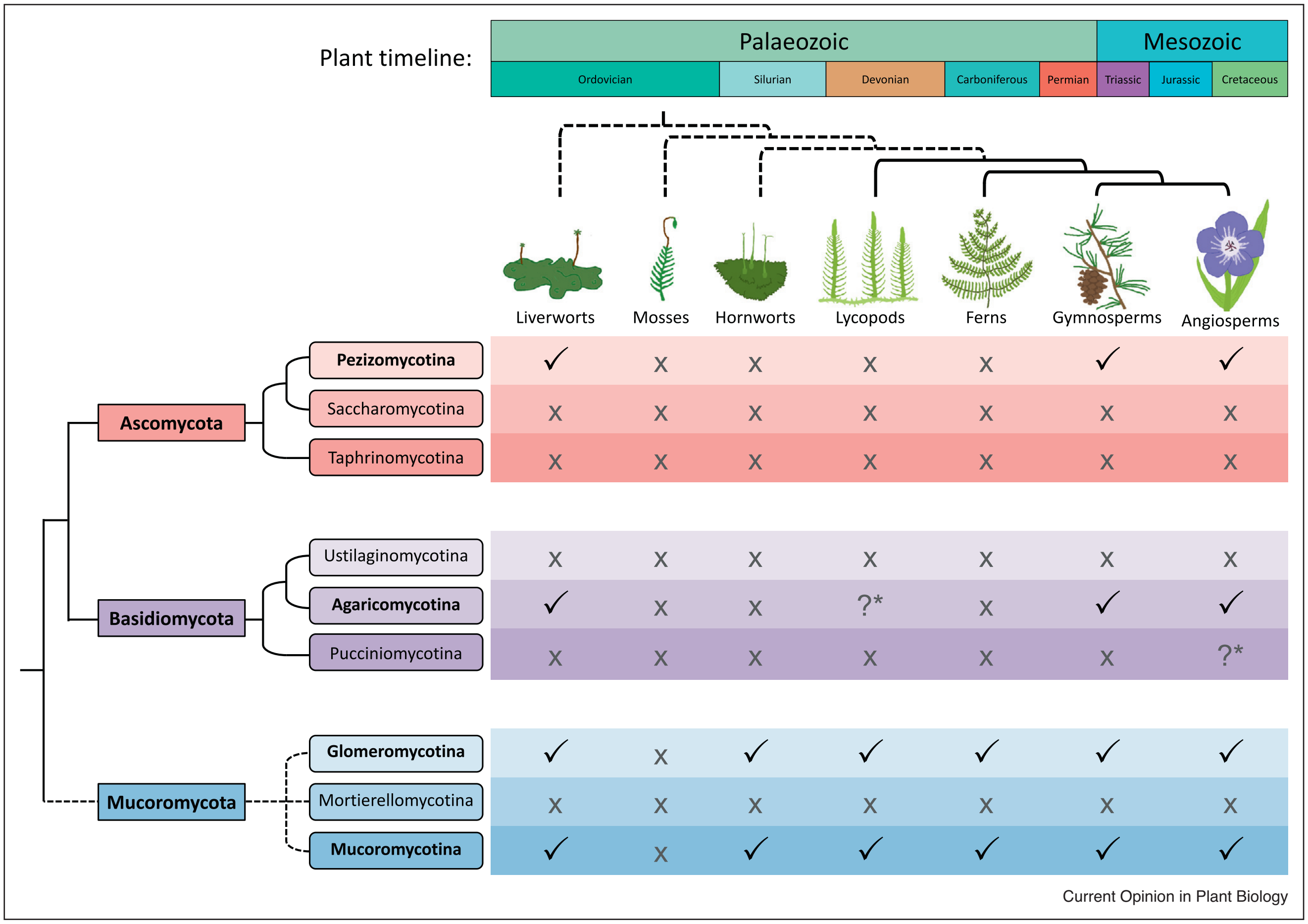
Introduction

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



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