Tansley review

Unity in diversity: structural and functional insights into the ancient partnerships between plants and fungi

Author for correspondence:
Katie J. Field
Tel: +44 0113 3432849
Email: k.field@leeds.ac.uk

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Katie J. Field[1] **and Silvia Pressel**[2]

[1]Centre for Plant Sciences, School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, LS2 9JT, UK; [2]Department of Life Sciences, Natural History Museum, Cromwell Road, London, SW7 5BD, UK

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Summary

Mycorrhizal symbiosis is an ancient and widespread mutualism between plants and fungi that facilitated plant terrestrialisation > 500 million years ago, with key roles in ecosystem functioning at multiple scales. Central to the symbiosis is the bidirectional exchange of plant-fixed carbon for fungal-acquired nutrients. Within this unifying role of mycorrhizas, considerable diversity in structure and function reflects the diversity of the partners involved. Early diverging plants form mutualisms not only with arbuscular mycorrhizal Glomeromycotina fungi, but also with poorly characterised Mucoromycotina, which may also colonise the roots of 'higher' plants as fine root endophytes. Functional diversity in these symbioses depends on both fungal and plant life histories and is influenced by the environment. Recent studies have highlighted the roles of lipids/fatty acids in plant-to-fungus carbon transport and potential contributions of Glomeromycotina fungi to plant nitrogen nutrition. Together with emerging appreciation of mycorrhizal networks as multi-species resource-sharing systems, these insights are broadening our views on mycorrhizas and their roles in nutrient cycling. It is crucial that the diverse array of biotic and abiotic factors that together shape the dynamics of carbon-for-nutrient exchange between plants and fungi are integrated, in addition to embracing the unfolding and potentially key role of Mucoromycotina fungi in these processes.

I. Introduction

The evolution of symbiosis, 'the living together of unlike organisms' (de Bary, 1879), has been central to the evolution of complex life on Earth. One of the most important terrestrial symbioses is that which occurs between an estimated 85% of land plants (Brundrett & Tedersoo, 2018) and fungi belonging to the basal phylum of Mucoromycota, which comprises the two

subphyla Glomeromycotina and Mucoromycotina (Bidartondo *et al.*, 2011; Spatafora *et al.*, 2016), as well as the 'higher' fungal phyla Basidiomycota and Ascomycota (Smith & Read, 2008). These fungi form intimate, usually mutualistic symbioses known as mycorrhizas or mycorrhiza-like in nonvascular plants lacking true roots (Read *et al.*, 2000), where mutualism is defined as being characterised by the bidirectional exchange of resources between partners to their mutual fitness benefit (Raven & Allen, 2003).

Mycorrhizal partnerships are thought to play a key role in the global carbon (C) cycle, through the allocation of photosynthetically fixed host plant C to fungal symbionts (van der Heijden *et al.*, 2015) and by affecting soil C sequestration processes (Soudzilovskaia *et al.*, 2015). It is estimated that plants direct generally 10–20% and up to 50% of their photosynthates to their fungi, with ecosystem C cycling and storage being strongly influenced by the predominant mycorrhizal type of the ecosystem (Averill *et al.*, 2014; Soudzilovskaia *et al.*, 2015). In return, mycorrhizal fungi may provide host plants with up to 80% of their phosphorus (P) requirements (van der Heijden *et al.*, 2017) while also making significant contributions towards plant nitrogen (N) and micronutrient needs (Smith & Read, 2008). Mycorrhizas are often defined by their structural characteristics, with ectomycorrhizal fungi (ECMF) growing within the apoplast between host cells, while endomycorrhizal fungi, including arbuscular, ericoid and orchid mycorrhiza-forming groups, penetrate the host plant cell wall, forming complex intracellular fungal structures such as arbuscules, hyphal coils and hyphal pelotons (Brundrett & Tedersoo, 2018; Fig. 1).

The most widespread (*c.* 74% of all plant species) association involves arbuscular mycorrhiza-forming fungi of the Glomeromycotina (AMF) (van der Heijden *et al.*, 2015) with other types of mycorrhizas (ectomycorrhizas, ericoid and orchid mycorrhizas) formed by later diverging Basidiomycota or Ascomycota fungi through multiple independent conversions of AM (Wang & Qiu, 2006). Several plant families or species within mycorrhizal families have lost, independently, their ability to form mycorrhizal associations (nonmycorrhizal (NM)) (Wang & Qiu, 2006). NM plants fall broadly into two categories: those with alternative nutritional strategies (e.g. parasitism, carnivory, specialised roots for phosphorous (P)-mining such as cluster roots) and those from habitats nonconducive to mycorrhizas (e.g. epiphytic, aquatic, heavily disturbed habitats) (Brundrett, 2009). The lack of mycorrhiza-like associations in mosses, an entire clade (Pressel *et al.*, 2010), remains somewhat puzzling. It has been proposed that their multicellular rhizoids with terminal ramifications of 2 μm in diameter might afford similar nutritional advantages to mycorrhizas (Field *et al.*, 2015a). Mycoheterotrophy, whereby achlorophyllous, nonphotosynthetic, plants gain organic carbon and other essential elements from their fungi, is also considered a derived condition that evolved independently over 40 times within plant lineages (Leake, 1994; Wang & Qiu, 2006; Merckx *et al.*, 2009). Glomeromycotina are aseptate, filamentous fungi (Spatafora *et al.*, 2016) which occur almost ubiquitously in clades across the land plant phylogeny. Their presence in all early diverging lineages of major clades of land plants supports arbuscular mycorrhizas as the ancestral type (Wang & Qiu, 2006). These obligately biotrophic fungi form characteristic intracellular structures within the host plant roots including highly branched, tree-like arbuscules in *Arum*-type colonisations that give them their common name of arbuscular mycorrhizal fungi, tightly wound hyphal coils (in *Paris*-type colonisations), vesicles and intercellular hyphae (Fig. 1). In plants without roots (i.e. the bryophytes: hornworts and liverworts) AMF tend to inhabit a distinct region within the thallus from which the rhizoids develop and form both arbuscules and coils alongside vesicles and strictly intracellular hyphae (Ligrone *et al.*, 2007; Pressel *et al.*, 2010).

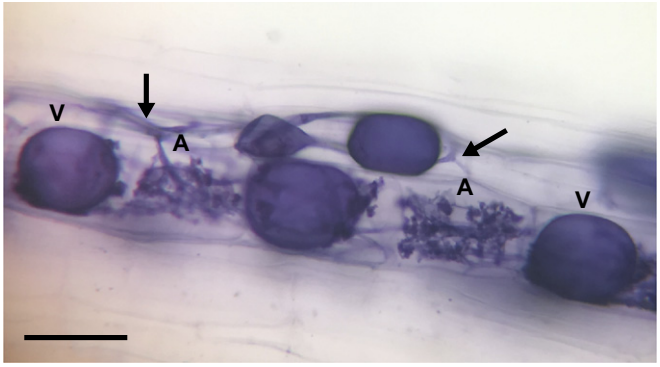

Fig. 1 Trypan Blue-stained typical *Arum*-type intracellular fungal structures produced during colonisation by the arbuscular mycorrhizal fungus *Rhizophagus irregularis* of vascular plant root cells (here, *Triticum aestivum*), with vesicles (V) and arbuscules (A) with interconnecting hyphae (arrows). Bar, 10 μm. Image courtesy of A. J. Elliott (University of Leeds, UK).

Recent discoveries are now revealing a hitherto unappreciated role of facultative saprotrophic Mucoromycotina fungi in mycorrhizal and mycorrhiza-like associations with early diverging land plant clades (Bidartondo *et al.*, 2011; Field *et al.*, 2015b), potentially extending to angiosperms (Orchard *et al.*, 2017a,b; Hoysted *et al.*, 2018). Such discoveries are now questioning, for the first time, the paradigm of AM as the ancestral type. Others are challenging our notion of AMF: their potential, and so far largely ignored, role in plant host nitrogen nutrition (e.g. Thirkell *et al.*, 2016) and how the AM symbiosis is better considered as a many-to-many interaction rather than a one-to-one, wherein fungi and plant partners form complex networks through which resources are shared (Leake *et al.*, 2004; Selosse *et al.*, 2006; van der Heijden *et al.*, 2015). These findings have potentially major implications for further understanding the origin and roles of mycorrhizal symbiosis in shaping terrestrial ecosystems – past, present and future.

This review aims to explore the considerable diversity in structure, function and response to environmental variables that exists within the unifying role of different mycorrhiza-forming fungi in C-for-nutrient exchange with plant partners. We will focus in particular on the mycorrhizal and mycorrhiza-like associations formed by plants with Glomeromycotina and Mucoromycotina fungi within the ancient phylum Mucoromycota and on how the latest research on these partnerships is leading the way to a paradigm-shifting view on the origin, evolution, and past and future responses to the environment of this key symbiosis between plants and fungi. Along the way, we identify current challenges and

potential exciting new avenues of investigation emerging from these latest developments in mycorrhizal research.

II. An ancient, and diverse, symbiosis

The prevalence of mycorrhiza-like and mycorrhizal associations in the earliest diverging clades of land plants points towards plant–fungal mutualisms having ancient origins with potentially critical significance in the initial establishment of a land flora > 500 million yr ago (Ma). In early diverging thalloid liverworts (Marchantiopsida (Complex thalloid) and Pellidae (Simple thalloid I), glomeromycotean fungal associates take on a *Paris*-type colonisation pattern, producing arbuscules and vesicles with large, colonising hyphae spreading from cell to cell (Fig. 2). Fungal colonisation occupies taxon-specific zones within the thallus, with the fungus gaining access to the plant tissue via rhizoids, specifically the smooth rhizoids in Marchantiopsida (Pressel *et al.*, 2010). In the more derived leafy liverworts (Jungermanniales), mutualistic associations with Ascomycota fungi are widespread (including *Pezoloma ericae* (D.J. Read) Baral & Kreiglsteiner, 2006 (syn. *Rhizoscyphus ericae* (D.J. Read); *Hymenoscyphus ericae* (D.J. Read); *Pezizella ericae* (D.J. Read); the same mycobiont as in ericoid mycorrhizas (Kowal *et al.*, 2018)). These fungi colonise rhizoids, inducing swelling of their tips, and form dense hyphal coils and, in many taxa, penetrate the host stems (Pressel *et al.*, 2008, 2010; Kowal *et al.*, 2016; Upson *et al.*, 2007; Fig. 2). Fewer leafy liverworts associate with Basidiomycota fungi, predominantly with members of the *Sebacina vermifera* species complex (Pressel *et al.*, 2010, and references therein) whilst the Aneuraceae, the only thalloid family with basidiomycetous endophytes, harbour preferentially members of the genus *Tulasnella* (Bidartondo *et al.*, 2003; Kottke *et al.*, 2003; Fig. 2). Therefore, fungal diversity in liverwort–fungus associations parallels that in 'higher' vascular plant–fungus symbioses (Pressel *et al.*, 2010; Field *et al.*, 2015a).

Recently, it has been shown that several extant, early diverging land plant clades are also colonised by members of the poorly characterised fungal subphylum Mucoromycotina, within Mucoromycota (Spatafora *et al.*, 2016). Thus, the earliest diverging Haplomitriopsida liverworts (*Treubia* and *Haplomitrium*) associate exclusively with Mucoromycotina fungi (Bidartondo *et al.*, 2011; Fig. 2), whilst several thalloid liverworts form partnerships with both mucoromycotean and glomeromycotean mycobionts, sometimes harbouring both fungi simultaneously (Field *et al.*, 2016a). These liverwort–Mucoromycotina associations are nutritionally mutualistic (Field *et al.*, 2016a) and therefore represent mycorrhiza-like symbioses. The occurrence of both fungi, either singly or in simultaneous 'dual colonisations', has also been observed throughout the hornworts (Desirò *et al.*, 2013) and the lycopods (Rimington *et al.*, 2015) and in one fern genus, *Anogramma* (Bidartondo *et al.*, 2011; Fig. 2). However, their mutualistic, mycorrhizal nature in these lineages remains to be established and is the subject of current investigations.

The first plants to colonise Earth's terrestrial land masses faced significant abiotic challenges. The biological soil crust (Edwards *et al.*, 2015) onto which the earliest bryophyte-like (Wellman *et al.*, 2003), rootless plants (Kenrick & Strullu-Derrien, 2014) first emerged was probably scarce in plant-accessible mineral nutrients and atmospheric CO_2 concentrations were very high compared to those of today (Berner, 2006; Mills *et al.*, 2018). However, long before the migration of plants onto Earth's terrestrial surfaces, the land masses were probably colonised by diverse microbes including fungi (Blair, 2009; Berbee *et al.*, 2017). A major evolutionary hypothesis posits that the formation of mutually beneficial partnerships between ancient plants and fungi was key to the establishment and evolutionary success of the terrestrial flora (Nicolson, 1967; Pirozynski & Malloch, 1975; Krings *et al.*, 2012). It has been proposed that these arbuscular mycorrhiza-like associations provided the earliest embryophytes with access to growth-essential nutrients, such as P (Pirozynski & Malloch, 1975), from skeletal mineral soils in exchange for plant-fixed organic carbon-based compounds (see Jiang *et al.*, 2017; Keymer *et al.*, 2017) in much the same way as the vast majority of land plants interact with their fungal symbionts today.

Strong support for this hypothesis was first provided by compelling evidence from fossil ecosystems, such as the Rhynie Chert, showing beautifully preserved fungal structures including arbuscule-like structures (Remy *et al.*, 1994; Taylor *et al.*, 1995), vesicles (Taylor *et al.*, 1995), and even spores and germination shields (Dotzler *et al.*, 2006) within the cells of ancient land plants – all remarkably similar to the fungal structures characteristic of extant arbuscular mycorrhizal associations (Smith & Read, 2008). Based on the striking structural homology between ancient, fossilised plant–fungus interactions and modern plant–Glomeromycotina partnerships, it was concluded that members of this fungal sub-phylum were probably involved in the ancestral plant–fungus symbiosis (Remy *et al.*, 1994; Taylor *et al.*, 1995). Subsequently, further corroborating evidence was provided by molecular, physiological and cytological studies. These established: (1) that the divergence dates of Glomeromycotina fungi fit within the timeframe of plant terrestrialisation (Simon *et al.*, 1993; Redecker *et al.*, 2000; Blair, 2009; Berbee *et al.*, 2017); and (2) that Glomeromycotina fungal associations present in extant early diverging lineages of land plants, that is liverworts (Pressel *et al.*, 2010) and ferns (Field *et al.*, 2012, 2015c; Pressel *et al.*, 2016), are nutritional mutualisms, although they provide greater nutrient returns to nonvascular liverworts compared with vascular ferns when grown under simulated Palaeozoic CO_2-rich atmospheres (Field *et al.*, 2012). Other studies examining fitness and productivity in liverworts with Glomeromycotina fungal associates have demonstrated clear benefits to the plants in terms of growth, asexual reproduction and photosynthetic output by associating with Glomeromycotina fungal partners (Humphreys *et al.*, 2010). Indeed, not only are the genes and biochemical pathways necessary for the formation and maintenance of symbiotic fungal associations – the symbiotic 'toolkit' – ubiquitous across the entire land plant phylogeny (Wang *et al.*, 2010; Delaux *et al.*, 2013; Oldroyd, 2013), this being strongly indicative of vertical inheritance from the earliest land plants, but also components of this 'toolkit' have been shown to be present within ancestral lineages of charophytic algae (Delaux *et al.*, 2015).

More recently, however, the long-held paradigm that Glomeromycotina fungi formed the ancestral plant–fungus symbiosis

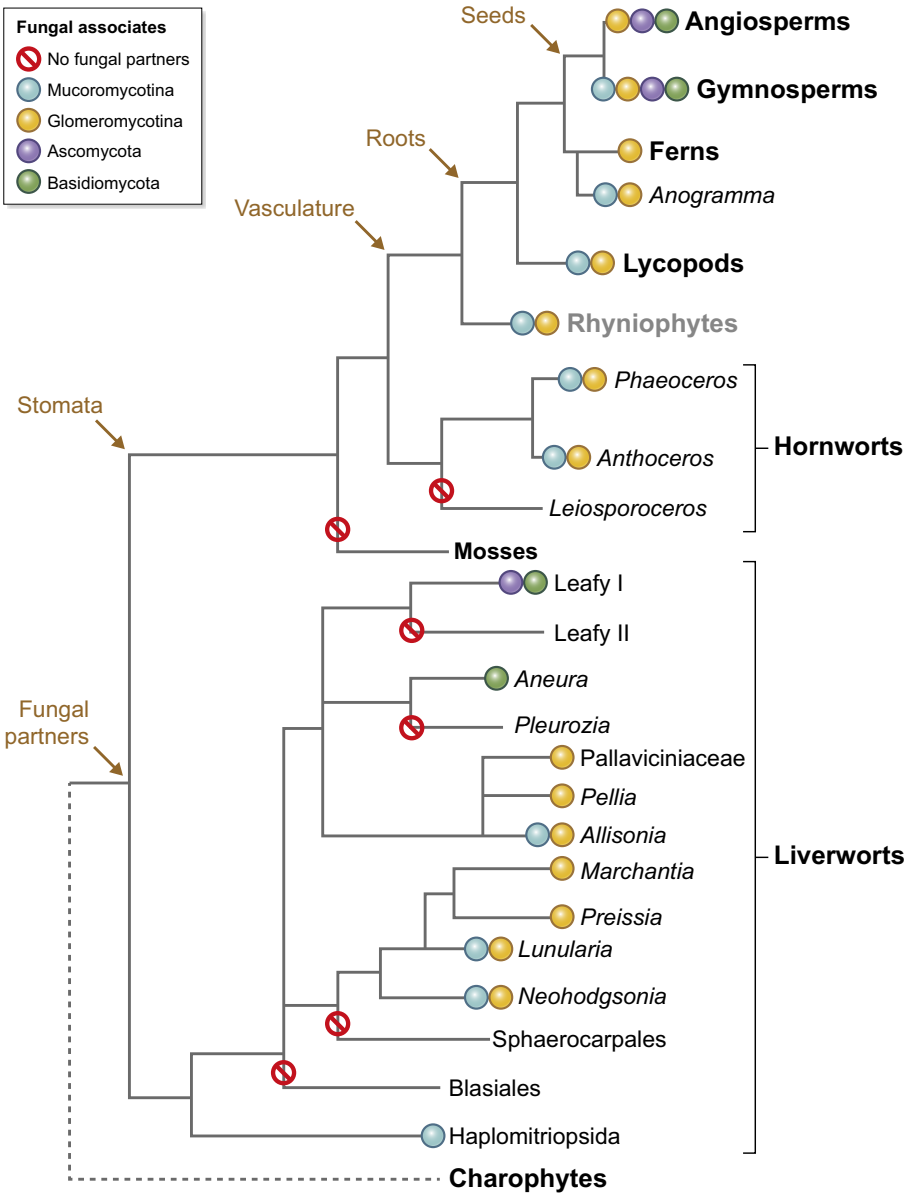

Fig. 2 Schematic land plant phylogeny (following Hedges & Kumar, 2009) with indication of fungal partner diversity detected in members of each plant clade (Bidartondo *et al.*, 2011; Desirò *et al.*, 2013; Strullu-Derrien *et al.*, 2014; Field *et al.*, 2015a,b; Rimington *et al.*, 2015). Key land plant physiological innovations are indicated with arrows. The latest research has now identified a liverwort–moss clade as sister to all other land plants (Puttick *et al.*, 2018), suggesting ancestral land plants were more complex than previously assumed.

has been challenged by the discovery that partially saprotrophic Mucoromycotina fungi, rather than Glomeromycotina, engage in nutritionally mutualistic partnerships with the earliest diverging Haplomitriopsida liverworts (Bidartondo *et al.*, 2011; Field *et al.*, 2015b; Fig. 2). Additionally, members of both fungal sub-phyla appear to form mutualistic mycorrhiza-like associations with early diverging simple and complex thalloid liverworts (Bidartondo *et al.*, 2011; Field *et al.*, 2015b) and are also widespread in hornworts and lycopods (Desirò *et al.*, 2013; Rimington *et al.*, 2015), although their functioning in early diverging vascular plant lineages is yet to be determined. The presence of Mucoromycotina fungi in early diverging land plant clades and resolution of Glomeromycotina as more closely related to Dikarya (Ascomycota and Basidiomycota) than Mucoromycotina (Schüßler *et al.*, 2001; James *et al.*, 2006; Bidartondo *et al.*, 2011) points to Mucoromycotina as the more likely symbionts involved in facilitating plant terrestrialisation (Feijen *et al.*, 2017) during the Ordovician (Edwards *et al.*, 2014; Morris *et al.*, 2018). However, other studies have presented contrasting topologies in which Glomeromycotina pre-date Mucoromycotina and are, possibly, the earliest diverging lineage of the Mucoromycota (Chang *et al.*, 2015; Spatafora *et al.*, 2016; Uehling *et al.*, 2017). Considerable uncertainties also remain regarding the timing of the divergence of Mucoromycota, hitherto estimated to pre-date the origin of land plants by some 100 million yr (Berbee *et al.*, 2017) and of the emergence of embryophytes, with latest estimates placing this major event earlier than generally assumed, in a middle Cambrian–Early Ordovician interval (Morris *et al.*, 2018). Given these large uncertainties, four evolutionary scenarios remain probable: (1) Glomeromycotina as the ancestral type (Mondo *et al.*, 2012; Chang *et al.*, 2015; Spatafora *et al.*, 2016); (2) Mucoromycotina as the ancestral type (Bidartondo *et al.*, 2011; Field *et al.*, 2015b); (3) dual colonisations involving

both fungal subphyla as the ancestral type (Rimington *et al.*, 2015; Field *et al.*, 2016a); and (4) symbiotic interactions between the common ancestor of Mucoromycota and early land plants, or even their algal ancestors (Selosse & Strullu-Derrien, 2015; Feijen *et al.*, 2017).

In line with the general trend for greater emphasis to be placed on examination of the rhizosphere depicted in Rhynie Chert fossils (Taylor *et al.*, 2003; Krings *et al.*, 2012) and with reports of mucoromycotean fungal symbionts in liverworts (Bidartondo *et al.*, 2011), re-examination of Rhynie fossils has revealed a potentially greater diversity of fungi forming symbioses with early plants than was previously thought (Strullu-Derrien *et al.*, 2014). Analysis of the Rhynie Chert fossil plant *Horneophyton lignieri* showed that there were two distinct, intra- and intercellular fungal associates inhabiting its aerial axes and corms, respectively; these formed fungal structures comparable to those observed in both modern Mucoromycotina and Glomeromycotina symbioses. Thus, the intercellular colonisation of the *Horneophyton* corm is highly reminiscent of that of mucoromycotean fungi in *Truebia* (Duckett *et al.*, 2006; Pressel *et al.*, 2010; Field *et al.*, 2015b), hornworts and lycopods, whilst the intracellular finely branched arbuscule-like structures and terminal spores within the aerial tissues conform to typical glomeromycotean colonisation patterns. Interpretation of early fossilised fungal remains in putative mutualistic associations with plants must, however, also consider a potential interaction between early embryophytes and the ancestor of Mucoromycotina and Glomeromycotina fungi. If indeed they represent this scenario, then questions regarding drivers of divergence of the two lineages gain greater prominence; why have both types of symbioses, sometimes simultaneous within the same individual, persisted in modern plants? In a similar vein, the phylogenetic affinity of early land plant fossils hitherto considered, by and large, as stem tracheophytes might require re-evaluation. The latest phylogenetic analyses aimed at resolving uncertainties of the relationships among bryophytes and between bryophytes and tracheophytes have found strong support for a clade of mosses and liverworts, or 'Setaphyta', suggesting that the ancestral embryophyte was more complex than hitherto assumed from topologies in which liverworts are the sister lineage to all other embryophytes (Puttick *et al.*, 2018). Regardless, the body of evidence that currently exists encompassing palaeobotanical, molecular, physiological and cytological data provides compelling support for the idea that the first associations between ancient plants and symbiotic fungi were nutritionally mutualistic and more diverse – in terms of both fungal identity and symbiotic function – than previously assumed (Selosse & Le Tacon, 1998; Read *et al.*, 2000; Wang & Qiu, 2006; Parniske, 2008; Bonfante & Selosse, 2010; Stürmer, 2012; Field *et al.*, 2015a).

III. Structural diversity in ancient plant–fungal partnerships

These recent discoveries of diverse fungal partners in early diverging lineages of land plants, involving members of both Mucoromycotina and Glomeromycotina subphyla, have spearheaded a re-evaluation of the until-recently puzzling range of fungal colonisation patterns observed across basal land plant clades. The cytology of colonisation in extant Mucoromycotina-exclusive symbioses (Bidartondo *et al.*, 2011; Field *et al.*, 2015b), that is those of *Treubia* (Duckett *et al.*, 2006; Fig. 3a,b) and *Haplomitrium* (Carafa *et al.*, 2003), shows a distinctive extracellular proliferation of the fungus forming coarse hyphae (2–3 μm) (Fig. 3b) and thick-walled spore-like structures in the mucilage-filled intercellular spaces of the thallus in *Treubia* (Duckett *et al.*, 2006) and within the thick layer of mucilage enveloping the underground axes of *Haplomitrium* (Carafa *et al.*, 2003). Similar patterns of extracellular colonisation, unknown in Glomeromycotina-only symbioses, have also been observed in hornwort thalli (Ligrone, 1988; Desirò *et al.*, 2013) and in the protocorm and gametophytes of lycopods (Duckett & Ligrone, 1992; Schmid & Oberwinkler, 1993), both of which we now know also harbour Mucoromycotina alongside Glomeromycotina symbionts (Desirò *et al.*, 2013; Rimington *et al.*, 2015). Also based on structural similarities with mucoromycotean cytology in *Treubia* was the recent re-evaluation of the fungal endophyte in the corm of the Rhynie fossil *Horneophyton ligneri*, and its reassignment to the Mucoromycotina (Strullu-Derrien *et al.*, 2014). A now overdue re-evaluation of another fossil plant, *Nothya aphylla*, might well lead to a similar conclusion (Krings *et al.*, 2007; Strullu-Derrien *et al.*, 2014; Field *et al.*, 2016b). Mucoromycotina fungi colonising the cells in the thallus midrib and underground axes of *Treubia* and *Haplomitrium*, respectively, also form distinctive structures comprising thin hyphae (0.5–1 μm) forming tightly wound coils with numerous terminal, small (10–15 μm) and short-lived 'lumps' or swellings (Duckett *et al.*, 2006; Carafa *et al.*, 2003; Fig. 3a). However, a similar pattern of intracellular colonisation by mucoromycotean symbionts is yet to be described in liverwort–Mucoromycotina symbioses other than those of Haplomitriopsida. In thalloid liverworts known from molecular studies to be symbiotic with both fungi (and which all lack intercellular spaces), for example *Neohodgsonia*, *Allisonia* and *Fossombronia* (Fig. 3c–g), it has not yet been possible to separate the two mycobionts on the basis of anatomy alone (Field *et al.*, 2015a, 2016a). The cytology of colonisation in these liverworts exhibits a range of fungal structures, including terminal arbuscules on trunk hyphae (Fig. 3c), arbusculated coils with intercalary arbuscules (Fig. 3d), tightly wound coils (Fig. 3e) and vesicles of varying diameters (15–45 μm) (Fig. 3f), that parallel those in liverwort–Glomeromycotina partnerships except for a greater variation in hyphal sizes (down to < 2 μm) (Fig. 3g). In this context, it is interesting to note that Beck *et al.* (2005, 2007) in their studies of arbuscular mycorrhizas in the neotropical tree *Alzatea verticillata* found a much greater structural diversity than previously reported in glomeromycotean symbionts in 'higher' plants. They characterised distinct morphotypes including one, morphotype III, structurally comparable to fine root endophytes by virtue of very thin hyphae (up to 1.5 μm), knobbly intercalary swelling, lack of vesicles and fine, fan-shaped branching. Parallel molecular analyses revealed diverse Glomeromycotina fungi and nine sequences from an unknown fungus clustering as a sister group to *Endogone* (Mucoromycotina) (Beck *et al.*, 2007).

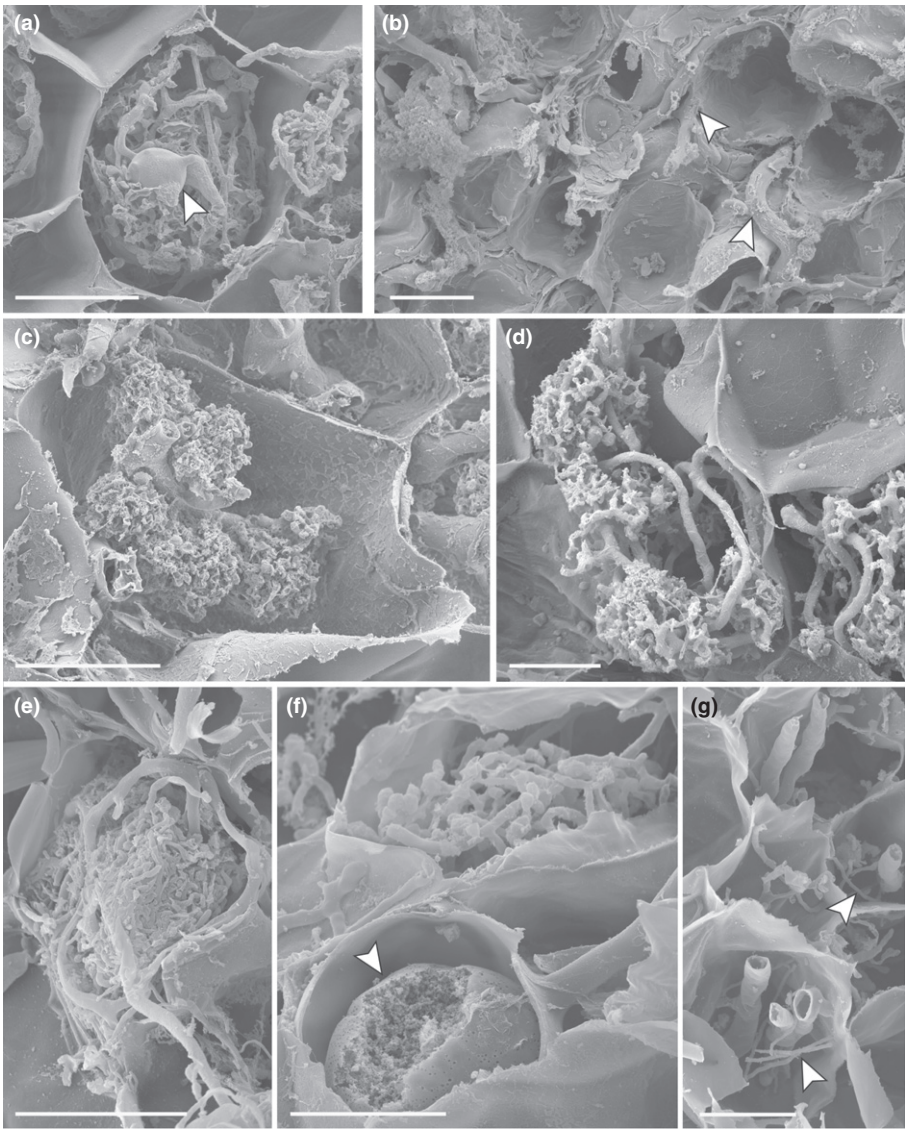

Fig. 3 Scanning electron micrographs showing fungal colonisation in the liverworts (a, b) *Treubia lacunosa*, (c, d) *Neohodgsonia mirabilis* and (e–g) *Fossombronia foveolata*. (a) Typical intracellular fungal colonisation by Mucoromycotina fungi in *Treubia*, comprising a hyphal coil with a terminal swelling; (b) coarse extracellular hyphae in the thallus of *Treubia* (arrowed). (c) Arbuscule terminal on a trunk hyphae and arbusculated coil (d) in the thallus of *Neohodgsonia* colonised by both Glomeromycotina and Mucoromycotina fungi. (e) Thin hyphae forming a tightly wound coil; a vesicle (arrowed) and an arbuscule (f) and coarse and thin (arrowed) hyphae colonising the same cells (g) in the thallus of *Fossombronia* in dual symbiosis with Mucoromycotina and Glomeromycotina fungi. Bars, 20 μm.

More recently, Orchard *et al.* (2017a) have proposed the reclassification of fine root endophytes (FRE) in the Mucoromycotina, rather than the Glomeromycotina. FRE have a global distribution and apparently colonise numerous vascular plant families (Orchard *et al.*, 2016, 2017b), often co-occurring with AMF in the same host, as well as having been described in bryophytes and ferns (Hoysted *et al.*, 2018, and references therein). Colonisation by FRE is, like AMF, characterised by the presence of arbuscules and arbuscule-like structures (Orchard *et al.*, 2016, and references therein), while the small diameter of their hyphae, and vesicles, is considered a distinctive morphological trait, clearly separating FRE from AMF, which consistently develop coarser (> 3 μm in diameter) hyphae and larger vesicles (Orchard *et al.*, 2016, 2017a).

What these studies clearly highlight is that there is considerably more diversity, both structural and in terms of the identity of the fungal symbionts involved, than hitherto appreciated across the land plant phylogeny. While some fungus-specific characters have been identified (Beck *et al.*, 2007; Strullu-Derrien *et al.*, 2014; Field *et al.*, 2015b), others such as the arbuscule can no longer be considered diagnostic of a particular fungal group, being found in both glomeromycotean and mucoromycotean colonisations or indeed lacking all together from some lower land plants in exclusive association with Glomeromycotina fungi (e.g. *Psilotum*), where fungal colonisation is characterised by prominent hyphal coils with small terminal vesicles (Winther & Friedman, 2009; Strullu-Derrien *et al.*, 2014). Assignment of fungal structures to a given fungal clade in plants colonised by diverse fungi is therefore not possible and immunocytochemical and molecular cytogenetic approaches are currently being developed to overcome this problem. Also requiring further investigation is the potential role(s) in nutrient exchange of the various structures, other than arbuscules, now characterised in Glomeromycotina and/or Mucoromycotina associations. Structural considerations aside, recent research (Orchard *et al.*, 2017a) showing FRE sequences closely related to several Mucoromycotina sequences from

liverworts (Field *et al.*, 2015b, 2016a,b; Rimington *et al.*, 2015) raises important questions on the occurrence, diversity and functional roles of Mucoromycotina associations, including FRE, across the land plant phylogeny, as recently highlighted by Hoysted *et al.* (2018).

IV. Mycorrhizal unity in host plant nutrition

Mycorrhizas are unified in participating in bi-directional exchange of resources between partners, whereby the fungus provides the plant with soil nutrients in return for photosynthesis-derived C (Smith & Read, 2008). The nutritional role of mycorrhizas was first established through the pioneering work of Mosse (1957) and others (e.g. Baylis, 1959; Daft & Nicolson, 1966; Murdoch *et al.*, 1967; Hattingh *et al.*, 1973), with a wealth of subsequent isotope tracer studies characterising the transfer and assimilation of fungal-acquired P to plants as a key feature of the arbuscular mycorrhizal symbiosis. Given their strictly biotrophic nature, AMF are considered to be entirely dependent on the host plant for their C requirements and to contribute significantly to plant P nutrition (Smith & Smith, 2011), with a negligible role in host N nutrition (Read, 1991; Hodge & Fitter, 2010). Nitrogen is mainly assimilated by plants as inorganic NH_4^+ or NO_3^- released by soil microbes through decomposition and nitrification, although the majority of N in the soil is present in plant-inaccessible organic forms (Vitousek & Howarth, 1991). As obligate biotrophs with no degradative capability it has long been thought that Glomeromycotina fungi are unable to utilize organic N sources from within the soil and that they therefore do not contribute to host plant N nutrition (Hodge & Fitter, 2010). Indeed, Tisserant *et al.* (2013) showed that the arbuscular mycorrhiza-forming fungus *Rhizophagus irregularis* lacks genes encoding plant cell wall-degrading enzymes. However, several studies have now shown that AMF hyphae acquire compounds from ^{15}N-labelled organic nutrient patches (St. John *et al.*, 1983; Hodge *et al.*, 2001; Leigh *et al.*, 2009), probably as microbial decomposition products (Leigh *et al.*, 2009; Hodge & Fitter, 2010), and a plant ammonium transporter that is mycorrhiza-specific and preferentially activated in cells containing arbuscules has been discovered (Guether *et al.*, 2009a,b). The extra radical hyphae of the fungus are thought to act as a major conduit between the microbial decomposer communities within the soil and the host plant, providing decomposers with photosynthates (Hodge & Fitter, 2010) and influencing bacterial community assembly during decomposition processes (Toljander *et al.*, 2007; Drigo *et al.*, 2010). However, whether the fungus then transfers the decomposition products to the host plant in exchange for C, leading to plant N assimilation (Ames *et al.*, 1983; Azcón *et al.*, 2003; Kaiser *et al.*, 2015; Thirkell *et al.*, 2016), or uses this N principally for its own growth and metabolism, thus essentially competing for soil N resources with its host plants (Hodge & Fitter, 2010) remains debated. While Thirkell *et al.* (2016) showed that AMF access to organic matter resulted in increased host plant N content and biomass, other studies have reported no effect on these two host plant parameters (Hodge *et al.*, 2001; Herman *et al.*, 2012) or even a reduction in biomass (Reynolds *et al.*, 2005). However, it should be noted that contrasting responses to mycorrhization have also been reported in terms of P (Corrêa *et al.*, 2015, and references therein). These may relate to the degree to which plants depend on fungal symbionts for nutrient uptake and the ease and/or pathway(s) by which a plant is able to acquire its own P (Smith *et al.*, 2010), underlining the notion that overall plant growth responses to mycorrhizal colonisation are not uniformly positive (e.g. Klironomos, 2003; Hoeksema *et al.*, 2010).

There is clear evidence that some fungal genotypes provide far greater nutritional benefits to plant partners than others (Munkvold *et al.*, 2004). Indeed, it has been shown that colonisation by multiple, diverse fungal partners may bring nutritional benefits over and above those when plants are colonised by a single fungus over the course of multiple seasons (van der Heijden *et al.*, 2006; Jansa *et al.*, 2008). Additionally, plant identity must also play a decisive role, with life history traits being key determining factors. There are also numerous examples of AM partnerships where plant growth is retarded upon colonisation by AMF (e.g. Klironomos, 2003; Hoeksema *et al.*, 2010). It is possible that in such cases the fungus imparts alternative, non-nutritional benefits to the plant partner, including enhanced defence capacity (Cameron *et al.*, 2013) and the potential role of the root as a refuge for the fungus under unfavourable environmental conditions (Field *et al.*, 2016b). These are both important factors that may contribute to the net fitness of each symbiont yet are often overlooked, with the main thrust of mycorrhizal physiological research remaining focused on C-for-nutrient exchange between symbionts.

Given the ecological role of AMs in N cycling (Hodge & Storer, 2015), unravelling the role of AMF in host plant N nutrition and potential C-for-N trades between symbionts (Corrêa *et al.*, 2015; Thirkell *et al.*, 2016) is crucial. These considerations must now also be extended to symbioses involving Mucoromycotina fungi, in particular following the recent demonstrations that these, on a par with AMF, are nutritionally mutualistic, participating in bi-directional exchange of plant-fixed C for mineral nutrients (Field *et al.*, 2015b, 2016a,b). Being facultative saprotrophs, Mucoromycotina fungi (Field *et al.*, 2015b) may be able to gain both C and N from organic sources, in a similar manner to some ECMF (Smith & Read, 2008; but see Lindahl & Tunlid, 2015), and would be in a position to then transfer N to their plant partners whilst remaining less reliant on the hosts to meet their C requirements. It should be noted, however, that the notion that ECMF are able to enzymatically liberate N from soil organic matter and to then transfer N to host plants is far from settled (Pellitier & Zak, 2018, and references therein). Recent studies have shown that ECM have a reduced complement of genes encoding plant cell wall-degrading enzymes than their saprotrophic ancestors – although the occurrence of these genes varies considerably across ECMF lineages – and thus have limited capacity to decompose soil lignocellulose (Martin *et al.*, 2008; Kohler *et al.*, 2015). Interestingly, the repertoire of genes associated with such functions has been shown to be much greater in Mucoromycotina fungi not only than AMF but also ECMF, although only nonsymbiotic species have been analysed so far (Tisserant *et al.*, 2013). Inclusion of Mucoromycotina species known to form mycorrhizas or mycorrhiza-like associations in future such studies would seem critical. Indeed, following the

recent placement of FRE in the Mucoromycotina (Orchard *et al.*, 2017a), determining potential differences in nutritional modes and requirements between Mucoromycotina and Glomeromycotina fungi might have important implications for our understanding of mycorrhizas and their role in nutrient cycling. The potential non-nutritional roles of mucoromycotean fungal symbionts have also not yet been explored, representing another major potential avenue for future research.

V. Plant-to-fungus carbon transfer

Plant-to-fungus C transfer is another fundamental aspect of mycorrhizal partnerships, particularly in AM symbioses where the fungi, being obligate biotrophs, are entirely reliant on their host plants for organic C (Jennings, 1995; Smith & Read, 2008). In mycorrhizal partnerships, plants may direct up to 50% of photosynthates to their mycobionts (Douds *et al.*, 2000; Graham, 2000; Taylor *et al.*, 2009; Soudzilovskaia *et al.*, 2015); thus, these symbioses contribute significantly to global C cycles, with AM alone determining the flow of an estimated 5 billion tons of C annually (Bago *et al.*, 2000).

The position of the plant–fungal interfaces is highly significant in a nutritionally mutualistic symbiosis for a reciprocal exchange of resources to occur between partners. In AM symbioses, the transport of plant-fixed C to the fungus is widely thought to be confined to the highly branched arbuscules (*Arum*-types) or tightly wound coils (*Paris*-types) produced by the fungus inside plant host cells (Smith & Read, 2008). These structures have a large surface area to volume ratio (Smith & Read, 2008) which would facilitate a rapid exchange of resources between symbiotic partners. However, while P transporters have been localised, unambiguously, to the peri-arbuscular membrane (Javot *et al.*, 2007; Pumplin & Harrison, 2009) the role of fungal membrane-bound transporters in regulating and facilitating movement of C from plant to fungus is less clear (Fitter, 2006; Parniske, 2008), particularly given that plants transfer C in a variety of forms (Keymer *et al.*, 2017; Luginbuehl *et al.*, 2017; Roth & Paszkowski, 2017). Recently published studies have confirmed the intriguing prospect that lipid/fatty acids play a role in transferring C from plants to AMF, initially raised in 2005 by Trépanier *et al.* (Jiang *et al.*, 2017; Keymer *et al.*, 2017; Luginbuehl *et al.*, 2017). However, quantification of fatty acid fluxes between symbionts and the relative proportions of sucrose : fatty acids transferred between symbionts remain unknown.

Although the underpinning mechanistic basis for C transport is equivocal (Field *et al.*, 2016b) – particularly when plant-to-fungus fatty acid and lipid transport is taken into account (Jiang *et al.*, 2017; Keymer *et al.*, 2017; Luginbuehl *et al.*, 2017) – it remains highly probable that the movement of C-based compounds across the plant–fungal interface is active, and therefore must involve membrane-bound transporters. However, even the most recent models for C transport between symbionts are based on the assumption that hexose sugars form the major substrate for exchange, thus outlining a pressing need for further functional studies to investigate diversity in fungal C acquisition. These considerations aside, it has been shown previously that plant-derived hexoses are converted into tricylglycerol lipid droplets upon transfer to AMF and are subsequently transported to fungal sinks (Parniske, 2008). The genes encoding transporters assumed to be involved in such hexose transfers between symbionts have been known to occur in the Glomerales for several years (Doidy *et al.*, 2012), and their expression has been shown to be present in the fungal arbuscular membrane (Helber *et al.*, 2011). However, the expression of such transporters, including the AM fungal monosaccharide *MST2*, is not restricted to the fungal arbuscular membrane but also occurs throughout the length of the fungal hyphae, within both the intra- and extramatrical mycelium (Helber *et al.*, 2011). This pattern of expression raises the hypothesis that, for hexoses at least, transfer and assimilation from plant to fungus is not restricted to the arbuscules and that both inter- and intracellular hyphae are also involved in the process (Gianinazzi-Pearson *et al.*, 1991; Fitter, 2006). It is critical that this hypothesis is now tested through comprehensive experimentation to determine the extent to which uptake via hyphal transporters contributes to the total movement of C from plant to fungus. Similarly, detailed studies are now needed to quantify and assess the degree to which plant lipid/fatty acid transfer to fungal partners contributes to overall C fluxes between symbionts and the wider rhizospheric communities. Given the apparent diversity in functioning between plant and fungal taxa (e.g. Kiers *et al.*, 2011; Lendenmann *et al.*, 2011; Walder *et al.*, 2012; Merrild *et al.*, 2013; Field *et al.*, 2015c) such experiments should strive to encompass as much plant and fungal diversity as is feasible within a given experimental system. Crucially, future research should seek to identify the positions of the plant–fungus interfaces and C transfer mechanisms of the Mucoromycotina fungi that form mutualistic symbioses with plants.

VI. From individuals to networks

A wealth of laboratory studies, from transformed root organ culture-based experiments to whole plant microcosms, have investigated the plant-to-fungus C transfer dynamics and C–P trades between symbionts across plant and fungal lineages. The tightly controlled conditions inherent to these laboratory-based investigations on mycorrhizal C transfer (see Box 1), often limit – albeit necessarily – the range of fungal partners made available to experimental plants. In nature, mycorrhizal plants are likely to interact with a much wider repertoire of fungal symbionts, especially because mycorrhizal fungi colonise multiple plants simultaneously and form huge underground hyphal networks that may link plants of the same and different species together (Leake *et al.*, 2004). C fluxes within such complex systems have important repercussions on wider ecosystem structure and function (van der Heijden *et al.*, 1998) and, given the variation in functioning of different symbiotic fungi (e.g. Kiers *et al.*, 2011; Lendenmann *et al.*, 2011; Walder *et al.*, 2012; Merrild *et al.*, 2013; Field *et al.*, 2015b), it is highly probable that fungal diversity plays a key role in these processes.

Several lines of research suggest tight coupling of mycorrhizal nutrient uptake with plant C transfer to fungal symbionts, including molecular evidence of both P and C transporter expression (Harrison *et al.*, 2002; Roth & Paszkowski, 2017;

Box 1 Untangling carbon-for-nutrient exchange dynamics: experimental considerations

It has been suggested that the persistence and stability of mycorrhizas across evolutionary time-scales is the result of stabilisation where so-called 'generous' plants are 'rewarded' with greater nutrient returns from their fungi for their C 'investment', and vice versa (Kiers & van der Heijden, 2006; Hammer *et al.*, 2011; Kiers *et al.*, 2011). There are significant issues to consider when interpreting results from microcosm experiments using transformed root organ cultures that are quite unlike the complex networks formed by mycorrhizal fungi in nature (Leake *et al.*, 2004) that support such a mechanism. In these, plants cannot generate photosynthates, thereby removing the source element from any symbiotic source–sink relationship. Fungal competition, for example for nutrients and space, is also removed, probably affecting regulation of resource exchange dynamics away from those in natural systems. Finally, it is almost impossible to determine whether measured plant nutrient gains represent nutrients released by fungi into plant tissue or whether nutrients are withheld within the intraradical mycelium (Walder & van der Heijden, 2015).

To understand resource exchange between symbionts, photosynthate supply to the fungal partner(s) is often manipulated, commonly by shading the host plant. Shaded plants invariably suffer growth retardation (see supporting information in Fellbaum *et al.*, 2014) alongside reduced respiration and nutrient demands. Reduced transpirational pull of shaded plants means they cannot exert their full influence on soil nutrient depletion zones (Hepworth *et al.*, 2015), potentially affecting plant–fungal C-for-nutrient exchange as an experimental artefact. Alternatively, the amount of CO_2 available for photosynthesis can be altered. In such experiments, fungal-acquired nutrient transfer to the plant is not always linked in a linear manner to plant C transfer (Cameron *et al.*, 2008; Field *et al.*, 2012, 2015a, 2016a; Zhang *et al.*, 2015). A common limitation is that single growth chambers for each CO_2 condition are often used in these experiments, raising the possibility that observations occur through chamber effects rather than solely CO_2 effects (Werner *et al.*, 2018). Future studies must seek to reduce similar pseudoreplication by multiple chambers for each CO_2 treatment, or by rotating plants and CO_2 conditions between paired growth chambers (e.g. Field *et al.*, 2015b, 2016a).

Sawers *et al.*, 2017). However, in many cases where fluxes of nutrients between symbionts are quantified, a tight coupling of mycorrhizal nutrient uptake with plant C transfer does not always hold true (e.g. Lendenmann *et al.*, 2011; Walder *et al.*, 2012; Merrild *et al.*, 2013; Field *et al.*, 2015c). In these studies, a distinct diversity in mycorrhizal resource exchange between plants and their fungal partners has been demonstrated, particularly where plants and fungi are not limited in their symbiotic options, instead forming common mycorrhizal networks. This evidence of a nonlinear relationship between C and nutrient exchanges between plant and fungal symbionts suggests such nutritional mutualisms are driven instead by mechanisms involving source–sink and mass flow dynamics. It is key that a combination of techniques to quantify and characterise the exchange of resources between partners are now coupled with transcriptomics and genomics approaches, and that such research is expanded to include diverse mycorrhiza-forming fungal groups rather than focusing solely on Glomeromycotina symbioses. Furthermore, given recent demonstrations of a potentially important role of AMF in plant N nutrition, these considerations should also be extended to possible C–N trade (Smith & Smith, 2011; Corrêa *et al.*, 2015; Thirkell *et al.*, 2016) as well as possible interactions between P and N transport in the AM symbiosis (Cruz *et al.*, 2007; Fellbaum *et al.*, 2012; Bücking & Kafle, 2015).

Plant communities are often highly diverse, encompassing many species with a variety of life histories and with plant diversity driving diversity in mycorrhizal fungal communities and vice versa (Kottke *et al.*, 2013). Such diversity translates into differences in the flow of C and nutrients through the associated mycorrhizal networks. It follows that resource exchange within mycorrhizal networks is often asymmetrical, with some plant species benefitting, in terms of C invested and nutrients obtained, much more than others (van der Heijden *et al.*, 1998, 2015). An extreme example of this are communities that include mycoheterotropic (either partial or full) plants. Mycoheterotrophic species rely fully on C and nutrients from mycorrhizal networks linking them with surrounding autotrophic plants (Leake, 1994; Merckx *et al.*, 2009; Hynson *et al.*, 2013). They are often achlorophyllous (e.g. the liverwort *Aneura mirabilis* which parasitises a Basidiomycota fungus (Bidartondo *et al.*, 2003)), and may even spend part of their lifecycles below ground as is the case in many lycophyte and fern species (Fig. 4). In these species, the subterranean gametophytes and early sporophytes are entirely nonphotosynthetic and rely on their fungal symbiont for nourishment. This subterranean phase of the life-cycle may last several years, or may re-occur throughout the plant's life-cycle (Winther & Friedman, 2007), such as is the case for the ophioglossoid fern *Ophioglossum vulgatum*. Upon commencement of autotrophy in this species, it has been shown by isotope tracer experiments on wild-collected *O. vulgatum* (Field *et al.*, 2015c) that the plant 'repays' C back into the mycorrhizal network it is connected to, although this may not be the case in all myco-heterotrophic plant species. A 'take now, pay later' mode of symbiosis has, however, been observed in several orchids (Cameron *et al.*, 2006, 2008) where germination and growth of young seedlings is fuelled exclusively by mycorrhizal fungi. It is likely that in such cases specificity and intergenerational fidelity are key factors in stabilising mutualistic symbioses (Leake *et al.*, 2008). It follows that in communities containing mycoheterotrophic plants, in addition to the variation in fungal C demands inherent to a diverse microbial community, the flow of C from plants to rhizosphere may become limited and this in turn may influence soil nutrient cycling and availability.

Even in communities that do not involve mycoheterotrophic plants, there is strong evidence for asymmetry in C-for-nutrient exchange. By using the characteristic C isotope signatures of C_3 and C_4 plants, Walder *et al.* (2012) showed that flax (*Linum usitatissimum*) contributes relatively little to a common mycelial network (CMN) but gained the vast majority of the available P and N while interconnected sorghum (*Sorgum bicolor*) allocated substantially more C to the CMN but received few nutrients in return. Most research efforts to date have been driven on the whole by the idea that mycorrhizal fungi are supplied with C derived from

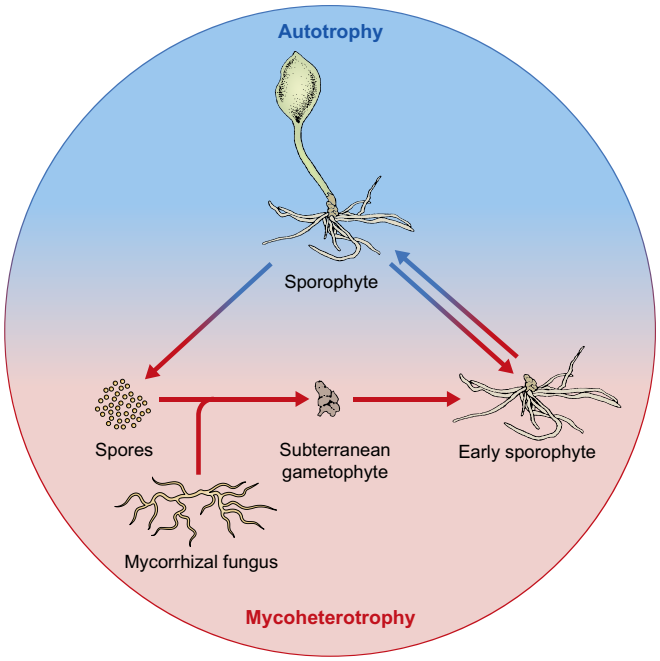

Fig. 4 Schematic diagram showing key phases of the *Ophioglossum vulgatum* life-cycle where the plant is initially reliant on its fungal symbiont, and therefore surrounding plants, for its entire carbon (C) (mycoheterotrophy) and nutrient uptake before becoming able to generate its own C through photosynthesis (autotrophy). Sporophytes oscillate seasonally between autotrophic and mycoheterotrophic lifestyles and thus represent a variable source and sink for C within the common mycorrhizal network (Field *et al.*, 2015c).

recent plant photosynthetic activity (Merryweather & Fitter, 1995). A potential role of plant C reserves – particularly in plant species with large capacity for C storage such as bulb-forming and tuberous plants (Merryweather & Fitter, 1995) – has been largely overlooked. This may have led to underestimates of the C 'cost' of mycorrhizas on their host plants. Furthermore, latest confirmations that mycorrhizal fungi acquire C from host plants as fatty acids (Jiang *et al.*, 2017; Keymer *et al.*, 2017; Luginbuehl *et al.*, 2017), as well as carbohydrates, represent another potentially large underestimate of the C sink strength of mycorrhizas. In many studies, C flux between symbionts is quantified according to instantaneous measures of C at a single given time point. This does not allow for any temporal variation in metabolic processes for photosynthates vs fatty acids or lipids. As such, it is entirely possible that C fluxes from plants to fungi have been underestimated and, if this is the case, then the overall flux of C to mycorrhizas on a global scale might have been also grossly underestimated.

Clearly, it is crucial that future avenues of research maintain a holistic viewpoint of the whole plant and soil microbial communities to fully understand and appreciate the complexity of C fluxes between plants and soil at an ecosystem scale. This point is particularly pertinent when alternative soil microbial C and nutrient cycling processes are considered. A significant proportion of photosynthates are moved below ground for production of the fruiting bodies of ECMF and in extraradicular vesicles in AMF. A further substantial proportion of plant-fixed C is released into the rhizosphere by plant roots and fungal hyphae (Drigo *et al.*, 2010; Kaiser *et al.*, 2015; Galloway *et al.*, 2018). These C-based exudates stimulate microbial decomposition activities, which in turn increase nutrient availability through depolymerisation of soil organic matter (Kaiser *et al.*, 2015). Furthermore, unravelling how CMNs influence plant establishment, survival, physiology, growth and defence chemistry and especially whether and how C and other resources are potentially shared between linked plants (Gorzelak *et al.*, 2015, and references therein) might have tremendous consequences for our understanding of plant interactions (Fitter *et al.*, 1998). It is also critical that C transfer between symbionts at the plant–fungal interface is better characterised, particularly in the Mucoromycotina/FRE where it is almost completely unexplored. Given the apparent unity and variation in functioning between plant and fungal taxa, such experiments should seek to encompass as much plant and fungal diversity as is feasible within the given experimental system.

VII. Diverse responses of mycorrhizal functioning to dynamic environments

As outlined previously, the environment plays a critical role in determining plant and rhizosphere community structure and function. Indeed, mycorrhizal functioning, in terms of bidirectional C-for-nutrient exchange between symbionts, has been repeatedly shown to be influenced by changes in the abiotic environment. Throughout the 500 million-yr history of terrestrial plant life on Earth (Morris *et al.*, 2018), there have been considerable shifts in climate, particularly with respect to changes in atmospheric composition and temperature.

Atmospheric conditions, including CO_2 and O_2 concentrations, have varied throughout Earth's history. When plants first colonised the terrestrial environment, atmospheric CO_2 concentrations ($[CO_2]$) were > 1000 ppm (Royer, 2014). Both climate models and proxies suggest that the global environment underwent major changes throughout the Palaeozoic, with a general decline in atmospheric $[CO_2]$ being coincident with a rise in O_2 and the evolution of the terrestrial biosphere (Berner, 1991, 2006; Bergman *et al.*, 2004; Lenton *et al.*, 2016). According to these models, and corroborated by proxies such as fossilised leaves (Franks *et al.*, 2014) and palaeosols (Breecker *et al.*, 2010; Royer, 2014), CO_2 levels in the atmosphere are likely to have reached modern concentrations by the end of the Carboniferous, and thus land plant–fungal symbioses evolved under a CO_2 atmosphere much greater than that of today. Early diverging land plant–fungal partnerships, whether involving exclusively Mucoromycotina fungi (Field *et al.*, 2015b), or both Mucoromycotina and Glomeromycotina fungal associates (Field *et al.*, 2016a), have been shown to respond very differently to changing atmospheric $[CO_2]$ when compared with liverwort–Glomeromycotina exclusive symbioses (Field *et al.*, 2012). These findings demonstrate significant diversity in mycobiont responses to changes in atmospheric CO_2, although the underpinning physiology for these differences remains unknown. Of course, changing atmospheric $[CO_2]$ is not limited to Earth's deep history; modern atmospheric $[CO_2]$ reached the symbolic milestone of 400 ppm in May 2013 (as reported for Mauna Loa, Hawaii, by Richard Monastersky in

Nature, 2 May 2013) and has since increased to 403.38 ppm (September 2017). These concentrations are thought to have last occurred in the Pliocene *c.* 3 Ma when mean temperatures on Earth were *c.* 2–3°C higher than today (Martínez-Botí *et al.*, 2015). Climate predictions suggest that [CO_2] will continue to increase unless drastic measures are taken to curb anthropogenic CO_2 emissions, with current [CO_2] expected to double by 2070 (Pachauri *et al.*, 2014).

Such changes in atmosphere are known to affect plant growth and productivity, with experiments and computer models showing gains in both under increased atmospheric [CO_2] (Ainsworth & Long, 2005). While much of the total photosynthate produced is thought to be transported to fungal mycelium below ground (Rillig & Allen, 1999), its precise fate can vary according to plant life history traits. The additional photosynthates produced under elevated atmospheric CO_2 may be stored as starch within specialised structures (e.g. bulb, rhizomes, tubers; Merryweather & Fitter, 1995), or it may be exuded directly into the soil in a variety of high- (Galloway *et al.*, 2018) or low-molecular-weight compounds (Poole, 2017). Changes in the allocation and fluxes of C between source and sink plant tissues are likely to affect mycorrhizas, particularly given that they form the critical interface between the majority of land plants and the soil.

While mycorrhizas themselves occupy environments that are of inherently high [CO_2] (Fitter *et al.*, 2000), it is reasonable that increased abundance of photosynthates in below-ground plant structures in response to rising atmospheric [CO_2] would lead to greater plant C assimilation by mycorrhizal fungi (Drigo *et al.*, 2010). Indeed, it has been shown that even moderate increases in atmospheric [CO_2] can lead to a 36% increase in root colonisation and a mean 47% increase in hyphal growth of mycorrhizal fungi across a range of land plants (Treseder, 2004). This trend is echoed across arbuscular and ectomycorrhizal fungal species (Staddon & Fitter, 1998; Alberton *et al.*, 2005) and it seems likely to be driven by increased allocation of photosynthates to fungal partners by the host plants. Alternatively, increased atmospheric [CO_2] might facilitate fungal growth and root colonisation indirectly, by enhancing plant growth (Staddon & Fitter, 1998) or by causing substantial changes to the community composition of the symbiotic fungi. Such an effect has previously been observed, with the ratio of Glomeracea to Gigasporaceae fungi increasing significantly under increased atmospheric [CO_2] (Cotton *et al.*, 2015).

The direct quantification of movement of plant C and fungal-acquired mineral nutrients using isotope tracers has shed important new light on the impact of varying atmospheric [CO_2] on C-for-nutrient exchanges between plants and their symbiotic fungi (see Field *et al.*, 2012, 2015a, 2016a; Zhang *et al.*, 2015). Both Glomeromycotina and Mucoromycotina fungi (and dual fungal symbioses involving both fungal partners) gain a greater proportion of recently fixed photosynthates when grown under an elevated atmospheric [CO_2] compared to current ambient conditions (Drigo *et al.*, 2010; Field *et al.*, 2012, 2015b, 2016a), decreasing further in response to subambient atmospheric [CO_2] (Zhang *et al.*, 2015). Nutrient transfer from fungus to plant appears to respond differently to changing [CO_2] according to both fungal and plant host identity (Field *et al.*, 2012, 2015b, 2016a; Werner *et al.*, 2018). For instance, Glomeromycotina-associated nonvascular plants exposed to elevated atmospheric [CO_2] assimilate more fungal-acquired ^{33}P tracer than under ambient atmospheric [CO_2] (Field *et al.*, 2012; Werner *et al.*, 2018). By contrast, ^{33}P tracer uptake via fungal symbionts in vascular plants appears to be either maintained across CO_2 treatments, or is reduced under the higher [CO_2] (Field *et al.*, 2012). Interestingly, this contrasts with the responses of Mucoromycotina symbioses in liverworts, the only group to have been tested so far (Field *et al.*, 2015b, 2016a). Potential resource exchanges between Mucoromycotina and vascular plants, and how these might be influenced by changes in atmospheric [CO_2], remain to be determined. Given that symbioses involving Mucoromycotina fungi are much more widespread than initially thought (Bidartondo *et al.*, 2011; Rimington *et al.*, 2015; Orchard *et al.*, 2017b), their responses to changes in atmospheric [CO_2] may be far more significant than previously assumed, emphasising an urgent need for more functional studies of a wider variety of plant–fungal symbioses.

In conjunction with changing atmospheric [CO_2], temperature has also been shown to play an influential role in mycorrhizal colonisation and function. Indeed, there have been major shifts in Earth's global temperatures throughout history with average surface temperatures ranging from between 20 and 22°C around the time plants first colonised the land to the 300 Ma 'icehouse' conditions in the Permo-Carboniferous where ice sheets extended into the subtropics (Mills *et al.*, 2018). These changes in global ambient temperatures together with the persistence of mycorrhizas and mycorrhiza-like associations across similar timescales demonstrate the potential plasticity and tolerance of the symbiosis to changes in abiotic conditions, although it is unlikely the symbionts we see today are identical to those that persisted at the dawn of land plant–fungal symbiosis. However, it remains critical that we test how modern mycorrhizal plasticity translates into function in order to understand how a changing climate may affect nutrient fluxes between symbionts in the past, present and, importantly, future. Plants grown under high vs ambient atmospheric [CO_2] (700 vs 350 ppm) and correspondingly increased temperature (15 vs 10°C) showed enhanced mycorrhizal colonisation and P uptake with temperature being the critical determining factor (Gavito *et al.*, 2003). This finding is in line with several other studies showing similar increases in AMF proliferation with rising temperature (Zhang *et al.*, 2005; Castro *et al.*, 2010). These observations lend support to the hypothesis that when exposed to elevated atmospheric [CO_2] and higher temperatures, plant productivity is enhanced and greater proportions of photosynthates are transferred to fungal partners. Given recent discoveries that C is transferred between symbionts not only as hexose molecules but also as fatty acids and lipids, it is now imperative that this hypothesis is tested and elaborated upon to determine the identities, quantities and relative proportions of C-based molecules that are transferred between partners under changing environmental conditions, including ambient temperatures and atmospheric O_2 concentrations.

VIII. Summary of future research direction

Recent advancements in mycorrhizal research, as summarized in this review, present us with tremendous opportunities to

further understand the diversity, biology, ecology and evolution of mycorrhizas. They also raise new challenges, with several outstanding key questions. The recent discovery that Mucoromycotina fungi form mutualistic partnerships with early diverging land plant clades (Bidartondo *et al.*, 2011; Field *et al.*, 2015a,b, 2016a) and also colonise the roots of numerous vascular plant families (Orchard *et al.*, 2017a) raises alternative hypotheses on the origin and evolution of mycorrhizas and on the potential importance of Mucoromycotina fungi in past and present terrestrial ecosystems. However, we know very little of the occurrence, diversity and functional roles of these fungi across the land plant phylogeny (Hoysted *et al.*, 2018). It remains unknown whether the contrasting responses observed in liverwort–Mucoromycotina mutualisms to changes in [CO_2] (Humphreys *et al.*, 2010; Field *et al.*, 2015b, 2016a) extend to vascular plant–Mucoromycotina associations, or indeed whether these also represent mutually beneficial symbioses.

Given that Mucoromycotina fungi are considered facultative saprotrophs, it might be expected that they afford different nutritional benefits to their host plants than the obligate biotroph arbuscular mycorrhizal Glomeromycotina. However, hardly anything is known of the nutritional modes of mycorrhizal Mucoromycotina fungi or indeed of their colonisation patterns, location of plant–fungus interfaces and nutrient transfer mechanisms. Recent genomic studies have indicated that the repertoire of genes encoding plant cell wall-degrading enzymes in Mucoromycotina fungi is much greater than in AMF (Tisserant *et al.*, 2013), although only nonsymbiotic Mucoromycotina species were analysed. It is critical that similar future studies include species known to form mycorrhizas/mycorrhiza-like associations. Even our understanding of the roles of AMF in host plant nutrition and the mechanistic basis for C-for-nutrient exchanges remains patchy. Recently it has been shown that AMF might have a hitherto unappreciated role also in plant host N nutrition (Hodge & Fitter, 2010; Kaiser *et al.*, 2015; Thirkell *et al.*, 2016). Given the ecological role of AMs in N cycling (Hodge & Storer, 2015), unravelling the role of AMF in host plant N nutrition and potential C-for-N trades between symbionts (Corrêa *et al.*, 2015; Thirkell *et al.*, 2016) is now crucial. Recent discoveries of a role of lipid/fatty acids in C transfer from plants to AMF (Jiang *et al.*, 2017; Keymer *et al.*, 2017; Luginbuehl *et al.*, 2017) also invite further studies not least to quantify and assess the degree to which plant lipid/fatty acid transfer to fungal partners might contribute to overall C fluxes between symbionts and the wider rhizospheric communities. Understanding these processes will have important consequences for improving current estimates of the role of mycorrhizas in ecosystem C cycling, as will also an unfolding appreciation of common mycorrhizal networks as multi-species resource-sharing systems. Mycorrhizal fungi colonise multiple plants simultaneously and form extensive underground hyphal networks, potentially linking plants of the same and different species together (Leake *et al.*, 2004). Resource exchange within these networks is often asymmetrical, reflecting the diversity and different life histories of the plants and fungi involved (van der Heijden *et al.*, 2015). An extreme example is that of communities which include mycoheterotrophic plants, which potentially limit the flow of C from plants to the rhizosphere, impacting soil nutrient cycling and availability. It is therefore crucial that future research efforts maintain a holistic viewpoint of the whole plant and soil microbial communities to fully understand and appreciate the complexity of C fluxes between plants and soil at an ecosystem scale.

Furthering our understanding of the diversity, biology and ecology of symbiotic Mucoromycotina fungi, of the roles in and mechanistic basis of C-for-nutrient exchanges in both Mucoromycotina– and Glomeromycotina–plant symbioses, and of the impacts of mycorrhizal networks on ecosystem nutrient cycling also has important implications for determining the influence – past, present and future – of the environment on this key partnership between plants and fungi. Recent advances in mycological research, including the development of high-throughput molecular tools (van der Heijden *et al.*, 2015) and ever more sophisticated isotope tracer techniques to quantify plant-to-fungus nutrient exchange dynamics (Field *et al.*, 2015b, 2016a; Zhang *et al.*, 2015), present us with unrivalled opportunities to dissect the 'diversity within unity' of this ancient and widespread mutualistic partnership between plants and fungi, its past roles in facilitating plant terrestrialistation > 500 Ma, and present and future roles in ecosystem functioning.

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ORCID

Katie J. Field http://orcid.org/0000-0002-5196-2360

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