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Mycorrhizal ecology and evolution: the past, the present, and the future

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Received: 29 July 2014

Accepted: 30 November 2014

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Contents

Summary	1406	VI. Mycorrhizal genomics and symbiotic molecular crosstalk	1416
I. Introduction	1407	VII. Conclusions and future research	1418
II. Biodiversity of mycorrhizal associations	1408	Acknowledgements	1418
III. Carbon and nutrient cycling and ecosystem multifunctionality	1410	References	1419
IV. Mycorrhizal networks	1411		
V. Evolution and partner selection	1413		

New Phytologist (2015) **205**: 1406–1423
doi: 10.1111/nph.13288

Key words: arbuscular mycorrhizal fungi, biodiversity, ectomycorrhizal fungi, ericoid, mutualism, orchid, plant–microbe interactions, population, symbiosis.

Summary

Almost all land plants form symbiotic associations with mycorrhizal fungi. These below-ground fungi play a key role in terrestrial ecosystems as they regulate nutrient and carbon cycles, and influence soil structure and ecosystem multifunctionality. Up to 80% of plant N and P is provided by mycorrhizal fungi and many plant species depend on these symbionts for growth and survival. Estimates suggest that there are c. 50 000 fungal species that form mycorrhizal associations with c. 250 000 plant species. The development of high-throughput molecular tools has helped us to better understand the biology, evolution, and biodiversity of mycorrhizal associations. Nuclear genome assemblies and gene annotations of 33 mycorrhizal fungal species are now available providing fascinating opportunities to deepen our understanding of the mycorrhizal lifestyle, the metabolic capabilities of these plant symbionts, the molecular dialogue between symbionts, and evolutionary adaptations across a range of mycorrhizal associations. Large-scale molecular surveys have provided novel insights into the diversity, spatial and temporal dynamics of mycorrhizal fungal communities. At the ecological level, network theory makes it possible to analyze interactions between plant–fungal partners as complex underground multi-species networks. Our analysis suggests that nestedness, modularity and specificity of mycorrhizal networks vary and depend on mycorrhizal type. Mechanistic models explaining partner choice, resource exchange, and coevolution in mycorrhizal associations have been developed and are being tested. This review ends with major frontiers for further research.

I. Introduction

Frank (1885) was probably the first to recognize the widespread nature of associations between plant roots and mycorrhizal fungi (Frank & Trappe, 2005). In the following 100 yr, the partners and processes involved in this symbiosis have been described (Phillips & Hayman, 1970; Harley & Smith, 1983; Gardes & Bruns, 1993) and we now know that mycorrhizal associations are present in almost all ecosystems, from deserts to tropical forests to arable land (Read, 1991; Brundrett, 2009). Four major mycorrhizal types have been described based on their structure and function, namely arbuscular mycorrhiza (AM), ectomycorrhiza (EM), orchid mycorrhiza and ericoid mycorrhiza (see Fig. 1 and Table 1 for a short description of each type). Mycorrhizal fungi live inside the cortex of plant roots, on the surface of the root, or around the

epidermal cells of the root. The hyphae of these fungi also grow out from the roots into the soil where they forage for nutrients that are limiting to plant growth, especially nitrates and phosphates, but organically bound nutrients are also acquired by some mycorrhizal types (e.g. EM and ericoid mycorrhizal fungi) (Read & Perez-Moreno, 2003). These nutrients as well as other benefits are then delivered to their host plants in return for carbohydrates (Smith & Read, 2008). Consequently, the mycorrhizal symbiosis exerts a strong influence on plant growth and fitness.

The mycorrhizal symbiosis is of key interest to biologists and ecologists because mycorrhizal fungi influence plant productivity and plant diversity, and mycorrhizal fungi connect plants below ground via a hyphal network allowing the movement of resources among coexisting plants. Additionally, the symbiosis plays a key role in the cycling of carbon (C), nitrogen (N), and phosphorus (P)

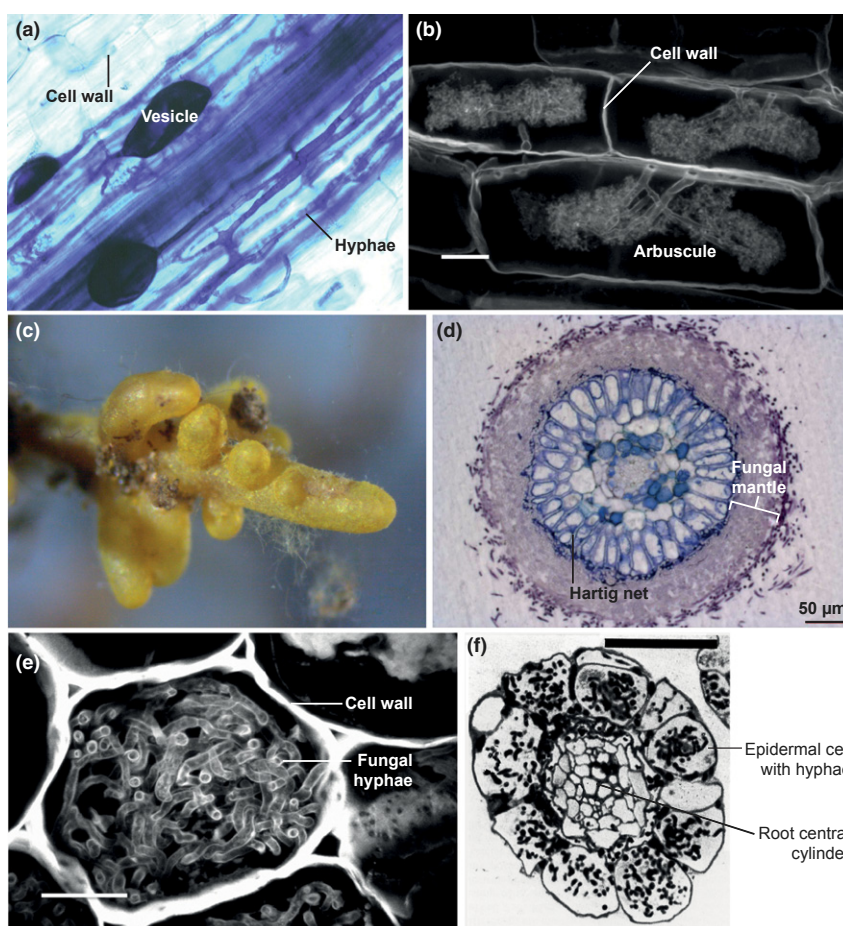


Fig. 1 Typical structures of arbuscular mycorrhizas (a, b), ectomycorrhizas (c, d), orchid mycorrhizas (e), and ericoid mycorrhizas (f). Arbuscular mycorrhizas are distinguished from other mycorrhizal types by the formation of extensive amounts of fungal hyphae that run parallel to the endodermis inside the root cortex (a, trypan blue-stained clover root colonized by *Glomus intraradices*, $\times 150$; photo courtesy of Marcel G. A. van der Heijden). Arbuscular mycorrhizal fungi are named after so-called arbuscules, tree-like structures that are formed by the fungus inside cortical root cells (b, *Pisum sativum* root cells with arbuscules; bar, 50 μm ; photo courtesy of Ryan Geil, published with kind permission from Peterson *et al.* (2004) and NRC press, © Canadian Science Publishing or its licensors). Primary and secondary roots of ectomycorrhizal plants are often completely surrounded by a fungal mantle and the largest part of the fungus remains outside the root, hence the name ectomycorrhiza. Shown is an ectomycorrhiza formed between the fungus *Russula ochroleuca* and the tree *Fagus sylvatica* (c, $\times 40$; photo courtesy of Marc Buée, INRA) and a cross-section of an ectomycorrhizal root between the fungus *Pisolithus microcarpus* and *Populus trichocarpa*. All the typical features of ectomycorrhiza are shown, including a loose external mantle, an aggregated internal mantle, and a Hartig net encasing elongated epidermis root cells. (d, bar, 50 μm ; photo courtesy of Maira de Freitas Pereira, INRA). Root cells of an orchid (*Paphiopedilum sanderianum*) colonized fungal hyphae, forming a peloton (e, Photo courtesy of Carla Zelmer, bar, 50 μm ; published with kind permission from Peterson *et al.* (2004) and NRC press, © Canadian Science Publishing or its licensors). Ericoid mycorrhizal root of *Calluna vulgaris* showing large epidermal cells colonized by hyphae (f, bar, 150 μm ; photo courtesy of Paola Bonfante).

Table 1 Numbers of plant and fungal species forming arbuscular mycorrhizal, ectomycorrhizal, orchid mycorrhizal, or ericoid mycorrhizal associations

Mycorrhizal type	Major groups of plants ¹	Number of plant species hosting mycorrhizal fungi ¹	Fungal identity	Total estimated number of fungal taxa
Arbuscular mycorrhiza	Most herbs, grasses and many trees, many hornworts ² and liverworts ³	200 000	Glomeromycota	300–1600 ⁴
Ectomycorrhiza	Pinaceae and Angiosperms (mostly shrubs and trees, mostly temperate) ⁵ , some liverworts ⁶	6000	Basidiomycota and Ascomycota	20 000 ⁷
Orchid mycorrhiza	Orchids	20 000–35 000	Basidiomycota	25 000 ⁸
Ericoid mycorrhiza	Members of the Ericaceae, some liverworts ⁶	3900	Mainly Ascomycota, some Basidiomycota ⁹	> 150 ¹⁰
Nonmycorrhizal plant species ¹¹	Brassicaceae, Crassulaceae, Orobanchaceae, Proteaceae etc.	51 500		0

¹The taxonomic affiliation of the major fungal groups and the major groups of plants forming mycorrhizal associations are shown after Brundrett (2009). The distinction between mycorrhizal categories is not necessarily strict (e.g. some plant species form dual associations with both AM and EM fungi (e.g. Egerton-Warburton & Allen, 2001; Onguene & Kuyper, 2001) while some fungal species can form both ectomycorrhizas and ericoid mycorrhizas (Villarreal-Ruiz *et al.*, 2004; Grelet *et al.*, 2009) or orchid and ectomycorrhizas (Taylor & Bruns, 1997)).

²After Desiro *et al.* (2013).

³After Ligrone *et al.* (2007).

⁴After Öpik *et al.* (2013) and Kivlin *et al.* (2011).

⁵Families such as Myrtaceae, Fabaceae, Fagaceae, and Dipterocarpaceae contain many members that form associations with EM fungi (after Brundrett, 2009).

⁶After Read *et al.* (2000).

⁷After Rinaldi *et al.* (2008) and Tedersoo *et al.* (2010).

⁸See Supporting Information Table S1 and Fig. S1 for calculations.

⁹See Section II.

¹⁰After Walker *et al.* (2011).

¹¹A wide range of ruderal plant species and several plant species with specialized root structures (e.g. cluster roots and proteoid roots) do not associate with mycorrhizal fungi (Lambers & Teste, 2013).

in ecosystems (see Section III.2, Table 2). Given that the vast majority of the Earth's plant species form at least one of the four mycorrhizal associations and given the amount of resources that can move above or below ground because of the mycorrhizal symbiosis, it is likely that the role of the symbiosis in global nutrient cycling is significant.

It is not our intention in this review to give a detailed description of the biology of each of the four mycorrhizal types, as these have been covered in detail elsewhere (Smith & Read, 2008). Here we provide an overview of recent developments in mycorrhizal research, focusing on the ecology, evolution, and genomics of mycorrhizal associations. We identify research gaps and propose new avenues of research. First, we discuss the biodiversity of mycorrhizal associations and provide global estimates of the number of fungal and plant symbionts involved in various mycorrhizal associations. Second, we emphasize that mycorrhizal fungi are important drivers of global C and nutrient cycles and we discuss how these symbiotic fungi deliver an important number of ecosystem services, including services that can be directly used by humans. Third, we discuss the evolution of the mycorrhizal symbiosis and propose factors that influence plant–fungal coexistence and contribute to the evolutionary stability of these associations. And finally, we discuss recent insights into fungal genomes and the genetic mechanisms driving symbiosis development and evolution. Here we consider any long-term, intimate association between two organisms to be a 'symbiosis', while reserving mutualism only for those interactions known to be beneficial to both partners.

II. Biodiversity of mycorrhizal associations

Mycorrhizal associations are extremely abundant in the plant kingdom. Estimates suggest that *c.* 74% of all plant species form AMs with fungi of the Glomeromycota clade (Smith & Read, 2008; Brundrett, 2009), *c.* 2% of plants form EM associations, *c.* 9% of plants form orchid mycorrhizas and *c.* 1% of plants form ericoid mycorrhizas (Brundrett, 2009). Some plant species, such as poplars and eucalypts, also form dual symbiotic associations (e.g. with AM and EM fungi; Egerton-Warburton & Allen, 2001; Villarreal-Ruiz *et al.*, 2004). Almost all ecosystems are dominated by mycorrhizal plants (Read, 1991) with the exception of early successional communities, intensively managed arable fields and extremely P-impooverished soils that are dominated by plants with cluster roots (Lambers *et al.*, 2008).

For many plant species, it is now firmly established whether they form mycorrhizal associations (see Harley & Harley, 1987; Wang & Qiu, 2006; Akhmetzhanova *et al.*, 2012 for extensive plant species lists). Recent studies also revealed that lower land plants, in particular species of hornworts and liverworts, associate with AM, EM, or ericoid mycorrhizal fungi (Read *et al.*, 2000; Schüssler, 2000; Ligrone *et al.*, 2007; Pressel *et al.*, 2010). By contrast, the number of fungal partners involved in the symbiosis is less clear and varies depending on mycorrhizal type (Table 1). In the following we provide estimates of the number of known fungal symbionts for each mycorrhizal type, for the first time including a total estimate of fungi having the ability to form mycorrhizal associations. Key questions for further research include a better investigation of

Table 2 Influence of mycorrhizal associations on various ecosystem processes

Ecosystem process	Mycorrhizal type	Estimated mycorrhizal contribution to ecosystem process*
<i>Carbon cycle</i>		
Plant productivity	AM	0–80% ¹
	EM	0–80% ²
	Ericoid	0–50% ³
	Orchid	100% (protocorms) ⁴
Decomposition	Unknown (green orchids) ⁵	
	AM	0–10% ⁶
	EM	0–30% ⁷
<i>Nitrogen cycle</i>		
Plant nitrogen acquisition	AM,	0 to –20% ⁸
	EM, ericoid	0–80% ⁹
Reduction of N leaching losses	AM, EM, ericoid	0–50% (NO ₃ [–]) ¹⁰
Denitrification, N ₂ O losses	AM, EM	Unknown (see text) ¹¹
<i>Phosphorus cycle</i>		
Plant phosphorus uptake	AM	0–90% ¹²
	EM	0–70% ¹³
	Ericoid	0–80% ¹⁴
	Orchid	100% (protocorm) ¹⁵
	Unknown (green orchids) ¹⁶	
<i>Regulation of plant diversity</i>		
Stimulation of plant diversity	AM	0–50% ¹⁷
Reduction of plant diversity	AM	–20 to 0% ¹⁸
<i>Other ecosystem processes strongly affected by mycorrhizal fungi</i>		
Soil aggregation	AM, EM	¹⁹
Seedling survival	AM, EM, ericoid	²⁰
	Orchid	²¹

AM, arbuscular mycorrhiza; EM, ectomycorrhiza.

^{1–21}Selected references and additional remarks are given in Supporting Information Table S2.

*Estimates vary widely; in some ecosystems mycorrhizal fungi are major drivers of several ecosystem processes (e.g. especially in undisturbed and less disturbed ecosystems with poor nutrient availability), while in other ecosystems (e.g. highly disturbed ecosystems and intensively managed agroecosystems) mycorrhizal fungi are less important.

mycorrhizal fungal communities in a range of habitats, especially the tropics, which are less well investigated. In order to do that, the species concept for most groups of mycorrhizal fungi needs additional attention. The development of new and better primers (targeting longer DNA sequences – e.g. those described in Krüger *et al.*, 2009) for AM fungi or including different barcoding genes would further such knowledge. Specific attention should be paid to resolving the many ‘unknown’ taxa in environmental DNA sequencing datasets.

So far, 244 species of Glomeromycota have been described based on morphological characteristics of the spores (Schüssler, 2014; for additional information on AM fungal taxonomy, see Oehl *et al.*, 2011). Estimates of global AM fungal richness based on environmental ribosomal DNA sequences range from 341 (Öpik *et al.*, 2013) to 1600 operational taxonomic units (OTUs) (Koljalg *et al.*, 2013), or even higher (Kivlin *et al.*, 2011). These 300–1600 AM fungal taxa associate with *c.* 200 000 plant species (Brundrett, 2009), showing that host specificity must be very low. In fact, so far

no convincing evidence has been presented demonstrating that AM fungi are host-specific, although host preferences and host selectivity have been widely reported (Helgason *et al.*, 1998; Vandenkoornhuys *et al.*, 2003; Torrecillas *et al.*, 2012). Most plant communities typically host between 1 and 75 AM fungal OTUs (Oehl *et al.*, 2010; Verbruggen *et al.*, 2012), indicating that local species richness of AM fungi is very high compared with the global species richness. Richness and composition of AM fungal communities depend on host plant, climate, and soil conditions (Öpik *et al.*, 2006). Land use intensification often leads to reduced AM fungal richness (Helgason *et al.*, 1998; Verbruggen *et al.*, 2010). Interestingly, natural communities of AM fungi are largely composed of uncultured taxa (Ohsowski *et al.*, 2014) and it will be a challenge to investigate whether these uncultivated fungi differ functionally from cultured taxa.

The number of EM fungal species is thought to be higher than for AM fungi and estimates suggest that there are *c.* 20 000 EM fungi (Rinaldi *et al.*, 2008; Tedersoo *et al.*, 2012). This estimate is based on a range of traits, including morphological, molecular, and isotope studies (Tedersoo *et al.*, 2012; a color atlas of ectomycorrhizas by Agerer (1987–2012) shows the morphological diversity of EM). The number of EM fungi might even be higher based on high sequence diversity of EM roots in several field studies. Most EM fungi are, in contrast to AM fungi, at least in part saprotrophic as they can be grown on artificial agar media without host plants. However, the loss of lignocellulose-degrading enzymes in most EM fungi (see Section V.1) makes many of them dependent on their host plant photoassimilates under field conditions. It is not unusual that temperate and boreal forests are dominated by a few tree species (e.g. pines or oaks) while diverse EM fungal communities occur below ground (Malloch *et al.*, 1980; Taylor *et al.*, 2000), and several hundreds of fungal species can coexist in a single forest (Richard *et al.*, 2005; Buée *et al.*, 2009, 2011). It has been estimated that *c.* 6,000 plant species form associations with EM fungi (Table 1). Many EM fungi have a broad host range while others are more specific and colonize certain hosts or host genera (Molina *et al.*, 1992).

Less attention has been paid to fungi forming mycorrhizas with orchids and ericoid plants. Fungi forming mycorrhizas with orchids typically live as saprotrophs in the soil or form endophytic/EM associations with neighboring trees (Dearnaley *et al.*, 2013). Orchid seeds are extremely small (0.3–14 µg) and in natural ecosystems seedlings of most orchids are completely dependent on colonization by fungi. Orchid seedlings (protocorms) lack chlorophyll and rely on nutrients and C that they obtain from these fungi (Rasmussen, 1995). In recent years, molecular identification techniques have shown that many orchids have host-specific fungal associates (usually between one and 10 taxa per orchid; Martos *et al.*, 2012; Jacquemyn *et al.*, 2015), although higher numbers have also been reported (Jacquemyn *et al.*, 2010; Kartzinel *et al.*, 2013). New fungal taxa colonizing orchids are continuously being described (e.g. Atractiellales; Kottke *et al.*, 2010) and the total number of fungi forming orchid mycorrhizas may be as much as 25 000 or even more (this estimate is derived from Supporting Information, Fig. S1 and Table S1).

Even less is known about the fungi forming ericoid mycorrhizas with species of the Ericaceae, such as *Erica*, *Calluna*, *Rhododendron*,

or *Vaccinium* (e.g. cranberry), which are mostly common under acid and infertile heathland conditions. Well-known ericoid fungi belong to the Helotiales (Ascomycetes) and are soil saprotrophs. Recent evidence suggests that some ericoid mycorrhizal fungi may act as plant endophytes and some Basidiomycetes are also thought to form ericoid mycorrhizal associations (see Section V.1). Some fungi can also form both ericoid and EM associations with different host plants (Villarreal-Ruiz *et al.*, 2004; Grelet *et al.*, 2009). Interestingly, it has been found that a sebacinoid fungus forming ericoid associations with *Calluna* also colonized neighboring gametophytes of a lycopod (Horn *et al.*, 2013), pointing to even more complex associations than previously thought. While earlier work indicated that there are only very few fungi forming these ericoid mycorrhizas (Smith & Read, 2008), a study by Walker *et al.* (2011) indicated that there are many more fungi colonizing plants of the Ericaceae, with 129 fungal Helotiales OTUs detected in three ericoid plant species at one location. Moreover, Sebaciniales (Basidiomycetes) were also discovered to be widespread ericoid mycorrhizal fungi (Selosse *et al.*, 2007) and there may be many more ericoid fungal partners, e.g. in Trechisporales (Vohník *et al.*, 2012). The lack of available data makes it currently difficult to estimate the number of ericoid mycorrhizal fungi.

Overall, these estimates suggest that 40 000–50 000 fungal species form mycorrhizal associations (Table 1). This represents c. 0.5–10% of the total number of 0.5–10 million fungal species estimated to be present on Earth (Blackwell, 2011; Taylor *et al.*, 2014). Note that many of these fungi are facultative mycorrhiza-forming fungi and also have a saprotrophic lifestyle (e.g. most orchid mycorrhizal fungi are thought to be soil saprotrophs). Importantly, plants also associate with a wide range of fungal endophytes (e.g. dark septate endophytes and some Sebaciniales), which might be beneficial under some conditions (Jumpponen & Trappe, 1998; Waller *et al.*, 2005; Weiss *et al.*, 2011; Shakya *et al.*, 2013). Although they improve plant growth and provide resistance to stress and pathogens (Rodríguez *et al.*, 2009), these fungal endophytes do not form a specialized plant–fungal interface for resource exchange and we currently do not consider them as mycorrhizal associates (see also Section V.1).

III. Carbon and nutrient cycling and ecosystem multifunctionality

1. Effects on C cycling

There is increasing evidence that mycorrhizal fungi play a key role in the biogeochemical cycles in terrestrial ecosystems (Table 2). Glasshouse experiments and field studies suggest that plants allocate between 10 and 20% of their photosynthates to AM fungi (Jakobsen & Rosendahl, 1990; Johnson *et al.*, 2002; Nottingham *et al.*, 2010). Approximately 20%, and sometimes up to 50%, of assimilates can be allocated to EM fungi and ericoid mycorrhizal fungi (Hobbie & Hobbie, 2008). This, together with the fact that almost all terrestrial ecosystems, and some agricultural ecosystems, are dominated by EM, ericoid or AM forming trees, shrubs and herbs, indicates that mycorrhizal fungi probably play a key role in the global C cycle. Heavily managed agricultural ecosystems are not

included because the abundance of AM fungi is often reduced as a result of heavy fertilization, soil disturbance, and cultivation of nonmycorrhizal crops (e.g. oil rapeseed, sugar beet). Still, the majority of crops (e.g. maize, cereals, soybean, potato, rice grown under nonpaddy conditions) are colonized by AM fungi in the field and thus allocate C to the fungal compartment below ground. The recent observations that mycorrhizal fungi are important regulators of C dynamics because of impaired degradation of fungal residues (Clemmensen *et al.*, 2013) and that C storage is increased in EM-dominated vs AM-dominated ecosystems (Phillips *et al.*, 2013; Averill *et al.*, 2014) further support the role of mycorrhizal fungi in the terrestrial C cycle.

2. Effects on N and P cycles

Mycorrhizal fungi provide significant amounts of N and P to their host plants in natural ecosystems, especially those with reduced soil nutrient availability. Experiments with single plants and plant communities have shown that AM fungi contribute up to 90% of plant P (Table 2; Jakobsen *et al.*, 1992; Leake *et al.*, 2004; Smith & Smith, 2011). The contribution of AM fungi to plant N nutrition is less pronounced, often negligible and depends on factors such as soil water content, soil pH, and soil type (Tobar *et al.*, 1994; Mäder *et al.*, 2000; Hodge & Storer, 2014). Moreover, AM fungi can immobilize significant amounts of N in mycelia (Hodge & Fitter, 2010).

Ectomycorrhizal fungi and ericoid fungi can acquire significant amounts of (organic) N and P, sometimes representing up to 80% of plant N and plant P (Simard *et al.*, 2002; Read & Perez-Moreno, 2003; Hobbie & Hobbie, 2006). While many experiments have been performed under controlled conditions in the glasshouse in sterilized soil, relatively few studies have been performed under field conditions because of experimental constraints (Read, 2002). A number of important tools and techniques have been developed to provide evidence for the role of mycorrhizal fungi in natural ecosystems, including hyphal bags or compartments (Babikova *et al.*, 2013; Veiga *et al.*, 2013), rotated cores (Johnson *et al.*, 2005), comparison of wild-type and mycorrhiza-deficient plant mutants (Facelli *et al.*, 2014), tree trenching (Hogberg *et al.*, 2001), or isotopes (Hobbie & Hobbie, 2006). Furthermore, stable isotope probing can be used to follow the fate of N and/or C (Drigo *et al.*, 2010) through mycorrhizal networks.

While many studies have focused on nutrient uptake, relatively few have considered that mycorrhizal fungi could also contribute to the reduction of nutrient losses (e.g. efficient nutrient uptake reduces the risk of nutrient loss as a result of leaching or denitrification). Yet, mycorrhizal fungi can significantly reduce N (up to 70 kg N ha⁻¹ yr⁻¹) and P (up to 150 g P ha⁻¹ yr⁻¹) leaching losses (Asghari *et al.*, 2005; Asghari & Cavnagaro, 2012; Bender *et al.*, 2015). Even in the absence of a plant growth response, AM fungi have been shown to reduce nutrient leaching losses (van der Heijden, 2010). Interestingly, AM fungi can reduce leaching losses of both organic and inorganic nutrients (Bender *et al.*, 2015). This might indicate that AM fungi acquire organic nutrients in line with a few earlier observations (Koide & Kabir, 2000), and this is important because significant amounts of organic nutrients can be

lost through leaching. Nutrient leaching losses also depend on the dominant mycorrhizal type (AM or EM) of the vegetation (Midgley & Phillips, 2014). By preventing nutrient losses, mycorrhizal fungi can enhance nutrient-use efficiency and ecosystem sustainability. Such ecosystem services are especially important in nutrient-poor ecosystems where plant productivity is nutrient-limited. Further work needs to test whether reducing nutrient losses is a general effect of mycorrhizas in ecosystems. AM fungi were recently shown to reduce emissions of N_2O , an important greenhouse gas with a 300 times higher global warming potential than CO_2 (Bender *et al.*, 2014). Such effects may be indirect, as AM fungi influence bacterial communities inhabiting the rhizosphere and mycorrhizosphere (Johansson *et al.*, 2004; Scheublin *et al.*, 2010), and AM fungi may induce shifts in denitrifying communities (Veresoglou *et al.*, 2012).

3. Plant productivity, ecosystem functioning, and multifunctionality

Mycorrhizal fungi play a key role in ecosystems and influence various important ecosystem functions (Table 2). They are well known to enhance plant productivity (Johnson *et al.*, 1997; Lekberg & Koide, 2005; Hoeksema *et al.*, 2010), although negative effects on plant biomass have also been repeatedly reported in natural (Francis & Read, 1994; Hoeksema *et al.*, 2010; Veiga *et al.*, 2013) and agricultural ecosystems (Ryan & Graham, 2002). Growth responses are also plant species-dependent: some plant species, especially those with relatively thick roots rely much more on mycorrhizal fungi than do plants with fine roots, such as grasses (Baylis, 1975; Hetrick *et al.*, 1992). Growth responses to AM fungi fall along a continuum from mutualism to parasitism (Johnson *et al.*, 1997), and even within the life cycle of a plant, the benefit obtained from the symbiosis can vary. Usually seedlings benefit more from the symbiosis than do adult plants (Jones & Smith, 2004). So far, relatively few studies have investigated how changes in mycorrhizal communities in the field alter plant growth and ecosystem functioning, and most glasshouse studies compare the effects of mycorrhiza with a nonmycorrhizal control, which is a very rare situation in nature.

Mycorrhizal fungi provide a wide range of other ecosystem functions and have a large impact on seedling establishment (van der Heijden & Horton, 2009), litter decomposition (Lindahl *et al.*, 2007), soil formation, and soil aggregation (Rillig & Mummey, 2006). Furthermore, mycorrhizal fungi can provide resistance to drought (Auge, 2001), heavy metals, disease, pathogens and stress (Newsham *et al.*, 1995). Effects are often variable between studies and context-dependent (e.g. depending on host plant, fungal species, environmental conditions). It has also been proposed that AM fungi extend the niche of plants (Klironomos *et al.*, 2000), and many plants would not be able to coexist with other plants without AM fungi (van der Heijden *et al.*, 2008).

A wide range of studies showed that mycorrhizal fungi modify competitive interactions between plants (Fitter, 1977; Wagg *et al.*, 2011). Consequently, plant community structure and diversity are altered depending on the presence (Grime *et al.*, 1987; Hartnett & Wilson, 1999; O'Connor *et al.*, 2002) and/or composition of

mycorrhizal fungal communities (van der Heijden *et al.*, 1998; Vogelsang *et al.*, 2006). A recent study showed that AM fungi influence the temporal stability of a plant community (Yang *et al.*, 2014) by differentially influencing plant species and reducing temporal variability in productivity. Some studies also showed that the introduction of mycorrhizal fungi into new habitats supports plant invasion (Nunez *et al.*, 2009; Dickie *et al.*, 2010). Moreover, the suppression of mycorrhizal networks by some invasive plants (Stinson *et al.*, 2006; Vogelsang & Bever, 2009) can modify plant community structure and impair seedling establishment of mycorrhizal plants.

It is difficult to summarize the overall impact of mycorrhizal fungi on ecosystems, because so many variables are influenced simultaneously. One way to solve this is to summarize the effects of a range of ecosystem functions and calculate an overall response index. In biodiversity research, multiple ecosystem functions are summarized into a so-called ecosystem multifunctionality index (*sensu* Hector & Bagchi, 2007). We used this metric and applied it to data from an earlier experiment (van der Heijden *et al.*, 1998). We observed that the presence of AM fungi significantly enhanced ecosystem multifunctionality compared with a nonmycorrhizal situation (Fig. S2). Similarly, EM fungi provide a range of ecosystem services (Table 2) and thus contribute to ecosystem multifunctionality. These observations confirm a recent study showing that soil biodiversity positively correlates with ecosystem multifunctionality (Wagg *et al.*, 2014). In this study, mycorrhizal fungi were one of the drivers of the positive effects of soil biodiversity on ecosystem multifunctionality, especially through their positive effects upon plant diversity.

IV. Mycorrhizal networks

The view of the mycorrhizal association as a one fungus–one plant association is practical for studying the physiology and ontogeny of the interaction, but does not hold ecologically. Most plant roots are colonized by multiple mycorrhizal fungi and most mycorrhizal fungi are not host-specific, colonizing various host plants at the same time. As a consequence, plants are usually interconnected by mycorrhizal mycelial networks in so-called ‘wood-wide-webs’ (Simard *et al.*, 1997). For example, in some temperate forests, trees (e.g. oak, pine, birch) are interconnected by EM fungal networks, while understory shrubs, grasses, and herbs are interconnected by AM fungi. In some communities, even a third and a fourth network are formed between ericoid and orchid mycorrhizal plants (Fig. 2). There are possible hubs between these networks; for example, some EM fungi may form ericoid mycorrhizas (Villarreal-Ruiz *et al.*, 2004; Bougoure *et al.*, 2007), and some trees or tree seedlings form dual symbiosis with EM and AM fungi (Egerton-Warburton & Allen, 2001; Onguene & Kuyper, 2001; Wagg *et al.*, 2008). However, there is still debate about the abundance and exact functional role of such hubs.

1. Carbon and nutrient transfer in mycorrhizal networks

The existence of mycorrhizal networks implies that C and nutrients can be transferred from one plant to another through fungal hyphae.

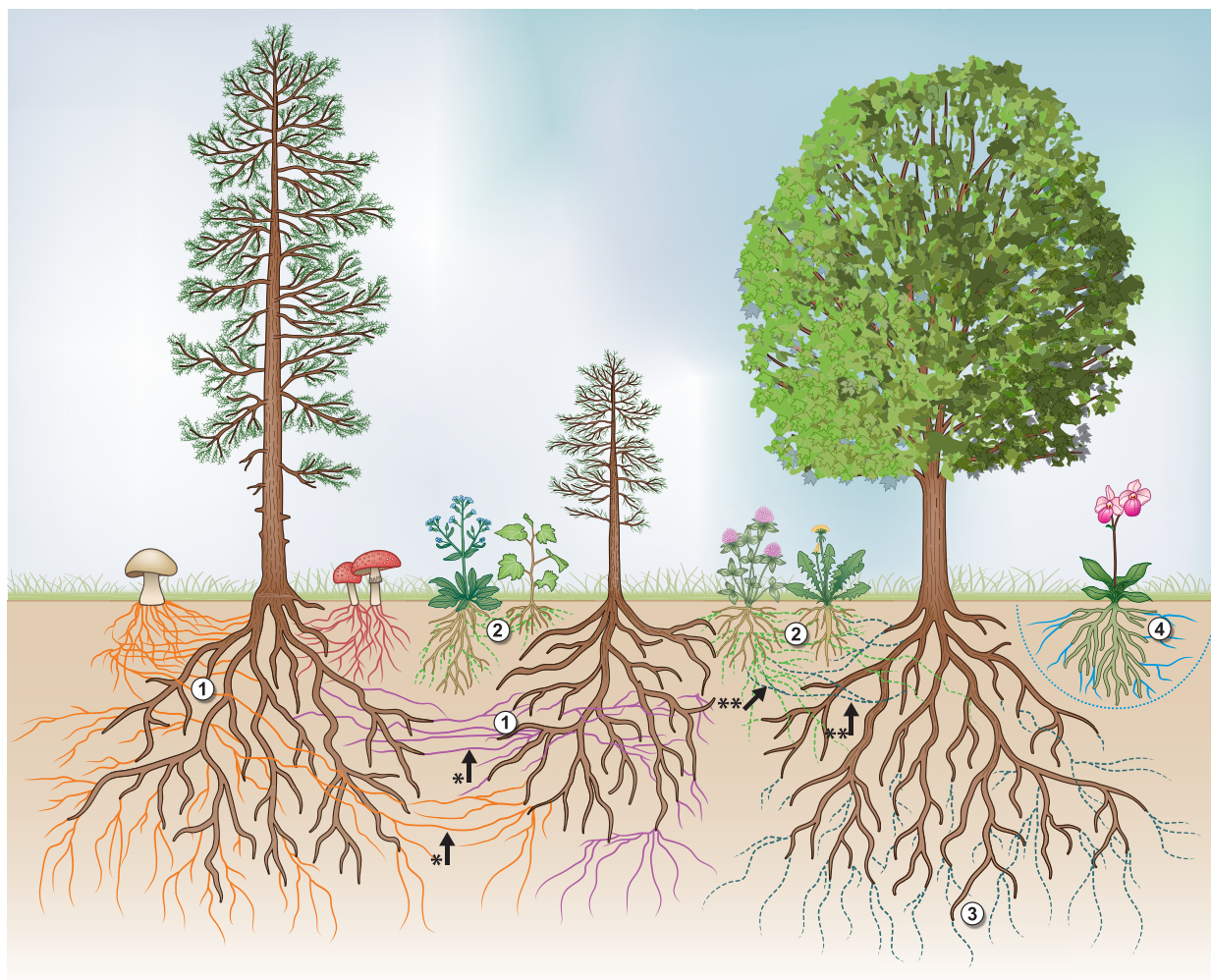


Fig. 2 Drawing of a hypothetical plant community consisting of plant species that associate with different types of mycorrhizal fungi and which form three separate underground networks. (1) Trees forming networks with ectomycorrhizal (EM) fungi (solid thin lines) are interconnected (see arrow*); (2) various plant species and a tree (3) form arbuscular mycorrhizal (AM) networks and are also interconnected (see dashed lines, arrow**), and (4) an orchid forms a third underground network. The different colors represent different mycorrhizal fungal species for EM fungi (solid thin lines) and AM fungi (dashed thin lines). Note that other combinations are possible (e.g. temperate forests with EM trees often harbor an understory of shrubs (e.g. *Vaccinium*) that form ericoid mycorrhizal associations). In these forests some fungi form both EM and ericoid mycorrhizal associations, meaning that there might be interlinkages between the two networks (composite by Ursus Kaufmann, Agroscope).

In boreal forests, mature trees allocate significant amounts of C into mycorrhizal networks. Part of that C has subsequently been found in small shaded tree saplings connected to the same mycorrhizal network, leading to the suggestion that there is interplant C transfer (Simard *et al.*, 1997). Similarly, several studies suggest that nutrients (e.g. N) move from one plant to another through these hyphal networks (Sellesse *et al.*, 2006). The latter would be important for intercropping systems (e.g. mycorrhizal networks could potentially move N from an N-fixing plant to a nonN-fixing plant). The significance of interplant C and nutrient transfer has been, and continues to be, widely debated (Fitter *et al.*, 1998; Selosse *et al.*, 2006). Unequivocal evidence is difficult to obtain because many control treatments are required (e.g. plant roots or mycorrhizal fungi may exude C or nutrients that are subsequently taken up by neighboring plants or mycorrhizal networks). Interestingly, there are indications that chemical signals are transferred through mycorrhizal networks (MNs) from one plant to another (Song

et al., 2010; Barto *et al.*, 2011; Babikova *et al.*, 2013) and that those signals may help plants to protect themselves against herbivores and pathogens (Pozo & Azcon-Aguilar, 2007; Babikova *et al.*, 2013). The ecological significance of interplant transfer of chemical signals, and why such signaling pathways have evolved need to be confirmed under field conditions.

Mycorrhizal networks are important for seedling establishment in perennial vegetation (Grime *et al.*, 1987; van der Heijden & Horton, 2009). The fact that seedlings that germinate in perennial communities, with existing mycelial networks, often become quickly colonized by mycorrhizal fungi (e.g. within 3–6 d after seedling emergence; Read *et al.*, 1976; Dickie *et al.*, 2002) is probably very important because small seedlings then have immediate access to a low-cost 'nutrient adsorption machine', provided and maintained by the surrounding vegetation (Newman 1988). Note, however, that root colonization of seedlings can be slow in the absence of mycelial networks, such as in early

successional sites with annual plants, areas with strip-mine reclamation, intensively managed (and ploughed) agricultural fields, arid environments where growth is reduced (long fallow) or after major stand-destroying disturbances such as fire (Allen & Allen, 1980; Kipfer *et al.*, 2010; Karasawa & Takebe, 2012). Mycorrhizal networks are absent or low in abundance in such communities because of regular soil disturbance destroying mycorrhizal networks or the absence of permanent vegetation cover that is needed to maintain mycorrhizal networks.

Plants investing the largest amount of C into mycorrhizal networks often obtain the largest amount of nutrients in return, indicating that resource exchange is, at least to some extent, controlled (Kytöviita *et al.*, 2003; Kiers *et al.*, 2011). By contrast, other studies found that one plant species can maintain a mycorrhizal network, while other plants connected to it benefit more for their nutrition (Grime *et al.*, 1987; Walder *et al.*, 2012). Walder *et al.* (2012) made use of natural differences in $^{13}\text{C}/^{12}\text{C}$ isotope composition between C_3 and C_4 plants to assess resource exchange in mycorrhizal networks. They found that one plant species (*Linum usitatissimum*) invested little C into the mycelial network, while obtaining up to 90% of plant N and P through those networks. By contrast, the other plant species (*Sorghum bicolor*) that invested most C in the mycorrhizal network received little in terms of enhanced nutrient uptake. This example shows that resource exchange in mycorrhizal networks is not necessarily balanced and that one plant species can benefit much more from mycorrhizal networks than others.

The most extreme examples of unequal resource exchange in mycorrhizal networks are probably mycoheterotrophic plants. These plants are completely achlorophyllous and depend on C and nutrients obtained from mycorrhizal networks that link them to surrounding plants (Leake, 1994). Mycoheterotrophic plants act as epiparasites and it is still unclear whether these plants supply anything at all to mycorrhizal networks. Mycoheterotrophy arose through convergent evolution in land plants. Several orchids, members of Gentianaceae, Ericaceae, and Polygalaceae, and even some species of liverworts are mycoheterotrophic (Merckx, 2013). Moreover, some green plants were recently discovered to recover part of their C from EM fungal networks, mixing mycohetero- and autotrophy (mixotrophy; Selosse & Roy, 2009; Merckx, 2013).

2. Mycorrhizal interaction networks

At a larger scale, the study of interaction networks has become very popular for visualizing interactions between species (e.g. pollinator networks or plant–frugivore networks) and for understanding their functioning and evolution (Bascompte *et al.*, 2003; Thebault & Fontaine, 2010). Such interaction networks can be applied to mycorrhizal associations and make it possible to show which plant species are linked to which mycorrhizal fungi and vice versa. The assembly of mycorrhizal interaction networks has recently been revealed for AM (Montesinos-Navarro *et al.*, 2012), orchid (Martos *et al.*, 2012; Jacquemyn *et al.*, 2015) and EM (Bahram *et al.*, 2014) associations. These studies show that AM interaction networks are nested, meaning that there are several generalist fungi

(e.g. *Rhizophagus irregularis* (formerly *Glomus intraradices*), *Funneliformis mosseae* (formerly *Glomus mosseae*)) that associate with almost all plants present in a particular ecosystem, while other fungi are more specific and interact with a subset of the plant species that interact with the widespread generalists (Öpik *et al.*, 2003, 2006; Verbruggen *et al.*, 2012). This nested assembly pattern generates highly asymmetrical interactions and organizes the community cohesively around a central core of interactions (Bascompte *et al.*, 2003). By contrast, orchid interaction networks are modular (subsets of species that interact more with a group of partners than with other groups; Martos *et al.*, 2012; Jacquemyn *et al.*, 2015) and this often reflects the high specificity between partners in orchid symbioses. EM interaction networks display an intermediate structure, showing some modularity and nestedness (Bahram *et al.*, 2014), with generalist EM fungal species having a broad host range, colonizing many trees in a forest, and more specialized EM fungi associating with particular hosts. Overall, these findings and the comparison between mycorrhizal types point towards a relationship among mycorrhizal specificity, modularity, and nestedness (Fig. 3). Interestingly, using network theory, it is possible to test whether there are completely independent underground networks and ‘guilds’ of interconnected plant species building upon earlier work on mycorrhizal guilds (Read, 1989; Kottke *et al.*, 2008).

V. Evolution and partner selection

1. Diversification of mycorrhizal symbioses

Considerable information has been gained about the evolution of mycorrhizal symbioses in the last decade. Based on its wide phylogenetic distribution and the presence of 450 million-yr-old fossils of mycorrhizal fungal-like structures (Redecker *et al.*, 2000), the AM symbiosis is considered ancestral among land plants, and it probably allowed their transition from water to land (Selosse & Le Tacon, 1998). Whether AM fungi evolved from soil saprotrophs or from biotrophic fungi parasitizing early land plants remains unknown. This calls for more research on symbiotic fungal associations in the closest extant relatives of land plants such as Charo- and Coleochaetophyta.

Two facts support AM symbioses as being homologous in all major land plant lineages. First, the signaling transduction pathway controlling the AM symbiosis, the so-called SYM pathway (Oldroyd, 2013; see Section VI.2), is also present in earliest branching land plants (e.g. hornworts and liverworts contain orthologs of the *Medicago truncatula dmi3* gene coding for a calcium- and calmodulin-dependent kinase required for the establishment of both nodulation and AM symbiosis (Wang *et al.*, 2010). Second, a mycorrhiza-specific phosphate transporter is conserved among evolutionarily distant plant species (Karandashov *et al.*, 2004). However, an exclusive role of Glomeromycota in early fungal–plant symbioses was recently challenged by the discovery that the earliest branching land plants also associate with fungi within the Mucoromycotina, a basal fungal lineage close to the Glomeromycota (Bidartondo *et al.*, 2011; Desiro *et al.*, 2013). Further support challenging this paradigm is the discovery of fungal

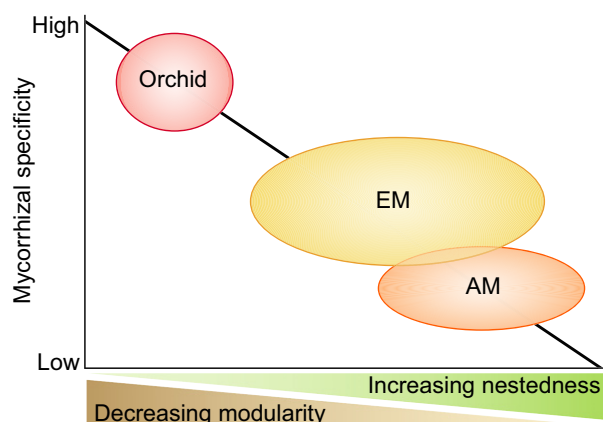


Fig. 3 Proposed relationship between host specificity, nestedness, and modularity in associations between plants and mycorrhizal fungi. Arbuscular mycorrhizas (AM), ectomycorrhizas (EM) and orchid mycorrhizas (orchid). Nestedness is a measure of order in ecological communities. A nested plant–mycorrhizal fungal community is cohesively organized around a central core of interactions of fungi with a broad host range that associate with almost all plant species in the community and other fungi that are more specific and interact with a subset of plant species that also interact with the generalist species. Modularity is defined as a subset of species that interact more with a group of partners than with other groups.

fossils of the Mucoromycotina in 400 million-yr-old plant material from the Rhynie Chert (Strullu-Derrien *et al.*, 2014). To what extent these two symbioses overlap in function (e.g. enhanced plant nutrition) in extant plants should now be investigated. The recent observation that there is reciprocal exchange of C and nutrients in a symbiosis between a liverwort and a member of the Mucoromycotina (Field *et al.*, 2015) suggests that Mucoromycotina form mutualistic associations and it might even indicate that there is some overlap in function with mycorrhizal fungi. It is still unclear to what extent the Mucoromycotina also colonize more recent plant lineages, such as flowering plants, and this is an area for further investigation.

Ectomycorrhizal associations are much younger than the AM symbiosis and evolved *c.* 100–200 million yr ago during a period of rapid angiosperm radiation in the Jurassic and Cretaceous (Brundrett, 2002). The oldest known fossils to have ericoid mycorrhizas were found *c.* 80 million yr ago (Brundrett, 2002). The evolutionary history of EM fungi has been investigated in more detail than for fungi forming other mycorrhizal types. The EM fungal lifestyle has evolved multiple times from saprotrophic lineages of wood and litter decayers through convergent evolution as shown by multigene phylogenies (James *et al.*, 2006) and phylogenomic analyses (Eastwood *et al.*, 2011; Floudas *et al.*, 2012). Tedersoo & Smith (2013) proposed that the ability to form EM evolved independently at least 80 times in fungi.

Phylogenomic reconstructions based on sequenced Agaricomycotina species suggests that EM clades evolved from wood and litter decayers (Floudas *et al.*, 2012; A. Kohler *et al.*, unpublished). Examination of the available *Laccaria bicolor* and *Tuber melanosporum* genomes (Martin *et al.*, 2008, 2010) and the new genomes released by the Mycorrhizal Genomics Initiative consortium (MGI) (Table 3; A. Kohler *et al.*, unpublished) concurs with the hypothesis that the mycorrhizal lifestyle is associated with a

massive loss of lignocellulose-degrading genes compared with the saprotrophic ancestors (Martin & Selosse, 2008; Eastwood *et al.*, 2011; Plett & Martin, 2011; Floudas *et al.*, 2012; Wolfe *et al.*, 2012). The loss of lignocellulose-degrading enzymes in the EM fungi studied so far (mostly in the Agaricomycotina) made them dependent on their host plant photoassimilates as a C source. Thus, the evolution of EM fungi is first characterized by a loss-of-function entailing dependency on the host, which may explain why reversion to free life has, to our knowledge, not been documented for EM lineages.

More recently, orchids and plants within the Ericaceae family independently evolved mycorrhizal associations by recruiting new fungal lineages (e.g. Ceratobasidiaceae, Tulasnellaceae and Sebaciniales in orchids; Sebaciniales and Helotiales in the Ericaceae) that form coils within roots cells (Selosse *et al.*, 2009). Many of these fungi have a free-living, saprotrophic stage but may also have an endophytic stage, that is, a diffuse growth within living plant tissues, without apparent infection symptoms or symbiotic organs such as arbuscules formed by AM fungi or a fungal mantle formed by fungi in ectomycorrhizal associations. It has been speculated that many mycorrhizal lineages evolved from former root endophytes, because endophytism could act as a symbiotic ‘waiting room’ predisposing the fungus to evolution towards a tighter mutualism with some hosts (Selosse *et al.*, 2009). Similarly, several endophytic lineages also contain EM fungi (e.g. within the Helotiales and Sebaciniales or within the genus *Hygrocybe*) (Seitzman *et al.*, 2011; Tedersoo & Smith, 2013), perhaps indicating that these fungi recently switched to an EM lifestyle. The genome of dozens of endophytic fungi currently sequenced within the framework of the Joint Genome Institute 1000 Fungal Genomes project should provide long-awaited information on their evolution, and confirm their possible intermediate complexity between free-living saprotrophs and mycorrhizal fungi.

2. Evolutionary stability and maintenance of mutualism in mycorrhizal symbioses

The symbiosis between plants and mycorrhizal fungi is widespread and very old (see Section V.1). Thus, this symbiosis can be considered to be evolutionarily stable. However, the mechanisms contributing to evolutionary stability and to plant–fungal coexistence are only partly understood. Key questions are whether plants and fungi have the ability to regulate resource exchange (C and nutrients) and whether they can detect and sanction nonbeneficial partners or specifically select for beneficial ones. Also, did plants or fungi evolve any specific mechanisms to control the exchange of C for nutrients? Furthermore, how do plants interact with multiple fungi at a molecular level (e.g. is the establishment of a particular fungus in a root segment influenced by the presence of other established fungi)? The evolutionary biology of the mycorrhizal symbiosis is a research area with many unanswered questions.

Mycorrhizal fungi vary in effectiveness and some fungi deliver many more nutrients to plants compared with other plants (Jakobsen *et al.*, 1992; Lendenmann *et al.*, 2011). Vice versa, plant species differ in the amounts of C they can deliver to mycorrhizal fungi (Walder *et al.*, 2012). Thus, selection forces should exist that

Table 3 Genome size and gene number for mycorrhizal fungi with completely sequenced genomes produced within the framework of the JGI-INRA Mycorrhizal Genomics Initiative (Grigoriev *et al.*, 2011; Martin *et al.*, 2011)

Species	Genome size	Gene no.
Arbuscular mycorrhizal fungi		
1 <i>Rhizophagus irregularis</i> DAOM 181602 v1.0	91 083 792	28 232
Ectomycorrhizal fungi		
2 <i>Amanita muscaria</i> Koide v1.0	40 699 759	18 153
3 <i>Boletus edulis</i> v1.0	46 637 611	16 933
4 <i>Cenococcum geophilum</i> 1.58 v2.0	177 557 160	14 748
5 <i>Choiromyces venosus</i> 120613-1 v1.0	126 035 033	17 986
6 <i>Clavulina</i> sp.	41 635 769	15 452
7 <i>Cortinarius glaucopus</i> AT 2004 276 v2.0	63 450 306	20 377
8 <i>Gyrodon lividus</i> BX v1.0	43 048 674	11 779
9 <i>Hebeloma cylindrosporum</i> h7 v2.0	38 226 047	15 382
10 <i>Laccaria amethystina</i> LaAM-08-1 v1.0	52 197 432	21 066
11 <i>Laccaria bicolor</i> v2.0	60 707 050	23 132
12 <i>Morchella conica</i> CCBAS932 v1.0	48 213 273	11 600
13 <i>Meliniomyces bicolor</i> E v2.01.3*	82 384 847	18 619
14 <i>Paxillus involutus</i> ATCC 200175 v1.0	58 301 126	17 968
15 <i>Paxillus rubicundulus</i> Ve08.2 h10 v1.0	53 011 005	22 065
16 <i>Piloderma croceum</i> F 1598 v1.0	59 326 866	21 583
17 <i>Pisolithus microcarpus</i> 441 v1.0	53 027 657	21 064
18 <i>Pisolithus tinctorius</i> Marx 270 v1.0	71 007 534	22 701
19 <i>Rhizopogon vinicolor</i> AM-OR11-026 v1.0	36 102 320	14 469
20 <i>Scleroderma citrinum</i> Foug A v1.0	56 144 862	21 012
21 <i>Suillus brevipes</i> v1.0	51 712 595	22 453
22 <i>Suillus luteus</i> UH-Slu-Lm8-n1 v1.0	37 014 302	18 316
23 <i>Terfezia boudieri</i> S1 v1.0	63 234 573	10 200
24 <i>Tricholoma matsutake</i> 945 v3.0	175 759 688	22 885
25 <i>Tuber aestivum</i>	131 544 163	9344
26 <i>Tuber magnatum</i> v1.0	192 781 443	9433
27 <i>Tuber melanosporum</i> v1.0	124 945 702	7496
28 <i>Wilcoxina mikolae</i> CBS 423.85 v1.0	117 288 895	13 093
Ericoid mycorrhizal fungi		
13 <i>Meliniomyces bicolor</i> E v2.01.3*	82 384 847	18 619
29 <i>Meliniomyces variabilis</i> F v1.03	55 857 776	20 389
30 <i>Rhizoscyphus ericae</i> UAMH 7357 v1.0	57 408 471	16 784
31 <i>Tulasnella calospora</i> AL13/4D v1.0	62 392 858	19 659
Orchid mycorrhizal fungi		
32 <i>Tulasnella calospora</i> AL13/4D v1.0	62 392 858	19 659
33 <i>Sebacina vermifera</i> MAFF 305830 v1.0	38 094 242	15 312

Genome sequences and annotations can be assessed through the JGI MycoCosm portal (<http://genome.jgi-psf.org/programs/fungi/index.jsf>; Grigoriev *et al.*, 2014). Sequenced fungi forming arbuscular mycorrhizal, ectomycorrhizal, ericoid mycorrhizal or orchid mycorrhizal associations are shown.

**Meliniomyces bicolor* forms both ectomycorrhizal and ericoid mycorrhizal associations.

favor the detection of beneficial partners and the efficiency of the symbiosis (*sensu* Koide & Elliott, 1989). Recent work revealed that AM fungi allocated more mineral nutrients to the most C-rewarding plants, while, reciprocally, plants allocated more C to the fungus providing the highest mineral nutrition, that is, P (Bever *et al.*, 2009; Kiers *et al.*, 2011) or N (Fellbaum *et al.*, 2014). Thus, these studies indicate that plants and fungi both have the ability to detect and selectively reward beneficial symbionts. This analogy with a 'biological market' has been used to explain the evolutionary stability of the symbiosis between plants and AM fungi. It is still

unclear whether preferential resource allocation to beneficial symbionts is also occurring in complex mycorrhizal networks with many different symbionts or in other mycorrhizal associations (e.g. EM, ericoid or orchid mycorrhizas) and this is an issue that deserves attention. The fact that plants usually have reduced root colonization levels when soil fertility is high (e.g. when fungal symbionts are not beneficial for the plant) or when light intensities and C availability are low (Smith & Read, 2008; Smith & Smith, 2011) further demonstrates that plants, at least in part, have the ability to regulate this symbiosis.

Several observations question the view of a biological market where partners control the exchange of C against mineral nutrients as a sole mechanism for understanding plant–fungal coexistence in mycorrhizal associations. First, mycoheterotrophic (Leake, 1994; Merckx, 2013) and mixotrophic plants (Sellesse & Roy, 2009; see Section IV.1) bypass the previous market logic. The fungi reverse the C flow, and provide no sugar for the mineral nutrients they obtain. Moreover, mycoheterotrophic plants feeding on EM networks extract N more efficiently from their fungus than autotrophic plants (Merckx, 2013; Gonneau *et al.*, 2014). It is possible that mycoheterotrophic plants provide other benefits to the fungi (e.g. vitamins or protection; Selosse & Rousset, 2011), but this has not been convincingly proven. Second, a meta-analysis by Hoeksema *et al.* (2010) revealed that in *c.* 10% of the studies, mycorrhizal fungi reduced plant growth. This suggests that plants do not necessarily benefit from the symbiosis and are unable to exclude fungal symbionts under deleterious conditions. It also indicates that mycorrhizal fungi are regularly 'cheating' and that the plant is not in full control of the symbiosis. Third, many plant species are not C-limited, but grow in nutrient-limited soils, and plant photosynthates are a luxury commodity under these conditions (Kiers & van der Heijden 2006). Hence, for such plants there is no strong selection pressure to reward beneficial fungi or develop defense mechanisms against less effective fungi (e.g. because C delivery to less beneficial symbionts does not directly reduce plant fitness). Moreover, the biological market theory offers a view where each partner acts independently, but there is evidence for manipulations of the host gene expression by the colonizing symbionts through effector proteins (see Section VI.2). These effector proteins counteract the plant immune system and further work should test whether such effector proteins facilitate the establishment of other (nonbeneficial) symbionts. Plants can control their N-fixing bacterial symbionts by using secreted effector polypeptides (Kondorosi *et al.*, 2013), and the possibility that host plants release effector-like proteins to control the penetration of mycorrhizal fungi deserves further study. Clearly, resource exchange regulation and biological market theory are not the only factors that explain plant–fungal coexistence and evolutionary stability in the mycorrhizal symbiosis.

VI. Mycorrhizal genomics and symbiotic molecular crosstalk

1. Mycorrhizal genomics

Genome sequences are now available for several mycorrhizal fungi and are valuable for resolving long-standing issues about their

biology, evolution, and ecology. The fungal lineages containing EM species are separated by tens or hundreds of millions of years (James *et al.*, 2006), but they share remarkable morphological and metabolic similarities. To identify the genetic innovations that led to convergent evolution of the mycorrhizal lifestyle from saprotrophic species, large-scale comparative genomics projects have recently been implemented (Grigoriev *et al.*, 2011; Martin *et al.*, 2004, 2011). Additional questions that can be addressed using a genomics approach include the following: What accounts for the diversity of mycorrhizal lifestyles (e.g. AM, EM, orchid, ericoid)? How do the genes that mycorrhizal fungi use to colonize their hosts compare with those of fungal pathogens? Which genes are responsible for the molecular crosstalk with their host plants? Which genes are controlling the nutrient exchange between partners? Do mycorrhizal fungal genomes have features that help symbionts to survive environmental changes?

As of 2014, the nuclear genomes of three mycorrhizal fungi (*L. bicolor*, *T. melanosporum* and *R. irregularis*) have been published (Martin *et al.*, 2008, 2010; Tisserant *et al.*, 2013). This resource has provided unprecedented knowledge about the structure and functioning of the mycorrhizal fungal genomes and their interactions with plants (Martin & Selosse, 2008; Plett & Martin, 2011; Lanfranco & Young, 2012; Martin & Kohler, 2014). It has also led to the identification of master genes with crucial roles in symbiosis formation, such as those coding for mycorrhiza-induced small secreted proteins (MiSSPs) controlling plant immunity and development (Kloppholz *et al.*, 2011; Plett *et al.*, 2011, 2014a,b).

The MGI, an international effort, is aiming to sequence the nuclear and mitochondrial genome of 50 fungal species that are able to form various types of mycorrhizal symbioses, that is, EM, AM, ericoid and orchid mycorrhizas. Comparative genomics should facilitate the identification of the genetic mechanisms that underpin the establishment and evolution of ecologically relevant mycorrhizal symbioses and characterization of genes selectively associated with particular symbiotic patterns (Plett & Martin, 2011). The fungal species have been selected based on: their phylogenetic position, their ecological relevance, and their ability to establish different types of mycorrhizal symbiosis. As of writing, assemblies annotated with gene models are publicly available for 33 mycorrhizal fungi (Table 3), including 26 ectomycorrhizal species, four ericoid species, two orchid mycorrhizal species and one arbuscular mycorrhizal fungal species (see the JGI MycoCosm database at: <http://genome.jgi-psf.org/programs/fungi/index.jsf>).

Genomes of mycorrhizal fungi are estimated to range in size from c. 36 Mb, as in the case of *Rhizopogon vinicolor*, to 193 Mb, as in *Tuber magnatum* (Table 3). Repetitive DNA, mostly in the form of transposable elements, is responsible for the bulk of the variation (Martin *et al.*, 2008, 2010; Murat *et al.*, 2013). The repetitive DNA content ranges from 3.6% for *Hebeloma cylindrosporum* to 58.3% for *T. magnatum*. Predicted gene contents range from c. 7500 for *T. melanosporum* to c. 28 000 genes for *R. irregularis* (Table 3). It remains to be determined whether the number of genes relates to the mycobionts' ability to infect an increasing number of plant species (i.e. determine host range specificity). The compact gene repertoire of *T. melanosporum* might be a product of selection

for such host specialization. By contrast, expansion of the gene repertoire, as observed in *L. bicolor* and *R. irregularis*, may be selected to exploit the diversity of rhizospheric and *in planta* environments when in association with multiple hosts in diverse soil habitats.

One of the most surprising observations to be drawn from the comparison of *L. bicolor* and *T. melanosporum* genome-wide transcript profiling is that there are only a few similarities between genes induced by *T. melanosporum* and *L. bicolor* during the development of the ectomycorrhizal symbiosis (Martin *et al.*, 2010). Both species have symbiosis-specific gene expression, but in neither case are the genes expressed during symbiosis the same, except a few membrane sugar transporters and a GH5 glycosyl hydrolase (Martin *et al.*, 2010; Plett *et al.*, 2014b). Transcript profiling of EM roots from a dozen EM interactions suggests that the genes required for mutualism were reinvented each time it developed in evolutionary history, although similar functional categories (e.g. nutrient transporters, small secreted proteins) appear to be convergently expressed (Kohler *et al.*, in press). Importantly, the functional categories of genes expressed in *R. irregularis* in the AM symbiosis are similar to those observed in the EM symbiosis, in a remarkable case of convergent molecular evolution (Kohler *et al.*, in press).

2. Molecular crosstalk in mycorrhizal symbioses

The genes responsible for the establishment of the AM symbiosis and molecular crosstalk between plant and fungus (i.e. the SYM signaling pathway) are currently being revealed (Parniske, 2008; Bonfante & Genre, 2010; Oldroyd, 2013). Strigolactones have been discovered as plant signaling molecules attracting AM fungi (Akiyama *et al.*, 2005; Besserer *et al.*, 2006; Kretschmar *et al.*, 2012) and, reciprocally, AM fungi secrete lipochitooligosaccharides that stimulate the formation of AM (Maillet *et al.*, 2011). Moreover, transcriptome profiling has highlighted a number of different genes that may be involved in the establishment and maintenance of the symbiosis. Induced expression of genes coding for membrane transporters and MiSSPs during the symbiotic interaction, and the lack of expression of hydrolytic enzymes acting on plant cell wall polysaccharides are hallmarks of the *R. irregularis* transcriptome (Tisserant *et al.*, 2013). While it is not fully understood how AM and EM mycorrhizal fungi have acquired the ability to avoid plant defenses, current research suggests that a combination of differential gene expression of fungal effectors, such as the proteins MiSSP7 and SP7 (Kloppholz *et al.*, 2011; Plett *et al.*, 2011, 2014a), actively counteract local defense responses and plant immunity. For example, the most highly symbiosis-induced *L. bicolor* gene, MiSSP7, is coding for a secreted protein, altering gene expression in poplar roots (Plett *et al.*, 2011). MiSSP7 is a 7 kDa protein that is secreted from fungal hyphae, internalized within plant cells, after which it localizes to the nucleus (Plett *et al.*, 2011). The nuclear localization of MiSSP7 is essential for the formation of the fungal Hartig net (Plett *et al.*, 2011). MiSSP7 acts by binding to the key regulator of the jasmonate (JA) signaling pathway, the repressor protein JASMONATE ZIM-domain (JAZ) PtJAZ6. Binding of MiSSP7 to PtJAZ6 stabilizes the JAZ protein to suppress JA-

dependent defenses that would otherwise preclude the formation of the Hartig net and thus the symbiosis (Plett *et al.*, 2014a). The effector protein SP7 from *R. irregularis* (Kloppholz *et al.*, 2011) is also targeted to the host nucleus where it binds to the pathogenesis-related transcriptional factor ERF19 during the AM interaction.

The next critical step is to elucidate the functions of the > 200 000 clade-specific orphan genes with unknown function found in the mycorrhizal genomes sequenced so far and give a biochemical, physiological, and ecological interpretation of this information. This will require an efficient integration of bioinformatics tools and genome-wide functional analyses, including gene disruption, transcriptomics, and proteomics, in order to determine gene function. The greatest challenge will be to simultaneously monitor transcriptional profiles of multiple mycorrhizal fungi *in situ* over time to answer questions about how these microorganisms interact with their host(s) and environment and with each other, and how these interactions influence ecosystem stability. An interesting avenue to investigate is also to monitor molecular crosstalk in symbiotic associations where resource transfer and growth outcomes vary (e.g. using mycorrhizal (such as *Medicago*) and nonmycorrhizal model plants (such as *Arabidopsis*; Veiga *et al.*, 2013) and plants that vary in mycorrhizal responsiveness (Plett *et al.*, 2014c)).

3. From population genetics towards population genomics

Genomics studies of mycorrhizal fungi have largely focused on individual fungal species (see Section VI.1), while metagenomics studies have concentrated on describing fungal diversity and community structure based on numbers of recognizable OTUs detected in the environment (see Section II). The markers that have mostly been used in metagenomic studies are located in the rDNA, and clustering of those sequences into OTUs usually gives a resolution to the genus or species level, but probably not at a finer intraspecific scale (Lindahl *et al.*, 2013). This leaves a gap where little knowledge currently exists about the genomic variation among individuals of a given mycorrhizal fungal species both within populations and among populations of different geographic origin.

Population genetics of AM fungi is restricted to only a handful of species (Stukenbrock & Rosendahl, 2005; Croll *et al.*, 2008). This is largely because AM fungi are obligate biotrophs and can only be cultured together with plant roots. Furthermore, it is difficult to isolate many different individuals of one AM fungal species from a given location, coupled with the difficulty of culturing the fungi in a clean system to obtain AM fungal DNA that is free of contaminant DNA (Koch *et al.*, 2004). Because of this, suitable markers have only been developed for *R. irregularis* and only from one population located in Switzerland (Croll *et al.*, 2008; Börstler *et al.*, 2010). Studies by Croll *et al.* (2008) and Börstler *et al.* (2010) revealed very high degrees of genetic variability of *R. irregularis* in a very small area (Croll *et al.*, 2008; Börstler *et al.*, 2010). Interestingly, an isolate of the same species but originating in Canada was not genetically very different from the Swiss isolates and actually clustered within the Swiss *R. irregularis* population (Croll *et al.*, 2008). Many AM fungal species, including *R. irregularis*, are unusual in that they have a seemingly worldwide distribution, which is often not observed for EM fungi (Vincenot *et al.*, 2012; Dearnaley *et al.*, 2013). Isolates of

R. irregularis are now greatly needed from other geographically distant populations in order to study gene flow between populations, genetic and phenotypic differentiation among populations, and in order to shed light on how AM fungi are dispersed. Given the large within-population variation in ecologically relevant quantitative traits in these fungi or in their plant hosts after inoculation with these fungi, the development of mycorrhizal fungal population genomics is an important area to develop further our understanding of the ecologically relevant degrees of genomic variation in mycorrhizal fungi.

While population genetics has told us much about the ecology of mycorrhizal fungi themselves, looking at within-species and within-population genetic variation in mycorrhizal fungi, and coupling this with their phenotypic variation, can allow us to estimate the potential importance of such diversity for plant ecology and plant communities (Johnson *et al.*, 2012). Experimental studies on both EM and AM fungal populations indicate considerable within-species or within-population variation in how these fungi affect plant growth or key phenotypic traits of the fungi that should influence plant growth (Wagner *et al.*, 1989; Koch *et al.*, 2004; Munkvold *et al.*, 2004). In some of these studies, the genetically different fungi were isolated from the same population and all isolates were maintained in a common environment before the estimates of variation in quantitative traits, such as effect on plant size (Koch *et al.*, 2004); fungal nitrate reductase and acid phosphatase activity (Wagner *et al.*, 1989); ability to form mycorrhiza and host specificity (Hedh *et al.*, 2009); and nickel tolerance (Jourand *et al.*, 2010). These experiments allow us to conclude that the wide range of within-population variation observed in some mycorrhizal fungal phenotypic traits probably has a genetic basis, and points to the strong potential ecological importance of within-population genetic variation in AM and EM fungi. The recent sequencing of the genomes of a range of mycorrhizal fungal species (Table 3) and the genome resequencing of multiple strains of these fungi from different geographic origins will greatly facilitate the development of genome-wide markers for future population genomic studies.

VII. Conclusions and future research

In this review, we have summarized recent advances in mycorrhizal biology, evolution, and ecology. This research has confirmed that mycorrhizal fungi play a key role in terrestrial ecosystems and are major drivers of global C and nutrient cycles (Table 2). High-throughput molecular techniques have uncovered the unexpected diversity of mycorrhizal associations and their spatial and temporal dynamics in temperate, boreal, and tropical ecosystems. The numerous biochemical, genetic and transcriptomic efforts described earlier are currently being aided by a massive effort to sequence the genomes of multiple fungal symbionts (Table 3). Data produced from these projects will serve as building blocks for an extensive framework enabling scientists to ask a broad spectrum of biological, ecological, evolutionary, and other questions about role of mycorrhizal fungi in plant growth and evolution, soil structure and responses to environmental changes, and global C and nutrient cycles.

A number of key questions still need to be answered. First, the molecular crosstalk between plants and mycorrhizal fungi is only beginning to be revealed and is clearly delayed compared with knowledge on other plant–microbe interactions (e.g. rhizobia–legume associations, *Phytophthora*–solenaceous crops). It is largely unclear which genes are responsible for the establishment and maintenance of the mycorrhizal symbiosis. Thus, the exploration of symbiotic gene networks and master transcriptional factors in the molecular dialogue between plant and fungus is a key challenge to understand plant–fungal coexistence and the factors responsible for the establishment of the mycorrhizal symbiosis. Moreover, a further major advance will be to link molecular data and metabolic pathways with ecophysiological and ecological processes such as the acquisition of nutrients or the protection against stresses and diseases.

Second, while the individual genomes of various mycorrhizal fungi are now available (Table 3) and metagenomes of fungal communities associating with plant roots are being revealed (Gottel *et al.*, 2011; Shakya *et al.*, 2013), complete plant microbiomes (all fungi and bacteria associating with plant roots) are largely missing (Hacquard & Schadt, 2014). The advance of sequencing technology and bioinformatics will also make it possible to further explore mycorrhizal networks (e.g. see Tedersoo *et al.*, 2014) and interactions with other organisms in complete foodwebs, including interactions with bacteria colonizing the hyposphere (Johansson *et al.*, 2004; Scheublin *et al.*, 2010) or even endosymbiotic bacteria living inside mycorrhizal hyphae (Bianciotto *et al.*, 1996). It is also still a major challenge to understand interactions between mycorrhizal fungi and other members of underground foodwebs and how mycorrhiza interact with other soil biota to drive ecosystem functioning. A major challenge is also to reveal the fluxes of energy, metabolites, signaling molecules, and nutrients through mycorrhizal networks.

Third, the tools for studying interaction networks now allow better visualization of the mycorrhizal association at the level of the fungal and the plant community. Interestingly, such network analyses revealed that plant–fungal interactions in the major mycorrhizal types may differ in important characteristics such as specificity, nestedness, and modularity (Fig. 3).

Fourth, coevolutionary processes between plants and mycorrhizal fungi are still poorly understood, especially the physiological mechanisms responsible for partner choice, and, more broadly, for the stability of mycorrhizal mutualism. Biological market models to explain associations between plants and mycorrhizal fungi are appealing, but need to be further developed and extended. It is also intriguing to investigate newly acquired symbionts (e.g. forming ericoid mycorrhizas) or ancient symbionts (e.g. the Mucoromycotina) and how they coevolve with their hosts.

Fifth, new methods for large-scale production of AM fungi (Ijdo *et al.*, 2011) and seed coating technology with AM fungi (Vosátka *et al.*, 2012) have been developed in recent years. This makes application in horticulture and agriculture cheaper and more reliable. For instance, the use of *in vitro* produced AM fungal propagules have led to significant yield increases in the globally important food security crop cassava (Ceballos *et al.*, 2013), following earlier reports of beneficial effects of mycorrhizal fungi on several important agricultural crops (Plenchette *et al.*, 1983;

Sieverding *et al.*, 1991). Now we need to develop biogeochemical models that help us to predict when, and under what conditions, application of mycorrhizal technology is profitable. Similarly, it is still unclear how variation in plant responsiveness to mycorrhizal colonization is regulated. Finally, mycorrhizal associations are increasingly included in global models, for instance for understanding C or nutrient cycling. Improving such models is a further major frontier.

Major advances have been made in the field of mycorrhizal research. It all started with the discovery that mycorrhizal associations are abundant and important for plant nutrition. Now, more than 100 yr later, the ecological function of this symbiosis is much better understood, the biodiversity and evolution of this symbiosis is no longer a black box, genomes of a wide range of mycorrhizal fungi have been sequenced, and molecular interactions establishing the symbiosis are starting to be revealed.

Acknowledgements

We are grateful to all participants of the 33rd New Phytologist Symposium ‘Networks of power and influence: ecology and evolution of symbioses between plants and mycorrhizal fungi’ at Agroscope, in Zurich, Switzerland, for stimulating and thought-provoking discussions. M.G.A.vdH. acknowledges financial support from Agroscope and the Swiss National Science Foundation (grant nos 137136 and 143097), and Florian Walder, Valexia Provent, Klaus Schläppi, and Franz Bender for discussion and assistance. The Mycorrhizal Genome Initiative is supported by INRA, the US Department of Energy (DOE) Joint Genome Institute (contract no. DE-AC02-05CH11231), the Oak Ridge National Laboratory Scientific Focus Area for Genomics Foundational Sciences, and the Region Lorraine Research Council. M.-A.S. acknowledges the Muséum national d’Histoire naturelle for internal funding, and Maarja Öpik for discussions. F.M.M. acknowledges the invaluable support of his MGI collaborators Drs Igor Grigoriev, David Hibbett, Annegret Kohler, Claude Murat, Emmanuelle Morin, and Kerrie Barry. F.M.M.’s laboratory is part of the Laboratory of Excellence ARBRE (ANR-11-LABX-0002-01). The three reviewers and the Editor Ian Dickie provided many helpful comments.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Relationship between the number of orchid species and the total number of novel fungal taxa associating with orchid roots.

Fig. S2 Ecosystem multifunctionality of an experimental plant community grown with AM fungi (AMF) or without AM fungi (NM).

Table S1 Selected studies used to calculate the relationship between number of orchid species and number of novel fungal taxa depicted in Fig. S1

Table S2 Influence of mycorrhizal associations on various ecosystem processes

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