Fungal Ecology xxx (2016) 1–10

Contents lists available at ScienceDirect

Fungal Ecology

journal homepage: www.elsevier.com/locate/funeco

Ericoid fungal diversity: Challenges and opportunities for mycorrhizal research

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ARTICLE INFO

Article history:
Received 21 January 2016
Received in revised form
27 June 2016
Accepted 8 July 2016
Available online xxx

Corresponding Editor: Maarja Öpik

Keywords:
Biogeography
Community assembly
Diversity
Ericaceae
Ericoid mycorrhiza
Mycorrhizal fungi
Mycorrhizal research
Plant-fungal symbioses

ABSTRACT

Ericoid mycorrhiza occur only within the plant family Ericaceae, yet are globally widespread and contribute to carbon and nutrient cycling in many habitats where harsh conditions limit decomposition and plant nutrient uptake. An increasingly diverse range of fungi are recognized as ericoid symbionts and patterns in the distribution of ericoid taxa are beginning to emerge across scales. However, the true diversity of ericoid mycorrhizal fungi remains unresolved due to limited sampling from some regions and challenges associated with delineating mycorrhizal taxa from the broader fungal community associated with ericoid plants. Interpreting patterns in the diversity and distributions of ericoid mycorrhizal fungi will ultimately require improved understanding of their functional ecology and functional diversity, which is currently limited to a few well studied species. Fortunately, many ericoid taxa are amenable to experimental manipulation and continued ericoid mycorrhizal research promises to improve general understanding of the ecology and evolution of mycorrhizal symbioses.

1. Introduction

Mycorrhizal fungi colonize the roots of most terrestrial plant species, enhancing nutrient uptake in exchange for photosynthetically derived sugars and making them key drivers of carbon and nutrient cycling in many ecosystems (van der Heijden et al., 2008). In the plant family Ericaceae, the extra-fine terminal roots of most species, which lack root hairs and are known as hair-roots, are colonized by fungi that form ericoid mycorrhiza (ErM; Smith and Read, 2008). An ErM, which includes both the plant and fungal components of the symbiotic complex, is a morphologically distinct mycorrhiza characterized by the formation of compact intracellular hyphal coils in enlarged epidermal hair-root cells which function as the sites of nutrient exchange (for detailed ErM morphology see, Bonfante-Fasolo and Gianinazzi-Pearson, 1979; Read, 1983). Although ErM plants account for just 1% of angiosperm species (Brundrett, 2009), they have a nearly global distribution and are often abundant in habitats with harsh edaphic conditions, primarily where acidic soils, low temperatures or low soil moisture limit the uptake of soil nutrients by plants and slow the degradation of organic matter (Read, 1991; Cairney and Meharg, 2003; Mitchell and Gibson, 2006). ErM are particularly abundant in heathlands and the boreal forest understory, habitats which account for approximately 70% of the terrestrial surface of the Northern Hemisphere (Read et al., 2004). The proliferation of ericaceous plants in these environments has been attributed to symbiosis with ErM fungi (ErMF), which help to detoxify acidic soil conditions and provide access to recalcitrant organic nutrient pools (Näsholm et al., 1998; Read et al., 2004). However, ErMF remain understudied relative to the more common mycorrhizal types, arbuscular and ectomycorrhizae (AM and ECM, respectively), and definitive data on the mycorrhizal status and functional roles of many taxa associated with ErM roots are lacking.

Based primarily on studies of Northern Hemisphere heathlands, ErM were historically viewed as a highly specialized symbiosis, including only a narrow range of plants and fungi (Harley and Smith, 1983; Straker, 1996). The proliferation of culture-independent molecular methods (Perotto et al., 1996; Allen et al., 2003) and the increasing availability of globally-distributed data (Bruzone et al., 2015) have challenged these early views. While ErM plants remain phylogenetically constrained to the family Ericaceae,

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http://dx.doi.org/10.1016/j.funeco.2016.07.004
1754-5048/

an increasingly diverse range of fungi are recognized as forming ErM (but see Lehnert et al., 2009 and Okuda et al., 2011 for descriptions of symbioses resembling ErM in the Diapensiaceae and neotropical ferns, respectively). Furthermore, the identification of ErM associated fungi from contrasting environments and across environmental gradients has revealed patterns in fungal community composition (e.g., Bougoure et al., 2007; Gorzelak et al., 2012), though the factors driving these patterns are not yet well understood. Molecular methods have also revealed a diverse assemblage of other fungal symbionts within ErM roots, including dark-septate endophytes (DSE), ECM fungi and saprotrophs (e.g., Bougoure et al., 2007; Walker et al., 2011). New evidence that some DSE and ECM fungi can form hyphal coils resembling ErM in ericaceous plants (Villarreal-Ruiz et al., 2012; Lukešová et al., 2015), and reports of novel taxa forming ErM in resynthesis trials (Vohník et al., 2012), have begun to blur the distinctions between these classifications, raising new questions about the functional relationships amongst a broad range of fungi found in ErM roots. Greater focus on the functional diversity among putative ErMF, along with the abiotic and biotic factors that influence the structure and function of ErM associated fungal communities as a whole, is needed to advance understanding of the ErM symbiosis.

While uncertainty surrounding the phylogenetic and functional diversity of ErMF presents a clear challenge to ErM research, several features of the symbiosis are well-suited for manipulative experimentation. Most notably, many fungi associated with ErM roots are highly saprophytic and, as a result, many potentially mycorrhizal taxa can be readily isolated and maintained in pure culture (Leake and Read, 1991). Although culture collections such as this are known to bias against some taxa (Allen et al., 2003; Bougoure and Cairney, 2005a), the ability to consistently and relatively quickly obtain pure-culture collections of potentially mycorrhizal fungi lies in stark contrast to AM fungi, which can only be cultured *in planta*, or ECM fungi, which are often difficult to isolate in pure culture (Hobbie et al., 2001). One factor that may have slowed progress in ErM research is the fact that many ericaceous plants grow slowly or are difficult to propagate. Fortunately, some species such as *Calluna vulgaris* and many *Vaccinium* spp., have proven to function as broadly compatible ErM host plants, amenable to axenic culture for experimentation (e.g., Villarreal-Ruiz et al., 2012) and some *Rhododendron* and *Gaultheria* species have also been used to establish *in vitro* plant-fungal co-cultures (Xiao and Berch, 1999; Grunewaldt-Stöcker et al., 2013). The potential to obtain culture collections of ErMF from contrasting environments or plant hosts and experimentally manipulate ErM under controlled conditions represents a largely untapped resource for mycorrhizal research and has the potential to advance both our understanding of the ErM symbiosis and mycorrhizal symbioses more broadly. However, to realize this potential for ErM research, a more complete understanding of the species and functional diversity of ErMF is needed.

Conclusive determination of the mycorrhizal status of a fungus is complicated by the fact that mycorrhizal symbioses exist along a continuum of mutualistic to parasitic interactions and outcomes for either partner can vary with the abiotic and biotic environment (Johnson et al., 1997). Brundrett (2004) recognized this functional variability and suggested an inclusive definition of mycorrhizae that requires experimental evidence of both the formation of a specialized symbiotic interface resulting from synchronized plant-fungal development (i.e., ericoid hyphal coils) and direct plant-fungal resource exchange, without stipulating a net benefit to either partner (Brundrett, 2004); however, evidence for the latter is lacking for many ErM associated fungi (Leake and Read, 1991). Given the uncertainty surrounding the range of taxa capable of forming ErM, this review will distinguish between those fungi that have been experimentally determined to form functional ErM (*sensu* Brundrett, 2004) and those for which only limited or circumstantial evidence is currently available. In addition, the broader community of fungi associated with ErM roots, including ErMF and taxa with uncertain mycorrhizal status, will be referred to as ErM associated fungi. To facilitate continuing advances in ErM research, this review has three primary goals: (1) Assess the current state of knowledge on ErMF diversity and the unique challenges associated with delineating ErMF from the broader community of ErM associated fungi. (2) Identify emerging biogeographic patterns for ErMF across global, regional and local scales. (3) Identify focal areas for future ErM research and research opportunities where continued study of ErM may enhance general understanding of the ecology and evolution of mycorrhizal symbioses.

2. Diversity of ericoid mycorrhizal fungi

A broad range of potentially mycorrhizal ascomycetous and basidiomycetous fungi are often identified in ErM roots using both culture-based and culture-independent molecular methods. However, mycorrhizal status has only been experimentally confirmed for a few species, making the definitive identification of ErMF from among the broader community of ErM associated fungi challenging. Unlike AM fungi (Glomeromycota), ErMF are not monophyletic (Smith and Read, 2008), precluding a simple phylogenetic prescription. In addition, many putative ErMF occur within lineages that encompass functionally diverse groups of plant and soil associated fungi, limiting the ability to infer mycorrhizal status from phylogenetic information alone. Furthermore, unlike ECM, in which individual root tips are typically colonized by a single mycorrhizal species (Smith and Read, 2008), ErM roots are characterized by multiple occupancy, with multiple putative mycorrhizal taxa occurring in close proximity (Setaro et al., 2006; Perotto et al., 2012). Even the proper identification of ericoid hyphal coils within roots requires careful attention to detail due to the common presence of non-mycorrhizal endophytes which can form intracellular structures, such as loose hyphal coils or sclerotia, that could be mistaken for ErM (Usuki and Narisawa, 2005; Lukešová et al., 2015). Following the basic principals of Koch's postulates, mycorrhizal resynthesis experiments, in which individual fungi are isolated and reinoculated onto axenic host plants, are the primary method used for determining the mycorrhizal status of fungi associated with ErM roots (Leake and Read, 1991). However, the recalcitrance of some putative ErMF to pure culture techniques requires alternative approaches (Setaro et al., 2006; Selosse et al., 2007).

Among ascomycetous ErMF, *Rhizoscyphus ericae* (formerly *Hymenoscyphus ericae* and *Pezizella ericae;* Read, 1974; Zhang and Zhuang, 2004) was the earliest to be identified and experimentally confirmed to be mycorrhizal (Pearson and Read, 1973; Stribley and Read, 1974). With the advancement of molecular and phylogenetic methods, many additional sterile isolates from ErM roots that could not be classified morphologically were recognized as being closely related to *R. ericae*, forming a species complex known as the *R. ericae* aggregate (REA; Vrålstad et al., 2000, 2002). Hambleton and Sigler (2005) further refined the REA which now includes the ErMF species *Meliniomyces variabilis*, which has also been experimentally shown to exchange C and N with host plants (Grelet et al., 2009a), along with the ECM species *Meliniomyces bicolor* and *Cadophora finlandica*, and numerous other related mycorrhizal species and non-mycorrhizal endophytes. Experimentation with ErM associated REA species other than *R. ericae* and *M. variabilis* has largely focused on the formation of ericoid hyphal coils *in vitro* and a greater effort to understand the functional variability among these species is needed to fully understand the extent of functional ErM formation in this species aggregate.

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Although early work focused on *R. ericae* as the sole ErMF, a second group of ascomycetous species isolated from ErM roots and identified as members of the genus *Oidiodendron*, were eventually shown to form ericoid hyphal coils in resynthesis experiments (Couture et al., 1983; Dalpé, 1986). Although later molecular approaches identified some phylogenetic variability amongst ErM associated *Oidiodendron* isolates, most appear to be very closely related to *Oidiodendron maius* and may or may not represent distinct species (Lacourt et al., 2002). Research on the functional aspects of ErM formation by *O. maius* has largely focused on the role of the mycobiont in improving heavy metal tolerance in the host (Daghino et al., 2015), though some investigations into enhanced host nutrient uptake have helped confirm the mycorrhizal status of this species (Xiao and Berch, 1999; Vohník et al., 2005). *O. maius* conspecifics and related species have also been isolated from soils and ECM roots, suggesting that this species is not restricted to association with ErM plants (Bergero et al., 2000; Rice and Currah, 2006).

There are many reports of other ascomycetous fungi that can form hyphal coils with ErM plants in resynthesis trials. Three helotialean isolates that could not be resolved between the families Dermateaceae or Hyaloscyphaceae were shown by Grelet et al., (2009b) to form ericoid hyphal coils and exchange C and N with *Vaccinium* spp. *in vitro*, demonstrating that at least some non-REA Helotiales can form functional ErM. In the genus *Leohumicola*, several isolates were shown by Grunewaldt-Stöcker et al. (2013) and Bizabani (2015) to form ericoid hyphal coils and repress the growth of oomycete root-rot pathogens, though evidence for nutrient exchange was not reported. Isolates with affinity to the genus *Capronia* have also been reported to form ericoid hyphal coils in resynthesis experiments (Allen et al., 2003). Although no functional data is currently available for *Capronia*-like species, the observation that similar taxa are often observed as significant components of sequencing based surveys of ErM associated fungal communities (Walker et al., 2011; Wurzburger et al., 2012; Lukešová et al., 2015) has led many ErM researchers to consider these taxa putative ErMF. Other ascomycetous fungi reported to form hyphal coils resembling ErM in resynthesis experiments with ericaceous plants include *Acremonium strictum* (Xiao and Berch, 1996; Monreal et al., 1999), *Geomyces pannorum* (Vohník et al., 2007), members of the *Phialocephala–Acephala* complex (Walker et al., 2011; Lukešová et al., 2015) and isolates with affinities to the genera *Cadophora* (Monreal et al., 1999; Bizabani and Dames, 2015), *Cryptosporiopsis* (Chambers et al., 2008; Walker et al., 2011; Bizabani, 2015) and *Lachnum* (Walker et al., 2011). The mycorrhizal status of these associations remain questionable and many reports of *in vitro* associations resembling ErM are likely to be the result of opportunistic colonization by non-mycorrhizal species that primarily function as endophytes, necrotrophs or root-associated saprotrophs. However, it is also possible that some of these associations represent nascent mycorrhizal symbioses and further study of their potential functional significance and the conditions under which they occur is warranted. In addition, both culture-based and culture-independent survey methods regularly yield poorly resolved taxa that match closely with other unidentified ascomycetous fungi associated with ErM roots (e.g., Bougoure et al., 2007; Zhang et al., 2009). This suggests that an even broader range of ascomycetous fungi, some of which may be difficult or impossible to culture, may have potential to form ErM.

The presence of basidiomycetous fungi in ErM roots was recognized in some of the earliest ErM research using morphological characteristics of intracellular hyphae (Bonfante-Fasolo, 1980; Peterson et al., 1980). However, the inability to successfully culture any basidiomycetes from ErM roots initially prevented their identification. Based on observations of basidiocarps associated with ErM plants and subsequent immunofluorescent staining of colonized roots, a *Clavulina* sp. was the first basidiomycete suspected of forming ErM (Seviour et al., 1973). Englander and Hull (1980) later provided evidence for bi-directional transfer of isotopically labeled C and P between naturally occurring ericaceous plants and *Clavulina* sp. fruiting bodies, but they were unable to conclusively determine if the symbiosis was mycorrhizal or represented some other saprotrophic or necrotrophic association. Molecular methods eventually revealed that species in the order Sebacinales are common inhabitants of ErM roots, sometimes as the dominant taxa in sequencing based community profiles (Berch et al., 2002; Allen et al., 2003). Ultrastructural observations further support the formation of ErM by Sebacinales, which can be distinguished by their electron-opaque cell walls and dolipore septa with imperforate parenthesomes, while ascomycetes have electron-translucent cell walls and simple septal pores with Woronin bodies (Setaro et al., 2006). Selosse et al. (2007) combined targeted molecular methods and ultrastructural observations to show that Sebacinales in the family Serendipitaceae *nom. prov* (formerly Sebacinales Clade B; Weiß et al., 2016) form ericoid hyphal coils in many ericoid plants and these taxa are now widely regarded as putative ErMF. However, these enigmatic species have not yet been successfully isolated in pure culture, complicating experimental confirmation of their mycorrhizal status and limiting understanding of their functional significance.

Recently, a basidiomycetous species with affinity to the Trechisporales was cultured and identified by Vohník et al. (2012) as a co-dominant symbiont of some *Vaccinium* spp. in Norway. In resynthesis experiments these isolates were shown to form intracellular structures with a unique morphology that the authors described as a “sheathed-ericoid” mycorrhiza. Although conclusive evidence of resource exchange was not provided, the isolates did enhance plant growth *in vitro* and, combined with strong circumstantial evidence for ErMF in the Sebacinales, this finding has dramatically broadened the phylogenetic range of putative ErMF.

There is accumulating evidence that some ErMF colonize non-ericaceous hosts and some fungi typically classified as ECM or DSE may also be capable of forming ErM, blurring the distinction between these functional classifications (Vrålstad, 2004; Zijlstra et al., 2005; Grelet et al., 2010; Vohník and Albrechtová, 2011; Vohník et al., 2013). Villarreal-Ruiz et al. (2004) were the first to conclusively show that a REA isolate collected from an ECM host, *Pinus sylvestris*, could simultaneously form ECM in an ectotrophic host and ericoid hyphal coils in an ericaceous host. Grelet, Johnson, et al. (2009) later demonstrated that the ECM species *M. bicolor* could form functional ErM with *Vaccinium vitis-idaea* roots, exchanging C and N with ErM plants. Similarly, Villarreal-Ruiz et al. (2012) found that *Laccaria bicolor*, a basidiomycetous ECM species, extensively colonized multiple ErM plants *in vitro*, forming hyphal coils that resembled typical ErM. Among species commonly identified as DSE, numerous species belonging to the *Phialocephala–Acephala* species complex (Lukešová et al., 2015) along with *Heteroconium chaetospira* (Usuki and Narisawa, 2005) were also experimentally shown to colonize ErM plants, forming intracellular structures resembling ericoid hyphal coils, though the functional significance of these structures are unclear.

It is clear from the diversity of confirmed and possible ErMF, and the recent discovery of novel putative ErMF lineages, that the true diversity of ErMF has not yet been circumscribed (Fig. 1). Renewed focus on resynthesis experiments that include tests for bi-directional nutrient transfer is needed to clarify the mycorrhizal status of many fungi capable of forming hyphal coils in ericaceous plants. For unculturable taxa, this may ultimately require methods such as laser microdisection (Gomez and Harrison, 2009), stable isotope probing (DNA-SIP; Dumont and Murrell, 2005), or taxon

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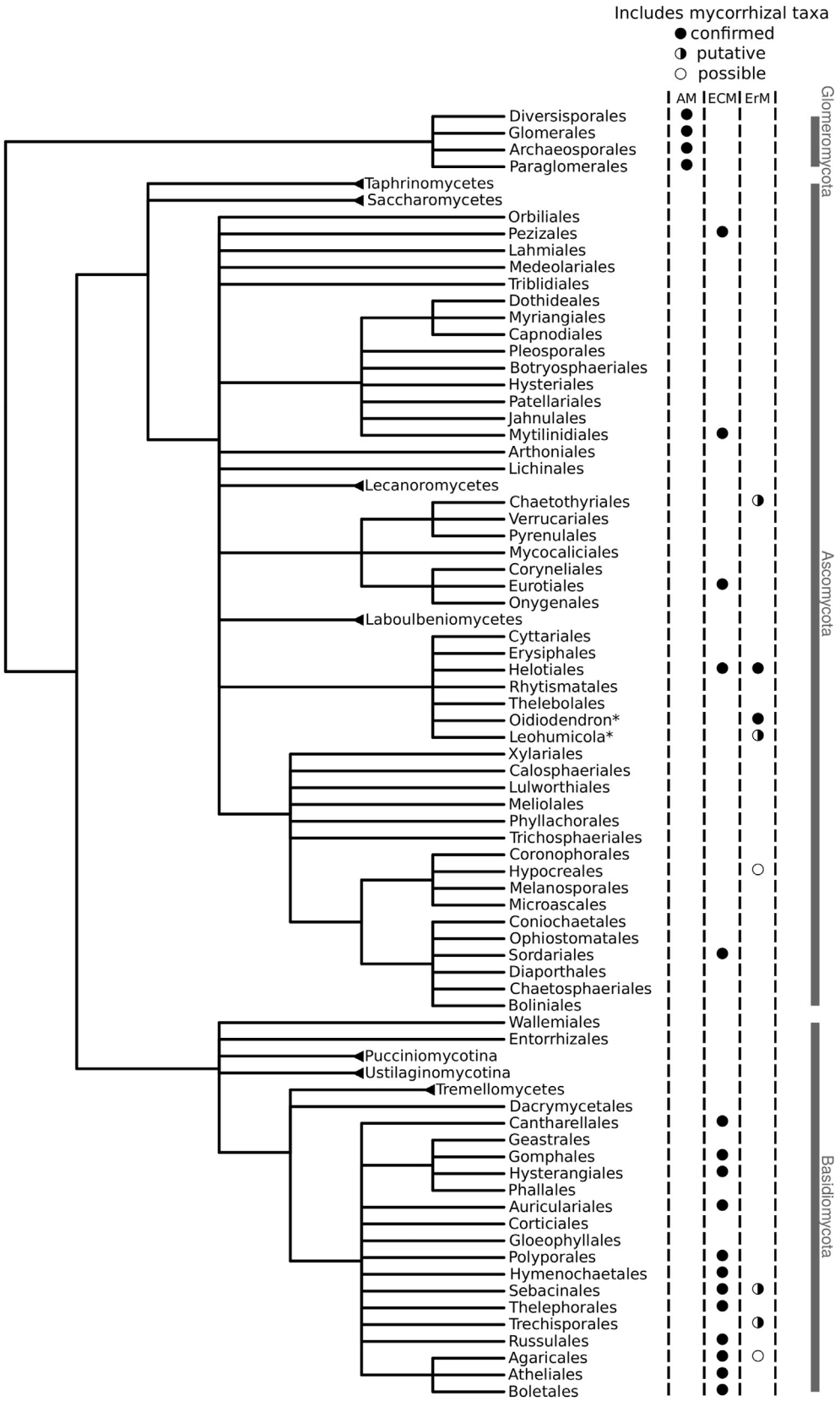

Fig. 1. Distribution of mycorrhizal taxa across a subset of the Fungal Tree of Life (McLaughlin et al., 2009) including phyla Glomeromycota, Ascomycota and Basidiomycota at the order level. Branches with no known or suspected mycorrhizal taxa are collapsed to class (suffix -mycota) or sub-phyla (suffix -mycotina). Filled circles aligned with fungal orders indicate at least one species is known to form arbuscular mycorrhiza (AM; Schüßler et al., 2001) or ectomycorrhiza (ECM; Tedersoo and Smith, 2013). For ericoid mycorrhiza (ErM), fungal orders are identified based on the highest level of confidence in mycorrhizal status available for lower level taxa. Confirmed mycorrhizal taxa have direct experimental evidence of *in vitro* resynthesis of ericoid hyphal coils and plant-fungal nutrient exchange. Putative mycorrhizal taxa have multiple lines of circumstantial evidence indicating mycorrhizal status, but lack conclusive experimental evidence of resource exchange. Possible mycorrhizal taxa have only been shown to form hyphal coils in ericaceous plants *in vitro*, which may be the result of opportunistic colonization by non-mycorrhizal species. *The genera *Oidiodendron* and *Leohumicola* are *incerti ordini* and are included here because they contain known and putative ErM fungi, respectively.

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specific fluorescent *in situ* hybridization coupled with nano-scale secondary ion mass spectrometry (FISH-NanoSIMS; Behrens et al., 2008). It is likely that the formation of hyphal coils in ErM roots by some fungi simply represents opportunistic colonization without the formation of true mycorrhizal symbioses, however, it is also possible that the functional classifications of these associations vary with environmental conditions or host ontogeny (Brundrett, 2004), forming ecologically significant mycorrhizal symbioses only under particular conditions (Moeller and Neubert, 2016). Ultimately, the mycorrhizal status of some ErM associated fungi may remain ambiguous, underscoring both the lack of a sharp distinction between functional classifications and the general difficulties associated with any functional definition of a mycorrhiza (Jones and Smith, 2004). However, as a more comprehensive understanding of ErMF ecology and diversity begins to emerge, it may become easier to confidently assign mycorrhizal status to some ErM associated species without direct experimental evidence, an accepted practice for some ECM fungi (Tedersoo and Smith, 2013).

3. Biogeography of ericoid mycorrhizal fungi

Limited sampling of ErM from many regions relative to the geographic distribution of ericaceous plants currently precludes conclusive identification of global biogeographical patterns of ErM mycobiont community composition. The lack of data from much of the Southern Hemisphere is particularly striking considering that diversity hot spots for the Ericaceae include the South African fynbos, montane regions in the Neotropics and Papua New Guinea (Oliver, 2000; Luteyn, 2002; Bruzone et al., 2015). Some early studies of ErMF from South Africa suggested that ErM associated fungi in the fynbos are predominantly ascomycetes, including *Oidiodendron* spp. and Helotiales, but not *R. ericae* conspecifics (Straker, 1996). Bizabani (2015) recently confirmed these findings, using both molecular and culture-based approaches which revealed *Meliniomyces*, *Phialocephala*, *Cadophora*, *Cryptosporiopsis*, *O. maius*, and Chaetothyriales, but not *R. ericae*. In South America, Bruzone et al. (2015) recently reported for the first time on the identities of fungi associated with two species of *Gaultheria* from NW Patagonia, expanding the geographic range of data available for the Southern Hemisphere. Using culture-independent methods they found that Sebacinales were the dominant members of ErM associated fungal communities, though culturable isolates included primarily non-REA Helotiales, Hypocreales and *O. maius*. One notable exception to the dearth of data from the Southern Hemisphere is Australia, where fungi associated with a variety of endemic ericaceous genera have been investigated, revealing diverse assemblages of ascomycetous fungi, primarily groups of helotialean species outside of the REA and some *O. maius* related species (McLean et al., 1999; Chambers et al., 2000; Cairney and Ashford, 2002; Midgley et al., 2004; Bougoure and Cairney, 2005a,b; Curlevski et al., 2009).

There is considerably more data available for the Northern Hemisphere and global geographic patterns are beginning to emerge for some ErMF. For example, Sebacinales have been increasingly identified as dominant components of ErM associated fungal communities in North America and the Neotropics (Berch et al., 2002; Allen et al., 2003; Kottke et al., 2008; Bruzone et al., 2015). Setaro and Kron (2011) reported close phylogenetic relationships among ErM associated Sebacinales across this range, leading them to suggest a history of concerted migration. In contrast, members of the REA, including *R. ericae* and *M. variabilis*, are dominant ErMF across many boreal and subarctic habitats and much of temperate Eurasia (Grelet et al., 2010; Ishida and Nordin, 2010; Kjøller et al., 2010; Gorzelak et al., 2012). *O. maius*, on the other hand, appears to be a cosmopolitan species, having been detected in studies that span the globe (e.g., Australia, Bougoure and Cairney, 2005a; South Africa, Bizabani, 2015; China, Zhang et al., 2009; USA, Wurzburger et al., 2012), though rarely as the dominant mycobiont at any given site. There are also many other groups of poorly understood, possible ErMF which can be locally dominant in sequencing based surveys, such as undescribed members of the Chaetothyriales or Helotiales (Lukešová et al., 2015), and much more data is needed before a comprehensive picture of the global biogeography of ErMF can emerge.

Despite the fact that dispersal mechanisms remain largely unknown for most ErMF due to the cryptic nature of their reproductive strategies, there is some evidence for broad dispersal limitation in ErMF communities (Hutton et al., 1997). However, other factors, such as abiotic filtering or historical contingency (i.e., priority effects), are also likely to have influenced global distribution patterns. The global distribution of *R. ericeae*, for example, appears to exclude Southern Hemisphere Ericaceae, yet *R. ericeae* isolates capable of forming ErM in laboratory trials have been isolated from a leafy liverwort present on a number of sub-Antarctic islands (Upson et al., 2007). This suggests that factors other than dispersal limitation have shaped the global biogeography of this species.

It is possible that differential global distribution patterns among ErMF have arisen as a result of differential traits among fungal taxa. For example, the cosmopolitan species *O. maius* can occur as a free-living saprotroph in soil (Rice and Currah, 2006), potentially allowing it to disperse widely and independently of ErM plants. Some ErMF in the REA are known to colonize the roots of ECM trees (Grelet et al., 2010; Vohník et al., 2013), which are dominant plants in the boreal forest, giving REA species multiple niches and potentially contributing to their abundance in this habitat. In contrast, putative ErMF in the Sebacinales have not been observed to colonize co-occurring non-ericaceous plants, even when closely related fungi occur as endophytes or other mycorrhizal types (Kottke et al., 2008; Garnica et al., 2016). In addition, all attempts to culture ErM associated Sebacinales have failed thus far, further suggesting that at least some of these species may be obligate ErM symbionts, restricted to migration with suitable ericaceous plants (Setaro and Kron, 2011). However, related orchid mycorrhizal Sebacinales, also in the family Serendipitaceae, which have been successfully cultured, appear to be phylogenetically interspersed with ErM forming lineages (Weiß et al., 2016), and much more study is need to properly characterize the ecological distinctions among these taxa.

At the regional scale, environmental gradients have been used to explore the factors influencing the community composition of ErM associated fungi. Gorzelak et al. (2012) found that fungal communities associated with *Vaccinium membranaceum* changed across an elevation gradient; dominant culturable fungi shifted from *Phialocephala fortinii* to *R. ericae* with increasing elevation. Bougoure et al. (2007) examined the fungal community associated with *Vaccinium myrtillus* across a vegetation gradient and found distinct communities of putative ErMF in heathland, forest understory and the joining ecotone. These transitions may reflect both a response to abiotic factors and interactions with co-occurring non-ErM vegetation, which may host some ErMF as endophytes or ECM (Zijlstra et al., 2005; Grelet et al., 2010; Vohník et al., 2013). Hazard et al. (2014) identified soil nitrogen as explaining more than 50% of the variation in ErM associated fungal communities sampled across sites with varying land use history in Ireland. However, experimental nitrogen additions in boreal forest plots by Ishida and Nordin (2010) did not alter the community composition of ErM associated fungi. This latter result is surprising given the role of ErMF in facilitating nitrogen uptake in ericaceous plants (Read 1996) and the fact that nitrogen additions are known to impact the community composition of other types of mycorrhizal fungi

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(Lilleskov et al., 2001; Treseder, 2004).

At the local scale, there is also evidence that both abiotic and biotic factors influence the fine scale structure of ErM associated fungal communities. Within individual plants, Wurzburger et al. (2012) found that many putative ErMF were differentially abundant between organic and mineral soil horizons, and that roots from the organic horizon had significantly greater fungal diversity. Gorzelak et al. (2012) used co-occurrence analysis to show that fungi associated with *V. membranaceum* tended to co-occur more often than expected by chance, suggesting that facilitation may influence ErMF community composition. Evidence for plant-fungal partner specificity in ErMF community composition is currently mixed. Kjøller et al. (2010) found that fungal communities associated with four ErM plants in a subarctic mire were spatially structured at scales of just a few meters, yet were indistinguishable among plants co-occurring in small hummocks. Similarly, Walker et al. (2011) found no difference in fungal communities associating with three ErM plants in the Arctic tundra. However, Bougoure et al. (2007) detected differences in fungal communities associated with two co-occurring ErM plants in a Scots pine understory, but was unable to determine if this was a result of host micro-habitat preference. There is also some evidence that intraspecific partner specificity can influence the composition of ErM associated fungal communities. Sun et al. (2012) reported a correlation between the community composition of putative ErMF and intraspecific genetic variation in *Rhododendron decorum*. Midgley et al. (2004) found that different genotypes of a single putative ErMF species were segregated among two co-occurring ericaceous plants in an Australian dry sclerophyll forest. These contrasting results suggest that host specificity may be relatively weak and context dependent in ericaceous plant-fungal networks. It is likely that fine scale variation in ErMF community composition is linked to both the compositional and functional diversity of the local fungal community and the degree to which host distributions are correlated with fine scale variation in soil conditions, such as organic matter content.

The available data are only beginning to elucidate the factors driving ErMF community composition across scales. Recent analyses of large molecular barcoding databases for AM and ECM fungi have revealed patterns of high and low endemism, respectively, at a global scale (Davison et al., 2015; Tedersoo et al., 2012). The emerging patterns for some ErMF discussed above suggest that the global biogeography of ErMF may be similar to ECM fungi, with patterns of endemism revealed at large spatial scales. This is not surprising considering the phylogenetic overlap between ErMF and ECM fungi. Because ErM are common in boreal and heathland ecosystems, playing a role in regulating some of the largest terrestrial carbon stocks, a better understanding of how ErMF community composition is linked to environmental conditions could be important for predicting how these ecosystems will respond to anthropogenic global change factors and influence climate change predictions (Olsrud et al., 2004; Clemmensen et al., 2013, 2015). However, detailed understanding of the functional ecology of ErMF is almost entirely limited to studies of *R. ericae* and *O. maius*. Unraveling the drivers of ErMF community composition across scales will ultimately require a greater focus on manipulative experiments and diverse mycobiont communities, which have been largely lacking from ErM research and are needed to provide causal explanations for observed patterns.

4. Research opportunities for ericoid mycorrhizal systems

In a recent review, Perotto et al. (2012) identified *O. maius* as having significant potential as a model organism for studying the molecular basis of mycorrhizal symbioses; *O. maius* readily grows and reproduces asexually in culture, producing uninucleated conidia that germinate to produce haploid mycelium in which all nuclei will carry the same mutation. Abbà et al. (2009) took advantage of these features and used *Agrobacterium*-mediated transformation to disrupt the superoxide dismutase gene in *O. maius*, resulting in the first targeted knock-down of a fungal gene involved in the establishment of mycorrhizal symbiosis. Advances in understanding the molecular bases of heavy metal tolerance in *O. maius* (Di Vietro et al., 2014; Khouja et al., 2015; Khouja et al. 2013; Chiapello et al., 2015), a trait linked to the success of ErM host plants in otherwise inhospitable environments (Cairney and Meharg, 2003), has also focused attention on this species as a model organism (Daghino et al., 2015). Additionally, the complete *O. maius* genome was recently published (Kohler et al., 2015), setting the stage for continuing advances using *O. maius* as a model mycorrhizal fungus. While the study of plant-fungal interactions in mycorrhizal symbioses occurs across scales, from genes and molecular interactions to communities and ecosystems, the potential for ErM symbioses and the broader community of ErM associated fungi to serve as model study systems in a variety of contexts has been largely ignored. The remainder of this review will explore research areas in which ErMF and ErM associated fungal communities could provide particularly well-suited study systems to advance the understanding of the ecology and evolution of mycorrhizal symbioses.

4.1. Community assembly

Research on mycorrhizal fungi has generally focused on the function of individual fungi and the composition and function of mycobiont communities, with less attention given to processes that influence the local assembly of the mycobiont community itself. In a recent analysis of AM fungal communities at scales ranging from individual plants to global, Davison et al. (2016) found evidence of phylogenetic clustering that increased with spatial extent and habitat heterogeneity, suggesting that processes related to dispersal, host preference and environmental filtering were general drivers of assembly. However, experimental work is needed to understand the conditions under which individual factors are more or less important for assembly processes. For example, Johnson (2015) recently identified the effect of species' arrival timing, or priority effects, as an area needing further research. Some experimental work on priority effects in AM and ECM fungi indicates that these historical effects can be important factors influencing the community assembly of mycorrhizal fungi (Kennedy et al., 2009; Werner and Kiers 2015), but the conditions under which priority effects are important and the functional consequences for interacting plant and fungal species are largely unknown. There is also increasing interest in understanding how the composition of regional species pools can influence local community assembly processes (Cornell and Harrison, 2014; Pärtel et al., 2016), a topic that is virtually unexplored in microbial symbiont communities. Local factors that influence the assembly of mycorrhizal fungi, such as competitive or facilitative interactions between symbionts, also require further study, particularly in the case of ErM (Thonar et al., 2014).

Many unique features of the biology and morphology of the ErM symbiosis are well-suited for the study of symbiont community assembly processes. First, ErMF tend to colonize only the outermost epidermal root cells of ericaceous hair-roots by entering from the root surface, with little cell-to-cell hyphal penetration (Massicotte et al., 2005). This suggests that colonized cells can be considered individual units, each challenged and potentially colonized by a variety of fungi present in the rhizosphere (Perotto et al., 2012). As a result, multiple species, or even genotypes of the same species can occupy an individual ericoid root in close proximity (Midgley et al.,

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2004). Second, the broader community of ErM associated fungi interacting with an individual plant can be extremely diverse (e.g., Bougoure et al., 2007) and many of these symbionts can be isolated in pure culture. Finally, numerous methods have been described for establishing ErMF in microcosms using axenic seedlings and individual fungal isolates (Vohník et al., 2012). By extending these methods to include pairs or entire communities of ErM associated fungi, and tracking community assembly outcomes using molecular methods (e.g., Sikes et al., 2016), many aspects of community assembly in mycorrhizal symbiont communities could be experimentally tested using ErM systems.

4.2. Local adaptation and co-evolution

Mycorrhizae have been implicated in the local adaptation of plants to their soil environment (Schultz and Miller, 2001; Johnson et al., 2010; Doubková et al., 2012), however many questions remain regarding the conditions under which different patterns of adaptation and co-adaptation occur in mycorrhizal symbioses. Because ErM plants are highly mycotrophic, relying on their fungal symbionts for nutrient uptake (Smith and Read, 2008), it can be expected that edaphic conditions are particularly important for the evolutionary trajectory of both plant and fungal traits related to the symbiotic exchange. There is also evidence that intraspecific variation exists in the production of extracellular enzymes and in the uptake of different forms of nutrients by ErM fungi. For example, Grelet et al. (2009b), reported differences in nitrogen use efficiency by three non-REA helotialean ErMF, including two with identical internal transcribed spacer regions, and further demonstrated that these differences affected *Vaccinium* host plants *in vitro*. While data on the functional diversity among the broader community of potential ErMF is sparse, the ability to easily isolate and culture distinct species and genotypes of putative ErMF from sites with contrasting edaphic conditions offers the opportunity to explore the functional diversity of ErMF in the context of the local adaptation of plant-fungal symbioses.

It is also possible that host benefits other than nutrient uptake play a role in the local adaptation of mycorrhizal symbioses. For example, colonization by mycorrhizal fungi is known to increase host resistance to pathogens (Newsham et al., 1995). Grunewaldt-Stöcker et al. (2013) recently demonstrated that some putative ErMF can protect plants from oomycete root rot pathogens *in vitro* and that the strength of protective benefits varied amongst isolates. Theory suggests that pathogen pressure should increase with nutrient availability while the benefit of nutritional symbionts should decrease (Thrall et al., 2007), suggesting that adaptation to higher nutrient availability could involve increased pathogen protection. Another benefit that can be conveyed to ericaceous plants by ErMF is protection against toxic compounds in soils, particularly heavy metals (Bradley et al., 1981; Sharples et al., 2000). By comparing ErMF from sites contaminated by industrial activity and neighboring uncontaminated sites, strains of both *R. ericae* and *O. maius* have been shown to develop adaptive resistance to a variety of heavy metals (Martino et al., 2000; Sharples et al., 2001; Vallino et al., 2011). However, while the mechanisms of adaptive heavy metal resistance are well documented in some ErMF, the potential for co-evolutionary response between symbiont and host requires further study (Vallino et al., 2011).

4.3. Evolution of plant-fungal symbioses

The ErM symbiosis is believed to be the youngest of the major mycorrhizal types, originating in the most recent common ancestor of the Ericaceae ~117 mya (Cullings, 1996; Schwery et al., 2015). While most plants in the family Ericaceae form ErM, the basal genus in the family, *Enkianthus*, associates with AM fungi (Glomeromycota), as do related families within the order Ericales (Obase et al., 2013). The mycorrhizal types arbutoid and monotropoid, are also recognized within the Ericaceae in the subfamilies Arbutoideae and Monotropoideae, respectively (Smith and Read, 2008). Arbutoideae and Monotropoideae symbionts include typical ECM fungi and root colonization shares some morphological characteristics with both ErM and ECM. The basal position of *Enkianthus* within the Ericaceae suggests that association with AM fungi is the ancestral mycorrhizal state from which the other mycorrhizal associations evolved (Obase et al., 2013). Furthermore, *Enkianthus* also harbors typical ErM taxa as endophytes without forming ErM (Obase and Matsuda, 2014), presenting an opportunity to study the role of host evolution in the establishment of mycorrhizal symbioses during diversification with a single plant lineage. Through the use of comparative genomics and transcriptomics, it should be possible to identify genes associated with distinct mycorrhizal types and track the evolution of those genes through ancestral state reconstruction across the Ericaceae. In addition, there are some reports of other ericaceous species concurrently forming both ErM and AM (Koske et al., 1990; Urcelay, 2002). These species could hold clues to the evolutionary process of transition between mycorrhizal types, however, the functional significance of these dual associations, which may simply represent opportunistic colonization by AM fungi predominantly associated with neighboring hosts, and the extent of the phenomenon within the Ericaceae remain unexplored.

5. Conclusions

Given their global distribution and prominent role in carbon and nutrient cycling in some of the largest terrestrial biomes, ErM symbioses remain understudied relative to other mycorrhizal types. New evidence has dramatically expanded the phylogenetic range of fungi known to form ErM and has blurred the distinction between ErMF and other co-existing fungal symbionts. Continued efforts to elucidate the factors influencing ErMF community composition using molecular methods will require a more comprehensive documentation of ErM fungal diversity, which can only be achieved through continued sampling of understudied regions and resynthesis experiments that include tests for nutrient exchange. While the lack of functional data for most putative ErMF presents significant challenges to current ErM research, many ErM symbionts are amenable to isolation and laboratory culture, presenting opportunities for experimentation that could be exploited to advance understanding of the ecology and evolution of both ErM and mycorrhizal symbioses more broadly.

Acknowledgments

The author is supported by funding from Stanford University, Department of Biology. Thanks is due to Tadashi Fukami, Gwen Grelet, Christina R. Leopold, Maarja Öpik, Kabir G. Peay and two anonymous reviewers who all provided critical feedback and constructive comments that substantially helped improve this manuscript.

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