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Ericoid fungal diversity: Challenges and opportunities for mycorrhizal research

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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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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.