

COMMENTARY

Revisiting mycorrhizal dogmas: Are mycorrhizas really functioning as they are widely believed to do?

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Abstract Since the discovery of mycorrhizas, dogmas have been developed regarding their function, ecology, and distribution. We explore if these dogmas are valid, and if there are research biases toward regions inhabited by most researchers and away from regions inhabited by most plant species. We found, first, that the mycorrhizal status is known in less than 1% of plant species, with few having proven mycorrhizal benefits for growth and development. Second, the mycorrhizal status of a plant species varies within families, even genera. Third, mycorrhizas are important for phosphorus acquisition only within a narrow phosphorus range. Fourth, mycorrhizal plants are not uniform in their response to environment; taxonomy, phylogeny and continental history strongly drive mycorrhizal diversity. For example, the center of diversification of Ericaceae and Orchidaceae is in the neotropics, rather than, as recently claimed, in cold and high-latitude climates. Understanding the importance of mycorrhizas at the family-wide and biome-wide level is therefore conflicted by a research bias toward research-intensive regions outside the phylogenetic hotspots of diversification. The current precepts on mycorrhizas provide important starting points for hypotheses to robustly test when and where mycorrhizas play a role in determining ecological trajectory. The time has come to move forward and revisit past assumptions and update the dogmas, rather than assume functional significance in terms of nutritional benefits from studies on extraneous regions and species. We conclude that non-nutritional benefits deserve far greater attention.

1 Introduction

The term mycorrhiza was coined by Frank (1885), to describe the association of a fungus (μυκησ, mukès) and a root (ρίζα, rhiza). Mycorrhizas are symbiotic structures, and mycorrhizal fungi are symbiotic microorganisms that colonise plant roots, providing benefits primarily in exchange for carbon. This group of fungi has been extensively studied because of their perceived importance for crop and forest production and ecosystem functioning. Several subgroups of mycorrhizal fungi are recognized, depending on their phylogenetic placement, morphological association with plant roots, and taxonomy of their associated plant hosts. Since their first discovery, dogmas have been developed regarding their function, ecology, and distribution. The current dogma on mycorrhizal fungi, as expressed in recent reviews and textbooks, comprises four overarching claims (Smith and Read, 2008; Brundrett and Tedersoo, 2018; Tedersoo et al., 2020):

- 1) Most vascular plant species are mycorrhizal.
- 2) Being mycorrhizal or not is a taxonomic trait: plant families are typically mycorrhizal or not.
- 3) Mycorrhizal colonisation implies plant benefits in terms of enhanced phosphorus (P) uptake.
- 4) The ecology and distribution of mycorrhizal fungi depends on the mycorrhizal subgroup to which they belong.

These claims are widely accepted, but often not adequately tested empirically. We explore if these claims are experimentally validated, and if there is a strong bias toward regions

We dedicate this paper to Professor Sir David Read FRS, who has been instrumental in mycorrhizal research, especially in Orchidaceae and Ericaceae. He inspired many, often while enjoying the products that plants and microbes can provide, and continues to do so.

Received August 2, 2020; accepted October 30, 2020

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inhabited by most researchers and away from regions inhabited by most plant species. In scrutinising these four claims, we fully acknowledge that mycorrhizas have numerous non-nutritional benefits. We also focus on two major global plant groups (Ericaceae and Orchidaceae) from which these dogmas have been particularly pervasive.

2 The major claims

2.1 Most vascular plant species are mycorrhizal

It is generally accepted that 80%–90% of vascular plant species form some sort of mycorrhizal association. There are numerous reports on mycorrhizal structures in a vast number of plants (Wang and Qiu, 2006; Brundrett, 2009, 2017) that strongly support the claim that we can, indeed, consider most vascular plant species to be mycorrhizal. Studies such as these extrapolate to global patterns by evaluating the currently known mycorrhizal status of the species that have been tested. For example, Wang and Qiu (2006) evaluated the mycorrhizal status of 3617 plant species around the world, concluding that most plant species are indeed mycorrhizal. However, it is estimated that there are around 374 000 plant species in the world (Christenhusz and Byng, 2016), meaning we know the mycorrhizal status of less than 1% of all plant species. Hence, globally, the mycorrhizal status of most plant species remains unknown. It is likely that these estimations are correct, based on current knowledge, but, as explained below, extrapolations and assumptions of mycorrhizal status may be erroneous in the absence of clear experimental evidence of presence. This extends to the burgeoning number of large-scale molecular screenings of soils and plants for microbial presence where experimental evidence of functional importance is assumed. Such an approach leads to over-estimations of the diversity and abundance of microbial diversity in and on plant roots with cautionary notes such as “... ‘omics approaches’... have not been matched by increases in our understanding of the ecology of such communities or links between community composition, diversity and ecosystem function” (Prosser, 2013). We propose that, when studying mycorrhizal associations, mycorrhizal status should not be assumed; rather, easy checks such as root colonisation scoring should be carried out. When attempting to infer mycorrhizas to functional benefits, mycorrhizal presence must be corroborated with functional significance *in planta*, with demonstrated ecological benefit. Otherwise, our appetite for experimentation will dwindle, while descriptive, correlative activities such as sequencing continue to grow (Prosser, 2013). Only with appropriate corroboration will we have a grasp of the real role of mycorrhizas in driving diversification and plant persistence.

2.2 Mycorrhizal status is dependent on plant family

The mycorrhizal status of a plant species is often assumed based on the general trend of the plant family it belongs to. For example, one of the earliest and most studied of mycorrhizal

families, the Orchidaceae (Selosse et al., 2011), have well-known obligate symbionts, at least during germination, though not always persisting into the mature plant, particularly in epiphytic taxa (Rasmussen and Rasmussen, 2009). For these reasons, we will discuss this family in more detail below, in Section 4. The claim that mycorrhizal status is strongly determined by taxonomy is more controversial in arbuscular mycorrhizal and ectomycorrhizal plant families. For example, in the typically mycorrhizal Fabaceae, there are numerous non-mycorrhizal genera, e.g., *Lupinus* (Lambers et al., 2013), or species, e.g., *Daviesia cordata* and *D. decurrens* (Brundrett and Abbott, 1991) and *Kennedia coccinea* (Ryan et al., 2012). Likewise, within Cactaceae, there are many non-mycorrhizal species, with up to 10% of studied Cactaceae being non-mycorrhiza (Wang and Qiu, 2006). It is possible that this percentage may be even higher, as a recent study found another Cactaceae species, *Discocactus placentiformis*, being non-mycorrhizal (Abrahão et al., 2014). What many of the ‘exceptions’ that have been scrutinised have in common is that these ‘exceptional’ species have an alternative P-acquisition strategy that depends on the release of carboxylates, sometimes involving specialized structures such as cluster roots in *Lupinus* (Gardner et al., 1981) and *Daviesia* species (Nge et al., 2020; Brundrett and Abbott, 1991). Much of the research on ericoid mycorrhizas has been restricted to cold biomes in the northern hemisphere. From these, there is no strong evidence that Ericaceae acquire nutrients without involvement of ericoid mycorrhizas, but this is largely because very few species have been scrutinised and areas where they are most diverse have been largely ignored. We will discuss this family separately, therefore.

Within typical non-mycorrhizal families, there are exceptions of mycorrhizal species as well. For example, in the grassland community on serpentine soil in California two species from non-mycorrhizal families, *Arenaria douglasii* (Caryophyllaceae) and *Streptanthus glandulosus* (Brassicaceae) are mycorrhizal (Hopkins, 1987). Similarly, *Costularia comosa* in the Cyperaceae (Lagrange et al., 2011; Bourles et al., 2020), and *Hakea verrucosa* in the Proteaceae (Boulet and Lambers, 2005) form associations with arbuscular mycorrhizal fungi. Both of these species naturally occur in soils that are rich in nickel. Since some mycorrhizas intercept metals (Bethlenfalvay and Franson, 1989; Hashem, 1995; Canton et al., 2016), whereas carboxylates mobilise them (Gardner et al., 1982; Lambers et al., 2015), high concentrations of toxic metals are likely a driving force to associate with mycorrhizal symbionts in non-mycorrhizal families. This shows that environments where particular plant species within a family have evolved can be a strong driver of their mycorrhizal status. Therefore, assuming the mycorrhizal status of a species evolved in a nutrient-poor semiarid environment based on the status of a relative that evolved in cold and fertile environments may be erroneous. Tedersoo et al. (2020) recently proposed a genus-level classification of mycorrhizal status of plants. This is a step forward into updating the mycorrhizal dogmas and will improve understanding, particularly if broad species screenings across

biomes and climatic zones are undertaken.

2.3 Mycorrhizal fungi benefit P uptake

Numerous studies have shown that mycorrhizal fungi increase P uptake by plants (Smith and Read, 2008). Even when mycorrhizas provide no growth benefit, the mycorrhizal P-uptake pathway may well be very important for net P acquisition (Smith et al., 2003; Smith et al., 2011). Some have also shown that benefits are greater under lower nutrient availability (Bolan et al., 1987). However, there are also many studies that show that mycorrhizal fungi provide no growth or P benefit (Bethlenfalvay et al., 1982; Jacott et al., 2017), questioning the nature of their symbiosis (Johnson et al., 1997), and begging the question: does the presence of mycorrhizal fungi result in increased nutritional status? Many other studies have shown that mycorrhizas increase uptake of water (Marulanda et al., 2003; Poca et al., 2019), nitrogen (Bowen and Smith, 1981; Javelle et al., 2003), and micro-nutrients (Ferrol et al., 2016; Watts-Williams and Cavagnaro, 2018), provide competitive advantage via allelochemical interactions (Francis and Read, 1994; 1995), improve soil structure (Rillig and Mummey, 2006; Zhang et al., 2017), protect against metal toxicity (Ferrol et al., 2016; Shi et al., 2019) and defend against herbivorous insects (Hill et al., 2018; Kadam et al., 2020) and pathogens (Albornoz et al., 2017; Mustafa et al., 2017). In fact, recent studies have linked these “non-P” benefits of mycorrhizas during plant–soil feedback in structuring plant communities (Lambers et al., 2018). These studies have advanced our knowledge on the benefits of mycorrhizas beyond P uptake, which is a great step forward. This claim of the mycorrhizal dogma is arguably the one where most advancement has been made out of the four, clearly showing a gradual shift toward a more holistic view on the function of mycorrhizas. More studies on these benefits and their context-dependency require investigation. We do not argue that there are no benefits of the mycorrhizal symbiosis. Our tenet is that to appreciate those benefits, we have to look beyond the current dogma and not jump to conclusions based on limited and often unsupported experimental evidence.

There is a bias toward plant species that are of economic or ecological importance. Most crop species are nutrient demanding and may heavily rely on mycorrhizas if nutrient availability is relatively low (Wright et al., 2005; Jacott et al., 2017). Even when mycorrhizas do enhance P uptake of crop plants, the magnitude and importance of this uptake has been questioned (Ryan and Graham, 2018). Hence, the widely held belief that mycorrhizas must enhance a plant's P acquisition deserves further scrutiny, rather than extrapolation based on a limited number of species from specific habitats and conditions. First, arbuscular mycorrhizas only enhance P acquisition in a very narrow range of P concentrations in the rhizosphere solution (Parfitt, 1979) or bulk soil (Pairunan et al., 1980). Other mycorrhizas such as ectomycorrhizas may access more P, if the mycorrhizal hyphae release carboxylates (Arvieu et al., 2003), but this has never been tested using a

similar experimental design as used by Parfitt (1979). While suppression of arbuscular mycorrhizas is commonly reported at high P supply (Abbott et al., 1984; Reddell et al., 1997), suppression is also common at a very low P availability (Bolan et al., 1984; Bolan et al., 1987). This provides clear evidence that arbuscular mycorrhizas do not enhance P uptake above or below a specific range of P availability. This is supported and extended for ectomycorrhizas based on results using in-growth cores in severely P-impooverished natural habitats (Teste et al., 2016). Yet, paradoxically, mycorrhizal plant species are common in severely P-impooverished habitats (Zemunik et al., 2015). This is accounted for by the role of mycorrhizas in boosting plant defense (Albornoz et al., 2017; Lambers et al., 2018). This important role of mycorrhizas has been known (Marx, 1972), yet the assumption is often made that mycorrhizas must be important for P acquisition, even when the evidence points in the opposite direction, at least in severely nutrient-impooverished habitats, as outlined above.

We argue that in severely P-impooverished systems, mycorrhizas play a pivotal ecological role, but that role is not to enhance P acquisition (Laliberté et al., 2015; Albornoz et al., 2017). Some of the most P-impooverished ecosystems occur in the southern hemisphere in seasonally-dry regions, namely the fynbos in the Cape Floristic Region of South Africa (Allsopp et al., 2014), campos rupestres in south-eastern Brazil (Fernandes, 2016), and kwongan in south-western Australia (Lambers, 2014). Due to their high plant diversity and depauperate nutrient availability, these regions must be included in studies aimed to better understand global patterns and ecological significance of mycorrhizas.

2.4 Ecology of mycorrhizal plants as dependent on their subgroup

Each mycorrhizal subgroup (e.g., ectomycorrhizal and arbuscular mycorrhizal plants species) is thought to be driven by a different set of environmental factors, or that they respond differently to the same factors. For example, it is widely accepted that arbuscular mycorrhizal plants tend to dominate in early successional habitats where soil pH and available P is higher, while ectomycorrhizal plants dominate in late-successional habitats, where soils are more acidic and P is mostly sorbed or in organic form (*i.e.*, not readily available) (Lambers et al., 2008). This claim is supported by evidence in the northern hemisphere where young soils are colonised by fast-growing arbuscular mycorrhizal plants that also form symbioses with N₂-fixing bacteria (Francis and Read, 1994). However, arbuscular mycorrhizal plants remain dominant in the vegetation across a 2-million year soil chronosequence in kwongan heath in south-western Australia (Zemunik et al., 2015), compounded by these hyperdiverse ecosystems being non-successional (Hopper, 2009). This shows that mycorrhizal subgroups are not uniform in their response to environment and that similarly to the mycorrhizal status of plants, taxonomy, evolution and continental history are strong drivers of mycorrhizal diversity (Dickie et al., 2013). Hence, as raised above,

oversimplification and extrapolation to global patterns from limited data of environmental drivers of mycorrhizas can be flawed. We provide examples to illustrate these points below.

3 On Ericaceae

The Ericaceae is one of the 11 largest families of vascular plants (Christenhusz and Byng, 2016), having a cosmopolitan distribution and comprising more than 125 genera and almost 4500 species (Luteyn, 2002). The species in this family radiated in oligotrophic regions, such as well-leached soils and epiphytic habitats; much of the ecological functions of their unique ericoid mycorrhizas have been established on a few well-studied Ericaceae from post-glacial landscapes (Leake and Read, 1989, 1991, 1994). Yet, the diversification of the Ericaceae is not in cold tundra, boreal forests, and montane habitats (Schwery et al., 2015), where most studies have been conducted. Globally, richness of ericoid mycorrhizal plants species is greatest in tropical, subtropical and warm temperate (Mediterranean) regions. They also represent an important vegetation component in cool temperate and arctic regions, but without the high species diversity of warmer regions (Kohout, 2017).

In a recent review, the habitats where ericoid mycorrhizal plants are abundant was described as “highly acidic soils with mostly high organic content, usually cold tundra, boreal forests, and montane habitats” (Tedersoo et al., 2020). These authors consider that Ericaceae achieve competitive advantage and large population densities by establishing ericoid mycorrhizal symbioses with selected groups of ubiquitous humus saprotrophs that have evolved efficient enzymes to access nutrients in recalcitrant organic compounds in strongly acidic environments. The authors of this review based their claims on two previous publications (Read, 1991; Soudzilovskaia et al., 2019). First, Soudzilovskaia et al. (2020) acknowledge that data on ericoid mycorrhizal vegetation were unreliable. Second, data for most of the southern hemisphere were absent for ericoid mycorrhizal plants, with a bias toward higher latitude ericaceous species or species of horticultural value (*Vaccinium* species) (Hashem, 1995; Kula et al., 2018; Millaleo et al., 2020). Dominance of ericoid mycorrhizas associated with a very small number of Ericaceae might be due to a range of plant traits, rather than demonstrated competitive advantage of ericoid mycorrhizal fungi.

Ericaceae have ericoid mycorrhizas that function to promote plant growth (Read, 1991; Treu et al., 1995; Cairney, 2000) (Fig. 1). In holomycotrophic Ericaceae such as *Sarcodes*, *Pyrola* and *Monotropa* (previously considered to be distinct from the Ericaceae), ericoid mycorrhizas function as life critical components (Jacquemyn and Merckx, 2019). However, for all other Ericaceae, experimental evidence of *in planta* growth and development is demonstrated to a limited degree in only a few of the 4000 species in the family (Dixon et al., 2002). What we know is that ericoid mycorrhizas, among other attributes, intercept manganese (Mn) in the soil profile (Hashem, 1995), which would account for a low leaf Mn concentration [Mn].

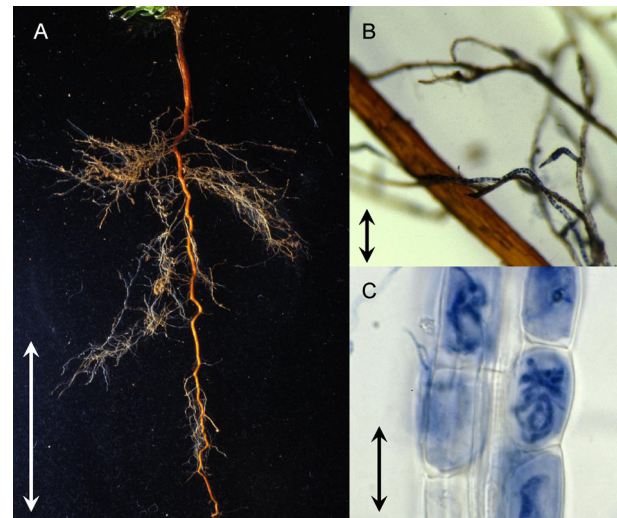


Fig. 1 The mycorrhizal system in Ericaceae. Four year-old plant of *Astroloma xerophyllum* (Ericaceae) showing (A) fine roots, central brown tap root (Bar = 100 mm) and (B) interspersed in the fine roots are hair roots, here stained with cotton blue (note fine intracellular blue stained ericoid mycorrhiza) (Bar = 0.2 mm). (C) Endophytic ericoid mycorrhiza stained with cotton blue (Bar = 200 μ m). Photos: Kingsley W. Dixon.

However, some Ericaceae, for example, *Vaccinium corymbosum* (highbush blueberry), exhibit high leaf [Mn] (Millaleo et al., 2020) which is typically associated with a carboxylate-releasing P-acquisition strategy (Lambers et al., 2015). Carboxylate release in some Ericaceae might therefore account for the large variability in leaf [Mn] (Bouwens and Longin, 1979; Pillon et al., 2018) and often high leaf [Mn] (Korcak, 1987; Wojtuń et al., 2017; Kula et al., 2018) in Ericaceae. Again, there are no broad survey data for Ericaceae foliar [Mn], which, if collected across the range of biomes where the family occurs, would provide a surrogate for showing how far and wide mycorrhizal activity and carboxylate release occur in the family (Zhou et al., 2020; Lambers et al., 2021). The paucity of isotopic studies of mycorrhiza-mediated N and C nutrition as undertaken in orchids (see Gebauer et al., 2016 and references therein) in the Ericaceae (Bell and Pate, 1996) is surprising, given the capacity of the tool to resolve relative nutritional competency of the mycorrhizal associates (Jacquemyn and Merckx, 2019).

Taking a more global view on diversity, rather than abundance, outside postglacial landscapes, the area with the highest Ericaceae species richness in Europe and the Mediterranean is the Western Mediterranean (Ojeda et al., 1998). In the southern Mediterranean, the Ericaceae is represented by three genera and 10 species in Morocco, generally distributed on non-calcareous soils in forests, scrubland and desert regions as well as in montane environments (Hamim et al., 2017) (Fig. 2). In the Neotropics, a hotspot for Ericaceae, the species are Andean-centered, adapted to moist, open and cool montane environments with many being epiphytes (Luteyn, 2002). Overall, species

richness increases nearer the Equator, with the highest species numbers concentrated in Colombia and Ecuador between 1000 m and 3000 m, with 46 genera and about 800 species of Ericaceae native to the Neotropics (Luteyn, 2002). In Europe, a single species of Ericaceae (*Calluna vulgaris*) can dominate a landscape (Fig. 2A). However, we do not know if this dominance is based on its ericoid mycorrhizal status or related to other traits such as aluminum resistance (Ojeda et al., 2000).

As one of the most species-rich genera of flowering plants, *Erica* is remarkable because >80% of the >800 species are endemic to the smallest floral kingdom, the Cape Floristic Region of South Africa (Pirie et al., 2017). Australia hosts just 596 species across 35 genera (D. Crayn, pers. comm.) (Fig. 3) with centers of diversity and abundance in the temperate south-west and south-east forests, shrublands and montane regions (<https://www.ala.org.au/>), characterized by impoverished soils (Rossel and Bui, 2016; Kooyman et al., 2017). In Yunnan, China, ericaceous species richness, which includes many *Rhododendron* species, shows a unimodal relationship with mean annual temperature and mean annual precipitation, and the elevational pattern of species richness is shaped by the combined effects of climate and competition (Wang et al., 2018). Zhang et al. (2018) analyzed nutrient concentrations in 32 Ericaceae from 161 sites across southern China, from 27 m to 4906 m above sea level, none of which qualify as cold tundra or boreal forest habitats, and only some were associated with montane areas, all of which Tedersoo et al. (2020) consider major habitats for Ericaceae.

In conclusion, the distribution of Ericaceae is geographically, edaphically and ecologically more widespread and diverse than suggested in a recent review (Tedersoo et al., 2020) and it is premature to draw global generalisations on their functioning based on a limited number of regionally-biased studies. Based on what we know about carboxylate release and leaf [Mn], their P-acquisition strategies are likely more variable than suggested. Rather than give the impression that the research on P nutrition on Ericaceae has been well established, we suggest to explore their P acquisition strategies in greater detail, using stable isotopes (Gebauer et al., 2016) as well as leaf [Mn] as a proxy for rhizosphere carboxylates (Lambers et al., 2015; Zhou

et al., 2020). This then needs to be followed up with actual measurements and controlled plant growth benefit studies (Pang et al., 2018; Lambers et al., 2021).

4 The orchids

Outside of crops, the Orchidaceae are among the most studied of all plant groups in terms of their mycorrhizal associates. This is despite the minor ecological importance of the family in ecosystem function (Dixon et al., 2003; Swarts and Dixon, 2017). This investigator bias stems from a variety of factors associated with the charismatic appeal of the family, the experimental ease of investigating their orchid mycorrhizal system and, for terrestrial species, the obligate mycorrhizal requirement for germination and early growth that is rapidly and easily synthesized under laboratory conditions (Fig. 4). Yet, this major horticultural family, with an estimated annual trade of 1.1 billion units of mostly epiphytic taxa (Hinsley et al., 2017), relies on plants germinated and grown without mycorrhizal fungi (Swarts and Dixon, 2017). Clearly, further studies are required before we extrapolate how this very large family functions based on studies of only a small fraction of all species.

For terrestrial orchids examined under laboratory conditions, all have an obligate requirement for mycorrhizal fungi for germination and seedling growth, although the reliance on mycorrhizal fungi in later stages of plant development is less clear (Rasmussen and Rasmussen, 2009). Carbon is the bulk commodity traded between chlorophyllous orchids and their associated fungi, with nutrients flowing to the orchid from the fungus (and vice versa), but to varying degrees (Gebauer et al., 2016). In mycoheterotrophic orchids, carbon as well as other plant nutrients including nitrogen are provided to the orchid (Gebauer and Meyer, 2003; Gebauer et al., 2016). Orchid mycorrhizal types for mixotrophic orchids exploit a wide range of organic compounds including phytate as a P source (Nurfadilah et al., 2013), while genetic studies show that different genera of orchid mycorrhizal fungi can or cannot access nitrate and nitrite pools (Fochi et al., 2017).

The degree of mycorrhiza-mediated nutrition in the adult phase under field conditions has been examined using



Fig. 2 (A) *Calluna vulgaris* forms dense stands on acidic peat soils where the ericoid mycorrhizas provide access to nutrients that would otherwise not be available to its roots. (B) *Rhododendron* sp. is a dominant small tree in natural high-altitude grasslands in peat-based soils in Sri Lanka. Photos: A: Marga Speelman-Lambers; B: Kingsley W. Dixon.

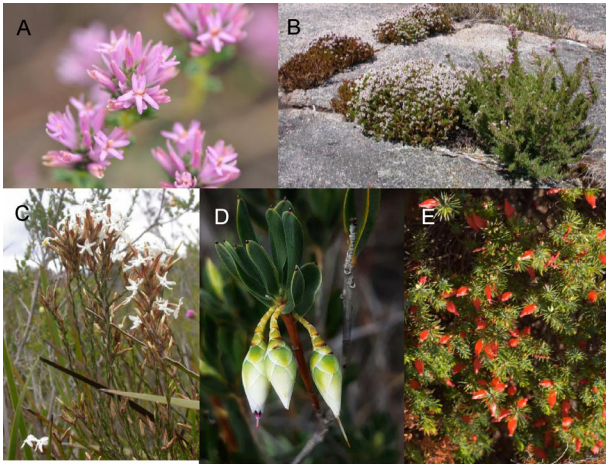


Fig. 3 Unlike *Calluna vulgaris* in Europe, Ericaceae in the South-west Australian Biodiversity Hotspot are common and widespread in most ecosystems from coastal to montane and can be co-dominant as an understorey family, although, unlike *Calluna vulgaris* in Europe, single species dominance is rare, with many species contributing to the abundance of the Ericaceae. (A) *Andersonia gracilis*, a declared rare flora species (<https://florabase.dpaw.wa.gov.au/browse/profile/6309>); (B) *Andersonia lehmanniana*; (C) *Lysinema conspicuum*; (D) *Conostephium pendulum*; (E) *Styphelia tortifolia*. Photos: A: Hongtao Zhong; B, C, E: Hans Lambers; D: Sophie Zhang.

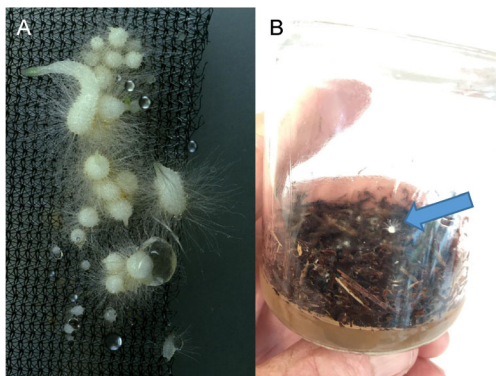


Fig. 4 (A) Eight-week old *Caladenia arenicola* orchid seedlings grown on oats macerated in agar inoculated with a mycorrhizal fungus. (B) Six-week old *Caladenia huegelii* seedling incubated in the dark that germinated and grew 40 mm on glass from sterilised leaf mulch (*Allocasuarina fraseriana* mulch) inoculated with a mycorrhizal fungus indicating that the mycorrhiza can supply the developing orchid seedling with all required nutrients for early growth. Photos: Kingsley W. Dixon.

surrogate measures based on isotopic enrichment (Liebel et al., 2010; Gebauer et al., 2016). These studies show low to highly-variable levels of mycorrhiza-associated enrichment for many in situ adult orchid plants. Predictably, holomycotrophic species such as many *Neottia* species are highly enriched with such extreme nutritional linkages being taxonomic exceptions, rather than the rule, as holomycotrophy occurs in just 0.8% of

orchid species (Merckx and Freudenstein, 2010). Studies of the degree of P nutrition are more complex and under-researched in orchids in the absence of easily deployed isotopic tools. However, P transfer must occur to a significant degree, given that symbiotic media for germination and growth of orchids utilize complex plant materials such as macerated oat agar with the mycorrhiza capable of supplying all nutrients to the generally achlorophyllous early stages of orchid germination (Swarts and Dixon, 2017). Despite the experimental ease for testing fungal efficacy, there is a large number of studies where orchid tissues are sequenced to investigate endomycorrhizas. However, in the absence of experimental testing of the benefit of sequenced fungi, such studies potentially overestimate mycorrhizal diversity and potentially understate functionally important endophytes (as discussed in Prosser, 2013). McCormick et al. (2018) highlight that distinguishing between mycorrhizal associates and non-mycorrhizal endophytes requires germination studies, which can be problematic for orchids that change mycorrhizal ‘species’ depending on season, ecology and life stage.

As with the Ericaceae, the center of diversification of the family is in the neotropical Andean region, with a second major diversification node in Asian tropical and subtropical regions (Christenhusz et al., 2018). Similarly, within the 30 000 species of orchids (Govaerts et al., 2016), 30% of species are temperate terrestrial taxa, on which much of the mycorrhizal research has been done, with little for the remaining >60% of the family that are tropical epiphytes. Understanding the importance of mycorrhizas at the family-wide and biome-wide level (see Tedersoo et al., 2020) is therefore conflicted by the current research bias toward terrestrial taxa, associated with research-intensive regions (USA, Europe and Australia) that are outside the phylogenetic hotspots of diversification. In addition, mycorrhizal nutritional studies would benefit from a focus on adult orchid nutrition and the importance in defining orchid distributional status.

5 Perspectives

Recent reviews promote the concept that mycorrhizas are invariably important to enhance a plant’s growth and development, with a major focus on P acquisition. We accept the pivotal ecological importance of mycorrhizas, but argue that their importance for P acquisition is relevant only in a narrow critical range of P availability and should be examined across centers of plant diversity. The current emphasis of mycorrhizal research on centers of academic richness provides an outstanding research platform for investigating broader issues across the globe. This is particularly so for understanding nutrient dynamics, because plants acquire P without mycorrhizas in situations of very low P availability. Below a critical range, P mobilisation based on the release of root exudates (carboxylates and phosphatases, often in combination; Zhong et al., 2020) is the dominant mechanism to acquire P (Raven et al., 2018). In that very low range, mycorrhizas may provide benefits masked by investigator focus on P acquisition

(Albornoz et al., 2017). Because of this variation in P-acquisition strategies and the role of environment, we must evaluate the mycorrhizal status of a plant and the role of mycorrhizal fungi on a case-by-case basis, rather than extrapolate from small regional studies. We conclude that the current dogma on mycorrhizas provides an invaluable starting point for developing hypotheses to robustly test when and where mycorrhizas play a role in determining ecological trajectory (Teste et al., 2016). The time has come to move forward, as an overwhelming amount of research indicates that we must revisit and update the dogmas (Lambers et al., 2021).

Acknowledgments

This research was supported by an ARC-funded Discovery Project grant (DP130100005) awarded to HL and KD is supported by the Australian Research Council Industrial Transformation Training Centre for Mine Site Restoration (Project Number 389 ICI150100041).

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