



## Tansley insight

# Evolutionary history of mycorrhizal symbioses and global host plant diversity

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## Summary

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**Key words:** evolution, habitat specialization, host plant diversity, mycorrhizal associations, plant nutrition.

The majority of vascular plants are mycorrhizal: 72% are arbuscular mycorrhizal (AM), 2.0% are ectomycorrhizal (EcM), 1.5% are ericoid mycorrhizal and 10% are orchid mycorrhizal. Just 8% are completely nonmycorrhizal (NM), whereas 7% have inconsistent NM–AM associations. Most NM and NM–AM plants are nutritional specialists (e.g. carnivores and parasites) or habitat specialists (e.g. hydrophytes and epiphytes). Mycorrhizal associations are consistent in most families, but there are exceptions with complex roots (e.g. both EcM and AM). We recognize three waves of mycorrhizal evolution, starting with AM in early land plants, continuing in the Cretaceous with multiple new NM or EcM lineages, ericoid and orchid mycorrhizas. The third wave, which is recent and ongoing, has resulted in root complexity linked to rapid plant diversification in biodiversity hotspots.

## I. Introduction

There are four main types of mycorrhizas based on the criteria of morphological differentiation of root tissues and host plant lineages: arbuscular mycorrhizas (AM), ectomycorrhizas (EcM), ericoid mycorrhiza (ErM) and orchid mycorrhizas (OrM) (see descriptions in Box 1). Mycorrhizal associations have key roles in maintaining plant productivity in natural and agricultural habitats, and are the key sources of energy for many fungal taxonomic groups, yet there are major gaps in knowledge about the evolutionary history of these partnerships. Here we summarize the global diversity of mycorrhizal and nonmycorrhizal (NM) plants, provide regional host plant summaries and briefly address

data quality issues in mycorrhizal lists and their consequences. Finally, we provide a brief update on the evolutionary history of mycorrhizal associations, based on information published in the book '*Biogeography of mycorrhizal symbioses*' (Tedersoo, 2017a) and other sources.

## II. Mycorrhizal plant diversity at global and local scales

A phylogenetic approach for summarizing mycorrhizal host plant diversity works well because the majority of plant species belong to genera, families or orders with consistent mycorrhizal status, indicating strong phylogenetic conservatism of the mycorrhizal

**Box 1** Mycorrhizal types

Mycorrhizal associations and their subtypes are described in more detail in Table B1 using the morphological definitions of Brundrett (2004) and additional criteria concerning potential reciprocal benefits criteria, phylogenetic relatedness and association with characteristic fungi (Tedersoo & Brundrett, 2017).

Arbuscular mycorrhizas (AM) are defined by the presence of arbuscules that normally form in root cortex cells (Fig. 1). Based on the morphology of fungal hyphae within roots, linear and coiling subtypes are distinguished, with additional variants within them. In particular, AM associations of myco-heterotrophic plants are often highly divergent (Leake, 1994).

Ectomycorrhizas (EcM) are defined by the presence of a Hartig net and mantle (Fig. 1). Besides the basic type, ectendo (thin mantle, some intracellular colonization; in *Pinus* and *Larix* with some ascomycete groups), arbutoid (variable mantle, sparse intracellular colonization; in Arbutaceae hosts), pyroloid (variable mantle, heavy intracellular colonization; in Pyroleae hosts), monotropoid (thick mantle, heavy intracellular colonization, hyphal digestion), pisonioid (transfer cells in Hartig net; Pisonia hosts), gnetoid (symbiotic interface as finger-like projection above root epidermis; in *Gnetum* hosts) and superficial (sparse mantle with no or poorly developed Hartig net; Mediterranean Cistaceae, Australian AM–EcM groups) subtypes can also be recognized.

Ericoid mycorrhizas (ErM) are limited to members of Ericaceae, excluding some subfamilies (Monotropoideae, Arbutoideae and Enkianthoideae), but including the Diapensiaceae. Fungi are various groups of Helotiales, Chaetothyriales, Serendipitaceae and potentially other Agaricomycetes. Fungi colonize each epidermal cell separately from the root surface, forming densely interwoven coils (Fig. 1).

Orchid mycorrhizas are confined to the Orchidaceae and involve 'saprotrophic' fungi from the Tulasnellaceae and Ceratobasidiaceae families, supplemented by Serendipitaceae and Pezizales and multiple EcM groups occurring in some achlorophyllous orchids that evolved more recently. Mycorrhizal fungi are stimulated to form densely branched or coiled structures termed as pelotons inside root cells; older cells are lysed and 'digested' by the plant (Fig. 1).

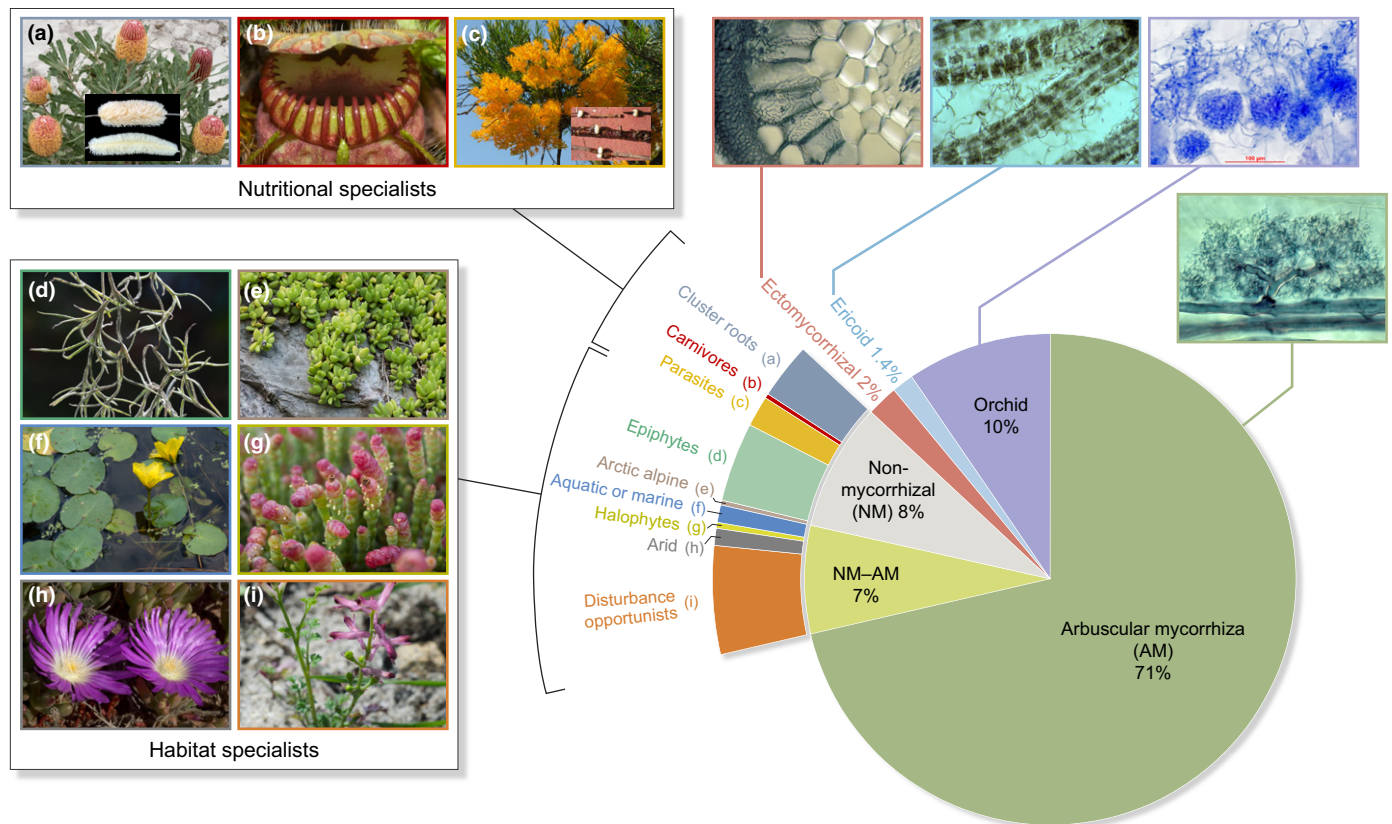
**Table B1** Characteristics of principal mycorrhizal types

	Arbuscular	Ectomycorrhizal	Ericoid	Orchid
Morphological characters	Arbuscules present; vesicles present/absent; colonization from root surface mycelia or from neighbouring cells	Hartig net present; differentiated hyphal mantle present; no intracellular colonization	Hyphal coils in cells present; each cell is separately colonized from root surface; no (or patchy, undifferentiated) mantle	Hyphal pelotons within root cells present; old pelotons digested by plant; colonization from root surface mycelia or from neighbouring cells
Plant dependency	Mostly obligatory (survival with reduced competition)	Mostly obligatory (survival with reduced competition)	Obligatory	Obligatory for seedling development and adult nutrition
Benefits supplied to plants	Nutrition (mineralized nutrients), limited protection	Nutrition (mineralized, simple organic nutrients), protection	Nutrition (mineralized, simple organic nutrients), limited protection?	Nutrition (mineralized, organic nutrients, carbon energy), limited protection?
Benefits to fungi	Carbon energy, habitat, deep water from trees	Carbon energy, deep water from trees	Carbon energy? Habitat in roots and soil via allelopathy	None (probably cannot support fungi)
Presence of cheating associations	In plants (multiple groups)	In plants (Monotropoideae, Pyroleae), fungi conditionally	Not known	All germinating seedlings, and many adult plants (at least partially)
Plant associations: phylogenetic groups	Vascular plants, thalloid bryophytes; multiple switches to other states (see text)	Two Gymnospermae lineages, 28 Angiospermae lineages; multiple losses to AM and NM states	Ericaceae, Diapensiaceae (Ericales), partial reversion to AM reported in Hawaii (Koske <i>et al.</i> , 1992)	Orchidaceae; no losses known
Fungal associations: phylogenetic groups	Glomeromycota, (or Mucoromycota)	Four Endogonomycetes lineages, 33–34 Pezizomycetes lineages, 45–48 Agaricomycetes lineages (Tedersoo & Smith, 2017)	Groups within Helotiales, Chaetothyriales, Serendipitaceae, Pekloderma	EcM and saprotrophic Agaricomycetes and Pezizomycetes, especially Tulasnellaceae, Ceratobasidiaceae and Serendipitaceae (Sebacinales)

trait (Brundrett, 2009; Maherali *et al.*, 2016). However, some families are more complex due to specialized or multifunctional roots (e.g. AM and EcM). Fig. 1 illustrates revised estimates of the diversity of mycorrhizal and NM plants, based on 135 years of published information and recently available large-scale plant phylogeny (Zanne *et al.*, 2014) and mycorrhizal data, which includes extensive coverage of both temperate and tropical ecosystems (Brundrett, 2009; Tedersoo, 2017a). This analysis confirms the overall importance of AM, which occurs in 72% of

flowering plant species, with  $\geq 2\%$  EcM, 1.5% ErM, 10% OrM and 7% inconsistent AM (NM–AM); 8% remain NM. These numbers are similar for all vascular plants, with 71% species being AM and 2.2% EcM (Brundrett, 2017b). In ferns, *c.* 67% of species are AM (Lehnert *et al.*, 2017) and *c.* 25% of bryophytes are mycorrhizal, mostly with AM; however, mosses, the largest group of bryophytes, are normally NM (Davey & Currah, 2006; Pressel *et al.*, 2010).

The general consistency in mycorrhiza development within most plant families allows phylogenetic information about mycorrhizal



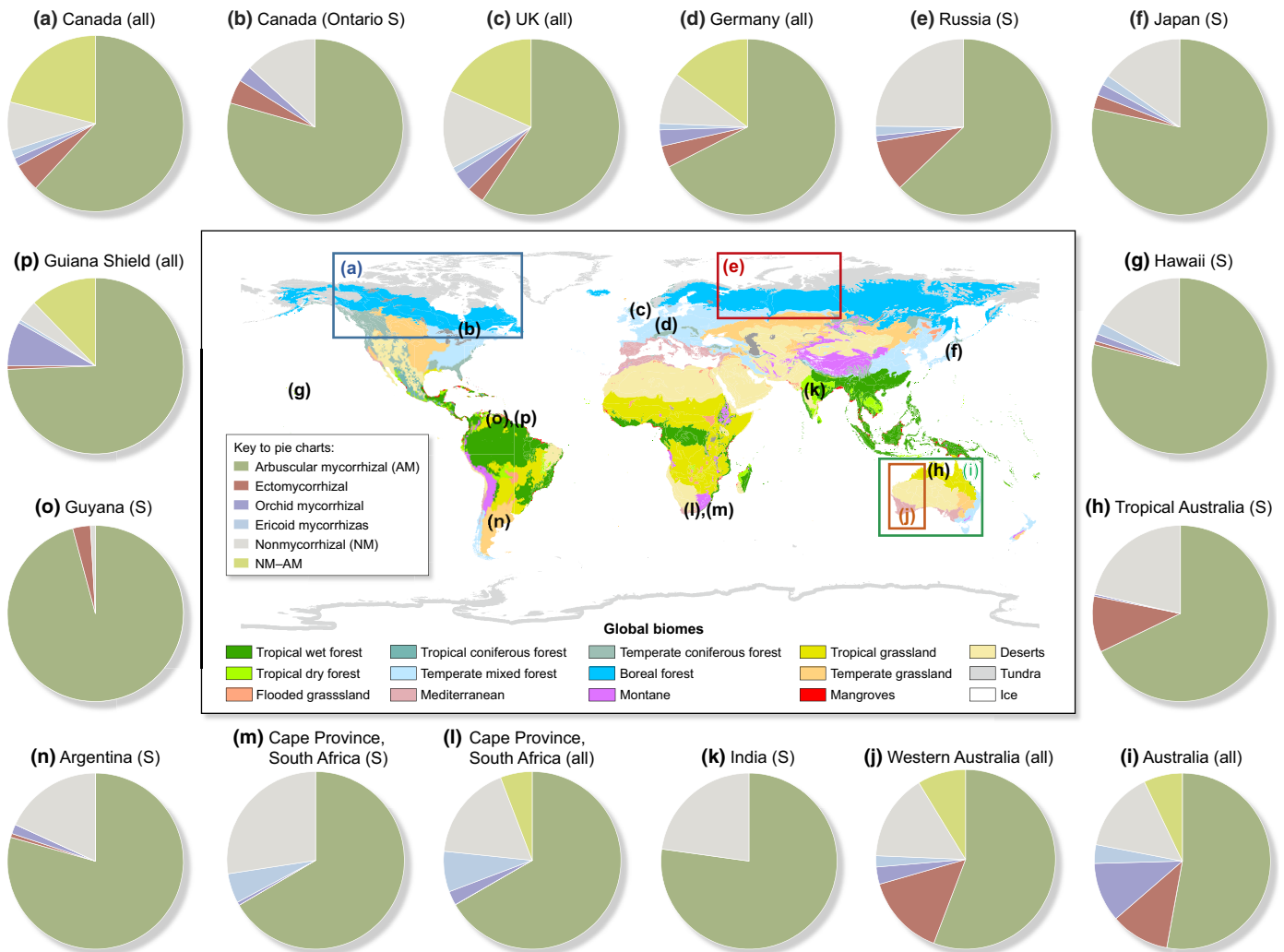
**Fig. 1** Pie chart showing the taxonomic diversity of plants with different types of mycorrhizas, nonmycorrhizal (NM) roots, or inconsistent mycorrhizas (arbuscular mycorrhiza (AM)–NM). Exploded pie segments show plants assigned to the categories NM and NM–AM, which are combined and then reallocated to groups based on mineral nutrition or habitat specializations. These specialized plants are assigned to categories at the family level, based on the most important strategy for each family (families often include several of these strategies). Note that these specialized habitats also include many mycorrhizal plants, but NM and NM–AM plants are much more common than elsewhere. Inset photos show mycorrhizal structures (right side) or examples of specialized plants (left side). Data are from Brundrett (2017b).

status to be extended to produce regional-scale estimates of host and nonhost plant diversity (Fig. 2). These comparisons reveal that most plant communities are dominated by mycorrhizal plants in most ecosystems, EcM plants are rare or absent in many tropical habitats, whereas NM plants are more common and diverse in some arid and degraded habitats, as well as arctic and alpine regions (Brundrett, 2009; Gerz *et al.*, 2016; Swaty *et al.*, 2016; Soudzilovskaia *et al.*, 2017). In particular, plants with NM cluster roots have centres of diversity in extremely poor soils in Mediterranean habitats of Western Australia and South Africa (Lambers *et al.*, 2010). It is also remarkable that Australia is a global centre of diversity for plants with EcM roots, NM roots or carnivorous nutrition, with *c.* 33%, *c.* 15% and *c.* 25% of global species, respectively (Brundrett, 2017a). Furthermore, Australia contributes to 17% of diversity of EcM plant species and 10% of plant parasites.

Ectomycorrhizas are the most frequently acquired mycorrhizal associations due to multiple independent gains and some losses of symbiosis (Tedersoo & Brundrett, 2017). We resolved conflicting information and missing data for many EcM plant taxa, resulting in a revised estimate of 6000–7000 EcM plant species, with a further 1500–2500 species that belong to Australian groups with complex roots in which EcM occurs in some species but not others, such as

Myrtoideae (Myrtaceae) *Acacia* (Fabaceae), Mirbelieae (Fabaceae) and Casuarinaceae (Brundrett, 2017b; Tedersoo & Brundrett, 2017). These groups include many species with both EcM and AM roots and require further investigation (Fig. 3). Our maximum estimate includes 335 ectomycorrhizal plant genera (8500 species) in 30 monophyletic lineages. We also identified a further 22 plant genera (76 species) that may also be EcM due to phylogenetic sister relationships to known EcM hosts, but require further investigation (Tedersoo & Brundrett, 2017).

Rapid phylogenetic radiation has occurred in some NM plant groups that have secondarily lost their mycorrhiza-forming capacity permanently, or intermittently depending on habitat and co-occurring plants (NM–AM). We estimate that there are 30–50 separate evolutionary origins of NM or NM–AM plants, including several occasions within some families (Brundrett, 2017b). Many NM and NM–AM plants are habitat specialists that grow in environments where plant productivity is limited by soil or climatic conditions, or nutritional specialists such as carnivores, parasites and cluster-rooted species, where mycorrhizas are redundant (Fig. 1). There also is an over-representation of NM plants in waterlogged, cold and saline soils, as well as in epiphytic, freshwater, marine and disturbed habitats (Fig. 1). For example, 15 of the top 17 weed plant families listed by Daehler (1998) have NM



**Fig. 2** Regional-scale case studies of mycorrhizal diversity shown as pie charts with locations shown on a global vegetation map. These charts were produced by assigning mycorrhizal status to all of the species in a region based on phylogeny (All; data from Brundrett, 2009, 2017b; Lambers *et al.*, 2010), or from studies where roots of many species were sampled (S). Note that letters refer to sampling locations, except where associated with polygons that show the approximate boundaries of regional studies. These samples were from 2970 spp. from Russia (Akhmetzhanova *et al.*, 2012), 1037 spp. from Japan (Maeda, 1954), 147 spp. from Hawaii (Koske *et al.*, 1992), 247 species from tropical Australia (Brundrett *et al.*, 1995), 332 spp. from South Africa (Allsopp & Stock, 1993), 215 spp. from Guiana (Bereau *et al.*, 1997; McGuire *et al.*, 2008), 329 spp. from India (Muthukumar & Udaiyan, 2000) and 286 spp. from Argentina (Fontenla *et al.*, 2001; Fracchia *et al.*, 2009). NM and NM-AM plants were not distinguished in these surveys. This figure includes many of the most important habitats on earth, but extreme habitats where mycorrhizas may be less common are not well represented at this scale. Simplified global vegetation patterns follow Olson *et al.* (2001).

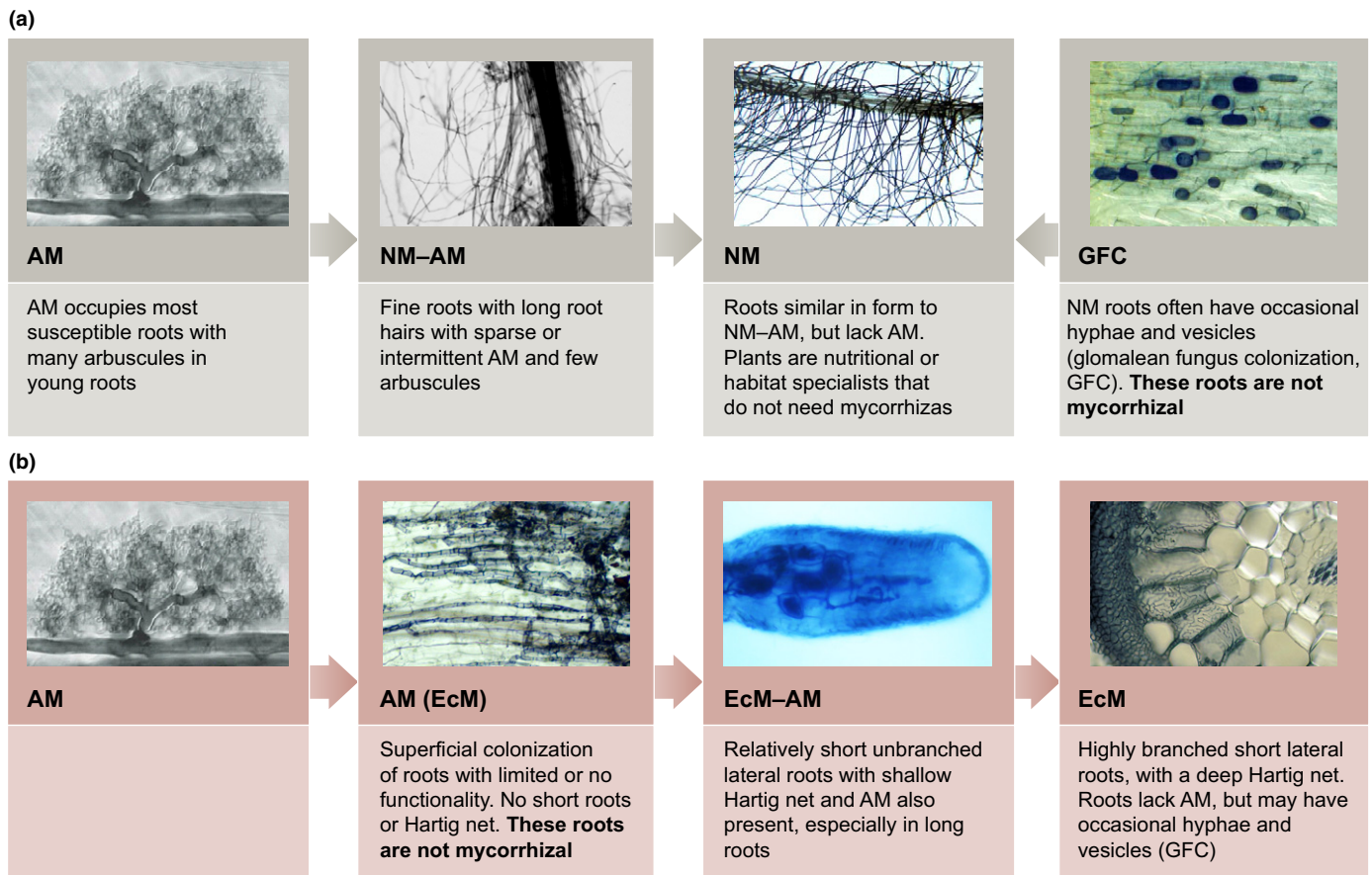
roots. By contrast, mycorrhizal plants usually dominate most mid- and late-successional habitats (Fig. 2).

### III. Mycorrhizal evolution in plants: a brief update

Switching from AM to NM or AM to EcM roots and reversal of carbon flow in mycoheterotrophic associations are the three most common trends in mycorrhizal evolution (Box 1; Fig. 3). Additionally, potential losses of EcM associations occur in the Fagales, Fabales, Asterales and Myrtales that may be attributed to the evolution of association with nitrogen-fixing bacteria, of shrubby or herbaceous life forms or following the shift to wetland habitats (Tedersoo & Brundrett, 2017).

Taking the accumulated information together, we recognize three waves of mycorrhizal evolution which resulted in new nutritional mechanisms in plants (Fig. 4). The second and third waves consist of multiple origins of mycorrhizal (especially EcM) and NM plant lineages and extend over a considerable time period.

The first wave represents the origin of AM associations in early terrestrial plants over 450 Myr ago (Ma) (Taylor & Osborn, 1996; Brundrett, 2002). The fossil record for land plants starts in the Ordovician at *c.* 470 Ma, but interpreting these early clues is complicated due to major gaps in the fossil record and difficulties in linking early cryptosporic land plants to modern lineages (Wellman, 2014). The first well-preserved fossils of mycorrhizal rhizomes originate from the Devonian Rhynie chert (407 Ma) and show



**Fig. 3** Evolution flowchart showing intermediate categories in the evolution of (a) nonmycorrhizal (NM) or (b) ectomycorrhizal (EcM) roots from arbuscular mycorrhizas (AM), as well as opportunistic activity by fungi that sometimes causes errors in diagnosis.

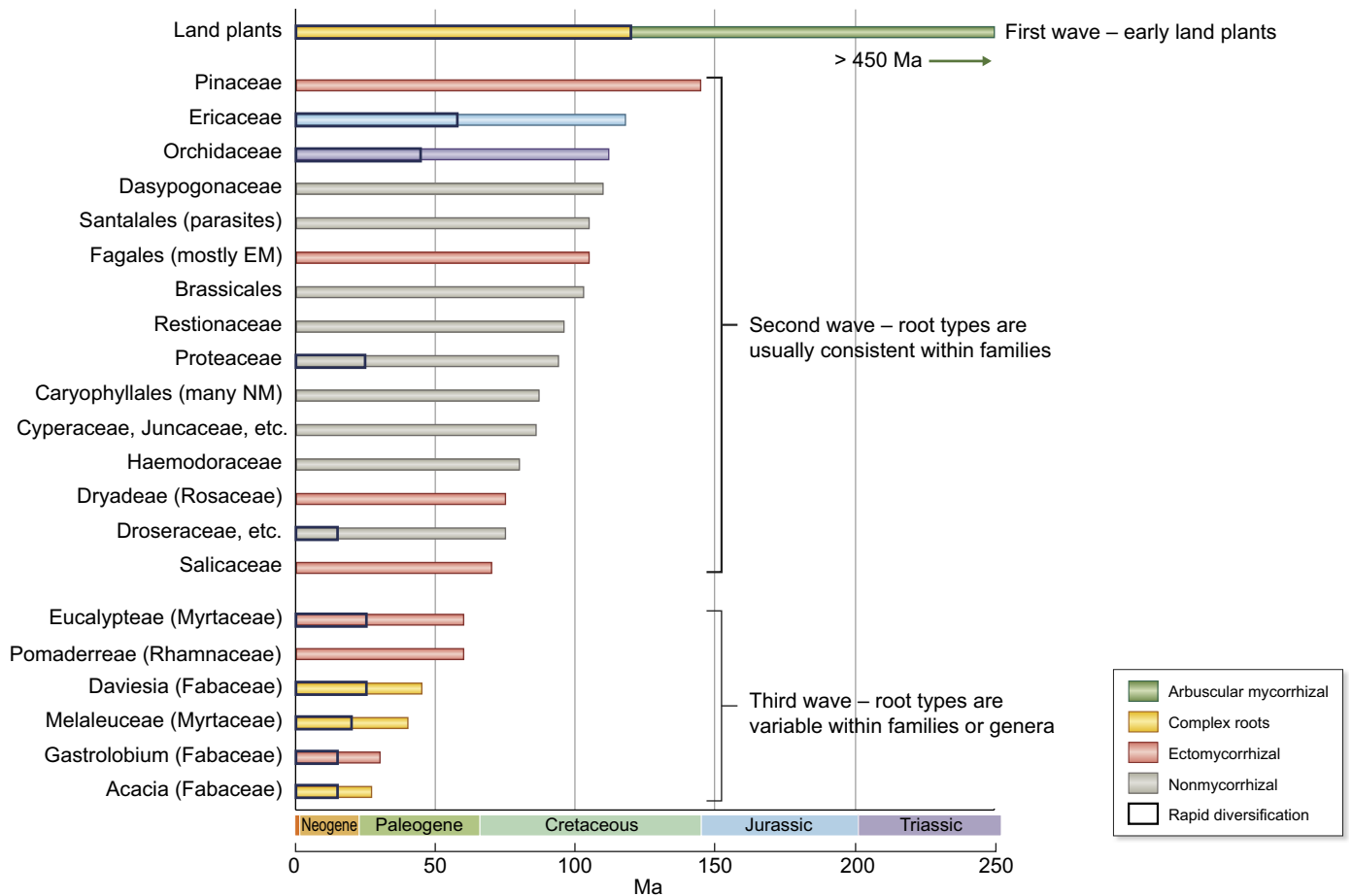
remarkably similar mycorrhizal and spore morphology to modern equivalents (Taylor & Osborn, 1996; Krings *et al.*, 2007), but the first AM fungus-like spores have been detected in substrates 50 Myr earlier from the Ordovician (Pirozynski & Dalpé, 1989; Redecker *et al.*, 2000). Due to limited evidence from the first 60 Myr of life on land, it is unclear if mycorrhizal fungi arrived with the first plants or when plant complexity rapidly increased in the Silurian. This is further complicated by the fact that some plant symbiosis genes pre-date land plants (Delaux *et al.*, 2015; Martin *et al.*, 2017). Both fossil evidence and molecular studies support a single origin for AM (Brundrett, 2002; Bravo *et al.*, 2016). For example, genomic studies have revealed common mechanisms for signalling and regulation of mycorrhizal associations that are shared with nitrogen-fixing associations and the common loss of symbiotic genes in NM plants (Delaux *et al.*, 2015; Bravo *et al.*, 2016; Kamel *et al.*, 2017).

Reduced mycorrhizal dependency may have evolved in some ferns and Equisetales (horsetails) with fine roots with long root hairs. However, reduced AM colonization in ferns is primarily correlated with their occupation of epiphytic habitats during their rapid radiation in the Cenozoic (Schuettpeitz & Pryer, 2009; Lehnert *et al.*, 2017). The NM bryophyte lineages are also ancient, but some modern bryophytes have relationships with AM or more recently evolved fungi (Box 1).

As shown in Fig. 4, the second major wave of mycorrhizal evolution occurred in the Cretaceous with the origins of the

Orchidaceae, Ericaceae and multiple families with EcM or NM roots, as well as parasitic plants carnivorous plants and nitrogen-fixing symbioses (Brundrett, 2002, 2017b; Raven & Andrews, 2010; Li *et al.*, 2015). Although the EcM Pinaceae evolved in the Late Triassic or Jurassic (Zanne *et al.*, 2014; Falcon-Lang *et al.*, 2016; Smith *et al.*, 2017), most of the remaining independent origins of nutrition strategies that are consistent within families date from the Cretaceous. Evolution of EcM and nitrogen-fixing bacterial associations was particularly common in the eurousid group of angiosperms in the Late Cretaceous and early Cenozoic (Werner *et al.*, 2014; Li *et al.*, 2015; Tedersoo & Brundrett, 2017). This plant group may have specific genetic preconditions for entering microbial symbioses (Werner *et al.*, 2014). Late Cretaceous angiosperm radiation has been linked to lower atmospheric CO<sub>2</sub>, increasing aridity and fires, as well as plant colonization of aquatic, cold or disturbed habitats (Wing & Boucher, 1998; Gomez *et al.*, 2015; Cardinal-McTeague *et al.*, 2016; Carpenter *et al.*, 2017).

The third wave of root diversification commenced in the Palaeogene *c.* 65 Ma and is still underway (Fig. 4). It includes lineages of plants with recently acquired root traits that are often inconsistent within families called 'New Complex Root clades' (NCR; Brundrett, 2017a,b). This wave, which peaked over the past 30 Myr, is linked to a very high diversity of both EcM and NM plants in certain plant families (Brundrett, 2017a; Tedersoo,



**Fig. 4** Summary of evolution trends illustrated by designating three waves of mycorrhizal evolution, using clades identified by Tedersoo & Brundrett (2017) and Brundrett (2017b). Ages of clades are estimates based on multiple data sources for each family, especially those summarized by the Angiosperm Phylogeny Website (Stevens, 2001 onwards). Some clades of ectomycorrhizal (EcM) and nonmycorrhizal (NM) plants are omitted due to limited dating evidence. Ma, million years ago.

2017b). This is a global phenomenon, but NCR clade plants are most common in Australia, which provides a preview of future soil conditions elsewhere. Australian soils are very old, deep and highly leached (Henderson & Johnson, 2016). Outside Australia, examples of NCR clades include EcM of sedges in the genus *Kobresia* (Cyperaceae) and EcM or NM cluster roots in some members the Fabaceae, such as *Lupinus* spp. (Brundrett, 2017b; Tedersoo & Brundrett, 2017). Other less common trends found in one or more plant lineages include switching from NM to EcM (Freudenstein *et al.*, 2016), Ericoid to EcM, and from balanced to myco-heterotrophic associations in plants (Box 1; Brundrett, 2002). Because the third wave of mycorrhizal evolution is linked to climate and soil conditions, it may be being accelerated by the Anthropocene epoch, with the increasing importance of disturbed habitats, as well as aridification and warming of most global ecosystems that can cause shifts in dominant mycorrhizal types in vegetation (Swaty *et al.*, 2016; Tedersoo, 2017b). It is also expected that invasive plants (including many NCR species) will continue to be spread globally along with their co-introduced soil microorganisms, where they will also interact with novel symbiotic partners (Tedersoo, 2017b).

Both the second and third waves of mycorrhizal evolution are linked to climate change as well as increasing habitat and soil

complexity, which presumably resulted in a competitive advantage for more specialized root types (Brundrett, 2017b). Mycorrhizal evolution tends to be a staged process starting from AM roots and progressing forward to specialized, NM or EcM roots with some reversions. Fig. 3 illustrates how plants that acquire a new nutrition strategy maintain the old one, at least initially (Brundrett, 2017a, b). The majority of lineages where plants transition from AM to EcM reach an endpoint with fully EcM roots, but others have retained multifunctional roots (EcM–AM). In the case of *Allocauarina* spp. (Casuarinaceae), plants have EcM and AM as well as nitrogen fixation and cluster roots. Other examples of EcM–AM include many members of the Australian Myrtaceae and as well as the panglobal Fabaceae, in which mycorrhizal status varies within some genera (Brundrett, 2017a,b; Tedersoo & Brundrett, 2017). Contradictory published information is common for plants bearing multifunctional roots such as Australian *Melaleuca* and *Acacia* species, where individual species, in addition to AM, have abundant EcM, occasional EcM or no EcM (Fig. 3). Some plants which predominantly have EcM associations, such as *Alnus*, *Eucalyptus* and *Salix* also have AM as seedlings, or when growing in extreme habitats (Lodge, 1989; Chen *et al.*, 2000; Pölme *et al.*, 2016). This variability becomes problematic if researchers focus on

one type of mycorrhiza, only examine seedlings or use a relaxed definition of EcM (Brundrett, 2017b).

Plants that appear to remain in an intermediate evolutionary state such as dual EcM–AM associations have multifunctional roots that may provide them with greater ecological flexibility, but overlapping functional roles would also come at a greater cost. However, these plants are often highly competitive suggesting that soil fertility is the most important factor limiting plant productivity in their habitats (Brundrett, 2009). For example, Australian eucalypts and acacias with multifunctional roots are important in plantation forestry and some are highly invasive weeds (Hui *et al.*, 2014). Despite the success of families that acquired new root trait changes in the second and third wave of mycorrhizal evolution, the majority of vascular plants (72–80%) have retained AM associations throughout their evolutionary history on land.

#### IV. Conclusions and perspectives

Transitions between nutrition strategies, especially gains or losses of EcM and NM strategies, are more common than previously thought, but completely new mycorrhizal types emerge very rarely. The plant groups undergoing frequent shifts in biotic associations with mycorrhizal fungi and nitrogen-fixing bacteria include the fabids clade of eurosids. Genomics and transcriptomics tools offer high-resolution insights into changes in genetic structure and gene expression profiles related to initiation and loss of symbioses (Garcia *et al.*, 2015; Delaux, 2017). These may include polyploidization events leading to functional shifts in gene paralogues, (e.g. MADS-box genes) which facilitate adaptive morphological radiation and diversification in plants (Van de Peer *et al.*, 2017). It is highly likely that similar processes occur during the acquisition of symbiotic associations with fungi and nitrogen-fixing bacteria through mechanisms that may involve phytohormones, defence suppressor and transportation factors (Delaux *et al.*, 2015; Garcia *et al.*, 2015).

We recognize three waves of mycorrhizal evolution, starting with the origin of AM in early land plants and continuing with a period of major root diversification in the Late Cretaceous, when EcM (except Pinaceae) and NM roots appeared, and ericoid and orchid mycorrhizas evolved. The third ongoing wave of mycorrhizal evolution is related to substantial climate change since the Palaeocene, which is linked to development of specialized nutrition strategies and multifunctional (e.g. EcM and AM) roots in a few plant families. Plants with such multifunctional roots are subject to rapid morphological and taxonomic diversification, especially on nutrient-impoorished soils in seasonally dry habitats. It is likely that plant lineages with newly acquired mycorrhizas do not function in the same way as ancient mycorrhizal lineages and may be regulated by a different suite of symbiotic genes (Delaux *et al.*, 2015; Maherali *et al.*, 2016). In particular, the southwest Australian biodiversity hotspot provides the opportunity to compare association ages and intensity for EcM, as a tool to better understand the evolution, physiology and genomics of mycorrhizas.

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

**Supplementary Material S1** Mycorrhiza slides for teaching.

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