Chapter 19
Evolution of Ectomycorrhizal Symbiosis in Plants

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19.1 Introduction

Ectomycorrhizal (EcM) symbiosis has evolved multiple times in plants and fungi (Brundrett 2009; Tedersoo and Smith 2013). Similarly to fungi in general, there is a lot of controversy in understanding the fungal root association of plant species. This can be partly attributed to environmental impact in arbuscular mycorrhizal (AM) associations, where facultatively mycorrhizal plants are common and development of root fungal structures depends on edaphic, floristic and climatic conditions as well as seasonality and ontogeny of plants (Smith and Read 2008). By contrast, the vast majority of EcM plants are obligately mycotrophic, and conflicts in assignment of mycorrhizal status seem to arise more from alternative definitions of the association (Brundrett 2009).

Here we define EcM and EcM-like associations based on the structure, phylogeny and putative function. At least two of these three criteria should be met for considering the associations to be EcM. First, Hartig net and fungal mantle (sheath) are the main structural characteristics of EcM, but these may be incompletely developed or patchy, as often seen in the EcM of herbs and shrubs. EcM associations of the ectendomycorrhiza subtype may additionally exhibit intracellular hyphal development that is characteristic to certain plant-fungal combinations

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(Yu et al. 2001). Second, EcM plants form phylogenetically distinct groups, although reversal to non-EcM habit (unlike in EcM fungi) or switch to mycoheterotrophy may have occurred. Pyroloid and monotropoid subtypes of EcM in Pyroleae and Monotropeae, respectively, are linked to the arbutoid subtype of Arbuteae within Ericaceae and are considered as EcM (Brundrett 2004). Similarly, mycorrhiza of *Pisonia* spp. with transfer cells is considered as a subtype of EcM. Third, EcM associations should also be essentially beneficial to both partners, but Monotropeae, Pterosporeae and perhaps Pyroleae do not fulfil this criterion. The phylogeny criterion clearly places Monotropeae and Pterosporeae among EcM associations but keeps orchids separate as they have evolved exclusively intracellular associations with EcM fungi secondarily and even photosynthetic orchids provide little if any benefits to fungi (Cameron et al. 2008). Furthermore, EcM plants also associate with mutualistic fungi from well-known EcM fungal lineages (Tedersoo and Smith 2013), with no known exceptions. The first EcM plant group that evolved certainly developed EcM associations with ‘previously unrecognised’ fungi. Theoretically, newly emerging EcM plants may associate with novel fungal groups, but this has not yet happened or these evolving associations have not persisted (see below). From this perspective, superficial root associations of *Entoloma clypeatum* group and Rosaceae (and *Ulmus*) and Helotiales-*Graffenrieda* (Melastomataceae) are to be considered non-EcM.

The oldest known EcM associations involve Pinaceae. The fossil records of unequivocal mycorrhizal structures of Pinaceae date back to the Eocene, although genera of the family evolved in the Late Jurassic or Early Cretaceous (LePage 2003). Since the Late Cretaceous and throughout Tertiary, many extant EcM groups of plants and fungi have evolved (Chaps. 1 and 20), followed by subsequent radiation and dispersal. In the last decade, several plant families have been deeply studied from the phylogenetic and biogeographic perspective that greatly adds to our understanding of the evolution of functional traits as well as biotrophic interactions with fungi, actinomycetes and other organisms (e.g. Werner et al. 2014).

In this synthesis, we critically assess the EcM status of plant genera based on published literature, personal observations as well as phylogenetic evidence. We also propose a number of genera that are potentially EcM based on their phylogenetic position but with no known root-level study. Finally, we discuss the issues in recognition of EcM symbiosis, ongoing evolution and groups with dual mycorrhiza.

19.2 Data Sources

We have compiled global literature about mycorrhizal status of plants for >10 years, also retrieving decades old literature based on the citations in Harley and Harley (1987), Wang and Qiu (2006), Koele et al. (2012) as well as Google Scholar. We carefully evaluated the descriptions of mycorrhizal status of EcM and putatively EcM plants. We also noted the inoculation and synthesis trials and growth benefits of plants. Based on the methodology, sample size and conflicts with other sources, we determined the reliability of particular studies when interpreting the mycorrhizal status.

Studies on plant phylogeny and molecular dating were searched from Google Scholar by combining names of particular plant genera, families or orders with 'phylogeny' and 'molecular dating' and 'biogeography' as key words. In addition, we searched the Angiosperm Phylogeny Website (www.mobot.org) for additional sources of literature as they often referred to information hidden in supplementary materials and not found by web search engines. We also used the tree file of the most comprehensive vascular plant phylogeny (Zanne et al. 2014). These different sources of phylogenetic information were combined to separate EcM plant genera into monophyletic lineages, allowing reversals to non-EcM habit. We refer to these lineages by taxon names, because in nearly all cases, the lineages fit into particular species, genera, (sub)tribes, (sub)families or orders.

Our consideration of mycorrhizal associations is based on genus level, because members of the same genus usually share the same mycorrhizal status, with multiple notable exceptions in Australian plants (Wang and Qiu 2006; Brundrett 2009). Most economically and ecologically important woody genera have been revised based on molecular phylogenetic tools, which has increased the value of the generic rank. Species-level information is also too sparse for specific conclusions. Plant taxonomy and species richness follows the Plant List (www.theplantlist.org). We follow Werner et al. (2014) and Benson et al. (2004) regarding rhizobial and actinorhizal associations, respectively.

19.3 Evolution of Ectomycorrhizal Habit

Critical evaluation of mycorrhizal and plant phylogenetic literature enabled us to distinguish 30 plant lineages that most probably evolved EcM associations independently (Fig. 19.1; Table 19.1). Searches through plant phylogenies revealed that 335 plant genera can be considered EcM (Table 19.2). Of these groups, 184 (54.9%) plant genera were regarded as ectomycorrhizal based on direct morphological evidence, whereas the remaining 151 genera were considered as belonging to EcM groups based on the monophyly criterion, although only AM has been reported in nine of these genera (see Supporting Information: http://dx.doi.org/10.15156/BIO/587454). The 335 putatively EcM genera were comprised of ca. 8500 species based on the Plant List (except Miller and Seigler 2012 for *Acacia s.str.*). Since <10% of these species exhibit reports on mycorrhizal status, it is highly possible that several genera and multiple species do not function as ectomycorrhizal (see Sect. 19.4.10). We estimate that approx. 6000–7000 species from 250 to 300 genera are truly capable of forming EcM associations.

Phylogenetic analyses revealed 22 potentially EcM genera (comprising 76 species) that represented sister groups to known EcM plant lineages or critical clades

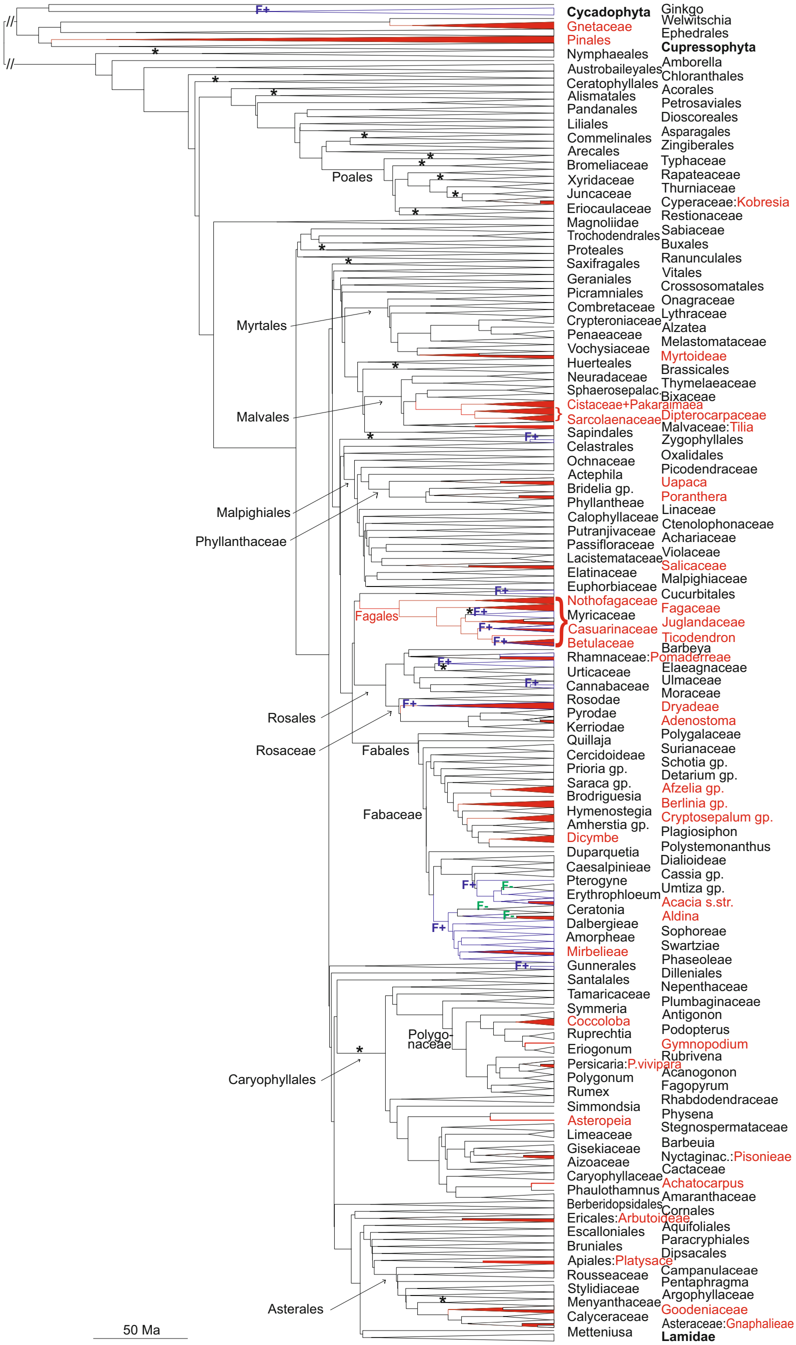

Fig. 19.1 Distribution of 30 ectomycorrhizal plant lineages (red branches and names) in the collapsed dated spermatophyte phylogram of Zanne et al. (2014), with improved taxonomic resolution of Fabaceae from LPWG (2017) and de la Estrella et al. (2017). *Asterisks* indicate

within large EcM groups that had secondarily lost EcM habit in certain occasions (see Sect. 19.7; Fig. 19.2). Thus, the root systems of representative species of these 170 genera nested within or closely affiliated to EcM groups certainly warrant further investigation for better understanding the evolution and distribution of EcM habit.

Taxonomic analysis of EcM plant lineages revealed that EcM habit evolved mostly from AM ancestors, which is consistent with Brundrett (2009). However, EcM symbiosis evolved in at least five occasions from non-mycorrhizal or facultatively AM-dependent ancestors (*Coccoloba*, *Persicaria vivipara*, *Gymnopodium* and Pisonieae within Caryophyllales and *Kobresia* within Poales). The latter finding is in a strong conflict with Maherali et al. (2016) who suggested that only AM habit can be ancestral to EcM habit. However, the authors excluded most of the above-mentioned groups from their final analysis, which must have strongly biased their results.

Of all 30 EcM plant lineages, *Gnetum* and Pinaceae represent gymnosperms, whereas all others belong to angiosperms The Fabaceae family alone includes seven EcM groups. The Myrtoideae represent the most genus-rich and species-rich EcM plant group (Table 19.2). Two additional Australian groups, viz. *Thysanotus* and *Lobelia*, are considered to possess EcM-like root associations, with distinct root anatomy and uncertain mode of nutrition (see Sect. 19.5; Chap. 17).

Integrating the information from community studies of EcM fungi and EcM plant lineages as described here reveals that there are no plant lineage-specific fungal lineages, although certain plant genera may associate with narrow fungal clades. This indicates that the evolution of EcM symbiosis in plants is linked to pre-existing fungal lineages and vice versa. This is a parsimonious scenario that would require critical modification of gene expression in only a single partner to become connected into a mycorrhizal network of a particular type. The lack of unique plant-fungal combinations furthermore indicates that the evolution of the first EcM plant-fungus association was an extremely rare event, which probably occurred and persisted only once or a few times. Unfortunately, there is no information, whether Pinaceae represent the very first EcM plant lineage or whether there was another, now extinct gymnosperm group. Strikingly, all known EcM fungal lineages are much younger than Pinaceae, suggesting that extinct groups of EcM fungi may have primarily associated with plants in the Jurassic period.

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Fig. 19.1 (continued) major reversal events to predominantly non-mycorrhizal habit according to Brundrett (2009). To illustrate the evolution of EcM symbiosis in tripartite associations with nitrogen-fixing rhizobia and *Frankia* actinobacteria, these interactions are indicated as branches and clades in blue; F+ and F− (*green*) denote evolution and loss of N fixation, respectively. Data about N fixation are derived from Werner et al. (2014) and searches of literature for minor uncovered Fabaceae groups. Taxa above the order rank are highlighted in bold. The *bar* indicates rough age estimates for higher taxa (Zanne et al. 2014), but these are not refined for Detarioideae and relatively recently derived EcM plant groups

Table 19.1 Plant lineages and their predicted age (Ma)

Lineage	Reliability of EcM habit	Stem age/crown age (reference)	Stem/crown age (Zanne et al. 2014)
Pinaceae	High	325–340/175–198 (Leslie et al. 2012; Lu et al. 2014)	267/238
Gnetum	High	130/26 (Won and Renner 2006)	87/75
Fagales	High	98/94 (Larson-Johnson 2015)	103/82
Pisonieae	High	<37/nd (Tank et al. 2015)[a]	29/26[a]
Achatocarpus	Low	<52/nd (Tank et al. 2015)	12/nd
Coccoloba	High	52/24 (Schuster et al. 2013)	20/14[a]
Gymnopodium	Low	35/nd (Schuster et al. 2013)	15/nd
Persicaria vivipara	High	<28/nd (Schuster et al. 2013)	7/nd
Asteropeiaceae	Medium	nd/nd	34/nd
Acacia	High (mostly AM-EcM or AM)	27/24 (Murphy et al. 2003)	0.9/0.8[a]
Aldina	High	<18/nd (Lavin et al. 2005)	34/nd
Mirbelieae	High (mostly AM-EcM)	52/50 (Toon et al. 2014)	50/45
Afzelia group	High	35/30 (de la Estrella et al. 2017)[a]	7.3/4.1[a]
Berlinia group	High	59/57 (de la Estrella et al. 2017)	15/13[a]
Cryptosepalum group	High	53/34 (de la Estrella et al. 2017)	nd/nd
Dicymbe	High	24/18 (de la Estrella et al. 2017)	nd/nd
Salicaceae	High (mostly EcM-AM)	45/33 (Davis et al. 2005)[a]	46/34[a]
Uapaca	High (mostly EcM-AM)	<<80/nd (Xi et al. 2012)	43/16
Poranthera	Medium	<<80/nd (Xi et al. 2012)	25/19
Pomaderreae	High	55/41 (Onstein et al. 2015)	43/30
Dryadeae	High	75/67 (Chin et al. 2014)	81/73
Adenostoma	Low (AM-EcM)	nd/nd	15/nd
Dipterocarpaceae-Cistaceae	High	33/23 (Wikström et al. 2001)[a]	73/49[a]
Tilia	High	32/17 (Richardson et al. 2015)[a]	14/8[a]
Gnaphalieae	Medium (mostly AM-EcM or AM)	12–16/10–14 (Bergh and Linder 2009)	5.2/4.4

(continued)

Table 19.1 (continued)

Lineage	Reliability of EcM habit	Stem age/crown age (reference)	Stem/crown age (Zanne et al. 2014)
Goodeniaceae	Medium (mostly AM-EcM or AM-NM	78/67 (Jabaily et al. 2014)	54/49
Myrtaceae	High (mostly EcM-AM)	85/72 (Thornhill et al. 2015)	66/63
Platysace	Medium	33/nd (Nicolas 2009)	70/15
Arbutoideae *s.lat*	High	110/102 (Schwery et al. 2015)	51/49
Kobresia	High (mostly EcM-NM)	$<$10/nd (Starr et al. 2004; Escudero et al. 2012)	5.0/4.5

Reliability indicates the number of studies and proven evidence for EcM formation in particular groups

nd not determined

[a] Values considered underestimates by us (questionable calibration or rate shifts or conflicting fossil evidence; see also Chap. 20)

Divergence times for only a small proportion of EcM fungal lineages have been studied, with oldest groups dating back to the Mid-Cretaceous (Chap. 1). Among the unstudied groups, there are no lineages that could be suspected of being really ancient, although the */cantharellus* and */clavulina* and some pezizalean lineages such as /tuber-helvella (Bonito et al. 2013) may potentially exceed 100 million years.

Given that certain EcM fungi associate with liverworts, it is possible that the necessary genetic mechanisms of establishing mutualism evolved long before the modern EcM anatomy evolved. However, phylogenetic evidence suggests that the association of Aneuraceae spp. (incl. *Aneura* = *Cryptothallus mirabilis*) with EcM *Tulasnella* sp. and ericoid mycorrhizal (ErM) fungi has evolved secondarily and relatively recently (Pressel et al. 2010). Except for a few instances, most of the potentially ancient associations with Endogonales in liverworts, hornworts and other lower plants are unrelated to endogonaceous EcM lineages (Yamamoto et al. 2015), but certainly more sequence data are required from both liverwort thalli, and roots of vascular plants are needed to understand their role in EcM and AM symbioses (Orchard et al. 2017). Taken together, it is more likely that the partially mycoheterotrophic lower plants switched to EcM plant lineages rather than these were ancestrally present in these bryophytes and then evolved to associate with EcM gymnosperms and angiosperms.

Table 19.2 Overview of ectomycorrhizal plant genera arranged by lineages

Taxon	No spp.	References (EcM status)	References (phylogeny)
Pinaceae			
Abies	47	Noack (1889), Sarauw (1903)	Lu et al. (2014)
Cathaya	1	Hu and Wang (1984)	Lu et al. (2014)
Cedrus	3	Sarauw (1903), Noelle (1910)	Lu et al. (2014)
Keteleeria	3	Ge et al. (2012)	Lu et al. (2014)
Larix	11	Sarauw (1903), McDougall (1914)	Lu et al. (2014)
Nothotsuga	1		Lu et al. (2014)
Picea	38	Frank (1885), Noack (1889)	Lu et al. (2014)
Pinus	113	Frank (1885), Noack (1889)	Lu et al. (2014)
Pseudolarix	1	Noelle (1910)	Lu et al. (2014)
Pseudotsuga	4	Noelle (1910), McDougall and Jacobs (1927)	Lu et al. (2014)
Tsuga	9	Noelle (1910), McDougall (1928)	Lu et al. (2014)
Gnetum			
Gnetum	39	Fassi (1957), St. John (1980)	Won and Renner (2006)
Fagales[a]			
Alfaroa (Jug)	8		Larson-Johnson (2015)
Allocasuarina (Cas)	59	McGee (1986), Brundrett and Abbott (1991)	Larson-Johnson (2015)
Alnus (Bet)	37	Frank (1888), Masui (1926)	Larson-Johnson (2015)
Betula (Bet)	98	Frank (1888), Peyronel (1922)	Larson-Johnson (2015)
Carpinus (Bet)	40	McDougall (1914), Doak (1927)	Larson-Johnson (2015)
Carya (Jug)	18	McDougall (1914), Doak (1927)	Larson-Johnson (2015)
Castanea (Fag)	8	Frank (1885), Mangin (1910)	Larson-Johnson (2015)
Castanopsis (Fag)	132	Maeda (1954), Haug et al. (1991)	Larson-Johnson (2015)
Casuarina (Cas)	14	Tandy (1975), Warcup (1980) (AM dominates)	Larson-Johnson (2015)
Chrysolepis (Fag)	2	Trappe (1964), Longway (2015)	Larson-Johnson (2015)
Colombobalanus (Fag)	1		Larson-Johnson (2015)
Corylus (Bet)	17	Frank (1885), Mangin (1910)	Larson-Johnson (2015)
Engelhardia (Jug)	12	Haug et al. (1991), (1994), AM: Sharma et al. (1986)	Larson-Johnson (2015)

(continued)

Table 19.2 (continued)

Taxon	No spp.	References (EcM status)	References (phylogeny)
Fagus (Fag)	10	Kamienski (1882); Frank (1885)	Larson-Johnson (2015)
Formanodendron (Fag)	1		Larson-Johnson (2015)
Lithocarpus (incl. *Pasania*) (Fag)	334	Asai (1934), Haug et al. (1994)	Larson-Johnson (2015)
Nothofagus (Noth)	34	Frank (1888), Morrison (1956)	Larson-Johnson (2015)
Notholithocarpus (Fag)	1	Kennedy et al. (2003)	Larson-Johnson (2015)
Oreomunnea (Jug)	2	Corrales et al. (2016)	Larson-Johnson (2015)
Ostrya (Bet)	9	Lohman (1926), Doak (1927)	Larson-Johnson (2015)
Ostryopsis (Bet)	2	Bai et al. (2003)	Larson-Johnson (2015)
Quercus (incl. *Cyclobalanopsis*) (Fag)	431	Frank (1885), Noack (1889)	Larson-Johnson (2015)
Ticodendron (Tic)	1	Põlme et al. unpubl.	Larson-Johnson (2015)
Trigonobalanus (Fag)	1		Larson-Johnson (2015)
Pisonieae			
Guapira	79	Moyersoen (1993), Haug et al. (2005)	Cuenoud et al. (2002), Douglas and Manos (2007)
Neea	72	Janos (1980), St. John (1980)	Cuenoud et al. (2002), Douglas and Manos (2007)
Pisonia	20 of 24	Ashford and Allaway (1982), Lodge (1996)	Cuenoud et al. (2002), Douglas and Manos (2007)
Achatocarpus			
Achatocarpus	10	Alvarez-Manjarrez and Garibay-Orijel (2015)	Cuenoud et al. (2002)
Coccoloba			
Coccoloba	172	Kreisel (1970), Moyersoen (1993)	Cuenoud et al. (2002), Schuster et al. (2013)
Gymnopodium			
Gymnopodium	2	Bandala et al. (2011)	Schuster et al. (2013)

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Table 19.2 (continued)

Taxon	No spp.	References (EcM status)	References (phylogeny)
Persicaria vivipara			
Persicaria vivipara	2 of 66	Hesselman (1900), Costantin and Magrou (1926)	Cuenoud et al. (2002), Schuster et al. (2013)
Asteropeiaceae			
Asteropeia	8	Ducousso et al. (2008), Tedersoo et al. (2011)	Cuenoud et al. (2002)
Acacia			
Acacia s. stricto	ca 1000	Warcup (1980), McGee (1986)	Murphy et al. (2003)
Aldina			
Aldina	22	Meyer (1991), Moyersoen (1993)	Ramos et al. (2016)
Mirbelieae			
Aenictophyton	1		LPWG (2017)
Almaleea	5		Crisp and Cook (2003)
Aotus	14		Crisp and Cook (2003)
Bossiaea	49	AM: Zemunik et al. (2015)	Zanne et al. (2014)
Brachysema	11	Warcup (1980)	Crisp and Cook (2003)
Callistachys	1		Crisp and Cook (2003)
Chorizema	16	Warcup (1980)	Crisp and Cook (2003)
Daviesia	78	Warcup (1980), Meers et al. (2010), Teste et al. (2017), AM: Bellgard (1991), NM: Brundrett and Abbott (1991)	Crisp and Cook (2003)
Dillwynia	21	Warcup (1980), McGee (1986)	Crisp and Cook (2003)
Erichsenia	1		Crisp and Cook (2003)
Euchilopsis	1		Crisp and Cook (2003)
Eutaxia	7	Warcup (1980)	Crisp and Cook (2003)
Gastrolobium	36	Lamont et al. (1985), Teste et al. (2017)	Crisp and Cook (2003)
Gompholobium	35	Warcup (1980), Kope and Warcup (1986), Brundrett and Abbott (1991), Meers et al. (2010), AM: Zemunik et al. (2015), AM: Bellgard (1991)	Crisp and Cook (2003)
Isotropis	12	AM: Zemunik et al. (2015)	Crisp and Cook (2003)

(continued)

Table 19.2 (continued)

Taxon	No spp.	References (EcM status)	References (phylogeny)
Jacksonia	37	Warcup (1980), Reddell and Milnes (1992), Zemunik et al. (2015), AM: Brundrett and Abbott (1991)	Crisp and Cook (2003)
Jansonia	1		Crisp and Cook (2003)
Latrobea	5		Crisp and Cook (2003)
Leptosema	6		Crisp and Cook (2003)
Mirbelia	26	Warcup (1980), Bellgard (1991)	Crisp and Cook (2003)
Muelleranthus	1		LPWG (2017)
Oxylobium	17	Warcup (1980), Brundrett and Abbott (1991)	Crisp and Cook (2003)
Phyllota	10		Crisp and Cook (2003)
Platylobium	4	Warcup (1980), Meers et al. (2010)	Crisp and Cook (2003)
Podolobium	1		Crisp and Cook (2003)
Pultenaea	103	Warcup (1980), Warcup (1985)	Crisp and Cook (2003)
Sphaerolobium	18		LPWG (2017)
Stonesiella	1		Crisp and Cook (2003)
Urodon	2		Crisp and Cook (2003)
Viminaria	1	Warcup (1980), Bell and Yasmeen (2010), AM: Brundrett and Abbott (1991), AM: de Campos et al. (2013)	Crisp and Cook (2003)
***Afzelia* group**			
Afzelia	14	Fassi and Fontana (1962), Jenik and Mensah (1967)	de la Estrella et al. (2017)
Intsia	2	Alexander and Högberg (1986), Alexander (1989)	de la Estrella et al. (2017)
***Berlinia* group**			
Anthonotha	30	Peyronel and Fassi (1960), Fassi and Fontana (1962)	de la Estrella et al. (2017)
Aphanocalyx	14	as *Monopetalanthus*: Fassi and Fontana (1962), Newbery et al. (1988)	de la Estrella et al. (2017)
Berlinia	16	Newbery et al. (1988), Alexander (1989)	de la Estrella et al. (2017)
Bikinia	10	as *Monopetalanthus*: Onguene (2000)	de la Estrella et al. (2017)
Brachystegia	34	Peyronel and Fassi (1960), Fassi and Fontana (1962)	de la Estrella et al. (2017)

(continued)

Table 19.2 (continued)

Taxon	No spp.	References (EcM status)	References (phylogeny)
Didelotia	12	Newbery et al. (1988), Alexander (1989)	de la Estrella et al. (2017)
Englerodendron	2		de la Estrella et al. (2017)
Gilbertiodendron	26	Peyronel and Fassi (1960), Fassi and Fontana (1962)	de la Estrella et al. (2017)
Icuria	1		de la Estrella et al. (2017)
Isoberlinia	5	Alexander and Högberg (1986), Högberg and Piearce (1986)	de la Estrella et al. (2017)
Isomacrolobium	12		de la Estrella et al. (2017)
Julbernardia	11	Peyronel and Fassi (1960), Fassi and Fontana (1962)	de la Estrella et al. (2017)
Librevillea	1		de la Estrella et al. (2017)
Michelsonia	1		Gervais and Bruneau (2002)
Microberlinia	2	Newbery et al. (1988), Alexander (1989)	de la Estrella et al. (2017)
Monopetalanthus	2		Bruneau et al. (2001)
Oddoniodendron	3		de la Estrella et al. (2017)
Pellegriniodendron	1	Alexander (1989), Riviere et al. (2001)	Bruneau et al. (2001)
Pseudomacrolobium	1		LPWG (2017)
Tetraberlinia	7	Newbery et al. (1988), Alexander (1989)	de la Estrella et al. (2017)
Toubaouate	1	Onguene (2000)	de la Estrella et al. (2017)
***Cryptosepalum* group**			
Cryptosepalum	11	Alexander (1989), Rivière (2004)	de la Estrella et al. (2017)
Paramacrolobium	1	Peyronel and Fassi (1960), Fassi and Fontana (1962)	de la Estrella et al. (2017)
Dicymbe			
Dicymbe	15	Henkel et al. (2000, 2002)	de la Estrella et al. (2017)
Salicaceae			
Populus	29	Frank (1885), Stahl (1900)	Davis et al. (2005), Chen et al. (2010)
Salix	475	Frank (1885), Stahl (1900), Hesselman (1900)	Davis et al. (2005), Chen et al. (2010)
Uapaca			
Uapaca	49	Redhead (1974), Högberg (1982)	Wurdack et al. (2004)

(continued)

Table 19.2 (continued)

Taxon	No spp.	References (EcM status)	References (phylogeny)
Poranthera			
Poranthera	14	Warcup (1980), Kope and Warcup (1986), McGee (1986), Bellgard (1991), Teste et al. (2017), non-EcM: Chap. 17	Wurdack et al. (2004), Vorontsova et al. (2007)
Pomaderreae			
Blackallia	1		Ladiges et al. (2005)
Cryptandra	57	Warcup (1980), Brundrett and Abbott (1991)	Ladiges et al. (2005)
Papistylus	2		Onstein et al. (2015)
Polianthion	4		Onstein et al. (2015)
Pomaderris	70	Ashton (1975), Warcup (1980)	Ladiges et al. (2005)
Serichonus	1		Onstein et al. (2015)
Siegfriedia	1		Ladiges et al. (2005)
Spyridium	40	Warcup (1980), Zemunik et al. (2015), AM: McGee (1986)	Ladiges et al. (2005)
Stenanthemum	14	Zemunik et al. (2015)	Ladiges et al. (2005)
Trymalium	30	Warcup (1980, 1985), Brundrett and Abbott (1991)	Ladiges et al. (2005)
Dryadeae			
Cercocarpus	5	Thomas (1943), Trappe (1964), Williams (1979), AM: Rose (1980)	Potter et al. (2007)
Chamaebatia	2	Trappe (1964)	Potter et al. (2007)
Cowania	1		Potter et al. (2007)
Dryas	9	Hesselman (1900), Jessen (1914)	Potter et al. (2007)
Purshia	6	AM: Williams (1979), AM: Rose (1980)	Potter et al. (2007)
Adenostoma			
Adenostoma	2	Cooper (1922), Allen et al. (1999a,b)	Potter et al. (2007)
Dipterocarpaceae-Cistaceae[b]			
Anisoptera (Dipt)	11	Singh (1966), Chalermpongse (1987)	Dayanandan et al. (1999)
Cistus (Cist)	21	Chevalier et al. (1975), Fontana and Giovannetti (1978)	Guzmán and Vargas (2009)
Cotylelobium (Dipt)	6	Hong (1979), de Alwis and Abeynayake (1980)	Dayanandan et al. (1999)
Crocanthemum (Cist)	20		Guzmán and Vargas (2009)
Dipterocarpus (Dipt)	69	Singh (1966), de Alwis and Abeynayake (1980)	Dayanandan et al. (1999)
Dryobalanops (Dipt)	7	Singh (1966), Hong (1979)	Dayanandan et al. (1999)
Eremolaena (Sarc)	3		Aubriot et al. (2016)

(continued)

Table 19.2 (continued)

Taxon	No spp.	References (EcM status)	References (phylogeny)
Fumana (Cist)	9	Chevalier et al. (1975), Kovacs and Szigetvari (2002)	Guzmán and Vargas (2009)
Halimium (Cist)	8	Buscardo et al. (2012)	Guzmán and Vargas (2009)
Helianthemum (Cist)	90	Peyronel (1930), Boursnell (1950)	Guzmán and Vargas (2009)
Hopea (Dipt)	102	Van Roosendael and Thorenaar (1924), Singh (1966)	Dayanandan et al. (1999)
Hudsonia (Cist)	3	Malloch and Thorn (1985), Massicotte et al. (2010)	Guzmán and Vargas (2009)
Lechea (Cist)	17	Malloch and Thorn (1985)	Guzmán and Vargas (2009)
Leptolaena (Sarc)	8	Ducousso et al. (2004, 2008)	Aubriot et al. (2016)
Marquesia (Mon)	3	Alexander and Högberg (1986), Högberg and Piearce (1986)	Gunasekara (2004)
Mediusella (Sarc)	2		Aubriot et al. (2016)
Monotes (Mon)	30	Högberg (1982), Alexander and Högberg (1986)	Dayanandan et al. (1999)
Neobalanocarpus (Dipt)	1	Singh (1966), Zainudin (1990)	Dayanandan et al. (1999)
Pakaraimaea (Pak)	1	Moyersoen (2006)	Dayanandan et al. (1999)
Parashorea (Dipt)	14	Noor (1981), Lee (1988)	Gunasekara (2004)
Pentachlaena (Sarc)	3		Aubriot et al. (2016)
Perrierodendron (Sarc)	5		Aubriot et al. (2016)
Pseudomonotes (PsM)	1	Vasco Palacios et al. unpubl.	Morton et al. (1999)
Rhodolaena (Sarc)	7		Aubriot et al. (2016)
Sarcolaena (Sarc)	8	Ducousso et al. (2004, 2008)	Dayanandan et al. (1999), Aubriot et al. (2016)
Schizolaena (Sarc)	22	Ducousso et al. (2004, 2008)	Aubriot et al. (2016)
Shorea (Dipt)	194	de Voogd (1933), Singh (1966)	Dayanandan et al. (1999)
Stemonoporus (Dipt)	15		Dayanandan et al. (1999)
Tuberaria (Cist)	12	Proctor (1960)	Guzmán and Vargas (2009)
Upuna (Dipt)	1		Dayanandan et al. (1999)
Vateria (Dipt)	2	Alexander and Högberg (1986)	Dayanandan et al. (1999)
Vateriopsis (Dipt)	1	Tedersoo et al. (2007a,b)	Gunasekara (2004)

(continued)

Table 19.2 (continued)

Taxon	No spp.	References (EcM status)	References (phylogeny)
Vatica (Dipt)	65	Singh (1966), Santoso (1988)	Dayanandan et al. (1999)
Xerochlamys (Sarc)	7		Aubriot et al. (2016)
Xyloolaena (Sarc)	5		Aubriot et al. (2016)
Tilia			
Craigia	2		Nyffeler et al. (2005), within Tilia: Zanne et al. (2014)
Tilia	44	McDougall (1914), Peyronel (1922)	Nyffeler et al. (2005)
Gnaphalieae			
Acanthocladium	1		Bayer et al. (2002)
Acomis	4		Bayer et al. (2002)
Actinobole	4		Bayer et al. (2002), Bergh and Linder (2009)
Ammobium	2		Bayer et al. (2002)
Anaphalioides	8		Breitwieser and Ward (2003)
Anemocarpa	3		Bayer et al. (2002)
Angianthus	19	Warcup and McGee (1983), Kope and Warcup (1986), Warcup (1990), AM: Zemunik et al. (2015)	Bayer et al. (2002), Bergh and Linder (2009)
Apalochlamys	1		Bayer et al. (2002)
Argentipallium	6		Bayer et al. (2002), Bergh and Linder (2009)
Argyroglottis	1		Bayer et al. (2002); Bergh and Linder (2009)
Argyrotegium	4		Breitwieser and Ward (2003)
Asteridea	11	Warcup (1990), AM: Chap. 17	Bayer et al. (2002)
Bellida	1		Bayer et al. (2002)
Blennospora	3	Warcup (1990)	Bayer et al. (2002)
Calocephalus	9		Bayer et al. (2002)
Calomeria	2		Bayer et al. (2002)
Cassinia	37		Bayer et al. (2002)
Cephalipterum	1		Bayer et al. (2002)
Cephalosorus	1	Warcup (1990)	Bayer et al. (2002)
Chondropyxis	1	Warcup (1990)	Bayer et al. (2002)
Chrysocephalum	9		Bayer et al. (2002)
Cryptocoryne	2	Warcup and McGee (1983)	Bayer et al. (2002)
Chthonocephalus	7		Bayer et al. (2002)

(continued)

Table 19.2 (continued)

Taxon	No spp.	References (EcM status)	References (phylogeny)
Coronidium	10		Schmidt-Lebuhn et al. (2015)
Decazesia	1		Bayer et al. (2002), Bergh and Linder (2009)
Dithyrostegia	2		Bayer et al. (2002)
Eriochlamys	4	Warcup (1990)	Bayer et al. (2002)
Erymophyllum	5	Warcup and McGee (1983), Warcup (1990), AM: Teste et al. (2017)	Bayer et al. (2002)
Euchiton	17	AM: Meers et al. (2010)	Breitwieser and Ward (2003)
Ewartiothamnus	1		Breitwieser and Ward (2003)
Feldstonia	1		Bayer et al. (2002)
Fitzwillia	1	Warcup (1990)	Bayer et al. (2002), Bergh and Linder (2009)
Gilberta	1		Bayer et al. (2002)
Gilruthia	1		Bayer et al. (2002)
Gnephosis	17	Warcup (1990), AM: Teste et al. (2017)	Bayer et al. (2002)
Haeckeria	3		Bayer et al. (2002), Bergh and Linder (2009)
Haegiela	1		Zanne et al. (2014)
Haptotrichion	2		Zanne et al. (2014)
Helichrysum (Australian spp.)	30 of 536	Warcup and McGee (1983), McGee (1986), Warcup (1990), AM: Meers et al. (2010)	Bayer et al. (2002), Bergh and Linder (2009)
Hyalochlamys	1		Bayer et al. (2002)
Hyalosperma	9		Bayer et al. (2002)
Ixiolaena	1		Bayer et al. (2002), Bergh and Linder (2009)
Ixodia	1	Warcup (1990)	Bayer et al. (2002)
Lawrencella	2		Bayer et al. (2002)
Leiocarpa	11		Zanne et al. (2014)
Lemooria	1		Bayer et al. (2002)
Leptorhynchos	10	Warcup and McGee (1983), Warcup (1990)	Bayer et al. (2002)
Leucochrysum	7		Bayer et al. (2002), Bergh and Linder (2009)
Leucogenes	4		Breitwieser and Ward (2003)

(continued)

Table 19.2 (continued)

Taxon	No spp.	References (EcM status)	References (phylogeny)
Leucophyta	1		Bayer et al. (2002)
Millotia	16		Bayer et al. (2002), Bergh and Linder (2009)
Myriocephalus	15		Bayer et al. (2002)
Odixia	2		Bayer et al. (2002)
Ozothamnus	53	AM: Teste et al. (2017)	Bayer et al. (2002), Bergh and Linder (2009)
Parantennaria	1		Zanne et al. (2014)
Pithocarpa	2		Bayer et al. (2002), Bergh and Linder (2009)
Pleuropappus	1		Bayer et al. (2002)
Podolepis	20	Warcup and McGee (1983), McGee (1986), Warcup (1990), Teste et al. (2017)	Bayer et al. (2002), Bergh and Linder (2009)
Podotheca	6	Warcup (1990), AM: Teste et al. (2017), Chap. 17	Bayer et al. (2002)
Pogonolepis	2	Warcup and McGee (1983)	Bayer et al. (2002), Bergh and Linder (2009)
Polycalymma	1		Bayer et al. (2002), Bergh and Linder (2009)
Pterochaeta	1		Bayer et al. (2002)
Pycnosorus	6		Bayer et al. (2002), Bergh and Linder (2009)
Quinetia	1		Bayer et al. (2002), Bergh and Linder (2009)
Quinqueremulus	1		Bayer et al. (2002)
Raoulia	26		Breitwieser and Ward (2003)
Rhodanthe	46	Warcup and McGee (1983), Teste et al. (2017)	Bayer et al. (2002)
Rutidosis	10	Warcup and McGee (1983), Warcup (1990)	Bayer et al. (2002)
Schoenia	6		Zanne et al. (2014)
Siemssenia	1		Zanne et al. (2014)
Siloxerus	4		Bayer et al. (2002), Bergh and Linder (2009)

(continued)

Table 19.2 (continued)

Taxon	No spp.	References (EcM status)	References (phylogeny)
Sondottia	2	Warcup (1990)	Bayer et al. (2002), Bergh and Linder (2009)
Toxanthes	1	McGee (1986)	Bayer et al. (2002)
Trichanthodium	3	Warcup (1990)	Bayer et al. (2002)
Triptilodiscus	1	Warcup (1990)	Bayer et al. (2002)
Waitzia (Waitzea)	5	Warcup and McGee (1983), Kope and Warcup (1986), Warcup (1990)	Bayer et al. (2002)
Xerochrysum	8		Bayer et al. (2002)
Goodeniaceae			
Anthotium	4		Gustafsson et al. (1996), Jabaily et al. (2014)
Brunonia	1	Warcup (1980, 1985)	Gustafsson et al. (1996), Jabaily et al. (2014)
Calogyne	1	Reddell and Milnes (1992)	Gustafsson et al. (1996), Jabaily et al. (2014)
Coopernookia	6		Gustafsson et al. (1996), Jabaily et al. (2014)
Dampiera	69	McGee (1986), Bellgard (1991), AM: Brundrett and Abbott (1991), AM: Teste et al. (2017)	Gustafsson et al. (1996), Jabaily et al. (2014)
Diaspasis	1		Gustafsson et al. (1996), Jabaily et al. (2014)
Goodenia	ca 200	Warcup (1980, 1985), McGee (1986), AM: Teste et al. (2017)	Gustafsson et al. (1996), Jabaily et al. (2014)
Scaevola	ca 120	Zemunik et al. (2015), Teste et al. (2017), AM: Asai (1934), AM: Peterson et al. (1985), AM: Koske (1988), AM: Brundrett and Abbott (1991)	Gustafsson et al. (1996), Jabaily et al. (2014)
Selliera	ca 5		Gustafsson et al. (1996), Jabaily et al. (2014)
Velleia	29		Gustafsson et al. (1996), Jabaily et al. (2014)
Verreauxia	1		Gustafsson et al. (1996), Jabaily et al. (2014)

(continued)

Table 19.2 (continued)

Taxon	No spp.	References (EcM status)	References (phylogeny)
Myrtaceae[c]			
Actinodium (Cha)	1		Thornhill et al. (2015)
Agonis (Lept)	6	Brundrett and Abbott (1991)	Thornhill et al. (2015)
Allosyncarpia (Euc)	1	Reddell and Milnes (1992)	Thornhill et al. (2015)
Angophora (Euc)	13	Tandy (1975), Bellgard (1991)	Thornhill et al. (2015)
Arillastrum (Euc)	1	Buyck et al. (2012), Jourand et al. (2014)	Thornhill et al. (2015)
Astartea (Cha)	9		Lam et al. (2002)
Asteromyrtus (Lept)	7	Reddell and Milnes (1992)	Thornhill et al. (2015)
Astus (Cha)	4		Zanne et al. (2014)
Babingtonia (Cha)	2		Lam et al. (2002)
Backhousia (Back)	11	Reddell et al. (1996)	Thornhill et al. (2015)
Baeckea (Cha)	47	McGee (1986), Bellgard (1991)	Thornhill et al. (2015)
Balaustion (Cha)	1		Zanne et al. (2014)
Barongia (Kan)	1		Wilson et al. (2005)
Beaufortia (Mel)	20		Thornhill et al. (2015)
Callistemon (Mel)	37	Warcup (1980)	Thornhill et al. (2015)
Calothamnus (Mel)	44	Zemunik et al. (2015), Teste et al. (2017)	Thornhill et al. (2015)
Calytrix (Cha)	80	Langkamp and Dalling (1982), McGee (1986), Reiter et al. (2013), AM: Brundrett and Abbott (1991), AM: Zemunik et al. (2015), AM: Teste et al. (2017)	Thornhill et al. (2015)
Chamelaucium (Cha)	13		Thornhill et al. (2015)
Choricarpia (Back)	2		Thornhill et al. (2015)
Cloezia (Tri)	6		Thornhill et al. (2015)
Conothamnus (Mel)	1		Thornhill et al. (2015)
Darwinia (Cha)	52	AM: Zemunik et al. (2015)	Thornhill et al. (2015)
Eremaea (Mel)	16	Zemunik et al. (2015), Teste et al. (2017)	Thornhill et al. (2015)
Eucalyptopsis (Euc)	2	L. Tedersoo, unpubl.	Thornhill et al. (2015)
Eucalyptus (incl. *Corymbia*) (Euc)	755	Samuel (1926), Pryor (1956), Trappe (1964), Chilvers and Pryor (1965)	Thornhill et al. (2015)
Euryomyrtus (Cha)	8		Thornhill et al. (2015)
Harmogia (Cha)	1		Thornhill et al. (2015)
Homalocalyx (Cha)	11		Thornhill et al. (2015)
Homalospermum (Lept)	1		O'Brien et al. (2000)
Homoranthus (Cha)	23		Thornhill et al. (2015)
Hypocalymma (Cha)	24	AM: Brundrett and Abbott (1991), AM: Teste et al. (2017)	Thornhill et al. (2015)

(continued)

Table 19.2 (continued)

Taxon	No spp.	References (EcM status)	References (phylogeny)
Kardomia (Cha)	6		Thornhill et al. (2015)
Kjellbergiodendron (Loph)	1		Thornhill et al. (2015)
Kunzea (Lept)	42	Baylis (1962), Bellgard (1991)	Thornhill et al. (2015)
Lamarchea (Mel)	2		Thornhill et al. (2015)
Leptospermum (Lept)	91	Tandy (1975), Cooper (1976)	Thornhill et al. (2015)
Lophostemon (Loph)	5	Reddell and Milnes (1992), Reddell et al. (1996)	Thornhill et al. (2015)
Lysicarpus (Kan)	1		Thornhill et al. (2015)
Malleostemon (Cha)	6		Lam et al. (2002)
Melaleuca (Mel)	264	Warcup (1980), Alexander and Högberg (1986)	Thornhill et al. (2015)
Micromyrtus (Cha)	50		Thornhill et al. (2015)
Mitrantia (Kan)	1		Wilson et al. (2005)
Neofabricia (Lept)	3		O’Brien et al. (2000)
Ochrosperma (Cha)	6		Thornhill et al. (2015)
Pericalymma (Lept)	4	Brundrett and Abbott (1991)	Thornhill et al. (2015)
Petraeomyrtus (Mel)	1		Thornhill et al. (2015)
Phymatocarpus (Mel)	1		Thornhill et al. (2015)
Pileanthus (Cha)	8	Zemunik et al. (2015)	Thornhill et al. (2015)
Regelia (Mel)	3		Thornhill et al. (2015)
Rinzia (Cha)	12		Lam et al. (2002)
Ristantia (Kan)	3		Wilson et al. (2005)
Sannantha (Cha)	15	Jourand et al. (2014)	Thornhill et al. (2015)
Scholtzia (Cha)	13	AM: Zemunik et al. (2015), AM: Teste et al. (2017)	Lam et al. (2002)
Seorsus (Cha)	4		Zanne et al. (2014)
Sphaerantia (Kan)	2		Thornhill et al. (2015)
Stockwellia (Euc)	2		Thornhill et al. (2015)
Taxandria (Lept)	12		Zanne et al. (2014)
Thaleropia (Tri)	3		Thornhill et al. (2015)
Thryptomene (Cha)	32	Reiter et al. (2013), Teste et al. (2017)	Thornhill et al. (2015)
Triplarina (Cha)	7		Lam et al. (2002)
Tristania (Tri)	1	Tandy (1975), Alexander and Högberg (1986)	Thornhill et al. (2015)
Tristaniopsis (Kan)	42	Perrier et al. (2006), Prin et al. (2012)	Thornhill et al. (2015)
Welchiodendron	1		Wilson et al. (2005)
Verticordia (Cha)	111	AM: Brundrett and Abbott (1991), AM: Teste et al. (2017)	Thornhill et al. (2015)

(continued)

Table 19.2 (continued)

Taxon	No spp.	References (EcM status)	References (phylogeny)
Whiteodendron (Loph)	1		Wilson et al. (2005)
Xanthomyrtus (Tri)	25		Thornhill et al. (2015)
Xanthostemon (Xan)	49	Richards et al. (2003), AM: Reddell and Milnes (1992)	Thornhill et al. (2015)
Platysace			
Platysace	27	Warcup (1980), Bellgard (1991), Teste et al. (2017), non-EcM: Chap. 17	Nicolas (2009)
Arbutoideae *s.lat* [d]			
Allotropa (Mon)	1	Castellano and Trappe (1985), Bidartondo (2005)	Bidartondo (2005), Kron and Luteyn (2005)
Arbutus (Arb)	10	Dufrenoy (1917), Zak (1974)	Hileman et al. (2001), Kron and Luteyn (2005)
Arctostaphylos (incl. *Arctous*) (Arb)	60	Christoph (1921), Peyronel (1930)	Hileman et al. (2001), Kron and Luteyn (2005)
Cheilotheca (Mon)	2	Bidartondo (2005)	Bidartondo (2005), Kron and Luteyn (2005)
Chimaphila (Pyr)	5	Largent et al. (1980), Massicotte et al. (2008)	Bidartondo (2005), Kron and Luteyn (2005)
Comarostaphylis (Arb)	10	Osmundson et al. (2007), Kühdorf et al. (2015)	Hileman et al. (2001), Kron and Luteyn (2005)
Hemitomes (Mon)	1	Castellano and Trappe (1985), Bidartondo (2005)	Bidartondo (2005), Kron and Luteyn (2005)
Moneses (Pyr)	2	Christoph (1921), Massicotte et al. (2008)	Bidartondo (2005), Kron and Luteyn (2005)
Monotropa (Mon)	1	Kamienski (1882), Frank (1887)	Bidartondo (2005), Kron and Luteyn (2005)
Monotropastrum (Mon)	1	Matsuda and Yamada (2003), Bidartondo (2005)	Bidartondo (2005), Kron and Luteyn (2005)
Monotropsis (Mon)	1	Bidartondo (2005)	Bidartondo (2005), Kron and Luteyn (2005)
Ornithostaphylos (Arb)	1		Hileman et al. (2001), Kron and Luteyn (2005)

(continued)

Table 19.2 (continued)

Taxon	No spp.	References (EcM status)	References (phylogeny)
Orthilia (Pyr)	1	Christoph (1921), Malloch and Malloch (1982)	Bidartondo (2005), Kron and Luteyn (2005)
Pityopus (Mon)	1	Bidartondo (2005)	Bidartondo (2005), Kron and Luteyn (2005)
Pleuricospora (Mon)	1	Castellano and Trappe (1985), Bidartondo (2005)	Bidartondo (2005), Kron and Luteyn (2005)
Pterospora (Pter)	2	Castellano and Trappe (1985), Bidartondo (2005)	Bidartondo (2005), Kron and Luteyn (2005)
Pyrola (Pyr)	30	Kramar (1901), Christoph (1921)	Bidartondo (2005), Kron and Luteyn (2005)
Sarcodes (Pter)	1	Bidartondo (2005)	Bidartondo (2005), Kron and Luteyn (2005)
Xylococcus (Arb)	1	L. Tedersoo, unpubl.	Zanne et al. (2014)
Kobresia			
Kobresia	ca 30 of 58	Fontana (1963), Haselwandter and Read (1980)	Starr et al. (2004)

References to EcM status indicate time of first description and conflicting evidence. The generic and species nomenclature and the number of accepted species follow the Plant List, with specifications from phylogenetic studies in case of unsplit genera (*Acacia s.lat*) or unresolved groups (Goodeniaceae, *Kobresia*, *Pisonia*, *Persicaria*, *Helichrysum*). More references are provided in Supporting Information: http://dx.doi.org/10.15156/BIO/587454

[a] *Bet* Betulaceae, *Cas* Casuarinaceae, *Fag* Fagaceae, *Jug* Juglandaceae, *Noth* Nothofagaceae, *Tic* Ticodendraceae

[b] *Cist* Cistaceae, *Dipt* Dipterocarpoideae, *Mon* Monotoideae, *Pak* Pakaraimaeaceae, *PsM* Pseudomonotoideae, *Sarc* Sarcolaenaceae

[c] *Back* Backhousieae, *Cham* Chamelaucieae, *Kan* Kanieae, *Lept* Leptospermeae, *Loph* Lophostemoneae, *Mel* Melaleuceae, *Tri* Tristanieae, *Xant* Xanthostemoneae

[d] *Arb* Arbuteae, *Euc* Eucalypteae, *Mon* Monotropeae, *Pter* Pterosporeae, *Pyr* Pyroleae

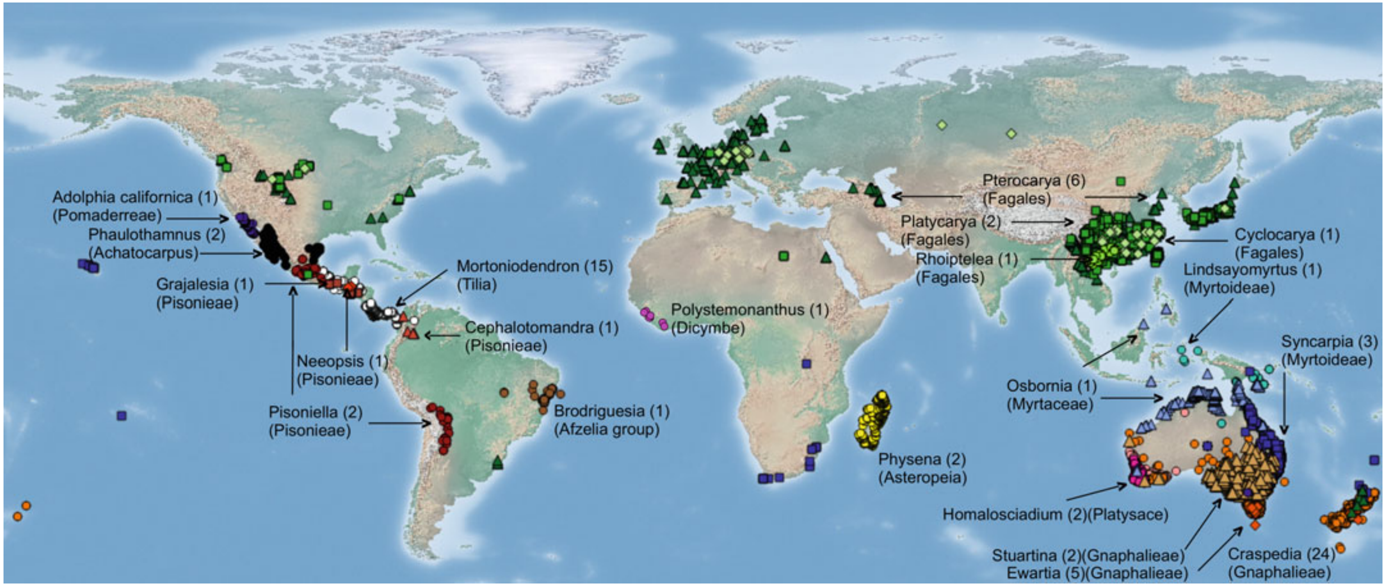

Fig. 19.2 Native and assisted distribution of top 22 most wanted plant genera that have no information about mycorrhizal status but are placed in sister position to known EcM lineages. Colours are grouped according to phylogenetic affinities as indicated in parentheses, and closely related genera are further distinguished by symbols. Numbers in parentheses indicate the number of species. Note that the European and American distribution of the three Juglandaceae genera represents their introduced range. Similarly, Hawaiian and South African distribution of *Syncarpia* indicates its introduced range. All data are based on GBIF (accessed 17.12.2016) records that include coordinates

19.4 Ectomycorrhizal Plant Lineages

19.4.1 Pinales

Pinaceae is the oldest extant ectomycorrhizal plant group that consists of 11 extant genera of trees. The genera *Pinus* and *Picea* were described as ectomycorrhizal in the pioneering study of Frank (1885), but similar root structures were described several decades earlier. Within Pinaceae, only the narrowly endemic genera *Nothotsuga* and *Pseudolarix* remain unconfirmed in terms of EcM habit but are also expected to have EcM. In natural conditions, short roots of Pinaceae are typically fully converted to EcM, but in *Cedrus* EcM colonisation typically remains <50% in native habitats (L. Tedersoo, unpubl.). In contrast to other EcM plant genera, species of *Pinus* exhibit characteristic bifurcately branching root tips. Pinaceae serve as hosts for a wide variety of fungi, but the local diversity in Pinaceae habitats tends to be lower than that in temperate deciduous forests (Tedersoo et al. 2012, 2014) probably because of highly acidic needle litter. Several small and recently evolved EcM fungal lineages are associated only with Pinaceae (Tedersoo and Smith 2013), but this could be due to their preference for acidic soils and paucity of studies of angiosperm roots in conifer forests. It is notable that older fungal lineages tend to have included Pinaceae in their host range relatively recently, indicating that the ancient fungal associations were phylogenetically relatively restricted. The family Pinaceae diverged from other extant gymnosperms roughly 340–320 Ma and radiated to extant genera since 198–175 Ma (average estimates: Leslie et al. 2012; Lu et al. 2014), although one conflicting study indicates only half that age (Crisp and Cook 2011).

19.4.2 Gnetales

The genus ***Gnetum*** is another gymnosperm group that forms EcM. In contrast to Pinaceae, this group represents mostly climbers, from which two species of trees evolved once in Indo-Malay. Similarly to Pinaceae, the root system of *Gnetum* is coarse with thick and conspicuous EcM. However, the EcM anatomy of *Gnetum* is substantially different from those of Pinaceae and any other plant (Brundrett 2009: Fig. 7a). The fungal interface in *Gnetum* occurs above the epidermis and consists of many fingerlike projections (root hairs) in a matrix of hyphae. Epidermal cells in these roots are also exceptionally narrow and densely packed. The level of EcM colonisation varies strongly, but all plants seem to be EcM (L. Tedersoo, unpubl.). *Gnetum* is characterised by extremely low EcM fungal richness that is restricted to a few species of *Scleroderma* in the liana-forming species (Bechem and Alexander 2012). The tree-forming *G. gnemon* exhibits somewhat greater fungal richness with still a prominent role of *Scleroderma* (Tedersoo and Põlme 2012). Although *Gnetum* diverged from the AM *Welwitschia* 130 Ma, modern groups of *Gnetum* radiated since 26 Ma, indicating its recent rather than ancient origin (Won and Renner 2006).

19.4.3 Fagales

The order **Fagales** is likely to be the oldest angiosperm EcM group that is represented by mostly trees and bushes both in the Northern and Southern Hemispheres. Since >80% of genera of Fagales are EcM, it is likely that EcM habit is ancestral in this group (Larson-Johnson 2015). Nothofagaceae represents the earliest diverging branch with current distribution in relicts of Gondwana. Within Betulaceae (incl. Coryloideae), *Alnus* is the only genus to associate with N_2-fixing *Frankia* actinobacteria. The monotypic Central American Ticodendraceae family is closely related to Betulaceae, and it has been proven EcM very recently (S. Põlme et al. unpubl.). The Southern Hemisphere Casuarinaceae family represents a sister group to Betulaceae + Ticodendraceae (Larson-Johnson 2015). Within this group, association with *Frankia* actinobacteria has probably evolved independently. EcM formation is normally present in the genus *Allocasuarina* but more occasional in *Casuarina*. AM symbiosis is always present in their roots, but nodules and EcM may be secondarily lacking, depending on species, plant age and soil properties (Reddell et al. 1986). Two additional Casuarinaceae genera, *Ceuthostoma* and *Gymnostoma*, have probably fully lost their capacity to form EcM (Duhoux et al. 2001), but certainly more information is needed. Fagaceae are certainly the most widely distributed family of Fagales that comprise only EcM-forming genera such as *Quercus* and *Fagus*. Besides the Casuarinaceae family, Juglandaceae represents another group that contains both EcM-forming and non-EcM members. The genera *Engelhardia*, *Oreomunnea*, *Alfaroa* and *Carya* form a monophyletic group that has been proven to associate with EcM fungi. Besides the EcM groups, Juglandaceae comprise at least one non-EcM genus, i.e. *Juglans*. Although sporadic reports on EcM exist, the root systems of *Juglans* have an architecture similar to that of *Fraxinus* with elongated short roots that is not seen in any EcM groups (except *Alnus*). There are several genera of Juglandaceae endemic to East Asia (*Cyclocarya*, *Pterocarya*, *Platycarya*) with no information about their mycorrhizal status. Within Fagales, the actinorhizal family Myricaceae seems to have completely lost the capacity to form EcM (but see the probably incorrect report of Sharma et al. 1986). At the family level, there is no information about the mycorrhizal status of Rhoipteleaceae, a narrow endemic of South China. Given the accumulated information, we hypothesise that Fagales gained the EcM-forming ability once, with multiple consequent losses. Development of actinorhizal symbiosis may be one of the causes for these losses (Myricaceae, Casuarinaceae) and for reduced EcM colonisation (Casuarinaceae, *Alnus*). This does not, however, explain the non-EcM habit of *Juglans* that typically inhabits EcM-dominated forests. It is possible that the strongly allelopathic biocide juglone has evolved to prevent EcM formation in *Juglans* spp., in which this substance is particularly abundant. The evolutionary history of Fagales has been relatively well established compared with other plant groups due to outstanding fossil record and economic importance. The EcM Fagales diverged from Hamamelidaceae some 98 Ma. The extant fagalean families diverged between 94 Ma and 72 Ma. The putatively non-EcM groups

Gymnostoma, Myricaceae, *Juglans* and *Ceuthostoma* diverged from the closest EcM taxa 59 Ma, 56 Ma, 45 Ma and 43 Ma, respectively (Larson-Johnson 2015). Members of Fagales differ strongly in EcM colonisation and the diversity of fungi supported. The actinorhizal genera *Alnus* and these of Casuarinaceae exhibit relatively low level of colonisation, and these groups harbour a limited set of fungi (Põlme et al. 2013), although molecular data are virtually lacking for Casuarinaceae. *Quercus* spp. and Juglandaceae spp. are typically moderately colonised by EcM fungi, whereas most groups in Betulaceae (except *Alnus*), Fagaceae and Nothofagaceae are heavily colonised (>90%). These three families harbour very high diversity of EcM fungi both in Northern and Southern Hemispheres (Tedersoo et al. 2012, 2014). Several EcM fungal lineages are specific to *Nothofagus* spp. or shared with neighbouring plants in Australia (Tedersoo et al. 2010a).

19.4.4 Caryophyllales

Six phylogenetically distinct groups of EcM plants are recognised within the order of Caryophyllales (Cuenoud et al. 2002; Schuster et al. 2013). The Pisonieae tribe, *Achatocarpus* and *Asteropeia* belong to Nyctaginaceae, Achatocarpaceae and Asteropeiaceae families, respectively, whereas *Persicaria vivipara*, *Coccoloba* and *Gymnopodium* belong to Polygonaceae.

Within the **Pisonieae** tribe, trees and shrubs belonging to *Pisonia*, *Neea* and *Guapira* contain EcM species. All species of the two latter genera are always EcM, but not all species of *Pisonia* form EcM (Hayward and Hynson 2014). Most of the EcM *Pisonia* species occur in South and Central America, whereas *P. grandis* inhabits much of the tropical Oceania (Chap. 20). Except for *P. sandwichiensis* in Hawaii, several phylogenetically distant endemic species of *Pisonia* inhabiting the islands of Pacific and Indian oceans are non-ectomycorrhizal and should be transferred to a new genus (Hayward and Hynson 2014). In addition to the genera *Pisonia*, *Neea* and *Guapira*, the monotypic *Pisoniella* belongs to this group based on phylogenetic analyses (Douglas and Manos 2007). On a morphological basis, *Neeopsis*, *Grajalesia* and *Cephalomandra* may also be related to this EcM group (Douglas and Spellenberg 2010), but no phylogenies are available for these small genera. Species and genera of Pisonieae exhibit extremely specific (*P. grandis*: Suvi et al. 2010) or strongly specific (*Neea*, *Guapira*: Tedersoo et al. 2010b) associations with EcM fungi. In all these genera, the EcM colonisation may be very low, and seedlings are not always associated with EcM fungi (L. Tedersoo, pers. obs.). In *P. grandis*, specific transfer cells extending from Hartig net to epidermal cells are characteristic anatomic features of EcM (Ashford and Allaway 1982). No specific age estimates exist for the EcM group, but most probably EcM habit evolved between 35 Ma and 20 Ma (Douglas and Manos 2007; Zanne et al. 2014).

Achatocarpus is a small family of trees in Central and South America. The EcM habit of *Achatocarpus* sp. was convincingly illustrated only recently, and several fungal groups are associated (Alvarez-Manjarrez and Garibay-Orijel 2015; J. Alvarez-Manjarrez, pers. comm.). *Phaulothamnus* constitutes a sister genus to *Achatocarpus*, but there is no information about its mycorrhizal status so far. There are no specific phylogenetic or biogeographic studies involving Achatocarpaceae, but Zanne et al. (2014) estimate this group to date back to <12 Ma.

The Polygonaceae is a predominantly non-mycorrhizal family, but there are some conflicting reports (Andrade et al. 2000) that may be derived from attention to AM colonisation. The South and Central American genus ***Coccoloba*** contains only EcM species that are among the dominant trees in maritime sand dunes or subcanopy trees, bushes or lianas. The EcM roots of *C. uvifera* in sand dunes are relatively much broader and more heavily colonised by fungi compared with scattered *Coccoloba* spp. tree individuals in a rain forest habitat in Ecuador (L. Tedersoo, unpubl.). Fungi associated with *Coccoloba* spp. in both habitats exhibit relatively greater diversity than in Nyctaginaceae but lower diversity compared with South American Dipterocarpaceae and Fabaceae, suggesting certain level of specificity (Tedersoo et al. 2010b). The genus *Coccoloba* diverged from AM ancestors around 52 Ma and radiated 24 Ma (Schuster et al. 2013).

The Central American genus ***Gymnopodium*** was only recently suggested to be EcM, and so far, published molecular and morphological evidence at the root tip scale is lacking (Bandala et al. 2011). *Gymnopodium* forms monodominant stands and supports tens of fungal species that are mostly shared with *Coccoloba* in neighbouring habitats (Bandala et al. 2011). *Gymnopodium* is a relatively young EcM group since its stem age was estimated to date back 35 Ma (Schuster et al. 2013).

In contrast to these three South and Central American EcM groups, ***Persicaria vivipara*** (also known as *Polygonum* and *Bistorta*) represents a perennial herb that is distributed throughout the circumarctic habitat and many glacial refugia in the alpine areas of Europe, Asia and North America. Since there is no recent taxonomic work on the genus *Persicaria* and closely related genus *Polygonum*, it remains unknown whether any other species of this group exhibit EcM habit as there are only a few and unreliable reports as well as some taxonomic confusion. Besides *P. vivipara*, the only reliable report on EcM is derived from *Polygonum weyrichii* in Japan, where all plants exhibited low but consistent colonisation across different habitats (Titus and Tsuyuzaki 2002; Tsuyuzaki et al. 2005) and perhaps *P. paronychia* (both not transferred to *Persicaria*) in dunes of Western North America (Zak 1973). In spite of conflicting reports about the EcM status of *P. vivipara*, we have observed that all individual plants of this species in Estonia and Scandinavia are colonised by EcM fungi, but the level of colonisation usually remains <50% (L. Tedersoo, unpubl.). The root systems and EcM tips of *P. vivipara* are among the finest and shortest among all EcM groups (Massicotte et al. 1998). *P. vivipara* associates with multiple fungi and lacks host specificity relative to other arctic and alpine herbs and shrubs (Botnen et al. 2014). *P. vivipara* seems to be a relatively recently evolved EcM group, with the estimated stem age < 28 million years (Schuster et al. 2013), but probably much less in case of better taxon sampling (<7 million years; Zanne et al. 2014).

Asteropeiaceae represents a monogeneric family of small trees and bushes that is distributed in Madagascar. The EcM status of *Asteropeia* was first reported in the year 2008 (Ducousso et al. 2004). The roots and EcM tips of *A. micraster* are extremely narrow and difficult to locate without a stereomicroscope. EcM root tips are sparsely distributed along the long root and contribute to ca. 50% of all root tips. Roots of *A. micraster* typically inhabit the fermentation horizon, while other EcM plants spread their roots more commonly in mineral soil in SW Madagascar (Tedersoo et al. 2011; unpubl.). *Asteropeia* associates with a broad range of EcM fungi, most of which are shared with other local EcM plant families (Tedersoo et al. 2011). *Asteropeia* appears to be an ancient group at the base of Caryophyllales, but no age estimates exist for this genus. According to Zanne et al. (2014), the stem age of *Asteropeia* dates to around 34 Ma. *Asteropeia* is sister to *Physena* (Physenaceae), another Malagasy endemic with no known mycorrhiza information (Cuenoud et al. 2002; Ducousso et al. 2008).

19.4.5 Fabales

The order Fabales represents an extremely large and ecologically important group of herbs, shrubs and trees that has several times independently evolved and multiple times subsequently lost the N_2-fixing capacity in association with rhizobial *Proteobacteria* (Werner et al. 2014). In addition to this rhizobial association, the typically obligately AM Fabaceae have evolved EcM habit at least seven times. The large Detarioideae subfamily itself contains four distantly related EcM clades that we term as the *Berlinia* group and the *Afzelia* group, following Bruneau et al. (2008), and *Cryptosepalum* group and *Dicymbe* (monogeneric) following the same logic. The distinctness of these four lineages is sufficiently supported in an inclusive and specifically focused phylogenetic study of de la Estrella et al. (2017) but not in earlier studies with less genes and representative taxa (e.g. Bruneau et al. 2008; Smith et al. 2011). The age for the entire Fabaceae and particularly Detarioideae and *Acacia* is greatly underestimated by Zanne et al. (2014) compared with strictly focused studies of de la Estrella et al. (2017) and Miller et al. (2013).

Acacia s.lat. (Mimosoideae) constitutes a large polyphyletic genus (nearly 1400 species) that has EcM-forming representatives only in the Australian *Phyllodina* group (*Racosperma*), known as ***Acacia s.str.*** (unfortunately not recognised as such in the Plant List). *Acacia s.str.* is the largest EcM genus with ca. 1000 accepted species (Miller and Seigler 2012) that represent small trees, bushes and shrubs, which are typically heavily colonised by rhizobia. Partly due to multiple symbiotic partners, certain species of *Acacia* are among the fastest-growing trees in the world. Most species of *Acacia s.str.* Seem to be facultatively EcM, because very often individual plants lack EcM and the level of colonisation commonly remains <10%. There is a tendency for larger species of *Acacia s.str.* (small or large trees) to have both EcM and AM, whereas the shrubs in this genus tend to have AM only (Chap. 17). Only about 50 species have been examined for mycorrhizas, of which about half have AM and the rest have both EcM and AM roots (Ducousso and Thoen 1991; M. Brundrett unpubl.). In some cases, EcM roots are poorly developed and may be nonfunctional. The conditions required for EcM fungi are poorly understood, but these are probably related to soil texture and organic matter or paucity of certain micronutrients. The EcM fungal diversity associated with species of *Acacia s.str*. Remains unknown, although only a few species from several EcM fungal genera are found under *Acacia* spp. in Australia and exotic plantations (M. Brundrett, pers. obs.). *Acacia s.str*. Diverged from other Mimosoideae 27–24 Ma and radiated shortly thereafter (Murphy et al. 2003; Miller et al. 2013).

Aldina is a small genus of South American trees that belongs to the subfamily Papilionoideae (papilionoid legumes). Root systems of *Aldina* are heavily mycorrhized (>90%) and support a large number of fungal species that are mostly shared with *Dicymbe* spp. (Smith et al. 2011; L. Tedersoo, unpubl.). The global plant phylogeny suggests that the divergence of *Aldina* from other legumes dates back >34 Ma (Zanne et al. 2014). *Aldina* spp. do not associate with rhizobia. The ‘igapó’ riparian forests of *Aldina* were the main source of mycological collections of R. Singer in the 1970s and 1980s.

The **Mirbelieae** tribe (sometimes also referred to as Bossiaeeae; papilionoid legumes) represents a group of Australian shrubs and bushes that are most widely distributed in the seasonally dry Mediterranean habitats in P-impoverished soils. Most if not all taxa of the Mirbelieae exhibit root symbiosis with rhizobia. Multiple species have been shown to be EcM, but reports from individual studies are often contradictory. The genera *Pultenaea*, *Gompholobium* and *Mirbelia* are consistently EcM and possess well-developed mantle and Hartig net (Chap. 17). Based on the individual reports of genera, it appears that EcM habit is inherent to the core group of Mirbelieae (Warcup 1980). Published information indicates that EcM habit may have been secondarily lost in certain species and genera. In his pioneering work, J. Warcup inoculated seedlings of Mirbelieae with a number of EcM fungal isolates and demonstrated >tenfold growth benefit of inoculation, although the nature of the control treatment was unspecified. These inoculation trials revealed that at least the tested fungal isolates were not selective among host plant group, allowing us to speculate that some Mirbelieae associate with a broad range of Australian EcM fungi. While there is no information about the colonisation level of Mirbelieae root systems, the EcM structures of most taxa appear poorly developed and only partly matching the morphological EcM definition. The widespread genus *Gastrolobium* is associated with a wide diversity of fungi, many of which form hypogeous fruit bodies that are an important food source for animals (Lamont et al. 1985). The EcM group radiated around 40 Ma (Crisp and Cook 2003; Schrire et al. 2005). Along with species assigned to Mirbelieae, Warcup (1980) reported EcM on *Hardenbergia* and *Kennedia*, but these groups belong to Phaseoleae, and only AM has been found in more recent studies (e.g. Brundrett and Abbott 1991).

When referring these groups as Mirbelieae, Warcup (1980) may have misidentified the plants. Furthermore, some species of *Daviesia* have NM cluster roots, but EcM and/or AM have been reported in others (Table 19.2; Chap. 17).

The ***Afzelia* group** (Detarioideae, caesalpinioid legumes) comprises two closely related genera, *Afzelia* and *Intsia*. Bruneau et al. (2008) identified the South American genus *Brodriguesia* as a well-supported sister taxon to these genera within the *Afzelia* group, but there is no information about the mycorrhizal status of *B. santosii* that is endemic to E Brazil. The roots of *I. bijuga* are heavily colonised by EcM fungi (>70%; L. Tedersoo et al. unpubl.), but we have no such data for *Afzelia* spp. In a few studies, *I. bijuga* associated with a wide array of fungi with no obvious specificity patterns in the Seychelles and Madagascar (Tedersoo et al. 2007b, 2011). Species of the *Afzelia* group do not associate with rhizobia. The age and ancestral distribution of the *Afzelia* group are not known, and the dating of EcM habit would strongly depend on the mycorrhizal status of *Brodriguesia*. The stem age of the entire group (incl. *Brodriguesia*) is 62 Ma (de la Estrella et al. 2017).

The ***Berlinia* group** (Detarioideae) represents at least 20 genera of large dominant trees and subcanopy trees in African miombo woodlands and rain forests. Several rain forest taxa of the *Berlinia* group (e.g. *Gilbertiodendron* and *Microberlinia*) form monodominant stands in the mainly AM matrix. Through extremely recalcitrant litter, these trees seem to control the soil conditions that favour proliferation of their symbionts and suppress seedlings of small-seeded arbuscular mycorrhizal plants. The roots are typically heavily colonised (>50%) by EcM fungi, although there are great differences in mycorrhiza density and root branching among tree genera (L. Tedersoo, unpubl.). Individual species and the *Berlinia* group as a whole establish non-specific associations with EcM fungi (Diedhiou et al. 2010; Tedersoo et al. 2011). Species of the *Berlinia* group do not associate with rhizobia. The *Berlinia* group diverged from other Amherstieae 59 Ma and radiated 57 Ma (de la Estrella et al. 2017).

The ***Cryptosepalum* group** (Detarioideae) consists of *Cryptosepalum* spp. and *Paramacrolobium coeruleum* that represent large and small trees in rain forests and miombo woodlands of Africa. *C. exfoliatum* forms monodominant stands in the dry deciduous forests biome in NE Zambia (L. Tedersoo, pers. obs.). The roots of *C. exfoliatum* are heavily colonised (>50%) by EcM fungi (L. Tedersoo, unpubl.). Fungal symbionts of *Cryptosepalum* spp. and *P. coeruleum* are shared with species belonging to the *Berlinia* group (Diedhiou et al. 2010; Tedersoo et al. 2011). Species of the *Cryptosepalum* group do not associate with rhizobia. The *Cryptosepalum* group diverged from other Detarioideae 53 Ma and radiated 34 Ma (de la Estrella et al. 2017).

Dicymbe (Detarioideae) is a genus of trees that is distributed in South America. Several species of *Dicymbe* form monodominant stands that may be codominated with *Aldina* spp. (Henkel 2003). Roots of *Dicymbe* species are heavily colonised by EcM fungi, and the mycobionts are shared with *Aldina* spp. and *Pakaraimaea* (Smith et al. 2011, 2013). *Dicymbe* spp. do not associate with rhizobia. The genus *Dicymbe* diverged from *Polystemonanthus dinklagei* 24 Ma and radiated

18 Ma (de la Estrella et al. 2017). Treatment of *Dicymbe* as a separate EcM plant lineage is important, because it is the only EcM Detarioideae group in South America and it does not belong to the large African *Berlinia* group that was previously hypothesised to have dispersed to South America. Nonetheless, mycorrhizal status of the West African *P. dinklagei* is not known, and thus it is still possible that EcM ancestors of the *Dicymbe* group evolved in Africa.

19.4.6 Malpighiales

Several families of Malpighiales contain EcM groups. Unfortunately, those in Phyllanthaceae and Euphorbiaceae have not been dated using a taxonomically focused approach.

The core group of **Salicaceae** is the most widely recognised EcM lineage within Malpighiales, consisting of *Populus* and *Salix* (including the monotypic *Chosenia*). The EcM Salicaceae are widely distributed from the arctic tundra to temperate forests, extending into tropical areas in riparian habitats. Species of *Salix* and *Populus* differ greatly in the structure and size of roots and EcM tips as well as the degree of EcM colonisation. All examined species of *Salix* and *Populus* are ectomycorrhizal, although several species include individuals that are non-EcM. Low level of EcM colonisation is characteristic to certain phylogenetic groups as well as individuals inhabiting permanently waterlogged conditions (Lodge 1989; Tedersoo et al. 2013). *Populus* spp. associate with a highly diverse set of fungi, a few of which are genus specific. *Salix* spp. associate with fewer fungal species, and the proportion of *Salix*-specific fungal taxa is greater (Tedersoo et al. 2013). Calibrated phylogenies indicate that EcM Salicaceae diverged from AM groups 45 Ma, whereas *Populus* and *Salix* were separated 33 Ma (Davis et al. 2005). Fossil records, however, suggest that modern Salicaceae *s.str.* Evolved 60–55 Ma (Collinson 1992), which we believe is more likely.

Uapaca (Phyllanthaceae) is a genus of small trees in miombo woodlands and rain forests of Africa and Madagascar. Many rain forest *Uapaca* spp. have stilted roots. Fine roots of *Uapaca* are much broader compared with those of other EcM angiosperms. The broad, brittle, red-brown ‘fine’ roots are characteristic to all studied species of *Uapaca*. Certain large root clusters are heavily mycorrhizal, whereas others are colonised by AM fungi (L. Tedersoo, pers. obs.). *Uapaca* spp. associate with a diverse community of EcM fungi that is shared with the *Berlinia* group and Dipterocarpaceae in Africa and Asteropeiaceae, Sarcolaenaceae and *Intsia* (*Afzelia* group) in Madagascar (Tedersoo et al. 2011). *Uapaca* diverged from other Phyllanthaceae <50 Ma and diverged at around 16 Ma (Zanne et al. 2014), but these figures are probably underestimates.

Poranthera (Phyllanthaceae) is a genus of small herbs and shrubs that is distributed in Australia and New Zealand. Several independent authors have consistently interpreted *Poranthera* as an EcM genus but with low level of colonisation and some individuals uncolonised. Some West Australian material examined did not have EcM roots as these are normally defined (Chap. 17). Inoculated fungi displayed 30–40-fold growth benefit to *Poranthera* sp. in sterile soils (Kope and Warcup 1986). However, these experiments need to be repeated, since growth responses of this magnitude are only likely in cases where fungi detoxify sterilised soils and control plants die. There is no information about the natural fungal associations of *Poranthera*, although EcM has been successfully synthesised with fungi from Myrtoideae (Kope and Warcup 1986). There is limited phylogenetic information about *Poranthera*, although the global analysis of Zanne et al. (2014) suggests they would have split from other Euphorbiaceae around 26 Ma and radiated 19 Ma, which we consider realistic.

19.4.7 Rosales

Pomaderreae is a coherent tribe of Rhamnaceae that is mostly represented by small trees and shrubs in Australia and New Zealand. Unlike some other Rhamnaceae, Pomaderreae spp. do not associate with N_2-fixing *Frankia* actinobacteria. *Adolphia californica* forms a sister taxon to the Pomaderreae (Onstein et al. 2015), but nothing is known about its mycorrhizal or actinorhizal status. The root system of *P. apetala* is heavily colonised by EcM fungi (>90%) and associates with a great diversity of mycobionts. The associated fungi display remarkably strong host preference for either *Pomaderris* or *Nothofagus* + *Eucalyptus* (Tedersoo et al. 2008). Molecular studies indicate that Pomaderreae split from other Rhamnaceae 55 Ma and radiated 41 Ma. Phylogenies indicate that the 'Pomaderreae' genera *Alphitonia* and *Granitites* are placed outside this tribe and are most probably AM (Onstein et al. 2015).

Dryadeae (Rosaceae) represents a tribe of small trees (*Cercocarpus*) and shrubs (*Dryas*) that associate with both EcM fungi and *Frankia* actinobacteria. While *Dryas* and *Cercocarpus* are consistently EcM, available information suggest that *Chamaebatia* is associated with at least *Cenococcum* (Trappe 1964), but *Purshia* forms only AM (studies not focused on EcM: Williams 1979; Rose 1980). Information about *Cowania* is lacking completely. Root systems of *Dryas* are moderately colonised by EcM fungi (>50%; L. Tedersoo, unpubl.), but such information is lacking for other groups. Both *Dryas* and *Cercocarpus* appear to associate with a broad diversity of EcM fungi with no evidence for host specificity (McDonald et al. 2010; Botnen et al. 2014). Dryadeae diverged from other Rosaceae tribes 75 Ma and radiated to currently recognised genera 67 Ma (Chin et al. 2014) that is in a good agreement with a global analysis (Zanne et al. 2014).

Adenostoma is a small genus of bushes not associated with *Frankia* actinobacteria in Western North America. *A. fasciculatum* has been reported to form EcM with poorly developed mantle and Hartig net (Cooper 1922; Allen et al. 1999a), but *A. sparsifolium* has only AM (Allen et al. 1999a). Allen et al. (1999b) observed production of EcM fungal fruit bodies in monospecific *Adenostoma* patches far from other EcM vegetation, indicating its performance as a functional host. Notably, however, *Adenostoma* does not facilitate recruitment of tree seedlings that contrasts with local Arbutoideae (Horton et al. 1999). Taken together, we interpret *Adenostoma* as a facultatively EcM plant genus. We have no information about the root structure, EcM mycobionts or evolutionary history of *Adenostoma*. The global analysis of Zanne et al. (2014) indicated its separation from extant sister groups <15 Ma.

19.4.8 Malvales

The order Malvales contains two EcM plant groups, viz. Dipterocarpaceae-Cistaceae and *Tilia*. Malvales is a relatively young group that dates back to 80–70 Ma based on multiple studies focused on the entire angiosperms (e.g. Wikström et al. 2001; Zanne et al. 2014; Tank et al. 2015). Unfortunately, phylogenetic relationships within Malvales are poorly resolved and the divergence estimates accounting for continental disjunctions are strongly conflicting with clock-based estimates.

We define the EcM **Dipterocarpaceae-Cistaceae group** as a clade that includes all genera of Cistaceae, Pakaraimaeaceae, Dipterocarpaceae *s.lat.* (incl. Monotoideae and Pseudomonotoideae) and Sarcolaenaceae. Close phylogenetic association of Dipterocarpaceae *s.lat.*, and in particular the genus *Pakaraimaea* and Cistaceae, has been evident for a long time (Wikström et al. 2001; Ducousso et al. 2004) but considered as an artefact of poor taxon sampling. Strikingly, modern in-depth phylogenetic analyses confirm these early findings (Zanne et al. 2014; Horn et al. 2016, J. Horn, pers. comm.), indicating that the present assumptions about the evolution and biogeography of these groups need to be drastically revised. From the belowground perspective, the monophyly of Dipterocarpaceae-Cistaceae makes sense, because both groups are well known as EcM hosts. Due to great ecological differentiation and the lack of geographic overlap probably within the last 30 My, these subgroups share no fungal species besides *Cenococcum geophilum*. The roots of all examined species of the Dipterocarpaceae subgroup are of average thickness for angiosperms and appear to be heavily colonised by EcM fungi (>70%), except *Monotes* which has relatively lower colonisation level (<30%) and low level of branching. Relatively low branching and low level of colonisation is as also characteristic of Cistaceae (L. Tedersoo, pers. obs., but see Massicotte et al. 2010). Furthermore, Cistaceae exhibit relatively fine roots and EcM tips compared with other EcM groups. In Mediterranean *Cistus* species, the mantle and Hartig net are often poorly developed, but this may be characteristic of pezizalean symbionts that have been frequently studied in this context. Species of the Dipterocarpaceae subgroup associate with multiple mycobionts and display no host specificity in Asia, Africa, Madagascar or South America (Tedersoo et al. 2011; Peay et al. 2015). This also applies to *Pakaraimaea dipterocarpacea* that is endemic to sandy soils of the Guyana shield (Smith et al. 2013). Little is known about the fungal diversity associated with Cistaceae, but sequence data suggests that Cistaceae associate with a phylogenetically diverse set but species-poor assemblages of EcM fungi (data available in UNITE: www.unite.ut.ee), many of which are Cistaceae specific (e.g. *Hebeloma* spp., *Cortinarius* spp.: Comandini et al. 2006). According to early vascular plant phylogenies, the Dipterocarpaceae-Cistaceae group diverged from other taxa 33 Ma and radiated to families since 23 Ma (average values from Wikström et al. 2001), which are anecdotally low values. Later, the stem and crown age of this group was pushed back to 73 and 49 Ma, respectively (Zanne et al. 2014). Given the slow evolution and continental disjunctions in these woody plants, the age of Dipterocarpaceae *s.lat.*, Cistaceae and *Pakaraimaea* is almost certainly underestimated (Moyersoen 2006; see also Chap. 20).

Tilia is a small genus of bee-pollinated trees that also includes *Craigia* nested therein. The Central American *Mortoniodendron* spp. form a sister group to *Tilia* and *Craigia* (Nyffeler et al. 2005), but there is no information about the mycorrhizal status of this genus. Roots of *Tilia* are heavily colonised by EcM fungi (>90%), and fungal richness tends to be among the highest of all EcM plants (Tedersoo et al. 2014, unpubl.), although no *Tilia*-specific EcM fungal species are known. In contrast to most other EcM trees, litter of *Tilia* species is nutrient rich and degrades rapidly. Richardson et al. (2015) estimate the stem age and crown age for *Tilia* + *Craigia* at 32 and 17 Ma, respectively, but these are certainly underestimates based on the fossil record (Chap. 20).

19.4.9 Asterales

Gnaphalieae (Asteraceae) is a tribe of herbaceous plants (as Inuleae; Warcup and McGee 1983; Warcup 1990) that is comprised of a large number of genera, some of which have been reported as EcM but many others are probably fully non-EcM. Apart from the image of *Podolepis* by Warcup and McGee (1983), the majority of reported associations lack a Hartig net, and the occurrence of a mantle is inconsistent and may require the presence of companion EcM plants. The same genera, or even species, of Asteraceae examined in Australia were reported to be EcM and AM or AM only in different studies (Table 17.2). It seems most likely that all Asteraceae are predominantly AM plants and the role of EcM-like associations on their roots requires further study. Only the crown group of this tribe with Australian distribution comprises EcM members (clades D-X; cf. Bayer et al. 2002). The taxonomy of Gnaphalieae is poorly resolved, with many currently recognised genera being polyphyletic (Bayer et al. 2002). Especially the genus *Helichrysum* stands out in terms of polyphyly as certain species belong to the EcM clade, whereas others belong to the neighbouring non-EcM clades (Smissen et al. 2004). Certain species have distributed from Australia to neighbouring islands, but to our knowledge, the mycorrhizal status of the EcM core group of Gnaphalieae has not been addressed outside Australia. Likewise, there is no information about the natural mycobionts of Gnaphalieae. Warcup (1980) also described the genus

Isoetopsis as EcM, but this genus is closely related to *Aster* (Bayer and Cross 2002), and the report is almost certainly incorrect. The EcM status of most genera and vast majority of species remains poorly understood, but the groups that may have EcM evolved in the time frame of 10–16 Ma (Bergh and Linder 2009).

Goodeniaceae represents another Australian-centred family of herbs and shrubs that are reported as EcM or without EcM, sometimes in the same species. The root system of Goodeniaceae has typically low level of superficial fungal colonisation along with AM, and the roots generally lack a Hartig net (see Fig. 17.5); yet, inoculation with EcM fungi was reported to provide plants 10–100x growth benefits in sterile soils (Warcup 1985), but these experimental results have been questioned (Chap. 17). Information about natural mycobionts of Goodeniaceae is lacking, but EcM-like associations were synthesised using fungi from Myrtoideae (Warcup 1985). Many Goodeniaceae spp. are halophytes or hydrophytes, and these are very unlikely to be ectomycorrhizal. Molecular dating studies suggest that Goodeniaceae is an ancient group that separated from its sister groups 78 Ma and radiated 67 Ma (Jabaily et al. 2014). However, the Cretaceous origin of Goodeniaceae is probably overestimated (Zanne et al. 2014 report around 55 Ma for stem age).

19.4.10 Myrtales

The order Myrtales contains probably a single EcM group—the subsection of **Myrtoideae** that bear dry seeds. The Myrtoideae subfamily has complex mycorrhizal relationships, especially in Australia. Altogether 95 species of Australian Myrtoideae have been assessed for mycorrhizas: 35% with EcM, 36% with AM and EcM and 29% with AM only (M. Brundrett, unpubl.). To illustrate the present knowledge about Myrtoideae mycorrhizal status from a phylogenetic perspective, we mapped the confirmed lineages on a dated tree (Fig. 19.3). Species within many genera of Myrtoideae differ greatly in their consistency of EcM status, level of EcM colonisation and root morphology, which requires further investigation (Brundrett 2009). It is also common for them to have both AM and EcM in their roots. Despite conflicting evidence or a lack of information about the mycorrhizal status of many Myrtoideae genera, there are well-resolved EcM clades, which are phylogenetically centred around *Eucalyptus*, *Leptospermum* and *Melaleuca*. In the crown group of Myrtoideae, the Myrteae, Syzygeae and Metrosidereae tribes have probably secondarily switched to arbuscular mycorrhizal habit (Thornhill et al. 2015), although conflicting and probably incorrect reports on EcM of *Campomanesia* and *Ugni* exist from South America and that of *Syzygium kuranda* from Australia. Evidence that the Myrtoideae gained many of their EcM symbionts from *Nothofagus* in the Late Cretaceous is provided by low specificity of fungi between eucalypts and southern beeches (Tedersoo et al. 2008). General observations suggest that large trees such as *Eucalyptus s.lat.* Host many EcM fungi, whereas bushes and shrubs support relatively low fungal diversity based on fruit-body

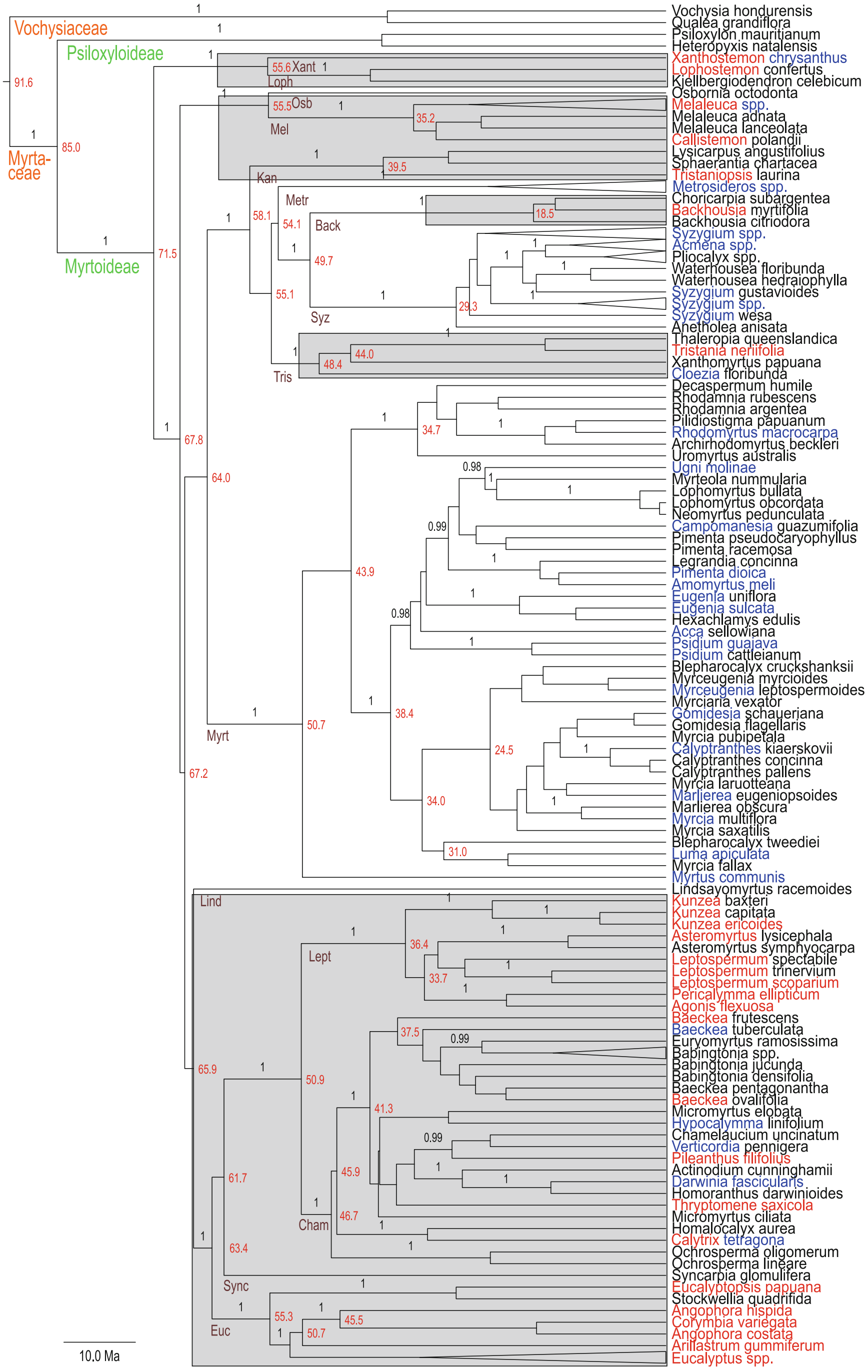

Fig. 19.3 Distribution of mycorrhizal types in the phylogeny of Myrtoideae (Myrtaceae). The backbone tree is adapted from Thornhill et al. (2015). Numbers at nodes and above branches

records (Chap. 17). Interestingly, Myrtoideae are able to associate with indigenous fungi of the Seychelles, Madagascar and continental Africa (Tedersoo et al. 2007b, 2011; Buyck 2008), but not with those of Europe (Pennington et al. 2011). The EcM Myrtoideae diverged from other groups around 85 Ma and radiated 72 Ma. The AM groups evolved probably secondarily between 25 Ma and 65 Ma (Thornhill et al. 2015).

19.4.11 Apiales

Platysace (Apiaceae) represents a single EcM genus in Apiales. The Australian endemic perennial herb genus *Platysace* forms a sister group to *Homalosciadium*, another Australian genus (Nicolas 2009), for which there is no available information about mycorrhiza status. Phylogenies suggest that *Platysace* and *Homalosciadium* diverged ca. 35 Ma, but these were separated from other subfamilies of Apiaceae some 78–84 Ma (Nicolas 2009) that are probably overestimates. *Platysace* spp. have been reported to form a well-developed mantle and Hartig net, and individuals exhibit consistent colonisation (Bellgard 1991; Zemunik et al. 2015), but other plants in the same genera have been shown to be AM only (Table 19.2). The occurrence of EcM in this group requires further investigation since the rest of this family seems to be consistently AM. There is no available information about the root structure, EcM colonisation and associated mycobionts.

19.4.12 Ericales

Ericaceae is one of the largest plant families on earth that is particularly well-known for ericoid mycorrhiza (ErM; Chap. 9). At the base of Ericaceae, however, the AM Enkianthoideae forms a successive sister group to the large ErM and relatively small EcM lineage (Schwery et al. 2015). The ErM lineage comprises subfamilies Cassiopoideae, Harrimanelloideae, Ericoideae, Styphelioideae and Vaccinioideae (Chap. 9), whereas the monophyletic EcM group contains Arbutoideae, Pyroloideae and Monotropoideae (tribes Monotropeae and Pterosporeae: Kron

◄

Fig. 19.3 (continued) indicate divergence times and Bayesian posterior probabilities, respectively. Names highlighted in *red* and *green* denote EcM habit and non-EcM habit, respectively (highlights covering genus name only indicate that different species were assessed for mycorrhiza status). Clades believed to be dominated by EcM habit are shaded. Abbreviated names under major branches indicate tribe names: *Back* Backhousieae, *Cham* Chamelaucieae, *Euc* Eucalypteae, *Kan* Kanieae, *Lept* Leptospermeae, *Lind* Lindsayomyrteae, *Loph* Lophostemoneae, *Mel* Melaleuceae, *Metr* Metrosidereae, *Myrt* Myrteae, *Osb* Osbornieae, *Sync* Syncarpieae, *Syz* Syzygieae, *Tris* Tristanieae, *Xant* Xanthostemoneae and Luteyn 2005) that we refer to collectively as ***Arbutoideae s.lat***. Of these individual subfamilies, Monotropoideae comprises fully non-photosynthetic, so-called mycoheterotrophic plants that form monotropoid subtype of EcM with usually a thick mantle, intensive intracellular root colonisation of hyphae and extensive digestion of hyphal coils (Smith and Read 2008). Most of the Pyroloideae form pyroloid subtype of EcM that has low to moderate intracellular colonisation and usually lacks a mantle (Smith and Read 2008), but mantle development is a function of plant species, fungal species and habitat (L. Tedersoo unpubl.). Nearly all species of *Pyrola*, *Orthilia* and *Moneses* are partially mycoheterotrophic, whereas *Chimaphila* appears to gain little if any carbon from forest trees via EcM fungi (Tedersoo et al. 2007a; Hynson et al. 2012). Only members of the Arbutoideae subfamily appear fully autotrophic, although they form arbutoid mycorrhiza with intracellular colonisation in addition to a Hartig net and a poorly or fully developed mantle (Smith and Read 2008). Since the fungi and many anatomical features of these specific mycorrhiza types are shared with typical EcM, we continue to consider these as specific subtypes of EcM. While Arbutoideae and *Pyrola*, *Orthilia* and *Chimaphila* from Pyroloideae associate with an extremely wide range of EcM fungi, *Moneses* (Pyroloideae) and members of the entire Monotropoideae display substantial selectivity for specific fungal groups that are often unrelated (Bidartondo et al. 2015). *Moneses* associates with *Amphinema* and *Tylospora* species (Hynson et al. 2015; L. Tedersoo, unpubl.). Both the ErM and EcM groups diverged from the putatively AM ancestor 110 Ma and radiated further since 102–103 Ma (Schwery et al. 2015). Besides this most recent and comprehensive study, other age estimates for Ericaceae and mycorrhizal groups therein are 1.3–3 times more recent, but these conflict with the fossil record.

19.4.13 Cyperales

The genus ***Kobresia*** is a perennial genus of sedges, part of which are EcM in arctic and alpine habitats of the Northern Hemisphere. We consider ectomycorrhizal only the ‘uniseriate’ group (cf. Starr et al. 2004), which is monophyletic within the paraphyletic *Carex* and contains proven EcM plant species (e.g. *K. myosuroides*, syn. *K. bellardii*). *Kobresia* species outside this core clade are probably non-EcM. However, not all individuals (or perhaps populations) of *K. myosuroides* are EcM, suggesting the facultative nature of EcM mutualism at least in some habitats. *Kobresia* is the dominant plant group in the Tibetan Plateau and other Central Asian lowlands, where the EcM habit is consistently reported in several species. The EcM colonisation of individual plants is relatively low, and EcM roots are arranged as unbranched pinnate terminal roots (resembling the structure of *Alnus* spp.) branching off the main feeder root (L. Tedersoo, unpubl.). *Kobresia* spp. associate with multiple fungal partners that are not specific to this genus (Gao and Yang 2010). The diversity appears to be, however, relatively low (Tedersoo et al. 2012), but this may result from the tundra and grassland habitat, where EcM plant relative abundance is low compared to forest habitats. Phylogenetic analyses suggest that *Kobresia* is a relatively recently evolved EcM group as the large paraphyletic genus *Carex* dates back 21 Ma (Escudero et al. 2012), which pushes the divergence date of EcM *Kobresia* to <10 Ma (Starr et al. 2004) or <5 Ma (Zanne et al. 2014). The EcM roots of *Kobresia* seem be derived from dauciform roots, which are swollen lateral roots produced by many members of the Cyperaceae (Chap. 21).

19.5 Groups Forming EcM-Like Associations

We have taken a precautionary approach to assigning EcM status to taxa where such evidence is poor or conflicting and descriptions are lacking or open to multiple ways of interpretation. We briefly discuss these taxonomic groups below.

Multiple groups of orchids form the orchid type of endomycorrhiza with typical EcM fungi that colonise root cells, but these associations are morphologically and functionally distinct from EcM (Dearnaley et al. 2012). Certain thalloid liverworts of Aneuraceae family also establish symbiosis with EcM fungi inside the cells of their belowground and aboveground tissues (Bidartondo and Duckett 2010). In both cases, associations with EcM fungi have evolved secondarily, and EcM fungi and their tree hosts are to a greater or lesser extent exploited by orchids and liverworts as the fungal hyphae are digested inside the root cells, indicating mixotrophic and mycoheterotrophic interactions. Notably, these associations are distributed only in the mycorrhizosphere of EcM plants and never distant from EcM vegetation. There is no evidence that orchids and thalloid liverworts can sustain EcM fungi in the absence of other EcM vegetation (Cameron et al. 2008). As obviously non-mutualistic for the exploited fungi, we do not consider these interactions here. Evolution and biogeography of these mixotrophic and mycoheterotrophic plants has been comprehensively addressed in Merckx (2013).

Lobelia is a paraphyletic cosmopolitan genus of contrasting life forms that evolved in Neotropics 55 Ma and spread further to Africa and Australia (17 Ma; Antonelli 2009). The Australian annual *Lobelia* spp. have been demonstrated to form a strange form of root symbiosis with both EcM and AM fungi, but perennial species had only AM (Fraser 1931; Warcup 1988). The mycorrhizal isolates displayed 1–100x growth benefits to plants (Warcup 1988), suggesting functional and beneficial associations to their hosts. However, field samples of other *Lobelia* spp. only had AM in their roots (Brundrett and Abbott 1991). Given the strange seedling development belowground (Fraser 1931), we speculate that some *Lobelia* species may display mixotrophic lifestyle briefly as seedlings, but their mycorrhizas do not conform to the definition of EcM and require further study.

Thysanotus (Laxmanniaceae, Asparagales) is a genus of monocot herbs endemic to Australia, except two species distributed west to East Asia and Indo-Malay (Sirisena 2010). The Australian species have been reported to form ‘thysanotoid’ mycorrhizal associations with both AM and EcM fungi (Chap. 17). Aseptic synthesis experiments recovered up to twofold growth benefits that were evident in the presence of another mycorrhizal plant (McGee 1988). These experiments suggest that *Thysanotus* spp. may exhibit mixotrophic associations with EcM or endophytic fungi. Given the association with EcM fungi and formation of EcM-like sheath but not Hartig net, the Australian *Lobelia* and *Thysanotus* warrant further mycological, ecological and physiological research to resolve their mycorrhizal status.

19.6 Some Remarkable Examples of Incorrect Reports

The topic of diagnosis and misdiagnosis of mycorrhizal associations is discussed in detail elsewhere (Brundrett 2009), so we present only a few striking cases that have taken root or become influential in mycorrhizal ecology. Both false-positive and false-negative reports about the EcM status of plants are common. False-negative observations are at least partly related to the fact that only AM colonisation has been assessed or insufficient fresh/living material has been studied. False-positive EcM reports may be derived for multiple reasons:

(1) The authors consider any hyphal network on the root surface as a mantle that is indicative of EcM (work of J. Warcup and his followers, early and middle twentieth-century researchers).
(2) Consideration of a weft of dark septate endophytic (DSE) hyphae as poorly developed EcM of *Cenococcum* (work of T. Dominik and his students).
(3) Careless tracing of roots leading to sample contamination (e.g. EcM reports in ferns, work of early researchers).
(4) Misidentification of plant species (suspected in some reports of J. Warcup).
(5) Careless suggestion of mycorrhiza type based on fruiting habits of fungi without clear belowground evidence (work of B. Peyronel, R. Singer, D. Pegler and that of many other mycologists; summarised in Trappe 1962).
(6) Influence from former publications and wishful thinking.
(7) A general tendency to exaggerate the significance of observed fungal structures in an attempt to publish a ‘more interesting’ story.

Some of these incorrect or incomplete reports have been widely accepted and further cited by other authors without critical reassessment (e.g. Daft et al. 1985; Wang and Qiu 2006; Smith and Read 2008; Phillips et al. 2013; Fisher et al. 2016; Maherali et al. 2016; Lin et al. 2017). In particular, Maherali et al. (2016) assessed the evolution of gains and losses of EcM associations in plants based on mapping mycorrhizal status to phylograms of Zanne et al. (2014). In contrast to this review, they considered *Calliandra*, *Gleditsia*, *Lonchocarpus*, *Robinia* and *Senegalia* (all Fabaceae), *Cerasus* and *Padus* (both Rosaceae), *Graffenrieda* (Melastomataceae) and *Ceratopetalum* (Cunoniaceae) as ectomycorrhizal, representing nine additional EcM lineages. For most of these genera, there is ample evidence for the occurrence of only AM in the literature (members of Fabaceae and Rosaceae), or the described structures cannot be considered EcM (*Ceratopetalum*, *Graffenrieda*). Furthermore, Maherali et al. (2016) ignored altogether 11 EcM plant lineages as described here, although many of these are well established.

In Europe, there are multiple reports of EcM occurrence in Rosaceae, especially in the fruit tree genera *Malus*, *Pyrus* and *Prunus* as well as closely related *Crataegus*, *Padus* and *Sorbus*. These reports are particularly evident in the East European and Russian literature published in the 1950s and 1960s. The same authors describe these plants as EcM or non-EcM in their different studies but provide no illustrative evidence. Most commonly, *Cenococcum* has been reported as a putative symbiont, suggesting that dense colonisation of DSE may have resulted in incorrect assignment of the EcM status. Furthermore, fine roots of Rosaceae exhibit swollen tips; if these become old and turn brown, it is tempting for an inexperienced eye to suspect EcM association. That could be, however, easily checked by examining the squashed root tip under a stereomicroscope. Another example comes from *Juniperus communis* that is known to be AM, but there are several EcM reports that probably represent misidentification of roots. For example, Reinsvold and Reeves (1986) described a tuberculate EcM of '*J. osteosperma*' that is clearly donated by a neighbouring *Pinus* individual. Notably, the roots of pines may distribute >30 m from the trunk even when mature trees are <5 m high. There are several records of EcM in the nitrogen-fixing *Elaeagnus angustifolia* (Elaeagnaceae) in Russia, although reports of the same species and other *Elaeagnus* species from Europe and North America have revealed only AM (see Daft et al. 1985).

In North America, Grand (1971) reported tuberculoid EcM from *Photinia* (Rosaceae), but their images remind us of suilloid mycorrhiza of *Pinus*. More recent reports suggest AM or NM habit for *Photinia* spp. Several physiological experiments have been performed based on inoculation of *Ulmus americana* with EcM fungi. It is anecdotal, because *Ulmus* spp., incl. *U. americana*, are non-EcM and form AM based on multiple reports and authors' personal observations. Morphological studies of these roots by Brundrett et al. (1990) and others have clearly shown that they consistently have AM associations and also have structural features that would make EcM formation unlikely or impossible (suberised epidermis and exodermis). Certain companies (established by former EcM researchers) also promote universal EcM inoculum that supposedly benefits the growth of all trees, including AM trees and *Alnus*.

Of Asian records, *Elaeocarpus* (Elaeocarpaceae) has been reported and illustrated to be an EcM genus in Taiwan (Haug et al. 1994), but multiple previous and subsequent studies indicate only AM colonisation for members of this genus. *Pimelodendron* (often misspelled *Pimeleodendron*) is a small euphorbiaceous genus of trees that is distributed in the Sunda Islands and New Guinea. *P. amboinicum* was reported as EcM two decades ago in New Guinea (Verbeken and Walleyn 1999), but these records remain unconfirmed. More recent stable isotope analyses of EcM and AM plant leaves place *P. griffithianum* deeply into the AM category (Tanaka-Oda et al. 2015). Based on original studies (Tian et al. 2003 and their earlier research), *Robinia pseudoacacia* has been misinterpreted as

EcM by Wang and Qiu (2006). The original descriptions by Bratek et al. (1996) indicated either AM or some intracellular colonisation of *Mattirolomyces terfezioides*, which is not an EcM fungus.

In South America, many authors have carelessly claimed that certain plant species host putatively EcM fungi. Oft-cited examples include *Allophylus* (Sapindaceae), *Pradosia* (syn. *Glycoxylon*; Sapotaceae), *Haematoxylum* (syn. *Haematoxylon*; Fabaceae), *Swartzia* (Fabaceae) and *Inga* (Fabaceae). Later it appeared that not all these fungi were in fact ectomycorrhizal (*Gyrodon rompelii*, *Phlebopus* spp.); *Aldina*, Pisonieae and *Coccoloba* represented local hosts (Meyer 1991; Moyersoen 1993). Other commonly cited South American EcM associations were reported by Thomazini (1974) who claimed that *Campomanesia* (Myrtoideae) and *Bauhinia* (Fabaceae) form EcM in Brazil. Furthermore, Frioni et al. (1999) reported EcM associations in *Gleditsia*, *Senegalia* (as *Acacia bonariensis*), *Calliandra*, *Prosopis* and *Lonchocarpus*. However, multiple more recent studies have been unable to confirm these findings, reporting only AM. *Graffenrieda* (Melastomataceae) has been described to possess a specific type of ectendomycorrhiza (Haug et al. 2004). Given its phylogenetic position, poorly developed mantle-like structure and association with typical root endophytic/ fungi related to *Rhizoscyphus ericae*, we interpret this as somewhat differentiated root endophytic interaction rather resembling ericoid mycorrhiza.

In Africa, Högberg and Piearce (1986) suggested EcM habit for *Faurea* (Proteaceae) and *Pericopsis* (Fabaceae), which are commonly cited as examples of African EcM plants. However, several other studies as well as the first author's observations suggest that these trees are not EcM in Africa or elsewhere. Recently, Bechem et al. (2014) conducted an extensive survey of mycorrhizal status in plants of Cameroon, reporting EcM habit for *Angylocalyx*, *Baikiaea*, *Baphia*, *Calpocalyx*, *Dialium* and *Hymenostegia* (all Fabaceae), *Antidesma* (Phyllanthaceae), *Leptonychia* (Malvaceae) and *Soyauxia* (Peridiscaceae) in addition to known EcM members of the *Berlinia* group and *Uapaca*. Roughly half of these findings are not supported by previous studies at genus level, but others lack independent evidence.

In Australia, the floristic distribution of EcM habit is particularly complicated, because commonly accepted EcM plants such as shrubs in the Myrtoideae other than eucalypts may have poorly developed mycorrhiza structures. The pioneering work of Warcup (1980) can be regarded as the most confusing, because he was the primary describer of EcM in multiple plant groups, but he also followed a relaxed criterion for EcM by considering plants with a hyphal weft on a root surface as mycorrhizal. Because he rarely provided illustrations and did not describe the methods used in synthesis trials, his findings have been heavily criticised (Brundrett and Abbott 1991; Brundrett 2009). Nonetheless, subsequent evidence has confirmed some of his striking findings, whereas others appear very unlikely in the context of plant phylogeny and subsequent studies (mycorrhizas.info/ozplants). Therefore, we consider the genera *Lasiopetalum* (Sterculiaceae), *Thomasia* (Sterculiaceae), *Pimelea* (Thymelaeaceae), *Opercularia* (Rubiaceae) and *Isoetopsis* (Asteraceae) as insufficiently supported for EcM habit. Based on updated phylogenetic and mycorrhizal information, we also consider doubtful and unlikely the EcM status of the following Australian genera: *Ceratopetalum* (Cunoniaceae), *Astroloma* (Ericaceae), *Comesperma* (Polygalaceae), *Erythrophleum* (Fabaceae) and *Stylidium* (Stylidiaceae, Asterales). The latter genus represents a group of perennial herbs in Australia that is reported as EcM with poor mantle and Hartig net development by Warcup and his students. Interestingly, several species of *Stylidium* are reported to be protocarnivorous, but this is not supported by substantial evidence. Other doubtful examples of EcM in Australian plants, where more recent studies have only found AM, are listed in Table 17.2. Most discrepancies between earlier and more recent studies of Australian plants result because the Hartig net was used to define EcM in recent studies but not in the past.

Multiple putatively incorrect false-positive reports of EcM have propagated themselves across studies and along research projects. Some of these may represent intermediate steps in the AM to EcM evolutionary continuum but in many cases can be more easily explained as the results of misidentification of fungal structures. We acknowledge that there certainly are cases where a continuum of AM to EcM host plants occurs in the same family or genus, and these are worthy of further study. Some of the worst cases of misidentification warrant published corrections for research articles or PhD theses. However, designation of EcM is complex and the status of some plants cannot be fully resolved by us at this time. This complexity arises because evolution of the EcM symbiosis is an ongoing process that is initiated at the level of plant individuals and populations.

19.7 Losses and 'Facultative' EcM Associations

Several EcM plant groups stand out as possessing poorly developed mycorrhizal structures and/or inconsistent root colonisation. Furthermore, some groups comprise multiple species with non-EcM populations (Fagales, Myrtoideae, Dryadeae, *Acacia s.str.*, Mirbelieae, Goodeniaceae, Gnaphalieae), which indicates secondary losses of EcM habit. Maherali et al. (2016) found more losses of EcM habit than gains. Although this is probably true, their analysis was based on incorrectly assigned mycorrhizal types and exclusion of many EcM taxa. Our review suggests that there are two floristic features characteristic of such facultative EcM habit and loss of it: herbaceous or shrubby life form and nitrogen-fixing strategy. It is remarkable that EcM evolution—both gains and losses—is closely related to the nitrogen-fixing habit as seen in Fagales, Fabaceae, Rhamnaceae and Rosaceae that altogether comprise nine EcM groups. Furthermore, there are reports about non-EcM habit for nearly all nitrogen-fixing EcM plants. *Frankia*-associating Myricaceae, some members of Casuarinaceae and perhaps some Dryadeae such as *Purshia* have lost EcM associations. Similarly, certain *Acacia* spp. and Mirbelieae spp. associated with rhizobia seem to have lost EcM capacity completely. A deeper look into the Fabaceae phylogeny (Werner et al. 2014; de la Estrella et al. 2017) indicates that the *Berlinia* group, *Cryptosepalum* group, *Dicymbe* and *Afzelia* group evolved EcM associations before the two major Fabaceae groups evolved rhizobial symbiosis. By contrast, the genus *Aldina* evolved EcM associations after the nitrogen-fixing trait was lost in its papilionoid ancestors. The Fabaceae phylogeny also suggests that plants either evolved associations with rhizobia first and then evolved EcM associations with subsequent losses of these EcM associations in some groups (*Acacia s.str.*, Mirbeliae). Such losses of EcM are not seen in non-nodulating lineages of Fabaceae (*Berlinia* group, *Afzelia* group, *Cryptosepalum* group, *Dicymbe, Aldina*; Fig. 19.1). In Fagales, however, the genus *Alnus* and the whole Casuarinaceae evolved actinorhizal associations when ectomycorrhizal (Larson-Johnson 2015). EcM habit was lost in certain Casuarinaceae, and it was reduced in *Alnus* as compared to the sister taxa. Within the Rhamnaceae family, EcM habit in Australian Pomaderreae and actinorhizal state in the Chilean Colletiae and NW American *Ceanothus* is phylogenetically unrelated (Onstein et al. 2015). In Rosaceae, Dryadeae exhibit both EcM and actinorhizal associations, whereas *Adenostoma fasciculatum* hosts only EcM fungi. Thus, it remains unclear whether the EcM habit or actinorhizal association evolved first in Dryadeae, but it is probable that EcM evolved first considering the pathways in *Adenostoma* and *Alnus*. Construction of dated phylogenies of *Frankia* and evolutionary history of symbiosis-related genes in plants may provide an answer to this question.

Root-associated actinobacteria and rhizobia have the potential to render EcM habit redundant for plants, because much of the nutritional benefit of EcM symbiosis is related to nitrogen acquisition. Actinorhizal plants have usually established their niche in early successional habitats that have poorly developed soils with limited nitrogen and little carbon but ample mineral phosphorus supply, except its poor availability at extreme pH values. High phosphorus demand by nitrogen-fixing microbes usually requires assistance of mycorrhizal fungi, probably depending on soil properties and other mycorrhizal benefits. If EcM fungi become too costly for maintenance in terms of carbon energy or phosphorus trade, plants may simply avoid such associations and exploit AM fungi. Except for Myricaceae and *Daviesia* (Mirbelieae), most rhizobial and actinorhizal plants have high dependency on mycorrhiza.

Low level of EcM formation in non-actinorhizal plants is characteristic to arctic and alpine habitats on the one hand (*Persicaria vivipara*, *Kobresia*) and the summer dry Mediterranean biome (Cistaceae in Europe, many plant groups in Australian semidry habitats) on the other hand. Both habitats suffer from severe seasonal drying of soil and paucity of nutrients. The vegetation in these ecosystems is dominated by herbs and shrubs, which may provide insufficient energy to sustain EcM mycobionts. If there are no large EcM trees maintaining the EcM mycelium network, EcM associations may be non-beneficial to plants in AM-dominated communities. Apart from herbs and shrubs, slowly growing trees may also display reduced EcM colonisation in heavily drought-stressed conditions (Lodge 1989; Swaty et al. 2004), further reinforcing the hypothesis of low carbon availability. EcM fungi may not be efficient enough in organic-poor substrates that are derived from low rates of leaf litter accumulation or frequent fires. Over time, Mediterranean and arctic plants may have evolved low colonisation and mycorrhiza biomass to optimise between benefits and costs of EcM mycobionts.

Similarly to seasonally very dry habitats, wetland plants tend to have reduced EcM colonisation. Since EcM fungi have high oxygen demand due to active metabolism, anoxic environments are not optimal for EcM growth. This has been shown experimentally for *Salix*, *Melaleuca* and *Casuarina* species which have both EcM and EM roots and grow in wet habitats but primarily form AM roots when soil is waterlogged (Lodge 1989; Watson et al. 1990; Khan 1993).

Arctic and alpine habitats are dominated by herbs and shrubs, for many of which there are conflicting reports about the mycorrhizal status. Dwarf *Betula* and *Salix* as well as *Dryas*, *Bistorta vivipara* and certain *Kobresia* species are nearly always EcM. In addition to these well-established EcM groups, individuals of *Potentilla* spp., *Saxifraga* spp., *Cassiope tetragona* and *Pedicularis* spp. are strikingly commonly reported as EcM by independent researchers in different regions, although most studies treat these as NM or AM (Table 19.3). Arctic species of *Potentilla* (Rosaceae) have been reported as EcM in four studies but only AM or NM in 15 studies. *Saxifraga oppositifolia* (Saxifragaceae) has been considered EcM in three studies but NM or AM in 13 studies. Kohn and Stasovski (1990) reported

Table 19.3 Conflicting reports for EcM and non-EcM status in selected arctic and alpine plants

Genus	References
Pedicularis (Lamiales: Orobanchaceae)	Stutz (1972), Kohn and Stasovski (1990), Väre et al. (1992), AM: Dominik et al. (1954), AM: Mikeladze (1960), NM: Katenin (1972), NM: Baikalova and Onipchenko (1988), NM: Treu et al. (1996), AM/NM: Clemmensen and Hansen (1998), NM: Onipchenko and Zobel (2000), NM: Cripps and Eddington (2005), NM: Cázares et al. (2005), AM: Li and Guan (2008)
Cassiope (Ericales: Ericaceae)	Stutz (1972), Miller and Laursen (1978), Miller (1982), Kohn and Stasovski (1990), ErM: Bledsoe et al. (1990), ErM: Väre et al. (1992), ErM: Michelsen et al. (1996), ErM: Clemmensen and Hansen (1998), ErM: Treu et al. (1996), ErM: Cázares et al. (2005)
Saxifraga (Saxifragales: Saxifragaceae)	Stutz (1972), Read and Haselwandter (1981), Kohn and Stasovski (1990), AM: Stahl (1900), AM: Costantin and Magrou (1926), NM: Daubenmire (1941), AM: Thomas (1943), AM: Nespiak (1953), AM: Katenin (1972), NM: Baikalova and Onipchenko (1988), NM: Väre et al. (1992), NM: Treu et al. (1996), AM/NM: Clemmensen and Hansen (1998); NM: Ruotsalainen et al. (2004), NM: Cázares et al. (2005), non-EcM: L. Tedersoo, unpubl.
Potentilla (Rosales: Rosaceae)	Thomas (1943), Bledsoe et al. (1990), Clemmensen and Hansen (1998), Cázares et al. (2005), AM: Schlicht (1889), AM: Jessen (1914), AM: Klecka and Vukolov (1935), NM: Daubenmire (1941), AM: Nespiak (1953), AM: Mikeladze (1960), AM: Read and Haselwandter (1981), AM and NM: Lesica and Antibus (1986), AM: Baikalova and Onipchenko (1988), NM: Kohn and Stasovski (1990), AM: Väre et al. (1997), AM: Onipchenko and Zobel (2000), AM: Kovacs and Szigetvari (2002), NM: Cripps and Eddington (2005), non-EcM: L. Tedersoo, unpubl.

EcM colonisation in 75% of *S. oppositifolia* individuals but none of *S. tricuspidata* individuals in the Canadian Arctic. In *Cassiope tetragona*, EcM root tips in addition to intracellular colonisation have been recovered in four studies, while six studies report only ErM. In Ellesmere Island, 44% of *C. tetragona* individuals were considered EcM (Kohn and Stasovski 1990). In the hemiparasitic *Pedicularis capitata*, EcM was reported in two out of eight individuals, but *P. hirsuta* was non-mycorrhizal (Kohn and Stasovski 1990). Across all studies, EcM has been reported in *Pedicularis* spp. three times but AM or NM associations ten times. Many other arctic plant genera have been reported as EcM only once or twice (e.g. *Silene*, *Campanula*, *Homogyne*; Read and Haselwandter 1981), but these are likely to be incorrect. In all these four above-mentioned arctic/alpine EcM groups, the EcM habit has been described for one or a few closely related species. If not systemically incorrect, these results suggest either a recent evolutionary shift to EcM strategy or facultative EcM habit for a group of species. It is possible that in *C. tetragona* and *S. oppositifolia*, EcM trait is characteristic of populations and has not become a common trait for a species. Therefore, also population-level analyses are urgently needed to shed further light into the ongoing EcM evolution and adaptive EcM to non-EcM balance in plants. From this perspective, some of the orphan EcM reports may actually represent recent evolutionary trends that cannot be captured in other congeneric species or populations of the same species. The alternative explanation of a highly facultative nature of EcM habit is also likely, because both local and regional processes (soil moisture, pH, limiting nutrients, neighbouring plants, climate) may affect the potential benefits of EcM habit and thus associations with EcM fungi. Nonetheless, in the era of molecular identification technologies, we urge that the authors confirm their unconventional findings of EcM habit with molecular tools or at least voucher the material for such possibility. We also strongly recommend that such novel findings be illustrated for a possibility of alternative interpretation (e.g. Haug et al. 2004).

Besides nitrogen-fixing bacteria, many EcM plants exhibit dual root colonisation with AM fungi. This seems to be a relic of the ancestral AM habit in vascular plants (Cazares and Smith 1996), but it certainly represents an adaptation for nutrition early in ontogeny or at low availability of EcM inoculum. In Salicaceae, much of the EcM colonisation level is phylogenetically determined (Tedersoo et al. 2013), but it depends on soil moisture (as above; Lodge 1989) and nutrient demand (van der Heijden 2001) at the individual and species levels. This indicates that dual mycorrhizal symbiosis may secure the plant host with sufficient nutrients and plants can optimise among the mycorrhiza types or even among fungal individuals (AM fungi: Werner and Kiers 2015) to maximise nutritional benefits. In natural conditions, most dual mycorrhizal plants in Fagaceae, Salicaceae and Myrtoideae become more dominated by EcM fungi at the sapling stage (Dominik 1956; Chen et al. 2000; Egerton-Warburton and Allen 2001), which can be explained by improved carbon availability and accumulation of recalcitrant litter with nutrients in the organic form that favours EcM symbionts over AM mutualists.

19.8 Conclusions

Our study took a critical view on the EcM status of plants and assigned 335 putatively EcM genera with roughly 8500 species into 30 phylogenetically well-delimited lineages. Because of multiple reversals to AM-only habit in several species-rich Australian EcM groups, we believe that around 250–300 genera and 6000–7000 species can be considered consistently ectomycorrhizal, but there is an urgent need for additional analyses especially in Australia and Central America. Based on phylogenetic evidence, the multiple losses of EcM habit in favour to AM (or NM in Myricaceae) and decline in EcM colonisation are related to the evolution of symbiotic nitrogen fixation and reduction of trees and bushes to shrubs and herbs, that is, a common adaptation to harsh Mediterranean and arctic/alpine climate. We also point to multiple potentially erroneous reports, many of which have propagated themselves in the literature, in a hope to better inform subsequent ecological and mycorrhizal studies.

Refining our knowledge about the mycorrhizal status of both fungi and plants will strongly improve our understanding about the evolution of EcM symbiosis. Furthermore, it will have strong implications on our understanding of ecosystem functioning on landscape and global scales due to differential nutritional balance that potentially affects all guilds of soil organisms (Phillips et al. 2013; Averill et al. 2014; Soudzilovskaia et al. 2015; Fisher et al. 2016). Mistakes in mycorrhizal type assignments in modelling studies of ecosystem function may severely bias our understanding of the ecosystem processes and biodiversity. For example, a number of meta-analysis and regional studies of mycorrhizal importance or functioning have included many misallocations of host plants in their datasets, so their results are in doubt. We recommend that an agreed list of EcM hosts be developed as an essential resource for future mycorrhizal and ecological studies. This would be based on the comprehensive summary we have provided here, with resampling and/or reassessing taxa where required.

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