New Phytologist

Tansley review

Ectomycorrhizal associations in the tropics – biogeography, diversity patterns and ecosystem roles

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Received: *1 December 2017*
Accepted: *20 February 2018*

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New Phytologist (2018) **220:** 1076–1091
doi: 10.1111/nph.15151

Key words: altitudinal gradients, Dipterocarpaceae, Fabaceae, fungal diversity, monodominance, nitrogen cycling, tropical forest.

Summary

Ectomycorrhizal (ECM) associations were historically considered rare or absent from tropical ecosystems. Although most tropical forests are dominated by arbuscular mycorrhizal (AM) trees, ECM associations are widespread and found in all tropical regions. Here, we highlight emerging patterns of ECM biogeography, diversity and ecosystem functions, identify knowledge gaps, and offer direction for future research. At the continental and regional scales, tropical ECM systems are highly diverse and vary widely in ECM plant and fungal abundance, diversity, composition and phylogenetic affinities. We found strong regional differences among the dominant host plant families, suggesting that biogeographical factors strongly influence tropical ECM symbioses. Both ECM plants and fungi also exhibit strong turnover along altitudinal and soil fertility gradients, suggesting niche differentiation among taxa. Ectomycorrhizal fungi are often more abundant and diverse in sites with nutrient-poor soils, suggesting that ECM associations can optimize plant nutrition and may contribute to the maintenance of tropical monodominant forests. More research is needed to elucidate the diversity patterns of ECM fungi and plants in the tropics and to clarify the role of this symbiosis in nutrient and carbon cycling.

I. Introduction

Tropical forests are known for their high diversity of plants, animals and microorganisms (Arnold *et al.*, 2000; Wright, 2002). Although the diversity of most organismal groups increases closer to the equator, plant symbiotic ectomycorrhizal (ECM) fungi generally do not follow this trend. Tedersoo *et al.* (2014a) demonstrated a peak in ECM fungal diversity at middle latitudes. This pattern is putatively driven by a lower abundance and diversity of host plants in the tropics. However, other factors also may be important, including high soil temperatures and rapid decomposition rates that lower the availability of organic matter and reduce vertical

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stratification of the soil profile (Tedersoo *et al.*, 2012a, 2014a). These processes may lead to poor differentiation of soil microhabitats and few organic substrates for ECM fungi. Conversely, specific tropical locales with high host densities can have ECM fungal diversities that rival those of higher latitude forests (Smith *et al.*, 2011; Henkel *et al.*, 2012).

Tropical forests vary significantly in their structure and plant species composition. Due to varying local weather, altitude and soil conditions it can be difficult to categorize tropical forests (Richards, 1996). For the purpose of this review we apply a broad definition of tropical forests as those that occur between latitudes 23.5°N and 23.5°S. Four tropical forest biomes can be recognized that differ mainly in the amount and seasonality of precipitation and in their altitudinal range (modified from Chapin *et al.*, 2011): (1) lowland tropical rainforests, which occur at < 1500 m above sea level (asl), are found near the Equator along the Intertropical Convergence Zone (ITCZ), have high precipitation and relatively low seasonality or short dry seasons; (2) tropical dry forests, which are located north and south of the ITCZ and have pronounced wet and dry seasons with dry seasons lasting 4–7 months; (3) tropical savannas, that are grasslands with reduced tree cover and highly seasonal precipitation; and (4) tropical montane forests, which occur at > 1500 m asl, have consistently cooler annual temperatures, and high precipitation with low seasonality. The purpose of this review is to synthesize the available data on ECM plants and fungi in the tropics, and elucidate their patterns of diversity, community structure and overall functioning in tropical ecosystems.

II. Historical overview

The first studies describing mycorrhizal associations of tropical plants were carried out in Java and Trinidad and documented only arbuscular mycorrhizas (AM) (Janse, 1896; Johnston, 1949). The first reports of putative ECM associations in the tropics were by Palm (1930) who observed fruiting bodies of *Boletus* growing near native *Pinus merkussi* in Sumatra and native *Pinus cubensis* in Guatemala, consistent with the confirmed ECM status of Pinaceae at higher latitudes (Melin, 1921). Fassi (1957) documented an ECM association between a *Scleroderma* (Boletales) species and the gymnosperm liana *Gnetum africanum* (Gnetaceae), and Peyronel & Fassi (1957) described ectomycorrhizas of the Congolian rainforest tree *Gilbertiodendron dewevrei* (Fabaceae). Subsequently Peyronel & Fassi (1960), Fassi & Fontana (1961, 1962), and Redhead (1968) documented ECM associations of several additional African Fabaceae. Jenik & Mensah (1967) described the morphology of ectomycorrhizas on *Afzelia africana* (Fabaceae). During the 1980s, several authors reported additional African ECM plants, including the widespread genus *Uapaca* (Phyllanthaceae), from woodlands and rainforests (Högberg & Nylund, 1981; Högberg, 1982; Högberg & Piearce, 1986; Newbery *et al.*, 1988; Alexander, 1989; Thoen & Ba, 1989).

Singh (1966) provided the first evidence of an ECM status for southeast Asian Dipterocarpaceae, confirming the symbiosis on 13 species from Malaysia. Hong (1979) later reported a list of ECM fungi potentially associated with Dipterocarpaceae. Ectomycorrhizal associations were subsequently described for several additional Dipterocarpaceae species (de Alwis & Abeynayake, 1980; Alexander & Högberg, 1986) and Smits (1983) focused on ECM manipulation for propagating valuable dipterocarp timber species.

In Central and South America, Singer & Morello (1960) described montane forests dominated by *Alnus jorullensis* or *Quercus humboldtii*, members of plant genera considered ECM in higher latitude forests. Singer (1963) then published an extensive list of ECM fungi from *Quercus humboldtii* forests in Colombia, including descriptions of many new species. Singer & Araujo (1979) hypothesized that several tree species from the Brazilian Amazon were ECM based on their spatial association with ECM fungal fruiting bodies, but confirmed ectomycorrhizas only on one *Aldina* species (Fabaceae). Their report of putative ECM associations for *Swartzia* (Fabaceae), *Glycoxylon* (Sapotaceae) and *Psychotria* (Rubiaceae) were not supported by later studies (McGuire *et al.*, 2008; Brundrett, 2009; Tedersoo & Brundrett, 2017). In Venezuela, Moyersoen (1993) reported the ECM status of *Aldina* and multiple species in Nyctaginaceae. A subsequent study also documented ECM in *Pakaraimaea dipterocarpacea* (Cistaceae) (Moyersoen, 2006). In Guyana, Henkel *et al.* (2002) documented ectomycorrhizas on three species of *Dicymbe* (Fabaceae) as well as *Aldina insignis*. Subsequent studies of monodominant *Dicymbe corymbosa* forests documented a large number of new ECM fungal species and genera in these ecosystems (Henkel *et al.*, 2012).

The idea that ECM associations were rare or nonexistent in the tropics became established based on early studies that found primarily AM associations (Malloch *et al.*, 1980) despite some early evidence of ECM associations in tropical forests. Publications on tropical ECM associations have been scattered across a variety of journals (and languages) in plant biology and mycology, and this situation likely contributed to a communication breakdown and lack of synthesis. For example, macrofungal surveys and monographs had repeatedly demonstrated that certain tropical forests were rich in ECM fungi (e.g. Heinemann, 1954; Corner & Bas, 1962; Singer, 1963; Buyck *et al.*, 1996). Nonetheless, the idea that ECM associations were rare in the tropics persisted throughout much of the 20th century. In recent years, the development of affordable molecular tools and easier access to tropical forests have spurred research on tropical ECM from 1990 to 2017 (Fig. 1). The field has grown considerably in the past 20 yr, with many studies describing new plant–fungal associations and community diversity patterns along ecological gradients (Figs 1, 2).

III. Identities and distributions of tropical ectomycorrhizal plants

In a recent global review of ECM plant lineages, Tedersoo & Brundrett (2017) reported 184 ECM genera based on direct morphological evidence. They also estimated that 6000–7000 species from 250 to 300 plant genera are likely ECM based on their phylogenetic affinities. In the tropics we found direct evidence for ECM associations in 283 plant species from 73 genera in 18 families. We provide a global synopsis of all known ECM plant species from tropical regions (Table 1; Fig. 3; Supporting

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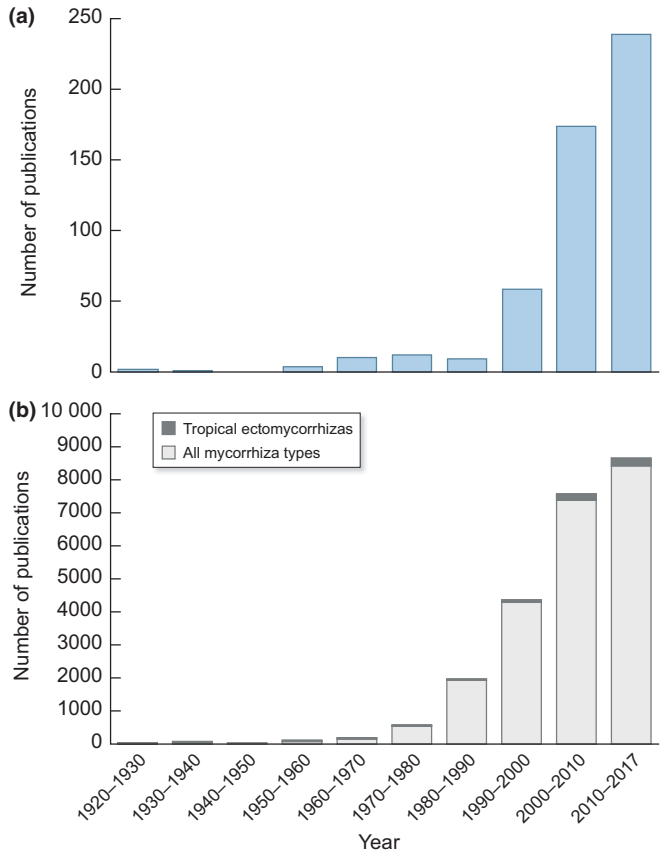

Fig. 1 Number of publications on Web of Science with the search terms 'ectomycorrhiza*' and 'tropical' found anywhere in the paper from 1986 to 2017 with the manual addition of early records from 1930 to 1985. (a) Blue bars show the total number of publications about tropical ectomycorrhizas per decade since 1920 ($n = 507$). (b) Number of publications about tropical ectomycorrhizas per decade (dark gray bars) as compared to research on all mycorrhiza types (light gray bars). The number of citations for all mycorrhiza research was determined with the search term 'mycorrhiza*'.

Information Table S1). Mycorrhizal surveys from tropical forests are summarized in Table S2. This synthesis shows that Africa has the highest number of confirmed ECM plants (120 species), followed by the Neotropics (60 species, including Central and South America and the Caribbean), Asia (59 species) and Oceania (44 species, including Melanesia, Micronesia, Polynesia and Australasia) (Fig. 3; Table 1). In Africa, Asia and Oceania, most ECM species belonged to one dominant family: in Africa 58% of ECM plant species belonged to Fabaceae, in Asia 83% to Dipterocarpaceae, and in Oceania 64% to Myrtaceae. By contrast, the number of ECM plant species in the Neotropics was more evenly distributed among Nyctaginaceae (23%), Pinaceae (18%), Fagaceae (18%), Polygonaceae (13%) and Fabaceae (12%) with seven additional families accounting for the remaining 15%. Only a few genera have been studied on multiple continents. This minimal overlap is mostly due to the restricted geographical distribution of many ECM plant genera. Our results indicate that the number of tropical plant species that form ECM may be greatly underestimated. For example, there are only 61 confirmed ECM Dipterocarpaceae species but the family has > 450 species in 13 genera (Dayanandan *et al.*, 1999; Tedersoo & Brundrett, 2017). Expanded study of this family should greatly increase the number of confirmed tropical ECM plant species. Similarly, there are 88 species of Fabaceae confirmed to form ECM but there may be many more. Fabaceae subfam. Detarioideae, which contains nearly all of the known ECM species within prominent ECM genera such as *Brachystegia, Dicymbe* and *Gilbertiodendron*, has 760 species from 84 genera (Legume Phylogeny Working Group, 2017), but only 60 species have been confirmed so far to form ECM (Smith *et al.*, 2011).

IV. Dominance of tropical forests by ECM trees

Tree diversity is high in the tropics and individual plots can have an order of magnitude greater number of species than comparable plots from higher latitude forests (Wright, 2002; ter Steege *et al.*, 2003). However, in specific locales throughout the tropics some undisturbed forests are dominated (> 60% of stand basal area; Table 2) by a single canopy tree species with ample conspecific recruitment (i.e. 'persistent monodominance' *sensu* Connell & Lowman, 1989) or co-dominated by multiple confamilial species (e.g. Newbery *et al.*, 1988). In such forests the dominant species escape density- and distance-dependent mechanisms that normally limit the abundance of individual tree species in the tropics (Janzen, 1970; Henkel *et al.*, 2005). Monodominant forests are found in all tropical regions but are particularly well represented in Africa (Richards, 1996; Peh *et al.*, 2011a).

Mechanisms that drive tropical monodominance are not fully understood and are under active study (e.g. Fukami *et al.*, 2017; Kearsley *et al.*, 2017). Several mechanisms have been proposed to drive tropical monodominance, including adaptation to extreme edaphic conditions or low disturbance rates favoring the dominant species via competitive exclusion. Multiple life-history traits often are present in the dominant tree species that may facilitate competitive exclusion, including chemical defense against herbivores, seedling shade-tolerance, mast seeding, coppicing regeneration and an ECM habit (Connell & Lowman, 1989; Hart *et al.*, 1989; Torti *et al.*, 2001; Woolley *et al.*, 2008).

Most tropical monodominant tree species are ECM (Table 2). This is striking because AM trees collectively dominate most tropical forests and ECM trees make up a small fraction of tropical tree diversity, ranging from *c.* 6% of species in the Neotropics to *c.* 19% in the Paleotropics (Table S2) (Brundrett, 2009; Fukami *et al.*, 2017). The predominance of ECM tree species that form tropical monodominant forests has led some to hypothesize a critical facilitative role of the ECM symbiosis (e.g. Connell & Lowman, 1989; Newbery *et al.*, 1997; Henkel *et al.*, 2005). Ectomycorrhizal tree species can form persistently monodominant forests, including *D. corymbosa* (Guiana Shield), *G. dewevrei* and *Julbernardia seretii* (Africa), and *Dryobalanops aromatica* and *Shorea curtisii* (southeast Asia) (Richards, 1996; Henkel, 2003).

Adult trees may enhance the performance of nearby conspecific seedlings through creation of interconnecting ECM fungal networks (EMN) (Simard *et al.*, 2012). At least two studies on

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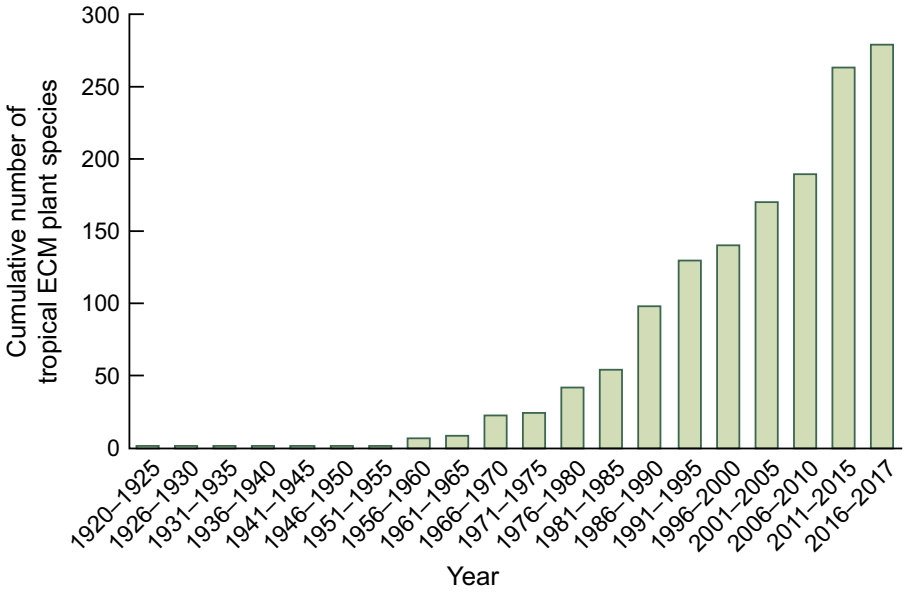

Fig. 2 Cumulative number of tropical ectomycorrhizal (ECM) plant species reported between 1924 and 2017 based on the literature review. See Supporting Information Table S2 for a complete list of publications.

Table 1 Plant families with confirmed tropical ectomycorrhizal (ECM) species and the number of species reported for each tropical region

Family*	Africa	Asia	Neotropical	Oceania	Total
Achatocarpaceae	–	–	1	–	1
Asteropeiaceae	1	–	–	–	1
Betulaceae	–	–	1	–	1
Cistaceae	–	–	1	–	1
Dipterocarpaceae	11	49	1	–	61
Fabaceae	70	1	7	10	88
Fagaceae	–	3	11	–	14
Gnetaceae	3	–	2	1	6
Goodeniaceae	–	–	–	1	1
Juglandaceae	–	1	2	–	3
Myrtaceae	–	3	–	28	31
Nothofagaceae	–	–	–	3	3
Nyctaginaceae	2	–	14	1	17
Phyllanthaceae	20	–	–	–	20
Pinaceae	–	2	11	–	13
Polygonaceae	–	–	8	–	8
Salicaceae	–	–	1	–	1
Sarcolaenaceae	13	–	–	–	13
Total per continent	120	59	60	44	283

*For references and additional information about the species see Supporting Information Table S1 and the literature cited therein.

tropical ECM trees found evidence that seedlings with access to EMNs perform better than those outside EMNs (Onguene & Kuyper, 2002; McGuire, 2007). Recent studies have found no evidence of active EMNs in forests dominated by ECM *O. mexicana* in Panama (Corrales *et al.*, 2016b) or multiple dipterocarp species in Borneo (Brearley *et al.*, 2016). Norghauer & Newbery (2016) provided evidence that a putative ECM fungal network may negatively affect the long-term survival of seedlings and saplings of *Microberlinia bisulcata* (Fabaceae) in Cameroon through deleterious juvenile-to-adult nutrient drains over multiple masting events.

The importance of EMNs also remains controversial because some positive effects could be due either to increased ECM fungal inoculum, to EMNs, or both, but these effects can be difficult to disentangle. For example, ECM seedlings growing near mature ECM trees can access a wider diversity and abundance of ECM fungal inoculum regardless of whether EMNs are present or not. Inoculum includes all structures used by fungi for dispersal, including spores, sclerotia and hyphae. Dispersed seeds of ECM plants depend on fungal inoculum for successful establishment, so the local scale spatial distribution of ECM fungal inoculum could affect the spatial patterns and local abundances of their host plant species. Seedlings growing next to conspecific mature trees and with greater access to fungal inoculum are colonized by more ECM fungal species (Dickie & Reich, 2005; Peay *et al.*, 2012). In tropical monodominant forests, seedlings and conspecific trees also have similar ECM fungal communities (Diédhiou *et al.*, 2010; Corrales *et al.*, 2016a; Ebenye *et al.*, 2017). Evidence from temperate systems also suggests that abundant ECM fungal inoculum can promote the establishment of ECM plants (Dickie & Reich, 2005; Dickie *et al.*, 2007). Conversely, Newbery *et al.* (2000) showed that ECM fungal inoculum was neither a prerequisite nor a guarantee of seedling establishment near conspecific adults in three sympatric African ECM Fabaceae.

Corrales *et al.* (2016b) hypothesized that ECM fungi in *O. mexicana*-dominated forests may slow the cycling of soil nitrogen (N), thereby reducing soil inorganic N availability. This could favor plants like *O. mexicana* that rely on ECM-mediated uptake of N directly from organic sources (Phillips *et al.*, 2013; Lindahl & Tunlid, 2015). Some studies have suggested that soils in monodominant forest have lower inorganic N and phosphorus (P) concentrations compared with adjacent mixed forest dominated by AM tree species (Torti *et al.*, 2001; Read *et al.*, 2006; Corrales *et al.*, 2016b), whereas others have found no differences (Hart *et al.*, 1989; Conway & Alexander, 1992; Henkel, 2003; Peh *et al.*, 2011b). However, most studies of tropical monodominant forests have measured total nutrient pools rather than focusing on plant-available

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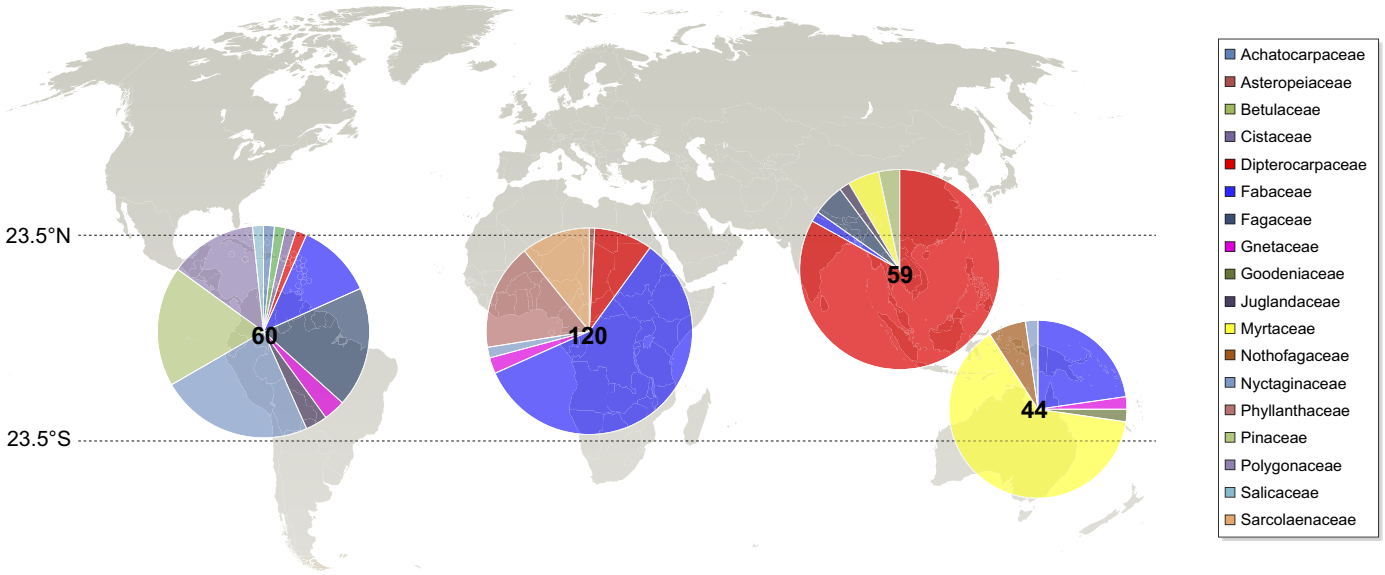

Fig. 3 Map depicting the total number of confirmed ectomycorrhizal (ECM) plant species and their distribution across different plant families as reported for tropical latitudes of Africa, Southeast Asia, Oceania and the Neotropics. Color-coded areas correspond to the number of species from specific plant families.

Table 2 List of reported monodominant ectomycorrhizal (ECM) and arbuscular mycorrhizal (AM) tree species in tropical forests (forest type refers to the type of tropical climate each monodominant species inhabits)

Monodominant species	Family	Continent	Type of mycorrhiza	Forest type	Reference for monodominance
Species with confirmed monodominance and ECM associations					
Alnus acuminata	Betulaceae	Neotropical	ECM/AM	Tropical montane forest	Kappelle & Brown (2001)
Dryobalanops aromatica	Dipterocarpaceae	Asia	ECM	Lowland tropical rainforest	Whitmore (1984)
Parashorea malaanonan	Dipterocarpaceae	Asia	ECM	Lowland tropical rainforest	Richards (1996)
Parashorea chinensis	Dipterocarpaceae	Asia	ECM	Tropical seasonal forest	van der Velden *et al.* (2014)
Shorea curtisii	Dipterocarpaceae	Asia	ECM	Lowland tropical rainforest	Grubb *et al.* (1994)
Gilbertiodendron dewevrei	Fabaceae	Africa	ECM	Lowland tropical rainforest	Conway (1992)
Dicymbe corymbosa	Fabaceae	Neotropical	ECM	Lowland tropical rainforest	Henkel *et al.* (2002)
Quercus humboldtii	Fagaceae	Neotropical	ECM	Tropical montane forest	León *et al.* (2009)
Quercus oleoides	Fagaceae	Neotropical	ECM	Tropical montane forest	Boucher (1981)
Oreomunnea mexicana	Juglandaceae	Neotropical	ECM	Tropical montane forest	Rzedowski & Palacio-Chávez (1977)
Colombobalanus excelsa	Fagaceae	Neotropical	ECM	Tropical montane forest	Parra-Aldana *et al.* (2011)
Species with confirmed monodominance and AM associations or unknown type of mycorrhizal association					
Cynometra alexandri	Fabaceae	Africa	AM	Lowland tropical rainforest	Hart *et al.* (1989)
Talbotiella gentii	Fabaceae	Africa	AM	Lowland tropical rainforest	Richards (1996)
Tetraberlinia tubmaniana	Fabaceae	Africa	Unknown	Lowland tropical rainforest	Connell & Lowman (1989)
Eusideroxylon zwageri	Lauraceae		Unknown	Lowland tropical rainforest	Richards (1996)
Aspidosperma excelsum	Apocynaceae	Neotropical	Unknown	Lowland tropical rainforest	Richards (1996)
Dacryodes excelsa	Burseraceae	Neotropical	AM	Lowland tropical rainforest	Richards (1996)
Celaenodendron mexicanum	Euphorbiaceae	Neotropical	Unknown	Tropical deciduous forest	Martijena & Bullock (1994)
Eperua falcata	Fabaceae	Neotropical	AM	Lowland tropical rainforest	Torti *et al.* (2001)
Mora excelsa	Fabaceae	Neotropical	AM	Lowland tropical rainforest	Torti *et al.* (2001)
Mora gonggrijpii	Fabaceae	Neotropical	Not ECM, likely AM*	Lowland tropical rainforest	Connell & Lowman (1989)
Mora oleifera	Fabaceae	Neotropical	Unknown	Lowland tropical rainforest	Holdridge *et al.* (1971)
Peltogyne gracilipes	Fabaceae	Neotropical	Unknown	Lowland tropical rainforest	Nascimento *et al.* (1997)
Pentaclethra macroloba	Fabaceae	Neotropical	Unknown	Lowland tropical rainforest	Connell & Lowman (1989)
Brosimum rubescens	Moraceae	Neotropical	Unknown	Tropical seasonal forest	Marimon *et al.* (2012)
Spirotropis longifolia	Fabaceae	Neotropical	AM	Lowland tropical rainforest	Fonty *et al.* (2011)

*T. W. Henkel & M. E. Smith (unpublished).

inorganic N and P (Hart *et al.*, 1989; Conway & Alexander, 1992; Peh *et al.*, 2011b). Although this N-cycling mechanism needs to be tested outside *O. mexicana* monodominant forests, it is possible that microbial competition for N may help to explain monodominance in some cases. Such a mechanism could work in concert with other mechanisms, such as ECM fungal networking.

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Proposed nutrient-based mechanisms are intriguing and require further study. However, Smith & Read (2008) noted that numerous glasshouse and field experiments involving ECM African Fabaceae and Asian Dipterocarpaceae have shown that although ECM fungal colonization increased nutrient uptake, it did not enhance plant growth (e.g. Brearley *et al.*, 2003; Neba *et al.*, 2016). This apparent unlinking of nutrient uptake and growth enhancement suggests that the benefits of ECM fungal colonization for forest-dominating tropical trees needs to be critically re-examined.

An alternative hypothesis that could explain monodominance is that ECM fungal colonization enables cumulative capture of nutrient reserves to facilitate mast seeding (Newbery, 2005; Smith & Read, 2008). As noted earlier, most monodominant lowland tropical tree species are ECM and exhibit mast seeding (e.g. *G. dewevrei* in Africa, Hart, 1995; mixed dipterocarps in Asia, Curran & Leighton, 2000; *D. corymbosa* in Guyana, Henkel *et al.*, 2005). Mast seeding yields abundant shade-tolerant seedlings and enables the persistence of the dominant species, but resource investment in masting is high. In *M. bisulcata* the dry mass of flowers, fruits and seeds during masts can be 55% of the annual leaf dry mass (Green & Newbery, 2002) and in *D. corymbosa* the reproductive dry mass during masting was 3.0 t ha^{-1} yr^{-1}, nearly double the average annual leaf litter dry mass. Furthermore, P investment during masting is five times greater than the P lost during annual leaf litterfall (Henkel *et al.*, 2005; T. W. Henkel, unpublished).

Available data suggest that there is a heavy nutrient drain on ECM trees due to masting and that nutrients, particularly P, are the limiting factor that controls masting (Janzen, 1974; Ashton, 1982; Newbery *et al.*, 1997; Newbery, 2005). For example, Ichie *et al.* (2005) found that threshold levels of P, N and carbohydrate reserves are required for masting in *Dryobalanops tempehes*. Recapture of short-supply P by ectomycorrhizal fungi was supported by the results of Chuyong *et al.* (2000) who found that P concentrations were higher in the leaves of four ECM Fabaceae than in nearby non-ECM trees, and that retranslocation of P before ECM litterfall was only half that of non-ECM tree species. Chuyong *et al.* (2002) showed that although litter of ECM tree species decomposed slower than litter of non-ECM plants, litter-bound P was mineralized faster, enabling rapid recycling by ectomycorrhizas. Nutrient accumulation mediated by ECM fungi was subsequently implicated as a causal factor in long-term masting cycles of *M. bisulcata* (Newbery *et al.*, 2006, 2013). Although none of these studies directly demonstrated uptake of soil nutrients by ECM fungi under field conditions, ECM associations are implicated as a contributing factor in masting and monodominance in ECM trees, at least in some ecosystems.

Although there have been advances in understanding tropical monodominance over the last 10 yr, more information about causes and ecosystem effects of monodominance at different spatial and temporal scales is needed to fully understand this phenomenon. The mycorrhizal status of several monodominant tree species has still not been examined and the number of monodominant ECM tree species is likely to increase as additional mycorrhizal surveys are conducted in tropical forests.

V. Biogeography of tropical ECM fungi

In contrast to the variable patterns seen in ECM plant hosts (Fig. 3), several important ECM fungal lineages are species-rich and dominant across most tropical forests (Tedersoo *et al.*, 2010a, 2012a). Surveys of ECM root tips and ECM fungal fruiting bodies have found that members of the /amanita, /russula–lactarius and /boletus ECM fungal lineages are speciose and widespread across the tropics (Tedersoo *et al.*, 2010a; Tedersoo & Smith, 2013; and references therein). The pantropical distribution of these speciose lineages suggests that they are adapted to tropical habitats. Root and soil-based studies often find that the /tomentella–thelephora and /sebacina lineages also are diverse and dominant, but have been undersampled due to their inconspicuous fruiting bodies (Kõoljalg *et al.*, 2000; Tedersoo *et al.*, 2014b). Phylogeographical evidence suggests that many ECM fungal lineages are likely to have originated in higher latitude regions and subsequently migrated into the tropics (Tedersoo *et al.*, 2010a, 2014a). There are at least three globally distributed ECM fungal lineages (/russula–lactarius, /clavulina and /inocybe) that probably have tropical origins (Buyck *et al.*, 1996; Alexander, 2006; Matheny *et al.*, 2009; Kennedy *et al.*, 2012).

Several other ECM fungal lineages also are locally important in tropical ecosystems but their diversity and dominance are variable depending on the continent, type of forest and tree hosts. Species in the /scleroderma–pisolithus lineage are prevalent in some forest types, and taxa in this group often dominate the roots of specific plant taxa, such as *Gnetum* and *Coccoloba* (Tedersoo & Põlme, 2012; Séne *et al.*, 2015). Members of the /clavulina lineage are common worldwide but are particularly diverse in several Neotropical forests (Morris *et al.*, 2009; Smith *et al.*, 2011; Uehling *et al.*, 2012). Species in the /cortinarius lineage can be common in montane tropical habitats or in sandy soils. This is probably due to the fact that most species are nitrophobic and have long-distance exploration types; these features may enhance their performance in low N soils (Roy *et al.*, 2016; Essene *et al.*, 2017; Geml *et al.*, 2017). Members of the /cantharellus and /inocybe lineages are highly diverse at some tropical sites but completely missing from others, with no obvious explanation for their distribution pattern (Tedersoo *et al.*, 2012a). Currently the /guyanagarika lineage, which consists of three *Guyanagarika* species, is the only ECM fungal lineage that is considered endemic to the tropics (Sánchez-García *et al.*, 2016).

Another noticeable pattern is the conspicuous absence from the tropics of some ECM fungal taxa that are well represented at higher latitudes. For example, most ECM Pezizales are either absent or species-poor in lowland tropical forests (Tedersoo *et al.*, 2010a). Despite extensive root tip sampling and fruiting body surveys in *Dicymbe* forests of Guyana, there are no records of ECM Pezizales (e.g. Henkel *et al.*, 2012; Smith *et al.*, 2017) and only a few ECM Pezizales have been reported from tropical Africa (Tedersoo *et al.*, 2012a). By contrast, some Mexican tropical dry forests dominated by *Quercus* host a high diversity of ECM Pezizales and may be biodiversity hotspots for these fungi (García-Guzmán *et al.*, 2017). Other lineages are apparently absent or species-poor in tropical ecosystems, including /albatrellus, /endogone1, /hygrophorus,

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/paxillus–gyrodon, /piloderma, /suillus–rhizopogon and /tricholoma (Tedersoo *et al.*, 2010a). These fungi likely evolved at higher latitudes but both geographical barriers and host incompatibilities have likely kept them from dispersing to the tropics. Alternatively, some taxa may require specific environmental conditions. For example, ECM Pezizales abound in forests with high soil pH and seasonal drought (Ge *et al.*, 2017) but these environmental features are lacking in many lowland tropical forests. Other groups such as truffle-like fungi are understudied in the tropics so their biogeography patterns remain poorly known (Sulzbacher *et al.*, 2017).

Biogeographical understanding of ECM fungi also is confounded by the fact that many regions in the tropics are still undersampled. For example, there are only a few studies of ECM fungal communities from Oceania (Adams *et al.*, 2006; Tedersoo & Põlme, 2012; Waseem *et al.*, 2017). Greater sequencing of ECM roots and sporocarp surveys from additional locations and host lineages are needed to fully elucidate the diversity and biogeographical patterns of tropical ECM fungi.

VI. Beta diversity patterns in tropical ECM fungal communities

Tropical ECM-dominated forests often are patchily distributed within a larger forest matrix of AM trees (Degagne *et al.*, 2009; Newbery *et al.*, 2013). Spatial effects may strongly influence diversity and community structure of ECM fungal communities found in discrete stands dominated by ECM trees (Bahram *et al.*, 2013). However, in tropical ecosystems soil, climate and vegetation variables are often spatially autocorrelated, making it challenging to separate environmental from purely distance effects (Ettema & Wardle, 2002; Bahram *et al.*, 2013). Bahram *et al.* (2013) studied distance effects on ECM fungal communities of tropical and nontropical forests, and found that distance decay was greater in tropical forests. They suggested that lower host density could explain tropical ECM fungal community structure because dispersal limitation of ECM fungi could create 'islands' of unique fungal communities (Bahram *et al.*, 2013). This situation is supported by data where widely dispersed ECM understory tree species are growing in hyperdiverse forests of AM trees in the Neotropics (Tedersoo *et al.*, 2010b). However, this argument does not consider that most ECM-dominated forests in the tropics have high host density. Accordingly, other factors besides geographical distance, such as soil fertility, soil vertical stratification, altitude, host specificity, coevolution of fungi with their hosts, and forest successional stage are likely to be important to explain the strong distance decay and high variation in tropical ECM fungal communities.

1. Community turnover across soil types and along soil fertility gradients

In some tropical systems ECM fungi can exhibit high community turnover along varying soil types and fertility gradients (Peay *et al.*, 2010a, 2015; Corrales *et al.*, 2016a). In tropical forests, the distribution of plant species strongly corresponds with soil nutrient availability at local, regional and landscape scales (Gartlan *et al.*, 1986; Itoh, 1995; Paoli *et al.*, 2006; John *et al.*, 2007). It is therefore challenging to develop studies on ECM fungal community variation along environmental gradients because of the many confounding factors.

Peay *et al.* (2010b) studied a diverse Dipterocarpaceae-dominated forest in Borneo and found high turnover of ECM fungal species between two different soil types (clay and sandy). Edaphic factors explained *c.* 25% of the variation in ECM fungi species composition. However, given the strong plant turnover associated with soils at this site, it was not possible to fully separate biotic vs abiotic effects in structuring the fungal communities. Functional variation in the ECM fungal community according to soil type was implied given that short-distance (Thelephorales and Russulales) and long-distance (Cortinariaceae) exploration mycorrhizas varied in their abundances between clay and sandy soils. A follow-up study in the same system by Peay *et al.* (2015) involving reciprocal seedling transplants showed that soil type was of greater importance for determining the ECM fungal community composition than host plant species, a finding further corroborated with belowground sequencing by Essene *et al.* (2017).

In a neotropical montane forest, Corrales *et al.* (2016b) sampled ECM fungi in *Oreomunnea mexicana* monodominant stands that were only 6 km apart but had contrasting soil fertility. They found strong ECM fungal species turnover between high and low fertility sites. However, soil fertility and annual precipitation were highly correlated so it was impossible to determine which factor was more important in structuring the fungal communities. Corrales *et al.* (2017) also studied the effect of N addition on the ECM fungi in the same study site and found that the artificially increased N availability strongly altered the fungal community composition. Nitrophilic genera such as *Laccaria* and *Lactarius* responded positively to N addition, whereas nitrophobic genera such as *Cortinarius* responded negatively. Studies from Borneo (Peay *et al.*, 2010b) and Panama (Corrales *et al.*, 2016a) also found significant phylogenetic clustering of fungal species by soil type. These results suggest that habitat filtering due to soil characteristics for specific functional traits is critical for structuring tropical ECM fungal communities. Phylogenetic clustering also is consistent with conserved functional traits among closely related ECM fungi (Peay *et al.*, 2010b).

By contrast, studies in the Guiana Shield employing above- and belowground sampling found that *D. corymbosa*-dominated forests on both sand and lateritic soils had similar ECM fungal communities (Smith *et al.*, 2017). Broader geographical overlap also was found in the ECM fungi symbiotic with canopy trees *D. corymbosa*, *D. altsonii*, *Dicymbe jenmanii*, *Aldina insignis* and *Pakaraimaea dipterocarpacea* (Smith *et al.*, 2011, 2013; Henkel *et al.*, 2012). Vasco-Palacios *et al.* (2018) corroborated this low Guiana Shield beta diversity on an even broader scale in a white sand forest dominated by *Dicymbe* and *Aldina* species in Colombia. At this site 42% of the 59 ECM fungal species recovered as sporocarps or on ECM root tips were conspecific with taxa from Guyana. Roy *et al.* (2016) emphasized the uniqueness and heterogeneity of ECM fungi from Amazonian white sand forests as compared to those of Guyana. However, given that *c.* 1000 km

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separates the Colombia and Guyana sites, there appears to be a broad regional pool of Guiana Shield ECM fungi that occur with a variety of host plants on multiple soil types.

2. ECM fungal community variation through the soil profile

Studies on variation of ECM fungal communities across soil layers (e.g. vertical stratification), have found contrasting results in different tropical forests. Tedersoo *et al.* (2011) found little variation in ECM fungal communities across soil horizons in each of four sites in Africa; soil horizon explained only 0.5% of the variance in the community. By contrast, two studies of monodominant forest of *Dicymbe corymbosa* in Guyana found evidence of vertical stratification. McGuire *et al.* (2013) compared fungal communities in leaf litter and mineral soil and found that different fungal lineages dominated in soil vs litter, and that ECM fungi may be less abundant in litter. In a more intensive study, Smith *et al.* (2017) examined ECM fungi from *D. corymbosa* root tips inhabiting aerially trapped litter, decayed wood, humus-rich root mounds and mineral soil. They found ECM fungi on roots in all strata and detected significant turnover of ECM fungal communities, particularly in the mineral soil, indicative of some degree of niche differentiation.

Differences in ECM host abundance, litter accumulation and litter quality may affect vertical stratification across tropical forest types. In some sites where ECM host plants are dominant (e.g. *D. corymbosa* monodominant forest), ECM fungi vertical stratification shows patterns similar to those observed in temperate ecosystems. The *D. corymbosa* system has extensive litter accumulation, which likely drives turnover of ECM fungal species between organic layers and mineral soils. It has been hypothesized that in some tropical forests tannin-rich litter with a high C:N ratio may decompose slowly, promote litter build-up and stratification, and lead to diversification of the ECM fungal community (Hättenschwiler *et al.*, 2011). The lack of vertical stratification found in other studies has been attributed to the high decomposition rates, which lead to poor soil horizon development and similar nutrient availability across soil horizons (Tedersoo & Nara, 2010; Tedersoo *et al.*, 2011).

3. Community turnover across altitudinal gradients

Richness and abundance of ECM fungi generally peak at 1500–2500 m asl in tropical montane cloud forests and then monotonically decrease at higher elevations (Gómez-Hernández *et al.*, 2012; Geml *et al.*, 2014, 2017; Looby *et al.*, 2016). These mid-elevation forests usually have higher precipitation, intermediate temperatures, and higher diversity and/or density of ECM host trees compared to forests upslope and downslope (Gómez-Hernández *et al.*, 2012; Geml *et al.*, 2014). Nonetheless, Geml *et al.* (2017) found peak ECM fungal richness in mid-elevation forests on Mt. Kinabalu, Borneo, even though ECM host density was putatively similar over a broader elevation gradient. This suggests that elevation-dependent abiotic factors probably also have a strong influence on ECM fungal diversity. It is well-established that temperature, relative humidity, soil pH, parent material, decomposition rates, forest productivity and plant community composition vary along tropical elevation gradients. This increases the difficulty of determining the causes of observed changes in the ECM fungal communities, which clearly require more study.

Another important consideration is that ECM trees found at higher elevation in many tropical sites are of higher latitude origin (e.g. *Quercus*, *Alnus*, *Leptospermum*) and with rare exceptions these do not occur at low elevations in the tropics. The very different evolutionary origins of hosts trees in montane vs lowland forests may strongly influence ECM fungal communities and their beta diversity (Morris *et al.*, 2008; Kennedy *et al.*, 2011).

4. Effects of host specificity on ECM fungal community structure

Studies of host specificity and host preferences in tropical ECM fungi have shown contrasting results, depending on the host species and the type of ecosystem. Most studies of host specificity in monodominant or codominant forests have found that ECM plants and fungi are generalists (Morris *et al.*, 2009; Diédhiou *et al.*, 2010; Smith *et al.*, 2011, 2013; Tedersoo *et al.*, 2011; Peay *et al.*, 2015). Diédhiou *et al.* (2010) studied several sympatric Fabaceae and *Uapaca* species in Guinea, and found that multi-host ECM fungi accounted for 89% of taxa and that ECM fungal communities on seedlings were dominated by host generalists. Tedersoo *et al.* (2011) found a similar result with Fabaceae and *Uapaca* in Central Africa and Madagascar where host plant species explained only 0.8–10.1% of the ECM fungal community variation. Smith *et al.* (2011, 2013, 2017) found that co-occurring species of Fabaceae and *P. dipterocarpacea* harbored many of the same ECM fungi across multiple sites in Guyana, suggesting that host preferences are weak in that region. Peay *et al.* (2015) found no evidence of host specificity in a reciprocal transplant experiment involving multiple species of Dipterocarpaceae. Conversely, Morris *et al.* (2009) found that host plant species was the most important determinant of ECM fungal community composition across a *Quercus*-dominated landscape in Mexico. Although some ECM fungi were shared across *Quercus* hosts, multiple abundant ECM fungi species were found on only one of the two sampled tree species.

In contrast to the more common scenario of low host preferences, there are some unusual plant species or genera that are associated with a specific and reduced set of ECM fungi. These include species of *Coccoloba* (Põlme *et al.*, 2017), *Pisonia* (Suvi *et al.*, 2010; Hayward & Hynson, 2014), *Alnus* (Kennedy *et al.*, 2011; Põlme *et al.*, 2013) and *Gnetum* (Tedersoo & Põlme, 2012). These associations could result from long-term coevolution between plants and fungi, strong environmental filtering, or a combination of both factors (Huggins *et al.*, 2014; Põlme *et al.*, 2017). Some species of *Coccoloba*, *Pisonia* and *Alnus* occur in stressful environmental settings of high salinity, low water availability, high concentrations of P and N, or low pH soils (for more details on *Alnus*, see Tedersoo *et al.*, 2009). Some of these ECM host plants are small trees, shrubs or lianas with low within-stand basal area and stem density. All of these factors may be important in structuring their ECM fungal communities.

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Hosts such as *Coccoloba uvifera*, *Pisonia grandis* and *Pisonia sandwicensis* inhabit stressful, saline coastal habitats and they always associate with a small suite of specific ECM fungi (Chambers *et al.*, 1998; Suvi *et al.*, 2010; Hayward & Hynson, 2014; Séne *et al.*, 2015). In the case of *Alnus*, specificity is linked to the co-migration of plants and their ECM fungi from the northern hemisphere (Kennedy *et al.*, 2011). A three-way interaction among *Alnus*, ECM fungi and *Frankia* bacteria likely promotes habitat filtering which excludes nonspecialist ECM fungi (Kennedy *et al.*, 2015).

In other cases, specificity does not seem to be driven by environmental factors and is more likely due to specialization of the symbionts. Studies of *Gnetum africanum* (Gnetaceae) in Africa found only a few closely related *Scleroderma* species as ECM fungal symbionts (Bechem & Alexander, 2012). Similar results were found in *Gnetum gnemon* from Papua New Guinea where only five ECM fungal species (including two *Scleroderma*) were detected (Tedersoo & Põlme, 2012). Tedersoo *et al.* (2010b) also found high host preferences in the Ecuadorian Amazon on several *Coccoloba*, *Guapira* and *Neea* species; each of the plant taxa exhibited low ECM fungal diversity and minimal symbiont sharing. More extensive sampling and additional studies are necessary to determine why some ECM plants harbor low-diversity communities even when there is not an obvious environmental determinant.

5. Role of tropical ECM fungi in nutrient cycling

Recent research primarily from temperate ECM-dominated systems has demonstrated that ECM fungi play an important role in carbon (C) and N cycling. In tropical forests, functional roles of ECM associations are poorly known and contrasting results have come from studies in different ecosystems. Averill *et al.* (2014) analyzed a global dataset (including several tropical forests) and found that soils in ECM-dominated forests have a higher C content than soils in AM-dominated forests. Mechanisms behind C accumulation are largely untested in tropical forests. One hypothesis is that ECM plants produce more litter with a higher C : N ratio (Jordan, 1985), but alternative mechanisms have been proposed (Chuyong *et al.*, 2000).

Decomposition rates also may play an important role. Singer & Araujo (1979) proposed that ECM fungi could alter the C cycle by slowing litter decomposition in lowland Amazonian forests via the 'Gadgil effect'. The Gadgil effect proposes that when ECM fungi dominate the soil microbial community, they induce 'direct cycling' of nutrients by competing with decomposer fungi for organic nutrients in litter (Fernandez & Kennedy, 2015). Whether a Gadgil effect is operating in tropical ECM-dominated forests is still an open question. Mayor & Henkel (2006) used litter from *Dicymbe* monodominant forest and mixed AM-dominated forests to establish a reciprocal litter transplant experiment. They severed both roots and ECM fungal mycelium via trenching. They found no differences in litter decomposition rates between forest types or between trenched and nontrenched areas. McGuire *et al.* (2010) also conducted a reciprocal litter transplant and trenching experiment in a nearby forest. They found that the litter decomposition rate in AM-dominated forest was almost double that of the *Dicymbe* forest and that saprobic microbes were more abundant and diverse in the litter placed in AM-dominated forest. Torti *et al.* (2001) used a similar approach to compare decomposition rates in an African *Gilbertiodendron* forest to nearby AM-dominated forest and also found that decay was twice as fast in the AM-dominated forest. The results of McGuire *et al.* (2010) and Torti *et al.* (2001) support the hypothesis of Singer & Araujo (1986) but further work is needed in other study systems to determine whether these results are applicable across different forests (see Chuyong *et al.*, 2000).

Ectomycorrhizal fungi compete with decomposer microorganisms for access to organic N and P from litter (Read & Perez-Moreno, 2003). Brearley *et al.* (2003) grew seedlings of three Dipterocarpaceae species with and without litter addition, and showed that litter increased the ECM fungal colonization and the growth rate of all three species. Brearley *et al.* (2005) then demonstrated in an *in vitro* experiment that three tropical ECM fungi utilized both inorganic and organic N sources. They also showed that foliar $\delta^{15}N$ was negatively correlated with ECM fungal colonization, suggesting increased organic nutrient uptake via ECM fungi.

Tropical forests have higher N availability than many temperate forests and therefore have a more open N cycle (Hedin *et al.*, 2009). Tropical ECM-dominated forests sometimes have lower soil inorganic N than AM-dominated forests and therefore N limitation could affect plant growth (Torti *et al.*, 2001; Read *et al.*, 2006). However, some ECM-dominated forests have similar soil N to nearby AM-dominated forest so it is challenging to make generalizations about effects of ECM fungi on N availability (Hart *et al.*, 1989; Henkel, 2003; Peh *et al.*, 2011b). Tedersoo *et al.* (2012b) measured stable isotopes in soils and plants in a lowland tropical forest in Africa with the presence of several ECM host plant species. They detected an open N cycle with soils enriched in $\delta^{15}N$, low organic matter accumulation and poor soil stratification. This high N availability might have been due to low ECM host plant abundance; this forest had high ECM plant diversity but ECM hosts accounted for $\leq$ 10% of the trees in the sampled plots (Sunderland *et al.*, 2004).

Waring *et al.* (2016) found higher protease activity and lower rates of mineralization and nitrification in lowland Costa Rican forests dominated by *Quercus oleoides* than in AM-dominated forests. However, they argued that this conservative N cycling was due not only to the presence of ECM fungi, but also to adaptations of both plants and microbial communities to low N availability conditions. Variation in functional traits in individual plants also may have contributed. Given the variation between different ecosystems and host plants, further research is needed to elucidate the role of ectomycorrhizas in soil N availability in tropical forests. Specifically, future studies should combine detailed transformations and losses of N with complete characterization of the plant and soil fungal communities.

Tropical forests are typically limited by P rather than N so tropical ECM fungi are hypothesized to play an important role in both N and P cycling. In Cameroon, stands with high ECM tree density had much higher available P in the litter than nearby

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Box 1 Elucidating tropical mycorrhizas – a case study

Mycorrhizal associations of *Alfaroa costaricensis* and *Ticodendron incognitum* in montane forests of Panama

Alfaroa costaricensis (Juglandaceae) and *Ticodendron incognitum* (Ticodendraceae) are tree species that occur in mid-elevation cloud forests of Panama and Costa Rica. Both species are found scattered in mixed forests or in forests dominated by the ECM trees *Oreomunnea mexicana* (Juglandaceae) or *Quercus* spp. (Fagaceae) (J. Dalling, unpublished). There have been no previous studies of the mycorrhizal status of *Alfaroa* and *Ticodendron* (Tedersoo & Brundrett, 2017).

The genus *Alfaroa* was phylogenetically placed within Juglandaceae subfam. Engelhardioideae (Manos *et al.*, 2007), which includes ECM-forming species of *Oreomunnea* and *Alfaropsis* (Haug *et al.*, 1994; Corrales *et al.*, 2016a). *Ticodendron incognitum* is placed in the monotypic family Ticodendraceae, sister to Betulaceae (Manos *et al.*, 2007). Within the Betulaceae, species of *Alnus* form symbioses with N-fixing bacteria and ECM fungi (Kennedy *et al.*, 2011; Li *et al.*, 2015), whereas *Betula, Corylus, Carpinus* and *Ostrya* species are ECM (Tedersoo & Brundrett, 2017). Thus, by phylogenetic affinity *Alfaroa* and *Ticodendron* are suspected to form ECM (Tedersoo & Brundrett, 2017).

Our assessment of the mycorrhizal status of *A. costaricensis* and *T. incognitum* illustrates the challenges of studying tropical ectomycorrhizas. We used Illumina MiSeq and fungal-specific ITS1 primers (Smith & Peay, 2014) to generate data from the roots of 15 *A. costaricensis* trees (three sites) and three *T. incognitum* trees (two sites) in Panama. We sampled 16 cm of fine roots from two root branches (32 cm of roots per tree). Root processing followed Smith *et al.* (2017). The host plant species was confirmed by chloroplast trnL intron sequencing with primers trnC and trnD from randomly selected root tips and from the pooled roots used for Illumina (Taberlet, 1991). Host plant and fungi sequences are available in International Nucleotide Sequence Database (INSD) (MG241340–MG241342) and SRA (SRP132838).

The roots of *A. costaricensis* were diagnostically ECM, with a well-defined fungal mantle and Hartig net (Fig. 4c,d). Despite moderate sampling effort we captured significant ECM fungal diversity. Illumina sequencing revealed 72 fungal operational taxonomic units (OTUs) associated with *A. costaricensis,* with the 22 most abundant (83% of sequences) belonging to ECM fungal genera. Sequences showed BLAST matches to 11 ECM fungal genera, including *Cortinarius, Lactarius*, *Russula* and *Tomentella* (Fig. 4a). These DNA sequences and the diagnostic root morphology confirm the ECM status of *Alfaroa*.

The case of *Ticodendron incognitum*, however, was not straightforward. Morphological analyses of *Ticodendron* roots did not reveal typical mantle formation and we were not able to observe a Hartig net from any of the samples. Instead we observed vesicles and arbuscules in all three root samples (Fig. 4e,f). Sequencing from the three *T. incognitum* trees generated 195 962 sequences. After quality control filtering and OTU picking (including discarding OTUs with < 1% of sequences per sample), we documented 45 OTUs. Six OTUs (64 478 sequences) were identified as 'fungi' or had no BLAST hits. These unknown fungi constituted 2–68% of the sequences from our samples. Twelve additional OTUs (24 715 sequences) could only be identified to order or class. The lack of phylogenetic resolution limited our ability to define the trophic modes of these root-associated fungi. The remaining 27 OTUS (105 874 sequences) were assigned to genus or species and were given a 'highly probable' trophic mode by FUNGUILD software (Nguyen *et al.*, 2016). This high level of uncertainty for some dominant taxa is particularly problematic for understudied ecosystems (Peay *et al.*, 2010b; Truong *et al.*, 2017).

Our analysis indicates that the different *Ticodendron* individuals had widely divergent fungal communities (Fig. 4b). Approximately 65% of sequences from sample 2 belonged to ECM fungi but no ECM morphology was detected (Fig. 4e,f). By contrast, sample 1 had no ECM fungal sequences and sample 3 had only two ECM fungi that constituted *c.* 20% of the reads. All plant sequences matched *Ticodendron* records from INSD.

Morphological evidence suggests that *Ticodendron* forms AM associations and there was no morphological evidence for ECM symbiosis. However, molecular data suggest that some individual roots may be colonized by ECM fungi. There are several hypotheses that might explain why ECM fungi were detected in roots without ECM morphology. One possibility is that ECM fungi were symbiotic with nearby *Oreomunnea* or *Quercus* trees but superficially colonized *Ticodendron*. Alternatively, ECM fungi may form a viable symbiosis with *Ticodendron* but without a typical ECM morphology. Lastly, it is possible that ECM root tips were present but that we were not able to visualize them. The most likely scenario is that ECM fungi present on nearby hosts colonized young *Ticodendron* roots without a viable symbiosis. We noted that sample 1 (which lacked ECM fungal sequences) was distant from any ECM host trees, whereas the other two samples (which had 20–65% ECM fungal sequences) were found at sites with *Oreomunnea* or *Quercus* nearby. Sato *et al.* (2015) found a similar case where ECM fungi colonized the roots of non-ECM trees growing in close proximity to dipterocarps. However, we cannot rule out the possibility that *Ticodendron* forms ECM under some conditions. Further sampling is needed to test this hypothesis.

stands with low ECM tree density even though both occur on sandy soils (Newbery *et al.*, 1997). These results suggest that ECM fungi may facilitate host plant access to organic P. The classic Amazonian *in situ* study of Herrera *et al.* (1978) used ^{32}P-labeled leaves to demonstrate the transfer of P from litter to living root tissue via fungi. If short-cycling of P to hosts via ECM fungi is significant, then ECM plants should have a competitive advantage compared to AM or nonmycorrhizal plants under low inorganic P conditions.

Fertilization experiments using sterile and inoculated seedlings found no effect of nutrient addition on the relative plant growth rate but did find a positive response to ECM fungal inoculation. In a multifactorial glasshouse experiment, Lee & Alexander (1994) found that seedlings of two Dipterocarpaceae species responded better to ECM fungal inoculation than to fertilization with P, K or both. Moyersoen *et al.* (1998) found that colonization by AM fungi was positively correlated with both P uptake and growth rate of AM plants at low P levels. By contrast, this study and others found that P uptake in ECM plants is positively correlated with ECM fungal colonization at both high and low P levels, but that increased P uptake is not reflected in plant growth rates (e.g. Brearley, 2012; Steidinger *et al.*, 2015). In another glasshouse experiment, Steidinger *et al.* (2015) found no differences between AM and ECM plants in

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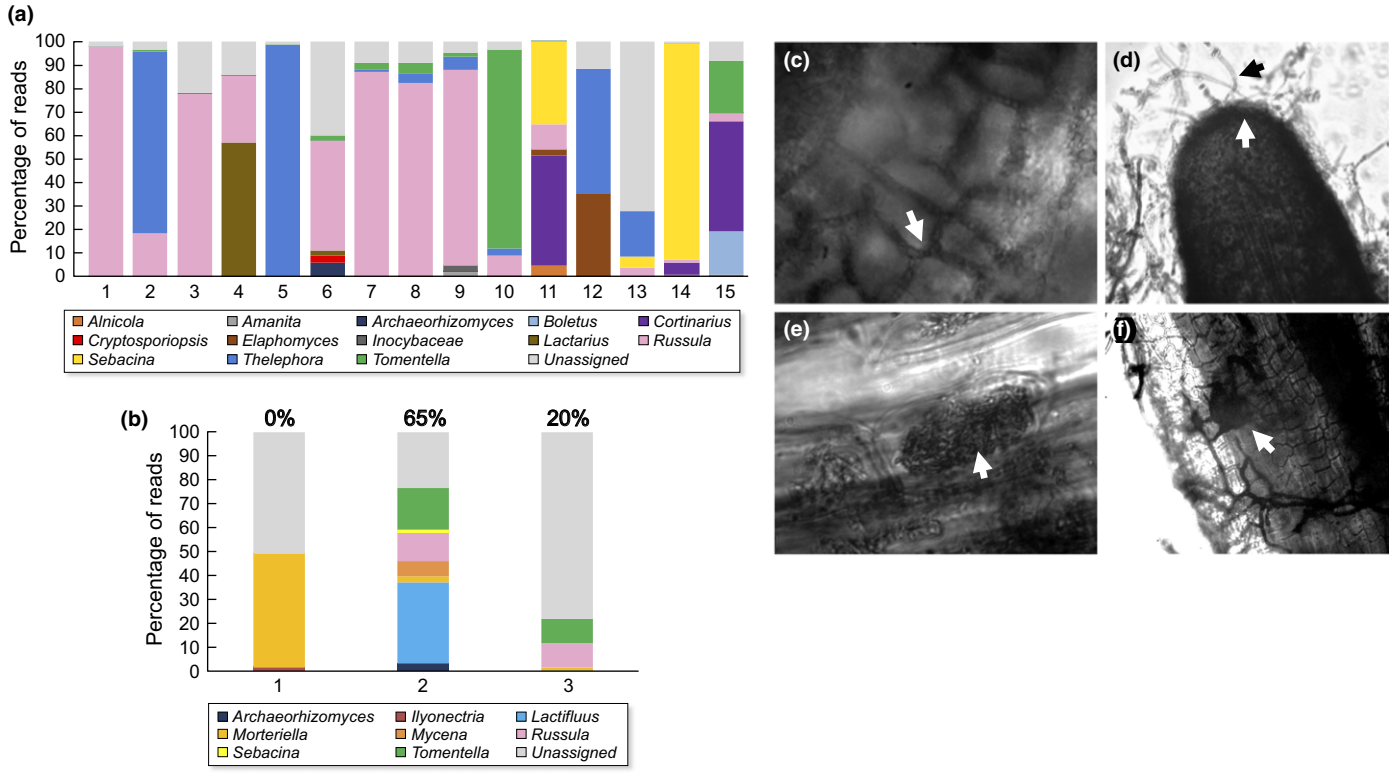

Fig. 4 Relative abundance per individual tree for all fungal operational taxonomic units (OTUs) with > 1% sequences per sample from (a) 15 *Alfaroa costaricensis* individuals and (b) three *Ticodendron incognitum* individuals. The proportion of sequences that correspond to known ectomycorrhizal (ECM) fungal taxa are shown in black text at the top of each bar. Stained roots of *Alfaroa costaricensis* (c) Hartig net as viewed at ×400 magnification (white arrow), (d) ECM root tip with fungal mantle (white arrow) and extraradical hyphae (black arrow) as viewed at ×200 magnification; and *Ticodendron incognitum* (e) arbuscule (white arrow) and (f) arbuscular mycorrhizal (AM) fungal hyphae and vesicle (white arrow) as viewed at ×400 magnification. All plants were collected at the Fortuna Forest Reserve in western Panama.

their ability to exploit P from organic sources, whereas nonmycorrhizal plants were better able to utilize organic P (Steidinger *et al.*, 2015). As with other fertilization experiments, Steidinger *et al.* (2015) found no direct effect of fertilization on seedling growth rates. This may be due to complex relationships between soil fertility, ECM fungal communities and host plant response which are dependent on species-specific functional traits that vary among different tropical ECM fungi.

Only one study to date has examined the enzymatic capabilities of tropical ECM fungi. Tedersoo *et al.* (2012b) measured enzyme activity and stable isotopes in ECM fungal-colonized and uncolonized root tips of several host plants in Gabon and performed molecular identification of the fungal symbionts and morphological characterization of the ECM mantle. Their found that β-glucosidase, phosphatase and cellobiohydrolase activities were higher in roots colonized by ECM fungi with long-distance exploration types, whereas laccase was higher in roots tips with contact exploration types. Furthermore, acid phosphatase and leucine aminopeptidase activities were highest in Atheliales, whereas Boletales had the highest cellobiohydrolase activity. Differences in enzymatic capabilities among ECM fungi could impact nutrient cycling because species with higher enzymatic capabilities may mine organic N and P and further slow the decomposition of residual soil organic matter (Lindahl & Tunlid, 2015). Furthermore, co-occurrence of ECM fungal species with different suites of enzymes and different substrate preferences may promote niche partitioning, species packing and higher local ECM fungal diversity (Smith *et al.*, 2017). Further studies on this topic are needed to establish the role of different species and functional groups in nutrient cycling, as well as their responses to anthropogenic ecological impacts.

VII. Conclusions and future research

Based on the available literature we conclude that tropical ECM systems are highly diverse and have notable geographical differences in the richness and composition of ECM plants and fungi.

Tropical regions have some prominent ECM plant families that dominate forests across large areas (e.g. Dipterocarpaceae, Fabaceae subfam. Detarioideae), whereas many other ECM plant taxa are a small component of diverse, AM-dominated forests. There is also a continuum ranging from scattered ECM plants in AM-hyperdiverse forests to monodominant or co-dominant forests of ECM trees. ECM fungal diversity generally follows the basal area of the host plants; diversity is generally low in forests with few hosts but rivals the diversity of temperate and boreal sites in ECM monodominant forests. The fungi in tropical ECM systems are

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generally less phylogenetically diverse than in temperate systems, but our review suggests that tropical ECM systems are exceedingly complex with a high beta and gamma diversity. Accordingly, further research is required to fully elucidate ECM fungal diversity patterns along soil and elevation gradients and at different spatial scales (e.g. local, regional and continental scales). To fully elucidate latitudinal diversity patterns it will be necessary to increase the sampling intensity in tropical areas and integrate data from all tropical biomes to reduce the temperate bias that exists in current datasets.

In many ECM-dominated systems, symbiotic fungal communities have not been sufficiently studied so the species composition and richness patterns are still unknown. This is particularly the case in Oceania where only a handful of studies have been completed; future studies are likely to yield interesting findings. Most studies on tropical ECM systems are from lowland rainforests or montane forests, whereas tropical dry forests and savannas have rarely been studied. Each host plant species is potentially associated with an endemic yet diverse fungal community and many taxa are likely undescribed. This is illustrated in multi-year sampling of *Dicymbe* forests in Guyana where > 70% of the fungi were new to science (Henkel *et al.*, 2012). This work also revealed the first example of a tropical-endemic ECM fungal lineage, *Guyanagarika* (Sánchez-García *et al.*, 2016). It is also crucial to improve herbarium collections of tropical specimens paired with barcode DNA sequencing to advance tropical fungal systematics and the description of unknown fungal diversity (Roy *et al.*, 2016). Efforts to sequence local herbarium specimens in tropical countries will enrich international databases and help to clarify the trophic modes of the many OTUs that are recovered during metagenomic sequencing.

Our review also highlights the importance of documenting the mycorrhizal status of tropical plants because many plant lineages have never been studied and new ECM plant taxa are being revealed each year (Alvarez-Manjarrez *et al.*, 2018; Fig. 2). Ideally, studies of mycorrhizal status should combine detailed analysis of root morphology and metagenomic sequencing from roots to document ECM fungal diversity (Box 1; Table S2). Further studies also are needed to unveil the functional roles of tropical ECM fungi in nutrient cycling and to document the functional traits of different tropical ECM fungi. We know that ECM fungal taxa differ in their enzymatic capabilities, exploration types and growth rates, and that these factors are likely to impact soil C storage and nutrient availability. Given the complexity of natural tropical ecosystems, it will be critical to conduct glasshouse and *in vitro* studies coupled with field experiments to test the effects of ECM fungi in tropical ecosystem processes and to measure their responses to global change.

Extensive research during the last 25 yr has shattered the simplified idea that all tropical forests are dominated by AM associations and that tropical ECM associations are local oddities and unworthy of research attention. We now know that tropical ECM plants and fungi are diverse, and that each region or even local site may have its own unique ECM symbiotic diversity, structure and function. Mounting evidence suggests that ECM fungi are intimately involved in altering plant–soil feedbacks in tropical monodominance and that ECM associations have a major ecological impact across many tropical systems. It is an exciting time to study tropical ECM associations and we expect that there are significant discoveries just over the horizon.

Acknowledgements

Funding for A.C. was provided by the Ewel Postdoctoral Fellowship at the University of Florida and National Science Foundation (NSF) Dissertation Improvement Grant (1501483). Funding for M.E.S. was provided in part by NSF grant DEB 1354802. T.W.H. that was supported by NSF DEB-1556338. Special thanks go to Jim Dalling for providing plant community data from Panama and to Smithsonian Tropical Research Institute and ENEL green power for their logistic support during fieldwork. Specimens from Panama were collected under permit SC/P-9-15. We thank Dr David Newbery and two anonymous reviewers for invaluable critiques of an earlier version of the manuscript.

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Supporting Information

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

Table S1 List of confirmed ectomycorrhizal plant species from tropical regions

Table S2 Surveys of mycorrhizal status in tropical forests

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