BIOLOGICAL REVIEWS
Cambridge Philosophical Society
Biol. Rev. (2019), **94**, pp. 1857–1880.
doi: 10.1111/brv.12538

Mycorrhizal types differ in ecophysiology and alter plant nutrition and soil processes

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ABSTRACT

Mycorrhizal fungi benefit plants by improved mineral nutrition and protection against stress, yet information about fundamental differences among mycorrhizal types in fungi and trees and their relative importance in biogeochemical processes is only beginning to accumulate. We critically review and synthesize the ecophysiological differences in ectomycorrhizal, ericoid mycorrhizal and arbuscular mycorrhizal symbioses and the effect of these mycorrhizal types on soil processes from local to global scales. We demonstrate that guilds of mycorrhizal fungi display substantial differences in genome-encoded capacity for mineral nutrition, particularly acquisition of nitrogen and phosphorus from organic material. Mycorrhizal associations alter the trade-off between allocation to roots or mycelium, ecophysiological traits such as root exudation, weathering, enzyme production, plant protection, and community assembly as well as response to climate change. Mycorrhizal types exhibit differential effects on ecosystem carbon and nutrient cycling that affect global elemental fluxes and may mediate biome shifts in response to global change. We also note that most studies performed to date have not been properly replicated and collectively suffer from strong geographical sampling bias towards temperate biomes. We advocate that combining carefully replicated field experiments and controlled laboratory experiments with isotope labelling and -omics techniques offers great promise towards understanding differences in ecophysiology and ecosystem services among mycorrhizal types.

Key words: ectomycorrhiza, arbuscular mycorrhiza, ericoid mycorrhiza, plant mineral nutrition, ecosystem processes, comparative genomics, community dynamics, competition.

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I. INTRODUCTION

Plant nutrient-acquisition strategies involving mycorrhizal fungi constitute key functional traits that have strong effects on nutrient cycling, from individual plant to ecosystem level, with global consequences (Martin, Uroz & Barker, 2017). The vast majority of terrestrial plants provide carbon to root-associated mycorrhizal fungi, which in turn supply plants with soil-derived nutrients, offer increased resistance against abiotic stress and pathogens, and mediate communication with other plants and soil microbes (Smith & Read, 2008). By affecting competitive abilities of plant individuals, mycorrhizal associations drive plant population and community dynamics (Klironomos *et al.*, 2011; Tedersoo, Bahram & Zobel, 2019).

Mycorrhizal associations are classified into four principal mycorrhizal types with remarkable differences in anatomy, evolutionary history and functioning (Smith & Read, 2008; Brundrett & Tedersoo, 2018). Arbuscular mycorrhiza (AM) evolved in early land plants associating with members of Glomeromycota and Endogonomycetes to improve carbon to nutrient exchange *via* intracellular structures termed 'arbuscules' (Orchard *et al.*, 2017; Strullu-Derrien *et al.*, 2018). Ectomycorrhiza (EcM) evolved repeatedly since approximately 200 million years ago (mya) in 30 vascular plant lineages (Tedersoo & Brundrett, 2017) and >80 fungal lineages from saprotrophic ancestors (Tedersoo & Smith, 2017). EcM fungi cover the finest feeder roots by forming a hyphal sheath termed a 'mantle' and grow their hyphae tightly inbetween epidermal or cortical cells of the first and second-order feeder roots. Nutrient and carbon (C) exchange occurs in this so-called 'Hartig net'. Ericoid mycorrhizal (ErM) symbiosis evolved once in the crown group of Ericaceae and once in Diaspensiaceae (Ericales) *ca.* 100 mya. ErM fungi form intracellular hyphal structures – coils – in roots of their host plants, but act as non-symptomatic root endophytes in non-ericoid plants and saprotrophs in soil and organic material (Kohout, 2017). In orchid mycorrhiza (OM), species of orchids exploit EcM or saprotrophic fungi for nutrition, but provide little if any C benefits in return (Merckx, 2013) and are therefore excluded from this synthesis.

Based on observations on plant distribution, soil fertility and nutritional experiments, Read (1991) postulated that mycorrhizal types differentially affect ecosystem C and nutrient cycling. The mode of nutrition, anatomical and functional differences are linked to substantial mycorrhizal-type effects on plant biology. For example, AM fungi regulate intra- and interspecific plant competition and maintenance of diversity, productivity and stability (van der Heijden, Bardgett & van Straalen, 2008; Klironomos *et al.*, 2011), but there is little such evidence in other types of symbiosis. Partly because of ensheathing roots, EcM fungi are more efficient in protection against soil-borne pathogens, resulting in positive soil feedback in EcM trees but negative soil feedback in AM trees (Bennett *et al.*, 2017; Teste *et al.*, 2017) that affects population dynamics and community assembly (Johnson, Clay & Phillips, 2018).

Building on the seminal ideas of Read (1991), Chapman *et al.* (2006) proposed ecosystem nutrient cycling models for AM and EcM systems that principally differ in bypassing the microbial nutrient mineralisation loop in EcM habitats with lower litter quality and organic nutrient uptake. These models served the basis for the mycorrhiza-associated nutrient economy (MANE) framework explaining the mechanisms of more rapid nutrient cycling and higher losses in AM compared with EcM systems (Phillips, Brzostek & Midgley, 2013). Since then, research teams have tested related hypotheses in field studies, microcosm experiments and meta-analyses integrating plant ecophysiological, soil and climate data from the mycorrhizal-type perspective. Global modelling reveals that differences in the key ecosystem processes among mycorrhizal types are important from the perspectives of climate change and biosphere functioning (Averill, Turner & Finzi, 2014; Terrer *et al.*, 2016; Soudzilovskaia *et al.*, 2018; Sulman *et al.*, 2019).

Using a review and synthesis approach, our primary objective is to understand the fundamental differences among mycorrhizal types on ecosystem processes. We specifically aim to (1) determine principal differences in costs and benefits in tree nutrition; (2) evaluate the role of mycorrhizal types in C and nutrient cycling; and (3) estimate how mycorrhizal types ameliorate biotic and abiotic stress in trees. Finally, we critically assess analytical shortfalls and point to perspectives

in methodology and research directions for interdisciplinary advances of the field.

II. PLANT NUTRITION

(1) Overall nutritional benefits

According to the current paradigm, AM vegetation dominates in relatively nutrient-rich or phosphorus (P)-limited habitats, whereas EcM and ErM plants prevail in organic-rich soils of poor nitrogen (N) availability, which is attributable to relative nutrient limitation and differential capacity of the mycorrhizal fungi from different mycorrhizal types to access organic nutrients (Read, 1991; Read, Leake & Perez-Moreno, 2004; Smith & Read, 2008; Johnson *et al.*, 2015). AM fungi have very limited capacity for enzymatic degradation, although their hyphae are capable of nutrient uptake in mineral form from organic material (Hodge & Storer, 2015). Conversely, a series of experiments revealed that an EcM fungus *Paxillus* sp. may take up and transport 5–33% N and 37–62% P in detritus to its host tree (Leake *et al.*, 2004). ErM plants also take up large amounts of organic nutrients mobilised by their root-symbiotic fungi (Burke & Cairney, 2002).

A meta-analysis revealed that overall mycorrhizal benefits to plant growth are twice as strong at P limitation compared to low-N conditions, but no overall differences among mycorrhizal types exist (Hoeksema *et al.*, 2010). Given the large variance in parameter estimates and not accounting for other local-scale predictors such as soil origin, soil physicochemical or climatic parameters, it is plausible that local biologically meaningful differences in mycorrhizal growth benefits are blurred in such global analyses. Liu *et al.* (2018) demonstrated that tropical and subtropical EcM trees from Dipterocarpaceae, Fagaceae and Juglandaceae take up soil organic P more efficiently compared to several co-occurring AM tree species.

Some tree species such as members of Salicaceae, Myrtaceae and *Quercus* commonly associate with both AM and EcM fungi, the latter typically becoming dominant in closed-canopy communities. Of such dual mycorrhizal trees, *Acacia rostellifera* and *Melaleuca systena* preferentially hosted AM fungi in soils with P in mineral form but EcM fungi in soils with P in organic form (Albornoz *et al.*, 2016). Experiments using both AM and EcM inocula indicate that EcM fungi are usually relatively more efficient in plant N and P nutrition compared to AM fungi (Table 1). Furthermore, co-inoculated EcM and AM fungi synergistically enhance seedling growth and mineral nutrition as well as nodulation by rhizobia or actinobacteria in nitrogen-fixing trees (Table 1). The negative impact of co-inoculation on *Quercus* spp. may be related to the host's need to use seed C reserves to develop an extensive root system, for which several mycobionts may be too strong a C sink (Egerton-Warburton & Allen, 2001). The generally synergistic benefits of dual inoculations suggest that in spite of the greater C cost, fungal taxa belonging to different mycorrhizal types may complement each other in the acquisition of limiting nutrients or by displaying differential nutritional or non-nutritional benefits such as protection against stress or herbivores. Dual mycorrhizal trees represent an underutilized natural resource to test shifts in symbiotic associations across environmental gradients as well as costs and benefits of mycorrhizal fungi and broader functioning of the nutrient-to-carbon biological market.

(2) Roots and mycelium

In mycorrhizal systems, both roots and hyphae are involved in the release of exudates and enzymes, and in nutrient uptake and transport to plants, acting in a complementary fashion (Cheng *et al.*, 2016). Hyphae are two orders of magnitude thinner than feeder roots and an order of magnitude finer than root hairs, which tremendously increase the surface area per unit biomass and access to dissolved nutrients in soil including micropores (Smith & Read, 2008). Mycorrhizal plants grow their roots closer to the limiting nutrients to improve transport of nutrients from litter and organic horizon and weathered minerals in subsoil.

Because of nutritional differences among plant-mycorrhizal types and principal root traits, tree species differ greatly in their relative belowground allocation and investment into feeder roots or foraging mycorrhizal mycelium (Litton, Raich & Ryan, 2007; Eissenstat *et al.*, 2015; Brundrett & Tedersoo, 2018). In temperate forests, AM trees allocate relatively more C to root biomass than to mycobiont mycelium compared with EcM trees (Chen *et al.*, 2016; Cheng *et al.*, 2016). AM trees, especially those with thin roots, respond to nutrient-rich patches by targeted fine root production, whereas EcM trees respond by fungal mycelium proliferation (Chen *et al.*, 2016). Furthermore, amendment of organic materials triggers disproportionately greater belowground allocation in EcM compared to AM systems (Chen, Koide & Eissenstat, 2018*b*). In a Polish common-garden experiment, two AM *Acer* species exhibited twofold greater average root production and median life span than EcM broadleaved and coniferous trees (Withington *et al.*, 2006). These findings collectively suggest that, compared to AM trees, EcM plants invest relatively more into fungal biomass and hyphal exploration rather than into development and maintenance of feeder roots, and further indicate the relatively greater role of fungi in both mineral nutrition and transport (see Section III).

Many root traits of tree species and the rate of mycorrhizal colonisation are evolutionarily conserved (Ma *et al.*, 2018). All studied species of the ErM Ericaceae (but not Diaspensiaceae) exhibit ultra-narrow roots, in striking contrast to the EcM Monotropoideae and Pyroleae (Ericaceae) as well as the OM Orchidaceae with coarse roots (Smith & Read, 2008). AM and EcM associations both exist in tree species that produce very narrow or coarse roots (McCormack *et al.*, 2012; Brundrett & Tedersoo, 2018). In both temperate and tropical forests, feeder roots of AM trees are coarser than EcM tree roots and exhibit lower tissue density, an

Table 1. Response of dual mycorrhizal trees to inoculation with fungi of different mycorrhizal types alone or in combination

Tree species	Fungal species	EcM relative to AM	Dual mycorrhiza relative to single mycorrhiza type	Reference
Alnus incana	*Paxillus* sp., *Glomus fasciculatus*	Comparable growth, better nodulation	Synergistic growth, nodulation increase	Chatarpaul, Chakravarty & Subramaniam (1989)
Eucalyptus coccifera	Multiple	Better growth, P	Synergistic P increase	Jones, Durall & Tinker (1998)
E. globulus, *E. urophylla*	*Laccaria lateritia*, Glomeromycota 3 spp.	Better growth	Synergistic growth increase	Chen, Brundrett & Dell (2000)
Casuarina equisetifolia	*Pisolithus* sp., *Glomus fasciculatum*	Better growth, N, P; similar nodulation	Synergistic growth, P, nodulation increase,	Elumalai & Raaman (2009)
Salix repens	*Hebeloma leucosarx*, *Glomus mosseae*	Lower N, P (low nutrition); higher N, P (high nutrition)	Not determined	van der Heijden (2001)
Quercus agrifolia	*Pisolithus* sp., Glomeromycota 16 spp. mix	Higher P, lower N	Lower growth, N, P	Egerton-Warburton & Allen (2001)
Quercus costaricensis, *Eucalyptus grandis*	Mixed root inoculum	Better growth, N, P (eucalypt); similar (oak)	Not determined	Holste, Kobe & Gehring (2017)
Betula papyrifera (ectomycorrhizal)	*Pisolithus* sp., *Glomus intraradices*	Not determined	Adding EcM: growth increase in 3 of 9 populations	Lauermeier (2017)
Populus sp.	*Paxillus* sp., *Glomus mosseae*	Lower growth response	Synergistic growth increase	Aguillon & Garbaye (1990)
Eucalyptus marginata	*Scleroderma* sp., *Rhizophagus irregularis*	Better growth, N, P, S, K, Fe	No colonisation	Kariman *et al.* (2012)
Uapaca bojeri	*Scleroderma* sp., *Rhizophagus irregularis*	Comparable growth	Synergistic growth increase	Ramanankierana *et al.* (2007)
Acacia holosericea	*Pisolithus* sp., *Glomus aggregatum*	Comparable growth, lower P, Ca	Synergistic growth, nodulation, mycorrhizal colonisation	Founoune, Duponnois & Bâ. (2002)

AM, arbuscular mycorrhizal; EcM, ectomycorrhizal.

adaptation to support greater AM colonisation in cortical cells (Comas, Callahan & Midford, 2014; Ushio *et al.*, 2015). Similarly, greater root branching intensity in EcM trees can be ascribed to the development of colonisation sites for EcM fungi (Comas *et al.*, 2014). A global meta-analysis reveals that AM roots have somewhat greater specific root length and specific root area compared with EcM trees, indicative of their greater role in nutrient uptake from soil (Valverde-Barrantes *et al.*, 2018).

Globally, increasing root diameter, C:N ratio and calcium (Ca) concentration stimulate fine-root longevity but independently from mycorrhizal type (McCormack *et al.*, 2012). However, trees respond to soil nutrients and physical conditions by strongly altering root functional anatomy (Ostonen *et al.*, 2017), necessitating inclusion of site-specific effects, particularly soil nutrient concentration and temperature into global models. Based on the above case studies, we conclude that differences in adaptive root morphology among trees representing different mycorrhizal types is mainly associated with broad anatomical differences in mycorrhizal structure, especially for building up the symbiotic interface (i.e. Hartig net, arbuscules, coils or digestible pelotons). Partly and fully mycoheterotrophic plants exhibit relatively smaller root systems and coarse roots because of luxurious consumption of carbon and nutrients obtained by effectively cheating the associated fungi.

(3) Nutrient mobilisation and uptake

Nitrogen is usually the limiting macronutrient in temperate and boreal forests and tundra biomes, whereas P limitation is common in grasslands and subtropical and tropical habitats (Reich & Oleksyn, 2004). In terms of energy, diazotrophic fixation and NO_3^- are relatively costlier than simple amino acids and particularly NH_4^+ for N uptake. This is reflected in preferences for NH_4^+ in most plant and fungal species (Nygren *et al.*, 2012; Lilleskov *et al.*, 2019). Both fungi of different functional guilds and plants possess multiple NH_4^+ and NO_3^- and amino acid transporters to acquire simple N compounds (Casieri *et al.*, 2013; Giovannetti *et al.*, 2017; Nehls & Plassard, 2018). Goodale (2017) estimated that N uptake of EcM trees may exceed that of AM trees by 50% in temperate forests.

Although total soil P concentration is relatively higher in AM habitats, P may be less accessible to trees in AM-dominated than EcM-dominated patches owing to differences in their associated mycorrhizal fungi (Rosling *et al.*, 2016). Both plants and fungi are equipped with multiple phosphatases and P transporters to mobilise and take up P in inorganic form (Casieri *et al.*, 2013; Nehls & Plassard, 2018; Fig. 1A). Generally, AM and EcM trees exhibit roughly similar ability to take up mineral P, but rhizomorphic EcM fungi may have an advantage of immobile P acquisition over longer distances and from organic sources.

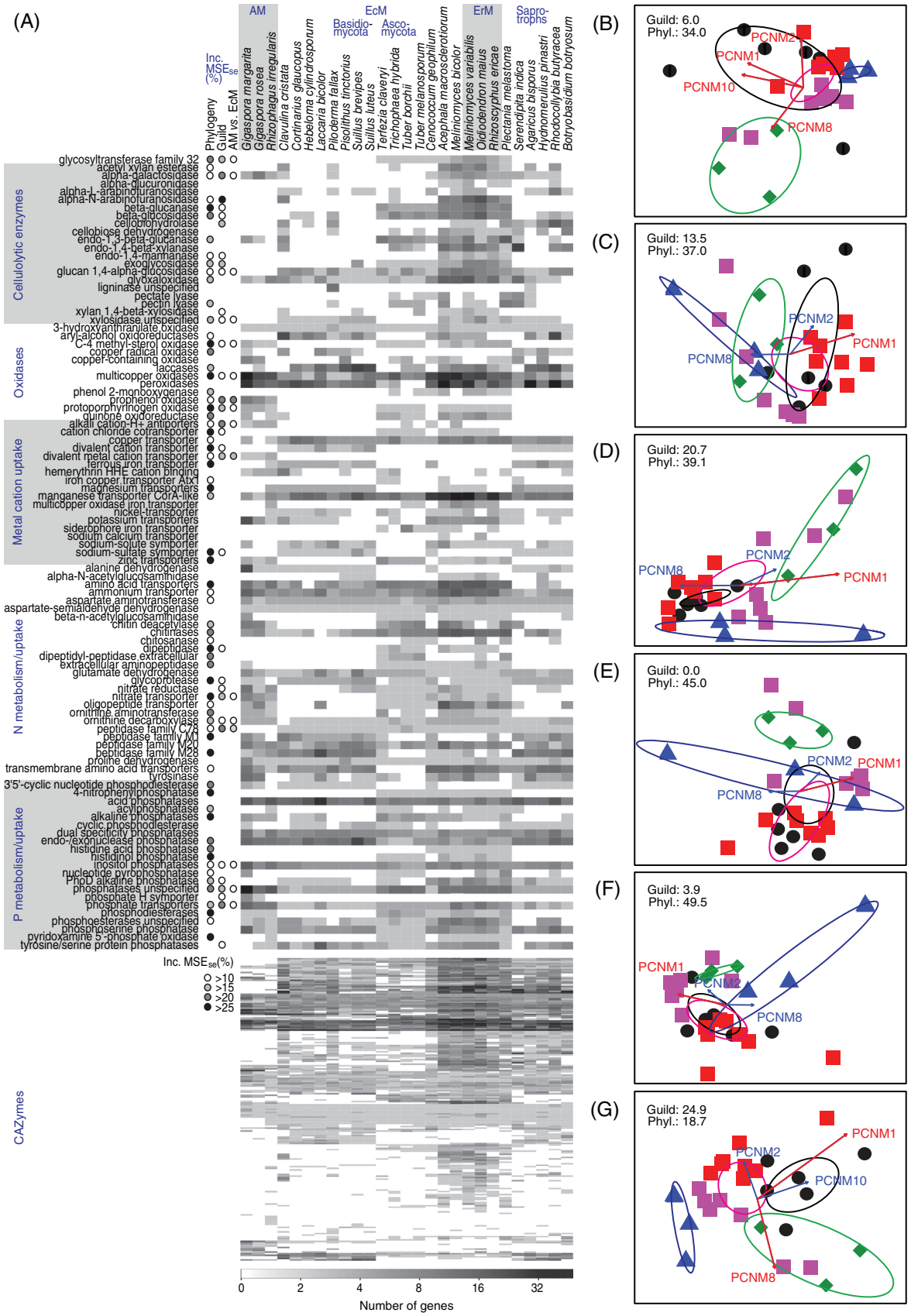

Fig. 1. Legend on next page.

Wood and litter saprotrophs belonging to Basidiomycota display the greatest decomposition activities, but genes responsible for efficient cellulolysis have been partly lost in mycorrhizal fungi to maintain the stability of symbiosis. While the ancestors of Glomeromycota and contemporary AM fungi lack a strong degradation machinery (Tisserant *et al.*, 2013; Chen *et al.*, 2018*a*), certain ascomycete and basidiomycete EcM and ErM symbionts are capable of producing Fenton radicals and polyphenol oxidases to release N from organic polymers (Wurzburger, Higgins & Hendrick, 2012; Lindahl & Tunlid, 2015; Adamczyk *et al.*, 2016). Although most EcM fungi have secondarily lost Mn-peroxidase genes, certain species of *Cortinarius* and *Hebeloma* possess and express these powerful oxidases to mobilise lignin-bound N (Bödeker *et al.*, 2014; Kohler *et al.*, 2015). To release P from organic compounds, EcM and ErM fungi usually possess multiple phosphomonoesterases (acid and alkaline phosphatases), phosphodiesterases and phytases. The oxidative enzymes as well as substantial amounts of oxalate and H^+ exuded by these fungi are thought to play an additional role in releasing P and micronutrients from complex organic molecules (Casieri *et al.*, 2013; Martino *et al.*, 2018).

Plant control over organolytic activities is relatively stronger under EcM trees in temperate forest soils (Brzostek & Finzi, 2011). In particular, activities of proteases, chitinases, polyphenol oxidases and acid phosphatases are relatively greater in EcM-dominated habitats (Phillips & Fahey, 2006; Brzostek & Finzi, 2011; Phillips *et al.*, 2013; Yin, Wheeler & Phillips, 2014; Midgley & Phillips, 2016), whereas cellulase activity is greater in AM-dominated habitats (Cheeke *et al.*, 2018) in temperate forests. Brzostek *et al.* (2015) demonstrated that girdling reduces soil N-acetyl-glucosamine and phenol oxidase activities relatively more in EcM-dominated compared to AM-dominated habitats, suggesting that much of these were expressed by EcM fungi. Except for lower β-glucosidase activity in EcM soils, roots and soils of EcM and AM trees exhibited no differences in key degradative enzyme activities in a Malaysian rain forest (Ushio *et al.*, 2015). At the root surface, EcM root tips exhibited greater activities of most enzymes compared to AM/non-mycorrhizal roots in an Afrotropical rain forest (Tedersoo *et al.*, 2012). ErM *Rhododendron* patches displayed greater soil polyphenol oxidase activity compared with soil under EcM trees in a temperate forest (Wurzburger & Hendrick, 2007).

Because a vast majority of mycorrhizal fungi are unculturable or extremely slow-growing using traditional methods, comparative genomics analyses enable us to shed light into the functional machinery of fungal taxa (Kohler *et al.*, 2015; Martino *et al.*, 2018). As published comparisons of AM and EcM fungal genomic contents are lacking so far, we focused our analysis on fungal individuals from distantly related taxonomic groups representing different mycorrhizal guilds. This comparative analysis demonstrates that phylogenetic relatedness among fungal species explains more variation in metabolism-related genes (19–50% in different functional gene groups) than nutritional strategies (0–25%; Fig. 1B–G), indicating a substantial evolutionary footprint. In particular, the EcM and ErM members of Helotiales (Ascomycota) harbour a relatively high abundance of organic nutrition-related genes that exceeds the oxidative gene repertoire of saprotrophic and EcM Basidiomycota. The EcM members of Agaricomycetes, Pezizomycetes, Dothideomycetes (*Cenococcum*) and Leotiomycetes differ particularly strongly in gene content, rendering generalization across EcM fungi difficult (Fig. 1A). The amount of carbohydrate-active enzymes (CAZymes) in genomes of ErM and saprotrophic fungi is greater than in EcM fungi, which in turn exceed that of AM fungi (one-way ANOVA: $F_{3,22} = 12.1$; $R^2_{adj} = 0.560$; $P < 0.001$; also valid when phylogeny is accounted for). Fungal guilds possess similar abundance of other metabolism-related genes, but differences occur in gene variant composition for most broad functions (Fig. 1B–G). Although Glomeromycota are believed to lack cellulolytic enzymes, our comparative genomics analyses indicate that AM fungi have a significantly greater abundance

Fig. 1. Genomic differences among arbuscular mycorrhizal (AM), ectomycorrhizal (EcM), ericoid mycorrhizal (ErM) and saprotrophic fungi. (A) Heat map of differences in genome families and groups of functional genes. (B–G) Non-metric multidimensional scaling (NMDS) graphs of fungal guilds (blue triangles, AM fungi; green diamonds, ErM fungi; purple squares, EcM Ascomycota; red squares, EcM Basidiomycota; circles, saprotrophs. (B) Genes encoding cellulolytic genes; (C) genes encoding oxidases; (D) genes encoding metal cation uptake/transport enzymes; (E) genes encoding nitrogen metabolism/uptake; (F) genes encoding phosphorus metabolism/uptake; (G) genes encoding various carbohydrate-active enzymes (CAZymes). Ellipses indicate 95% confidence intervals. Arrows represent phylogenetic eigenvectors (red, $P < 0.05$; blue, $0.05 < P < 0.1$). Variance explained (%; adjusted coefficient of determination × 100) is given in upper left corner. We compiled information from all available genomes of AM and ErM fungi and added a phylogenetically balanced set of EcM and litter saprotrophic fungi to test for differences in key metabolic and nutrition-related genes among fungal guilds and mycorrhizal types accounting for phylogeny. All genomes were downloaded from JGI (except *Gigaspora margarita* and *G. rosea*) and subjected to gene annotation using Augustus (Stanke *et al.*, 2006) trained on *Rhizopus oryzae*. Ribosomal RNA gene small and large subunits of these species were downloaded, subjected to maximum likelihood analysis and calculation of an ultrametric phylogram, followed by construction of phylogenetic eigenvectors (PCNM) and data analysis using multivariate ANOVA, non-metric multidimensional scaling (Põlme *et al.*, 2013) and random forest (following Tedersoo *et al.*, 2017). The most significant PCNM vectors contrast Basidiomycota *versus* Glomeromycota (PCNM1), Glomeromycota *versus* Pezizales (PCNM2), Helotiales and *Cenococcum versus* Agaricales (PCNM8), and *Serendipita versus* others (PCNM10). Protein models were functionally annotated using eggNOG-mapper (Huerta-Cepas *et al.*, 2017) and searched for CAZymes using dbCAN (http://csbl.bmb.uga.edu/dbCAN/).

of genes encoding α-galactosidases, multi-copper oxidases, prophenol oxidases and protoporphyrinogen oxidases compared with EcM fungi. So far, there is no evidence that these genes are functional or expressed in AM fungi. Partly due to much greater genome sizes, representatives of the three Glomeromycota species also possess more genes encoding alkali cation-H^+ transporters, divalent metal cation transporters, nitrate transporters, ornithine decarboxylases, inositol phosphatases, unspecified phosphatases and phosphate transporters compared with EcM fungi. By contrast, EcM fungi have more genes encoding glucan 1,4-α-glucosidases, xylosidases and extracellular peptidase family C78.

These analyses indicate that genomes of mycorrhizal fungal guilds display multiple metabolic differences and any comparisons are strongly confounded by phylogeny, which should be rigorously accounted for in subsequent studies. To understand genetic differences among AM fungi, gene catalogues from species belonging to Archaeosporomycetes and Paraglomeromycetes and, in particular, Endogonomycetes, are required (Chen *et al.*, 2018*a*). Likewise, genomic information from ErM symbionts belonging to Chaetothyriales and Sebacinales is warranted to understand whether the high metabolic gene content in hitherto-sequenced genomes can be ascribed simply to their helotialean origin or endophytic-ErM lifestyle. A large amount of work remains to be done to determine functionality and sites of expression of the inferred genes and patterns of protein transportation (Kohler *et al.*, 2015).

Due to anatomical traits of hyphae and mycorrhizal structures and differences in enzymatic activities, mycorrhizal types differ in the efficiency of nutrition and relative contribution of plant and fungal partners. Altogether 50–100% of N enters arctic plants *via* the EcM pathway (Hobbie & Hobbie, 2006), but such estimates for other biomes are lacking. Considering that the proportion of mycorrhizal roots is relatively low in arctic EcM plants, we expect that these estimates hold for other biomes as well. In experimental systems, AM fungi contribute 7–49% of N in their host plants (Hodge & Storer, 2015), but these values probably vary more greatly in natural systems. Although fungal contribution has received no quantitative assessment in ErM plant nutrition, Ericaceae proliferate in highly acidic nutrient-poor soils and there are enormous fungal growth benefits in experimental conditions, suggesting that ErM fungi provide a vast majority of nutrients to their host plants in spite of very fine roots.

(4) Nutritional benefits of mycorrhizal types: synthesis

The studies and meta-analyses described above collectively indicate that tree roots and fungi complement each other in nutrient capture and transportation, which is a function of phylogenetically determined feeder root diameter and mycorrhiza type. Both AM and EcM fungi primarily benefit P rather than N nutrition of plants, but the capacity to access these nutrients is greater in EcM fungi. Considering maintenance costs (see Section III), mycorrhizal fungal guilds provide roughly comparable net benefits, with EcM fungi tending to provide more resources under strong nutrient limitation and in organic soils. This is attributable to more extensive hyphal networks in soil and greater efficiency in liberating and transporting simple organic compounds. These differences between AM fungi and other guilds have received indirect support from multiple field studies using stable N isotopes as proxies of nutrition (Mayor *et al.*, 2015), from *in situ* and *in vivo* enzymatic assays (Table 2), and from our comparative genomics analysis (Fig. 1).

III. CARBON BUDGET

(1) Control over carbon flow

Photosynthetically fixed carbon is the main source of energy for AM and EcM fungi and the mycorrhizosphere microbiota (Buee *et al.*, 2009). Experiments using stable isotope tracers indicate that up to 12% of C in EcM fungi may originate from soil, probably as skeletons of nutrient-containing molecules (Hobbie *et al.*, 2014). These estimates are complicated, because soil-derived C is mostly respired (Hobbie *et al.*, 2014) or exuded as simple organic compounds. In several EcM model systems, plant-derived sucrose is transferred to the apoplast and converted to glucose and fructose by means of fungi-encoded invertase (glycosyltransferase family 32). While invertase is lacking in most EcM basidiomycetes, it occurs in EcM Helotiales, Pezizales, and in ErM fungi as multiple copies (Fig. 1A), suggesting that mechanisms controlling nutrient exchange are more complex and diverse than hitherto assumed. In AM fungi, invertase is not known and therefore, C transfer may be more under plant control (Casieri *et al.*, 2013). Reciprocal rewarding and sanctioning mechanisms for nutrient to carbon exchange have evolved in AM and EcM systems (Kiers *et al.*, 2011; Hortal *et al.*, 2017), but these remain to be addressed in ErM associations.

(2) Maintenance of mycorrhizal mycelium

Mycorrhizal fungi represent an important C cost to plants. In EcM and AM systems, respectively, 7–30% and 2–20% of photosynthetically fixed C is allocated to fungi within 6–72 h after initiation of $^{13}CO_2$ labelling, with an average twofold difference among mycorrhizal types (reviewed in Leake *et al.*, 2004). Notably, these experiments were performed in the exponential growth phase of the extraradical mycelium, which does not necessarily represent natural conditions with high standing mycelium biomass (Leake *et al.*, 2004; Hagenbo *et al.*, 2017).

In AM and EcM systems, mycorrhizal fungi represent up to one-third of soil microbial biomass (Leake *et al.*, 2004). The AM fungal mycelium is usually comprised of simple branching hyphae that explore soil 5–10 cm beyond root distribution in microcosms (Olsson, Jakobsen & Wallander, 2002; Allen, 2007). While AM fungi may contribute up to 5% of the feeder root biomass (Ouimette *et al.*, 2013), EcM

Table 2. Available information about relative effects of ectomycorrhiza (EcM) compared with arbuscular mycorrhiza (AM) on soil processes

Property	EcM effect relative to AM[1]	Region/biome	Main criticism	Reference
Foliage and soil P	Lower	IN, USA/warm temperate deciduous	*Acer* (AM) *vs.* multiple EcM trees	Rosling *et al.* (2016)
N cycling	Lower N leaching, nitrification, N_{min}, C degradation; greater C:N ratio, AP, NAG activities, microbial C and P	IN, USA/warm temperate	*Acer* (AM) *vs.* multiple EcM trees	Midgley & Phillips (2016)
Litter and soil C, N	Higher C:N ratio, lower labile N, slower N cycle	Global (meta-analysis)	Tropics: only exotic plantations; evergreen habit not considered	Lin *et al.* (2017)
Microbial respiration	Lower	GA, USA (microcosm)	Roots and hyphae disrupted = killed	Taylor *et al.* (2016)
Soil C, N, respiration	Higher C, C:N ratio, lower respiration, comparable pH, decomposition	N Sweden/tundra		Soudzilovskaia *et al.* (2015)
Microbial respiration, C input (priming) and C loss	Lower	NC, USA/warm temperate (microcosm)	2 AM *vs.* 3 EcM tree species	Wurzburger & Brookshire (2017)
Soil C, N, microbial biomass, enzymes, mineralisation	Lower pH, NO_3^-; similar enzymes, biomass, mineralisation	Liaoning, China/warm temperate	*Acer mono* misassigned to EcM, type II errors	Chen *et al.* (2018*c*)
Soil C, N, processes, plant traits, rhizosphere effects	Lower N, mineralisation, nitrification, decomposition, higher rhizosphere N effect	Yunnan, China/tropical evergreen	6 Dipterocarpaceae species *vs.* 8 AM tree species	Lin *et al.* (2018)
Soil C, N	Higher C/N, higher C in topsoil, Lower N, amino sugars, lower C in subsoil in 2 of 3 forests	E USA	Site-specific tests not given	Craig *et al.* (2018)
Soil C, N	Lower N, higher C/N	E USA		Zhu *et al.* (2018)
Soil C storage *vs.* N pollution	Higher at low N, similar at high N	Conterminous USA		Averill *et al.* (2018)
Soil C, N storage *vs.* eCO_2	Better at coping with N limitation at eCO_2 levels	Global (modelling)	Mycorrhizal type distribution relies on fungal sequences	Sulman *et al.* (2019)
Soil C storage	Forest-type dependent	E USA, regional scale		Jo *et al.* (2019)
Enzyme activities *vs.* C flow disruption (girdling)	Stronger negative effect for NAG, PhOx, greater nitrification, N mineralisation	IN, USA/warm temperate deciduous	*Acer* (AM) *vs. Quercus* (EcM): tiny plots/no trenching	Brzostek *et al.* (2015)
Microbial biomass, enzymes	Greater fungal biomass, necromass, fungi: bacteria ratio, AP, NAG activities, lower cellulases	IN, USA/warm temperate deciduous	*Acer* (AM) *vs.* multiple EcM trees	Cheeke *et al.* (2018)
Plant N acquisition, soil C *vs.* eCO_2	Greater soil priming, access to organic N, loss in soil C (in medium-N soils)	Global (metastudy)	EcM forests *vs.* AM grasslands, no truly low-N soils	Terrer *et al.* (2018)
Rhizosphere effects, enzymes	Greater differences from bulk soil, mineralisation, AP activities	NY, USA/temperate mixed	$N = 1–2$; confounding conifer/evergreen and pH effects	Phillips & Fahey (2006)
Fine root turnover	Comparable: depends on diameter, C:N ratio, Ca	PA, USA/warm temperate		McCormack *et al.* (2012)
Root turnover	Similar	Germany/temperate deciduous		Kubisch, Hertel & Leuschner (2016)

Table 2. Continued

Property	EcM effect relative to AM[1]	Region/biome	Main criticism	Reference
Soil properties, exudation, enzyme activities	Greater N_{org}:N_{min} C and N mineralisation, NAG, AG, PPO activities, root C exudation	IN, USA/warm temperate deciduous	2 EcM and 2 AM species	Yin *et al.* (2014)
Exudation, soil C storage (modelling)	Greater exudation, EcM but not AM retains previously stored C	IN, USA/warm temperate deciduous	*Acer* (AM) *vs.* multiple EcM trees	Sulman *et al.* (2017)
Exudation, biomass *vs.* drought	Exudation: comparable but greater in drought; growth: less reduced	Germany/temperate mixed (greenhouse)	Some measurements confounded by tree size	Liese *et al.* (2018)
Weathering: apatite	Greater Ca uptake	NH, USA/cool temperate	Ca/Sr ratio as a proxy	Blum *et al.* (2002)
Weathering: quartz, apatite	Greater Ca uptake	New Zealand/temperate deciduous	*Nothofagus vs.* multiple AM trees	Koele *et al.* (2014)
Weathering: plagioclase	Greater Ca uptake	England/temperate mixed (microcosm)	Confounding pH and C allocation effects	Quirk *et al.* (2012)
Weathering: chalk, marble, dolomite, limestone, basalt	Greater Ca uptake, residual pH effect	England/temperate mixed (microcosm)	Confounding C allocation effect	Thorley *et al.* (2015)
Weathering: basalt *vs.* eCO_2	Greater Ca uptake, C allocation (+increased benefits from eCO_2)	England (microcosm)	Confounding pH and C allocation effects	Quirk *et al.* (2014)
Foliar P	Higher (phylogeny effect)	Global (metastudy)	Mycorrhizal types misassigned in some cases	Koele *et al.* (2012)
Various	Slower litter decomposition; lower nitrification, pH; greater NAG, AP activites	IN, USA/warm temperate deciduous	*Acer* (AM) *vs. Quercus* (EcM); tiny plots/no trenching	Phillips *et al.* (2013)
N cycling	Higher N_{org}; lower nitrification	IN, USA/warm temperate deciduous	2 EcM and 2 AM tree species; 1 site	Phillips *et al.* (2013)
Soil chemistry, enzymatic activities	Higher phenolics, N_{tot}, pH, lower tannins; lower β-glucosidase activity	Malaysia/tropical mixed	EcM (2 spp.) and AM (3 spp.) not compared	Ushio, Kitayama & Balser (2010)
P acquisition	Similar	Panama/tropical evergreen	*Oreomunnea* (EcM) *vs.* 2 AM tree species	Steidinger *et al.* (2015)
P acquisition	Higher from organic sources	Malaysia, China/ (sub)tropical (common garden)		Liu *et al.* (2018)
Belowground respiration	Higher soil respiration, lower root respiration	Scotland/cool temperate (exotic plantations)	*Larix* (EcM) *vs. Acer* (AM)	Snell *et al.* (2016)

Table 2. Continued

Property	EcM effect relative to AM[1]	Region/biome	Main criticism	Reference
Soil enzymatic activities	Higher proteases, greater plant control over organolytic activities	PA, USA/cool temperate mixed	2 EcM *vs*. 2 AM tree species	Brzostek & Finzi (2011)
Root C exudation	similar	PA, USA/cool temperate mixed	Very limited sampling, no qualitative differences measured	Brzostek *et al.* (2013)
Litter decomposition	Slower, home-field advantage only in AM litter	IN, USA/warm temperate deciduous	No vegetation data	Midgley, Brzostek & Phillips (2015)
Litter decomposition	Slower in temperate trees, comparable in tropical trees	Global (meta-analysis)		Keller & Phillips (2019)
Root, leaf litter decomposition, soil provenance	Slower decomposition; greater soil C loss; no home-field advantage	IN, USA/warm temperate deciduous (microcosm)	1 EcM *vs*. 1 litter source; 1 EcM *vs*. 1 soil provenance; plant-free soil	Jacobs *et al.* (2018)
Root, leaf litter decomposition	Slower root decomposition	China/warm temperate	Mycorrhizal type misassigned in 40% of species	Sun *et al.* (2018)
Litter	Lower production, decomposition and turnover, greater fungal biomass	Guyana/tropical evergreen	1 EcM plant species *vs*. 3 mixed AM plots; $N = 6$ plots	McGuire *et al.* (2010)
Root litter decomposition	Faster	Global (metastudy)	Confounding sampling and climatic effects	See *et al.* (2019)
Response to drought	Greater retention of photosynthesis, root respiration better predicted by productivity	Germany/temperate deciduous (greenhouse)	2 EcM *vs*. 2 AM tree species	Meier *et al.* (2016)
Response to drought and temperature; respiration	EcM and AM dominate in sites where CO_2 flux is determined by temperature and precipitation, respectively	Global (metastudy)	Too few EcM-dominated sites for structural equation modelling	Vargas *et al.* (2010)

AP, acid phosphatase; eCO_2, elevated CO_2; NAG, N-acetyl-glucoseaminidase; N_{min}, mineral N; N_{org}, organic N; N_{tot}, total N; PhOx, phenol oxidase; PPO, polyphenol oxidase.

systems regularly develop a dense mantle of 5–7 hyphal layers on the root surface that may contribute 20–80% of mycorrhizal volume/biomass (Högberg *et al.*, 1996; Zeppa *et al.*, 2005; Ouimette *et al.*, 2013). While AM fungi and EcM and ErM ascomycetes do not produce hyphal strands, a majority of the EcM basidiomycetes develop undifferentiated or highly differentiated rhizomorphs, the latter of which may extend several decimetres and perhaps metres from roots (in Boletales; Agerer, 2001). Total hyphal length of AM fungi ranges from 2 to 35 m g^{-1} soil (20–1400 m m^{-1} root) in agricultural and experimental habitats, 40 to 100 m g^{-1} soil (440–1240 m m^{-1} root) in grasslands, and 240 to 800 m g^{-1} soil in tropical forests (Leake *et al.*, 2004; Powers, Treseder & Lerdau, 2005). In EcM systems, hyphal length varies from 1 to 600 m g^{-1} soil (300–8000 m m^{-1} root) in microcosm experiments, but it may exceed 6000 m g^{-1} soil in nutrient-poor forest habitats (Leake *et al.*, 2004; Wallander *et al.*, 2010). Both AM and EcM fungi display great within-group differences in the extent of mycelium and hence in potential maintenance cost to the host (Agerer, 2001; Maherali & Klironomos, 2007).

Hyphae of AM fungi are more ephemeral than those of EcM fungi. Using $^{14}CO_2$ labelling, Staddon *et al.* (2003) estimated that AM mycelium turns over in 5–6 days in a greenhouse. Since the authors did not consider respiration, these turnover rates are probably strong overestimates (Leake *et al.*, 2004). A better-controlled mesocosm experiment revealed an average AM hyphal residence time of 12 days (Allen, 2007). By contrast, ergosterol accumulation and standing fungal biomass suggest that EcM fungal hyphae turn over in 28–36 days in temperate coniferous forest soil (Ekblad *et al.*, 2013; Hendricks *et al.*, 2016). More recent estimates indicate EcM hyphal turnover in 25–500 days in a strong negative correlation with stand age (Hagenbo *et al.*, 2017). Longevity of EcM fungal rhizomorphs has been estimated at 7–22 months (Ekblad *et al.*, 2013), which roughly corresponds to the median age of roots (McCormack *et al.*, 2012).

(3) Plant carbon cost: synthesis

Ectomycorrhizal networks in soil are contrastingly more extensive compared to those of AM and ErM fungi due to the evolution of differentiated rhizomorphs in Basidiomycota. Although biomass of EcM fungi may exceed that of AM fungi by an order of magnitude, the 2–10-fold lower turnover of EcM hyphae renders the long-term costs of maintaining AM and EcM mycelium more comparable. Along with amino acids and other simple organic nutrients, EcM and ErM fungi take up carbon that is respired preferentially over plant-derived carbon, indicating that total C use by these symbionts is underestimated when solely measuring carbon flow from plant to fungus.

Information about the production, turnover and decomposition of the mycelium of different mycorrhizal types along soil fertility gradients would greatly improve our understanding of plant C costs and the relative role of mycorrhizal guilds in soil C release and sequestration (Clemmensen *et al.*, 2013), and how this may be affected by climate change and N deposition (Brzostek, Fisher & Phillips, 2014). Thus far, virtually nothing is known about C budget, exploration distance, biomass and turnover of the facultatively mycorrhizal ErM fungi.

IV. SOIL PROCESSES

(1) Nutrient cycling and mineral weathering

Mycorrhizal partners may alter ecosystem nutrient cycling due to differential access of mycorrhizal fungal guilds to organic and inorganic nutrients (Read, 1991; Read *et al.*, 2004; Phillips *et al.*, 2013; Fig. 2A). AM-dominated habitats exhibit relatively faster and more 'open' nutrient cycling (Phillips *et al.*, 2013; Lin *et al.*, 2017) because of higher litter quality (Cornelissen *et al.*, 2001; Keller & Phillips 2019), greater activities of litter and humus saprotrophs and bacteria (Taylor, Lankau & Wurzburger, 2016; Cheeke *et al.*, 2018) as well as higher concentration and transformation rates of inorganic nutrients compared with EcM and ErM systems (Phillips *et al.*, 2013; Yin *et al.*, 2014; Chen *et al.*, 2018*c*). Therefore, AM-dominated forests display relatively higher N leaching and nitrification processes (Phillips *et al.*, 2013; Midgley & Phillips, 2016). Increasing rates of nutrient cycling are reflected by relatively greater soil and microbial respiration in AM-dominated temperate and arctic habitats as based on field (Soudzilovskaia *et al.*, 2015; Snell, Robinson & Midwood, 2016) and microcosm (Taylor *et al.*, 2016) studies.

Physicochemical weathering of minerals represents a mechanism for counterbalancing nutrient losses to leaching. Weathering is particularly important in mineral nutrition of trees in P-limited and base-poor ecosystems (Smits & Wallander, 2017). Fungi have a high capacity to exude organic acids, siderophores and H^+ to liberate and dissolve mineral-bound micronutrients (Gadd, 2007). Although AM forests tend to be more P-limited, EcM symbiosis is inferred to be relatively more efficient in mineral weathering due to more abundant exudation of organic acids and release of chelators (Taylor *et al.*, 2009). The AM *Acer saccharum* and AM ferns obtain less Ca from the bedrock compared to various EcM trees in a mixed temperate forest (Blum *et al.*, 2002). Laboratory experiments reveal that EcM fungi acquire Ca more efficiently than AM fungi from plagioclase, basalt and several other minerals (Quirk *et al.*, 2012, 2014; Thorley *et al.*, 2015). By contrast, Koele *et al.* (2014) and Remiszewski *et al.* (2016) observed no differences in mineral weathering of quartz, apatite or granite between AM and EcM systems in New Zealand and NE USA, suggesting context dependency and that greater weathering rates may be attributable to soil acidity (Dickie *et al.*, 2014). Alternatively, biological weathering can be related to bacterial activity. For example, the common AM and EcM mycorrhizosphere-inhabiting *Burkholderia* spp. contribute to mineral weathering of biotite and hydroxyapatite (Fontaine *et al.*, 2016). Mineral weathering increases relatively more in EcM fungi compared with AM fungi at elevated CO_2

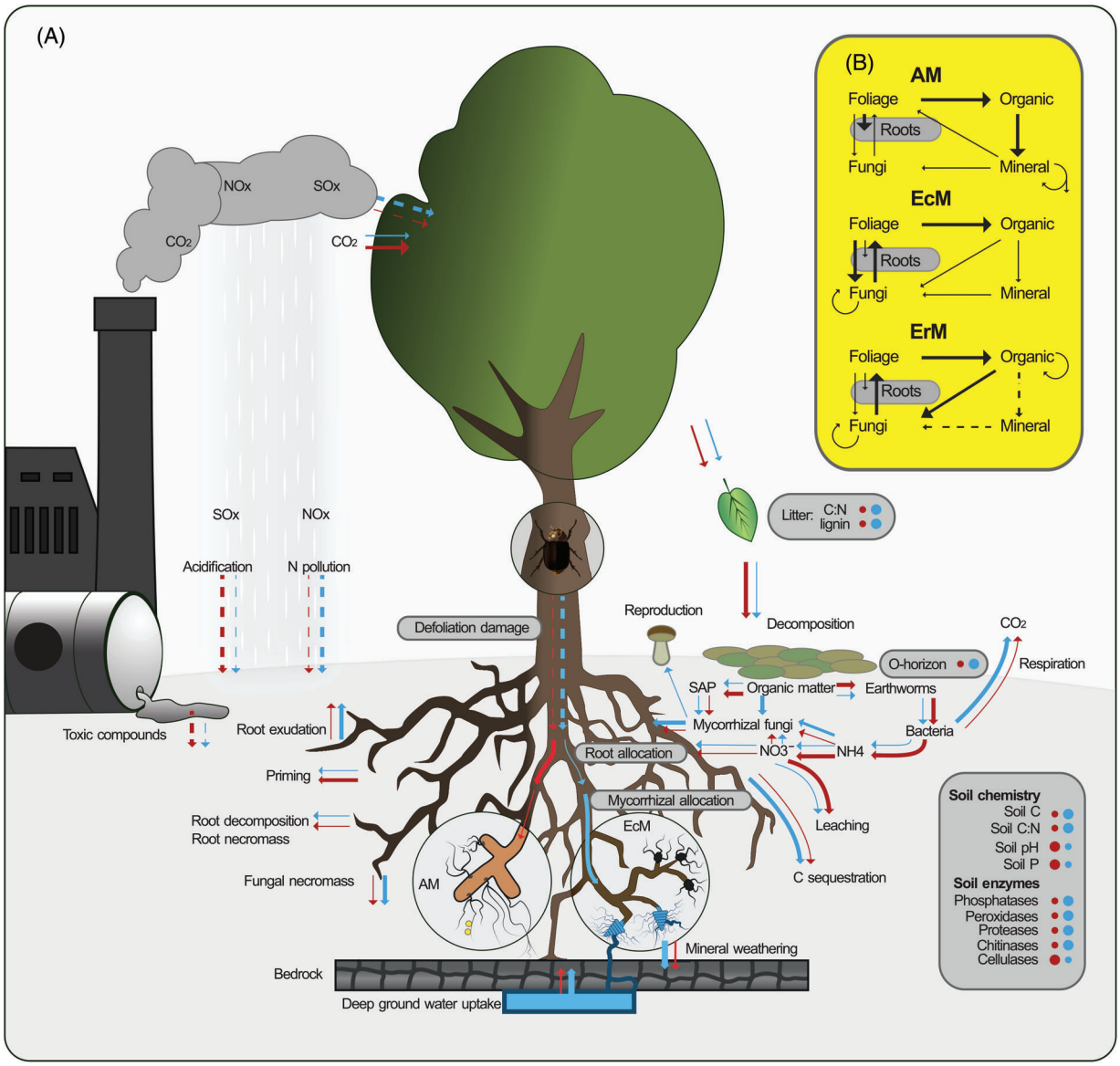

Fig. 2. Conceptual scheme of mycorrhizal type effects and response to ecosystem processes: (A) overall effects; (B) simplified model of C allocation and nutrient acquisition. In A, red and blue lines indicate arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM) effects respectively; dashed lines indicate negative effects; line width indicates relative effect strength. SAP, saprotroph. In B, line width indicates relative effect strength.

(eCO_2; Quirk *et al.*, 2014). Based on geochemical models, Taylor *et al.* (2011) speculated that the rise of EcM symbiosis in the Early Cretaceous successively enhanced weathering of cations that were deposited in ocean sediments as carbonates and thus reduced atmospheric CO_2 levels. However, Smits & Wallander (2017) heavily criticized their model input and challenged the validity of these findings. Whatever the driving mechanism, mineral weathering is similar or somewhat greater in EcM-dominated ecosystems.

(2) Decomposition

Early studies provide evidence that mycorrhizal types differ in soil and litter quality and litter decomposition rate (e.g. Cornelissen, 1996; Finzi, van Breemen & Canham, 1998; Augusto *et al.*, 2002; Hobbie *et al.*, 2007). Cornelissen *et al.* (2001) were the first to test this, demonstrating that temperate EcM and ErM plants shed more slowly decomposing leaf litter and exhibit slower growth compared with AM woody plants. However, the evergreen *versus* deciduous habit and phylogenetic relatedness of plants confound this analysis (Joly *et al.*, 2017; Ma *et al.*, 2018). Although leaves of EcM trees contain relatively more P and similar amounts of other nutrients, phylogeny accounts for much of the variation (Koele *et al.*, 2012), indicating no causal evolutionary effect of mycorrhizal type *per se* (Dickie *et al.*, 2014). Without considering phylogenetic autocorrelation, Lin *et al.* (2017) demonstrated that temperate EcM trees are associated with greater litter

and soil C:N ratio but lower labile N pool compared with AM trees in a meta-analysis. Another meta-analyses revealed that EcM and AM trees differ in leaf litter decomposition rates only in temperate but not tropical forests (Keller & Phillips, 2019). Some of these differences among studies may be attributable to differential nutrient resorption before shedding leaves. AM trees resorb more N in tropical habitats, whereas EcM trees resorb more N in temperate ecosystems, with strong climatic effects (Zhang *et al.*, 2018).

Globally, feeder roots of EcM and ErM woody plants decompose more slowly than those of AM trees (See *et al.*, 2019), although no clear differences among mycorrhizal types can be inferred from local multi-species experiments (Hobbie *et al.*, 2010; Lin *et al.*, 2011), suggestive of unaccounted roles of climatic and phylogenetic drivers. Decomposition of ectomycorrhizas is slower than non-EcM fine roots, which was originally ascribed to high chitin content of the fungal mantle (Langley & Hungate, 2003). Subsequent studies demonstrated that chitin is decomposed relatively rapidly, whereas the glomeromycotan glomalin and EcM fungal melanins and other hydrophobic proteins (hydrophobins) depolymerise slowly (Drigo *et al.*, 2012; Fernandez *et al.*, 2016). Recalcitrant residues of EcM and ErM fungal cell walls contribute much to boreal forest humus (Clemmensen *et al.*, 2013), especially when complexed with root-derived tannins (Adamczyk *et al.*, 2019). While the EcM fungal mycelium proliferates in organic soil horizons (Lindahl *et al.*, 2007), the AM fungal mycelium is mostly distributed in upper mineral soil layers (interpretation of data in Toju *et al.*, 2016) in forest ecosystems. Collectively, these studies suggest that residues of EcM and ErM fungi result in recalcitrant C accumulation mainly in topsoil, whereas both EcM and AM fungi contribute to C stored in mineral soil horizons.

Plants and microorganisms of different functional guilds compete for nutrients in soil (Franklin *et al.*, 2014). EcM fungi compete for the same organic nutrient sources with saprotrophs that have a much stronger capacity for degradation. Supported by ample energy from host trees, EcM fungi are able to outcompete saprotrophic fungi from partly decomposed organic material (Bödeker *et al.*, 2016), which may result in hampered degradation activity termed the Gadgil effect. The Gadgil effect is a widespread phenomenon across multiple biomes and it may be of particular importance in ecosystems dominated by N-limited EcM trees that shed recalcitrant litter (reviewed in Fernandez & Kennedy, 2016).

Plants and mycorrhizal fungi exude simple organic compounds to promote microbial activity, which is termed a priming effect. Plant and fungal species differ in quality and quantity of exudates (Smith, 1976; van Schöll, Hoffland & van Breemen, 2006; Toljander *et al.*, 2007). Exudation is several-fold greater in mycorrhizal than non-mycorrhizal plants (Fransson *et al.*, 2016) and tends to be greater in EcM- than AM-dominated temperate forest soils (Yin *et al.*, 2014). Microcosm studies suggest that AM trees exhibit relatively greater soil C input resulting in a stronger rhizosphere priming effect and hence more rapid soil C loss (Wurzburger & Brookshire, 2017). In a greenhouse experiment, EcM plant species and fungi but not AM systems enhance exudation in response to drought, which is probably an adaptation to secure microbial activity and continuous nutrition to plants (Liese *et al.*, 2018). The AM *Rhizophagus intraradices* releases mostly formiate, acetate and glucose (Toljander *et al.*, 2007), whereas EcM fungi and potentially ErM fungi exude large quantities of oxalate (van Schöll *et al.*, 2006; Fransson *et al.*, 2016). In particular, oxalate has a strong priming effect for soil C mineralisation by the bacterial community (Keiluweit *et al.*, 2015) and it stimulates the effects of ligninolytic enzymes (Dutton & Evans, 1996). Because oxalate is released along with H^+, it is difficult to distinguish the direct effect of protons from that of oxalate and oxidases (Smits & Wallander, 2017). The exudated sugars, organic acids and other compounds are utilised differently by microbes (Sasse, Martinoia & Northen, 2017), possibly promoting different C and nutrient cycling pathways (Keiluweit *et al.*, 2015).

(3) Soil carbon cycling

Mycorrhizal fungi, plants and other soil organisms produce hydrophobic proteins that improve soil physicochemical properties and C storage. AM fungi release glomalin that binds soil particles, further preventing erosion and leaching (Rillig & Mummey, 2006). EcM and ErM fungi produce other recalcitrant hydrophobins that improve soil aggregation, with substantial interspecific differences (Zheng, Morris & Rillig, 2014). In a field experiment, AM grasses and herbs promoted soil aggregation, whereas the EcM shrub *Helianthemum canum* and AM shrubs did not (Poirier *et al.*, 2018*a*), pointing to differences among life forms and perhaps mycorrhizal colonisation. Nonetheless, in nutrient-poor forests, EcM fungi produce extensive mycelial systems, which bind large patches of forest floor and strongly enhance phosphatase and phenoloxidase activities as well as oxalate exudation (Kluber *et al.*, 2010). The relative contribution of different mycorrhizal types to soil aggregation and the underlying mechanisms remain poorly understood, but warrant further exploration for selecting symbionts to control erosion, leaching and C losses.

Mycorrhizal types strongly affect soil C cycling *via* differences in litter decomposition and priming. Based on ecosystem models of enzymatic activities of excised root tips, Sulman *et al.* (2017) suggested that in newly established vegetation, EcM systems retain soil C of previous AM-dominated habitats, but AM vegetation slowly releases soil C originating from previous EcM-dominated forest. These models contradict the earlier suggestions that EcM fungi deplete accumulated soil C in exotic forestry plantations (Chapela *et al.*, 2001), indicating some context dependency or differences in accounting for active and passive losses. Based on soil C content and dominant vegetation, Averill *et al.* (2014) estimated that EcM forests store 1.7-fold C ha^{-1} more than AM-dominated forests globally, but much of this could be attributable to EcM dominance in colder habitats (Soudzilovskaia *et al.*, 2018) that exhibit slower C and nutrient cycling (Makkonen *et al.*, 2012). These results were recently extrapolated to all terrestrial biomes, further

suggesting that AM-dominated forest ecosystems store more carbon in aboveground biomass, whereas EcM-dominated systems store more carbon in soil (Soudzilovskaia *et al.*, 2018). However, three recent North American temperate forest studies revealed no overall mycorrhizal-type effect (Zhu *et al.*, 2018), opposite trends in deep soil (Craig *et al.*, 2018), or an interplay between forest type, mycorrhizal type and soil depth (Jo *et al.*, 2019).

Mycorrhizal plants and fungi influence soil carbon and nutrient cycling by altering soil acidity. The relatively recalcitrant leaf litter with high C:N ratio and ample organic acid exudation for weathering and polymer degradation purposes both result in relative soil acidification in EcM and ErM habitats (Finzi *et al.*, 1998; Wurzburger & Hendrick, 2007; Dickie *et al.*, 2014). Acidification dramatically reduces the abundance of earthworms (Phillips & Fahey, 2006) that play critical roles in soil aeration, litter fragmentation and transportation into deeper soil horizons. This certainly contributes to the development of deep litter layers in many EcM-dominated ecosystems and may explain relatively low rates of C sequestration in mineral soil (Craig *et al.*, 2018; Zhu *et al.*, 2018).

Acidification also reduces the abundance of bacteria and bacteria-to-fungi ratio (McGuire *et al.*, 2010; Bahram *et al.*, 2018; Cheeke *et al.*, 2018) due to relatively greater acidity stress in bacteria (Rousk, Brookes & Baath, 2010*b*). Soil pH has a strong effect on phylogenetic composition of bacteria and microfungi (Rousk *et al.*, 2010*a*). Lower bacterial abundance and their physiological stress lead to deceleration of soil biochemical processes, which may also contribute to the Gadgil effect. However, the main driver of the Gadgil effect seems to be competition for organic substrates for nutrient release or sources of energy by EcM and saprotrophic fungi, respectively (Fernandez & Kennedy, 2016).

(4) Effects of mycorrhizal types: synthesis

Mycorrhizal types differentially affect soil processes such as decomposition, C and nutrient cycling *via* release of enzymes, exudates and organic acids and plant-subsidised competition between free-living organisms. All these features taken separately but also synergistically hamper nutrient cycling and promote C accumulation in EcM systems, especially in topsoil. This view is, however, in some conflict with the microbial efficiency–matrix stabilisation model that emphasises the role of microbial C derived from high-quality litter and exudates in long-term soil C sequestration (Cotrufo *et al.*, 2013; Poirier, Roumet & Munson, 2018*b*). Based on the above reviewed evidence, we hypothesise that in AM systems deep soil C is rather derived from material transported by earthworms and microbial residues retained due to surplus in nutrient-rich conditions; likewise, C originates from recalcitrant litter that accumulates more in topsoil at least partly due to a paucity of transporting agents in EcM systems. High activities of the relatively non-selective termites and fewer differences between EcM and AM systems at low latitudes (Mayor *et al.*, 2015; Keller & Phillips, 2019) allow us to speculate that prevalence of priming- and litter-related processes may differ across biomes and along edaphic and climatic gradients. This hypothesis is partly supported by regional-scale vegetation analyses demonstrating that differences among mycorrhizal types may be strongly influenced by climate and soil texture in the USA (Jo *et al.*, 2019). Overall, these studies indicate that mycorrhizal-type effects on soil C sequestration are context dependent and require careful examination from litter to deep mineral soil in controlled experiments accounting for edaphic and climatic variables.

V. STRESS

(1) Physical damage

Damage to the foliage, stem or roots of host trees leads to a reduction in C flow belowground. EcM systems respond more strongly to induced stress by a relatively greater reduction of chitinase and phenol oxidase activity but stronger induction of nitrification and N mineralisation compared with AM-dominated systems (Brzostek *et al.*, 2015; Averill & Hawkes, 2016). This is related to the huge biomass of EcM fungal mycelium in forest soils, which becomes rapidly starved in C and ceases functioning (Kaiser *et al.*, 2010). Decline in EcM mycelium biomass results in N mobilisation from labile compounds and loss of resources to saprotrophic and mycoparasitic fungi and bacteria. Both EcM and AM associations may respond negatively to defoliation of host trees *via* reduced root colonisation, decline in species richness and shifts in composition towards less C-demanding fungal species (Barto & Rillig, 2010; Parker *et al.*, 2015).

(2) Water stress

Mycorrhizal fungi exhibit mechanisms to maintain host vigour under water stress. AM and EcM fungi induce expression of plant aquaporins during drought that conveys drought tolerance to plants by regulating root, shoot and stomatal conductance and hence transpiration of host plants (Allen, 2007; Lehto & Zwiazek, 2011). Due to greater mycelium biomass and the presence of rhizomorphs, EcM fungi are expected to transport soil water more efficiently (Allen, 2007) and perhaps access moisture in bedrock (Egerton-Warburton, Graham & Hubbert, 2003). Querejeta, Egerton-Warburton & Allen (2003) elegantly described the nocturnal uptake and transfer of deep ground water into oak EcM and AM extraradical mycelium and mycorrhizosphere soil. At dawn, water with dissolved nutrients is reabsorbed by hyphae and transferred to foliage to sustain transpiration and photosynthesis. Mycorrhizal seedlings recover from drought stress better than non-mycorrhizal seedlings (Auge, 2001; Lehto & Zwiazek, 2011). EcM trees retain their photosynthesis to a greater extent compared to AM trees (Meier *et al.*, 2016; Liese *et al.*, 2018). However, severely

water-limited systems (except Australian and Mediterranean semi-deserts) harbour AM but not EcM plants (Tedersoo, 2017), which may be related to the greater plasticity of AM hyphal production and withstanding highly negative water potentials (Querejeta, Egerton-Warburton & Allen, 2009; Vargas *et al.*, 2010).

Waterlogging reduces soil oxygen content and thus functioning of aerobic fungi and plants. Many wetland trees have evolved mechanisms for oxygen transport into feeder roots. In other trees, both EcM and AM root colonisation tends to decline in response to waterlogging. AM trees adapted to inundation gain nutritional benefits in waterlogged conditions, indicating mechanisms for oxygen supply to mycorrhizal fungi (Elzenga & van Veen, 2010). Given EcM formation in Salicaceae and *Alnus* in anoxic, waterlogged conditions, their mycorrhizal functionality is likely. In EcM fungi, the ability to tolerate waterlogging is related to mycelium hydrophobicity (Unestam & Sun, 1995). Nonetheless, in anoxic soils, EcM fungi are replaced by AM fungi, which can be ascribed to greater respiration, mycelial biomass and/or direct contact of the mantle with the substrate (Jurgensen *et al.*, 1996). EcM trees are generally uncommon in wetlands, except *Alnus* and *Salix* in temperate habitats and *Aldina* (Amazonia), *Uapaca* (Africa), *Casuarina* and *Melaleuca* (Australia) in tropical ecosystems (Tedersoo, 2017). Notably, a vast majority of these trees are EcM–AM dual mycorrhizal.

(3) Chemical stress

Plants are more sensitive to high concentrations of heavy metals, salts and toxins in the rhizosphere compared with microorganisms, but this could be at least partly related to the unanticipated rapid local selection for tolerant bacteria and fungi (Gadd, 2007; Amir *et al.*, 2014). All EcM and AM and ErM fungi are capable of ameliorating stress caused by various phytotoxic substances (Joner & Leyval, 2003; Amir *et al.*, 2014). EcM fungi may be relatively more efficient in protecting host plants due to the formation of the hyphal sheath as a barrier that reduces direct root contact with soil and accumulates certain elements. Besides vacuoles in the mantle of EcM fungi and intracellular vesicles in AM and ErM fungi, mycorrhizal fungi are able to immobilize cations and organic compounds into oxalate salts, metal-protein complexes and slime (bacterial biofilm) on the surface of extraradical hyphae (Amir *et al.*, 2014). Both EcM and AM fungi are able to promote tree growth in the presence of allelochemicals by ameliorating chemical stress (Javaid, 2007). Much of detoxification of allelochemicals and phenolic compounds takes place intracellularly by the mycorrhizosphere bacteria and extracellularly by saprotrophic fungi that have more efficient enzyme complexes compared with mycorrhizal fungi (Shukla, Singh & Sharma, 2010). Similarily to the Gadgil effect, the high competitive ability of EcM fungi may hamper detoxification of polyaromatic hydrocarbons by suppressing other more efficient microbes (Joner, Leyval & Colpaert, 2006).

(4) Nitrogen and Sulphur deposition

Increasing industrial gas emissions and human activities have caused shifts in climate and land use that have had strong effects on the competitive ability and distribution of mycorrhizal types (Soudzilovskaia *et al.*, 2018; Terrer *et al.*, 2018). Sulphur and nitrogen deposition *via* air pollution affects trees directly and indirectly through soil acidification (Section IV). Acid rains cause relatively greater damage to the foliage of conifers and other evergreen trees, resulting in dieback and replacement of Pinaceae by deciduous trees such as Fagales and Myrtoideae and ErM shrubs. Nitrogen deposition and fertilisation alter mycorrhizal dependency of trees, rendering especially EcM and ErM associations redundant for N uptake (Aerts, 2002). N deposition reduces both EcM and ErM root colonization and EcM mycelium biomass (Aerts, 2002) and fungal diversity (Lilleskov *et al.*, 2019), but responses of AM fungi are more variable (Treseder *et al.*, 2018). EcM fungal species with high affinity to ammonium and nitrate become more dominant in fungal communities (Lilleskov *et al.*, 2019). Using a meta-analysis, Kivlin, Emery & Rudgers (2013) demonstrated that EcM fungi exhibit marginally negative effects, whereas AM fungi provide positive growth responses to their host trees under N fertilisation. Surplus N turns the ecosystems P-limited and shifts the competitive balance towards AM symbiosis (Aerts, 2002; Hofland-Zijlstra & Berendse, 2010). Similarly to the direct effects of acid deposition on trees, increasing ultraviolet light and O_3 reduce the competitive ability of evergreen trees and affect mycorrhizal fungi *via* reduced C supply (Cairney & Meharg, 1999; Mohan *et al.*, 2014). Indeed, regional-scale studies in North America indicate that the growth and survival of the EcM understorey is decreasing relative to AM trees in sites receiving atmospheric N (Thomas *et al.*, 2010; Averill, Dietze & Bhatnagar, 2018).

Modelling reveals that tree C costs related to N uptake are greater for EcM symbionts than AM symbionts at high and medium soil N content, but these costs are comparable at low N (Brzostek *et al.*, 2014).

(5) Elevated CO_2

Elevated CO_2 stimulates photosynthesis and results in greater demand for soil nutrients, which in turn enhances belowground C allocation. In all mycorrhizal types, root colonisation, hyphal biomass and tree growth respond positively to eCO_2 (Treseder & Allen, 2000; Olsrud *et al.*, 2004; Alberton, Kuyper & Gorissen, 2005; Dong *et al.*, 2018). According to a meta-analysis, EcM and AM trees respond equally strongly positively to eCO_2, but EcM fungal extraradical mycelium increases by twice as much as AM mycelium (Alberton *et al.*, 2005). Enhancement of allocation to EcM fungi is 28% greater compared with AM fungi under low and medium soil N but 13% greater at high N (Terrer *et al.*, 2016). Increasing N demand leads to relatively greater belowground allocation and priming in EcM-dominated systems, resulting in net soil C loss (Terrer *et al.*, 2018). However, in boreal coniferous forests and potentially other

nutrient-poor ecosystems, strong N limitation may hamper productivity through N accumulation in thriving EcM mycelium, which is explained by the market theory (Franklin *et al.*, 2014). These studies collectively indicate that eCO_2 generally favours proliferation of EcM fungal mycelium over AM and saprotrophic mycelium, particularly in strongly and moderately N-limited habitats. In mixed forests, AM trees may further suffer from reduced nutrient availability and soil acidification. Greater amounts of mycelium may increasingly contribute to soil C sequestration under eCO_2 conditions (Ekblad *et al.*, 2016; Fernandez *et al.*, 2019).

(6) Temperature and precipitation

Shifts in temperature and precipitation affect soil moisture availability, which influences both photosynthesis and nutrient uptake. Temperature has a direct positive effect on tree growth and enzymatic activities given sufficient moisture and indirect effects through altered microbial activity and competitive balance (Brzostek & Finzi, 2011; Mohan *et al.*, 2014). Temperature effects on diversity, biomass and colonisation of mycorrhizal fungi are inconsistent among studies, which may result from confounding moisture effects (Pickles *et al.*, 2012) and adaptation to drought. For example, an experimental rise in temperature differentially affects EcM fungi in moist and dry tundra (Morgado *et al.*, 2015). Soil respiration is mostly driven by temperature in EcM-dominated habitats but by precipitation in AM-dominated habitats (Vargas *et al.*, 2010).

(7) Relative stress tolerance in mycorrhizal types: synthesis

AM and EcM fungi are obligate mutualists, whereas ErM and OM fungi may thrive as endophytes and saprobes. Therefore, damage to the host plant has probably a relatively small impact on ErM and OM fungi, or perhaps even benefits the latter guild. Compared with AM trees, EcM plants are more vulnerable to any disturbance or stress agent that results in reduced photosynthesis because of the high mycorrhizal mycelium biomass in the soil and relatively stronger reliance on their fungi for nutrient acquisition. Partly due to this, both a paucity and excess of soil moisture disfavour EcM associations. Although EcM fungal mycelium of many wetland tree species tolerates anoxic conditions, EcM structures are never observed in aquatic roots, where AM colonisation is sometimes high (Elzenga & van Veen, 2010).

In contrast to physiological stress, EcM symbionts can cope with chemical stress better than AM symbionts. By more extensive mycelium and hyphal cover around EcM root tips, EcM trees have more opportunities to access and lock up low molecular-weight harmful compounds in their biomass or hyphal surface (Amir *et al.*, 2014). Because many organic contaminants are phenolic compounds, the same enzymes and reactive compounds used for nutrient release from polymers act in decomposing the contaminants. As a result, EcM fungi may hamper decomposition of organic pollutants by generating unfavourable conditions for bacteria (Bahram *et al.*, 2018) as well as competing with saprotrophs over nutrients (Bödeker *et al.*, 2016).

Global climate change and associated pollution may alter limiting nutrients or magnify nutrient limitation, which results in optimisation of energy re-allocation in trees and fungi, and may further shift the competitive balance among host trees, fungal guilds and soil bacteria (Terrer *et al.*, 2018). Climate change factors affect the relative benefits of AM and EcM fungi to trees, but these shifts are context dependent and hard to predict because of too many influential parameters and genetic differences among plant and fungal species (Kivlin *et al.*, 2013). *Via* reduced competitive ability, N pollution is slowly shifting vegetation from EcM dominance to AM dominance in NE American temperate forests (Averill *et al.*, 2018). A similar situation may occur in E Asian and Central European regions subject to heavy N deposition. Shifts in dominant mycorrhizal types alter ecosystem C and nutrient cycling, generating positive or negative feedback loops with climate change.

VI. METHODOLOGICAL CONSIDERATIONS

(1) Sampling design and biases

For practical reasons, nutrition experiments on trees have been performed using seedlings or cuttings in artificial edaphic and climatic conditions, which are of limited relevance to natural ecosystems. To test ecophysiological differences among mycorrhizal types, most authors use only one or two tree species per guild, basically comparing maples with oaks, ignoring the inherent hierarchical study design of tree species nested within mycorrhizal type. Accumulation of similar studies with comparable results somewhat ameliorates these shortfalls, but further complicates interpretation when methods and results differ. In studies with multiple tree species and meta-analyses, the effects of mycorrhizal type and other traits should be corrected for phylogenetic non-independence, at least when inferring trait evolution (Dickie *et al.*, 2014).

To test for interspecific differences among mycobionts, different strains rather than pieces of the same culture should constitute replicates. Strains of the same species may have great differences in genome structure (Chen *et al.*, 2018*a*) and function (Hazard & Johnson, 2018). Likewise, spore material should ideally originate from fruit-bodies of different fungal individuals, i.e. collected at least several metres apart (Douhan *et al.*, 2011). In comparison, tree seeds and cuttings for inoculation are usually collected from several genetic individuals. As Glomeromycota are infected mostly using spores or soil inoculum, their genetic diversity is much higher than that of single-strain EcM and ErM inoculum.

There is an enormous temperate sampling bias in comparative mycorrhizal studies. Because of high research costs, >80% of information about differences in mycorrhizal types originates from temperate deciduous and mixed-forest

ecosystems, with extremely limited knowledge from tropical forest and tundra biomes. Given that tropical forests are more P-limited and harbour different EcM plant lineages, temperate studies may not adequately reflect mycorrhizal-type differences in tropical habitats (Zhang *et al.*, 2018; Keller & Phillips, 2019). Because the mycorrhizal trait input for global models is derived from temperate and boreal forest habitats, these nutrient-cycling models (Terrer *et al.*, 2016) may be somewhat biased. Therefore, meta-analyses should account for temperature and precipitation and their interaction with tested factors (Zhang *et al.*, 2018).

(2) Ecophysiological and molecular methods

Development of *in situ* methods such as ingrowth mesh bags, isotopic labelling systems, exudate analysis and real-time molecular identification have greatly benefited our understanding about ecosystem functioning and continue to offer great perspectives when combined with high-resolution -omics tools. While most biochemical and ecophysiological methods are equally well suited for different mycorrhizal systems, comparison of feeder root functioning is problematic, because EcM root tips are fully covered by fungal mantle, but the root surface of other mycorrhizal and non-mycorrhizal trees is sparsely covered by endophytes. Furthermore, much of the root surface is covered with a bacterial biofilm, which influences interpretation of enzymatic activities. Measurement of ecophysiological processes in extraradical mycelium represents a major bottleneck in understanding the functioning of mycorrhizal associations.

Phospholipid fatty acids (PLFAs), neutral lipid fatty acids (NLFAs) and ergosterol in the cell membrane, chitin in the cell wall and gene copy number-based polymerase chain reaction (PCR) are commonly used to quantify fungi and Glomeromycota therein, but most of these methods have serious shortfalls due to taxon coverage (Baldrian *et al.*, 2013; Table 3). DNA- and RNA-based molecular identification techniques have greatly improved our understanding of biodiversity and ecology of mycorrhizal fungi (Nilsson *et al.*, 2019). Well-curated reference databases enable distinguishing between EcM and AM fungi at the species level, but poorly so for ErM fungi because of highly fragmented information about the functionality of root-associated fungi of Ericaceae (Kohout, 2017). Besides species-level identification, high-throughput sequencing (HTS) methods allow determination of the relative proportion of fungal guilds. Perhaps due to the aseptate multinucleate mycelium, the relative abundance of Glomeromycota is strongly underestimated using ribosomal RNA (rRNA) gene markers (Dickie & St. John, 2016). Application of metagenomics, metatranscriptomics and proteomics techniques offers great opportunities for shedding light into the ecophysiology of mycorrhizal plant–fungus systems, but these methods rely heavily on scarce genome sequences and protein information from different fungal guilds (Nilsson *et al.*, 2019).

Stable isotope analyses are based on heavy isotope discrimination during photosynthesis and nutrient transport to trees that occurs in EcM but not in AM associations. While the ^{13}C:^{12}C ratio effectively discerns among trees with C3, C4 and mycoheterotrophic nutrition, the ^{15}N:^{14}N ratio has become a widely used proxy to discriminate among non-mycorrhizal and mycorrhizal guilds and nitrogen-fixing associations (Hobbie & Högberg, 2012; Merckx, 2013). Across biomes, relative ^{15}N enrichment is highest in non-mycorrhizal plants, followed by AM, EcM and ErM plants due to differential access to soil organic N pools (Craine *et al.*, 2009). These methods suffer from poor ability to distinguish among multiple processes that simultaneously discriminate against heavier isotopes (Table 3). The radioisotopes ^{14}C and ^{33}P are sometimes used in laboratory experiments to trace movement of labelled compounds, but safety regulations limit their use to a few laboratories. Stable isotope chemistry can also be linked to molecular identification *via* stable isotope probing (SIP) by selective sequence analysis of ^{13}C-enriched DNA. Although better suited to rapidly growing bacteria, recent technical advances enable detection of movement of plant-derived carbon through the soil food web, demonstrating a decline in the pathogen-to-mycorrhiza ratio during secondary succession (Hannula *et al.*, 2017).

(3) Perspectives

Given the paucity of truly well-replicated comparative studies (Table 2), particular care must be taken to consider the representativeness of experiments and to account for potential confounding effects and improve the signal-to-noise ratio inherent to field surveys (Ferlian *et al.*, 2018). Due to the strong temperate sampling bias, several fundamental issues regarding the relative ecophysiological and functional differences among mycorrhizal types remain open to interpretation. Replicated common-garden experiments involving multiple tree species are particularly useful for disentangling mycorrhizal-type effects from tree species effects in near-natural conditions. Another serious issue is misassignment of mycorrhizal types to study species, because this renders all subsequent analyses and interpretations incorrect (Brundrett & Tedersoo, 2019). If the raw data or means and variance are unavailable, it is almost impossible to re-analyse the data for re-interpretation and re-use it for meta-analyses that have greatly nourished our knowledge about processes shaping mycorrhizal-type effects on ecosystem function in recent years.

Regarding methods, there is much to achieve by integrating state-of-the-art analytical tools with experiments and field measurements. Strangely enough, few studies have combined ecophysiological methods and molecular identification tools; thus, we still know virtually nothing about the effects of mycorrhizal types on the rhizosphere microbial communities that are the actual consumers of exudates and key players in mineralisation, gas fluxes and decomposition. Metagenomics, metatranscriptomics, proteomics and metabolomics tools enable us to detect

Table 3. Pros and cons of currently used molecular methods to study differences in mycorrhizal types

Method	Target	Advantages	Disadvantages
PLFA 18:2ω6,9	Fungal biomass	Relatively precise	Present in plant membranes
NLFA 16:1ω5	Glomeromycota biomass	Relatively precise	Absent in Endogonomycetes?
Ergosterol quantity	Fungal biomass	Simple	Absent from Pezizales, Glomeromycota, Mortierellomycota
Chitin quantity	Fungal biomass	Simple	Includes necromass, animals; missing in arbuscules and Hartig net
In-growth meshbags	Hyphal production of mycorrhizal fungi	Simple	Sand unnatural substrate; saprotrophs sometimes abundant; many key mycorrhizal fungal taxa missed
qPCR	Biomass proxy for any taxon	Flexible, rapid	Difference in gene copy number; lack of truly specific primers for Fungi and Glomeromycota
Droplet digital PCR (ddPCR)	Biomass proxy for any taxon	Flexible, high-throughput, several parallel assays, precise	As above
DNA metabarcoding	Any: identification, relative abundance	Highly flexible, high-throughput, precise	Difference in gene copy number; PCR/primer bias
RNA (cDNA) metabarcoding	Any: identification, relative abundance	Highly flexible, high-throughput, active community, precise	Sample preparation; PCR/primer bias; high cost
Metagenomics	All: genes, identification	All-inclusive, high-throughput	Reference bias, high noise, high cost, guild assignment
Metatranscriptomics	All: transcribed genes, identification	All-inclusive, high-throughput, active genes, precise	Sample preparation, reference bias, ultra-high cost, guild assignment
Metaproteomics	All: proteins, functions	All-inclusive, high-throughput, translated proteins, precise	Sample preparation, ultra-high reference bias, inactive proteins, guild assignment
Stable isotopes: ^{15}N:^{14}N ratio	Ecosystem components: plant N nutrition	Simple, cheap	Confounding: soil depth, N form, transportation, leaching
Stable isotopes: ^{13}C:^{12}C ratio	Ecosystem components: plant photosynthesis, fungal C source	Simple, cheap	Little variation, soil ^{13}C driven by carbonates; depends on respiration, soil depth
Stable isotopes: ^{41}K, ^{44}Ca, ^{18}O, ^{2}H	Ecosystem components: plant mineral nutrition	Simple, high differences	Very specific questions; unknown fractionation processes
Radioisotopes: ^{33}P	Ecosystem components: plant P nutrition	Simple, good visualisation	Radioactive
Radioisotopes: ^{14}C	Ecosystem components: C partitioning belowground	Simple, good visualisation, double labelling with ^{13}C	Radioactive
Stable isotope probing (SIP)	Ecosystem components: C partitioning belowground	Identification of C users	High quantities needed; high cost

NLFA, neutral lipid fatty acid; PLFA, phospholipid fatty acid; qPCR, quantitative polymerase chain reaction.

Table 4. Important knowledge gaps and research needs to understand the functioning of mycorrhizal associations

Ecophysiology of ericoid mycorrhizal associations, particularly nutrient and energy budget of symbionts, and fungal role in the ability to grow in highly acidic, nutrient-poor soils
Relative nutritional benefits of mycorrhizal types along soil pH and nutrient gradients
Turnover of extraradical mycelium and its response to nutrient availability
Direct and indirect effects of mycorrhizal types on soil meiofauna and microbes: biomass, taxonomic and functional diversity
Quality and quantity of root exudates and priming in response to nutrient availability
Differences in mycorrhizal-type effects across biomes
Mycorrhizal type and soil nutrient-based predictive framework for whole-ecosystem C and nutrient economy

genome-encoded and expressed functions. Incorporation of ^{13}C, ^{14}C and ^{33}P into RNA-based SIP-type analyses might enhance the heavy isotope signal and enable us to address relative C or P nutrition of root-associated microbes. Multiple stable isotope tracers and carbon dot-labelled compounds could be simultaneously used to trace uptake of simple organic compounds. As all these methods are used in other fields of biology and chemistry, their integration requires collaboration between ecophysiologists, biochemists, molecular ecologists and modellers to be able to disentangle the direct and indirect effects of mycorrhizal types on ecosystem functions and processes and to extrapolate these globally. Table 4 lists some of the most pressing questions for understanding fundamental differences among mycorrhizal types and their effects on ecosystem functioning.

VII. CONCLUSIONS

(1) Ecophysiological studies suggest that mycorrhizal types differ in soil nutrition, in particular investment into roots *versus* mycelium and the relative contribution of mineral *versus* organic nutrients. Figure 2B integrates these findings and shows that AM trees invest relatively more C into feeder roots and rely on both mycelium and roots for uptake of nutrients in mineral form. Conversely, EcM trees invest into and benefit from soil mycelium relative more than AM associations. Compared with EcM trees, ErM shrubs invest relatively less into mycelium biomass, but acquire a relatively higher proportion of nutrients from organic sources.

(2) EcM associations tend to be relatively more efficient than AM associations in nutrient transfer to plants, which can be ascribed to acquisition of simple organic compounds, a more extensive mycelial network and more efficient means of transportation. In addition to nutrients transferred to plants, the extensive EcM mycelium locks up a substantial proportion of soil nutrients, rendering particularly saprotrophs and co-occurring AM plants nutrient-starved. EcM fungi require more carbon and oxygen for proper functioning, which makes this type of root symbiosis costlier to seedlings and plants in highly stressful habitats. While the EcM symbiosis in trees has evolved to function on its own in a highly competitive manner, the AM partners complement their poor organic nutrition capacity *via* stimulating the activities of saprotrophic fungi and bacteria. Because of greater decomposition efficiency of saprotrophic organisms, AM-dominated communities exhibit more rapid nutrient cycling and more losses to leaching (Fig. 2A).

(3) Our comparative genomics analysis demonstrates that guilds of mycorrhizal fungi serve mostly similar functions in mineral nutrient uptake and stress amelioration of host plants, but display relatively greater differences in CAZymes and oxidative enzymes to mobilise and take up macronutrients from organic material (Fig. 1). ErM fungi, in particular, possess more decomposition-related enzymes than many typical basidiomycetous saprotrophs. In contrast to the current paradigm, AM mycobionts do encode multiple putative ligninolytic enzymes, but there is no evidence for their extracellular degradation activity. Taken together, the genomic differences among mycorrhizal fungal guilds reflect ecophysiological traits of plant holobionts as well as their influence on biochemical processes and nutrient cycling at the ecosystem level.

(4) Pollution, changes in land use and climate have differential effects on mycorrhizal plants and ecosystems dominated by different mycorrhizal types, which affect global C and nutrient cycling and may trigger shifts in terrestrial biomes (Terrer *et al.*, 2016, 2018; Averill *et al.*, 2018; Sulman *et al.*, 2019). Although local- and global-scale modelling studies provide rough estimates on how individual global-change factors alter the balance among mycorrhizal types, it is critical to understand the interactive effects of these variables in different biomes accurately to predict global shifts in mycorrhizal types and associated ecosystem processes.

(5) Because of issues in experimental design and biases in geographical sampling (Table 2), many of the reported ecophysiological differences among mycorrhizal types require independent evaluation and confirmation across soil types and biomes. Direct and indirect effects of mycorrhizal types on soil nutrient cycling should be tested in parallel using path analysis of field and experimental data, to infer causality and direction of relationships. Integrating well-controlled experiments and ecophysiological methods with rapidly evolving -omics technologies offers deep insights into differences in ecophysiology, tree–fungal interactions and responses to global change among mycorrhizal types.

VIII. ACKNOWLEDGMENTS

We acknowledge funding from the Estonian Science Foundation grants 1399PUT, 1317PUT and MOBERC and Vetenskapsrådet grant 2017-05019. We thank the Joint Genome Institute and F. Martin for permission to use partly unpublished genomic data, and B. Waring and J. Powers

for constructive comments on an earlier version of the manuscript.

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(*Received 22 October 2018; revised 27 May 2019; accepted 30 May 2019; published online 3 July 2019*)