

## Tansley review

# The functional role of ericoid mycorrhizal plants and fungi on carbon and nitrogen dynamics in forests

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### Summary

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Ericoid mycorrhizal (ErM) shrubs commonly occur in forest understories and could therefore alter arbuscular (AM) and/or ectomycorrhizal (EcM) tree effects on soil carbon and nitrogen dynamics. Specifically, ErM fungi have extensive organic matter decay capabilities, and ErM plant and fungal tissues have high concentrations of secondary compounds that can form persistent complexes in the soil. Together, these traits could contribute to organic matter accumulation and inorganic nutrient limitation. These effects could also differ in AM- vs EcM-dominated stands at multiple scales within and among forest biomes by, for instance, altering fungal guild interactions. Most work on ErM effects in forests has been conducted in boreal forests dominated by EcM trees. However, ErM plants occur in *c.* 96, 69 and 29% of boreal, temperate and tropical forests, respectively. Within tropical montane forests, the effects of ErM plants could be particularly pronounced because their traits are more distinct from AM than EcM trees. Because ErM fungi can function as free-living saprotrophs, they could also be more resilient to forest disturbances than obligate symbionts. Further consideration of ErM effects within and among forest biomes could improve our understanding of how cooccurring mycorrhizal types interact to collectively affect soil carbon and nitrogen dynamics under changing conditions.

### I. Introduction

More than 90% of vascular plant species form mutualistic relationships with one or more types of mycorrhizal fungi (Brundrett & Tedersoo, 2018). One of the primary services of these fungi is to increase plant access to soil nutrients in exchange

for carbon (C) from photosynthesis (Smith & Read, 2008). These symbiotic fungi are therefore involved in aboveground–belowground transfers of C and nutrients, and as such, different types of mycorrhizal fungi can be associated with distinct ecosystem C and nitrogen (N) dynamics. Across biomes, for example, the relative abundance of arbuscular (AM), ecto- (EcM) and ericoid (ErM)

mycorrhizal plants aligns broadly with climate-associated gradients of soil organic matter (SOM) accumulation and inorganic nutrient limitation (Fig. 1; Read, 1991; Read & Perez-Moreno, 2003). Specifically, EcM and ErM plants are most abundant in high-latitude and high-elevation ecosystems characterized by slow decomposition rates, high SOM concentrations and stocks, and low inorganic N availability (Read, 1991; Kohout, 2017; Soudzilovskaia *et al.*, 2017, 2019). By contrast, AM plants are most abundant in lower latitude and lower elevation ecosystems with faster decomposition rates, lower SOM and higher N availability (Read, 1991; Soudzilovskaia *et al.*, 2017, 2019; Steidinger *et al.*, 2019).

Plant and fungal functional traits and nutrient acquisition strategies reflect and directly contribute to these broad biogeographic gradients (Fig. 1). For example, AM plants and fungi often have more nutrient-acquisitive traits (Cornelissen *et al.*, 2001; Averill *et al.*, 2019; Tedersoo & Bahram, 2019; Weigelt *et al.*, 2021), and AM fungi primarily enhance plant uptake of inorganic nutrients (Smith & Read, 2008). Ectomycorrhizal and ErM plants and fungi, by contrast, generally have more nutrient-conservative traits (Cornelissen *et al.*, 2001; Meers *et al.*, 2010; Clemmensen *et al.*, 2015; Averill *et al.*, 2019; Weigelt *et al.*, 2021) as well as the ability to, in many instances, access nutrients directly from organic matter (Read & Perez-Moreno, 2003). Together, these global patterns and functional differences suggest that AM, EcM and ErM plants and fungi each have distinct traits that, respectively, span a continuum linked to progressive inorganic N limitation (Fig. 1; Read, 1991; Read & Perez-Moreno, 2003).

Whether local relationships between mycorrhizal traits and C and N dynamics within biomes are consistent with these regional- and global-scale trends is increasingly being investigated (Fig. 1). In forests, for instance, AM and EcM trees can cooccur within stands, and a higher relative abundance (or 'dominance') of one vs the other appears to strongly influence ecosystem C and N cycling and storage (Phillips *et al.*, 2013; Lin *et al.*, 2017; Weemstra *et al.*, 2020). Understorey ErM plants are also common in forests (Mallik, 2003; Read *et al.*, 2004; Vrålstad, 2004; Nilsson & Wardle, 2005), but their effects are less often considered relative to those of AM and/or EcM trees. Publications on the relationships between AM and EcM plants and fungi and C and N dynamics have increased exponentially over the past three decades, whereas research on ErM associations has remained low and relatively constant (Fig. 2). Although only 2% of vascular plant species are EcM – compared to 78% that are AM (Brundrett & Tedersoo, 2018) – 60% of the world's tree stems are EcM (Steidinger *et al.*, 2019). As such, EcM plants make up a dominant component of plant biomass in forests despite their relatively low species richness. Ericoid mycorrhizal plants, by contrast, are primarily understorey shrubs (Soudzilovskaia *et al.*, 2020; Ward *et al.*, 2021; Fig. 3) and account for a relatively low proportion of both plant species richness (1.4% of vascular plants; Brundrett & Tedersoo, 2018) and biomass in forests.

The prevailing framework for understanding mycorrhizal effects on ecosystem C and N cycling has therefore focused primarily on the dominant mycorrhizal type(s) within an ecosystem based on its contribution to plant biomass (Soudzilovskaia *et al.*, 2017, 2019; Steidinger *et al.*, 2019). This approach is grounded in the mass ratio hypothesis, which posits that the traits of the dominant biomass

contributors will overwhelmingly control biogeochemical fluxes and stocks (Grime, 1998). However, traits of subdominant biomass contributors can also regulate ecosystem C and N dynamics (Nilsson & Wardle, 2005; Peltzer *et al.*, 2009; McLaren & Turkington, 2010), particularly when their functional traits are distinct from those of the dominant species (e.g. N<sub>2</sub>-fixing plants; Spehn *et al.*, 2002). Understorey ErM plants could therefore alter the direction and/or magnitude of AM and/or EcM tree effects through their distinct traits (Ward *et al.*, 2021; Fig. 4). Specifically, ErM plants and fungi could strengthen the magnitude of EcM plant and fungal effects if they have the same direction of effect (Read, 1991; Read & Perez-Moreno, 2003). Alternatively, ErM plant and fungal effects could contrast with those of EcM plants and fungi if they have the opposite direction of effect (Clemmensen *et al.*, 2021; Ward *et al.*, 2021). Finally, the effects of ErM plants and fungi could be redundant with those of EcM plants and fungi and therefore only influence C and N dynamics in AM-dominated stands (Ward *et al.*, 2021). Notably, these three alternative hypotheses each have different causal implications for AM vs EcM tree effects in forests where they cooccur with ErM shrubs (Ward *et al.*, 2021). As the distribution and abundance of AM, EcM and ErM plants shift in response to global changes, understanding the extent to which relationships among plant mycorrhizal types and forest C and N dynamics are driven by ErM shrubs and/or AM vs EcM trees will be critical for projecting future changes.

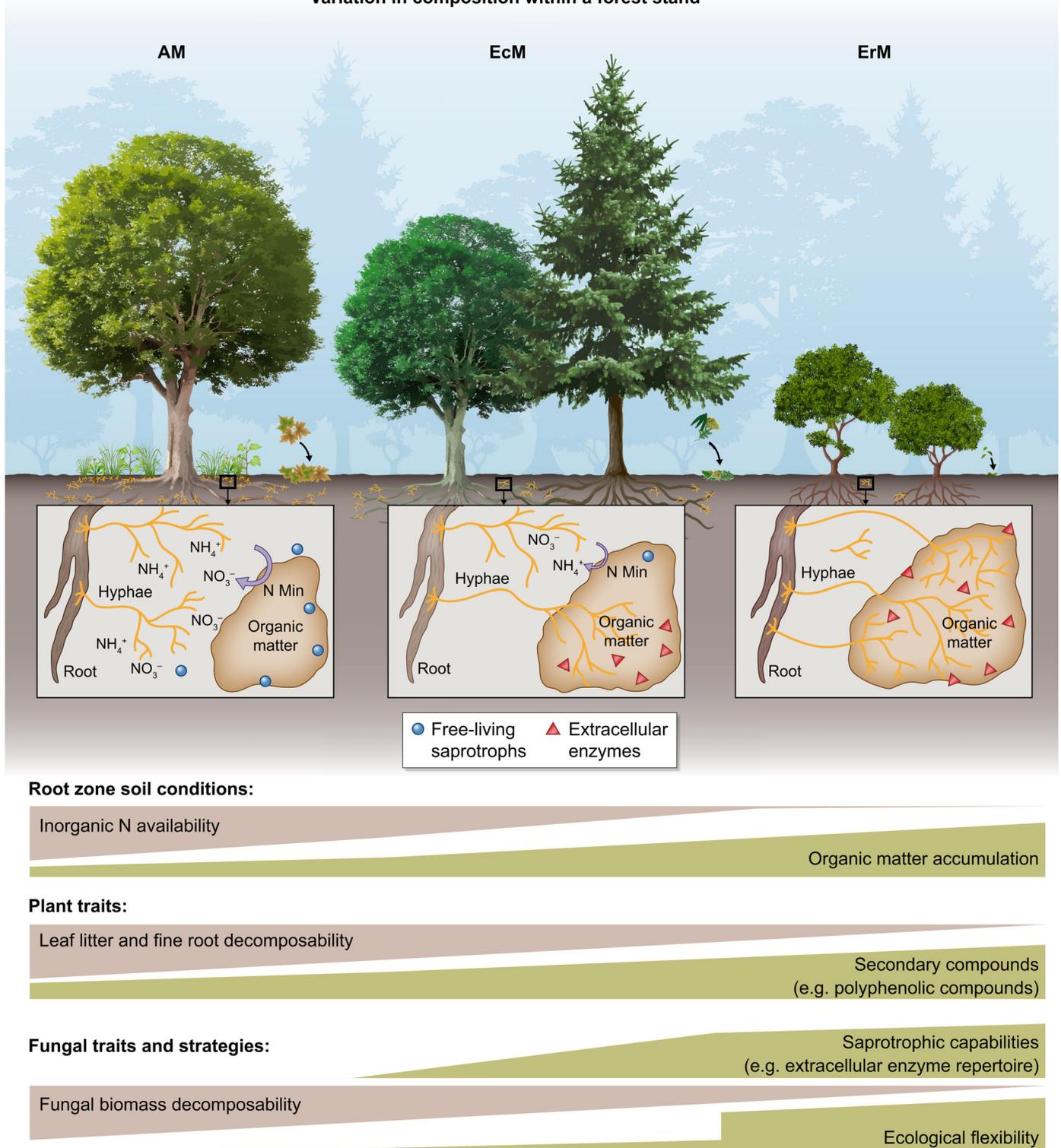
Here, we explore the potential role of ErM plants and fungi (Box 1) as regulators of C and N cycling in forests globally. We begin by reviewing the literature on ErM plant and fungal functional traits to evaluate how they might influence AM vs EcM tree effects on forest C and N dynamics (Section II). We then present hypotheses for how interactions among cooccurring fungal guilds could affect C and N cycling and storage within the soil profile (Section III; Fig. 4). Given the potential for ErM plant and fungal effects to differ in AM- vs EcM-dominated stands, we also estimate the distribution and abundance of ErM plants across global forest types defined by climate (i.e. boreal, temperate, tropical) and by dominant tree mycorrhizal type (i.e. AM vs EcM; Section IV). Finally, we synthesize the literature on the effects of ErM plants and fungi on forest soil C and N dynamics to identify potential knowledge gaps (Section V). Together, our review suggests that the AM vs EcM tree dominance framework should be extended to include the largely unmeasured influence of subdominant ErM shrubs on C and N dynamics across the approximately two-thirds of global forestlands in which they occur (Fig. 5; Table 1). More broadly, a focus on mycorrhizal trait variation – in addition to mycorrhizal trait dominance – could help to explain C and N cycling and storage in ecosystems where multiple mycorrhizal types cooccur in association with dominant and subdominant vegetation.

## II. Distinct ErM plant and fungal functional traits

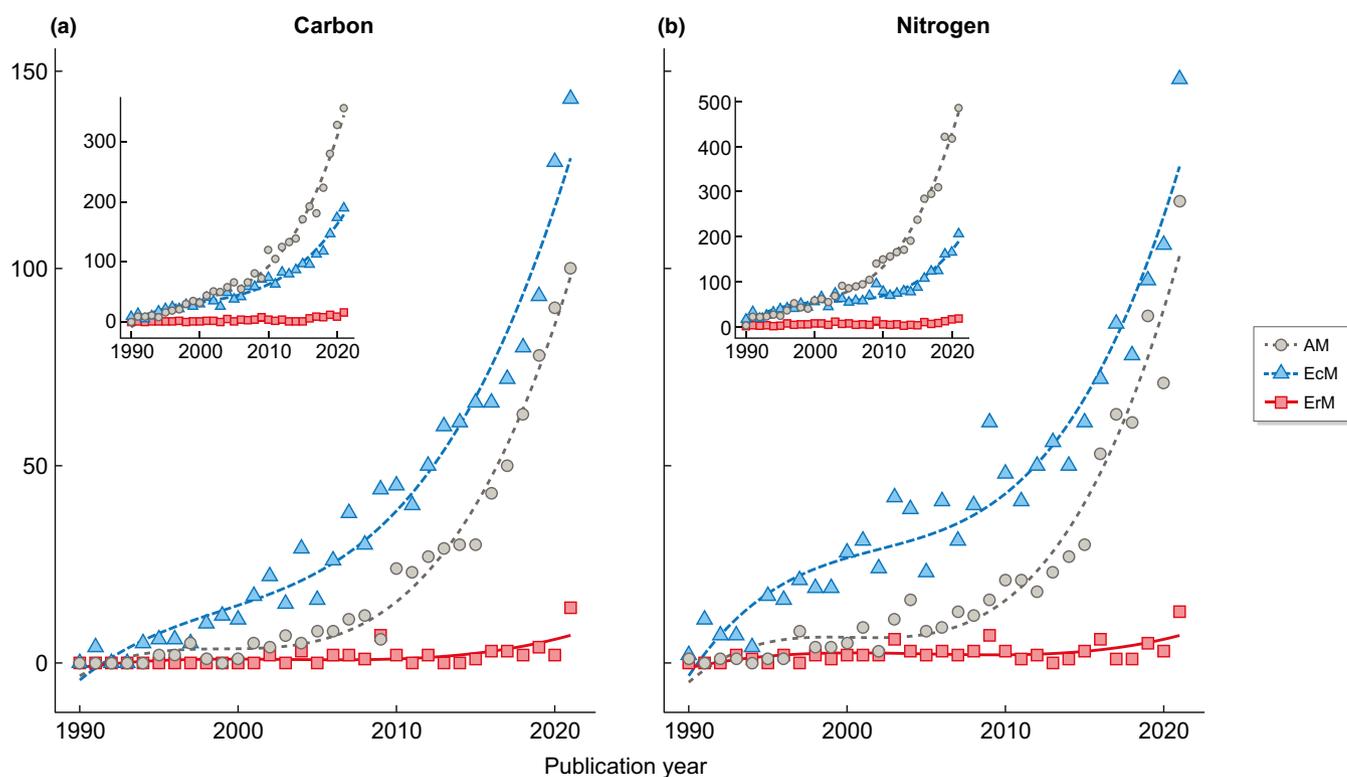
### 1. Extensive organic matter decay capabilities

Of particular relevance to understanding the effects of ErM fungi on C and N dynamics in forests is their extensive saprotrophic capabilities (i.e. ability to degrade organic compounds).

Variation in composition within a forest stand



**Fig. 1** Read (1991) and Read & Perez-Moreno (2003) hypothesized that the relative abundance of arbuscular (AM), ecto- (EcM) and ericoid mycorrhizal (ErM) plants vary predictably across broad, climate-associated gradients of decomposition rates, soil organic matter (SOM) accumulation and inorganic nitrogen (N) limitation owing to differences in plant and fungal functional traits among these groups. Whether similar relationships exist within forest stands in which ErM plants cooccur with AM and/or EcM trees is, however, a relatively unexplored question. Boxes depict the relative importance of different nutrient acquisition strategies under each plant mycorrhizal type: inorganic nutrient uptake (AM and some EcM fungi) and the degradation of organic nutrients (ErM and some EcM fungi). Wedges show the extent to which each trait or condition is hypothesized to differ among the three individual mycorrhizal groups, and the slopes on the wedges show potential variation within each group. Note that interactions between cooccurring understorey ErM shrubs and overstorey AM and/or EcM trees could also alter the magnitude or direction of these effects (Fig. 4). Specifically, the functional effects of ErM plants and fungi could either strengthen, contrast with or be redundant with the effects of cooccurring EcM trees and fungi.



**Fig. 2** The annual number of publications per year reporting arbuscular (gray circles; AM) and ecto- (blue triangles; EcM) mycorrhizal effects on (a) carbon and (b) nitrogen cycling has increased exponentially over the past three decades, whereas publications on ericoid mycorrhizal (ErM) effects (red squares) have remained low and relatively constant. Main plots show publications that included the search term 'forest', and the insets show publications for all ecosystem types. A publication search was conducted on Clarivate Analytics Web of Science for the years 1990–2021 using the search terms 'forest' (for the main plots only) plus 'carbon' or 'nitrogen' plus either 'arbuscular mycorrhiz\*', 'ectomycorrhiz\*' or 'ericoid mycorrhiza\*'. The search included the title, abstract, keywords and KeyWords Plus®, which is an index of terms that appear more than once in cited articles. Trend lines are smoothing splines.

Mycorrhizal fungi differ from free-living saprotrophs in that they primarily obtain C from plant photosynthate rather than from the decomposition of organic matter (Lindahl & Tunlid, 2015; Zak *et al.*, 2019). However, some mycorrhizal fungi possess genes that code for the production of extracellular enzymes involved in organic matter degradation, and the variety and abundance of these genes can be used as traits to characterize and compare the potential saprotrophic capabilities of different species and functional groups (Kohler *et al.*, 2015; Martino *et al.*, 2018; Miyauchi *et al.*, 2020). Some types of mycorrhizal fungi also use a nonenzymatic, oxidative mechanism to mine N from organic matter through the partial degradation of lignocellulose with hydroxyl radicals produced from the reaction of hydrogen peroxide with  $\text{Fe}^{2+}$  (i.e. the Fenton reaction; Shah *et al.*, 2016; Op De Beeck *et al.*, 2018; Nicolás *et al.*, 2019). This mechanism is similar to that used by brown-rot fungi and is retained in EcM species of Boletales that evolved from these wood-decaying saprotrophs (Lebreton *et al.*, 2021).

Whereas AM fungi have little to no organic matter-degrading abilities (Tisserant *et al.*, 2013), saprotrophic capabilities generally increase from EcM to ErM fungi (Read & Perez-Moreno, 2003). The ability of ErM fungi to mobilize N from a variety of organic compounds in plant litter and fungal biomass (e.g. chitin, cellulose, hemicellulose, pectin and polyphenolic compounds) has long been recognized (summarized in Smith & Read, 2008), and recent advances in genomic

sequencing efforts have strengthened this support. Specifically, these studies show that the four sequenced species of ErM fungi (*Oidiodendron maius* Barron, *Meliniomyces bicolor* Hambleton & Sigler, *M. variabilis* Hambleton & Sigler and *Rhizoscyphus ericae* (D.J. Read) Zhuang & Korf) have, on average, a higher number of plant cell wall-degrading enzyme- (PCWDE) coding genes than EcM fungi, and this includes enzymes involved in cellulose, lignin and pectin degradation (Kohler *et al.*, 2015; Martino *et al.*, 2018; Miyauchi *et al.*, 2020). Additionally, at least some ErM fungi can use the Fenton mechanism to degrade lignin (Burke & Cairney, 1998; Cairney & Burke, 1998).

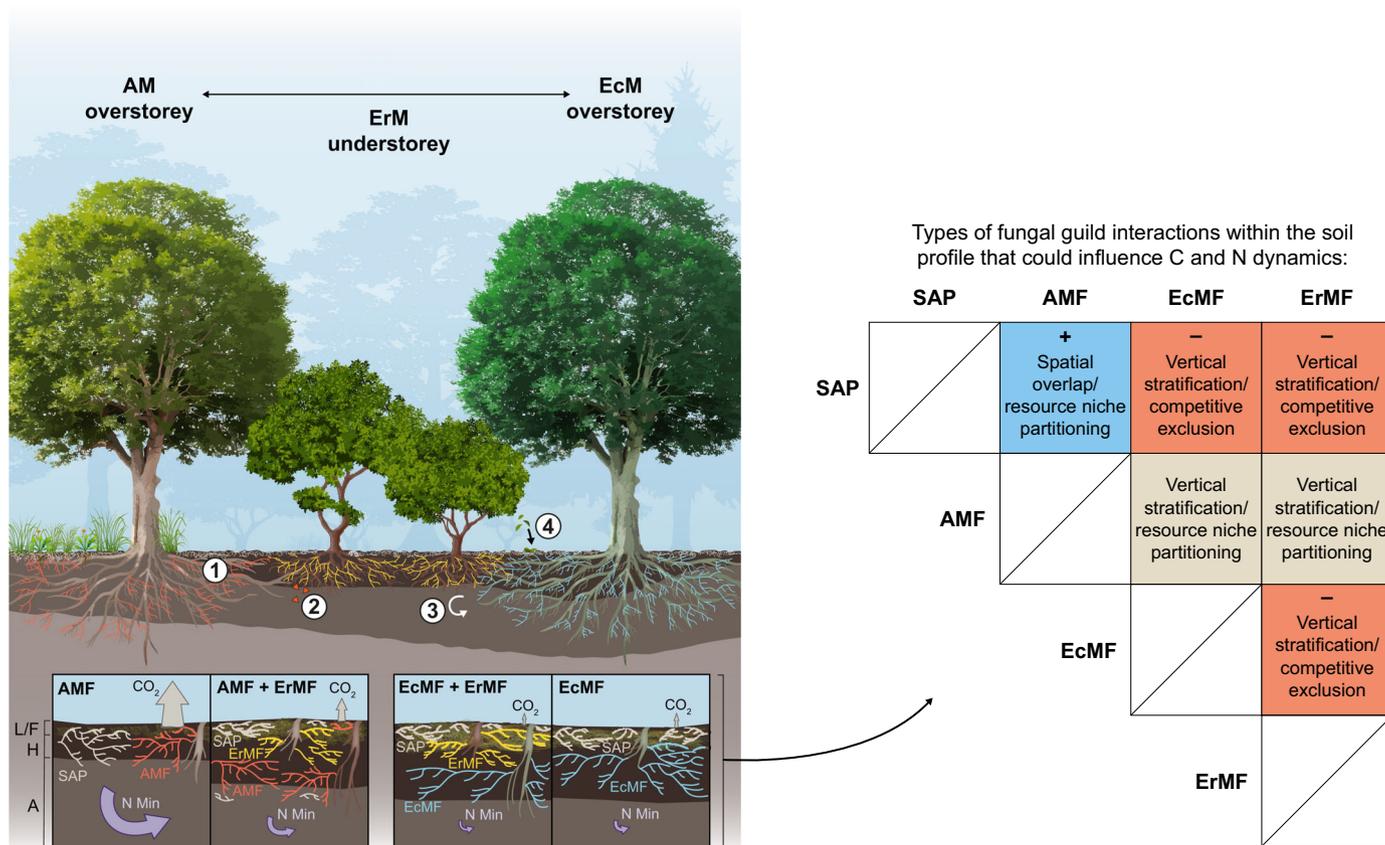
The evolutionary histories of the mycorrhizal groups shed light on differences in their saprotrophic traits. Arbuscular mycorrhizal associations evolved once in early land plants (van der Heijden *et al.*, 2015; Brundrett & Tedersoo, 2018) and function primarily as an extension of the root system by increasing plant access to inorganic nutrients from the soil water solution (Smith & Read, 2008). By contrast, EcM fungi evolved independently more than 80 times from diverse lineages of wood-decaying saprotrophs (Tedersoo & Smith, 2013), and the extent to which they retained genes involved in organic matter degradation varies immensely among individual taxa (Koide *et al.*, 2008; Pellitier & Zak, 2018; Zak *et al.*, 2019; Miyauchi *et al.*, 2020). The evolutionary transitions from saprotrophs to EcM fungi are, however, distinguished



**Fig. 3** Ericoid mycorrhizal plants make up a substantial component of the plant community in many forest types worldwide and often cooccur with other plant mycorrhizal types. Shown are example species for boreal, temperate and tropical forests globally: (a) marsh Labrador tea (*Rhododendron tomentosum* Harmaja), Finland; (b) bilberry (*Vaccinium myrtillus* L.), Ukraine; (c) common heather (*Calluna vulgaris* (L.) Hull), Estonia; (d) salal (*Gaultheria shallon* Pursh), Vancouver, Canada; (e) mountain laurel (*Kalmia latifolia* L.), Connecticut, USA; (f) rosebay rhododendron (*R. maximum* L.), North Carolina, USA; (g) tree rhododendron (*R. arboreum* Sm.), Nepal; (h) tree heather (*Erica trimera* (Engl.) Beentje), Rwenzori Mountain Range, Uganda; (i) tree rhododendron (*R. arboreum* Sm.), Sri Lanka; (j) neinei (*Dracophyllum latifolium* A. Cunn.), New Zealand; (k) *Cavendishia bracteata* (Ruiz & Pav. ex J.St.-Hil.) Hoerold, Ecuador; (l) giant grass tree (*Richea pandanifolia* Hook.f.), Tasmania, Australia. Photograph credits: (a) Ninara under a Creative Commons license CC BY 2.0 (<https://creativecommons.org/licenses/by/2.0/legalcode>); (b) Viacheslav Galievskiy under a Creative Commons license CC BY-SA 4.0 (<https://creativecommons.org/licenses/by-sa/4.0/legalcode>); (c) Urmas Ojango under a Creative Commons license CC BY-NC 2.0 (<https://creativecommons.org/licenses/by-nc/2.0/legalcode>); (d) Lauren ensworth under a Creative Commons license CC BY-SA 4.0 (<https://creativecommons.org/licenses/by-sa/4.0/deed.en>); (e) Elisabeth Ward; (f) James Lendemer; (g) Greg Willis under a Creative Commons license CC BY-SA 2.0 (<https://creativecommons.org/licenses/by-sa/2.0/legalcode>); (h) Albert Backer under a Creative Commons license CC BY-SA 4.0 (<https://creativecommons.org/licenses/by-sa/4.0/legalcode>); (i) © Vyacheslav Argenberg/<http://www.vasoplanet.com/> under a Creative Commons license CC BY 4.0 (<https://creativecommons.org/licenses/by/4.0/legalcode>); (j) Michal Klajban under a Creative Commons license CC BY-SA 4.0 (<https://creativecommons.org/licenses/by-sa/4.0/legalcode>); (k) Andreas Kay under a Creative Commons license CC BY-NC-SA 2.0 (<https://creativecommons.org/licenses/by-nc-sa/2.0/legalcode>); (l) J. J. Harrison/<https://www.jjharrison.com.au/> under a Creative Commons license CC BY-SA 3.0 (<https://creativecommons.org/licenses/by-sa/3.0/legalcode>). All photographs were cropped.

by convergent, widespread losses of PCWDE-coding genes and are therefore, in most instances, characterized by a reduction in genes involved in organic matter degradation (Kohler *et al.*, 2015). Ericoid mycorrhizal fungi also evolved from saprotrophs, but

unlike EcM fungi, they have retained an extensive repertoire of PCWDE-coding genes (Martino *et al.*, 2018). In fact, the number of PCWDE genes in ErM fungi is equal to or larger than that of many other species of soil and litter saprotrophs (Perotto



**Fig. 4** Hypothesized mechanisms through which interactions between ericoid mycorrhizal (ErM) plants and fungi and cooccurring fungal guilds could influence arbuscular (AM) vs ectomycorrhizal (EcM) tree dominance effects on carbon (C) and nitrogen (N) dynamics in forests. As an example of the types of fungal interactions that could potentially influence C and N dynamics, we show four hypothesized ways that ErM plants and fungi (ErMF; yellow) could suppress saprotrophic activity and hence overall organic matter decomposition rates. Numbers within the white circles denote these four hypothesized mechanisms, which are discussed in detail in the text and which collectively serve to increase the size of the surface organic horizons (the litter (L), fermentation (F) and humus (H) horizons) and, in turn, reduce nitrogen mineralization (N Min) rates. The four mechanisms are: (1) competitive interactions with free-living saprotrophs (SAP; white); (2) increased oxidative decomposition mechanisms that make substrates less suitable for hydrolytic decomposition; and the structural and biochemical traits of (3) below- and (4) above-ground plant and fungal inputs (e.g. condensed tannins, melanins). Boxes below the graphic depict how these effects might influence C and N cycling and the vertical partitioning of the soil environment in AM- vs in EcM-dominated stands where ErM plants and fungi cooccur. For instance, if AM fungi (AMF; red) and SAP have facilitative interactions whereas EcM fungi (EcMF; blue) and SAP have competitive interactions, then we would expect the addition of ErMF to have a greater negative effect on saprotrophic activity in AM-dominated stands because they disrupt the facilitative interaction. The matrix to the right of graphic shows hypothesized facilitative (+; blue) and competitive (-; red) pairwise interactions and how they might influence the vertical distribution of cooccurring fungal guilds within the soil profile, further developing mechanism 1. Alternatively, vertical stratification of fungal guilds could result from resource niche partitioning (beige). These hypothesized changes in the vertical distribution of roots and fungi driven by competitive exclusion or niche partitioning could, in turn, influence soil organic matter formation by shifting fungal guilds from organic to surface mineral (i.e. the A-horizon (A)) soil.

*et al.*, 2018). This trend suggests evolutionary pressure to retain – or potentially even enhance – saprotrophic traits (Perotto *et al.*, 2018) and therefore sets ErM fungi distinctly apart from most EcM fungi, which lost PCWDE genes relative to their saprotrophic ancestors (Kohler *et al.*, 2015).

There are several possible explanations for the high number of PCWDE-coding genes in ErM fungi. First, these genes increase the fitness of ErM fungi by enabling them to obtain limiting nutrients through organic matter degradation (Read & Perez-Moreno, 2003). This trait both strengthens their mutualistic partnership with plants, particularly in ecosystems in which nutrients are primarily available in organic forms, and enables ErM fungi to function as both symbiotrophs and saprotrophs

(Read & Perez-Moreno, 2003; Rice & Currah, 2006). Inferential support for this explanation comes from multiple studies showing that ErM fungi can obtain nutrients from a variety of organic compounds in the soil (summarized in Smith & Read, 2008; Wurzbürger & Hendrick, 2009). Second, because ErM fungi have relatively recent evolutionary origins (Schwery *et al.*, 2015; Martino *et al.*, 2018), they could be in a transitional stage from a primarily saprotrophic lifestyle (van der Heijden *et al.*, 2015; Perotto *et al.*, 2018; Genre *et al.*, 2020). Finally, PCWDE genes assist with plant cell wall penetration during ErM colonization of the host plant and therefore have at least some functions unrelated to organic matter degradation (Martino *et al.*, 2018; Genre *et al.*, 2020). Regardless of the extent to which some or all of these

**Box 1** Ericoid mycorrhizal symbioses: an overview of plant and fungal taxonomy.

Of the major mycorrhizal groups, ErM associations have the most recent evolutionary origins and lowest plant and fungal species richness. Ericoid mycorrhizal plants evolved from AM plant ancestors once in the Ericaceae and once in the Diapensiaceae c. 118 million years ago (Schwery *et al.*, 2015; Martino *et al.*, 2018). Overall, ErM plants include c. 4300 species, all of which are in Ericales, and they are dependent on ErM fungi for their nutrition (Brundrett & Tedersoo, 2018). Most species in Ericaceae (c. 93%) form ericoid mycorrhizas except the basal subfamilies, which form AM (Enkianthoideae) and EcM (Arbutoideae, Monotropoideae) associations (Selosse *et al.*, 2007; Freudenstein *et al.*, 2016; Lallemand *et al.*, 2016).

Ericoid mycorrhizal fungi are distinguished from other fungal associates by the formation of intracellular hyphal coils in root epidermal cells (Smith & Read, 2008). These fungi include diverse lineages of Ascomycota (e.g. Helotiales, Chaetothyriales) as well as some Basidiomycota (Selosse *et al.*, 2007; Vohník *et al.*, 2012a; Brundrett & Tedersoo, 2018). Identifying species of ErM fungi is, however, challenging (Leopold, 2016; Vohník, 2020). Ericoid mycorrhizal roots are often colonized by diverse assemblages of fungi, including multiple ErM species as well as endophytes (i.e. fungi in living plant tissue that do not cause symptoms) and other nonmycorrhizal fungi (Perotto *et al.*, 2012; Grelet *et al.*, 2016). Additionally, unlike AM and EcM fungi, many species of ErM fungi are facultative symbionts and can function independently of ErM plants as endophytes or saprotrophs (Rice & Currah, 2006; Smith & Read, 2008). Finally, there is some taxonomic overlap between ErM and EcM fungi (e.g. *Melinomyces* spp.; Villarreal-Ruiz *et al.*, 2004; Grelet *et al.*, 2010; Fehrer *et al.*, 2019), blurring the distinction between a few species in these guilds. Together, these reasons, among others (Leopold, 2016), make the number of ErM fungal species difficult to quantify.

explanations apply, the high number of saprotrophic genes in ErM fungi indicates that they have the potential to be functionally distinct from AM and EcM fungi.

Notably, the greater ability of some EcM fungi to degrade organic matter compared to AM fungi is one of the primary mechanisms thought to drive differences in C and N dynamics across gradients of AM vs EcM tree dominance in forests (Phillips *et al.*, 2013; Tunlid *et al.*, 2016; Frey, 2019; Zak *et al.*, 2019). Differences in organic matter decay capabilities among these mycorrhizal groups appear to influence the quantity and composition of SOM both directly through its degradation and indirectly through interactions with other fungal guilds (Fig. 4; Section III). For instance, competition between EcM fungi and soil saprotrophs for limiting organic N can suppress saprotrophic activity and hence collective decomposition rates, which, in turn, can increase soil C (Gadgil & Gadgil, 1975; Fernandez & Kennedy, 2016). Ectomycorrhizal fungi can also directly influence SOM composition through the targeted degradation of N-bearing molecules (Zak *et al.*, 2019) or by reducing organic C as a by-product of nutrient acquisition (Sterkenburg *et al.*, 2018; Clemmensen *et al.*, 2021; Lindahl *et al.*, 2021; Argiroff *et al.*, 2022). For each of these mechanisms, observed differences in C and N dynamics across

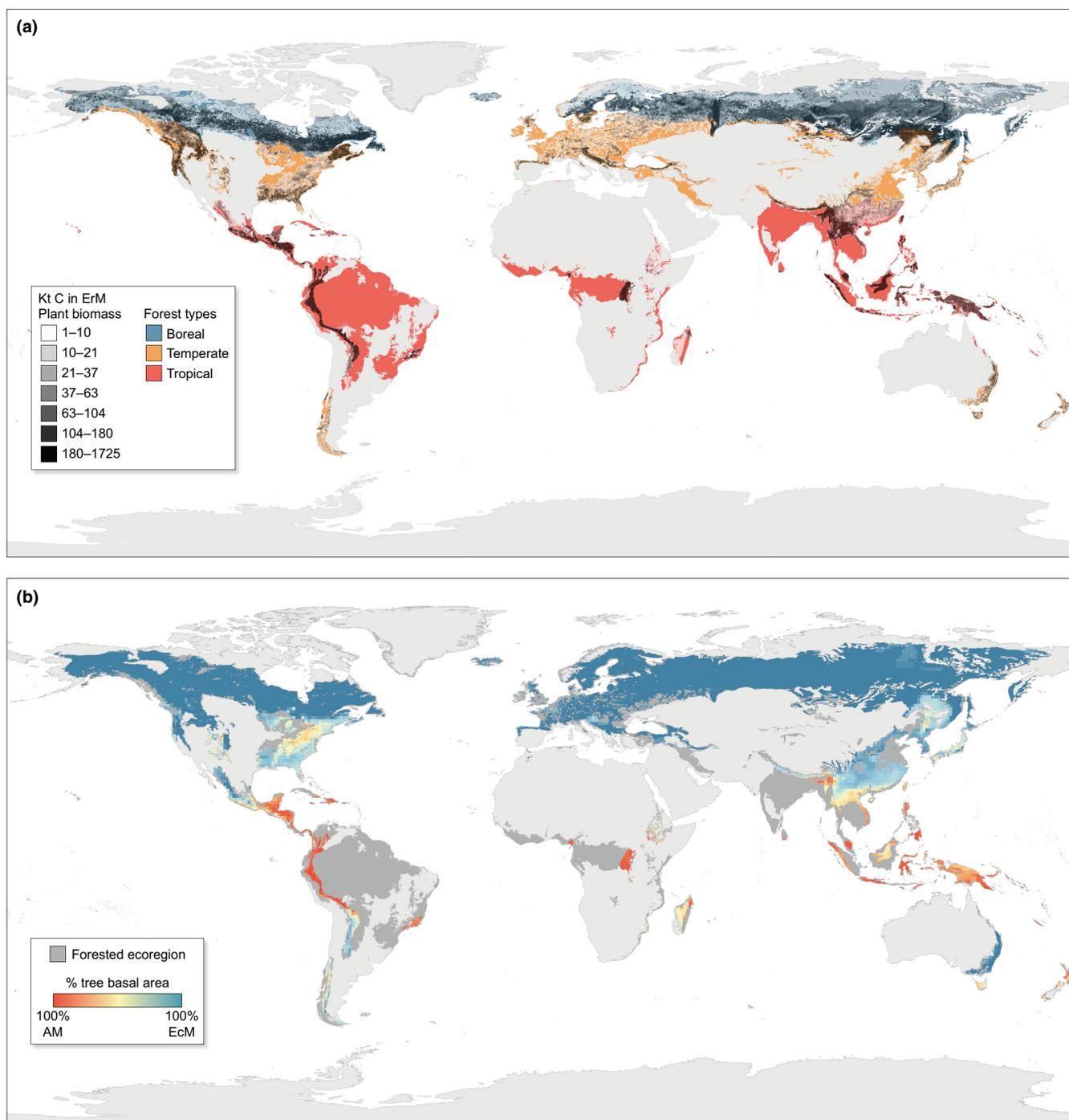
gradients of AM- vs EcM-dominated forests are ascribed, in part, to the differences in the organic matter-degrading abilities of EcM fungi compared to AM fungi. Extending the same logic would then suggest that ErM fungi, which have a higher variety and abundance of genes involved in organic matter degradation (Martino *et al.*, 2018; Perotto *et al.*, 2018; Miyauchi *et al.*, 2020), might also influence C and N dynamics in ways that strengthen EcM effects.

Although ErM fungi have, on average, higher organic matter decay capabilities than EcM fungi, wide variation in saprotrophic traits exists among individual lineages of EcM fungi (Koide *et al.*, 2008; Pellitier & Zak, 2018; Zak *et al.*, 2019). These functional differences within EcM fungi suggest that comparisons of EcM and ErM fungal effects on soil C and N dynamics in forests will probably depend on the characteristics of the individual species of fungi. For instance, several studies have highlighted the importance of ligninolytic EcM fungal taxa that have retained class II peroxidases from white-rot saprotrophs (Bödeker *et al.*, 2009, 2014; Lindahl *et al.*, 2021; Argiroff *et al.*, 2022). Although ascomycetous ErM fungi possess enzymes involved in the degradation of a wide variety of recalcitrant plant substrates, including lignin (Haselwandter *et al.*, 1990; Burke & Cairney, 1998, 2002; Wurzbarger *et al.*, 2012; Miyauchi *et al.*, 2020), they do not possess the enzymes needed to completely mineralize lignin C as is the case for white-rot fungi (Cairney & Burke, 1998; Vohník *et al.*, 2012b). In this instance, particular ligninolytic EcM fungi might enhance organic matter losses, whereas ascomycetous ErM fungi might contribute to its accumulation (Clemmensen *et al.*, 2021; Lindahl *et al.*, 2021). However, one basidiomycetous species of ErM fungus with ligninolytic capabilities has been described (Vohník *et al.*, 2012a), and other taxa could also potentially exist. Additionally – and in contrast to the ErM fungi that have been studied – many EcM fungi have highly reduced repertoires of genes involved in organic matter degradation, including many taxa common in forests (e.g. Boletales, Cantharellales, Russalales, Thelephorales; Lebreton *et al.*, 2021).

The above examples collectively highlight how trait variation within mycorrhizal groups might be as or more important than variation among groups. Individual species of EcM and ErM fungi could therefore have functional effects that either strengthen or contrast with one another. In other words, the degree to which differences in ecosystem C and N dynamics can be distinguished based on the relative abundance of AM, EcM and ErM plants – as well as the direction and magnitude of their overall effect – probably depends on the particular subset of species analyzed (Clemmensen *et al.*, 2021; Lindahl *et al.*, 2021). However, ErM fungi appear to have, on balance, consistently higher saprotrophic capabilities compared to AM and EcM fungi, though a greater number of sequenced species of ErM fungi is required to assess the generality of this trend across the range of fungal taxonomic groups that form ericoid mycorrhizas (Box 1).

## 2. Ecological flexibility and responses to forest disturbance

Ericoid mycorrhizal fungi are also ecologically and morphologically more versatile than AM and EcM fungi, which are obligate mutualists (Grelet *et al.*, 2016; Tedersoo *et al.*, 2020). Beyond



**Fig. 5** Global distribution of aboveground ericoid mycorrhizal (ErM) plant biomass carbon (C; grayscale) in boreal (blue), temperate (orange) and tropical (red) forests (a) and percentage of basal area made up by arbuscular mycorrhizal (AM; red) vs ectomycorrhizal (EcM; blue) trees in forests where ErM plants co-occur (b). Forest type data are from Olson *et al.* (2001), percentage EcM tree basal area data (1-degree resolution) are from Steidinger *et al.* (2019) and aboveground ErM biomass C data (15-arcmin resolution) are from Soudzilovskaia *et al.* (2019). Note that the shading classes for ErM plant biomass C are equal intervals rather than linear to better visualize the spatial extent of ErM plants because a disproportionately large amount of the pixels contain low biomass values.

forming mycorrhizal partnerships, ErM fungi are known to associate with nonErM plants as root endophytes (Bergero *et al.*, 2000; Vohník *et al.*, 2013), form hyphal coils in nonvascular liverworts (Upson *et al.*, 2007), form structures characteristic of dark septate endophytes on a range of plant hosts (Chambers

*et al.*, 2008), form ectomycorrhizas in EcM plants (Grelet *et al.*, 2009, 2010) and function as free-living saprotrophs (Rice & Currah, 2006). Species in the ErM genus *Meliniomyces* can even simultaneously form ectomycorrhizas with *Pinus* and ericoid mycorrhizas with cooccurring *Vaccinium* (Villarreal-Ruiz

**Table 1** Ericoid mycorrhizal (ErM) plants occur in approximately two-thirds of global forest land, c. 90% of which is dominated by EcM trees.

Forest type	Area with ErM plant biomass		Aboveground ErM plant biomass C in:					
	% of forest land area	% under EcM-dominated canopy	EcM-dominated forests		AM-dominated forests		Total per forest type	
			Gt Ca <sup>1</sup>	% of ErM C in all forest types <sup>2</sup>	Gt C <sup>1</sup>	% of ErM C in all forest types <sup>2</sup>	Gt C <sup>1</sup>	% of ErM C in all forest types <sup>2</sup>
Boreal	96.1	100	3.3	54.1	0.0003	0.005	3.3	54.1
Temperate	69.1	93.8	1.3	21.0	0.07	1.2	1.3	22.2
Tropical	29.3	36.7	0.2	3.4	1.2	20.3	1.4	23.7
All types	67.6	89.7	4.7	78.5	1.3	21.5	6.0	100

Most aboveground ErM plant biomass in forests is in EcM-dominated (c. 79%) and boreal (c. 54%) forest types. Yet tropical forests contain over 20% of total forest ErM plant biomass, and most of these forests are AM-dominated. For the area calculations, we used the Equal Earth map projection (Šavrič *et al.*, 2019) to estimate the area of all pixels (15-arcmin resolution) from the ErM plant biomass C dataset (Soudzilovskaia *et al.*, 2019) with values greater than zero. We classified EcM-dominated forests as pixels (1-degree resolution) with > 50% EcM tree basal area and AM-dominated forests as pixels with > 50% AM tree basal area (Steidinger *et al.*, 2019). Forest types include boreal forest/taiga in the boreal forest type; temperate broadleaf and mixed forests and temperate conifer forests in the temperate forest type; and tropical and subtropical coniferous forests, tropical and subtropical dry broadleaf forests, and tropical and subtropical moist broadleaf forests in the tropical forest type (Olson *et al.*, 2001). See Supporting Information Table S1 for the area calculations.

<sup>1</sup>Shown are estimates for ErM plant aboveground biomass carbon (C) stocks for boreal, temperate and tropical forests, delineated by areas with AM- vs EcM-dominated overstories.

<sup>2</sup>Shown are the percentages of ErM aboveground biomass C in each forest type out of total ErM aboveground biomass C in all forest types.

*et al.*, 2004; Grelet *et al.*, 2010). Despite some taxonomic overlap between ErM and EcM fungi (Fehrer *et al.*, 2019; Box 1), the ecological and morphological versatility of ericoid mycorrhizal-forming fungi differentiate them from most EcM fungi, which are obligate symbionts with more specialized plant partnerships.

The ability of ErM fungi to assume multiple ecological lifestyles and affiliate with a range of plant hosts could help them better respond to adverse and/or changing conditions compared to more specialized mycorrhizal groups (Bergero *et al.*, 2003; Durall *et al.*, 2005). As facultative symbionts with low host-plant specificity (Walker *et al.*, 2011), ErM fungi are less reliant on contemporary plant C inputs than more specialized, obligate symbionts, such as EcM fungi (Durall *et al.*, 2005; Tedersoo, 2015). As such, ErM fungi may be more resilient to losses in the photosynthetic capacity of their host plants caused by forest disturbances. Evidence also suggests that ErM fungi are less dispersal-limited than obligate symbiotrophs, such as EcM fungi, since they can be present in the soil in the absence of ErM plants (Bergero *et al.*, 2003; Vohník *et al.*, 2013; Tedersoo *et al.*, 2020). This trait may favor early-successional ErM plants over more dispersal-limited EcM plants following disturbance. Forest disturbances that increase the quantity of decomposing plant matter on the forest floor (e.g. windstorms) may also favor vegetation associated with mycorrhizal groups that can access organic nutrients through saprotrophic functions (Tedersoo, 2015). For instance, Kohout *et al.* (2021) found that the abundance of ErM fungi increased on decomposing tree roots following the experimental cutting of spruce seedling shoots.

Numerous studies have shown that canopy disturbances (e.g. logging) increase the abundance of saprotrophs and decrease the abundance of EcM fungi (Lindahl *et al.*, 2010; Štursová *et al.*, 2014; Mushinski *et al.*, 2018). Yet unlike EcM fungi, the abundance and/or diversity of ErM fungi often persists or even increases along with saprotrophic fungi in response to disturbance.

For instance, Chen *et al.* (2019) observed a higher relative abundance of ErM fungi following a tropical forest clear-cut. Likewise, in response to canopy tree mortality from a bark beetle infestation at a forest in Central Europe, ErM fungi remained present while the abundance of EcM fungi declined (Štursová *et al.*, 2014). In some instances, the persistence of ErM fungi may indicate that the disturbance did not damage understorey vegetation to the same extent as overstorey EcM trees. However, even in the absence of ErM plants, ErM fungi can exhibit a flexible ecological lifestyle that could help explain their relative success following forest disturbances (Bergero *et al.*, 2003; Vohník *et al.*, 2013). For example, Mushinski *et al.* (2018) found that the relative abundance of ErM fungi increased following removal of the surface organic horizon by timber harvesting despite the fact that ErM plants were not present at the site.

Like their fungal symbionts, some ErM shrubs also increase in abundance following forest disturbances (Mallik, 2003; Royo & Carson, 2006). For instance, loss of the American chestnut (*Castanea dentata* (Marsh.) Borkh.) and mortality of eastern hemlock (*Tsuga canadensis* (L.) Carrière) from invasive pests and pathogens are thought to have promoted the growth of the ErM shrub *Rhododendron maximum* L. (Fig. 3f) in southeastern US forests (Vandermaast & Van Lear, 2002; Ellison *et al.*, 2005). Mountain laurel (*Kalmia latifolia* L.; Fig. 3e), salal (*Gaultheria shallon* Pursh; Fig. 3d) and many other ErM plants also proliferate following timber harvesting in temperate and boreal forests in Europe and North America (Mallik, 2003; Joannis *et al.*, 2018). Additionally, many ErM plants in Neotropical montane forests have modes of reproduction, such as rhizomatous root systems, that allow them to rapidly colonize and establish in recently disturbed sites (Luteyn, 2002, 2004). Setaro & Kron (2011) hypothesized that severe storms may have facilitated the comigration of plants in Vacciniaceae (a tribe within Ericaceae) with their fungal symbionts from North America to Neotropical forests via islands, suggesting

that adaptations to disturbance may have favored the long-distance dispersal of these plants and fungi. Together, these studies show that some ErM plants and fungi can take advantage of forest canopy disturbances, many of which are increasing in frequency and severity due to anthropogenic changes (e.g. severe storms, fire, logging, loss of canopy species due to invasive species).

### 3. Structural and biochemical traits of plant and fungal tissues

In addition to their extensive organic matter-degrading abilities and ecological flexibility, ErM plants and fungi have distinct physical and biochemical litter traits that could favor organic matter accumulation and N limitation in forests. Because ErM plants are adapted to N-limited ecosystems, they tend to have more nutrient-conservative traits compared to AM and some EcM plants. Nutrient-conservative plant traits include low root and foliar nutrient concentrations (i.e. wide C : N), high nutrient resorption rates, and thick, persistent leaves (Michelsen *et al.*, 1998; Cornelissen *et al.*, 2001; Meers *et al.*, 2010; Schwery *et al.*, 2015; Xu *et al.*, 2020; Weigelt *et al.*, 2021). These traits are, in turn, associated with slower rates of leaf (Cornelissen *et al.*, 2001; Xu *et al.*, 2020; Clemmensen *et al.*, 2021), fine root (See *et al.*, 2019) and fungal biomass (Clemmensen *et al.*, 2015) decomposition compared to other mycorrhizal types.

One particularly important mechanism through which ErM plants and fungi contribute to organic matter accumulation and inorganic N limitation is through the production of secondary compounds in plant and fungal tissues. These include polyphenolic compounds (e.g. condensed tannins) in fine roots and leaves (Aerts, 2003; Joannis *et al.*, 2007; Wurzbürger & Hendrick, 2009; Adamczyk *et al.*, 2016) as well as melanin in fungal biomass (Clemmensen *et al.*, 2015). Melanins contribute to SOM accumulation because they constitute the recalcitrant fraction of fungal necromass and therefore regulate its decomposition and turnover (Fernandez & Koide, 2014; Fernandez *et al.*, 2019). A comparative genomic analysis found that ErM fungi possess a higher number of genes involved in melanin biosynthesis compared to other fungal guilds (Martino *et al.*, 2018). Indeed, in boreal forests, melanization of fungal mycelia is one of the primary mechanisms through which ErM fungi are thought to promote SOM accumulation relative to EcM fungi, which have more rapid mycelial turnover (Clemmensen *et al.*, 2015; Sterkenburg *et al.*, 2015; Lindahl & Clemmensen, 2016).

Plant-derived tannins also strongly regulate N cycling in forests by inhibiting microbial activity and binding with organic N to form persistent complexes with proteins and chitin in the soil (Northup *et al.*, 1995; Kraus *et al.*, 2003; Joannis *et al.*, 2007; Adamczyk *et al.*, 2019a). These tannin–organic N complexes reduce SOM decomposition rates and restrict N mineralization, thereby favoring the build-up of organic N and strongly limiting inorganic N availability (Kraus *et al.*, 2003). Notably, at least some ErM fungi possess the enzymes needed to mobilize N from the recalcitrant protein–tannin complexes formed through ErM foliar and root litter inputs (Leake & Read, 1990; Bending & Read, 1996; Joannis *et al.*, 2009; Wurzbürger & Hendrick, 2009). As such,

high concentrations of polyphenolic compounds in ErM plant litters are thought to promote the growth of ErM plants through a positive feedback mechanism by creating conditions under which ErM fungi are better competitors for soil nutrients than other fungal guilds (Aerts, 2003; Mallik, 2003; Joannis *et al.*, 2007; Wurzbürger & Hendrick, 2009). Indeed, many ErM plants can form persistent, monodominant layers in a range of forest types worldwide (Fig. 3). Likewise, the invasive status of several ErM plants (e.g. *Calluna vulgaris* (L.) Hull and *Rhododendron ponticum* L.; ISSG, 2013) could be partially explained by the creation of recalcitrant protein–tannin complexes that generate severe N limitation for plants that lack ErM fungi.

Although the humification and selective preservation models of SOM persistence have been refuted (Lehmann & Kleber, 2015), the initial biochemical traits of plant and fungal inputs – along with products arising through their decomposition – might increase the mean residence time of surface SOM pools, thereby favoring SOM accumulation under ErM plants relative to other plant mycorrhizal types (Adamczyk, 2021). For instance, ErM plants generally have higher concentrations of aromatic macromolecules, such as polyphenolic compounds and lignin, whose oxidative decomposition creates substrates with progressively more random molecular structures. These structural changes interfere with saprotrophic decomposition mediated by hydrolytic enzymes, which catalyze the decomposition of compounds with regularly ordered molecular structures (Lindahl & Clemmensen, 2016; Sterkenburg *et al.*, 2018). As such, the association of ErM fungi with high activities of oxidative enzymes (Wurzbürger & Hendrick, 2007, 2009), together with high input rates of compounds such as polyphenols, suggests that oxidative decomposition products probably accumulate in the presence of ErM plants and fungi. This SOM accumulation mechanism could be especially important in boreal forests with mineral-free soil horizons and high quantities of oxidized organic matter with long mean residence times (Lindahl & Clemmensen, 2016).

In addition to influencing overall SOM accumulation in surface organic horizons, the structural and biochemical traits of ErM plant and fungal tissues also probably affect the relative formation rates of SOM fractions with different turnover times. Specifically, more recalcitrant ErM plant and fungal tissues probably favor the build-up of particulate SOM fractions, which have a faster mean turnover time and hence shorter persistence (all else being equal) than mineral-associated fractions (Heckman *et al.*, 2022). In particular, the production of microbial residues (e.g. secondary products and necromass) is a dominant pathway by which C and N are transferred from particulate to mineral-associated SOM pools (Miltner *et al.*, 2012; Liang *et al.*, 2017), and the formation of these residues is dependent on the growth efficiencies of microbes on different organic compounds. Thus, the amount of C retained within microbial biomass vs respired as CO<sub>2</sub> (i.e. the growth efficiency) influences the proportion of decomposing inputs that can potentially persist in the longer term as mineral-associated SOM (Sokol *et al.*, 2019). Because microbial growth efficiencies tend to be higher on more labile substrates (Cotrufo *et al.*, 2013, 2015), higher quality AM plant and fungal litter inputs (Averill *et al.*, 2019; Keller & Phillips, 2019) could increase mineral-

associated SOM formation compared to inputs from EcM and ErM plants and fungi (Craig *et al.*, 2018; Cotrufo *et al.*, 2019). Therefore, the accumulation of particulate over mineral-associated SOM could make SOM stocks under ErM plants more vulnerable to loss under future disturbances, such as warming (Lehmann & Kleber, 2015; Cotrufo *et al.*, 2019; Lavalley *et al.*, 2020).

However, given the multiple mechanisms that contribute to SOM persistence, the directionality of the effects of ErM plant and fungal traits remains unclear. For instance, interactions between plant and fungal litter inputs are thought to increase the longer-term persistence of particulate SOM through the formation of tannin–organic N complexes (Clemmensen *et al.*, 2013, 2015; Adamczyk *et al.*, 2019b; Adamczyk, 2021). Further, and in contrast to the growth efficiency–recalcitrance relationship that favors the flow of more labile substrates via the microbial biomass to mineral surfaces, both labile and recalcitrant components of fungal necromass can sorb directly to mineral surfaces efficiently (See *et al.*, 2021). Fungal melanins, for instance, can persist in the soil for long timeframes, and evidence suggests that they probably interact with mineral surfaces (Fernandez *et al.*, 2019; Frey, 2019; See *et al.*, 2022). The high rates of melanization of ErM fungal mycelia when compared to EcM and AM fungi may therefore stimulate formation rates of persistent, mineral-associated SOM.

Together, the distinct biochemical traits of ErM plant and fungal tissues, as well as the efficiency and oxidative mechanisms by which ErM fungi break down these inputs, suggest that ErM effects on SOM formation rates and persistence will probably differ from AM and EcM effects. Yet further work is needed to resolve how ErM plants and fungi might influence overall soil C and N stocks and their persistence in the range of forest biomes in which they occur. In particular, the progressively lower qualities of AM, EcM, and ErM plant and fungal inputs suggest that ErM effects could strengthen the effects of EcM plants and fungi on particulate SOM accumulation. Such effects could be further augmented by interactions between distinct ErM biochemical traits and free-living saprotrophs, such as those mediated via high condensed tannin inputs that suppress free-living saprotrophic activity (Joanisse *et al.*, 2007). Next, we discuss how these fungal guild interactions could potentially influence C and N cycling and storage in the presence and absence of understorey ErM plants and their fungal symbionts (Fig. 4).

### III. Exploring interactive effects between ErM fungi and cooccurring fungal guilds

Competition, facilitation or niche partitioning between ErM fungi and other cooccurring fungal guilds could also influence SOM formation (Fernandez & Kennedy, 2016; Verbruggen *et al.*, 2017), and these effects could be different in AM- vs EcM-dominated forest stands (Fig. 4). Most of these hypothesized interactions have yet to be fully explored but are important areas of future research in forests where ErM fungi cooccur with AM, EcM and saprotrophic fungi. For instance, competition for resources and/or niche partitioning can cause vertical stratification of fungal guilds across gradients of substrate quality and abiotic conditions within the soil profile (Lindahl *et al.*, 2007; Clemmensen

*et al.*, 2015; Bödeker *et al.*, 2016; Sterkenburg *et al.*, 2018; Fig. 4). In particular, the relative abundance of free-living saprotrophs is often higher in the litter layer, whereas mycorrhizal fungi are more predominant in deeper organic horizons that are more enriched in N relative to C (Lindahl *et al.*, 2007; Clemmensen *et al.*, 2015; Bödeker *et al.*, 2016; Carteron *et al.*, 2021). The cooccurrence of multiple mycorrhizal types with different functional traits could strengthen differences in the depth distributions of fungal guilds and, consequently, their associated roots. For instance, Persson (1983) found that in the absence of ErM shrubs, EcM fine roots were most abundant in the upper organic horizons but that they shifted deeper into the humus–mineral soil transition zone in the presence of ErM fine roots. Likewise, Genney *et al.* (2000) found that ErM fine roots and fungi excluded AM grass roots from the organic horizon, driving them deeper into the surface mineral soil.

Competition-driven shifts in the depth distribution of roots associated with different mycorrhizal types could, in turn, influence mineral-associated SOM persistence. Depth is a strong predictor of SOM persistence for many reasons (Rumpel & Kögel-Knabner, 2011; Heckman *et al.*, 2022). Depending on the soil type, deeper horizons can have higher concentrations of clay surfaces that provide more binding area for mineral-associated SOM formation (Ahrens *et al.*, 2020). Facilitative interactions between AM fungi and saprotrophs that enhance rhizosphere deposition in deeper horizons could therefore increase sorption of low-molecular-weight C compounds to mineral surfaces (Craig *et al.*, 2018; Frey, 2019). Likewise, the production and turnover of fungal hyphae in deeper soils could also increase mineral-associated SOM formation because fungal necromass is a major component of the mineral-associated fraction (See *et al.*, 2022). Competitive exclusion of AM and/or EcM fine roots and fungi from the organic horizon by the presence of ErM roots and fungi could therefore enhance mineral-associated SOM formation. Alternatively, because saprotrophic activity is more energy-limited in deeper soils (Ahrens *et al.*, 2020), rates of mineral-associated SOM formation may be reduced in the presence of ErM plants and fungi. Specifically, this energy limitation could decrease production of microbial necromass and secondary products, which are dominant precursors for mineral-associated SOM formation (Sokol *et al.*, 2019). Although there is currently no empirical work assessing how changes in the depth distribution of roots and fungi in the presence of ErM plants affect SOM formation and persistence in mineral soils, it could, theoretically, be consequential for forest soil C stocks.

The cooccurrence of ErM shrubs in the understorey of AM- vs EcM-dominated stands could also influence SOM dynamics through interactions with saprotrophic fungi (Fig. 4; Verbruggen *et al.*, 2017). Specifically, high concentrations of condensed tannins in ErM leaf and root litter inputs might suppress microbial activity (Joanisse *et al.*, 2007), thereby reducing SOM decomposition and hence favoring its accumulation. Additionally, N retention in ErM fungal mycelia could also suppress microbial activity by exacerbating N limitation (Clemmensen *et al.*, 2015, 2021; Lindahl & Clemmensen, 2016). Finally, as oxidative decomposition mechanisms become increasingly prevalent in

deeper organic horizons, substrates may become less suitable for hydrolytic decomposition, which could further restrict saprotrophic activity (Lindahl & Clemmensen, 2016).

Each of these mechanisms could theoretically slow organic matter decomposition rates by suppressing saprotrophic activity and favoring SOM accumulation. These mechanisms are similar to the Gadgil effect, which predicts that EcM fungi can outcompete free-living saprotrophs for soil resources and hence reduce decomposition rates (Gadgil & Gadgil, 1975; Fernandez & Kennedy, 2016). Given that ErM fungi, like EcM fungi, also have extensive saprotrophic capabilities, they too could compete with free-living saprotrophs for organic nutrients, which could heighten the Gadgil effect and therefore strengthen EcM effects. Additionally, Kohout *et al.* (2010) found that the presence of ErM shrubs and fungi altered the composition of the EcM fungal community, setting up the possibility that the effects of within-guild variation in the saprotrophic capabilities of EcM fungi could be mediated by ErM plant and fungal abundance. Collectively, then, there appear to be multiple plausible pathways – all of which require empirical testing – through which ErM plants and fungi could modify forest soil C and N dynamics via interactions with other fungal guilds (Fig. 4).

#### IV. Global distribution of ErM plants in forests

The potential for ErM effects to differ in forests dominated by AM vs EcM trees could have consequences for the effects of ErM plants and fungi on C and N dynamics across different forest biomes globally. In particular, given latitudinal variation in the relative abundance of AM vs EcM trees – with AM trees becoming increasingly dominant in tropical forests and EcM trees in boreal forests (Steidinger *et al.*, 2019) – we might expect the effects of ErM plants to differ between these forest types. Likewise, variation in AM vs EcM tree dominance within these forest types (e.g. along elevational gradients) could also alter ErM effects. We therefore assessed the distribution and abundance of ErM plants in boreal, temperate and tropical forests globally as well as the extent to which they cooccur with AM and EcM trees. To do this, we used data on aboveground ErM plant biomass C (Soudzilovskaia *et al.*, 2019), global forest types (Olson *et al.*, 2001) and AM vs EcM tree basal area (Steidinger *et al.*, 2019). Given the coarse spatial grain of the aboveground ErM plant biomass C dataset (15-arcmin resolution), this analysis probably overestimates the area in which ErM plants are present in global forests. Nevertheless, this dataset is the most comprehensive available for ErM plant biomass at the global scale and so provides a reasonable basis from which to assess broad patterns in their distribution to serve as a starting point for future finer-scale work. For the full methods, see Supporting Information Methods S1.

Overall, we found that ErM plants occur in about two-thirds of the world's forest land and that *c.* 80% of aboveground ErM plant biomass is in EcM-dominated forests (Fig. 5; Table 1). The abundance and distribution of ErM plants are highest in boreal forests dominated by EcM trees followed by temperate and tropical forests, which have increasing proportions of AM tree basal area (Table 1). These results are therefore consistent with previously

described associations between AM, EcM and ErM plants and broad latitudinal gradients of climate-associated organic matter decomposition rates (Read, 1991; Read & Perez-Moreno, 2003; Soudzilovskaia *et al.*, 2019; Steidinger *et al.*, 2019). More specifically, boreal forests contain over half of all aboveground ErM plant biomass in forests, and ErM plants are present in *c.* 96% of boreal forest land area, virtually all of which is EcM-dominated (Table 1). In temperate and tropical forests, ErM plants occur in *c.* 70 and 30% of the land area, respectively, and each of these forest types includes about 20% of the total ErM plant biomass C (Table 1). As in boreal forests, the vast majority of ErM plant biomass C in temperate forests is in EcM-dominated stands (Fig. 5; Table 1). In tropical forests, however, most ErM plant biomass is in AM-dominated stands, and this stock constitutes *c.* 20% of all ErM plant biomass in forests globally (Fig. 5; Table 1).

Thus, although ErM plants generally have the highest abundance and most extensive distribution in high-latitude boreal forests dominated by EcM trees (Soudzilovskaia *et al.*, 2019; Table 1), they are also common in many temperate and tropical forests with higher abundances of AM trees (Figs 3, 5; Luteyn, 2002, 2004; Mallik, 2003; Kohout, 2017). Given that ErM plant and fungal effects on soil C and N cycling and storage can differ in AM- vs in EcM-dominated stands (Fig. 4; Ward *et al.*, 2021), this finding has important implications for potential variation in ErM effects across forest biomes globally. Namely, because the ecosystem biogeochemical effects of subdominant species can be more pronounced for species with higher functional trait divergence compared to the dominant species (Spehn *et al.*, 2002; Kuebbing & Bradford, 2019), the effects of understorey ErM plants could be greater in AM- than in EcM-dominated forest types. Whereas ErM and EcM plants and fungi both have traits associated with organic nutrient acquisition and hence are often associated with higher SOM, AM plants and fungi have traits specialized for mineral nutrient uptake and are therefore commonly associated with faster organic matter decomposition rates and higher inorganic N availability (Fig. 1; Read, 1991; Read & Perez-Moreno, 2003; Phillips *et al.*, 2013). The cooccurrence of understorey ErM plants with overstorey AM trees could therefore enhance SOM accumulation to a greater extent than they would under EcM trees. Indeed, an observational study conducted across an AM to EcM tree dominance gradient within a temperate forest found that understorey ErM shrubs had a greater effect on SOM and soil C and N concentrations in stands with a higher relative abundance of AM trees (Ward *et al.*, 2021). Whether similar variation in ErM plant and fungal effects occurs across different global forest types that vary in AM vs EcM tree dominance is an open question requiring further empirical work.

In addition to highlighting latitudinal variation in the distribution and abundance of ErM plants across different forest types, our analysis also affirms previously described elevational gradients within forests (Fig. 5). In tropical forests, for instance, ErM plants are largely restricted to montane regions (Fig. 5), some of which have among the highest ErM plant diversity in the world (Luteyn, 2002; Schwery *et al.*, 2015; Kohout, 2017). Several tropical montane forest regions are also dominated by ErM trees, such as tree rhododendrons (e.g. *Rhododendron arboreum* Sm.; Fig. 3g,i)

and tree heathers (e.g. *Erica trimera* (Engl.) Beentje; Fig. 3h), further emphasizing the importance of ErM plants in these ecosystems. Like boreal and temperate forests, tropical montane forests are characterized by humid climates and acidic soils with higher SOM compared to the weathered, nutrient-poor soils of lowland tropical forests (Luteyn, 2002; Kohout, 2017). Although EcM-dominated tropical forests also exist (Corrales *et al.*, 2018; Weemstra *et al.*, 2020), most tropical ErM plants appear to occur in AM-dominated stands (Fig. 5; Table 1). Classifications of tropical montane forests by AM vs EcM tree associations alone could therefore underestimate surface organic matter stocks in areas with ErM plants, and this could have implications for estimates of soil C stocks at the global scale. However, many tropical ErM plant species in these regions are also epiphytic (e.g. c. 50% of Neotropical Ericaceae; Luteyn, 2004) because ErM fungi can access organic nutrients from litter deposits in tree crevices (Luteyn, 2002; Rains *et al.*, 2003), and these arboreal species are unlikely to influence soil conditions. The extent to which high ErM plant abundance and diversity in tropical montane forests affect soil C and N dynamics is therefore less clear than their geographic distribution might suggest.

## V. Review of empirical work on ErM plant and fungal effects on forest C and N dynamics

Given the extensive distribution of ErM plants across global forests that vary in AM and EcM tree dominance (Fig. 5; Table 1), we reviewed empirical literature on ErM plant and fungal effects on forest C and N dynamics to evaluate how they might influence AM and EcM tree effects in boreal, temperate and tropical forest types. Through this synthesis, we found a discrepancy between the relatively large number of studies on ErM plant and fungal functional traits (reviewed in Section II) and the paucity of work that has directly measured their soil biogeochemical effects. Specifically, we found 25 publications with data on the effects of ErM plant or fungal abundance on belowground C and N processes in forests (Tables S2, S3). Owing to the low number of studies on this topic, we could not perform a meaningful metaanalysis and instead summarized the findings in Table 2. For the full literature search methods, see Methods S2, and for the lists of publication see Tables S2 and S3.

The geographic distribution of empirical work on ErM functional effects closely aligns with their abundance and distribution in forests globally (Fig. 5; Table 1). Specifically, most work on ErM effects on forest C and N dynamics has been conducted in boreal forests dominated by EcM trees. Of the 25 studies, about two-thirds were from boreal forests (16 out of 25), with the remainder from temperate forests (nine out of 25) and zero from tropical forests (Tables 2, S3). Similarly, over three-quarters were from EcM-dominated forests (19 out of 25), about one-quarter from forests with both AM and EcM trees (six out of 25), and zero from AM-dominated forests (Tables 2, S3). Given the positive association between ErM and EcM plant abundance in temperate forests (Ward *et al.*, 2021) and the extent to which ErM plants dominate boreal forest understories (Fig. 5; Table 1), these trends are to be expected. However, they also highlight a need to fill knowledge gaps on ErM plant and fungal effects on forest C and N

dynamics to ensure that research on this topic is representative of the global diversity of ErM plants and fungi and the forested ecosystems they inhabit (Leopold, 2016; Albornoz *et al.*, 2021). For instance, similar to previous work on the ecology and taxonomy of ErM fungi (Grelet *et al.*, 2016; Leopold, 2016; Bruzone *et al.*, 2017; Kohout & Tedersoo, 2017; Vohník, 2020; Albornoz *et al.*, 2021), as well as in ecology more broadly (Martin *et al.*, 2012; Bennett & Classen, 2020), our literature review highlights a strong Northern Hemisphere sampling bias (Table S3). Therefore, despite the high abundance and diversity of ErM plants in montane tropical forests (Fig. 5; Luteyn, 2002, 2004; Schwery *et al.*, 2015; Kohout, 2017), as well their occurrence in seasonally dry, nutrient-poor forests in Australia (Chambers *et al.*, 2008; Meers *et al.*, 2010), these ecosystems remain understudied relative to forests in northern latitudes.

Despite the relatively low number of studies on ErM functional effects (Fig. 2), our literature synthesis reveals some common trends for boreal and temperate forests. For example, inorganic N availability – as well as the processes that generate these nutrient forms (e.g. net N mineralization) – are generally lower when ErM plants and fungi are present (Tables 2, S3). Additionally, hydrolytic enzyme activity is more often suppressed in the presence of ErM plants and fungi, and two studies found elevated oxidative enzyme activity in association with ErM plants (Tables 2, S3). Total surface soil C and N concentrations and stocks, as well as soil C:N, are also generally higher in the presence of ErM plants and fungi (Tables 2, S3). Therefore, despite the relatively sparse availability of empirical evidence on the functional effects of ErM plants and fungi in forests, the data that exist generally support expectations of hypothesized ErM effects based on our review of their traits (Section II).

Notably, however, our synthesis also highlights some discrepancies. Across different studies, there were often an equal number of positive and neutral or negative and neutral results for the effects of ErM plants and/or fungi on a single soil variable (Table 2). This finding could, in part, be caused by our use of reported statistical significance to categorize soil responses. Because this approach prioritizes precision rather than effect sizes, biologically meaningful changes could have been scored as neutral (Bradford *et al.*, 2021). However, these results also raise the possibility that ErM plant and fungal effects are context-dependent and vary in, for instance, AM- and EcM-dominated stands, different forest biomes, or in relation to different fungal guilds or species. Overall, however, there are insufficient data to assess the nature of these contingent results and hence how ErM plants and fungi might influence the direction and/or magnitude of AM and EcM tree effects. Instead, our review highlights a need for further consideration of ErM effects within and among forest biomes – and especially in AM-dominated forests – to improve understanding of how co-occurring mycorrhizal types interact to collectively affect soil carbon and nitrogen dynamics.

## VI. Concluding remarks

The prevailing framework for understanding mycorrhizal effects on forest C and N dynamics weights the importance of trait

**Table 2** Summary of results from empirical studies on the effects of ericoid mycorrhizal (ErM) plants and fungi on soil organic matter (SOM), carbon (C) and nitrogen (N) dynamics in forests.

Soil C or N process	No. of publications			Direction of ErM effect		
	Boreal	Temperate	Tropical	Positive	Neutral	Negative
SOM stocks <sup>1</sup>	3	1	0	3	1	0
Total C concentrations <sup>2</sup>	3	4	0	6	3	2
Total N concentrations and stocks <sup>3</sup>	7	6	0	11	8	5
C : N	5	6	0	9	6	1
N availability <sup>4</sup>	10	5	0	4	22	26
C availability <sup>5</sup>	0	1	0	0	1	0
Microbial biomass <sup>6</sup>	3	3	0	5	3	2
Heterotrophic soil respiration <sup>7</sup>	4	0	0	2	3	1
Litter decomposition rate	3	1	0	1	2	2
C-targeting, hydrolytic enzyme activity <sup>8</sup>	4	2	0	0	18	5
N-targeting, hydrolytic enzyme activity <sup>9</sup>	3	3	0	1	9	6
SOM-targeting, oxidative enzyme activity <sup>10</sup>	3	1	0	2	7	0

In total, we found 25 publications, which included 16 from boreal forests, nine from temperate forests and zero from tropical forests. Sixteen of these studies were from ectomycorrhizal (EcM)-dominated forests, nine were from forests with both arbuscular mycorrhizal (AM) and EcM trees, and zero were from AM-dominated forests. Darker shades on the heat map illustrate a higher number of publications (yellow) or empirical observations (red). Note that a single publication could include multiple soil variables or multiple ErM plant or fungal treatments/comparisons. As such, the total number of observations exceeds the number of publications. Supporting Information Table S3 shows how we classified specific results for each variable from each study and Methods S2 provides further details on how we compiled Table S3.

<sup>1</sup>Includes C stock and organic horizon mass or depth.

<sup>2</sup>Includes %C and %SOM.

<sup>3</sup>Includes total %N, total N pools, organic matter N and N immobilization.

<sup>4</sup>Includes NH<sub>4</sub> and NO<sub>3</sub> concentrations, N mineralization rates, and dissolved organic and inorganic N.

<sup>5</sup>Includes dissolved organic C.

<sup>6</sup>Includes microbial biomass and microbial biomass C and N.

<sup>7</sup>Includes basal respiration and heterotrophic soil respiration.

<sup>8</sup>Includes β-glucosidase, β-glucuronidase, β-xylosidase and cellobiohydrolase.

<sup>9</sup>Includes amidase, chitinase, protease, leucine aminopeptidase and N-acetyl-β-D-glucosaminidase.

<sup>10</sup>Includes peroxidase, phenol oxidase and polyphenol oxidase.

dominance (i.e. mass-ratio effects *sensu* Grime, 1998) over trait variation and has therefore primarily focused on the relative influence of AM vs EcM trees. However, growing evidence suggests that functional trait abundance and diversity effects are both important predictors of ecosystem biogeochemical processes and therefore need to be assessed in tandem (Mouillot *et al.*, 2011; Dias *et al.*, 2013; Kuebbing & Bradford, 2019). Our review reveals the broad extent of global forests over which ErM plants occur and summarizes the multiple trait axes over which their effects might diverge from, or interact with, AM and EcM trees. As such, there is substantial evidence supporting a need to consider the potential influence of ErM plants and fungi on soil C and N cycling in the range of forest biomes in which they occur.

Owing to the relatively high abundance of ErM plants in EcM-dominated boreal forests (Read *et al.*, 2004; Nilsson & Wardle, 2005), there has been more research on ErM vs EcM effects in this biome (Clemmensen *et al.*, 2015, 2021; Adamczyk *et al.*, 2016; Table S3). Likewise, there is ample research on the effects of gradients of AM vs EcM tree dominance within and among forest biomes given that most trees associate with these two mycorrhizal types (Phillips *et al.*, 2013; Lin *et al.*, 2017; Steidinger *et al.*, 2019; Weemstra *et al.*, 2020). What is much less clear is how changes in ErM plant abundance might affect C and N dynamics in AM-dominated forests and in stands in which all three mycorrhizal types cooccur. As the distribution and abundance of AM, EcM and

ErM plants shift, it is important to understand both their individual and collective effects to project forest biogeochemical responses to changing conditions. Anticipated increases in the frequency and severity of canopy disturbances (Seidl *et al.*, 2017) could, for instance, favor the growth of ErM shrubs and the extent to which they cooccur with AM vs EcM trees. An extension of the mycorrhizal dominance framework to include ErM effects on C and N cycling – along with the data collected to test these effects – could therefore advance understanding of the ecosystem consequences of plant mycorrhizal associations under changing conditions.

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## Author contributions

EBW led and wrote the original manuscript with input from MAB, and all authors contributed to the final manuscript.

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## Data availability

Data sharing is not applicable to this article as no datasets were generated.

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Methods S1** Methods for calculating the distribution and abundance of ericoid mycorrhizal plants in arbuscular- vs ectomycorrhizal-dominated boreal, temperate and tropical forests at the global scale.

**Methods S2** Literature search methods used to collate publications and summarize results on ericoid mycorrhizal plant and fungal effects on carbon and nitrogen dynamics in forests.

**Table S1** Global forest land area with ericoid mycorrhizal plant biomass in different forest types used for the land area calculations in Table 1.

**Table S2** Full list of publications from the Web of Science search on the effects of ericoid mycorrhizal plants and fungi on carbon and nitrogen dynamics in forests.

**Table S3** Results from the 25 publications on the effects of ericoid mycorrhizal plants and fungi on soil carbon and nitrogen dynamics in forests that met our criteria for inclusion in Table 2.

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