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Atmospheric nitrogen deposition impacts on the structure and function of forest mycorrhizal communities: A review☆

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ABSTRACT

Humans have dramatically increased atmospheric nitrogen (N) deposition globally. At the coarsest resolution, N deposition is correlated with shifts from ectomycorrhizal (EcM) to arbuscular mycorrhizal (AM) tree dominance. At finer resolution, ectomycorrhizal fungal (EcMF) and arbuscular mycorrhizal fungal (AMF) communities respond strongly to long-term N deposition with the disappearance of key taxa. Conifer-associated EcMF are more sensitive than other EcMF, with current estimates of critical loads at 5–6 kg ha^{-1} yr^{-1} for the former and 10–20 kg ha^{-1} yr^{-1} for the latter. Where loads are exceeded, strong plant-soil and microbe-soil feedbacks may slow recovery rates after abatement of N deposition. Critical loads for AMF and tropical EcMF require additional study. In general, the responses of EcMF to N deposition are better understood than those of AMF because of methodological tractability. Functional consequences of EcMF community change are linked to decreases by fungi with medium-distance exploration strategies, hydrophobic walls, proteolytic capacity, and perhaps peroxidases for acquiring N from soil organic matter. These functional losses may contribute to declines in forest floor decomposition under N deposition. For AMF, limited capacity to directly access complexed organic N may reduce functional consequences, but research is needed to test this hypothesis. Mycorrhizal biomass often declines with N deposition, but the relative contributions of alternate mechanisms for this decline (lower C supply, higher C cost, physiological stress by N) have not been quantified. Furthermore, fungal biomass and functional responses to N inputs probably depend on ecosystem P status, yet how N deposition-induced P limitation interacts with belowground C flux and mycorrhizal community structure and function is still unclear. Current 'omic analyses indicate potential functional differences among fungal lineages and should be integrated with studies of physiology, host nutrition, growth and health, fungal and plant community structure, and ecosystem processes.

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1. Introduction

Trees and fungi form mycorrhizal symbioses, i.e., beneficial relationships between tree roots and root-inhabiting fungi in which the tree provides the fungi with carbon (C), whereas the fungi provide the tree with nutrients, including nitrogen (N) and phosphorus (P) along with other benefits such as improved water uptake and protection from pathogens (Smith and Read, 2010). Nitrogen deposition increases N availability and typically acidifies ecosystems (Tian and Niu, 2015; Stevens et al., 2018), both of which alter the interactions of mycorrhizal fungi with their hosts and their abiotic environment. In this review, we emphasize newer research and synthesize N deposition effects on mycorrhizal fungi in forests, especially insights from studies into the large-scale distribution and physiological potential of mycorrhizal fungi.

Although N deposition and N fertilization experiments differ in multiple ways, we consider the latter useful in providing

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mechanistic insights, especially studies that attempt to mimic N deposition via chronic inputs. Most studies on N deposition and arbuscular mycorrhizal fungi (AMF) are from non-forested ecosystems (see, e.g., Treseder and Allen, 2000, Pardo et al., 2011 and references therein; but see Van Diepen et al., 2007, 2010, 2011). For biological, practical and historical reasons, most research on N deposition effects in forests has focused on ectomycorrhizal fungi (EcMF) rather than AMF. In contrast with AMF, which produce belowground spores asexually, some EcMF produce large aboveground sporocarps, so a long record of the spatiotemporal patterns of reproduction can be related to trends in N deposition (Arnolds, 1991). Additionally, some EcMF can be grown in pure culture whereas AMF require a host, so physiological studies on EcMF interactions with N are more feasible. Finally, Sanger sequencing DNA barcoding can be applied without cloning to ectomycorrhizas, whereas AMF required cloning PCR products, which made it simpler to characterize communities of EcMF prior to next-generation sequencing. Several reviews have characterized various aspects of the relationship between N deposition and mycorrhizal fungi, e.g., Wallenda and Kottke (1998), Treseder (2004), and Lilleskov et al. (2011). Given the literature available and our focus on forests, the present review emphasizes EcMF and higher-latitude mycorrhizal responses to N while covering AMF and tropical studies where possible.

1.1. Mycorrhizal diversity and its role in relation to nitrogen

Almost all trees form one of two types of mycorrhizal associations, either arbuscular mycorrhiza (AM) or ectomycorrhiza (EcM), which differ in fungal partners. Almost all AMF belong to the Glomeromycotina (Mucoromycota), a monophyletic clade that evolved more than 400 million years ago (Spatafora et al., 2016). In contrast, EcMF evolved more than eighty times (Tedersoo & Smith, 2017), forming a convergent assemblage of fungi mainly belonging to the Basidiomycota and Ascomycota, plus a small number of Mucoromycotina (Mucoromycota). Major EcM host families include Pinaceae, Fagaceae, Betulaceae, Salicaceae, Cistaceae, Dipterocarpaceae, and Myrtaceae. Most other trees form AM. Trees forming functional symbioses with both AMF and EcMF are rare (e.g. some Myrtaceae and Salicaceae; Adjoud-Sadadou & Hargas, 2017).

The different types of mycorrhizal symbioses also differ in ecological niches. Read (1991) was first to explicitly link functional differences between EcM and AM symbioses to broad patterns of plant distributions, positing that gradients from AM to EcM dominance were parallel to increases in soil organic horizons, reliance on organic nutrients, and higher C:N and C:P litter. Furthermore, AM forests are typified by mull humus with thin to no organic horizons, whereas EcM forests generally have moder or mor humus with thicker organic horizons (Read, 1991). In support of this model, more recent syntheses have confirmed that, whereas AMF can take up inorganic N and amino acids (Hodge and Storer, 2015), they cannot mine organic N from complex organic matter using hydrolytic and oxidative enzymes, as many EcMF do (Read, 1991; Read and Perez-Moreno, 2003; Shah et al., 2016; but see Talbot et al., 2013). This model was extended by Phillips et al. (2013) in the MANE (mycorrhiza-associated nutrient economy) framework. Comparing AM and EcM stands in the same area, they found that, relative to EcM stands, AM stands had soils with a higher pH, higher nitrification and more decomposable litter, but lower activities of N− and P-cycling extracellular enzymes, a lower ratio of organic N to inorganic N, and lower amounts of dissolved organic carbon. A further difference between AM and EcM systems is the relative importance of P versus N limitation, with AM plants more commonly P-limited and EcM plants more commonly N-limited, as judged by their leaf N:P ratios (Rosling et al., 2016). There may also be parallel differences in root traits between EcM and AM trees (e.g., foraging strategy; Chen et al., 2016), although root traits may also vary independently of mycorrhizal type (Weemstra et al., 2016). Averill et al. (2014) found that temperate EcM forests had significantly higher C:N ratios of surface soil organic matter than temperate AM forests. This may be primarily attributed to lower N stocks rather than higher C stocks in EcM forests (Zhu et al., 2018; but see section 3.7). The conceptual framework for different niches of EcM and AM trees has been developed for temperate and boreal forests, and Tedersoo et al. (2012) argued that both AM and ECM tropical forests are equally characterized by an open and inorganic N cycle.

Another important mycorrhizal fungal trait is the extent and anatomy of extraradical hyphal development (termed exploration type). In EcMF, this morphological characteristic appears to track with other important attributes such as C demand, enzymatic capabilities, and presence of rhizomorphs for long-distance transport (Agerer, 2006; Hobbie & Agerer, 2010). EcMF have greater diversity of exploration types than AMF, whose exploration strategies are poorly characterized.

Under this general model of AM and EcM nutrient economies, we predict that N deposition, with resultant declines in N limitation and/or increases in P limitation (Li et al., 2016; Braun et al., 2010; Johnson, 2010) will affect EcM and AM forests differently; therefore, we will treat the two types separately. As mycorrhizal symbioses are drivers of differential responses, N deposition could result in plant-microbe-soil feedbacks and in legacies of N deposition that likely persist even if deposition levels have been substantially reduced (see below).

1.2. Spatiotemporal patterns and trends in N deposition

Human activities have more than doubled N fixation globally over natural rates, much of which is mobilized into the atmosphere from fossil fuel combustion and agriculture (Fowler et al., 2013). Because atmospheric N residence times are relatively short, and forests have high aerodynamic resistance, atmospheric deposition of NH_x, NO_y or organic N does not fall evenly over the Earth's surface. As a result, atmospheric N deposition can be locally elevated more than 10x over pre-industrial levels. During the 20th century, the highest N deposition levels were in Europe and eastern North America but with declines in Europe and increases in Asia, the latter now has the highest N deposition rates (Liu et al., 2013; Kanakidou et al., 2016). Hence, forests globally have experienced spatiotemporally variable deposition of anthropogenic N.

2. Patterns of taxonomic response at different scales

2.1. AM vs EcM responses

Given EcM and AM differences in mobilization of organic N sources, N deposition should favor AM over EcM host plants by relieving N limitation, all else being equal. Consistent with this hypothesis, N deposition is positively correlated with greater growth and recruitment of AM trees compared with EcM trees in North America (Averill et al., 2018). However, co-variation between N deposition and climate change in the dataset is reason for caution. If N deposition is indeed the cause of this pattern, there are major implications for the future of forest composition, structure, and function in regions experiencing elevated N deposition.

2.2. EcMF responses

Ectomycorrhizal fungal community composition changes in

both sporocarp and belowground studies (Lilleskov et al., 2011, Van der Linde et al., 2018). At local to regional scales, aboveground sporocarp surveys consistently indicate responses across EcMF genera and species ranging from negative for many nitrophobic species to positive for a few nitrophilic species (see below; Arnolds, 1991; Lilleskov et al., 2001, 2011). These changes in sporocarp production should affect long-term fungal population and community dynamics, but this is yet to be tested. Similarly, the belowground composition of EcMF communities in boreal and temperate forests shifts consistently with longer-term N inputs, driven by significant changes in the abundances of certain EcMF (Avis et al., 2003, 2008; Cox et al., 2010; Lilleskov et al., 2011; Jarvis et al., 2013; Suz et al., 2014; Morrison et al., 2016, Van der Linde et al., 2018; see below). In a tropical montane forest, N addition shifted ectomycorrhizal communities similarly to high-latitude forests (Corrales et al., 2017), but studies in lowland tropical forests, with warmer conditions and more weathered soils, are rare (See section 4.3).

Across both fruiting and belowground studies, *Thelephora* and *Laccaria* show largely positive responses, while *Cortinarius*, *Tricholoma*, *Piloderma,* Bankeraceae and *Suillus* show consistently negative responses, and species within *Russula*, *Lactarius*, Boletales, Thelephoraceae and Atheliaceae show divergent sensitivities to atmospheric N deposition (Lilleskov et al., 2011). At the species level, significant responses have been demonstrated for abundant fungi, most recently through the application of indicator analysis (Suz et al., 2014, Van der Linde et al., 2018, Fig. 1). EcM taxonomic richness seems most affected by pH, while EcM evenness and functional composition are more strongly influenced by N (Hobbie and Agerer, 2010; Suz et al., 2014, 2017).

Host identity and condition (e.g. foliar nutrient concentrations) are major predictors of EcMF community diversity (Cox et al., 2010; Suz et al., 2014; Bahram et al., 2014; Tedersoo et al., 2014). Intensive below-ground analysis across Europe shows: 1) EcMF specialists (i.e. limited to conifers or broadleaves) match or exceed generalists (i.e. with conifer and broadleaves) in both richness and relative abundance, 2) conifer specialists outnumber broadleaf specialist EcMF, and 3) conifer specialists respond more negatively to elevated N (Van der Linde et al., 2018). Based on both sporocarp and EcM data, the conifer-specific fungi – most showing abundant hyphae and rhizomorphs – declined more than broadleaf-specific and host generalist fungi over the 20th century in Europe when N deposition was increasing (Arnolds, 1991), and were more negatively affected by increasing N than broadleaf-specific and host generalist fungi (Van der Linde et al., 2018).

2.3. AMF responses

The AMF respond to N inputs in both temperate and tropical forests with strong declines in root colonization, spore density and external hyphal length (Treseder, 2004; Zhang et al., 2018; Sheldrake et al., 2018), particularly in soils with initially low N:P where N deposition causes both N and P to be in high supply (Johnson et al., 2003). There are only a few studies on AM forests (Van Diepen et al., 2007, 2010, 2011, 2013; Camenzind et al., 2014; Sheldrake et al., 2018); as in EcMF, there are reports of nitrophobic AMF species with high soil exploration capacity (e.g. Gigasporaceae and Acaulosporaceae) and nitrophilic fungi with limited soil exploration (e.g. Glomeraceae) (Egerton-Warburton & Allen, 2000; Treseder & Allen, 2002; Johnson et al., 2003; Egerton-Warburton et al., 2007; Chagnon et al., 2013; Treseder et al., 2018). Thus, as predicted by theoretical models (Johnson, 2010), the abundance and diversity of large-spored AM species declines, generally shifting in composition from Gigasporaceae under low N to Glomeraceae under high N (Eom et al., 1999; Egerton-Warburton et al., 2007; Antoninka et al., 2011; Allen et al., 2016; Chen et al., 2017; Williams et al., 2017; Jiang et al., 2018) and only rarely neutral or positive effects (Zheng et al., 2014). Small-spored fine root endophytes, which are anatomically and phylogenetically distinct from all other AMF, have recently been identified as Mucoromycotina rather than Glomeromycotina (Orchard et al., 2017; Hoysted et al., 2018) and appear to be insensitive to high N conditions (Allen et al., 2016). Decreases in overall AMF functional diversity may also decrease functional capabilities (Van der Heijden et al., 1998; Maherali & Klironomos, 2007).

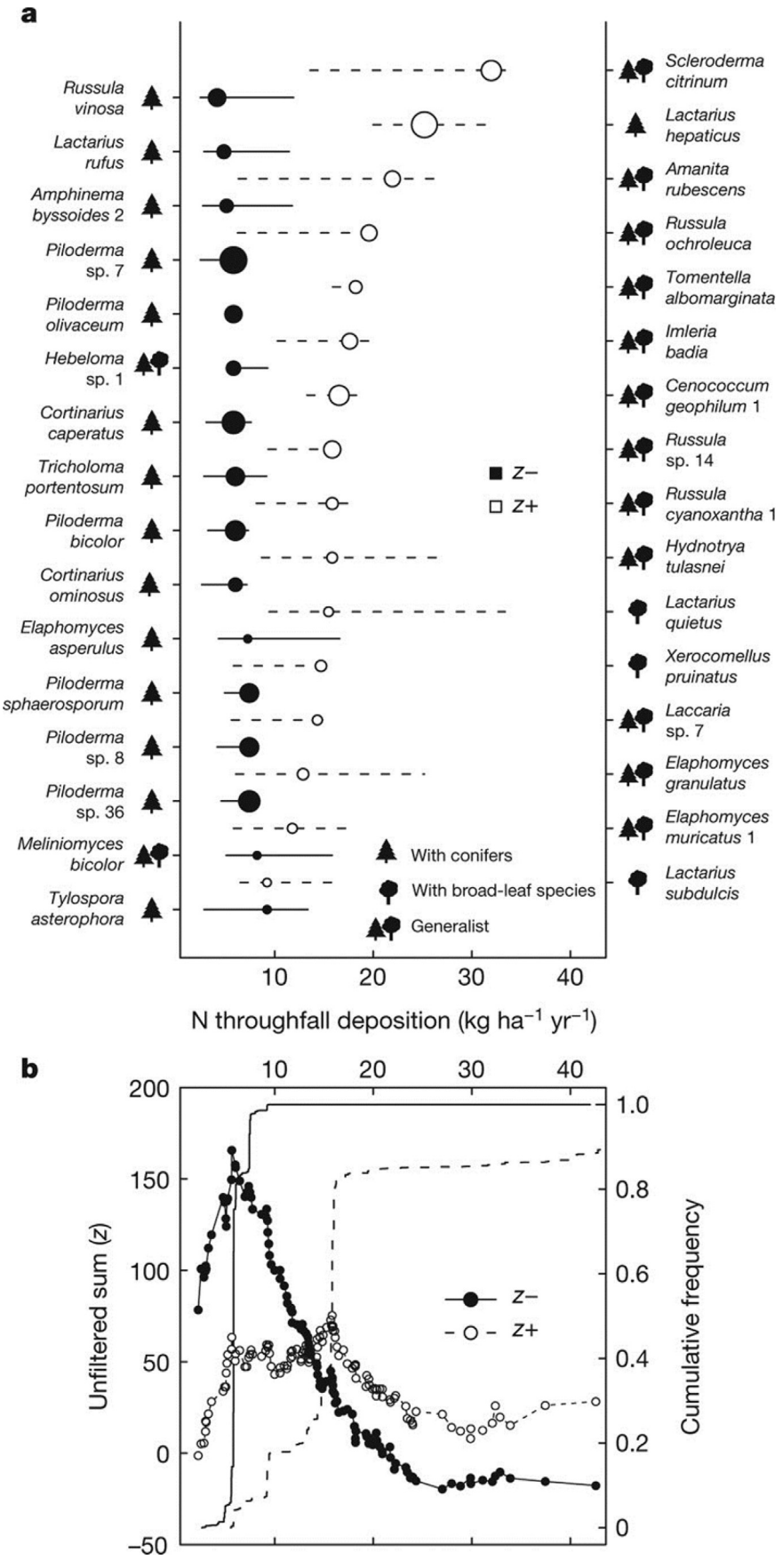
2.4. Interactions with other global change factors

The interactions of nitrogen deposition effects on mycorrhizal symbioses with the effects of other global-change factors, e.g., climate change, ozone, elevated CO_2, have been addressed in detail elsewhere (see, e.g., Mohan et al., 2014 and references therein) so will only be summarized here. Briefly, these can act by moderating or exacerbating N deposition effects on host C fixation and belowground C flux (CO_2, O_3, temperature, drought) or by altering soil resource availability (temperature, drought). Under elevated CO_2, mycorrhizal plants and fungi generally benefit (Alberton et al., 2005), although CO_2 fertilization effects are best explained by an interaction between N availability and mycorrhizal association (Terrer et al., 2016). EcM plants increased their biomass in response to elevated CO_2 regardless of N availability, apparently by accelerating N cycling (e.g., Drake et al., 2011; Phillips et al., 2012), whereas for AM plants, low N availability limits the biomass response to CO_2 fertilization. Thus, AM and EcM forests may differ in their responses to N deposition under rising CO_2 levels. By increasing belowground C allocation, elevated CO_2 may mitigate some negative impacts of atmospheric N deposition on EcMF, especially on nitrophobic species that are often more carbon-demanding (see below). In contrast, ozone damage on aboveground tissues of trees has potential negative effects on belowground carbon allocation and mycorrhizas (Andersen, 2003; Lilleskov, 2005; Mohan et al., 2014). The effects of ozone can sometimes moderate those of CO_2, e.g., on sporocarp production (Andrew et al., 2009), presumably by opposing effects on host C balance.

Climate change can have complex interactive effects on mycorrhizas. For example, warming in the absence of drought could both (a) reduce host carbon supply by increasing respiratory costs more than photosynthesis (Yamori et al., 2014) and (b) change soil resources by increasing N mineralization. Both could exacerbate N deposition effects on ecosystems, the former by reducing belowground C flux, and the latter by increasing soil inorganic N availability. However, in most warming studies, mycorrhizal hyphal abundance increases, but hyphal activity decreases (Mohan et al., 2014). Where moisture effects occur, one might expect a shift in hyphal anatomy and biochemistry, e.g., an increase in hydrophobic long-distance types or melanized hyphae with drought and increased hydrophilic taxa at higher humidity (Parts et al., 2013). These shifts could affect the ability of mycorrhizal fungi to forage for nutrients, interacting with N deposition in as yet untested ways.

2.5. Recovery from N deposition

Due to plant-soil feedbacks, acidification, litter accumulation and long-term storage of soil N, N deposition can have long-lasting legacies (Hasselquist & Högberg, 2014). While the direct effects of N are likely larger than the acidification effects (many EcMF evolved under acid soil conditions and most boreal forests occur on somewhat acidic soils), simultaneous eutrophication and acidification can leave legacies from which recovery can also be very slow (Kjøller et al., 2017).


a
Russula vinosa
Lactarius rufus
Amphinema byssoides 2
Piloderma sp. 7
Piloderma olivaceum
Hebeloma sp. 1
Cortinarius caperatus
Tricholoma portentosum
Piloderma bicolor
Cortinarius ominosus
Elaphomyces asperulus
Piloderma sphaerosporum
Piloderma sp. 8
Piloderma sp. 36
Meliniomyces bicolor
Tylospora asterophora
Scleroderma citrinum
Lactarius hepaticus
Amanita rubescens
Russula ochroleuca
Tomentella albomarginata
Imleria badia
Cenococcum geophilum 1
Russula sp. 14
Russula cyanoxantha 1
Hydnotrya tulasnei
Lactarius quietus
Xerocomellus pruinatus
Laccaria sp. 7
Elaphomyces granulatus
Elaphomyces muricatus 1
Lactarius subdulcis
z–
z+
With conifers
With broad-leaf species
Generalist
10
20
30
40
N throughfall deposition (kg ha−1 yr−1)
b
10
20
30
40
200
150
100
50
0
−50
1.0
0.8
0.6
0.4
0.2
0
Unfiltered sum (z)
Cumulative frequency
z–
z+

Reduced levels of N deposition lead to a slow recovery of EcMF community structure over many years. From sporocarp surveys, Van Strien et al. (2018) noted widespread recovery of fruiting by some EcMF since the 1990s in the Netherlands concurrent with reduced N deposition, although the most nitrophobic species had not recovered, probably because deposition is still above critical loads (21–35 kg ha^{-1} yr^{-1}). Nitrogen fertilization in Norway spruce led to residual fungal community effects even after 23 years (Choma et al., 2017) or 47 years of recovery (Strengbom et al., 2001). In a boreal Scots pine forest, EcM sporocarp production and species richness had recovered to control levels 23 years post-fertilization, but N availability was still elevated and the EcMF community was still enriched in nitrophilic taxa, especially *Lactarius* (Högberg et al., 2014; Hasselquist & Högberg, 2014).

Where EcM forests are replaced in the understory by AM saplings and trees, it is likely that the system becomes dominated by litter inputs characterized by lower C:N ratios, lower lignin content and hence higher leaf litter decomposability (Phillips et al., 2013). This functional group replacement will therefore speed up the N cycling rate, creating positive plant – soil feedbacks, which slow down the return to the previous EcM state. Thus, N deposition needs to be reduced to lower levels for recovery of EcM forests than for short-term maintenance of EcM forests. In AM forests, as N deposition may affect carbon cycling due to alterations in decomposition and humification rates, recovery may be slow, as feedbacks and legacies could also affect restoration here. Restoration methods tested with some success focus on removal of the forest floor (see e.g., De Vries et al., 1995; Baar and Kuyper, 1998; Smit et al., 2003) which would be difficult to implement at larger spatial scales.

2.6. Critical loads

Critical loads are "a quantitative estimate of an exposure to one or more pollutants below which significant harmful effects on specified sensitive elements of the environment do not occur according to present knowledge" (UBA, 2004). For mycorrhizal fungi this can be declines in abundance, diversity, or loss of species of EcMF. Wallenda & Kottke (1998) suggested a critical N load of 15–20 kg N ha^{-1} yr^{-1} for sporocarp production, and 20–30 kg ha^{-1} yr^{-1} for belowground EcMF communities in sensitive ecosystems. However, based on accumulation of data from long-term studies, more recent efforts (Bobbink and Hettelingh, 2011) estimated a critical load of 10–20 kg N ha^{-1} yr^{-1}, and Pardo et al. (2011); Pardo and Robin-Abbott, (2011) and Jarvis et al. (2013) estimated critical loads at 5–10 kg N ha^{-1} yr^{-1} for conifer-dominated ecosystems. Suz et al. (2014) defined a critical load for temperate European oak forests of 9.5–17 kg N ha^{-1} yr^{-1} depending on the level of EcMF community change. Recently, Van der Linde et al. (2018) estimated a critical load of 5–6 kg ha^{-1} yr^{-1} from 137 intensively monitored European ICP Forests plots using threshold indicator analysis of ectomycorrhizas. Although they included pine, spruce, beech and oaks, the critical load was largely determined by conifer ECM communities because few beech and oak occur in low-N deposition regions of Europe. There has been some partial community recovery in conifers and birch in the Netherlands (Van Strien et al., 2018) and a spruce site in Sweden (Choma et al., 2017) after reduction of deposition or cessation of fertilization, respectively. The EcMF associated with conifers are more sensitive to N deposition than broadleaf-associated EcMF (Arnolds, 1991; Cox et al., 2010, Van der Linde et al., 2018). Therefore, host-specific analysis should assign a lower critical load for conifer-dominated ecosystems than for deciduous ecosystems.

Estimates of critical loads for AMF in forests are sparse. Based on changes in AMF community structure and loss of fungal biomass in roots and soil (Van Diepen et al., 2007, 2010, 2011), a critical load for AMF in sugar maple-dominated forests of eastern North America was estimated at <12 kg ha^{-1} yr^{-1} (Pardo et al. (2011); Gilliam et al., 2011).

3. Causes and functional consequences of community change

Nitrogen deposition influences mycorrhizal fungi both directly (fungal- or soil-mediated) and indirectly (tree-mediated) (Smithwick et al., 2013). The relative importance of both pathways has long been disputed; here we suggest a middle ground of both viewpoints and propose how both pathways interact (Fig. 2). The impacts of these different pathways have been framed from the perspective of either fungal fitness (mycocentric) or plant fitness (phytocentric), both of which must be considered to understand the symbiosis.

3.1. Carbon supply from hosts

As N availability increases, *relative* C allocation (carbohydrates) to roots declines. Depending on circumstances, trees could also reduce *absolute* C allocation to roots and their associated mycorrhizal fungi. Whether absolute C flux belowground decreases will depend on how photosynthetic rates respond to higher N availability (Brassard et al., 2009) and the sinks for that photosynthate. In a meta-analysis, N addition reduced soil microbial biomass and respiration but not fine-root litter inputs to soil (Liu and Greaver, 2010). In several studies, elevated soil N leads to reduced fine-root density, mycelial biomass or production, or respiration (e.g., Kjøller et al., 2012; Almeida et al., 2018). Analysis of ^{13}C tracers indicated that N additions to forests can reduce *net* belowground C flux to EcM PLFAs (Högberg et al., 2010). Similarly, six years of fertilization at 100 kg N ha^{-1} yr^{-1} suppressed hyphal respiration (Hasselquist et al., 2012). Furthermore, nitrogen inputs decrease the abundance of EcMF relative to saprotrophic fungi (Morrison et al., 2016), consistent with the greater declines in EcMF than saprotroph sporocarps in regions with high N input (Arnolds, 1991) Despite these declines in abundance, extreme decreases in percentage of roots colonized at high N levels are often assumed (Franklin et al., 2014), but not consistently observed (Taylor et al., 2000; Peter et al., 2001; Treseder, 2004; Lucas & Casper, 2008; Corrales et al., 2017).

One model of the effect of N on C allocation is that, because leaves are stoichiometrically constrained by N availability, C allocation belowground declines when aboveground growth sinks are stimulated by high N availability (e.g. Ingestad & Ågren, 1991; Poorter and Nagel, 2000, but see Smithwick et al., 2013). These models avoid questions of ultimate causes of allocation toward mycorrhizal fungi, defining them as a sink like others (e.g., roots) directly feeding on host sugars, competing with other sinks in the process of balancing resource capture between above- and belowground resources. This model explains the common

Fig. 1. a) The belowground abundances of individual EcM species in relation to nitrogen deposition across 137 intensively monitored ICP Forests plots in Europe. Black symbols show species declining with increasing nitrogen deposition (*z*−) and open symbols depict species increasing with increasing nitrogen deposition (*z*+). The symbol size is proportional to the magnitude of the response (*z*-score). The horizontal lines represent 5th and 95th quantiles of values resulting in the largest change in species *z*-scores among 1000 bootstrap replicates. Tree shapes next to species names indicate host generalist, conifer- or broadleaf-specific species. **b**) In response to nitrogen deposition, a drastic mycorrhizal community shift occurs at 5.8 kg $ha^{-1}.yr^{-1}$, and a secondary shift occurs for positively-affected fungi at 15.5 kg $ha^{-1}.yr^{-1}$, based on the community-level output of accumulated *z*-scores per plot. Reproduced from Van der Linde et al., 2018

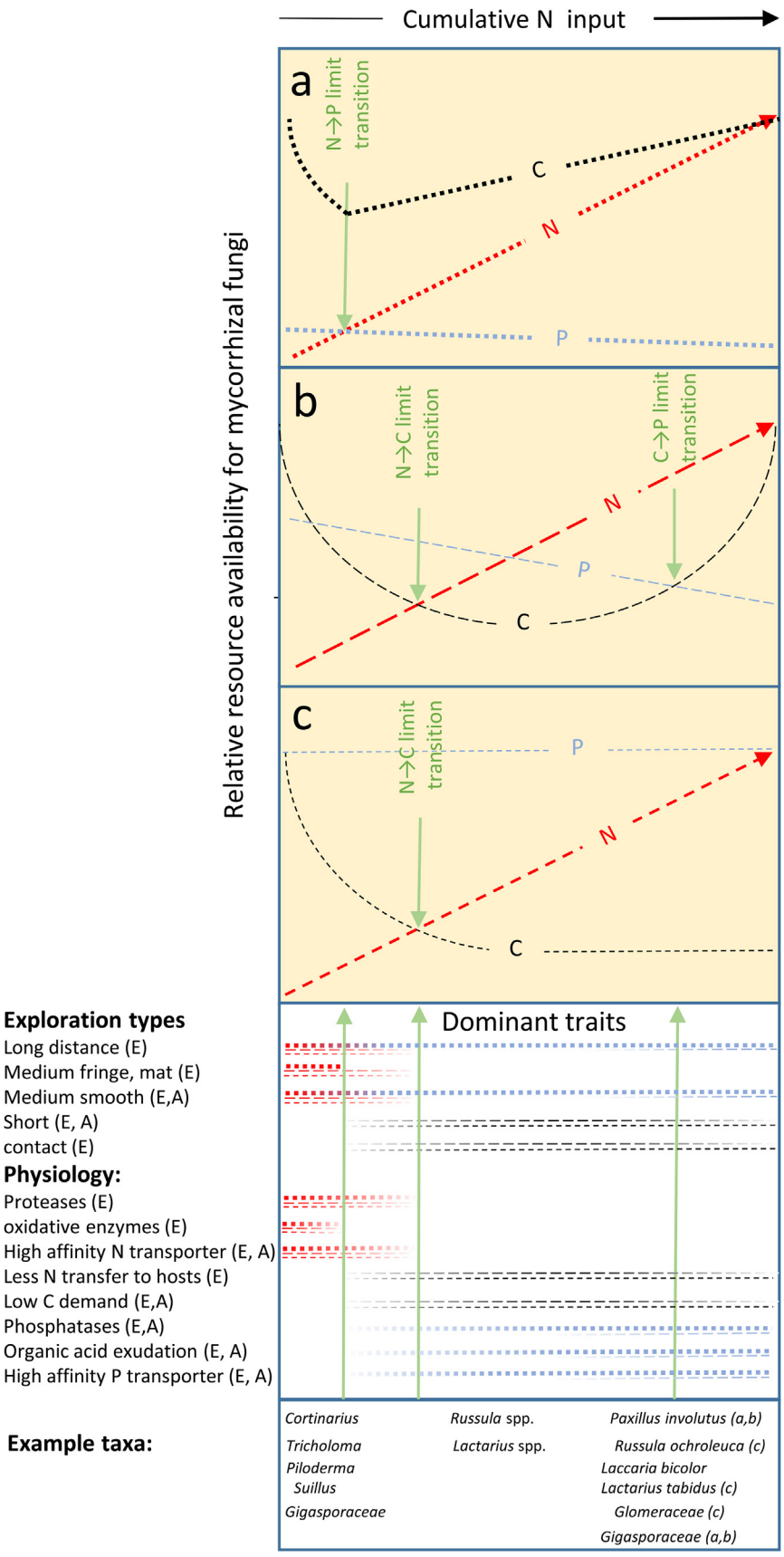


Fig. 2. As N availability increases, there are three scenarios of P availability represented in the three panels: a) low, b) medium, c) high; these are hypothesized to lead to different relative N and P limitation of hosts and resultant C flux belowground available for ectomycorrhizal activity; and would select differing dominant traits hypothesized to be associated with the shifting limitations. We assume that belowground C availability is high under low N or low P availability, but low under high N and P availability. In **scenario a)** P is very

observation of greater sensitivity of sporocarp production than root tip colonization to N deposition: with enhanced carbohydrate competition due to N deposition, sinks for C that are farthest from the source (EcMF sporocarps) suffer more than sinks closer to the source (EcM root tips), even though root tip density is usually also reduced under high N availability.

One approach to incorporating mycorrhizal fungi into such models is to hypothesize that under nutrient sufficiency the change in C balance shifts mycorrhizal fungal communities towards different suites of beneficial traits (Fig. 2). Because fungi also vary in their sensitivity to this reduction in carbon flux, large changes in species richness and species composition could occur.

These models have the virtue of simplicity, but there are two concerns here. First, this formulation ignores the potential for non-beneficial mycorrhizal interactions. These can occur if both plant and fungus are limited by the same nutrient (Treseder and Allen, 2002; Franklin et al., 2014) or if the plant cannot regulate carbon supply to mycorrhizal roots based on return for other benefits. The conditions under which plants can actively select for more mutualistic mycorrhizal fungal species on roots have still not been resolved. Preferential allocation to beneficial AMF occurs under some conditions (Bever et al., 2009; Kiers et al., 2011; Zheng et al., 2015), but the generality of this phenomenon has been questioned, especially under high N (Johnson, 2010, Walder and van der Heijden, 2015). There may also be evolutionary constraints to that solution for EcM trees, if the mechanism uses host N status as the regulating principle. In that case, under N deposition a tree might then reduce allocation to EcMF, including those fungal species specialized in P acquisition (but see section 3.3).

3.2. N-supply from soils

In addition to tree-mediated mechanisms, high soil N may directly affect mycorrhizal fungi, particularly EcMF. Species sensitivity is partly phylogenetically conserved (Lilleskov et al., 2011), that is many fungal genera can be classified along this gradient from nitrophobic to nitrophilic (section 2.2). Species sensitivity is also correlated with morphological and physiological fungal traits, such as hydrophobic mycelium, abundance of extraradical hyphae and rhizomorphs, ability to acquire N from organic sources, production of proteolytic enzymes, and the ^{15}N:^{14}N ratios in mycelium and sporocarps, due to both differential access to organic versus inorganic N sources and differential N allocation from fungus to tree (Hobbie & Agerer, 2010). One hypothesis is that differences in host specificity among EcMF are linked to differences in enzymatic capacities to acquire N directly from complex soil organic substrates and in resource exchange rate, e.g. if host-specific fungi transfer more soil N per unit of tree C than generalists (Gorissen & Kuyper, 2000; Molina & Horton, 2015). Alternatively, adaptations for mobilizing organic N may be more beneficial in the recalcitrant litter produced by most conifers than in deciduous litter. Host and soil pathways interact, as nitrophobic fungi are generally more C-demanding (Lilleskov et al., 2011), and hence respond more strongly to changes in C allocation by the tree.

Whether because of changes in host allocation, host selection, or soil-mediated direct effects, EcMF with organic N-mobilizing capacities decline with elevated soil N (Fig. 1). For example, elevated N greatly reduces the abundance of many *Cortinarius* species with strong peroxidative potential, which is hypothesized to be used to mobilize organic N (Bödeker et al., 2014; Lindahl and Tunlid, 2015). Although AMF are not known to have such organic N-mobilizing capacity, it is possible that AMF with high uptake of amino acids are differentially affected by deposition.

One hypothesized N-mediated community filtering mechanism was proposed by Wallander (1995). He proposed that under higher N, for species adapted to N deficiency that have obligate high N transfer rates to hosts, C will be used in acquiring and incorporating N into amino acids, and in the case of EcMF a significant amount of C will be transferred back to the host in amino acids transported from the fungus. For AMF, the fungus can transfer N as NH_4^+ (Govindarajulu et al., 2005), therefore the fungal carbon budget is more favorable because C skeletons from amino acids are retained by the fungus, although still at some cost related to hyphal transport as arginine (Hodge & Storer, 2015). Typically, studies do not distinguish between the effect of host C supply limitation vs. additional costs of N uptake and transfer. Without a full accounting of C costs of N and transfer to hosts and gross C flux into mycorrhizas, it will be difficult to distinguish the relative importance of the two as drivers of mycelial biomass, production and respiration. Their relative importance is worth distinguishing because, although both mechanisms enhance C limitation, which should select for fungi that can persist with low C supply from hosts, only the Wallander (1995) mechanism posits a C penalty to EcMF that transfer more N to hosts, providing an additional agent of community structuring.

3.3. N-mediated shifts in physiological potential

3.3.1. Shifting limitations and P mobilization

In an extremely N-poor ecosystem both trees and mycorrhizal fungi may be limited by N (Treseder et al., 2004, Fig. 2), resulting in a trap where plant growth can be constrained by N immobilization in the mycelium (Franklin et al., 2014; Püschel et al., 2016). With small increases in N availability the tree may still be N-limited, whereas the fungus is likely C-limited. With further increases in N the tree will no longer be N-limited. How do trees respond to those new conditions? In some cases, trees will likely maintain belowground C allocation, while in other cases they may not, selecting for fungi with a favorable N for C trade. As N is added, there are three potential host nutritional statuses likely to filter mycorrhizal fungi differently: 1) high overall nutrient availability, 2) limitation by cations, such as Mg or K, which is especially relevant with cation leaching due to acidification that normally accompanies N enrichment, 3) limitation by P, which can be exacerbated in acid soils by N deposition (Fig. 2). In the latter case, P limitation should stimulate belowground allocation (Ericsson, 1995). In support of this conceptual model, K and Mg limitation suppressed C allocation to root growth (Wickström and Ericsson 1995) and to EcMF growth, whereas P limitation stimulated C allocation to roots and EcMF growth (Hagerberg et al., 2003 and references therein). The

low, and hence limitation transitions rapidly from N to P and stays there, with relatively high C availability maintained by P limitation. In **scenario b)** P availability is higher, so as N increases, N and P are both readily available, and belowground C declines until N stimulates greater C flux belowground, or P availability declines because of uptake, acidification, or other factors, leading to greater P limitation and a steeper increase in belowground C availability. In **scenario c)** P availability is very high, and as N availability increases, neither N nor P is limited, and belowground C availability is reduced. (N→Mg limitation shift could also have an even more extreme effect on belowground C availability). Dominant traits are coded according to their association with a putative limiting resource: red = nitrogen limitation; blue = P limitation; black = C limitation, and dash style corresponds to those of the three scenarios with which they are associated. E and A after traits refer to putative EcMF and AMF traits, respectively. Note that AMF exploration types have not been formally defined and should differ from those described for EcMF, so the short and medium smooth types are considered approximations. (a), (b), and (c) after taxon names refer to the scenario in which that taxon is expected to possess some of the dominant traits under high N. Green vertical lines indicate transitions of nutrient and C limitations with increasing N in the three scenarios. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

spectrum of competitive fungal traits is likely to differ greatly among these three cases.

Case 1 and 2, C limitation. As discussed earlier, high overall fertility may sometimes reduce belowground C flux. If high overall fertility and limitation by nutrients affecting light harvest more than growth (e.g., Mg, K) reduce C allocation belowground, lower C demand would likely be a strongly selected trait (Fig. 2c). It has been noted that under many N fertilization scenarios the medium-distance fringe and mat, and sometimes long-distance, exploration types decline in abundance (Lilleskov et al., 2011; Treseder et al., 2018), being replaced by fungi with shorter-distance exploration types. If C limitation is a dominant community filter, one prediction would be that C limitation by any mechanism, regardless of site N status, might select for mycorrhizal communities with similar functional traits. Consistent with this, EcMF hemlock and birch seedling roots in densely shaded, low N availability rotting logs under hemlock canopies (Poznanovic et al. 2015), shared the same dominant taxa, *Tomentella sublilacina* and *Lactarius tabidus* (= *L. theiogalus*), as canopy spruce trees under high N deposition in Alaska (Lilleskov et al., 2002). This suggests that both low light availability and N deposition, by reducing belowground C allocation, may select similar dominants, despite large differences in N availability. Clearly, this hypothesis requires testing, especially in the case of cation limitation. Even if the same EcMF are selected by low C availability and high N availability, it remains to be tested whether these fungi can supply key nutritional or other benefits.

For AM fungi, a recent trait-based synthesis suggests that elevated N selects for certain genera over others (Treseder et al., 2018). In a regional deposition gradient, the N deposition-associated taxa conferred a smaller P benefit on hosts than those negatively associated with N deposition, yet these taxa did not produce fewer extraradical hyphae. However, in a parallel analysis based on a large global sampling, taxa that were more commonly found at lower soil C:N were found to have lower external hyphal length, providing an equivocal view of the links between the two (Treseder et al., 2018). The latter is consistent with a model of lower C supply and consequent lower P benefit, whereas the former does not link reduced P benefit to C supply. However, this synthesis study did not explicitly address whether the community response to N depends on variation in soil P (see Case 3). The regional gradient was on relatively P-rich soils, but soil P varied widely in the global study.

Case 3, P limitation. Under P limitation, C allocation belowground should increase (Ericsson, 1995), increasing C availability for fungi and increasing P demand for both fungal and host nutrition, which would favor a diversity of P-mobilizing strategies (Fig. 2a and b). Consistent with a model of P mediation of C supply to symbionts, Johnson et al. (2003) found that at a P-rich site, N addition decreased AMF biomass, whereas at P-limited sites N addition enhanced AMF biomass.

Under these conditions, additional potential trait combinations could be favored because the increased C and limiting P create niches for fungi with higher C demand, lower N-mobilizing capacity, and greater inorganic- or organic-P-mobilizing capacity (Johnson, 2010). Mycorrhizal fungi can enhance P mobilization via four mechanisms: high affinity transporters, increased soil exploration, mobilization of inorganically bound P, or mobilization of organically bound P. Although the diversity of P transporters in mycorrhizal fungi is unknown, with continued expansion of the pool of available fungal genomes (Martin et al., 2011; Grigoriev et al., 2014) and transcriptomes, the suite of transporters associated with taxa responding differentially to N deposition and resultant P limitation will become increasingly apparent.

Different fungal exploration types should vary in their ability to forage for P in soils (Plassard et al., 2011). In particular, given the low mobility of P in soils, contact and short-distance exploration types (e.g., many *Russula* and *Lactarius* species), would likely do a poor job of exploring for P. In contrast many of the medium-distance fringe and mat types that are suppressed by elevated N, and especially the medium-distance smooth exploration types that are not suppressed, should be more effective at P exploration. Some species with rhizomorphic long-distance exploration types are suppressed by elevated N (e.g., *Suillus* spp.) whereas others may be stimulated e.g., *Paxillus involutus*, *Tylopilus*, and *Imleria badia* (Lilleskov et al., 2011; Almeida et al., 2018), and would be especially good candidates for effective P scavengers under high-N conditions (Fig. 2a and b). Consistent with this, the nitrophilic *P. involutus* was more efficient at inorganic P uptake than the nitrophobic *Suillus bovinus* under similar conditions, although both are long-distance exploration types (Van Tichelen and Colpaert, 2000). Similarly, *I. badia* responded positively to P limitation enhanced by N additions, and preferentially colonized apatite ingrowth bags over quartz bags, apparently stimulated by primary inorganic P (Almeida et al., 2018).

For AM fungi, taxa in the Gigasporaceae have more extraradical hyphae than taxa in the Glomeraceae, so would be expected to be better at mobilizing P, but to be suppressed by low C availability (Treseder et al., 2018). Therefore, one might expect that Gigasporaceae would be favored under N or P limitation when C availability is high, but not under high N and P conditions (Fig. 2). Consistent with this, at P-rich sites, Gigasporaceae were most abundant under N limitation, whereas at a P-poor site, Gigasporaceae were most abundant under N fertilization (Johnson et al., 2003), suggesting an overarching role of C supply rather than N availability in their abundance. Additionally, Gigasporaceae greatly enhanced foliar P compared to most genera, including *Glomus* (Treseder et al., 2018).

The evidence for N-mediated increase in mycorrhizal taxa with high phosphatase activity is limited and mixed. Taniguchi et al. (2008) found higher phosphatase activity in EcMF from more N-rich forests (*Tomentella* and *Amanita* species) compared with those from more nutrient-limited forests (*Suillus* and *Rhizopogon* species). In contrast, in a montane tropical EcM forest, overall soil phosphatase activity was suppressed under elevated N inputs and was positively correlated with the abundance of the nitrophobic genus *Cortinarius* and negatively correlated with abundances of the nitrophilic genera *Russula* and *Tomentella* (Corrales et al., 2017). In these cases, understanding the P status of the soils will be critical, because high phosphatase activity should only be favored if P becomes limiting to growth. In the absence of P limitation, a decline in phosphatase activity could be associated with a decline in EcMF biomass. Although AM fungi also produce acid phosphatases, including free phosphatases in soil solution (Sato et al., 2015) nothing is known about AMF community members differing in phosphatase activity in response to the interaction of N deposition, C and P availability to the fungi.

High concentrations of exuded organic acids can mobilize inorganic P (Lambers et al., 2006). High rates of organic acid production were found in both nitrophilic (e.g., *Paxillus*) and nitrophobic (e.g., *Cortinarius*, *Piloderma*, *Suillus*) EcMF genera (Plassard et al., 2011), suggesting that potential for inorganic P mobilization spans the spectrum of tolerance of N deposition. However, other nitrophilic taxa show little capacity for organic acid exudation (e.g., *Thelephora*, *Tylospora*, *Laccaria bicolor*, *Hebeloma cylindrosporum*). The AM species *Rhizophagus clarus* had higher organic acid concentrations in the rhizosphere and host foliar P than four other AMF species across a range of soil aluminum concentrations (Klugh and Cumming, 2007). It is unknown whether P limitation under high N conditions could stimulate this species, as was found for Gigasporaceae (Johnson et al., 2003).

The above exemplifies the complexities involved in forms of P targeted and mechanisms of P mobilization, and our limited understanding of how P-mobilizing traits respond to shifts in both N and P limitation. Additionally, diverse traits could enhance P mobilization, pointing to a need to expand our profiling of phylogenetic distribution of suites of P-mobilizing traits to develop integrated estimates of the combined effect of the suite of traits, such as host stoichiometry.

3.3.2. Host stoichiometry

Given that EcMF capacities for uptake and transfer of different nutrients might shift under N enrichment, Lilleskov (2005) hypothesized that EcMF communities might shift the relative supply rate of different nutrients, at least partially buffering stoichiometric impacts on hosts. Surprisingly, effects of EcMF or AMF fungal taxa on host stoichiometry have been rarely investigated, although individual studies are suggestive. For example, Van der Heijden and Kuyper (2001) found that host N:P was regulated by fungal species, and the effect depended on substrate N:P. Similarly, Taniguchi et al. (2008) found that when seedlings were N-fertilized, those inoculated with ectomycorrhizal fungal isolates from high N sites had lower N:P than those inoculated with isolates from low N sites. Smith et al. (2015) found large fungal species effects on the stoichiometry of white spruce seedlings. Under unfertilized conditions *Amphinema* sp. (Atheliaceae) had a strong negative effect on host N:P ratio compared with *Thelephora terrestris* and another Atheliaceae species, apparently by preferentially supplying P. Some Atheliaceae are nitrophilic, whereas others are not, (Lilleskov et al., 2011), and it is unclear where these two Atheliaceae lie on that spectrum.

There is evidence that AMF species also differ in effects on host stoichiometry, suggesting that N-mediated community change could have stoichiometric consequences for hosts (e.g., Fellbaum et al., 2014). Johnson (2010) synthesized conceptual understanding of resource stoichiometry impacts on AMF communities and function. Although not explicitly addressing the issue of how the fungal community affects host stoichiometry, she emphasized the limited evidence of AM benefit to host N nutrition vs the extensive literature on AM benefit to P nutrition. If correct, this suggests that the dominant mechanism by which AMF affect host stoichiometry would be variation in the P supply rate, rather than the N supply rate.

3.4. EcM-AM comparisons

Given the apparent shifts from EcM to AM forest composition under N deposition in North America, it is critical to understand the functional consequences of such shifts. If we accept conceptual models in which, in contrast with EcMF, AMF lack the ability to mobilize polymeric or phenolically bound organic N from the environment but can access inorganic P effectively (Read, 1991), we might expect that increased N deposition would favor AMF, and the findings of Averill et al. (2018) are consistent with this. However, several experimental studies also suggest that AMF communities are less beneficial under N fertilization than under unfertilized conditions (e.g., Treseder et al., 2018), perhaps because high background P availability reduced the likelihood of a shift from N to P limitation and the potential for nutritional mutualism (Hoeksema et al., 2010). Key studies are needed to test the N–P interactions in AM trees.

At the level of EcM-AM comparisons, it is worth integrating this conceptual understanding with that of Albornoz et al. (2016), who found that on roots of *Acacia rostellifera*, an N_2-fixing dual mycorrhizal legume (where N supply should be sufficient), under high inorganic P availability AMF dominate, whereas as soils age and P is increasingly found in organic forms, EcMF dominate. They hypothesized that this trend was driven by the ability of the EcMF to access organic P via phosphatases, a function that is comparatively limited (Phillips et al., 2013; Rosling et al., 2016), but not absent (e.g., Sato et al., 2015) in AMF. This has relevance to differential AMF-EcMF responses to high N deposition.

3.5. New insights from phylogenetics and omics

Genomic methods are generating new insights into functional differences among and within groups that respond differentially to N deposition. The two sequenced Glomeromycotina genomes, *Rhizophagus irregularis* (Tisserant et al., 2013; Lin et al., 2014) and *R. clarus* (Kobayashi et al., 2018) revealed low copy number of CAZymes compared to many EcMF (Kuo et al., 2014; Kohler et al., 2015). Additionally, comparative genomics suggests the convergent loss of enzymes involved in the decay of lignocellulosic material in EcMF (Kohler et al., 2015), yet certain lineages appear to have retained high levels of oxidative activity, possessing Class II peroxidases hypothesized as potentially important mechanism for organic N mobilization (Lindahl & Tunlid, 2015). These peroxidases are largely absent in the Ascomycota and early-branching Basidiomycota (Sebacinales) that form some ectomycorrhizal and other mycorrhizal symbioses (Nagy et al., 2015).

Secreted proteases are also important in mobilizing organic N, and so we might expect taxa adapted to higher N conditions to possess a lower complement. Extracellular protease activity by many EcMF in the Ascomycota and Basidiomycota is well-documented (e.g., Talbot and Treseder, 2010) but lacking or greatly reduced in the Glomeromycotina (Hodge and Storer, 2015; Talbot et al., 2013). Consistent with this, the latter possess a reduced complement of serine proteases compared with saprotrophs and EcMF (Muszewska et al., 2017). A better understanding of the integrated function of secreted proteases will be necessary to link genomics to organismal function.

Within the EcMF, taxa that have a lower genomic potential or expression of genes involved in mining organic N appear likely to thrive under higher N availability. Although full genome analyses are only now under way, there are hints revealed in the recent literature. For example, *Laccaria bicolor* is tolerant of elevated N deposition (Lilleskov et al., 2011). Like most EcMF, *L. bicolor* possesses a broad suite of an estimated 116 secreted proteases (Martin et al., 2008), which is surprising given its low but variable growth on protein as a sole N source (Lilleskov et al., 2011). It is possible that experimental conditions do not always capture its enzymatic potential, for example, *L. bicolor* may extract N from soil fauna such as *Collembola* (Klironomos and Hart, 2001), perhaps via extracellular proteases that target animal protein. Some secreted proteases could be involved in functions other than nutrient mobilization (e.g., defense), and some modeled secreted proteases might not actually be transported into the soil. Consistent with this, Shah et al. (2016) found that *L. bicolor* had a smaller fraction of upregulated secreted peptidases when challenged with soil organic matter compared with *Paxillus involutus*, *Hebeloma cylindrosporum*, *Suillus luteus* and *Piloderma croceum*. The largest contrast was with *P. croceum*, a nitrophobic taxon that has both a larger number of secreted proteins and a larger fraction of those that are peptidases. These species also differed in their expressed suite of extracellular oxidative enzymes, which is also important for mobilizing N that is organically bound. Again, there is a need to characterize the integrated functioning of these suites of enzymes.

Since class II peroxidases are phylogenetically constrained (Bödeker et al., 2014), it is worth asking whether lineages possessing them are more sensitive to N deposition. A *Cortinarius* genome has 11 copies of Mn peroxidases, equivalent to white rot

fungi (Bödeker et al., 2014). The high sensitivity of this genus to N deposition is consistent with the hypothesis that EcMF with peroxidases are selected against under higher N conditions. Bödeker previously found class II peroxidases in 5 of 14 *Cortinarius* species screened, hence there is the possibility of infrageneric variation in presence of these enzymes. *Cortinarius* species also vary somewhat in their sensitivity, but whether this relates to peroxidase copy number or activity is untested. The only other sequenced EcM genomes with >1 copy of Class II peroxidases are Russulaceae and *Hebeloma* spp. The Russulaceae in particular vary widely in sensitivity to N deposition (Lilleskov et al., 2011, Van der Linde et al., 2018). They also have variable numbers of peroxidase gene copies. Elucidation of the distribution of these oxidative enzymes among N tolerant and sensitive species, and tests of their extracellular function, would be enlightening.

3.6. Implications of large-scale changes in tree nutrition

The preceding overview reveals clear functional diversity among and within mycorrhizal types, providing the potential for functional shifts as N, C and P shift in relative availability. However, it is still uncertain whether N inputs lead to changes in mycorrhizal community structure that are optimal for the plant or that show reduced benefit for the plant (e.g., in P acquisition). This has been challenging to investigate robustly using dominant organisms at ecosystem scales. However, strong declines in tree mineral nutrition at ICP Forests plots across Europe, including lowered P and higher foliar N:P of EcM trees, and negative health effects at least for conifers, even under N-limiting conditions (Veresoglou et al., 2014; Jonard et al., 2015), suggest that limits to the nutritional buffering capacity of EcMF communities at high N deposition levels have been reached. Arbuscular mycorrhizal trees were not abundant enough at ICP Forests sites to evaluate in these studies. Field surveys and experiments in AM and EcM forest ecosystems are needed to resolve the sign and magnitude of the integrated impact of N-mediated mycorrhizal fungal community change on host nutrition and plant community dynamics.

3.7. Nitrogen deposition, organic matter decomposition, and soil carbon storage

Whether changes in mycorrhizal communities in response to N deposition limit decomposition is an active area of research. In addition to direct nutritional and population effects on EcMF and trees, chronic N additions can suppress decomposition and increase soil carbon accumulation across AM and EcM temperate forests (Pregitzer et al., 2008; Frey et al., 2014). Changes in decomposition could be driven by multiple factors, including changing plant communities, litter chemistry, the environment, and both saprotrophic and mycorrhizal community function.

In this context, there has been a long-standing debate about whether EcMF have retained not only the capabilities for organic matter transformation, but also still have a facultative saprotrophic lifestyle. The evidence strongly indicates that EcMF lack a fully saprotrophic lifestyle, but that they can have substantial capabilities to transform soil organic matter, thereby affecting soil carbon pools and fluxes (Lindahl & Tunlid, 2015; Kuyper, 2017).

Gadgil and Gadgil (1971, 1975) proposed a conceptual model in which EcMF competitively suppressed decomposer activity, thereby reducing net decomposition. Although developed for EcMF, recent evidence suggests that this effect may also be seen with AMF (Leifheit et al., 2015). Fernandez and Kennedy (2016) summarized the potential mechanisms by which EcMF could suppress saprotrophs, one of which is especially relevant to this review, i.e., competition for N between both fungal guilds given high belowground C allocation which advantages EcMF. Under this model of fungal N competition, increased N deposition should reduce the Gadgil effect, accelerating saprotrophic activity, all else being equal. However, that does not seem to align with observations of reduced decomposition under N deposition, suggesting other mechanisms are at play.

An alternative mechanism is related to the peroxidative capabilities of certain EcMF (e.g., species of the genus *Cortinarius*; Bödeker et al., 2014) noted above, which could affect soil carbon dynamics, because peroxidases can cause extracellular mineralization of soil organic matter. These species show a high sensitivity to N deposition (Lilleskov et al., 2011), so their decline under N deposition could contribute to accumulation of soil organic matter. In fact, EcMF, which are less carbon-limited than saprotrophic fungi, may be more important in their contribution to the degradation of old soil organic matter than saprotrophic fungi (Lindahl et al., 2007).

Models linking the capacity of EcMF to acquire organic N from soil organic matter to transformations of soil organic matter by free-living heterotrophs vary widely in predictions. Whereas Orwin et al. (2011), in agreement with the Gadgil effect, predicted that EcMF will slow down decomposition, Moore et al. (2015) suggested that EcMF would increase decomposition under some scenarios. These predictions have a direct bearing on how N deposition could have cascading effects via changes in EcMF functioning into carbon pools and fluxes. Orwin's model, like that of Talbot (2008), predicts that, all other things being equal, decrease in EcM activity enhances decomposition rates, while some of Moore's models suggest the opposite. However, N deposition clearly slows decomposition of litter (Knorr et al., 2005) and soil organic matter, especially by fungi. For that reason, it is uncertain how declines of EcMF under N deposition would directly affect carbon storage.

Given possible shifts from EcM to AM forests under N deposition, it is important to determine the net effect of N deposition-mediated shifts between mycorrhizal types (EcM-AM) on C storage in the entire soil profile. Decomposition in organic horizons is only one determinant of soil carbon storage, and not necessarily the most important one (Schmidt et al., 2011). Most of the processes described above are primarily focused on the organic horizon, and as such influence the most vulnerable pool of soil carbon, yet interactions of partially degraded root and microbial inputs with mineral horizons are important determinants of total soil carbon storage (e.g., Torn et al., 1997; Doetterl et al., 2015). Averill et al. (2018) state that an observed shift from EcM to AM trees under N deposition was associated with decreased soil carbon storage, but other studies have found elevated mineral soil C and total organic C under AMF (Craig et al., 2018; Zhu et al., 2018). The Averill et al. (2018) analysis only extends to 20 cm depth in the mineral soil, and so captures effects on surface soil C, but would miss deeper soil carbon captured by the other studies. EcM forests are associated with greater C storage near the surface (Vesterdal et al., 2013; Craig et al., 2018) and so a bias toward surface sampling would overestimate soil C loss with decreased dominance of EcM trees.

4. The way forward—recommendations for future studies

There is a need to move the science forward on multiple fronts. Although we have a good picture of fungal community responses to N deposition in some boreo-temperate forests, the functional consequences are much less well sorted out. Additionally, our understanding of tropical community responses is still limited.

4.1. Integrating emerging 'omic resources with field and laboratory investigations of fungal functioning

A fruitful line of research will be to test the predictive utility of the genomic and transcriptomic information vs. *in situ* assays of taxon-specific enzymatic and nutrient-mobilizing potential under variable levels of inorganic N addition. Currently, our understanding of the obligate vs. facultative extracellular and intracellular *in symbio* deployment of the genomic arsenal of peptidases and oxidative enzymes possessed by EcMF is rudimentary (Talbot et al., 2013). We do not yet understand interactions between these enzymes in mobilizing N under field conditions (Pellitier & Zak, 2018). For example, if certain *Cortinarius* species express intense peroxidative capacity, which is non-specific in bonds targeted, then where, when, and how do they mobilize proteases to complement those enzymes? Are taxon-specific traits of organic and inorganic N and P uptake correlated? How much predictive power do genome analyses provide regarding enzymatic potential to target complex organic matter? Are these suites of genes regulated together by higher level transcription factors that are sensitive to N availability? Although these are fundamental questions about fungal ecophysiology, they have clear implications for understanding how function is likely to respond to N deposition.

4.2. Testing the concepts presented here in tropical forests

Most studies of N deposition impacts have been in temperate and boreal regions, yet lower latitudes deserve more attention given the rapid increase in N deposition, especially in Asia. Most tropical forests are dominated by AM trees, so it is important to understand how tropical AMF will respond functionally to N deposition. Given that P limitation predominates over N limitation in older, more weathered, tropical soils (Vitousek & Howarth, 1991), combined with the apparent specialization of AMF on P over N, functional shifts with N deposition might simply push systems to even greater emphasis on P acquisition. However, especially given the uncertainty about whether N deposition will enhance or inhibit AMF acquisition of P (Johnson, 2010; Treseder et al., 2018), the role of N in altering AMF nutrient acquisition in the tropics demands attention. Camenzind et al. (2014) found that in a high-elevation tropical forest, N additions decreased intraradical fungal abundance and reduced richness of Diversisporales but not of Glomerales, whereas P addition reduced Glomerales richness. Given the cooler environment and younger soils in montane forests, it remains to be determined whether this response is representative of warmer, more weathered low-elevation tropical forests.

Within EcMF, dominant tropical taxa are hypothesized to be poorly adapted for complex organic N uptake given the more open N cycle (Kuyper, 2012). As for AMF, this raises the question of whether tropical EcMF would be as sensitive to N deposition. Tropical EcM forests can form monodominant stands with substantial litter accumulation on nutrient-poor soils where organic N use could be beneficial (Connell and Lowman, 1989), and may reduce inorganic N availability (Corrales et al., 2016). Some tropical EcMF can grow on protein as a sole N source in sterile culture (Brearley et al., 2005), suggesting extracellular protease activity. Furthermore, tropical EcMF tend to be more diverse on low-nutrient soils (Corrales et al., 2018). For example, Peay et al. (2010) found that EcMF associated with Dipterocarpaceae were more diverse at low-fertility sites with sandy soils than high-fertility sites with clay soils, with all 12 identified Cortinariaceae restricted to low-fertility sites. Similarly, N fertilization of a montane tropical EcM forest led to community shifts identical to those at higher latitudes (Corrales et al., 2017). Given that the broadly dominant lineages in the tropics are the Russulaceae, *Amanita*, *Boletus*, *Sebacina*, and Thelephoracae (Corrales et al., 2018), none of which is known to predominantly harbor nitrophobic species, it is unclear whether the findings of Corrales et al. (2017) can be generalized across tropical EcM forests or limited to a small N-poor subset of ecosystems. Research is needed especially in subtropical China, considering its high levels of N deposition. In one such forest in Fujian, Fan et al. (2018) concluded that N deposition had increased both P limitation and EcM mobilization of organic phosphate.

4.3. Additional areas for further investigation

- Improved understanding of responses of AMF community structure and function to N deposition, with particular attention to integrated effects of C, N, and P limitations on functional organization of the community.
- Experimental tests of the effects of N deposition on shifts from EcM to AM tree dominance and their consequences for soil C storage.
- Refined critical loads, especially for EcM temperate broadleaf, AMF, and tropical forests.
- Improved understanding of the strength of legacies and feedbacks to predict recovery rates after reduction of N deposition.
- Improved understanding of mycorrhizal community mediation of shifts in P uptake rate and uptake mechanisms from different sources during the transition from N to P limitation.
- Robust data directly linking changes in 1) environment (soil, atmospheric), 2) mycorrhizal taxonomic and functional diversity, and 3) forest nutrition, growth, and health.
- Understanding the effects on ecosystem processes (e.g. nitrate leaching, greenhouse gas emissions) of transition to low-diversity nitrophile-dominated EcM forests with inorganic N enrichment.
- Expanded investigation into interactive effects of N deposition and other global change factors on mycorrhizal community structure and function.
- Mechanistically linking mycorrhizal fungi into models of forest C, N, and P cycling.
- Defining and testing C use efficiency and nutrient use efficiency by mycorrhizal fungi, especially in response to changing N and P availability.
- Increased understanding of the functioning of the mycorrhizas of N-fixing trees as a natural analog to N deposition.

5. Conclusions

Recent studies confirm the clear and strong sensitivity of mycorrhizal fungal communities to N inputs; this has clear conservation implications given their high beta diversity. The N impact on these communities is at all levels, including mycorrhizal types, as well as dominant families, genera, and species. The functional differences at the coarsest phylogenetic and functional level (Dikarya/EcM – Glomeromycotina/AM) are clear, suggesting N-mediated shifts from EcM to AM forests would reduce the capacity to access organic N, organic P, and soil carbon cycling. The functional shifts at finer taxonomic levels within EcMF suggest that functional suites of soil exploration types have declined under N deposition, with a probable loss of N– and C-mobilizing enzymatic potential, and continuing uncertainty about effects on P cycling. Genomics has opened up new areas of investigation, simultaneously revealing both the presence of diverse suites of putative extracellular hydrolytic and oxidative enzymes and our lack of understanding of the functional integration of these enzymes. Similarly, taxon-level understanding of traits relevant to C, N, and P dynamics is improving, suggesting that community functional

shifts may be contingent on P availability. How these trait suites are coupled and how they mediate the soil-fungal community-host system must be explored to understand the functional consequences of observed community shifts and to predict changes in ecosystem processes and forest condition under increased N deposition.

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