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Atmospheric Nitrogen Deposition to Global Forests

Lilleskov, Erik A.; Kuyper, Thomas W.; Bidartondo, Martin I.; Hobbie, Erik A.

https://doi.org/10.1016/B978-0-323-91140-5.00001-4

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Chapter 6

Impacts of nitrogen deposition on forest mycorrhizal communities

Erik A. Lilleskov[a], **Thomas W. Kuyper**[b], **Martin I. Bidartondo**[c,d] **and Erik A. Hobbie**[e]

[a]*Forestry Sciences Laboratory, Northern Research Station, USDA Forest Service, Houghton, MI, United States;* [b]*Soil Biology Group, Wageningen University and Research, Wageningen, the Netherlands;* [c]*Department of Life Sciences, Imperial College London, London, United Kingdom;* [d]*Royal Botanic Gardens, Kew, Richmond, United Kingdom;* [e]*Earth Systems Research Center, University of New Hampshire, Durham, NH, United States*

1. Introduction

Human activities have more than doubled nitrogen (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 residence times of reduced or oxidized atmospheric N 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 10 times over preindustrial levels. During the 20th century, the highest N deposition levels were in Europe and eastern North America, but peak deposition has now shifted to eastern Asia (Kanakidou et al., 2016; Liu et al., 2013). Hence, forests globally have experienced spatiotemporally variable deposition of anthropogenic N.

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) and fungi provide the tree with nutrients, including N and phosphorus (P), along with other benefits such as improved water uptake and protection against pathogens (Smith and Read, 2010). Nitrogen deposition increases N availability and typically acidifies soils (Stevens et al., 2018; Tian and Niu, 2015), both of which alter the interactions of mycorrhizal fungi with their hosts and their abiotic environment.

Although N deposition and N fertilization experiments differ in multiple ways, we consider the latter useful in providing mechanistic insights, especially studies that attempt to mimic N deposition via long-term chronic inputs. Most studies on N deposition and arbuscular mycorrhizal fungi (AMF) are from nonforested ecosystems (see, e.g., Treseder and Allen, 2000; Han et al., 2020; Pardo and Robin-Abbott, 2011) with some exceptions (Hu et al., 2022; Ma et al., 2021a; 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 asexual spores, many EcMF produce macroscopic aboveground sporocarps that have been widely monitored, especially in Europe, so a long record of the spatiotemporal patterns of their 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 mycorrhizal interactions with N are more feasible in EcMF than AMF. Historically, Sanger sequencing-based DNA barcoding could only be applied without cloning to EcMF, whereas AMF required more laborious cloning of PCR (polymerase chain reaction) products, allowing more rapid progress on EcMF community analyses. Recently, high-throughput sequencing has overcome this limitation, accelerating work on AMF community analysis. Several reviews have assessed the relationship between N deposition and mycorrhizal fungi (Lilleskov et al., 2011; Treseder, 2004; Wallenda and Kottke, 1998).

In this review, we synthesize N deposition effects on mycorrhizal fungi in forests, especially based on insights from studies into the large-scale distribution and physiological potential of mycorrhizal fungi. We do so by updating the review by Lilleskov et al. (2019) with a number of important studies that have come out in recent years.

Atmospheric Nitrogen Deposition to Global Forests. https://doi.org/10.1016/B978-0-323-91140-5.00001-4

2. Patterns of taxonomic response at different scales

2.1 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. The AMF belong to the Glomeromycotina and Endogonales (Mucoromycota), clades that evolved more than 400 million years ago (MYA) (Rimington et al., 2020; Spatafora et al., 2016). In contrast, EcMF evolved more than 80 times starting 150 MYA, forming a convergent assemblage of fungi mainly belonging to the Basidiomycota and Ascomycota, plus a small number of Endogonales (Mucoromycota) (Tedersoo and Smith, 2017). 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; Teste et al., 2020) and their responses to N enrichment are understudied (Karst et al., 2021).

The different types of mycorrhizal symbioses also differ in ecological niches. Read (1991) first explicitly linked functional differences between EcM and AM symbioses to broad patterns of plant distributions, positing that gradients from AM to EcM dominance paralleled 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, although AMF can take up 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 by Read (1991) was extended by Phillips et al. (2013) in the MANE (mycorrhiza-associated nutrient economy) framework. They compared forest stands in the same area and 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 C. 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 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 in 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). The conceptual framework for different niches of EcM and AM trees has been developed for temperate and boreal forests. In contrast to this framework, 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 and Agerer, 2010). EcMF have greater diversity of exploration types than AMF, whose exploration strategies are poorly characterized. The functional trait of having hydrophobic or hydrophilic mycelium of EcMF also links to differential sensitivity to N (Hobbie et al., 2022); again, variation in this trait among AMF is poorly known.

Given this conceptual model of AM and EcM nutrient economies, we predict that N deposition, with resultant declines in N limitation or increases in P limitation (Braun et al., 2010; Johnson, 2010; Li et al., 2016), 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-soil microbe-soil feedbacks and in legacies of N deposition that likely persist even if deposition levels are substantially reduced.

2.2 Arbuscular mycorrhiza versus ectomycorrhiza 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; Jo et al., 2019). If N deposition causes this pattern, there are major implications for the future of forest composition, structure, and function in regions experiencing elevated N deposition. However, covariation between N deposition and climate change in the dataset of Averill et al. (2018) is reason for caution.

2.3 Ectomycorrhizal fungal responses

In response to N deposition and fertilization, EcMF community composition has changed in both sporocarps and vegetative belowground (root tip and soil) EcMF communities (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). Changes in sporocarp production as a consequence of N deposition could 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; Jarvis et al., 2013; Lilleskov et al., 2011; Morrison et al., 2016; Suz et al., 2014; Van der Linde et al., 2018; see below). In the only study of how N addition modified EcMF communities in tropical forest, Corrales et al. (2017) concluded that N addition had similar effects in a tropical montane forest and in high-latitude forests. However, studies in lowland tropical forests, with warmer conditions and more weathered soils, are relatively rare but increasing (See Section 5.2).

In both sporocarp and belowground (root tip and soil) studies of impacts of atmospheric N deposition, *Thelephora* and *Laccaria* largely respond positively; *Cortinarius*, *Tricholoma*, *Piloderma*, Bankeraceae and *Suillus* consistently respond negatively; and species within *Russula*, *Lactarius*, Boletales, Thelephoraceae and Atheliaceae show divergent sensitivities (Lilleskov et al., 2011; Moore et al., 2021). 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. 6.1). Indicator values for macromycetes have also been proposed by Simmel et al. (2017) that reflect their relationship to soil nutrient status, including N and a range of other macronutrients. 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 (Bahram et al., 2014; Cox et al., 2010; Suz et al., 2014, 2021; Tedersoo et al., 2014; van der Linde et al., 2018). Intensive below-ground analysis across Europe shows: (1) EcMF specialists (i.e., associated with conifers *or* broadleaved trees) match or exceed generalists (i.e., associated with both conifer *and* broadleaved trees) in both richness and relative abundance, (2) conifer specialists outnumber broadleaf specialist EcMF, and (3) conifer specialists respond more negatively to elevated N than broadleaf specialists (Van der Linde et al., 2018). Based on both sporocarp and EcMF 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 spatial analyses reveal that they were also more negatively affected by increasing N than broadleaf-specific and host generalist fungi (Van der Linde et al., 2018).

2.4 Arbuscular mycorrhizal fungal responses

Four global-scale meta-analyses of the effects of N deposition or fertilization on AM fungi were recently published by Han et al. (2020), Ma et al. (2021a,b) and Hu et al. (2022). Both Han et al. (2020) and Ma et al. (2021a) found that N addition did not affect species richness and diversity of AM fungi. However, separate analyses for AMF abundance yielded very diverging results. In the study of Han et al. (2020), focusing on responses of AM in grassland, crop, and forest ecosystems, N addition reduced AM fungal abundance by 8% when averaged over all abundance indicators. In comparisons of the different abundance indicators assessed, fractional root colonization declined by 12%–20% and the AM-specific biomarker NLFA 16:1ω5 declined by ~32%–42%, whereas the length of extraradical mycelium and spore density were not affected. Caution should be used in interpreting NLFA, as it should not be considered as a measure of biomass, but rather of lipid storage in vesicles and spores, which can vary seasonally (see e.g., Van Diepen et al., 2007). The discrepancy in N effects on extraradical hyphal length and on the fatty acid biomarker was evident in both studies. This raises questions about the interpretation of earlier studies where only extraradical hyphal length was assessed, as lipid storage appears to be a more sensitive indicator.

In a subset analysis of data from Han et al. (2020) restricted to forests, the same pattern was seen, with N enrichment not significantly affecting species richness, diversity, and extraradical hyphal length, but AM root colonization declining 23% ($P = .016$, $n = 34$) and NLFA declining 24% ($P = .043$, $n = 8$) (our analysis of forest data from Han et al., 2020). Declines were greater in a recent meta-analysis focused on forests (Ma et al., 2021b), with AM biomass declining by 36% and AM root colonization declining by 31%. Ma et al. (2021b) also found greater declines in these two metrics for AM fungi than for EcM fungi (25% and 8%, respectively). However, they found N deposition significantly decreased biomass and length of EcM tree roots but not AM tree roots. This analysis did not control for all environmental conditions that might affect these responses, so direct comparisons should be made with caution. In contrast with the above studies, Hu et al. (2022) noted a small, nonsignificant, negative effect on AM fungal abundance (all metrics) across all ecosystems (−5%), but a significant increase in AM fungal abundance of 17% in forests. However, it was

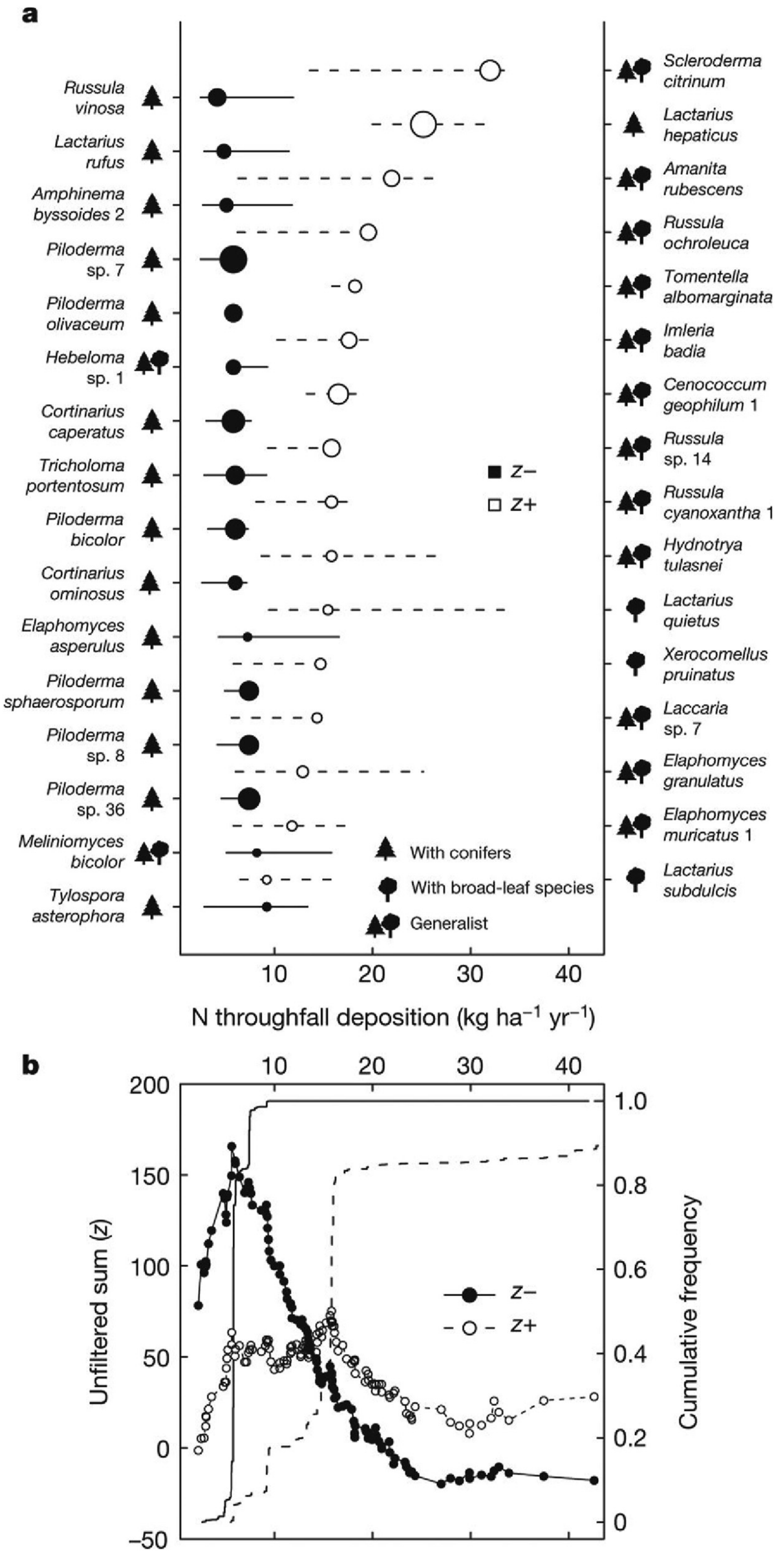

FIG. 6.1 (a) The belowground abundances of individual EcM species in relation to N deposition across 137 intensively monitored ICP forests plots in Europe. Black symbols show species declining with increasing N deposition ($z-$) and open symbols depict species increasing with increasing N deposition ($z+$). 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 N deposition, a drastic mycorrhizal community shift occurs at 5.8 kg^{-1} N ha^{-1} year^{-1}, and a secondary shift occurs for positively affected fungi at 15.5 kg^{-1} N ha^{-1}year^{-1}, based on the community-level output of accumulated z-scores per plot. *Reproduced from Van der Linde et al. (2018) with permission.*

impossible to determine whether initial environmental conditions and experimental design varied between experiments in forests and other ecosystem types. A deeper comparative analysis of the forest data subset from all of these studies is warranted to assess any assumptions, gaps, or biases inherent in the methods (e.g., data imbalances, abundance metrics, treatment of interactions), ambient environmental conditions (e.g., initial N status, pH, host composition), and experimental conditions. For example, the study by Hu et al. (2022) did not partition results by type of abundance metric used, whereas other studies found significant differences among these metrics.

The differential effect of N enrichment on intraradical and extraradical AMF mycelium suggests differential N sensitivity of various AM fungal families. However, studies disagreed on the nature of that response. Han et al. (2020) grouped AM fungi into rhizophilic (mainly root-inhabiting; belonging to Glomeraceae, Claroideoglomeraceae and Paraglomeraceae), edaphophilic (mainly soil-inhabiting; belonging to Gigasporaceae and Diversisporaceae), and ancestral (Acaulosporaceae, Archaeosporaceae, and Ambisporaceae) functional groups. These groups responded differently, with the abundance of the rhizophilic and ancestral guilds declining significantly by 30% and 50%, respectively, with higher N, whereas the abundance of the edaphophilic guild exhibited a nonsignificant decrease of 10%−12%. Curiously, these data contrast with earlier publications where the edaphophilic Gigasporaceae were considered nitrophobic and the rhizophilic Glomeraceae nitrophilic (Egerton-Warburton and Allen, 2000; Egerton-Warburton et al., 2007; Chagnon et al., 2013; Johnson et al., 2003; Treseder and Allen, 2002; Treseder et al., 2018). These earlier studies suggested that the AM fungal communities would shift from large-spored species of the Gigasporaceae under low N toward small-spored species of the Glomeraceae under high N (Allen et al., 2016; Antoninka et al., 2011; Chen et al., 2017; Egerton-Warburton et al., 2007; Eom et al., 1999; Jiang et al., 2018; Williams et al., 2017). Family level responses for two indices (the "N association index" and "Observed soil C:N") of Treseder et al. (2018) showed no correlation with the "N addition effects" of Han et al. (2020); our comparison).

As it is unclear what factors cause the different responses to N addition in forests, it is difficult to generalize how AMF respond to N addition. We cannot yet explain the opposing conclusions of those meta-analysis and the results from earlier studies. Tentative explanations for the discrepancies would include the direct effect of N enrichment on soil pH and the associated indirect effects on P availability, and the negative effects of N enrichment on plant species richness that could drive AM fungal species richness (Han et al., 2020; Ma et al., 2021a). A further possibility is that, as for EcMF, fungal family level taxonomy may be a poor predictor of N sensitivity. Treseder et al. (2018), who analyzed responses at the genus rather than family level, found that within the Glomeraceae, *Rhizophagus* species were more nitrophobic than *Glomus* and *Funneliformis* species. Sensitivity to N also varied within the Gigasporaceae, especially *Scutellospora* species (Treseder et al., 2018). To resolve these discrepancies, further studies of comprehensive standardized datasets at finer phylogenetic resolution are needed, with a goal of differentiating direct effects of N and indirect effects, e.g., those mediated through decline in pH, changes in P availability, N:P stoichiometry, host C transfer, and host plant community responses.

The most important predictor of the impact of N enrichment on AM fungal richness and diversity was the ratio of available N:available P (Han et al., 2020), which is consistent with the model of Johnson (2010). At high relative P supply (low N:P ratio), N enrichment had negative effects, whereas at low relative P supply (high N:P ratio) N enrichment increased richness and diversity of AM fungi. Other moderators (a decline in pH due to N enrichment; N addition rate, climatic parameters, and the effect of N enrichment on plant root biomass) were less important than the relative supply of soil N and P. Additionally, Han et al. (2020) noted that rhizophilic and edaphophilic taxa differed in their response to various predictors. For the rhizophilic guild the most important predictors were decline in pH, duration of the experiment, and the soil supply of N and P, whereas for the edaphophilic guild the most important predictors were changes in root biomass, decline in pH, and experimental duration. Ecosystem type (forest, grassland, cropland) was never an important predictor.

2.5 Ericoid mycorrhizal responses

Heathland plants of the family Ericaceae typically occur on nutrient-poor soils. As they are nitrophobic, N deposition on dry heathland has resulted in replacement of the Ericaceae species *Calluna vulgaris* by the grass *Deschampsia flexuosa*, while on wet heathlands the Ericaceae species *Erica tetralix* has been replaced by the grass *Molinia coerulea*. Accelerated succession to pine, birch and oak woodland may also be taking place due to N deposition. The role of the mycorrhizal partners of heathland plants in the replacement process has received less attention. Van Geel et al. (2020) noted a potential loss of ericoid mycorrhizal fungal species richness of 40% along an N deposition gradient in western Europe in both dry and moist heathlands and described potential implications for nutrient acquisition from recalcitrant organic sources and for pathogen resistance. Nitrogen deposition reduced mycorrhizal colonization in *Calluna vulgaris* with a more negative effect by ammonium than by nitrate (Hofland-Zijlstra and Berendse, 2009; Yesmin et al., 1996).

3. Critical loads of nitrogen and recovery from nitrogen deposition

3.1 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, harmful effects include declines in abundance, diversity, or loss of species of EcMF. Wallenda and Kottke (1998) suggested a critical N load of 15−20 kg N ha^{-1} $year^{-1}$ for sporocarp production and 20−30 kg N ha^{-1} $year^{-1}$ for belowground EcMF communities in sensitive ecosystems. More recently, syntheses including data from long-term studies estimated a critical load of 10−20 kg N ha^{-1} $year^{-1}$ (Bobbink and Hettelingh, 2011), with Pardo et al. (2011), Pardo and Robin-Abbott, (2011) and Jarvis et al. (2013) estimating critical loads at 5−10 kg N ha^{-1} $year^{-1}$ 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} $year^{-1}$, 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} $year^{-1}$ 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. The EcMF associated with conifers appear to be more sensitive to N deposition than broadleaf-associated EcMF (Arnolds, 1991; Cox et al., 2010; Van der Linde et al., 2018). However, there are no data from broadleaf forests with low N deposition, and empirical critical loads can only go as low as the range of plots sampled. Therefore, our critical load estimates for these ecosystems could be high. More data are required to determine whether we 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 N ha^{-1} $year^{-1}$ (Gilliam et al., 2011; Pardo et al., 2011).

3.2 Recovery from nitrogen deposition

Due to plant-soil microbe-soil feedbacks, acidification, litter accumulation, and long-term storage of soil N, N deposition can have long-lasting legacies (Hasselquist and 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 be slow (Kjøller et al., 2017).

Reduced levels of N deposition are followed by a slow partial recovery of EcMF community structure over many years. 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} $year^{-1}$). Nitrogen fertilization in Norway spruce led to residual fungal community effects even after recovery for 23 years (Choma et al., 2017) or 47 years (Strengbom et al., 2001). In a boreal Scots pine forest, EcM sporocarp production and species richness had recovered to control levels 14−21 years postfertilization, but N availability was still elevated and the EcMF community was still enriched in nitrophilic taxa, especially *Lactarius* (Hasselquist and Högberg, 2014; Högberg et al., 2014).

When EcM forests are replaced by AM forests as a consequence of N deposition and increased P limitation, it is likely that the system becomes increasingly 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 microbe-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 (Suz et al., 2021). Removal of the forest floor is one successful restoration method for EcMF (see e.g., Baar and Kuyper, 1998; De Vries et al., 1995; Smit et al., 2003) but would be difficult to implement at large spatial scales. This management practice also results in losses of exchangeable cations, causing the need for cation fertilization.

4. Causes and functional consequences of community change induced by nitrogen deposition

Nitrogen deposition influences mycorrhizal fungi both directly (fungal-mediated 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 between both viewpoints and propose how both pathways interact (Fig. 6.2). 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.

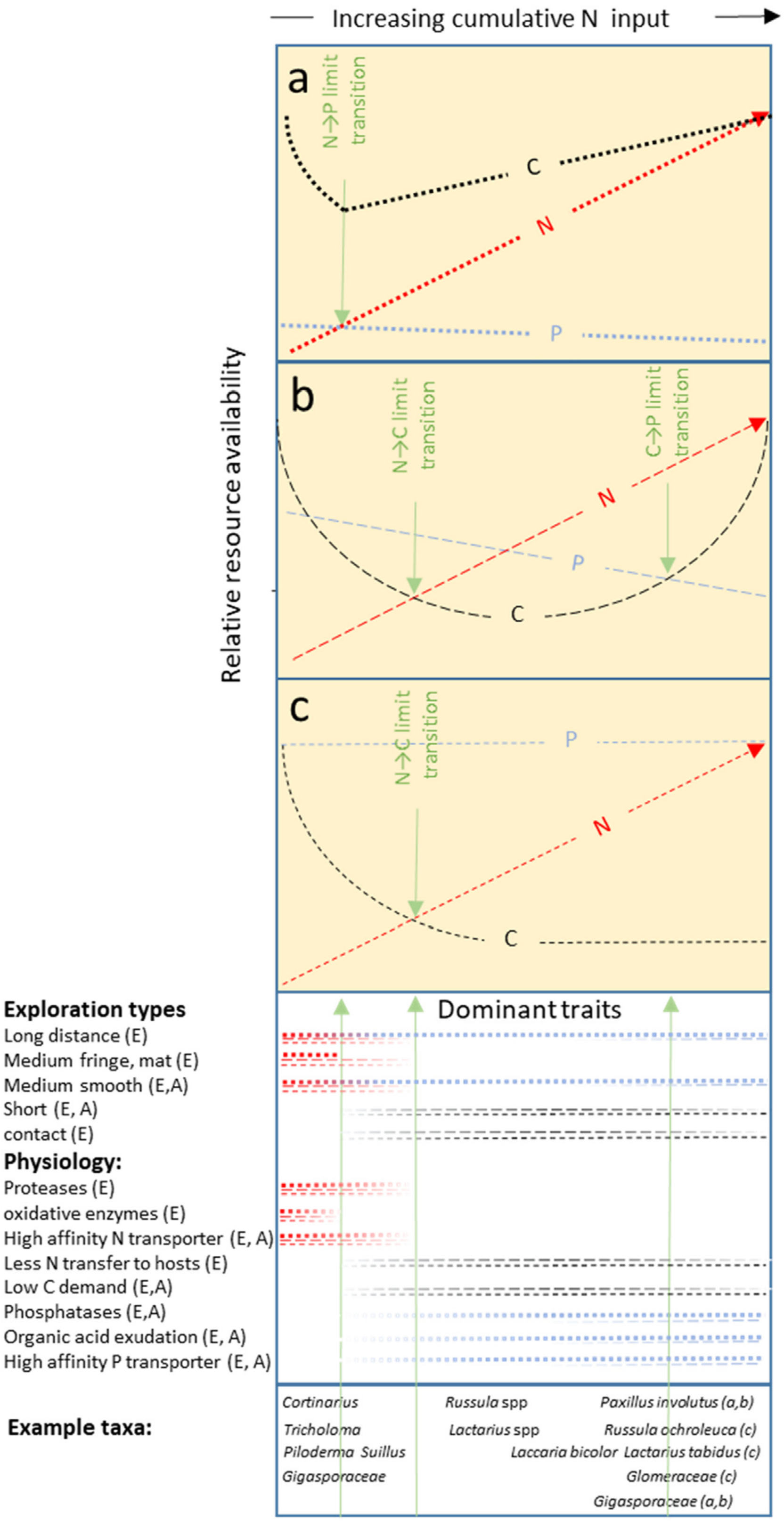

FIG. 6.2 As N availability increases three scenarios of P availability represented in the panels (a) low, (b) medium, and (c) high are hypothesized to lead to different relative N and P limitation of hosts and resultant C transfer from hosts available for ectomycorrhizal activity; and would select differing dominant traits hypothesized to be associated with the shifting limitations. We assume that belowground C transfer to mycorrhizas is high under low N or low P availability, but low under high N and P availability. In **(scenario a)** P is very 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 P availability declines because of uptake, acidification, or other factors, leading to P limitation and an 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. Dominant traits are coded according to their association with a putative limiting resource: red = N limitation; blue = P limitation; black = C limitation; and their dash style corresponds to those of the three scenarios with which they are associated. Putative EcMF and AMF traits are designated with E or A, 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 approximations. (a–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.

4.1 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 recent meta-analysis, Ma et al. (2021b) concluded that N addition reduced fine-root biomass and length of EcM trees by 13% and 17%, respectively, but increased fine-root biomass and length of AM trees by 10% and 42%, respectively. 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, 6 years of fertilization at 100 kg N ha^{-1} year^{-1} suppressed hyphal respiration, although fertilization at 20 kg N ha^{-1} year^{-1} doubled hyphal respiration (Hasselquist et al., 2012). Furthermore, N 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, decreases in percentage of roots colonized by EcMF at high N levels are often assumed (e.g., Franklin et al., 2014), but not consistently observed (Corrales et al., 2017; Lucas and Casper, 2008; Peter et al., 2001; Taylor et al., 2000; Treseder, 2004).

One class of models 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 and 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. These models are consistent with the common observation of greater sensitivity of sporocarp production than root tip colonization to N deposition (Lilleskov et al., 2011), as with enhanced carbohydrate competition due to N deposition, sinks for C that are farthest from the source (EcMF sporocarps) would be expected to 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 toward different suites of beneficial traits (Fig. 6.2). Because fungi vary in their sensitivity to the reduction in C 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 nonbeneficial mycorrhizal interactions. These can occur if both plant and fungus are limited by the same nutrient (Franklin et al., 2014; Treseder and Allen, 2002) or if the plant cannot regulate C 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 availability (Johnson, 2010; Walder and Van der Heijden, 2015). There may also be evolutionary constraints to that solution for EcM trees if the mechanism only uses host N status as the regulating principle. In that case, under N deposition a tree might then reduce allocation to EcMF, including to those fungal species specialized in P acquisition (but see Section 4.3). Köhler et al. (2018) found a positive relationship between EcMF species diversity and P uptake, suggesting that species losses driven by N addition might actually hamper P acquisition.

Furthermore, model formulations are needed that explain the differences between EcM and AM tree responses to N deposition. One approach can be found in a recent modeling effort that explicitly explored the differences between forests with inorganic and organic N economies, conceptualized as corresponding broadly with AM and EcM symbioses, respectively (Rotter et a1., 2020). They hypothesized that "reactive N deposition influences belowground plant investment (C allocation) in mycorrhizas more strongly if the competition between trees for available forms of N is indirect (organic nutrient economy) rather than direct (inorganic nutrient economy)." Their model predicts declines in investment in EcM with increasing N deposition, and also decline in fungi that are less efficient at mining N from organic matter. In contrast, this conceptual model predicts that N deposition will have no negative impact on tree allocation to AMF. This model was parameterized for a spruce and beech forest, even though both are EcM, because the authors could not find appropriate parameter estimates for AM forest. They argue that beech forests are intermediate between EcM conifer and AM forests in their N economies. In their model, these two tree species responded fundamentally differently in their allocation to mycorrhizal fungi under increasing N deposition. Spruce NPP peaked at an optimum allocation to mycorrhizas that shifted lower with N deposition, whereas there was a monotonic increase of NPP in beech with increase in allocation to mycorrhizal fungi. Clearly, this model should be challenged with more data and more realistic constraints. For example, there is no apparent upper threshold built into the inorganic nutrient economy model in which N availability no longer limits aboveground production, and therefore additional investments in mycorrhizas would not positively affect NPP; nor are other nutrients (e.g., P) considered.

4.2 Nitrogen 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), with many fungal genera partitioning along the gradient from nitrophobic to nitrophilic, whereas other genera contain species with divergent responses to N (Section 3.2). 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 and Agerer, 2010; Hobbie et al., 2022). 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 differing resource exchange rates, e.g., if host-specific fungi transfer more soil N per unit of tree C than generalists (Gorissen and Kuyper, 2000; Molina and 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 thought to be more C-demanding (Lilleskov et al., 2011), and hence respond more strongly to changes in C allocation (or C transfer to fungi) 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. 6.1). 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; Lindahl et al., 2021). Although AMF are not known to have such direct organic N-mobilizing capacity, it is possible that AMF with high uptake of amino acids are differentially affected by deposition.

One 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 C 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 and Storer, 2015). Typically, studies do not distinguish between the effect of host C supply limitation versus additional costs of N uptake and transfer. Without a full accounting of C costs of N uptake 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.

Differential ability to assimilate nitrate versus reduced N forms (such as ammonium or amino acids, Finlay et al., 1992) could also contribute to the differential responses of ectomycorrhizal taxa to N deposition. This could reflect both reduced capacity to acquire the N needed for growth and could also influence the C supply from plant hosts, if plants can modify their C flux of labile sugars to ectomycorrhizal fungi depending on the nutrient payoff. The ectomycorrhizal fungus *Paxillus involutus* assimilated nitrate in mycelia at half the rate of ammonium when grown monoxenically with *Fagus sylvatica* (Finlay et al., 1989), and growth on nitrate was only 20% that of growth on ammonium, glutamine, and the dipeptide alanyl-glutamine in axenic culture in eight taxa of *Suillus* and *Rhizopogon* (Antibus et al., 2018). Fungi with poor abilities to assimilate nitrate, such as many *Suillus* species, may acquire nitrate-derived N from their host plants, but this pathway of N acquisition appears to reduce fungal biomass. For example, in culture studies of *Pinus sylvestris* with the nitrophobic *Suillus bovinus* and the nitrophilic *Laccaria laccata* supplied with ammonium or nitrate, nitrate supply reduced colonization by *Suillus* but not *Laccaria*, with this reduction occurring at both high and low rates of N supply (Hobbie et al., 2008). Differential ability to assimilate nitrate provides another mechanism for variable sensitivity of ectomycorrhizal taxa to N deposition.

4.3 Nitrogen-mediated shifts in physiological potential

4.3.1 Shifting limitations and phosphorus mobilization

In an extremely N-poor ecosystem both trees and mycorrhizal fungi may be limited by N (Treseder et al., 2004; Fig. 6.2), 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, potentially 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 acidified soils by N deposition (Fig. 6.2). 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 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. 6.2C). Under many N fertilization scenarios, the medium-distance fringe and mat, and some 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, hemlock and birch seedling roots in densely shaded, low N availability rotting logs under hemlock canopies (Poznanovic et al., 2015), shared the same dominant EcMF 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 flux, 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 nutrients or other benefits.

For AM fungi, a trait-based synthesis suggested that elevated N selected for nitrophilic Glomeraceae over nitrophobic Gigasporaceae (Treseder et al., 2018; but see above). The authors noted that along a regional deposition gradient, the N deposition-associated taxa conferred smaller P benefits 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 had lower external hyphal length, providing an equivocal view of the links between the two (Treseder et al., 2018). The latter could result in lower P benefit in response to N inputs, whereas the former does not link reduced P benefit to N inputs. However, their 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. 6.2A 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. However, the extent to which such changes are ultimately driven by P-induced changes in C availability or by the N:P stoichiometry of soils (Han et al., 2020; Ma et al., 2021a) demands further study of actual C:N:P trade across the symbiotic interface.

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 P- 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 (Grigoriev et al., 2014; Martin et al., 2011) 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 also 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, such as *Paxillus involutus*, *Tylopilus felleus*, and *Imleria badia* (Almeida et al., 2019; Lilleskov et al., 2011), and would be especially good candidates for effective P scavengers under high-N conditions (Fig. 6.2A 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). *Paxillus involutus* is also able to mobilize P from primary inorganic forms (Almeida, 2019). 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., 2019).

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) driven by lower carbohydrate allocation to roots, or lower C transfer from plant hosts to their symbionts. Therefore, one might expect that Gigasporaceae would be favored under N or P limitation when C availability (or symbiotic C transfer) is high, but not under high N and P conditions when C availability/transfer is low (Fig. 6.2). Consistent with this, at P-rich grassland 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 from hosts rather than N availability in their abundance. Additionally, Gigasporaceae greatly enhanced foliar P compared to most genera, including *Glomus* (Treseder et al., 2018). However, studies are needed to determine whether C supply to fungal partners is regulated (at least in part) by C availability in roots or whether host nutrient stoichiometry triggers genetic regulation of transfer of host C to fungal partners, even in the absence of root C limitation. These alternate models should be readily testable given the widespread availability of metatranscriptomics linked with root metabolomics.

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, 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 and hosts 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 or their hyphal-wall associated bacteria (Jiang et al., 2021) also produce acid phosphatases, including free phosphatases in soil solution (Sato et al., 2015), virtually 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 or carboxylates can desorb and mobilize inorganic and organic 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 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* was associated with 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.

4.3.2 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 showing clear correlations between EcMF communities and foliar N:P along N deposition gradients are suggestive (Suz et al., 2021). 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 versus 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. However, indirect effects of N deposition on soil pH with cascading effects on P availability could explain why many studies observed negative effects of N enrichment on the AM symbiosis (Han et al., 2020; Ma et al., 2021a,b).

4.4 Fungal stoichiometry

Fungal stoichiometry itself should also be affected by N deposition, since the relative proportions of N forms available in the soil (e.g., nitrate versus reduced N forms) and the N uptake possible for a given unit of growth should change as soil N availability changes. In addition, C supply to fungi should generally decrease as nutrient status of plants increases. Nitrogen fertilization increased sporocarp N concentrations in *Suillus variegatus*, *Lactarius rufus*, and associated conifers in short-term fertilization experiments in Finland (Ohtonen, 1986). The C:N and N:P ratios of sporocarps have been correlated with foliar and soil C:N and N:P as a marker of N availability. Foliage, sporocarp and soil correlated in C:N across a podzolization gradient in *Pseudotsuga menziesii* stands in British Columbia (Kranabetter et al., 2019) and sporocarp C:N and F horizon C:N correlated across long-term N fertilization gradients in *Pinus sylvestris* stands in central Sweden (Hobbie et al., 2019). Interestingly, the slope of changes in log C:N between sporocarps and soil were very similar in these two studies, with British Columbia values at 0.37 (estimated graphically) and central Sweden values at 0.35 ± 0.05 (estimated from regression analysis). Similarly, ectomycorrhizal taxa increased in N concentration along an anthropogenic N deposition gradient in south-central Alaska (unpublished data, E. Lilleskov), with strong correlations with the inorganic N levels in the organic horizons and also with the P:Al ratio in sporocarps, according to the following equation:

$$\mathrm{Log_e\ N_{sporocarp}} = 1.43 \pm 0.23 \times \mathrm{mineral\ N_{organic\ soil}} + 0.162 \pm 0.034 \times \mathrm{Log_e\ P/Al_{sporocarp}} + [\mathrm{Species}] + 2.99 \pm 0.14\ (\mathrm{adjusted}\ r^2 = 0.72,\ n = 71),$$

where $N_{sporcarp}$ is the N concentration in sporocarps, *mineral* $N_{organic\ soil}$ is the concentration of exchangeable ammonium- + nitrate-N in organic soil, $P/Al_{sporocarp}$ is the ratio of total P to total Al in sporocarps, and *species* is a categorical variable for fungal species. The correlation with P:Al presumably indicated the positive relationship between P uptake and N uptake or between P and N availability. The consistent patterns here indicate that sporocarp N concentration or C:N stoichiometry could be useful metrics for the N status of a site, as affected by the history of N deposition.

4.5 Ectomycorrhizal to arbuscular mycorrhizal 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) and Jo et al. (2019) 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 more limited (Phillips et al., 2013; Rosling et al., 2016), but not absent (Jiang et al., 2021) in AMF. This has relevance to differential AMF-EcMF responses to high N deposition.

4.6 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* (Lin et al., 2014; Tisserant et al., 2013) and *R. clarus* (Kobayashi et al., 2018) revealed low copy number of CAZymes (carbohydrate-active enzymes involved in the breakdown of lignocellulose) compared to many EcMF (Kohler et al., 2015; Kuo et al., 2014). 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 a potentially important mechanism for organic N mobilization (Lindahl and 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 through oxidation of soil organic matter 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. We emphasize again the 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). Bödeker et al. (2014) also found evidence of peroxidase genes in numerous *Cortinarius* species, and enhanced soil peroxidase activity associated with some *Cortinarius* species' root tips. 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. *Cortinarius* species vary somewhat in their sensitivity to N deposition, 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), and also have retained variable numbers of peroxidase genes and other CAZymes (Looney et al., 2022). Elucidation of the distribution of these oxidative enzymes among N-tolerant and N-sensitive species, and tests of their extracellular function, would be enlightening.

The potential of metatranscriptomics lies in revealing not just genetic potential, but gene expression under changing soil nutrient availability. For example, after 25 years of fertilizing Norway spruce with balanced levels of nutrients, metatranscriptomic analyses revealed the change in coordination of mycorrhizal fungal gene expression with hosts as trees shift from nutrient-limited to nutrient-enriched (Law et al., 2022). Specifically, under low soil nutrients, there was strong gene network coordination of hosts with the nitrophobic symbionts *Piloderma* and *Cortinarius*. After fertilization this coordination broke down, and shifted to coordination of host gene networks with the widespread ascomycete, *Cenococcum geophilum*. In tandem with this, trees reduced expression of sugar efflux carriers and increased expression of defense-related genes, consistent with greater retention of C for host metabolism and a reduced support for symbiont metabolism. Although this complete fertilization differs from N fertilization and so inference is limited regarding effects of N deposition, these methods hold great promise for elucidating community functional responses to changing N availability in field settings.

4.7 Interactions with other global change factors

The interactive effects on mycorrhizal symbioses of N deposition with other global change factors, such as climate change, ozone, and elevated CO_2, have been addressed in detail elsewhere (see, e.g., Mohan et al., 2014 and references therein), so are only 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, 2021). Ectomycorrhizal plants increase their biomass in response to elevated CO_2 regardless of N availability, apparently by accelerating N cycling through enhanced N mining by oxidative enzymes (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 and the potential for N immobilization, elevated CO_2 may mitigate some negative impacts of atmospheric N deposition on EcMF, especially on nitrophobic species that are often more C-demanding (see below). In contrast, ozone damage on aboveground tissues of trees has potential negative effects on belowground C allocation and mycorrhizas (Andersen, 2003; Lilleskov, 2005; Mohan et al., 2014). Ozone can sometimes moderate effects of CO_2, e.g., on sporocarp production (Andrew and Lilleskov, 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 C 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.

4.8 Implications of large-scale changes in tree nutrition and tipping points

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 optimize or reduce plant fitness (e.g., in P acquisition). This has been challenging to investigate robustly using dominant organisms at ecosystem scales. However, strong imbalances 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 (Jonard et al., 2015; Veresoglou et al., 2014), 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.

A growing concern is that long-term anthropogenic N deposition can push ecosystems until a threshold is reached where an abrupt shift, or “tipping point”, to an alternative stable ecosystem state occurs that cannot be easily reversed and that need larger reductions in N input than would be predicted from critical loads only. Tipping point theory and its links with ectomycorrhizal feedbacks, phenotypic plasticity, and recovery from N deposition have only recently been investigated (Suz et al., 2021). There are large-scale environmental thresholds in EcM fungal communities linked to increasing N deposition and unbalanced tree foliar N:P ratios that indicate a tipping point in forest ecosystems. The precise tipping point will depend on tree species and their characteristic EcM fungal communities and will likely also vary to a smaller extent with climate and soil properties, but there is evidence that an ectomycorrhizal tipping point is a general phenomenon, at least in Europe. Large-scale repeated-measures data are still needed to quantify temporal change, but national observational and local experimental studies suggest that recovery demands strong reduction in N deposition (Högberg et al., 2011; Van Strien et al., 2018). Furthermore, if N deposition is not halted and forests remain persistently P-limited, a second tipping point may occur where EcM trees are displaced by AM trees, as appears to be happening in North America (Averill et al., 2018; Jo et al., 2019).

4.9 Nitrogen deposition, organic matter decomposition, and soil carbon storage

Whether changes in mycorrhizal communities in response to N deposition can increase C sequestration 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 C accumulation across AM and especially EcM forests (Frey et al., 2014, Kuyper et al., 2023 and references therein). Changes in decomposition could be driven by multiple factors, including changing plant communities, litter chemistry, the environment, and especially both saprotrophic and mycorrhizal community abundance, species richness and composition. 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 C pools and fluxes (Kuyper, 2017; Lindahl and Tunlid, 2015).

Gadgil and Gadgil (1971, 1975) proposed a conceptual model in which EcMF competitively suppress 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 favors 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 opposite mechanism, which relates the decline of EcMF to altered soil C dynamics and C sequestration, is related to the oxidative capabilities of certain EcMF (e.g., species of the genus *Cortinarius*; Bödeker et al., 2014), because these oxidative enzymes can cause extracellular oxidation of soil organic matter. These EcMF are highly sensitive to N deposition (Lilleskov et al., 2011), so their decline under N deposition could contribute to accumulation of soil organic matter. In fact, EcMF possessing suites of extracellular oxidative and hydrolytic enzymes capable of breaking down complex organic, which are less C-limited than saprotrophic fungi, may be more important in their contribution to the degradation of old, recalcitrant soil organic matter than saprotrophic fungi (Lindahl et al., 2007; Lindahl and Tunlid, 2015). Consistent with this hypothesis, Lindahl et al. (2021) found that C storage in Swedish boreal conifer forest soils was 33% lower when *Cortinarius* was present. This relationship was much stronger when a specific clade of this genus, *Cortinarius acutus* (*sensu lato*) was present. Although highly suggestive of a role for *Cortinarius* species in soil organic matter turnover, whether this link is causative or merely correlative requires additional testing. It also points to a need to expand predictions and tests of functional linkage of soil C degradation and sensitivity to N availability across the broad phylogenetic spectrum of EcMF.

Models linking the capacity of EcMF to acquire organic N from soil organic matter to transformations of soil organic matter by free-living saprotrophs 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 C pools and fluxes. Orwin's model, like that of Talbot et al. (2008), predicts that, all other things being equal, decreased EcM activity enhances decomposition rates, while some of Moore's models suggest the opposite. However, N deposition slows down decomposition of litter and soil organic matter, especially by fungi (Kuyper et al., 2023). The relative importance of N deposition on reducing EcMF and ligninolytic saprotrophic basidiomycetes, and hence on enhancing C storage, demands further study.

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 C storage, and not always the most important one across ecosystems (Schmidt et al., 2011). We currently do not know the extent to which oxidative-enzyme activity by EcMF affects C dynamics in both organic horizons with particulate organic matter of plant origin, and in mineral horizons with mineral-associated organic matter with a predominant microbial signature. 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 C storage (e.g., Torn et al., 1997; Doetterl et al., 2015). Averill et al. (2018) stated that an observed shift from EcM to AM trees under N deposition was associated with decreased soil C storage. However, this analysis only included the forest floor and the upper 20 cm in the mineral soil, and so captured effects on surface soil C, but could have missed deeper soil C. Other studies have found elevated mineral soil C effects and total organic C under AMF forests (Craig et al., 2018; Zhu et al., 2018). EcM forests are associated with greater C storage near the surface (Craig et al., 2018; Vesterdal et al., 2013) and so a bias toward surface sampling would overestimate soil C loss with decreased dominance of EcM trees.

5. 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 boreal and temperate forests, the functional consequences are much less well sorted out. Additionally, our understanding of fungal community responses is still limited in tropical forests.

5.1 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 versus in situ assays of taxon-specific enzymatic and nutrient-mobilizing potential under variable levels of inorganic N addition. Currently, our understanding of the obligate versus 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 and Zak, 2018). For example, if certain *Cortinarius* species express intense peroxidative capacity, which is nonspecific 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.

5.2 Testing the concepts presented here in tropical forests

Most studies of N deposition impacts have been conducted 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 and 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 axenic 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 at 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, Boletaceae, *Amanita*, *Sebacina*, and Thelephoraceae (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) in a tropical montane forest can be generalized across tropical EcM forests or are limited to a small N-poor subset of ecosystems. Research is especially needed in tropical and subtropical China, considering its high levels of N deposition (Du et al., 2014, 2016). 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.

Some N addition studies in tropical and subtropical Asia can suffer from interpretive challenges arising from high background N deposition. For example, in a tropical study, He et al. (2021) fertilized with N in a study system already experiencing deposition of $\sim 50\ \mathrm{kg\ N^{-1}\ ha^{-1}\ year^{-1}}$, with control plots lacking any dominant nitrophobic fungi, making it challenging to determine potential N deposition impacts. In this study, even at these high background deposition levels, there were still community shifts associated with N addition, e.g., increases in Russulaceae and declines in *Inocybe* spp. In a subtropical study, Zhao et al. (2020) added N to a mixed AMF and EcMF forest experiencing $\sim 19\ \mathrm{kg\ N^{-1}\ ha^{-1}\ year^{-1}}$ for 5 years, finding no significant effect on mycorrhizal relative abundance and a positive impact of soil NH_4^+-N on mycorrhizal richness. They did not distinguish impacts on AMF versus EcMF.

Again, given that baseline deposition is above critical loads for high-latitude ecosystems, there are challenges in determining N deposition impacts from this study. It is important to establish tropical and subtropical studies of mycorrhizal community response to N inputs (whether gradient or experimental studies) that include sites with the lowest possible N deposition levels.

5.3 Additional areas for further investigation

Some additional areas worthy of future investigation include, in no particular order.

- 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 spatial and temporal 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.

6. Conclusions

Recent studies confirm the clear and strong sensitivity of mycorrhizal fungal communities to N inputs, and this has clear conservation implications given their high beta diversity. The N impact on these communities occurs at all levels, including mycorrhizal types, as well as dominant families, genera, and species. The functional differences at the coarse levels of phylogeny (Dikarya − Glomeromycotina) and mycorrhizal type (EcMF−AMF) are clear, suggesting N-mediated shifts from EcM to AM forests would reduce soil C cycling pathways and the capacity to access organic N and organic P. 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 enzymatic potential for mobilizing organic N, 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.

Acknowledgments

MIB received support from NERC (NE/K006339/1) and EAH received support from the Center for Ecological Research, Kyoto University.

References

Agerer, R., 2006. Fungal relationships and structural identity of their ectomycorrhizae. Mycol. Prog. 5, 107−567.

Alberton, O., Kuyper, T.W., Gorissen, A., 2005. Taking mycocentrism seriously: mycorrhizal fungal and plant responses to elevated CO_2. New Phytol. 167, 859−868.

Albornoz, F.E., Lambers, H., Turner, B.L., Teste, F.P., Laliberté, E., 2016. Shifts in symbiotic associations in plants capable of forming multiple root symbioses across a long-term soil chronosequence. Ecol. Evol. 6, 2368−2377.

Allen, E.B., Egerton-Warburton, L.M., Hilbig, B.E., Valliere, J.M., 2016. Interactions of arbuscular mycorrhizal fungi, critical loads of nitrogen deposition, and shifts from native to invasive species in a southern California shrubland. Botany 94, 425−433.

Almeida, J.P., Rosenstock, N.P., Forsmark, B., Bergh, J., Wallander, H., 2019. Ectomycorrhizal community composition and function in a spruce forest transitioning between nitrogen and phosphorus limitation. Funct. Ecol. 40, 20−31.

Almeida, J.P., 2019. Biomass, Community Structure and Phosphorus Uptake of Ectomycorrhizal Fungi in Response to Phosphorus Limitation and Nitrogen Deposition (Doctoral Dissertation). Lund University.

Andersen, C.P., 2003. Source–sink balance and carbon allocation below ground in plants exposed to ozone. New Phytol. 157, 213–228.

Andrew, C., Lilleskov, E.A., 2009. Productivity and community structure of ectomycorrhizal fungal sporocarps under increased atmospheric CO_2 and O_3. Ecol. Lett. 12, 813–822.

Antibus, R.K., Hobbie, E.A., Cripps, C.L., 2018. Sporocarp δ^{15}N and use of inorganic and organic nitrogen in vitro differ among host-specific suilloid fungi associated with high elevation five-needle pines. Mycoscience 59, 294–302.

Antoninka, A., Reich, P.B., Johnson, N.C., 2011. Seven years of carbon dioxide enrichment, nitrogen fertilization and plant diversity influence arbuscular mycorrhizal fungi in a grassland ecosystem. New Phytol. 192, 200–214.

Arnolds, E., 1991. Decline of ectomycorrhizal fungi in Europe. Agric. Ecosyst. Environ. 35, 209–244.

Averill, C., Turner, B.L., Finzi, A.C., 2014. Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. Nature 505, 543–545.

Averill, C., Dietze, M.C., Bhatnagar, J.M., 2018. Continental-scale nitrogen pollution is shifting forest mycorrhizal associations and soil carbon stocks. Global Change Biol. 24, 4544–4553.

Avis, P.G., McLaughlin, D.J., Dentinger, B.C., Reich, P.B., 2003. Long-term increase in nitrogen supply alters above- and below-ground ectomycorrhizal communities and increases the dominance of *Russula* spp. in a temperate oak savanna. New Phytol. 160, 239–253.

Avis, P.G., Mueller, G.M., Lussenhop, J., 2008. Ectomycorrhizal fungal communities in two North American oak forests respond to nitrogen addition. New Phytol. 179, 472–483.

Baar, J., Kuyper, T.W., 1998. Restoration of aboveground ectomycorrhizal flora in stands of *Pinus sylvestris* (Scots pine) in The Netherlands by removal of litter and humus. Restor. Ecol. 6, 227–237.

Bahram, M., Harend, H., Tedersoo, L., 2014. Network perspectives of ectomycorrhizal associations. Fung. Ecol. 7, 70–77.

Bever, J.D., Richardson, S.C., Lawrence, B.M., Holmes, J., Watson, M., 2009. Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. Ecol. Lett. 12, 13–21.

Bobbink, R., Hettelingh, J.P., 2011. Review and Revision of Empirical Critical Loads and Dose-Response Relationships. Coordination Centre for Effects, National Institute for Public Health and the Environment (RIVM). www.rivm.nl/cce.

Bödeker, I.T.M., Clemmensen, K.E., dDe Boer, W., Martin, F., Olson, Å., Lindahl, B.D., 2014. EcM *Cortinarius* species participate in enzymatic oxidation of humus in northern forest ecosystems. New Phytol. 203, 245–256.

Brassard, B.W., Chen, H.Y., Bergeron, Y., 2009. Influence of environmental variability on root dynamics in northern forests. Crit. Rev. Plant Sci. 28, 179–197.

Braun, S., Thomas, V.F., Quiring, R., Flückiger, W., 2010. Does nitrogen deposition increase forest production? The role of phosphorus. Environ. Pollut. 158, 2043–2052.

Brearley, F.Q., Scholes, J.D., See, L.S., 2005. Nitrogen nutrition and isotopic discrimination in tropical ectomycorrhizal fungi. Res. Microbiol. 156, 184–190.

Camenzind, T., Hempel, S., Homeier, J., Horn, S., Velescu, A., Wilcke, W., Rillig, M.C., 2014. Nitrogen and phosphorus additions impact arbuscular mycorrhizal abundance and molecular diversity in a tropical montane forest. Global Change Biol. 20, 3646–3659.

Chagnon, P.L., Bradley, R.L., Maherali, H., Klironomos, J.N., 2013. A trait-based framework to understand life history of mycorrhizal fungi. Trends Plant Sci. 18, 484–491.

Chen, W., Koide, R.T., Adams, T.S., DeForest, J.L., Cheng, L., Eissenstat, D.M., 2016. Root morphology and mycorrhizal symbioses together shape nutrient foraging strategies of temperate trees. Proc. Natl. Acad. Sci. USA 113, 8741–8746.

Chen, Y.L., Xu, Z.W., Xu, T.L., Veresoglou, S.D., Yang, G.W., Chen, B.D., 2017. Nitrogen deposition and precipitation induced phylogenetic clustering of arbuscular mycorrhizal fungal communities. Soil Biol. Biochem. 115, 233–242.

Choma, M., Rappe-George, M.O., Bárta, J., Čapek, P., Kaštovská, E., Gärdenäs, A.I., Šantrůčková, H., 2017. Recovery of the EcM community after termination of long-term nitrogen fertilisation of a boreal Norway spruce forest. Fung. Ecol. 29, 116–122.

Connell, J.H., Lowman, M.D., 1989. Low-diversity tropical rain forests: some possible mechanisms for their existence. Am. Nat. 134, 88–119.

Corrales, A., Mangan, S.A., Turner, B.L., Dalling, J.W., 2016. An ectomycorrhizal nitrogen economy facilitates monodominance in a neotropical forest. Ecol. Lett. 19, 383–392.

Corrales, A., Turner, B.L., Tedersoo, L., Anslan, S., Dalling, J.W., 2017. Nitrogen addition alters ectomycorrhizal fungal communities and soil enzyme activities in a tropical montane forest. Fung. Ecol. 27, 14–23.

Corrales, A., Henkel, T.W., Smith, M.E., 2018. Ectomycorrhizal associations in the tropics–biogeography, diversity patterns and ecosystem roles. New Phytol. 220, 1076–1091.

Cox, F., Barsoum, N., Lilleskov, E.A., Bidartondo, M.I., 2010. Nitrogen availability is a primary determinant of conifer mycorrhizas across complex environmental gradients. Ecol. Lett. 13, 1103–1113.

Craig, M.E., Turner, B.L., Liang, C., Clay, K., Johnson, D.J., Phillips, R.P., 2018. Tree mycorrhizal type predicts within-site variability in the storage and distribution of soil organic matter. Global Change Biol. 24, 3317–3330.

De Vries, B.W., Jansen, E., Van Dobben, H.F., Kuyper, T.W., 1995. Partial restoration of fungal and plant species diversity by removal of litter and humus layers in stands of Scots pine in The Netherlands. Biodivers. Conserv. 4, 156–164.

Doetterl, S., Stevens, A., Six, J., Merckx, R., Van Oost, K., Pinto, M.C., Casanova-Katny, A., Muñoz, C., Boudin, M., Venegas, E.Z., Boeckx, P., 2015. Soil carbon storage controlled by interactions between geochemistry and climate. Nat. Geosci. 8, 780–783.

Drake, J.E., Gallet-Budynek, A., Hofmockel, K.S., Bernhardt, E.S., Billings, S.A., Jackson, R.B., Johnsen, K.S., Lichter, J., McCarthy, H.R., McCormack, M.L., 2011. Increases in the flux of carbon belowground stimulate nitrogen uptake and sustain the long-term enhancement of forest productivity under elevated CO_2. Ecol. Lett. 14, 349–357.

Du, E., Jiang, Y., Fang, J., de Vries, W., 2014. Inorganic nitrogen deposition in China's forests: status and characteristics. Atmos. Environ. 98, 474–482.

Du, E., de Vries, W., Han, W., Liu, X., Yan, Z., Jiang, Y., 2016. Imbalanced phosphorus and nitrogen deposition in China's forests. Atmos. Chem. Phys. 16, 8571–8579.

Egerton-Warburton, L.M., Allen, E.B., 2000. Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. Ecol. Appl. 10, 484–496.

Egerton-Warburton, L.M., Johnson, N.C., Allen, E.B., 2007. Mycorrhizal community dynamics following nitrogen fertilization: a cross-site test in five grasslands. Ecol. Monogr. 77, 527–544.

Eom, A.H., Hartnett, D.C., Wilson, G.W., Figge, D.A., 1999. The effect of fire, mowing and fertilizer amendment on arbuscular mycorrhizas in tallgrass prairie. Am. Midl. Nat. 142, 55–70.

Ericsson, T., 1995. Growth and shoot: root ratio of seedlings in relation to nutrient availability. In: Nutrient Uptake and Cycling in Forest Ecosystems. Springer, Dordrecht, pp. 205–214.

Fan, Y.X., Lin, F., Yang, L.M., Zhong, X.J., Wang, M.H., Zhou, J.C., Chen, Y.M., Yang, Y.S., 2018. Decreased soil organic P fraction associated with ectomycorrhizal fungal activity to meet increased P demand under N application in a subtropical forest ecosystem. Biol. Fertil. Soils 54, 149–161.

Fellbaum, C.R., Mensah, J.A., Cloos, A.J., Strahan, G.E., Pfeffer, P.E., Kiers, E.T., Bücking, H., 2014. Fungal nutrient allocation in common mycorrhizal networks is regulated by the carbon source strength of individual host plants. New Phytol. 203, 646–656.

Fernandez, C.W., Kennedy, P.G., 2016. Revisiting the ‘Gadgil effect’: do interguild fungal interactions control carbon cycling in forest soils? New Phytol. 209, 1382–1394.

Finlay, R.D., Ek, H., Odham, G., Söderström, B., 1989. Uptake, translocation and assimilation of nitrogen from ^{15}N-labelled ammonium and nitrate sources by intact ectomycorrhizal systems of *Fagus sylvatica* infected with *Paxillus involutus*. New Phytol. 113, 47–55.

Finlay, R.D., Frostegård, A., Sonnerfeldt, A.M., 1992. Utilization of organic and inorganic nitrogen sources by ectomycorrhizal fungi in pure culture and in symbiosis with *Pinus contorta* Dougl. Ex Loud. New Phytol. 120, 105–115.

Fowler, D., Coyle, M., Skiba, U., Sutton, M.A., Cape, J.N., Reis, S., Sheppard, L.J., Jenkins, A., Grizzetti, B., Galloway, J.N., Vitousek, P., 2013. The global nitrogen cycle in the twenty-first century. Phil. Trans. R. Soc. B 368, 20130164.

Franklin, O., Näsholm, T., Högberg, P., Högberg, M.N., 2014. Forests trapped in nitrogen limitation – an ecological market perspective on EcM symbiosis. New Phytol. 203, 657–666.

Frey, S.D., Ollinger, S., Nadelhoffer, K., Bowden, R., Brzostek, E., Burton, A., Caldwell, B.A., Crow, S., Goodale, C.L., Grandy, A.S., Finzi, A., 2014. Chronic nitrogen additions suppress decomposition and sequester soil carbon in temperate forests. Biogeochemistry 121, 305–316.

Gadgil, R.L., Gadgil, P.D., 1971. Mycorrhiza and litter decomposition. Nature 233, 133.

Gadgil, P.D., Gadgil, R.L., 1975. Suppression of litter decomposition by mycorrhizal roots of *Pinus radiata*. N. Z. J. For. Sci. 5, 33–41.

Gilliam, F.S., Goodale, C.L., Pardo, L.H., Geiser, L.H., Lilleskov, E.A., 2011. Eastern temperate forests, Chapter 10. In: Pardo, L.H., Robin-Abbott, M.J., Driscoll, C.T. (Eds.), Assessment of Nitrogen Deposition Effects and Empirical Critical Loads of Nitrogen for Ecoregions of the United States. Gen. Tech. Rep. NRS-80. Newtown Square, PA: US Department of Agriculture, Forest Service, Northern Research Station, pp. 99–116.

Gorissen, A., Kuyper, T.W., 2000. Fungal species-specific responses of ectomycorrhizal Scots pine (*Pinus sylvestris*) to elevated [CO_2]. New Phytol. 46, 163–168.

Govindarajulu, M., Pfeffer, P.E., Jin, H., Abubaker, J., Douds, D.D., Allen, J.W., Bücking, H., Lammers, P.J., Shachar-Hill, Y., 2005. Nitrogen transfer in the arbuscular mycorrhizal symbiosis. Nature 435, 819–823.

Grigoriev, I.V., Nikitin, R., Haridas, S., Kuo, A., Ohm, R., Otillar, R., Riley, R., Salamov, A., Zhao, X., Korzeniewski, F., Smirnova, T., 2014. MycoCosm portal: gearing up for 1000 fungal genomes. Nucleic Acids Res. 42, D699–D704.

Hagerberg, D., Thelin, G., Wallander, H., 2003. The production of ectomycorrhizal mycelium in forests: relation between forest nutrient status and local mineral sources. Plant Soil 252, 279–290.

Han, Y., Feng, J., Han, M., Zhu, B., 2020. Responses of arbuscular mycorrhizal fungi to nitrogen addition: a meta-analysis. Global Change Biol. 26, 7229–7241.

Hasselquist, N.J., Högberg, P., 2014. Dosage and duration effects of nitrogen addition on EcM sporocarps production and functioning: an example from two N-limited boreal forests. Ecol. Evol. 4, 3015–3026.

Hasselquist, N.J., Metcalfe, D.B., Högberg, P., 2012. Contrasting effects of low and high nitrogen additions on soil CO_2 flux components and ectomycorrhizal fungal sporocarp production in a boreal forest. Global Change Biol. 18, 3596–3605.

He, J., Jiao, S., Tan, X., Wei, H., Ma, X., Nie, Y., Liu, J., Lu, X., Mo, J., Shen, W., 2021. Adaptation of soil fungal community structure and assembly to long- versus short-term nitrogen addition in a tropical forest. Front. Microbiol. 12, 689674.

Hobbie, E.A., Agerer, R., 2010. Nitrogen isotopes in EcM sporocarps correspond to belowground exploration types. Plant Soil 327, 71–83.

Hobbie, E.A., Colpaert, J.V., White, M.W., Ouimette, A.P., Macko, S.A., 2008. Nitrogen form, availability, and mycorrhizal colonization affect biomass and nitrogen isotope patterns in *Pinus sylvestris*. Plant Soil 310, 121–136.

Hobbie, E.A., Chen, J., Hasselquist, N.J., 2019. Fertilization alters nitrogen isotopes and concentrations in ectomycorrhizal fungi and soil in pine forests. Fung. Ecol. 39, 267–275.

Hobbie, E.A., Bendiksen, K., Thorp, N.R., Ohenoja, E., Ouimette, A.P., 2022. Climate records, isotopes, and C:N stoichiometry reveal carbon and nitrogen flux dynamics differ between functional groups of ectomycorrhizal fungi. Ecosystems 25, 1207–1217.

Hodge, A., Storer, K., 2015. Arbuscular mycorrhiza and nitrogen: implications for individual plants through to ecosystems. Plant Soil 386, 1–9.

Hoeksema, J.D., Chaudhary, V.B., Gehring, C.A., Johnson, N.C., Karst, J., Koide, R.T., Pringle, A., Zabinski, C., Bever, J.D., Moore, J.C., Wilson, G.W., 2010. A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. Ecol. Lett. 13, 394–407.

Hofland-Zijlstra, J., Berendse, F., 2009. The effect of nutrient supply and light intensity on tannins and mycorrhizal colonisation in Dutch heathland ecosystems. Plant Ecol. 201, 661–675.

Högberg, M.N., Briones, M.J., Keel, S.G., Metcalfe, D.B., Campbell, C., Midwood, A.J., Thornton, B., Hurry, V., Linder, S., Näsholm, T., Högberg, P., 2010. Quantification of effects of season and nitrogen supply on tree below-ground carbon transfer to ectomycorrhizal fungi and other soil organisms in a boreal pine forest. New Phytol. 187, 485–493.

Högberg, P., Johannisson, C., Yarwood, S., Callesen, I., Näsholm, T., Myrold, D.D., Högberg, M.N., 2011. Recovery of ectomycorrhiza after ‘nitrogen saturation’ of a conifer forest. New Phytol. 189, 515–525.

Högberg, M.N., Yarwood, S.A., Myrold, D.D., 2014. Fungal but not bacterial soil communities recover after termination of decadal nitrogen additions to boreal forest. Soil Biol. Biochem. 72, 35–43.

Hu, H., He, L.Y., Ma, H.F., Wang, J.Y., Li, Y., Wang, J., Guo, X.Y., Ren, C.J., Bai, H.Y., Zhao, F.Z., 2022. Responses of AM fungal abundance to the drivers of global climate change: a meta-analysis. Sci. Total Environ. 805, 150362.

Ingestad, T., Ågren, G.I., 1991. The influence of plant nutrition on biomass allocation. Ecol. Appl. 1, 168–174.

Jarvis, S., Woodward, S., Alexander, I.J., Taylor, A.F.S., 2013. Regional scale gradients of climate and nitrogen deposition drive variation in ectomycorrhizal fungal communities associated with native Scots pine. Global Change Biol. 19, 1688–1696.

Jiang, S., Liu, Y., Luo, J., Qin, M., Johnson, N.C., Öpik, M., Vasar, M., Chai, Y., Zhou, X., Mao, L., Du, G., 2018. Dynamics of arbuscular mycorrhizal fungal community structure and functioning along a nitrogen enrichment gradient in an alpine meadow ecosystem. New Phytol. 220, 1222–1235.

Jiang, F., Zhang, L., Zhou, J., George, T.S., Feng, G., 2021. Arbuscular mycorrhizal fungi enhance mineralisation of organic phosphorus by carrying bacteria along their extraradical hyphae. New Phytol. 230, 304–315.

Jo, I., Fei, S., Oswalt, C.M., Domke, G.M., Phillips, R.P., 2019. Shifts in dominant tree mycorrhizal associations in response to anthropogenic impacts. Sci. Adv. 5, eaav6358.

Johnson, N.C., Rowland, D.L., Corkidi, L., Egerton-Warburton, L.M., Allen, E.B., 2003. Nitrogen enrichment alters mycorrhizal allocation at five mesic to semiarid grasslands. Ecology 84, 1895–1908.

Johnson, N.C., 2010. Resource stoichiometry elucidates the structure and function of AM across scales. New Phytol. 185, 631–647.

Jonard, M., Fürst, A., Verstraeten, A., Thimonier, A., Timmermann, V., Potočić, N., Waldner, P., Benham, S., Hansen, K., Merilä, P., Ponette, Q., 2015. Tree mineral nutrition is deteriorating in Europe. Global Change Biol. 21, 418–430.

Kanakidou, M., Myriokefalitakis, S., Daskalakis, N., Fanourgakis, G., Nenes, A., Baker, A.R., Tsigaridis, K., Mihalopoulos, N., 2016. Past, present, and future atmospheric nitrogen deposition. J. Atmos. Sci. 73, 2039–2047.

Karst, J., Wasyliw, J., Birch, J.D., Franklin, J., Chang, S.X., Erbilgin, N., 2021. Long-term nitrogen addition does not sustain host tree stem radial growth but doubles the abundance of high-biomass ectomycorrhizal fungi. Global Change Biol. 27, 4125–4138.

Kiers, E.T., Duhamel, M., Beesetty, Y., Mensah, J.A., Franken, O., Verbruggen, E., Fellbaum, C.R., Kowalchuk, G.A., Hart, M.M., Bago, A., Palmer, T.M., 2011. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. Science 333, 880–882.

Kjøller, R., Cruz-Paredes, C., Clemmensen, K.E., 2017. Ectomycorrhizal fungal responses to forest liming and wood ash addition: review and meta-analysis. In: Soil Biological Communities and Ecosystem Resilience. Springer, pp. 223–252.

Klironomos, J.N., Hart, M.M., 2001. Food-web dynamics: animal nitrogen swap for plant carbon. Nature 410, 651–652.

Klugh, K.R., Cumming, J.R., 2007. Variations in organic acid exudation and aluminum resistance among arbuscular mycorrhizal species colonizing *Liriodendron tulipifera*. Tree Physiol. 27, 1103–1112.

Kobayashi, Y., Maeda, T., Yamaguchi, K., Kameoka, H., Tanaka, S., Ezawa, T., Shigenobu, S., Kawaguchi, M., 2018. The genome of *Rhizophagus clarus* HR1 reveals a common genetic basis for auxotrophy among arbuscular mycorrhizal fungi. BMC Genom. 19, 465.

Kohler, A., Kuo, A., Nagy, L.G., Morin, E., Barry, K.W., Buscot, F., Canbäck, B., Choi, C., Cichocki, N., Clum, A., Colpaert, J., Copeland, A., Costa, M.D., Doré, J., Floudas, D., Gay, G., Girlanda, M., Henrissat, B., Hermann, ., Hess, J., Högberg, N., Johansson, T., Khouja, H.-R., LaButt, K., Lahrmann, U., Levasseur, A., Lindquist, E.A., Lipzen, A., Marmeissem, R., Martino, E., Murat, C., Ngan, C.Y., Nehls, U., Plett, J.M., Pringle, A., Ohm, R.A., Perotto, S., Peter, M., Riley, R., Rineau, F., Ruytinx, J., Salamov, A., Shah, F., Sun, H., Tarkka, M., Tritt, A., Veneault-Fourrey, C., Zuccaro, A., , Mycorrhizal Genomics Initiative Consortium, Tunlid, A., Grigoriev, I.V., Hibbett, D.S., Martin, F., 2015. Convergent losses of decay mechanisms and rapid turnover of symbiosis genes in mycorrhizal mutualists. Nat. Genet. 47, 410–415.

Köhler, J., Yang, N., Pena, R., Raghavan, V., Polle, A., Meier, I.C., 2018. Ectomycorrhizal fungal diversity increases phosphorus uptake efficiency of European beech. New Phytol. 220, 1200–1210.

Kranabetter, J.M., Harman-Denhoed, R., Hawkins, B.J., 2019. Saprotrophic and ectomycorrhizal fungal sporocarp stoichiometry (C: N: P) across temperate rainforests as evidence of shared nutrient constraints among symbionts. New Phytol. 221, 482–492.

Kuo, A., Kohler, A., Martin, F.M., Grigoriev, I.V., 2014. Expanding genomics of mycorrhizal symbiosis. Front. Microbiol. 4 (5), 582.

Kuyper, T.W., Janssens, I.A., Vicca, S., 2023. Impacts of nitrogen deposition on soil carbon dynamics in forests. In: Du, E., de Vries, W. (Eds.), Atmospheric Nitrogen Deposition to Global Forests: Spatial Variation, Impacts and Management Implications. Academic Press (Chapter 8).

Kuyper, T.W., 2012. Ectomycorrhiza and the open nitrogen cycle in an afrotropical rainforest. New Phytol. 125, 728–729.

Kuyper, T.W., 2017. Carbon and energy sources of mycorrhizal fungi: obligate symbionts or latent saprotrophs? In: NC Johnson, N.C., C Gehring, C., Jansa, J. (Eds.), Mycorrhizal Mediation of Soil—Fertility, Structure, and Carbon Storage. Elsevier, pp. 357–374.

Lambers, H., Shane, M.W., Cramer, M.D., Pearse, S.J., Veneklaas, E.J., 2006. Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. Ann. Bot. 98, 693–713.

Law, S.R., Serrano, A.R., Daguerre, Y., Sundh, J., Schneider, A.N., Stangl, Z.R., Castro, D., Grabherr, M., Näsholm, T., Street, N.R., Hurry, V., 2022. Metatranscriptomics captures dynamic shifts in mycorrhizal coordination in boreal forests. Proc. Natl. Acad. Sci. USA 119, e2118852119.

Leifheit, E., Verbruggen, E., Rillig, M., 2015. Arbuscular mycorrhizal fungi reduce decomposition of woody plant litter while increasing soil aggregation. Soil Biol. Biochem. 81, 323–328.

Li, Y., Niu, S., Yu, G., 2016. Aggravated phosphorus limitation on biomass production under increasing nitrogen loading: a meta-analysis. Global Change Biol. 22, 934–943.

Lilleskov, E.A., Fahey, T.J., Lovett, G.M., 2001. Ectomycorrhizal fungal aboveground community change over an atmospheric nitrogen deposition gradient. Ecol. Appl. 11, 397–410.

Lilleskov, E.A., Fahey, T.J., Horton, T.R., Lovett, G.M., 2002. Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska. Ecology 83, 104–115.

Lilleskov, E.A., Hobbie, E.A., Horton, T.R., 2011. Conservation of ectomycorrhizal fungi: exploring the linkages between functional and taxonomic responses to anthropogenic N deposition. Fung. Ecol. 4, 174−183.

Lilleskov, E.A., Kuyper, T.W., Bidartondo, M.I., Hobbie, E.A., 2019. Atmospheric nitrogen deposition impacts on the structure and function of forest mycorrhizal communities: a review. Environ. Pollut. 246, 148−162.

Lilleskov, E.A., 2005. How do composition, structure, and function of mycorrhizal fungal communities respond to nitrogen deposition and ozone exposure? In: Dighton, J. (Ed.), The Fungal Community. CRC Press, pp. 769−801.

Lin, K., Limpens, E., Zhang, Z., Ivanov, S., Saunders, D.G., Mu, D., Pang, E., Cao, H., Cha, H., Lin, T., Zhou, Q., Shang, Y., Li, Y., Sharma, T., Van Velzen, R., De Ruijter, N., Aanen, D.K., Win, J., Kamoun, S., Bisseling, T., Geurts, R., Huang, S.W., 2014. Single nucleus genome sequencing reveals high similarity among nuclei of an endomycorrhizal fungus. PLoS Genet. 10, e1004078.

Lindahl, B.D., Tunlid, A., 2015. Ectomycorrhizal fungi—potential organic matter decomposers, yet not saprotrophs. New Phytol. 205, 1443−1447.

Lindahl, B.D., Ihrmark, K., Boberg, J., Trumbore, S.E., Högberg, P., Stenlid, J., Finlay, R.D., 2007. Spatial separation of litter decomposition and mycorrhizal nitrogen uptake in a boreal forest. New Phytol. 173, 611−620.

Lindahl, B.D., Kyaschenko, J., Varenius, J., Clemmensen, K.E., Dahlberg, A., Karltun, E., Stendahl, J., 2021. A group of ectomycorrhizal fungi restricts organic matter accumulation in boreal forest. Ecol. Lett. 24, 1341−1351.

Liu, X., Zhang, Y., Han, W., Tang, A., Shen, J., Cui, Z., Vitousek, P., Erisman, J.W., Goulding, K., Christie, P., Fangmeier, A., 2013. Enhanced nitrogen deposition over China. Nature 494, 459.

Looney, B., Miyauchi, S., Morin, E., Drula, E., Courty, P.E., Kohler, A., Kuo, A., LaButti, K., Pangilinan, J., Lipzen, A., Riley, R., 2022. Evolutionary transition to the ectomycorrhizal habit in the genomes of a hyper-diverse lineage of mushroom-forming fungi. New Phytol. https://doi.org/10.1111/nph.17892.

Lucas, R.W., Casper, B.B., 2008. Ectomycorrhizal community and extracellular enzyme activity following simulated atmospheric N deposition. Soil Biol. Biochem. 40, 1662−1669.

Ma, X.C., Geng, Q.H., Zhang, H.G., Bian, C.Y., Chen, H.Y.H., Jiang, D.L., Xu, X., 2021a. Global negative effects of nutrient enrichment on arbuscular mycorrhizal fungi, plant diversity and ecosystem multifunctionality. New Phytol. 229, 2957−2969.

Ma, X.M., Zhu, B., Nie, Y.X., Liu, Y., Kuzyakov, Y., 2021b. Root and mycorrhizal strategies for nutrient acquisition in forests under nitrogen deposition: a meta-analysis. Soil Biol. Biochem. 163 art. 108418.

Martin, F., Aerts, A., Ahrén, D., Brun, A., Danchin, E.G., Duchaussoy, F., Gibon, J., Kohler, A., Lindquist, E., Pereda, V., Salamov, A., 2008. The genome of *Laccaria bicolor* provides insights into mycorrhizal symbiosis. Nature 452, 88−92.

Martin, F., Cullen, D., Hibbett, D., Pisabarro, A., Spatafora, J.W., Baker, S.E., Grigoriev, I.V., 2011. Sequencing the fungal tree of life. New Phytol. 190, 818−821.

Mohan, J.E., Cowden, C.C., Baas, P., Dawadi, A., Frankson, P.T., Helmick, K., Hughes, E., Khan, S., Lang, A., Machmuller, M., Taylor, M., 2014. Mycorrhizal fungi mediation of terrestrial ecosystem responses to global change: mini-review. Fung. Ecol. 10, 3−19.

Molina, R., Horton, T.R., 2015. Mycorrhiza specificity: its role in the development and function of common mycelial networks. In: Mycorrhizal Networks. Springer, Dordrecht, pp. 1−39.

Moore, J.A.M., Jiang, J., Post, W.M., Classen, A.T., 2015. Decomposition by ectomycorrhizal fungi alters soil carbon storage in a simulation model. Ecosphere 6, 29.

Moore, J.A., Anthony, M.A., Pec, G.J., Trocha, L.K., Trzebny, A., Geyer, K.M., Van Diepen, L.T.A., Frey, S.D., 2021. Fungal community structure and function shifts with atmospheric nitrogen deposition. Global Change Biol. 27, 1349−1364.

Morrison, E.W., Frey, S.D., Sadowsky, J.J., van Diepen, L.T.,A., Thomas, W.K., Pringle, A., 2016. Chronic nitrogen additions fundamentally restructure the soil fungal community in a temperate forest. Fung. Ecol. 23, 48−57.

Muszewska, A., Stepniewska-Dziubinska, M.M., Steczkiewicz, K., Pawlowska, J., Dziedzic, A., Ginalski, K., 2017. Fungal lifestyle reflected in serine protease repertoire. Sci. Rep. 7, 9147.

Nagy, L.G., Riley, R., Tritt, A., Adam, C., Daum, C., Floudas, D., Sun, H., Yadav, J.S., Pangilinan, J., Larsson, K.H., Matsuura, K., 2015. Comparative genomics of early-diverging mushroom-forming fungi provides insights into the origins of lignocellulose decay capabilities. Mol. Biol. Evol. 33, 959−970.

Ohtonen, R., 1986. The effect of forest fertilization on the nitrogen content of the fruit-bodies of two mycorrhizal fungi, *Lactarius rufus* and *Suillus variegatus*. Ann. Bot. Fenn. 23, 189−203.

Orwin, K.H., Kirschbaum, M.U.F., St John, M.G., Dickie, I.A., 2011. Organic nutrient uptake by mycorrhizal fungi enhances ecosystem carbon storage: a model-based assessment. Ecol. Lett. 14, 493−502.

Pardo, L.H., Robin-Abbott, M.J., 2011. Assessment of nitrogen deposition effects and empirical critical loads of nitrogen for ecoregions of the United States. In: Gen. Tech. Rep. NRS-80. Newtown Square, PA: US Department of Agriculture, Forest Service, Northern Research Station, p. 291.

Pardo, L.H., Fenn, M.E., Goodale, C.L., Geiser, L.H., Driscoll, C.T., Allen, E.B., Baron, J.S., Bobbink, R., Bowman, W.D., Clark, C.M., et al., 2011. Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. Ecol. Appl. 21, 3049−3082.

Parts, K., Tedersoo, L., Lohmus, K., Kupper, P., Rosenvald, K., Sober, A., Ostonen, I., 2013. Increased air humidity and understory composition shape short root traits and the colonizing ectomycorrhizal fungal community in silver birch stands. For. Ecol. Manag. 310, 720−728.

Peay, K.G., Kennedy, P.G., Davies, S.J., Tan, S., Bruns, T.D., 2010. Potential link between plant and fungal distributions in a dipterocarp rainforest: community and phylogenetic structure of tropical ectomycorrhizal fungi across a plant and soil ecotone. New Phytol. 185 (2), 529−542.

Pellitier, P.T., Zak, D.R., 2018. Ectomycorrhizal fungi and the enzymatic liberation of nitrogen from soil organic matter: why evolutionary history matters. New Phytol. 217, 68−73.

Peter, M., Ayer, F., Egli, S., Honegger, R., 2001. Above-and belowground community structure of ectomycorrhizal fungi in three Norway spruce (*Picea abies*) stands in Switzerland. Can. J. Bot. 79, 1134−1151.

Phillips, R.P., Meier, I.C., Bernhardt, E.S., Grandy, A.S., Wickings, K., Finzi, A.C., 2012. Roots and fungi accelerate carbon and nitrogen cycling in forests exposed to elevated CO_2. Ecol. Lett. 15, 1042−1049.

Phillips, R.P., Brzostek, E., Midgley, M.G., 2013. The mycorrhizal associated nutrient economy: a new framework for predicting carbon-nutrient couplings in temperate forests. New Phytol. 199, 41–51.

Plassard, C., Louche, J., Ali, M.A., Duchemin, M., Legname, E., Cloutier-Hurteau, B., 2011. Diversity in phosphorus mobilisation and uptake in ectomycorrhizal fungi. Ann. For. Sci. 68, 33–43.

Poorter, H., Nagel, O., 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO_2, nutrients and water: a quantitative review. Funct. Plant Biol. 27, 595–607.

Poznanovic, S.K., Lilleskov, E.A., Webster, C.R., 2015. Sharing rotting wood in the shade: ectomycorrhizal communities of co-occurringbirch and hemlock seedlings. Mycorrhiza 25, 153–164.

Püschel, D., Janoušková, M., Hujslová, M., Slavíková, R., Gryndlerová, H., Jansa, J., 2016. Plant–fungus competition for nitrogen erases mycorrhizal growth benefits of *Andropogon gerardii* under limited nitrogen supply. Ecol. Evol. 6, 4332–4346.

Read, D.J., Perez-Moreno, J., 2003. Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? New Phytol. 157, 475–492.

Read, D.J., 1991. Mycorrhizas in ecosystems. Experientia 47, 376–391.

Rimington, W.R., Duckett, J.G., Field, K.J., Bidartondo, M.I., Pressel, S., 2020. The distribution and evolution of fungal symbioses in ancient lineages of land plants. Mycorrhiza 30, 23–49.

Rosling, A., Midgley, M.G., Cheeke, T., Urbina, H., Fransson, P., Phillips, R.P., 2016. Phosphorus cycling in deciduous forest soil differs between stands dominated by ecto- and AM trees. New Phytol. 209, 1184–1195.

Rotter, P., Loreau, M., de Mazancourt, C., 2020. Why do forests respond differently to nitrogen deposition? A modelling approach. Ecol. Model. 425, 109034.

Sato, T., Ezawa, T., Cheng, W., Tawaraya, K., 2015. Release of acid phosphatase from extraradical hyphae of arbuscular mycorrhizal fungus *Rhizophagus clarus*. Soil Sci. Plant Nutr. 61, 269–274.

Schmidt, M.W., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D.A., Nannipieri, P., 2011. Persistence of soil organic matter as an ecosystem property. Nature 478, 49–56.

Shah, F., Nicolás, C., Bentzer, J., Ellström, M., Smits, M., Rineau, F., Canbäck, B., Floudas, D., Carleer, R., Lackner, G., Braesel, J., Hoffmeister, D., Henrissat, B., Ahrén, D., Johansson, T., Hibbett, D.S., Martin, F., Persson, P., Tunlid, A., 2016. Ectomycorrhizal fungi decompose soil organic matter using oxidative mechanisms adapted from saprotrophic ancestors. New Phytol. 209, 1705–1719.

Simmel, J., Bässler, C., Poschlod, P., 2017. Ellenberg indicator values for macromycetes – a methodological approach and first applications. Fung. Ecol. 27, 202–212.

Smit, E., Veenman, C., Baar, J., 2003. Molecular analysis of ectomycorrhizal basidiomycete communities in a *Pinus sylvestris* L. stand reveals long-term increased diversity after removal of litter and humus layers. FEMS Microbiol. Ecol. 45, 49–57.

Smith, S.E., Read, D.J., 2010. Mycorrhizal Symbiosis. Academic Press.

Smith, A.J., Potvin, L.R., Lilleskov, E.A., 2015. Fertility-dependent effects of ectomycorrhizal fungal communities on white spruce seedling nutrition. Mycorrhiza 25, 649–662.

Smithwick, E.A., Eissenstat, D.M., Lovett, G.M., Bowden, R.D., Rustad, L.E., Driscoll, C.T., 2013. Root stress and nitrogen deposition: consequences and research priorities. New Phytol. 197, 712–719.

Spatafora, J.W., Chang, Y., Benny, G.L., Lazarus, K., Smith, M.E., Berbee, M.L., Bonito, G., Corradi, N., Grigoriev, I., Gryganskyi, A., James, T.Y., 2016. A phylum-level phylogenetic classification of zygomycete fungi based on genome-scale data. Mycologia 108, 1028–1046.

Stevens, C.J., David, T.I., Storkey, J., 2018. Atmospheric nitrogen deposition in terrestrial ecosystems: its impact on plant communities and consequences across trophic levels. Funct. Ecol. 32, 1757–1769.

Strengbom, J., Nordin, A., Näsholm, T., Ericson, L., 2001. Slow recovery of boreal forest ecosystem following decreased nitrogen input. Funct. Ecol. 15, 451–457.

Suz, L.M., Barsoum, N., Benham, S., Dietrich, H.-P., Fetzer, K.D., Fischer, R., García, P., Gehrmann, J., Kristöfel, F., Manninger, M., Neagu, S., Nicolas, M., Oldenburger, J., Raspe, S., Sánchez, G., Schröck, H.W., Schubert, A., Verheyen, K., Verstraeten, A., Bidartondo, M.I., 2014. Environmental drivers of EcM communities in Europe's temperate oak forests. Mol. Ecol. 23, 5628–5644.

Suz, L.M., Kallow, S., Reed, K., Bidartondo, M.I., Barsoum, N., 2017. Pine mycorrhizal communities in pure and mixed pine-oak forests: abiotic environment trumps neighboring oak host effects. For. Ecol. Manag. 406, 370–380.

Suz, L.M., Bidartondo, M.I., Van der Linde, S., Kuyper, T.W., 2021. Ectomycorrhizas and tipping points in forest ecosystems. New Phytol. 232, 1700–1707.

Talbot, J.M., Treseder, K.K., 2010. Controls over mycorrhizal uptake of organic nitrogen. Pedobiologia 53, 169–179.

Talbot, J.M., Allison, S.D., Treseder, K.K., 2008. Decomposers in disguise: mycorrhizal fungi as regulators of soil dynamics in ecosystems under global change. Funct. Ecol. 22, 955–963.

Talbot, J.M., Bruns, T.D., Smith, D.P., Branco, S., Glassman, S.I., Erlandson, S., Vilgalys, R., Peay, K.G., 2013. Independent roles of ectomycorrhizal and saprotrophic communities in soil organic matter decomposition. Soil Biol. Biochem. 57, 282–291.

Taniguchi, T., Kataoka, R., Futai, K., 2008. Plant growth and nutrition in pine (*Pinus thunbergii*) seedlings and dehydrogenase and phosphatase activity of ectomycorrhizal root tips inoculated with seven individual ectomycorrhizal fungal species at high and low nitrogen conditions. Soil Biol. Biochem. 40, 1235–1243.

Taylor, A.F., Martin, F., Read, D.J., 2000. Fungal diversity in ectomycorrhizal communities of Norway spruce [*Picea abies* (L.) Karst.] and beech (*Fagus sylvatica* L.) along north-south transects in Europe. In: Carbon and Nitrogen Cycling in European Forest Ecosystems 2000. Springer, Berlin, Heidelberg, pp. 343–365.

Tedersoo, L., Smith, M.E., 2017. Ectomycorrhizal fungal lineages: detection of four new groups and notes on consistent recognition of EcM ectomycorrhizal taxa in high-throughput sequencing studies. In: Tedersoo, L. (Ed.), Biogeography of Mycorrhizal Symbiosis. Ecology Studies, vol. 230, pp. 125–142.

Tedersoo, L., Naadel, T., Bahram, M., Pritsch, K., Buegger, F., Leal, M., Kõljalg, U., Põldmaa, K., 2012. Enzymatic activities and stable isotope patterns of ectomycorrhizal fungi in relation to phylogeny and exploration types in an afrotropical rain forest. New Phytol. 195, 832–843.

Tedersoo, L., Bahram, M., Põlme, S., Kõljalg, U., Yorou, N.S., Wijesundera, R., Ruiz, L.V., Vasco-Palacios, A.M., Thu, P.Q., Suija, A., Smith, M.E., Sharp, C., Saluveer, E., Saitta, A., Rosas, M., Riit, T., Ratkowsky, D., Pritsch, K., Põldmaa, K., Piepenbring, M., Phosri, C., Peterson, M., Parts, M., Pärtel, K., Otsing, E., Nouhra, E., Njouonkou, A.L., Nilsson, R.H., Morgado, L.N., Mayor, May, T.W., Majuakim, L., Lodge, D.J., Lee, S.S., Larsson, K.H., Kohout, P., Hosaka, K., Hiiesalu, I., Henkel, T.W., Harend, H., Guo, L.D., Greslebin, A., Grelet, G., Geml, J., Gates, G., Dunstan, W., Dunk, C., Drenkhan, R., Dearnaley, J., De Kesel, A., Dang, T., Chen, X., Buegger, F., Brearley, F.Q., Bonito, G., Anslan, S., Abell, S., Abarenkov, K., 2014. Global diversity and geography of soil fungi. Science 346, 1256688.

Terrer, C., Vicca, S., Hungate, B.A., Phillips, R.P., Prentice, I.C., 2016. Mycorrhizal association as a primary control of the CO_2 fertilization effect. Science 353, 72−74.

Terrer, C., Phillips, R.P., Hungate, B.A., Rosende, J., Pett-Ridge, J., Craig, M.E., Van Groenigen, K.J., Keenan, T.F., Sulman, B.N., Stocker, B.D., Reich, P.B., Pellegrini, A.F.A., Pendall, E., Zhang, H., Evans, R.D., Carrillo, Y., Fisher, J.B., Van Sundert, K., Vicca, S., Jackson, R.B., 2021. A trade-off between plant and soil carbon storage under elevated CO_2. Nature 591, 599−603.

Teste, F.P., Jones, M.D., Dickie, I.D., 2020. Dual-mycorrhiza plants: their ecology and relevance. New Phytol. 225, 1835−1851.

Tian, D.S., Niu, S.L., 2015. A global analysis of soil acidification caused by nitrogen addition. Environ. Res. Lett. 10, 024019.

Tisserant, E., Malbreil, M., Kuo, A., Kohler, A., Symeonidi, A., Balestrini, R., Charron, P., Duensing, N., Dit Frey, N.F., Gianinazzi-Pearson, V., Gilbert, L.B., Handa, Y., Herr, J.R., Hijri, M., Koil, R., Kawaguchi, M., Krajinski, F., Lammers, P.J., Madclaux, F.G., Murat, C., Morin, E., Ndikumana, S., Pagni, M., Petitpierre, D., Requena, N., Rosikiewicz, P., Riley, R., Saito, K., San Clemente, H., Shapiro, H., Van Tuinen, D., Bécard, G., Bonfante, P., Paszowski, U., Schar-Hill, Y.Y., Tuskan, G., Young, J.P.W., Sanders, I.R., Henrissat, B., Rensing, S.A., Grigoriev, I.V., Corradi, N., Roux, C., Martin, F., 2013. Genome of an AM arbuscular mycorrhizal fungus provides insight into the oldest plant symbiosis. Proc. Nat. Acad. Sci. USA 110, 20117−20122.

Torn, M.S., Trumbore, S.E., Chadwick, O.A., Vitousek, P.M., Hendricks, D.M., 1997. Mineral control of soil organic carbon storage and turnover. Nature 389, 170−173.

Treseder, K.K., Allen, M.F., 2000. Mycorrhizal fungi have a potential role in soil carbon storage under elevated CO_2 and nitrogen deposition. New Phytol. 147, 189−200.

Treseder, K.K., Allen, M.F., 2002. Direct nitrogen and phosphorus limitation of arbuscular mycorrhizal fungi: a model and field test. New Phytol. 155, 507−515.

Treseder, K.K., Allen, E.B., Egerton-Warburton, L.M., Hart, M.M., Klironomos, J.N., Maherali, H., Tedersoo, L., 2018. Arbuscular mycorrhizal fungi as mediators of ecosystem responses to nitrogen deposition: a trait-based predictive framework. J. Ecol. 106, 480−489.

Treseder, K.K., 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO_2 in field studies. New Phytol. 164, 347−355.

UBA, 2004. Manual on Methodologies and Criteria for Modelling and Mapping Critical Loads and Levels and Air Pollution Effects, Risks, and Trends. Federal Environmental Agency (UmweltBundesAmt), Berlin, Germany.

Van der Heijden, E.W., Kuyper, T.W., 2001. Laboratory experiments imply the conditionality of mycorrhizal benefits for *Salix repens*: role of pH and nitrogen to phosphorus ratios. Plant Soil 228, 275−290.

Van der Linde, S., Suz, L.M., Orme, C.D., Cox, F., Andreae, H., Asi, E., Atkinson, B., Benham, S., Carroll, C., Cools, N., De Vos, B., Dietrich, H.-P., Eichhorn, J., Gehrmann, J., Grebenc, T., Gweon, H.S., Hansen, K., Jacob, F., Kristöfel, F., Lech, P., Manninger, M., Martin, J., Meesenburg, H., Merilä, P., Nicolas, M., Pavlenda, P., Rautio, P., Schaub, M., Schröck, H.-W., Seidling, W., Šrámek, V., Thimonier, A., Thomsen, I.M., Titeux, H., Vanguelova, E., Verstraeten, A., Vesterdal, L., Waldner, P., Wijk, S., Zhang, Y.X., Žlindra, D., Bidartondo, M.I., 2018. Environment and host as large-scale controls of ectomycorrhizal fungi. Nature 558, 243−248.

Van Diepen, L.T.A., Lilleskov, E.A., Pregitzer, K.S., Miller, R.M., 2007. Decline of arbuscular mycorrhizal fungi in northern hardwood forests exposed to chronic nitrogen additions. New Phytol. 176, 175−183.

Van Diepen, L.T.A., Lilleskov, E.A., Pregitzer, K.S., Miller, R.M., 2010. Simulated nitrogen deposition causes a decline of intra-and extra-radical abundance of arbuscular mycorrhizal fungi and changes in microbial community structure in northern hardwood forests. Ecosystems 13, 683−695.

Van Diepen, L.T.A., Lilleskov, E.A., Pregitzer, K.S., 2011. Simulated nitrogen deposition affects community structure of arbuscular mycorrhizal fungi in northern hardwood forests. Mol. Ecol. 20, 799−811.

Van Geel, M., Jacquemyn, H., Peeters, G., Van Acker, K., Honnay, O., Ceulemans, T., 2020. Diversity and community structure of ericoid mycorrhizal fungi in European bogs and heathlands across a gradient of nitrogen deposition. New Phytol. 228, 1640−1651.

Van Strien, A.J., Boomsluiter, M., Noordeloos, M.E., Verweij, R.J.T., Kuyper, T.W., 2018. Woodland ectomycorrhizal fungi benefit from large-scale nitrogen deposition in the Netherlands. J. Appl. Ecol. 55, 290−298.

Van Tichelen, K.K., Colpaert, J.V., 2000. Kinetics of phosphate absorption by mycorrhizal and non-mycorrhizal Scots pine seedlings. Physiol. Plantarum 110, 96−103.

Veresoglou, S.D., Peñuelas, J., Fischer, R., Rautio, P., Sardans, J., Merilä, P., Tabakovic-Tosic, M., Rillig, M.C., 2014. Exploring continental-scale stand health−N: P ratio relationships for European forests. New Phytol. 202, 422−430.

Vesterdal, L., Clarke, N., Sigurdsson, B.D., Gundersen, P., 2013. Do tree species influence soil carbon stocks in temperate and boreal forests? For. Ecol. Manag. 309, 4−18.

Vitousek, P.M., Howarth, R.W., 1991. Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13, 87−115.2.

Walder, F., Van der Heijden, M.G.A., 2015. Regulation of resource exchange in the arbuscular mycorrhizal symbiosis. Nat. Plants 1, 15159.

Wallander, H., 1995. A new hypothesis to explain allocation of dry matter between mycorrhizal fungi and pine seedlings in relation to nutrient supply. In: Nutrient Uptake and Cycling in Forest Ecosystems. Springer, Dordrecht, pp. 243−248.

Wallenda, T., Kottke, I., 1998. Nitrogen deposition and ectomycorrhizas. New Phytol. 139, 169−187.

Weemstra, M., Sterck, F., Kuyper, T.W., Mohren, F., vVan Ruijven, J., Visser, E., Mommer, L., 2016. Towards a multidimensional root trait framework: a tree root review. New Phytol. 211, 1159−1169.

Wikström, F., Ericsson, T., 1995. Allocation of mass in trees subject to nitrogen and magnesium limitation. Tree Physiol. 15, 339−344.

Williams, A., Manoharan, L., Rosenstock, N.P., Olsson, P.A., Hedlund, K., 2017. Long-term agricultural fertilization alters arbuscular mycorrhizal fungal community composition and barley (*Hordeum vulgare*) mycorrhizal carbon and phosphorus exchange. New Phytol. 213, 874−885.

Yamori, W., Hikosaka, K., Way, D.A., 2014. Temperature response of photosynthesis in C_3, C_4, and CAM plants: temperature acclimation and temperature adaptation. Photosynth. Res. 119, 101−117.

Yesmin, L., Gammack, S.M., Cresser, M.S., 1996. Effects of atmospheric nitrogen deposition on ericoid mycorrhizal infection of *Calluna vulgaris* growing in peat. Appl. Soil Ecol. 4, 49−60.

Zhao, A., Liu, L., Chen, B., Fu, W., Xie, W., Xu, T., Zhang, W., Ye, Q., Feng, H., Fu, S., 2020. Soil fungal community is more sensitive to nitrogen deposition than increased rainfall in a mixed deciduous forest of China. Soil Ecol. Lett. 2, 20−32.

Zheng, C., Ji, B., Zhang, J., Zhang, F., Bever, J.D., 2015. Shading decreases plant carbon preferential allocation towards the most beneficial mycorrhizal mutualist. New Phytol. 205, 361−368.

Zhu, K., McCormack, M.L., Lankau, R.A., Egan, J.F., Wurzburger, N., 2018. Association of EcM trees with high carbon-to-nitrogen ratio soils across temperate forests is driven by smaller nitrogen not larger carbon stocks. J. Ecol. 106, 524−535.