Manuscript Details

Manuscript number	ENVPOL_2018_2958_R2
Title	Atmospheric nitrogen deposition impacts on the structure and function of forest mycorrhizal communities: a review
Article type	Review Article

Abstract

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

Keywords	nitrogen deposition, mycorrhizal fungi, community response, function, critical loads
Corresponding Author	Erik Lilleskov
Corresponding Author's Institution	USDA Forest Service
Order of Authors	Erik Lilleskov, Thomas Kuyper, Martin Bidartondo, Erik Hobbie
Suggested reviewers	Kathleen Treseder, Louise Egerton-Warburton, Håkan Wallander, Richard Phillips, Björn Lindahl

Submission Files Included in this PDF

File Name [File Type]

Cover letter.docx [Cover Letter]

Response to comments from the editors and reviewers.docx [Response to Reviewers]

Highlights.docx [Highlights]

Graphical abstract.pdf [Graphical Abstract]

Lilleskov et al manuscript.docx [Manuscript File]

Figure 1.docx [Figure]

Figure 2 new.pdf [Figure]

Research Data Related to this Submission

There are no linked research data sets for this submission. The following reason is given:
No data was used for the research described in the article

United States Department of Agriculture **Forest Service** **Forestry Sciences Lab** **410 MacInnes Drive**
Houghton, MI 49931
(906)-482-6303 x 1322

November 21, 2018

Eddy Zeng, Editor
Special Issue
VSI: N Deposition and Forests
Environmental Pollution

Re: manuscript minor revisions for special issue

Dear Dr. Zeng:

Please find attached our minor revisions of the invited submission for the special issue on N Deposition and Forests. Thank you for your patience in waiting for this. If you need to communicate with me, please use the email address below.

Sincerely,

Erik Lilleskov, Research Ecologist
USDA Forest Service, Northern Research Station
Adjunct Professor, Michigan Technological University
410 MacInnes Drive
Houghton, MI 49931
e-mail: elilleskov@fs.fed.us, or
telephone: 906-482-6303, extension 1322.

Reviewer comments in italics, our responses in plain text.

Comments from the editors and reviewers:

-***Reviewer 2***

- The manuscript has revised properly. It can be accepted now.

-***Reviewer 3***

- The manuscript has been greatly improved and looks much better, so I recommend it to be accepted after consider the minor comments.

P85: comma
Fixed

P124: natural terrestrial?
That is over natural fixation, but not just terrestrial, it also includes marine fixation. Added the words "over natural rates"

P461-463: the example here could be more clear.
Revised for clarity.

Also, i think the graphical abstract should be more simplifed.

Agreed. We have significantly revised and simplified the graphical abstract.

-***Reviewer 4***

- I acknowledge the effort done by the authors to address the comments by 5 reviewers. I can see that most, if not all, of them have been satisfactorily addressed.
Very minor comments to this version:

Link 112-116 with the previous paragraph. Perhaps staring the sentence with "Another important fungal trait…".

Done. Added "Another"

Link 301-304 with the previous paragraph.

Done. Added: "One approach to incorporating mycorrhizal fungi into such models is to hypothesize…"

-***Reviewer 5***

-

The manuscript has improved considerably after revision. I only have a few additional comments that may improve it further:
Line 58: although it is true that N deposition usually acidifies the soil, it may sometimes have the opposite effects e.g. when N depositions is in the form of NH3 volatiles from animal husbandry.

Yes if all N is retained and not taken up by plants, but even with NH3 deposition if the N is taken up or becomes nitrified and leaches out, that does not alkalinize the soil because of the net production of H+ during uptake and nitrification/leaching. For the sake of brevity, we have added the word "typically" before "acidifies".

Line 155-157: It is confusing to state Lactarius as a genus that benefits from N deposition in line 155, and a genus that can both benefit and be inhibited by N deposition in line 157

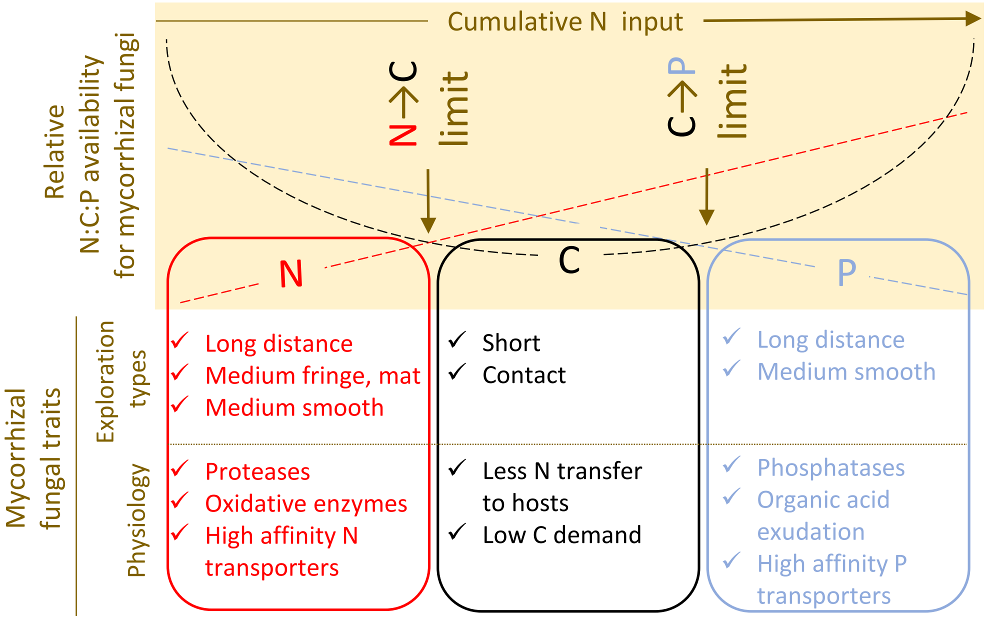
Agreed. We have removed the first mention of Lactarius. Thanks for catching that.

Line 366: Hagerberg et al 2003 is missing in the reference list

Added this reference- thanks.

Highlights

- Mycorrhizal fungal communities change in composition in response to N deposition.
- Critical loads for ectomycorrhizal fungi are lower for conifer than deciduous forests.
- Community shifts likely respond to and cause changes in C, N, and P cycling.
- Phylogenomic methods need integration with physiological and ecosystem studies.
- Tropical and arbuscular mycorrhizal communities are poorly understood.


Cumulative N input
Relative N:C:P availability for mycorrhizal fungi
N→C limit
C→P limit
N
C
P
Mycorrhizal fungal traits
Exploration types
Physiology
✓ Long distance
✓ Medium fringe, mat
✓ Medium smooth
✓ Proteases
✓ Oxidative enzymes
✓ High affinity N transporters
✓ Short
✓ Contact
✓ Less N transfer to hosts
✓ Low C demand
✓ Long distance
✓ Medium smooth
✓ Phosphatases
✓ Organic acid exudation
✓ High affinity P transporters

Title

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

Author names

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

Author affiliations

a. Forestry Sciences Laboratory, USDA Forest Service, Northern Research Station, 410 MacInnes Dr., Houghton, MI, 49931, USA

b. Soil Biology Group, Wageningen University and Research, Droevendaalsesteeg 3, NL-6708 PB Wageningen, Netherlands; Thom.Kuyper@wur.nl

c. Department of Life Sciences, Imperial College London, London SW7 2AZ, England; m.bidartondo@imperial.ac.uk

d. Comparative Plant & Fungal Biology, Royal Botanic Gardens, Kew, Richmond TW9 3DS, England.

e. Erik A. Hobbie, Earth Systems Research Center, University of New Hampshire, 8 College Road, Durham, New Hampshire, 03824-0322, USA; Erik.Hobbie@unh.edu

Corresponding author:

Erik A. Lilleskov
Forestry Sciences Laboratory, USDA Forest Service, Northern Research Station
410 MacInnes Dr
Houghton, MI 49931
Telephone: 906-482-6303 x 1322
Email: elilleskov@fs.fed.us

Abstract

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

Keywords: nitrogen deposition, mycorrhizal fungi, community response, function, critical loads

Capsule

Forest mycorrhizal fungal community composition responds strongly to N deposition across broad ranges of spatial, temporal and phylogenetic scales, with functional consequences—including altered tree nutrition and C, N, and P cycling—that are substantial but only partially understood.

1. Introduction

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

Although N deposition and N fertilization experiments differ in multiple ways, we consider the latter useful in providing mechanistic insights, especially studies that attempt to mimic N deposition via chronic inputs. Most studies on N deposition and arbuscular mycorrhizal fungi (AMF) are from non-forested ecosystems (see, e.g., Treseder and Allen 2000, Pardo et al. 2011b and references therein; but see van Diepen et al. 2007, 2010, 2011). For biological, practical and historical reasons, most research on N deposition effects in forests has focused on ectomycorrhizal fungi (EcMF) rather than AMF. In contrast with AMF, which produce belowground spores asexually, some EcMF produce large aboveground sporocarps, so a long record of the spatiotemporal patterns of reproduction can be related to trends in N deposition (Arnolds 1991). Additionally, some EcMF can be grown in pure culture whereas AMF require a host, so physiological studies on EcMF interactions with N are more feasible. Finally, Sanger sequencing DNA barcoding can be applied without cloning to ectomycorrhizas, whereas AMF required cloning PCR products, which made it simpler to characterize communities of EcMF prior to next-generation sequencing. Several reviews have characterized various aspects of the relationship between

N deposition and mycorrhizal fungi, e.g., Wallenda and Kottke (1998), Treseder (2004), and Lilleskov et al. (2011). Given the literature available and our focus on forests, the present review emphasizes EcMF and higher-latitude mycorrhizal responses to N while covering AMF and tropical studies where possible.

1.1 Mycorrhizal diversity and its role in relation to nitrogen

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

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

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

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

1.2 Spatiotemporal patterns and trends in N deposition

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

2. Patterns of taxonomic response at different scales

2.1 AM vs EcM responses

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

2.2 EcMF responses

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

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

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

2.3 AMF responses

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

Mucoromycotina rather than Glomeromycotina (Orchard et al. 2017, Hoysted et al. 2018) and appear to be insensitive to high N conditions (Allen et al. 2016). Decreases in overall AMF functional diversity may also decrease functional capabilities (van der Heijden et al. 1998, Maherali & Klironomos 2007).

2.4 Interactions with other global change factors

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

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

2.5 Recovery from N deposition

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

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

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

2.6 Critical loads

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

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

3. Causes and functional consequences of community change

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

3.1 Carbon supply from hosts

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

One model of the effect of N on C allocation is that, because leaves are stoichiometrically constrained by N availability, C allocation belowground declines when aboveground growth sinks are stimulated by high N availability (e.g. Ingestad & Ågren, 1991, Poorter and Nagel 2000, but see Smithwick et al. 2013). These models avoid questions of ultimate causes of allocation toward mycorrhizal fungi, defining them as a sink like others (e.g., roots) directly feeding on host sugars, competing with other sinks in the process of balancing resource capture between above- and belowground resources. This model explains the common observation of greater sensitivity of sporocarp production than root tip colonization to N deposition: with enhanced carbohydrate competition due to N deposition, sinks for C that are farthest from the source (EcMF sporocarps) suffer more than sinks closer to the source (EcM root tips), even though root tip density is usually also reduced under high N availability.

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

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

3.2 N-supply from soils

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

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

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

3.3 N-mediated shifts in physiological potential

3.3.1 Shifting limitations and P mobilization

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

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

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

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

Under these conditions, additional potential trait combinations could be favored because the increased C and limiting P create niches for fungi with higher C demand, lower N-mobilizing capacity, and greater inorganic 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 (Martin et al. 2011, Grigoriev et al. 2014) and transcriptomes, the suite of transporters associated with taxa responding differentially to N deposition and resultant P limitation will become increasingly apparent.

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

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

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

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

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

3.3.2 Host stoichiometry

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

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

3.4 EcM-AM comparisons

Given the apparent shifts from EcM to AM forest composition under N deposition in North America, it is critical to understand the functional consequences of such shifts. If we accept conceptual models in which, in contrast with EcMF, AMF lack the ability to mobilize polymeric or phenolically bound organic N from the environment but can access inorganic P effectively (Read 1991), we might expect that increased N deposition would favor AMF, and the findings of Averill et al. (2018) are consistent with this.

However, several experimental studies also suggest that AMF communities are less beneficial under N fertilization than under unfertilized conditions (e.g., Treseder et al. 2018), perhaps because high background P availability reduced the likelihood of a shift from N to P limitation and the potential for nutritional mutualism (Hoeksema et al. 2010). Key studies are needed to test the N-P interactions in AM trees.

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

3.5 New insights from phylogenetics and omics

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

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

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

Since class II peroxidases are phylogenetically constrained (Bödeker et al. 2014), it is worth asking whether lineages possessing them are more sensitive to N deposition. A *Cortinarius* genome has 11 copies of Mn peroxidases, equivalent to white rot fungi (Bödeker et al. 2014). The high sensitivity of this genus to N deposition is consistent with the hypothesis that EcMF with peroxidases are selected against under higher N conditions. Bödeker previously found class II peroxidases in 5 of 14 *Cortinarius* species screened, hence there is the possibility of infrageneric variation in presence of these enzymes. *Cortinarius* species also vary somewhat in their sensitivity, but whether this relates to peroxidase copy number or activity is untested. The only other sequenced EcM genomes with >1 copy of Class II peroxidases are Russulaceae and *Hebeloma* spp. The Russulaceae in particular vary widely in sensitivity to N deposition (Lilleskov et al. 2011, van der Linde et al. 2018). They also have variable numbers of peroxidase gene copies. Elucidation of the distribution of these oxidative enzymes among N tolerant and sensitive species, and tests of their extracellular function, would be enlightening.

3.6 Implications of large-scale changes in tree nutrition

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

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

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

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

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

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

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

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

4. The way forward—recommendations for future studies

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

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

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

4.2 Testing the concepts presented here in tropical forests.

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

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

4.3 Additional areas for further investigation

- Improved understanding of responses of AMF community structure and function to N deposition, with particular attention to integrated effects of C, N, and P limitations on functional organization of the community.

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

5. Conclusions

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

Acknowledgements

We thank Laura M. Suz and five anonymous reviewers for comments on the manuscript. MIB received support from NERC (NE/K006339/1) and EAH received support from the Center for Ecological Research, Kyoto University.

References

Adjoud-Sadadou D, Halli-Hargas R. 2017. Dual mycorrhizal symbiosis: an asset for eucalypts out of Australia? Can J Forest Res 47:500-5.

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

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

Albornoz FE, Lambers H, Turner BL, Teste FP, Laliberté E. 2016. Shifts in symbiotic associations in plants capable of forming multiple root symbioses across a long-term soil chronosequence. Ecol Evol 6:2368-77.

Allen EB, Egerton-Warburton LM, Hilbig BE, Valliere JM. 2016. Interactions of AMF, critical loads of nitrogen deposition, and shifts from native to invasive species in a southern California shrubland. Botany 94:425-33.

Almeida JP, Rosenstock NP, Forsmark B, Bergh J, Wallander H. 2018. Ectomycorrhizal community composition and function in a spruce forest transitioning between nitrogen and phosphorus limitation. Fun Ecol, doi.org/10.1016/j.funeco.2018.05.008

Andersen CP. 2003. Source–sink balance and carbon allocation below ground in plants exposed to ozone. New Phytol 157:213-28.

Andrew C, Lilleskov EA. 2009. Productivity and community structure of ectomycorrhizal fungal sporocarps under increased atmospheric CO2 and O3. Ecol Lett 12:813-22.

Antoninka A, Reich PB, Johnson NC. 2011. Seven years of carbon dioxide enrichment, nitrogen fertilization and plant diversity influence arbuscular mycorrhizal fungi in a grassland ecosystem. New Phytol 192:200-14.

Arnolds EE. 1991. Decline of ectomycorrhizal fungi in Europe. Agric Ecosys Env 35:209-44.

Averill C, Turner BL, Finzi AC. 2014. Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. Nature 505: 543-545.

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

Avis PG, McLaughlin DJ, Dentinger BC, Reich PB. 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 160:239-53.

Avis PG, Mueller GM, Lussenhop J. 2008. Ectomycorrhizal fungal communities in two North American oak forests respond to nitrogen addition. New Phytol 179:472-83.

Baar J, Kuyper TW. 1998. Restoration of aboveground ectomycorrhizal flora in stands of *Pinus sylvestris* (Scots pine) in The Netherlands by removal of litter and humus. Restoration Ecology 6:227-37.

Bahram M, Harend H, Tedersoo L. 2014. Network perspectives of ectomycorrhizal associations. Fungal Ecol 7:70-7.

Bever JD, Richardson SC, Lawrence BM, Holmes J, Watson M. 2009. Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. Ecol Lett 12:13-21.

Bobbink R, Hettelingh JP. 2010. Review and revision of empirical critical loads and dose-response relationships: Proceedings of an expert workshop, Noordwijkerhout, 23-25 June 2010. Rijksinstituut voor Volksgezondheid en Milieu RIVM; 2011 May 19.

Bödeker, ITM, Clemmensen KE, de Boer W, Martin F, Olson Å, Lindahl BD. 2014. EcM *Cortinarius* species participate in enzymatic oxidation of humus in northern forest ecosystems. New Phytol 203: 245-256

Brassard BW, Chen HY, Bergeron Y. 2009. Influence of environmental variability on root dynamics in northern forests. Critical Reviews in Plant Science 28:179-97.

Braun S, Thomas VF, Quiring R, Flückiger W. 2010. Does nitrogen deposition increase forest production? The role of phosphorus. Environ Pollut 158:2043-52.

Brearley FQ, Scholes JD, See LS. 2005. Nitrogen nutrition and isotopic discrimination in tropical ectomycorrhizal fungi. Res Microbiol 156:184-90.

Camenzind T, Hempel S, Homeier J, Horn S, Velescu A, Wilcke W, Rillig MC. 2014. Nitrogen and phosphorus additions impact arbuscular mycorrhizal abundance and molecular diversity in a tropical montane forest. Global Change Biol 20:3646-59.

Chagnon PL, Bradley RL, Maherali H, Klironomos JN. 2013. A trait-based framework to understand life history of mycorrhizal fungi. Trends in Plant Science 18:484-91.

Chen W, Koide RT, Adams TS, DeForest JL, Cheng L, Eissenstat DM. 2016. Root morphology and mycorrhizal symbioses together shape nutrient foraging strategies of temperate trees. P NATL A SCI USA 113: 8741-8746.

Chen YL, Xu ZW, Xu TL, Veresoglou SD, Yang GW, Chen BD. 2017. Nitrogen deposition and precipitation induced phylogenetic clustering of arbuscular mycorrhizal fungal communities. Soil Biol Biochem 115:233-42.

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

Connell JH, Lowman MD. 1989. Low-diversity tropical rain forests: some possible mechanisms for their existence. Am Nat 134:88-119.

Corrales A, Henkel TW, Smith ME. 2018. Ectomycorrhizal associations in the tropics–biogeography, diversity patterns and ecosystem roles. New Phytol, https://doi.org/10.1111/nph.15151

Corrales A, Mangan SA, Turner BL, Dalling JW. 2016. An ectomycorrhizal nitrogen economy facilitates monodominance in a neotropical forest. Ecol Lett 19:383-92.

Corrales A, Turner BL, Tedersoo L, Anslan S, Dalling JW. 2017. Nitrogen addition alters ectomycorrhizal fungal communities and soil enzyme activities in a tropical montane forest. Fungal Ecol 27:14-23.

Cox F, Barsoum N, Lilleskov EA, Bidartondo MI. 2010. Nitrogen availability is a primary determinant of conifer mycorrhizas across complex environmental gradients. Ecol Lett 13:1103-13.

Craig ME, Turner BL, Liang C, Clay K, Johnson DJ, Phillips RP. 2018. Tree mycorrhizal type predicts within-site variability in the storage and distribution of soil organic matter. Glob Change Biol, https://doi.org/10.1111/gcb.14132

De Vries BW, Jansen E, Van Dobben HF, Kuyper TW. 1995. Partial restoration of fungal and plant species diversity by removal of litter and humus layers in stands of Scots pine in the Netherlands. Biodiversity & Conservation 4:156-64.

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

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, and 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.

Egerton-Warburton LM, Allen EB. 2000. Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. Ecol Applic 10:484-96.

Egerton-Warburton LM, Johnson NC, Allen EB. 2007. Mycorrhizal community dynamics following nitrogen fertilization: a cross-site test in five grasslands. Ecol Monogr 77:527-44.

Eom AH, Hartnett DC, Wilson GW, Figge DA. 1999. The effect of fire, mowing and fertilizer amendment on arbuscular mycorrhizas in tallgrass prairie. The Amer 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 (pp. 205-214). Springer, Dordrecht.

Fan Y X, Lin F, Yang LM, Zhong XJ, Wang MH, Zhou JC, Chen YM, and Yang YS. 2018. Decreased soil organic P fraction associated with EcMF activity to meet increased P demand under N application in a subtropical forest ecosystem. Biol Fert Soils 54: 149-161.

Fellbaum CR, Mensah JA, Cloos AJ, Strahan GE, Pfeffer PE, Kiers ET, and 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 CW, Kennedy PG. 2016. Revisiting the ‘Gadgil effect’: do interguild fungal interactions control carbon cycling in forest soils? New Phytol 209:1382-94.

Fowler D, Coyle M, Skiba U, Sutton MA, Cape JN, Reis S, Sheppard LJ, Jenkins A, Grizzetti B, Galloway JN, 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 MN. 2014. Forests trapped in nitrogen limitation – an ecological market perspective on EcM symbiosis. New Phytol 203: 657–666.

Frey SD, Ollinger S, Nadelhoffer K, Bowden R, Brzostek E, Burton A, Caldwell BA, Crow S, Goodale CL, Grandy AS, Finzi A. 2014. Chronic nitrogen additions suppress decomposition and sequester soil carbon in temperate forests. Biogeochem 121:305-16.

Gadgil RL, Gadgil PD. 1971. Mycorrhiza and litter decomposition. Nature 233: 133.

Gadgil PD, Gadgil RL. 1975. Suppression of litter decomposition by mycorrhizal roots of *Pinus radiata*. New Zealand Forest Service.

Gilliam FS, Goodale CL, Pardo LH, Geiser LH and Lilleskov EA. 2011. Eastern temperate forests, Chapter 10. In: Pardo, LH; Robin-Abbott, MJ; Driscoll, CT, 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: 99-116., 80, pp.99-116.

Gorissen A, Kuyper TW. 2000. Fungal species-specific responses of ectomycorrhizal Scots pine (*Pinus sylvestris*) to elevated [CO_2]. New Phytol 46:163-8.

Govindarajulu M, Pfeffer PE, Jin H, Abubaker J, Douds DD, Allen JW, Bücking H, Lammers PJ, Shachar-Hill Y. 2005. Nitrogen transfer in the arbuscular mycorrhizal symbiosis. Nature 435:819.

Grigoriev IV, 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. Nucl Acids Res. 42(D1):D699-704.

Hagerberg D, Thelin G, Wallander H. 2003. The production of ectomycorrhizal mycelium in forests: relation between forest nutrient status and local mineral sources. Plant and Soil 252:279-90.

Hasselquist NJ, 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 NJ, Metcalfe DB, 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. Glob Change Biol 18:3596-605.

Hobbie EA, Agerer R. 2010. Nitrogen isotopes in EcM sporocarps correspond to belowground exploration types. Plant Soil 327:71-83.

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

Hoeksema JD, Chaudhary VB, Gehring CA, Johnson NC, Karst J, Koide RT, Pringle A, Zabinski C, Bever JD, Moore JC, Wilson GW. 2010. A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. Ecol Lett 13:394-407.

Högberg MN, Briones MJ, Keel SG, Metcalfe DB, Campbell C, Midwood AJ, 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 Phytologist 187:485-93.

Högberg MN, Yarwood SA, Myrold DD. 2014. Fungal but not bacterial soil communities recover after termination of decadal nitrogen additions to boreal forest. Soil Biol Biochem 72:35-43.

Hoysted GA, Kowal J, Jacob A, Rimington WR, Duckett JG, Pressel S, Orchard S, Ryan MH, Field KJ, Bidartondo MI. 2018. A mycorrhizal revolution. Current Opinion in Plant Biology 44:1-6.

Ingestad T, Ågren GI. 1991. The influence of plant nutrition on biomass allocation. Ecol Appl 1:168-74.

Jarvis S, Woodward S, Alexander IJ, Taylor AF. 2013. Regional scale gradients of climate and nitrogen deposition drive variation in ectomycorrhizal fungal communities associated with native Scots pine. Glob Change Biol 19:1688-96.

Jiang S, Liu Y, Luo J, Qin M, Johnson NC, 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, https://doi.org/10.1111/nph.15112

Johnson NC. 2010. Resource stoichiometry elucidates the structure and function of AM across scales. New Phytol 185: 631-647

Johnson NC, Rowland DL, Corkidi L, Egerton-Warburton LM, Allen EB. 2003. Nitrogen enrichment alters mycorrhizal allocation at five mesic to semiarid grasslands. Ecology 84:1895-908.

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. Glob Change Biol 21:418-30.

Kanakidou M, Myriokefalitakis S, Daskalakis N, Fanourgakis G, Nenes A, Baker AR, Tsigaridis K, Mihalopoulos N. 2016. Past, present, and future atmospheric nitrogen deposition. Journal of the Atmospheric Sciences 73:2039-47.

Kiers ET, Duhamel M, Beesetty Y, Mensah JA, Franken O, Verbruggen E, Fellbaum CR, Kowalchuk GA, Hart MM, Bago A, Palmer TM. 2011. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. Science 333:880-2.

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

Kjøller R, Nilsson LO, Hansen K, Schmidt IK, Vesterdal L, Gundersen P. 2012. Dramatic changes in ectomycorrhizal community composition, root tip abundance and mycelial production along a stand-scale nitrogen deposition gradient. New Phytol 194:278-86.

Klironomos JN and Hart MM. 2001. Food-web dynamics: animal nitrogen swap for plant carbon. Nature 410: 651.

Klugh KR, Cumming JR. 2007. Variations in organic acid exudation and aluminum resistance among arbuscular mycorrhizal species colonizing Liriodendron tulipifera. Tree Physiology 27:1103-12.

Knorr M, Frey S, and Curtis P. 2005. Nitrogen additions and litter decomposition: A meta-analysis. Ecology 86: 3252-3257.

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 Genomics 19:465.

Kohler A, Kuo A, Nagy LG, Morin E, Barry KW, Buscot F, Canbäck B, Choi C, Cichocki N, Clum A, Colpaert J. 2015. Convergent losses of decay mechanisms and rapid turnover of symbiosis genes in mycorrhizal mutualists. Nature Genetics 47:410.

Kuo A, Kohler A, Martin FM, Grigoriev IV. 2014. Expanding genomics of mycorrhizal symbiosis. Frontiers in Microbiology 4:5:582.

Kuyper TW. 2012. Ectomycorrhiza and the open nitrogen cycle in an afrotropical rainforest. New Phytol 125: 728-729

Kuyper TW. 2017. Carbon and energy sources of mycorrhizal fungi: obligate symbionts or latent saprotrophs? In: NC Johnson, C Gehring & J Jansa (eds), Mycorrhizal Mediation of Soil – Fertility, Structure, and Carbon Storage. Elsevier, p. 357-374.

Lambers H, Shane MW, Cramer MD, Pearse SJ, Veneklaas EJ. 2006. Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. Ann Bot 98:693-713.

Li Y, Niu S, Yu G. 2016. Aggravated phosphorus limitation on biomass production under increasing nitrogen loading: a meta-analysis. Glob Change Biol 22:934-43.

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

Lilleskov EA. 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, Third Edition. Pp 769-801.

Lilleskov EA, Fahey TJ, Lovett GM. 2001. Ectomycorrhizal fungal aboveground community change over an atmospheric nitrogen deposition gradient. Ecol Appl 11: 397-410.

Lilleskov EA, Fahey TJ, Horton TR, Lovett GM. 2002. Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska. Ecology 83:104-115

Lilleskov EA, Hobbie EA, Horton TR. 2011. Conservation of ectomycorrhizal fungi: exploring the linkages between functional and taxonomic responses to anthropogenic N deposition. Fungal Ecol 4: 174-183.

Lin K, Limpens E, Zhang Z, Ivanov S, Saunders DG, Mu D, Pang E, Cao H, Cha H, Lin T, Zhou Q. 2014. Single nucleus genome sequencing reveals high similarity among nuclei of an endomycorrhizal fungus. PLoS Genetics 10:e1004078.

Lindahl BD, Tunlid A. 2015. EcMF – potential organic matter decomposers, yet not saprotrophs. New Phytol 205: 1443-1447.

Lindahl BD, Ihrmark K, Boberg J, Trumbore SE, Högberg P, Stenlid J, Finlay RD. 2007. Spatial separation of litter decomposition and mycorrhizal nitrogen uptake in a boreal forest. New Phytol 173: 611-620.

Liu L, Greaver TL. 2010. A global perspective on belowground carbon dynamics under nitrogen enrichment. Ecol Lett 13:819-28.

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

Lucas RW, Casper BB. 2008. Ectomycorrhizal community and extracellular enzyme activity following simulated atmospheric N deposition. Soil Biology and Biochemistry 40:1662-9.

Maherali H, Klironomos JN. 2007. Influence of phylogeny on fungal community assembly and ecosystem functioning. Science 316:1746-8.

Martin F, Aerts A, Ahrén D, Brun A, Danchin EG, 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.

Martin F, Cullen D, Hibbett D, Pisabarro A, Spatafora JW, Baker SE, Grigoriev IV. 2011. Sequencing the fungal tree of life. New Phytol 190:818-21.

Mohan JE, Cowden CC, Baas P, Dawadi A, Frankson PT, 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. Fungal Ecol 10:3-19.

Molina R, Horton TR. 2015. Mycorrhiza specificity: its role in the development and function of common mycelial networks. In: Mycorrhizal networks (pp. 1-39). Springer, Dordrecht.

Moore, JAM, Jiang J, Post WM, Classen AT. 2015. Decomposition by EcMF alters soil carbon storage in a simulation model. Ecosphere 6: article 29.

Morrison EW, Frey SD, Sadowsky JJ, van Diepen LT, Thomas WK, Pringle A. 2016. Chronic nitrogen additions fundamentally restructure the soil fungal community in a temperate forest. Fungal Ecol 23:48-57

Muszewska A, Stepniewska-Dziubinska MM, Steczkiewicz K, Pawlowska J, Dziedzic A, Ginalski K. 2017. Fungal lifestyle reflected in serine protease repertoire. Scientific Reports 7:9147.

Nagy LG, Riley R, Tritt A, Adam C, Daum C, Floudas D, Sun H, Yadav JS, Pangilinan J, Larsson KH, Matsuura K. 2015. Comparative genomics of early-diverging mushroom-forming fungi provides insights into the origins of lignocellulose decay capabilities. Molecular Biology and Evolution 33:959-70.

Orchard S, Hilton S, Bending GD, Dickie IA, Standish RJ, Gleeson DB, Jeffery RP, Powell JR, Walker C, Bass D, Monk J. 2017. Fine endophytes (*Glomus tenue*) are related to Mucoromycotina, not Glomeromycota. New Phytol 213:481-6.

Orwin KH, Kirschbaum MUF, StJohn MG, Dickie IA 2011. Organic nutrient uptake by mycorrhizal fungi enhances ecosystem carbon storage: a model-based assessment. Ecol Lett 14: 493-502.

Pardo LH, Fenn ME, Goodale CL, Geiser LH, Driscoll CT, Allen EB, Baron JS, Bobbink R, Bowman WD, Clark CM, et al. 2011a Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. Ecol Appl 21:3049-82.

Pardo LH, Robin-Abbott MJ. 2011b. 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. 291 p.

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. Forest Ecol Manag 310:720-728.

Pellitier PT, Zak DR. 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 below-ground community structure of ectomycorrhizal fungi in three Norway spruce (*Picea abies*) stands in Switzerland. Canadian Journal of Botany 79:1134-51.

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

Phillips RP, Meier IC, Bernhardt ES, Grandy AS, Wickings K, Finzi AC. 2012. Roots and fungi accelerate carbon and nitrogen cycling in forests exposed to elevated CO_2. Ecol Lett 15:1042-9.

Plassard C, Louche J, Ali MA, 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. Functional Plant Biology 27(12):1191-.

Pregitzer KS, Burton AJ, Zak DR, Talhelm AF. 2008. Simulated chronic nitrogen deposition increases carbon storage in Northern Temperate forests. Glob Change Biol 14:142-53.

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 6:4332-46.

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

Read, DJ. 1991. Mycorrhizas in ecosystems. Experientia 47: 376-391.

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

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 61:269-74.

Schmidt MW, Torn MS, Abiven S, Dittmar T, Guggenberger G, Janssens IA, Kleber M, Kögel-Knabner I, Lehmann J, Manning DA, Nannipieri P. 2011. Persistence of soil organic matter as an ecosystem property. Nature 478:49.

Shah F, Nicolás C, Bentzer J, Ellström M, Smits M, Rineau F, Canbäck B, Floudas D, Carleer R, Lackner G, Braesel J. 2016. Ectomycorrhizal fungi decompose soil organic matter using oxidative mechanisms adapted from saprotrophic ancestors. New Phytol 209:1705-19.

Sheldrake M, Rosenstock NP, Mangan S, Revillini D, Sayer EJ, Olsson PA, Verbruggen E, Tanner EV, Turner BL, Wright SJ. 2018. Responses of AMF to long-term inorganic and organic nutrient addition in a lowland tropical forest. The ISME Journal 13:1. https://www.nature.com/articles/s41396-018-0189-7

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 AJ, Potvin LR, Lilleskov EA. 2015. Fertility-dependent effects of ectomycorrhizal fungal communities on white spruce seedling nutrition. Mycorrhiza 25:649-62.

Smith SE, Read DJ. 2010. Mycorrhizal Symbiosis. Academic Press.

Smithwick EA, Eissenstat DM, Lovett GM, Bowden RD, Rustad LE, Driscoll CT. 2013. Root stress and nitrogen deposition: consequences and research priorities. New Phytol 197:712-9.

Spatafora JW, Chang Y, Benny GL, Lazarus K, Smith ME, Berbee ML, Bonito G, Corradi N, Grigoriev I, Gryganskyi A, James TY. 2016. A phylum-level phylogenetic classification of zygomycete fungi based on genome-scale data. Mycologia 108:1028-46

Stevens CJ, David TI, Storkey J. 2018.Atmospheric nitrogen deposition in terrestrial ecosystems: Its impact on plant communities and consequences across trophic levels. Functional Ecology 32:1757–1769

Strengbom J, Nordin A, Näsholm T, Ericson L. 2001. Slow recovery of boreal forest ecosystem following decreased nitrogen input. Funct Ecol 15:451-7.

Suz, LM, Barsoum, N, Benham, S, Dietrich, H-P, Fetzer, KD, et al. 2014. Environmental drivers of EcM communities in Europe’s temperate oak forests. Molecular Ecology 23: 5628-5644.

Suz LM, Kallow S, Reed K, Bidartondo MI, Barsoum N. 2017. Pine mycorrhizal communities in pure and mixed pine-oak forests: Abiotic environment trumps neighboring oak host effects. Forest Ecol Manag 406:370-80.

Talbot, JM, Allison SD, Treseder KK. 2008. Decomposers in disguise: mycorrhizal fungi as regulators of soil dynamics in ecosystems under global change. Funct Ecol 22: 955-963.

Talbot JM, Bruns TD, Smith DP, Branco S, Glassman SI, Erlandson S, Vilgalys R, Peay KG. 2013. Independent roles of ectomycorrhizal and saprotrophic communities in soil organic matter decomposition. Soil Biology and Biochemistry 57:282-91.

Talbot JM, Treseder KK. 2010. Controls over mycorrhizal uptake of organic nitrogen. Pedobiologia 53:169-79.

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 40:1235-43.

Taylor AF, Martin F, Read DJ. 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 (pp. 343-365). Springer, Berlin, Heidelberg.

Tedersoo L, Bahram M, Põlme S, Kõljalg U, Yorou NS, Wijesundera R, Ruiz LV, Vasco-Palacios AM, Thu PQ, Suija A, Smith ME. 2014. Global diversity and geography of soil fungi. Science 346:1256688.

Tedersoo L, Smith ME. 2017. EcMF lineages: detection of four new groups and notes on consistent recognition of EcM taxa in high-throughput sequencing studies. In: L. Tedersoo (ed.), Biogeography of Mycorrhizal Symbiosis. Ecol Stud 230: 125-142.

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

Terrer C, Vicca S, Hungate BA, Phillips RP & Prentice IC. 2016. Mycorrhizal association as a primary control of the CO_2 fertilization effect. Science 353: 72-74.

Tian DS, Niu SL 2015. A global analysis of soil acidification caused by nitrogen addition. Environ Res Lett 10: article 024019

Tisserant E, Malbreil M, Kuo A, Kohler A, Symeonidi A, Balestrini R, Charron P, Duensing N, dit Frey NF, Gianinazzi-Pearson V, Gilbert LB, et al. 2013. Genome of an AM fungus provides insight into the oldest plant symbiosis. P Natl A Sci USAs 110:20117-22.

Torn MS, Trumbore SE, Chadwick OA, Vitousek PM, Hendricks DM. 1997. Mineral control of soil organic carbon storage and turnover. Nature 389:170.

Treseder KK. 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO_2 in field studies. New Phytol 164:347-55.

Treseder KK, Allen MF. 2000. Mycorrhizal fungi have a potential role in soil carbon storage under elevated CO_2 and nitrogen deposition. New Phytol 147:189-200.

Treseder KK, Allen MF. 2002. Direct nitrogen and phosphorus limitation of arbuscular mycorrhizal fungi: a model and field test. New Phytol 155:507-515

Treseder KK, Allen EB, Egerton-Warburton LM, Hart MM, Klironomos JN, Maherali H, Tedersoo L. 2018. AMF as mediators of ecosystem responses to nitrogen deposition: A trait-based predictive framework. J Ecology 106:480-9.

UBA. 2004. Manual on methodologies and criteria for modelling and mapping critical loads & levels and air pollution effects, risks, and trends. Federal Environmental Agency (UmweltBundesAmt), Berlin, Germany.

Van der Heijden MG, Boller T, Wiemken A. 1998. Sanders IR. Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. Ecology 79:2082-91.

Van der Heijden EW, Kuyper TW. 2001. Laboratory experiments imply the conditionality of mycorrhizal benefits for *Salix repens*: role of pH and nitrogen to phosphorus ratios. Plant Soil 228:275-90.

Van der Linde S, Suz LM, Orme CD, Cox F, Andreae H, Asi E, Atkinson B, Benham S, Carroll C, Cools N, De Vos B. 2018. Environment and host as large-scale controls of ectomycorrhizal fungi. Nature https://doi.org/10.1038/s41586-018-0189-9

Van Diepen LT, Entwistle EM, Zak DR. 2013. Chronic nitrogen deposition and the composition of active AMF. Appl Soil Ecol 72:62-8.

Van Diepen LT, Lilleskov EA, Pregitzer KS. 2011. Simulated nitrogen deposition affects community structure of AMF in northern hardwood forests. Mol Ecol 20:799-811.

Van Diepen LT, Lilleskov EA, Pregitzer KS, Miller RM. 2007. Decline of arbuscular mycorrhizal fungi in northern hardwood forests exposed to chronic nitrogen additions. New Phytol 176:175-83.

Van Diepen LT, Lilleskov EA, Pregitzer KS, Miller RM. 2010. Simulated nitrogen deposition causes a decline of intra-and extraradical abundance of arbuscular mycorrhizal fungi and changes in microbial community structure in northern hardwood forests. Ecosystems 13:683-95.

Van Strien, AJ, Boomsluiter M, Noordeloos ME, Verweij RJT, Kuyper TW. 2018. Woodland EcMF benefit from large-scale nitrogen deposition in the Netherlands. J Appl Ecol 55: 290-298.

Van Tichelen KK, Colpaert JV. 2000. Kinetics of phosphate absorption by mycorrhizal and non-mycorrhizal Scots pine seedlings. Physiol Plantarum 110:96-103.

Veresoglou SD, Peñuelas J, Fischer R, Rautio P, Sardans J, Merilä P, Tabakovic-Tosic M, Rillig MC. 2014. Exploring continental-scale stand health–N: P ratio relationships for European forests. New Phytol 202:422-30.

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

Vitousek PM, Howarth RW. 1991. Nitrogen limitation on land and in the sea: how can it occur?. Biogeochemistry 13:87-115.2.

Walder F, van der Heijden MG. 2015. Regulation of resource exchange in the arbuscular mycorrhizal symbiosis. Nature 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 (pp. 243-248). Springer, Dordrecht.

Wallenda T, Kottke I. 1998. Nitrogen deposition and ectomycorrhizas. New Phytol 139:169-87.

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

Williams A, Manoharan L, Rosenstock NP, Olsson PA, Hedlund K. 2017. Long-term agricultural fertilization alters arbuscular mycorrhizal fungal community composition and barley (*Hordeum vulgare*) mycorrhizal carbon and phosphorus exchange. New Phytol 213:874-85.

Zhang T, Chen HYH, Ruan H. 2018. Global negative effects of nitrogen deposition on soil microbes. The ISME Journal 12: 1817–1825

Zheng Y, Kim YC, Tian XF, Chen L, Yang W, Gao C, Song MH, Xu XL, Guo LD. 2014. Differential responses of arbuscular mycorrhizal fungi to nitrogen addition in a near pristine Tibetan alpine meadow. FEMS Microbiol Ecol 89:594-605.

Zheng C, Ji B, Zhang J, Zhang F, Bever JD. 2015. Shading decreases plant carbon preferential allocation towards the most beneficial mycorrhizal mutualist. New Phytol 205:361-8.

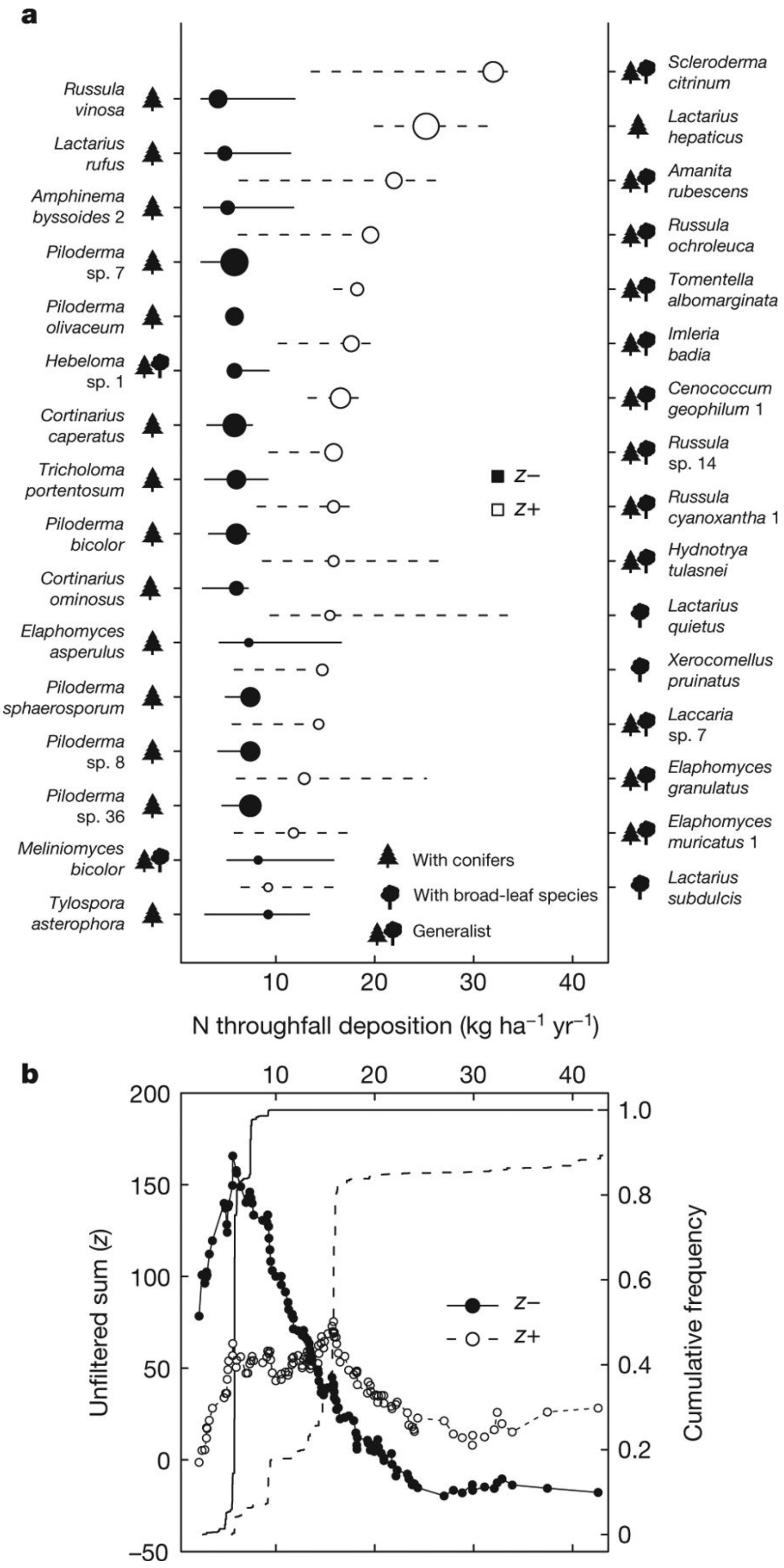
Zhu K, McCormack ML, Lankau RA, Egan JF, Wurzburger N. 2018. Association of EcM trees with high carbon-to-nitrogen ratio soils across temperate forests is driven by smaller nitrogen not larger carbon stocks. J Ecol 106:524-35.

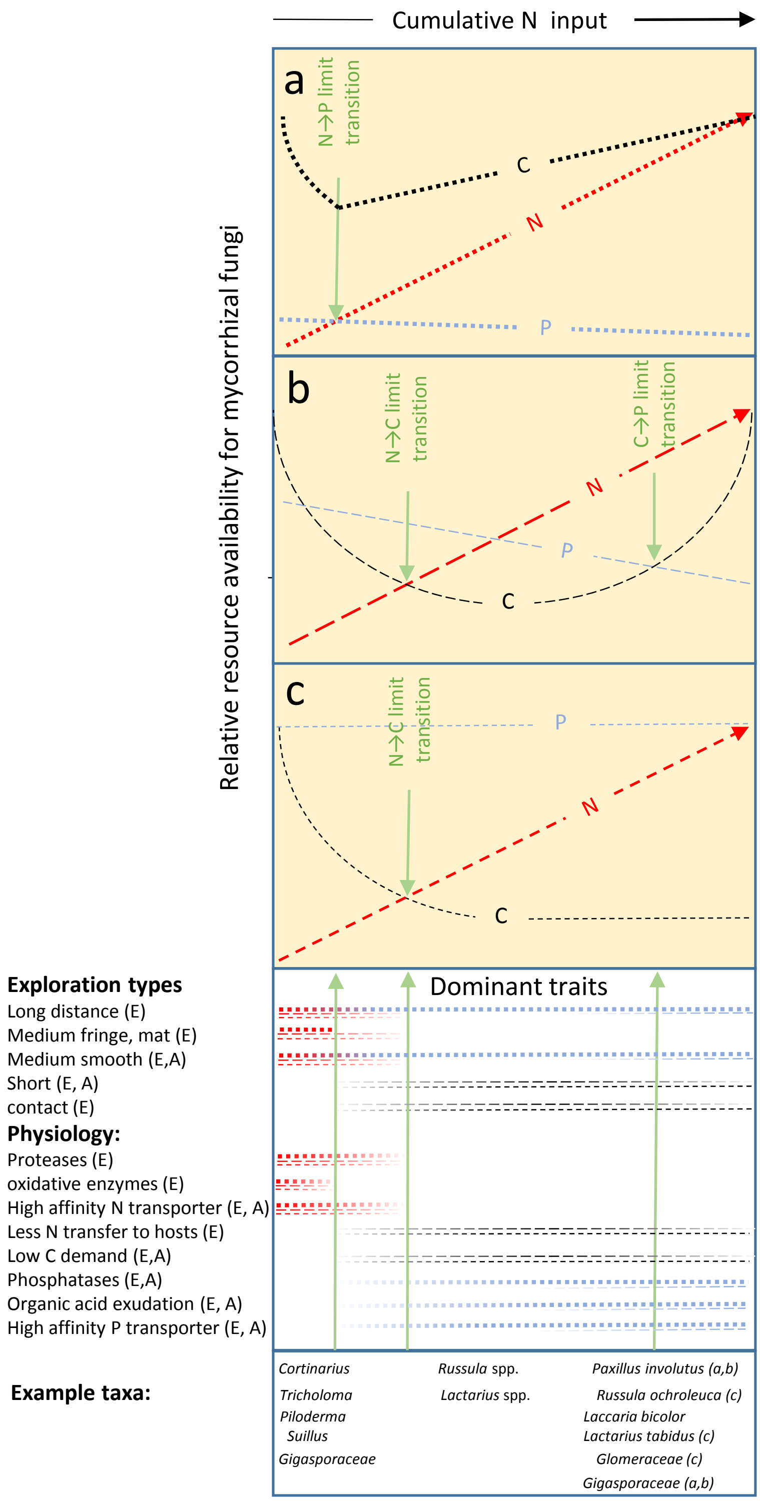
Figure legends

Fig. 1. a) The belowground abundances of individual EcM species in relation to nitrogen deposition across 137 intensively monitored ICP Forests plots in Europe. Black symbols show species declining with increasing nitrogen deposition (*z*−) and open symbols depict species increasing with increasing nitrogen deposition (*z*+). The symbol size is proportional to the magnitude of the response (*z*-score). The horizontal lines represent 5th and 95th quantiles of values resulting in the largest change in species *z*-scores among 1,000 bootstrap replicates. Tree shapes next to species names indicate host generalist, conifer- or broadleaf-specific species. **b**) In response to nitrogen deposition, a drastic mycorrhizal community shift occurs at 5.8 kg.ha^{-1}.yr^{-1}, and a secondary shift occurs for positively-affected fungi at 15.5 kg.ha^{-1}.yr^{-1}, based on the community-level output of accumulated *z*-scores per plot. Reproduced from van der Linde et al. 2018.

Fig.2. As N availability increases, there are three scenarios of P availability represented in the three panels: (a) low, b) medium, c) high; these are hypothesized to lead to different relative N and P limitation of hosts and resultant C flux belowground available for ectomycorrhizal activity; and would select differing dominant traits hypothesized to be associated with the shifting limitations. We assume that belowground C availability is high under low N or low P availability, but low under high N and P availability. In **scenario a)** P is very low, and hence limitation transitions rapidly from N to P and stays there, with relatively high C availability maintained by P limitation. In **scenario b)** P availability is higher, so as N increases, N and P are both readily available, and belowground C declines until N stimulates greater C flux belowground, or P availability declines because of uptake, acidification, or other factors, leading to greater P limitation and a steeper increase in belowground C availability. In **scenario c)** P

availability is very high, and as N availability increases, neither N nor P is limited, and belowground C availability is reduced. (N→Mg limitation shift could also have an even more extreme effect on belowground C availability). Dominant traits are coded according to their association with a putative limiting resource: red = nitrogen limitation; blue = P limitation; black = C limitation, and dash style corresponds to those of the three scenarios with which they are associated. E and A after traits refer to putative EcMF and AMF traits, respectively. Note that AMF exploration types have not been formally defined and should differ from those described for EcMF, so the short and medium smooth types are considered approximations. (a), (b), and (c) after taxon names refer to the scenario in which that taxon is expected to possess some of the dominant traits under high N. Green vertical lines indicate transitions of nutrient and C limitations with increasing N in the three scenarios.


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


Cumulative N input
Relative resource availability for mycorrhizal fungi
a
N→P limit transition
C
N
P
b
N→C limit transition
C→P limit transition
N
P
C
c
N→C limit transition
P
N
C
Dominant traits
Exploration types
Long distance (E)
Medium fringe, mat (E)
Medium smooth (E,A)
Short (E, A)
contact (E)
Physiology:
Proteases (E)
oxidative enzymes (E)
High affinity N transporter (E, A)
Less N transfer to hosts (E)
Low C demand (E,A)
Phosphatases (E,A)
Organic acid exudation (E, A)
High affinity P transporter (E, A)
Example taxa:
Cortinarius
Tricholoma
Piloderma
Suillus
Gigasporaceae
Russula spp.
Lactarius spp.
Paxillus involutus (a,b)
Russula ochroleuca (c)
Laccaria bicolor
Lactarius tabidus (c)
Glomeraceae (c)
Gigasporaceae (a,b)