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REVIEW

Biotic interactions with mycorrhizal systems as extended nutrient acquisition strategies shaping forest soil communities and functions

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Abstract

Plant nutrient acquisition strategies involving ectomycorrhizal (EcM) and arbuscular mycorrhizal (AM) associations, are key plant functional traits leading to distinct carbon (C) and nutrient dynamics in forests. Yet, little is known about how these strategies influence the structure and functioning of soil communities, and if such mycorrhizal effects may be more or less pronounced depending on the type of forest and various abiotic factors. Here we explore the potential interactions occurring between plant-EcM and plant-AM systems with the diverse soil organisms occurring in forest soils, and in the process draw attention to major issues that are worthy for future research directions. Based on these potential interactions, we suggest that EcM systems, especially those involving gymnosperms in colder climates, may select for a soil community with a narrow set of functions. These EcM systems may exhibit low functional redundancy, dominated by symbiotic interactions, where EcM fungi maintain low pH and high C/N conditions in order to tightly control nutrient cycling and maintain the dominance of EcM trees. By contrast, AM systems, particularly those involving deciduous angiosperm trees in mild and warmer climates, may facilitate a functionally more diverse and redundant soil community tending towards the dominance of competitive and antagonistic interactions, but also with a range of symbiotic interactions that together maintain diverse plant communities. We propose that the contrasting belowground interactions in AM and EcM systems act as extended nutrient acquisition traits that contribute greatly to the prevailing nutrient and C dynamics occurring in these systems.

Keywords: Arbuscular mycorrhizal (AM) fungi; Ectomycorrhizal (EcM) fungi; Mycorrhizal associations; Plant-microbial feedbacks; Microbiome, soil ecology; Holobiont; Rhizosphere; Biotic interactions

Introduction

Soil organisms play key roles in the population and community dynamics of plants and associated carbon (C) and nutrient dynamics in terrestrial ecosystems, by acting as decomposers of soil organic matter (SOM), nutrient transformers, plant mutualists, parasites/pathogens, grazers, and predators influencing patterns of plant diversity and productivity (Baldrian, 2017; Bever, Mangan, and Alexander, 2015; Tedersoo, Bahram, & Zobel, 2020). On a global scale communities of soil organisms are mainly shaped by abiotic

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factors, such as climatic conditions and soil properties (Bahram et al., 2018; Oliverio et al., 2020; Phillips et al., 2019; Van Den Hoogen et al., 2019). On a more local scale, however, plant identity and plant functional attributes may strongly influence the community and functioning of soil organisms through direct and indirect interactions, especially those associated closely with the rhizosphere, but also those inhabiting the bulk soil (Berg and Smalla, 2009; Prober et al., 2015; Urbanová, Šnajdr, and Baldrian, 2015). Thus, plants and interacting soil organisms may essentially act as an extended holobiont (Gilbert, Sapp, and Tauber, 2012).

The strongest and most integrated interaction of the plant-soil continuum is the association between plants and mycorrhizal fungi, a root symbiosis based on C and nutrient exchange (Smith and Read, 2010). Multiple lines of evidence suggest that mycorrhizal type, in particular ectomycorrhizal (EcM) and arbuscular mycorrhizal (AM) associations, is a key determinant of prevailing patterns of forest population and community dynamics, facilitating either co-occurrence or monodominance of tree species due to plant-mycorrhizal-soil feedbacks (Connell and Lowman, 1989; Peh, Lewis, and Lloyd, 2011). As both AM and EcM fungi associate with trees of different functional types and exist in boreal, temperate, and tropical forests, where they show contrasting dominance patterns (Öpik et al., 2010; Read, 1991; Read and Perez-Moreno, 2003; Soudzilovskaia et al., 2019), forest systems present a unique opportunity to explore contrasting ecosystem-plant-soil feedbacks.

Plant-EcM and plant-AM systems show great differences in their morphological, physiological, ecological, and phylogenetic properties (Table 1), and they are typically associated with low and high nutrient conditions, respectively, with contrasting nutrient acquisition strategies. This has led to the idea of the mycorrhizal-associated nutrient economy (MANE) (Phillips, Brzostek, and Midgley, 2013). Within this framework, AM- and EcM-dominated systems have distinct C, nitrogen (N) and phosphorus (P) cycling dynamics. AM systems tend to have high-quality litter that is rapidly decomposed by saprotrophs leading to high C mineralization, organic to inorganic N transformations, and nitrification (Phillips et al., 2013). Hence AM systems represent an inorganic nutrient economy, where AM fungi scavenge for inorganic nutrients released from litter and SOM by other soil organisms. By contrast, EcM systems tend to have low-quality litter with slow decomposition rates and most nutrients existing in organic form (Table 1). Supported by large C inputs from the host trees, EcM fungi are able to mine for organic N and P due to greater enzymatic capabilities compared to AM fungi, making less mineral N available for nitrification and losses via leaching, leading to a prevailing organic nutrient economy (Cheeke et al., 2017; Phillips et al., 2013).

However, the MANE framework is mainly based on temperate and boreal forests, and may or may not hold for tropical forests or even in temperate and boreal forests after accounting for different tree traits such as leaf habit (Averill, Bhatnagar, Dietze, Pearse, and Kivlin, 2019; Keller and Phillips, 2019; Lin, McCormack, Ma, and Guo, 2017). Furthermore, the biotic interactions occurring in soil that drive differences in nutrient and C cycling in EcM and AM systems are poorly characterised, and as most soil organisms are usually studied in isolation, we lack an understanding about the system-wide effects of trophic and ecological interactions on ecosystem functioning (Buchkowski, Bradford, Grandy, Schmitz, and Wieder, 2017; Phillips et al., 2013; Wall et al., 2008). EcM and AM systems, in combination with certain biotic and abiotic factors, may select for different soil communities and form holobionts with distinct functional properties. They are thus forming systems that exhibit *extended nutrient-acquisition strategies*, which have large implications for broad-scale C and nutrient dynamics. We propose that particular combinations of climates, trees, and mycorrhizal types influence soil community structures and ecosystem functions in contrasting ways. We also propose that EcM systems, primarily in temperate and boreal ecosystems, along with more closed nutrient cycles have a stronger and more direct influence on soil communities, leading to less functional redundancy by promoting more specialized soil organisms with a narrow set of functions that maintain a low nutrient status and slow nutrient cycling, compared to AM systems with more open and rapid nutrient cycles, and with high functional diversity and redundancy. We come to these hypotheses through exploring the interactions of EcM and AM fungi with different soil organisms in forests while considering that climatic biome and tree functional differences may strengthen or weaken specific ‘mycorrhizal effects’ on C and nutrient dynamics often associated with EcM and AM systems. We will subsequently discuss how these systems may be altered under environmental change and provide suggestions for future research needs.

Table 1. Overview of morphological, physiological, ecological, and phylogenetic properties of EcM and AM systems, for many properties using evidence mostly obtained from boreal and temperate ecosystems, with a clear need to investigate many of these properties in tropical ecosystems.

Property	**Ectomycorrhizal fungi(EcM)**	**Arbuscular mycorrhizal fungi (AM)**
Fungal taxa involved (Kivlin, Hawkes, and Treseder, 2011; Öpik et al., 2013; Brundrett and Tedersoo, 2018)	Around 20,000 different fungal taxa, mainly from the phylum Basidiomycota, but also Ascomycota and Zygomycota	250−1000 fungal taxa from the phylum Glomeromycota
Plant taxa involved (Brundrett and Tedersoo, 2018;)	2% of terrestrial plants, mainly woody	72% of terrestrial plants across a broad phylogeny
Specialized structures in and on host roots (Bonfante and Genre, 2010)	Intercellular hartig net and hyphal mantle ensheathing the root tip representing high fungal to root biomass.	Highly branched intracellular arbuscules representing less fungal to root biomass compared to a mantle and hartig net
External mycelium (Agerer, 2001; Chagnon et al., 2013	Extensive and varied with contrasting functional exploration types	Less extensive and more homogenous types
Reproductive and dispersal strategies (Horton, 2017; Vašutová et al., 2019)	Sexual or asexual reproduction, often production of fruiting bodies that facilitate wind and animal dispersal	Asexual reproduction, production of large asexual resting spores, relying on active and passive animal dispersal
Provision of C from host plants (Tedersoo and Bahram, 2019)	7−30% of photosynthates	2−20% of photosynthates
Hyphal turnover (Finlay and Read, 1986; Staddon, Ramsey, Ostle, Ineson, and Fitter, 2003; Olsson and Johnson, 2005; Wallander, 2006; Ekblad et al., 2013; Pepe, Giovannetti, and Sbrana, 2018)	2 weeks to 7 months, or even up to 2−10 years	4−5 days, to weeks and potentially months
Provision of nutrients to host plants (Smith, Smith, and Jakobsen, 2003; Smith and Smith, 2012; Phillips et al., 2013; Tedersoo and Bahram, 2019)	Organic and inorganic N acquisition is most important, but can also access inorganic P perhaps more efficiently than AM fungi	Inorganic P acquisition most important, and can acquire both inorganic and organic N, but may compete with host plants for N
Enzymatic capacity to break down organic matter (Tedersoo and Bahram, 2019)	Low to high enzymatic capacity for organic nutrient acquisition depending on EcM species/lineages, although less capacity compared to saprotrophic fungi	Lacking
Litter quality of hosts and decomposition (Read, 1991; Tedersoo and Bahram, 2019)	Low-quality, slower decomposition	High-quality, faster decomposition
Factors driving root colonization intensity, external mycelium production (Nilsson, Giesler, Bååth, and Wallander, 2005; Soudzilovskaia et al., 2015; Wang, Zong, and Li, 2019)	Colonization highest in acidic soils and mesic climates with constant precipitation. Mycelium production negatively correlated with nutrient availability	Colonization highest under continental climates with mild summers and high soil N availability. Mycelium production positively correlated with nutrient availability.
Proposed prevailing nutrient economy (Phillips et al., 2013; Averill et al., 2019; Tedersoo and Bahram, 2019)	Conservative closed organic nutrient economy	Rapid open/leaky inorganic nutrient economy
Relationship to top-soil C stocks (Soudzilovskaia et al., 2019)	EcM basal area fraction positively correlated with top-soil C stocks	AM basal area fraction negatively correlated with top-soil C stocks
Contribution to tree basal area across forest biomes (Steidinger et al., 2019)	>90% of boreal forest basal area, around 75% of temperate forest basal area, and < 30% of tropical forest basal area	60−70% of tropical forest basal area, > 20% of temperate forest basal area, and < 5% of boreal forest basal area
Plant-soil feedbacks (Bennett et al., 2017)	Neutral to positive	Negative

BOX 1. Tree and mycorrhizal types as key plant nutrient-acquisition traits across forest biomes

The EcM symbiosis requires a greater investment of C from the host plant than the AM symbiosis, equating to a more obligatory relationship with less autonomy for the host, a physical barrier between its roots and the soil environment, and a greater extension of its zone of influence in the soil (Table 1).Thus, EcM systems represent a more closed, stable and specialized active nutrient acquisition strategy that is less reliant on other soil organisms for nutrient transformation and more competitive against these organisms and AM trees under limiting nutrient conditions (Phillips *et al.*, 2013; Cheeke *et al.*, 2017; Averill *et al.*, 2019). However, EcM systems are perhaps more vulnerable to disturbance and environmental change due to less flexibility for the plant in the symbiosis, requiring more stable mesic conditions for success (Table 1). On the other hand, the AM symbiosis gives the plant more autonomy in the soil with greater root-soil contact (Tedersoo & Bahram, 2019), they have a greater reliance on other soil organisms for nutrient transformations (Phillips *et al.*, 2013), a greater competitive ability compared to EcM trees under high nutrient conditions, and a greater safety net for the plant against disturbance and environmental change due to a greater flexibility for the plant in the symbiosis (Table 1).

In addition to mycorrhizal types, trees can be angiosperms or gymnosperms, further divided into deciduous or evergreen, which differ in their distributions and commonality. Angiosperms tend to outcompete gymnosperms and become dominant in most tropical and temperate forests, while gymnosperms tend to dominate in cold and/or nutrient-poor soils, representing fast versus slow plant economic traits (Bond, 1989; Reich, 2014). Accordingly, gymnosperms have greater longevity of their organs (foliage, stems and roots), facilitated by the production of resins rendering protection from fungal and insect attack, whereas angiosperms tend to be more susceptible to such attacks (Brodribb et al., 2012). The deciduous habit is more common in angiosperms compared to gymnosperms for whom the evergreen habit is more common (Gower and Richards, 1990; Reich et al., 1997). And the greatest functional difference in fast versus slow plant economic traits in trees occurs between evergreen gymnosperms and deciduous angiosperms, with slower growth rates, conservative nutrient cycling, lower decomposition rates, and thicker litter layers under the former (Augusto *et al.*, 2015; Dawud *et al.*, 2017; Angst *et al.*, 2019).

Different tree and mycorrhizal types also exist across forest biomes that have varying aboveground biomass C stocks, soil C stocks, nutrient dynamics and climatic conditions (Read, 1991). Despite large climatic differences, tropical forests are usually more biomass C dense and contribute more to global forest aboveground biomass than temperate and boreal forests (Crowther et al., 2015; Liu et al., 2015). While boreal forests contribute around a half to total global forest soil C stocks despite only covering a third of the global forest area, tropical forests, despite accounting for over half of global forest area, contribute only around a third of global soil C (Scharlemann at al., 2014; Keenan et al., 2015). In addition, boreal forests have a belowground C flux of around two thirds of their gross primary production, compared to around a half in temperate forests, and around a third in tropical forests (Gill and Finzi, 2016). Tropical forests tend to have rapid nutrient cycles and produce high-quality litter compared to boreal forests that have slow nutrient cycles and low-quality litter, with temperate forests in between (Vitousek, 1982). Nitrogen becomes increasingly limiting from tropical to boreal forests, while phosphorus is more limiting in tropical forests, accordingly, although there is heterogeneity in nutrient limitations within biomes (Vitousek et al., 2010; Gill and Finzi, 2016).

These broad scale observations on C and nutrient dynamics across biomes warrant further attention for differences in tree functional traits including mycorrhizal type, given that boreal forests are dominated by gymnosperms, while temperate and tropical forests are dominated by angiosperms (Poulter et al., 2011; Augusto *et al.*, 2015; Crowther et al., 2015). Boreal gymnosperm forests potentially have around a two-fold higher soil C density, while in temperate and tropical forests soil C content appears to be more equal between gymnosperms and angiosperms (Zhong & Qiguo, 2001; Vesterdal *et al.*, 2013). Furthermore, around 60% of the worlds standing trees may be EcM-forming, distributed mostly across boreal and temperate forests, while AM-forming trees make up most of the remaining 40% concentrated mostly in the tropics (Steidinger *et al.*, 2019). Soil C is positively related to the abundance of EcM trees but differs depending on biome (Soudzilovskaia *et al.*, 2019a). The different leaf habits are also unequally distributed across biomes, deciduous trees are found mostly in temperate and tropical forests, and evergreen trees in boreal and tropical forests Poulter et al., 2011; Crowther et al., 2015). Understanding these traits across forest biomes is important as they may strengthen or weaken the prevailing closed versus open nutrient dynamics of EcM and AM systems, which may profoundly affect soil community structures and functions.

Ecosystem-tree-mycorrhizal interactions with soil organisms as extended nutrient-acquisition traits

Mycorrhizal fungi interact directly and indirectly with other soil organisms, while also moderating plant interactions with these organisms. Such interactions span a spectrum from inhibition to stimulation and direct competition to mutualism (Fitter and Garbaye, 1994), and drive and maintain distinct C and nutrient dynamics (Averill et al., 2019; Cheeke et al., 2017; Phillips et al., 2013; Read, 1991). While there is some overlap between EcM and AM in their interactions with soil organisms, they likely have contrasting effects when it comes to facilitation and inhibition of these organisms. EcM fungi, especially when associating with gymnosperms in temperate and boreal forests, represent a potentially greater facilitator or inhibitor of soil biotic activity compared to AM fungi. This is because of the greater physical presence of EcM in the soil, their greater enzymatic capacity and activity (Tedersoo and Bahram, 2019), their greater tolerance and potential maintenance of acidic soil conditions (Rosling, Lindahl, Taylor, and Finlay, 2004), and their contribution to and maintenance of high C/N ratios in the soil (Franklin, Näsholm, Högberg, and Högberg, 2014; Lin et al., 2017; Tedersoo and Bahram, 2019). This has the potential to trap systems in an N-limited state (Franklin et al., 2014), as it affects factors which other soil organisms are sensitive to (Bahram et al., 2018; Fierer, 2017).

Mycorrhizal interactions with saprotrophs

The interaction of mycorrhizal fungi with soil saprotrophs is considered to be a major factor influencing patterns of soil C and nutrient dynamics in forest soils (Averill, Turner, and Finzi, 2014; Brzostek, Dragoni, Brown, and Phillips, 2015; Fernandez and Kennedy, 2016; Sterkenburg, Clemmensen, Ekblad, Finlay, and Lindahl, 2018). These interactions are generally seen as either inhibitory or stimulatory (Fitter and Garbaye, 1994; Frey, 2019). The inhibition of soil saprotrophs, specifically saprotrophic fungi, by mycorrhizal fungi is known as the 'Gadgil effect', and refers to the phenomenon of EcM fungi suppressing the activity of fungal saprotrophs leading to decreased decomposition rates, or the removal of EcM from a system enhancing decomposition rates (Gadgil and Gadgil, 1971, 1975; Fernandez and Kennedy, 2016). This is thought to be driven primarily by the competition for organic matter colonization between EcM fungi and saprotrophic fungi. Fueled by a large input of C from host trees, some EcM fungi are able to proliferate and selectively mine for N in organic matter (Lindahl and Tunlid, 2015), in the process potentially outcompeting saprotrophic fungi and leading to C accumulation (Fernandez and Kennedy, 2016; Sterkenburg et al., 2018).

The 'Gadgil effect' has mostly been observed under temperate and boreal evergreen gymnosperm trees (Gadgil and Gadgil, 1971, 1975; Averill and Hawkes, 2016; Fernandez and Kennedy, 2016), and may not hold for deciduous angiosperm trees in the same systems (Fernandez, See, & Kennedy, 2019), nor under tropical evergreen angiosperm N-fixing trees (Mayor and Henkel, 2006). Furthermore, the presence of certain saprotrophic fungi can be higher in EcM gymnosperm forests compared to other EcM and AM forests (Awad et al., 2019; Bahram et al., 2020), although overall decomposition is still likely to be slow. While there is a lack of studies of the 'Gadgil effect' across different types of forests, it may be specific to EcM forming gymnosperms in boreal and temperate forests. Although first described in introduced *Pinus radiata* plantations in New Zealand (Gadgil and Gadgil, 1971, 1975), it may be most pronounced or at least saprotrophic activity most reduced in ecosystems with a significant ericoid mycorrhizal component (Clemmensen et al., 2015), which have an even greater saprotrophic capability than EcM fungi (Martino et al., 2018). Ericoid mycorrhizal fungi produce highly melanized mycelium that is resistant to decomposition (Clemmensen et al., 2015), and their hosts have very low-quality litter (Read, Leake, and Perez-Moreno, 2004). These factors suggest that ericoid mycorrhizal fungi and their plant symbionts may form an even more closed nutrient cycle in their zone of influence, outcompeting other fungal guilds for organic nutrient resources (Wurzburger and Hendrick, 2009). Something resembling the 'Gadgil effect' has been shown among certain tropical tree species, where the presence of mycorrhizal hyphae retarded root litter decomposition under tropical evergreen EcM gymnosperms as well as evergreen AM gymnosperms and angiosperms in the same system (Lin, Chen, and Zeng, 2019), suggesting that AM fungi may also suppress saprotrophic activity in forests, although this is not well supported.

When saprotrophs are C limited, and labile forms of C are quickly depleted, the exudation of labile C by tree roots and mycorrhizal fungi can stimulate saprotrophic breakdown of more complex C forms, for which they would otherwise be energy-limited to do so, a mechanism commonly known as 'priming' (Brzostek et al., 2015; Fernandez and Kennedy, 2016; Verbruggen, Pena, Fernandez, and Soong, 2017). Both EcM and AM fungi have been implicated in priming of decomposition (Clemmensen et al., 2015; Hodge, 2014), which is in contradiction to the 'Gadgil effect'. Even though most evidence for AM-induced priming comes from non-forest systems, AM fungi have been found to colonize both fresh and partially decayed litter in a variety of forests across biomes, as well as having higher colonization rates in upper organic soil layers (Bunn, Simpson, Bullington, Lekberg, and Janos, 2019; Sheldrake et al., 2017). From these observations it is tempting to speculate that AM fungi may engage in highly directed priming of saprotrophs via release of soluble C in nutrient-rich patches and scavenge for the mineralized nutrients released by saprotrophic activity (Bunn et al., 2019; Kaiser et al., 2015; Sheldrake et al., 2017).

However, it is relatively unknown whether decomposition of litter in AM systems is directly enhanced by the activity of AM fungi or is already rapid due to high-quality litter inputs, where AM colonization of litter may be inconsequential for overall C dynamics. In addition, plant roots may act as the main primers of soil saprotrophs and may do so in a more passive and diffuse way (Kuzyakov, Friedel, and Stahr, 2000; Shahzad et al., 2015), compared to mycorrhizal fungi (Kaiser et al., 2015). It is difficult to untangle the relative contribution of plant roots and mycorrhizal fungi to these processes (Verbruggen et al., 2017). Nevertheless, given that AM trees tend to have greater direct root-soil access compared to EcM trees, whose root-soil interactions are governed more tightly by EcM fungi, AM trees may be responsible for more priming through a combination of highly directed soluble C release by AM fungi and passive and general soluble C release by AM tree roots. This is in line with the more rapid nutrient cycling of AM systems with greater saprotrophic activity (Phillips et al., 2013), as there appears to be a greater capacity for AM systems to support a wider variety of saprotrophs, compared to EcM systems, where saprotrophic fungi that have efficient ligninolytic enzyme capabilities are more prominent (Bahram et al., 2020). In EcM systems, however, the high EcM mycelial biomass in the soil is likely a major resource for saprotrophs (Brabcová, Nováková, Davidová, and Baldrian, 2016), and has been shown to turnover rapidly (Clemmensen et al., 2015). Furthermore, EcM and fungal saprotrophs may co-exist by inhabiting different spatial niches especially in boreal forests with deep mor layers (Kyaschenko, Clemmensen, Karltun, and Lindahl, 2017).

Overall it is likely that mycorrhiza-saprotroph interactions occur on a spectrum of inhibition to stimulation and are likely to be spatially and temporally heterogenous. Thus, the so called ‘Gadgil’ and ‘priming’ effects are context-dependent and may both occur in the same system separated in space and time. In EcM systems, especially under N limitation such as boreal gymnosperm forests, regulation or suppression of decomposition is facilitated by the input of low-quality litter by EcM plants, allowing for a tighter control on C and nutrient cycling (Smith and Wan, 2019). AM systems, on the other hand, may favor stimulatory and neutral interactions with saprotrophs, relying on their activity for mineralization of organic nutrients that they scavenge for, with reduced control on C and nutrient cycling (Frey, 2019). Yet there is a lack of integration and consideration of these interactions across climatic biomes and tree types. Furthermore, most studies on mycorrhizal interactions with saprotrophs and patterns of decomposition focus on fungal saprotrophs, because fungi are considered the primary decay agents of complex plant-derived C (Baldrian, 2017). However, evidence suggests that the contribution of bacterial saprotrophs to forest soil decomposition has likely been underestimated (Lladó, López-Mondéjar, and Baldrian, 2017). Bacteria are extremely diverse and abundant in soils and have been shown to be capable of decomposing complex C substrates (López-Mondéjar et al., 2018). Compared to fungal saprotrophs who may be better suited to utilize plant compounds, bacteria may be better suited to utilize fungal and bacterial necromass (Lladó et al., 2017; López-Mondéjar et al., 2018), and may dominate in the decomposition of EcM mycelia in particular (Brabcová et al., 2016). It may well be that the activity of fungal saprotrophs promotes the activity of bacterial saprotrophs, through their substrate and decay stage niche separation (Romaní, Fischer, Mille-Lindblom, and Tranvik, 2006), further enhancing decomposition and partly explaining the contrasting C and nutrient dynamics in EcM and AM systems. Thus, the relative contributions of fungi and bacteria to decomposition in EcM and AM systems presents an important research area, as more complete decomposition of both plant and microbial biomass may require the activity of both saprotrophic bacteria and fungi (López-Mondéjar et al., 2018).

Mycorrhizal interactions with pathogens

Plant-soil feedbacks involving plant antagonists such as pathogens have long been recognized to influence patterns of forest diversity and plant succession (Connell, 1971; Janzen, 1970; Van Der Putten, 2000). The holobiont perspective combined with the contrasting patterns of interactions between trees and EcM and AM fungi with soil-borne pathogens (fungi, bacteria, protists, viruses, and nematodes) across climatic biomes adds a new perspective that may help explain distinct and differing plant and soil community dynamics and functioning.

Accumulating evidence points to relatively greater soil-borne pathogen prevalence in AM systems compared to EcM systems, resulting in greater negative plant-soil feedbacks in the former compared to positive and neutral feedbacks in the latter (Bahram et al., 2020; Bennett et al., 2017; Chen et al., 2019; Kadowaki et al., 2018; Teste et al., 2017). It is possible that if there are increased competition and interactions between different microbial groups in AM systems, this may lead to increased functional switching from saprotrophic or commensal microbes to pathogenic microbes in those capable of such switching, as proposed under the pathobiome concept (Vayssier-Taussat et al., 2014). Pathogens may also benefit from high nutrient access or less competition with AM fungi for colonizing roots of AM hosts (Ingham, 1988), compared to greater physical protection of EcM roots by EcM fungi (Branzanti, Rocca, and Pisi, 1999). In addition, a relatively stable source of N as shown in EcM trees facilitated by organic N acquisition by EcM fungi (Corrales, Mangan, Turner, and Dalling, 2016), may promote plant defense responses if N can be consistently allocated to secondary metabolite production (Blodgett, Herms, and Bonello, 2005). This greater activity of pathogens in AM systems leads to greater negative density dependence of AM trees and potentially drives plant community and population dynamics, facilitating higher tree species richness in AM-dominated systems (Chen et al., 2019; Laliberté, Lambers, Burgess, and Wright, 2015; Tedersoo, Bahram, & Zobel, 2020). By contrast, the suppression of pathogens by EcM trees may contribute to positive and neutral plant-soil feedbacks facilitating monodominant conspecific EcM systems from the tropics to the boreal forest (Connell and Lowman, 1989; Corrales et al., 2016; Dickie, Koele, Blum, Gleason, and McGlone, 2014; Tedersoo, Bahram, & Zobel, 2020). Recent evidence suggests that the Janzen-Cornell hypothesis may have limitations in explaining plant diversity. On a broad scale, monodominant EcM systems may be an exception rather than the rule and related more to edaphic factors (Ter Steege et al., 2019). It is also possible that mixed EcM/AM forests facilitate more diverse plant communities through a combination of negative, positive, and neutral plant-soil feedbacks (Bahram et al., 2020), that would create establishment mosaics for plants with differing regeneration niches (Mariotte et al., 2018). The next step in studying mycorrhizal-pathogen dynamics is to go beyond mere relative and absolute pathogen abundance analyses in these systems to analyzing actual pathogen attack or damage to mycorrhizal hosts, perhaps by detecting and quantifying necrosis (Minina et al., 2013), and relating this to mycorrhizal root colonization and community analysis.

One additional particular topic of interest for future research is the role of viruses in mycorrhizal systems, as viruses through cell lysis may be responsible for a large fraction of C that cycles in the soil food web (Kuzyakov and

Mason-Jones, 2018) And they are also key mediators of horizontal gene transfer within and potentially across kingdoms (Kimura, Jia, Nakayama, and Asakawa, 2008). Phages play an obvious role in controlling bacterial populations, but viruses also infect all other organisms in the soil (Pratama and van Elsas, 2018). A recent study showed that viruses that infect eukaryotic hosts, mostly fungi, appear to be more diverse than phages in soils (Starr, Nuccio, Pett-Ridge, Banfield, and Firestone, 2019). Thus, viruses of eukaryotes likely play an important role in fungal community dynamics, as well as C and nutrient dynamics in EcM systems with high fungal biomass, compared to AM systems where phages may play a greater role in bacterial community dynamics, as well as C and nutrient dynamics, due to higher bacterial biomass (Kimura et al., 2008; Kuzyakov and Mason-Jones, 2018). Such questions could be addressed by combining stable isotope probing with 'omics' techniques to unravel if mycorrhizal systems host distinct viral assemblages with contrasting C and nutrient flows through their associated viromes, but general studies into viral communities using amplicon sequencing will also be useful in advancing this research area.

Mycorrhizal interactions with soil grazers and predators

The contrasting food web dynamics of AM and EcM systems is driven by their contrasting dominant energy channels; where AM systems with more rapid nutrient cycling have a more bacterial-based energy channel and EcM systems with slower nutrient cycling have a more fungal-based energy channel (Phillips et al., 2013; Wardle et al., 2004). These energy channels may then merge at trophic levels due to the omnivorous feeding of many soil animals (Bengtsson, Setälä, and Zheng, 1996) or by the activity of protists who are major feeders on both bacteria and fungi (Geisen, 2016). Given their different nutrient economies, EcM and AM systems are expected to have very different food webs driven by multitrophic interactions, and hence these mycorrhizal associations influence the whole ecosystem surrounding plants including associated soil animals and protists.

The high bacterial to fungal biomass ratio of AM systems as well as less AM protection of roots should promote a higher density of bacterivores (primarily protists and nematodes) and herbivores (root-feeding invertebrates like nematodes), and their subsequent predators and pathogens (Antunes and Koyama, 2017; Persson, Bengtsson, Menge, and Power, 1996). The high fungal biomass of EcM systems should promote a higher density of fungivores (various invertebrates and protists), and their subsequent predators (Antunes and Koyama, 2017; Cromack, Fichter, Moldenke, Entry, and Ingham, 1988; Fitter and Garbaye, 1994). While little is known about the effect of mycorrhizal type on nematode community dynamics, evidence suggests that fungal-feeding nematodes have higher abundances under EcM trees, compared to bacterial-feeding nematodes under AM trees (Cesarz et al., 2013). This observation may however be ascribed to the strong pH effect on bacterial community structure (Fierer, 2017), rather than mycorrhiza *per se*. Furthermore, EcM fungi may provide more extensive and nutritious hyphae for fungivores compared to saprotrophic fungi which dominate AM forests (Anslan, Bahram, and Tedersoo, 2018; Cromack et al., 1988; Dighton, Zapata, and Ruess, 2000).

Protists may be key organisms that help to maintain higher diversity and system functioning in the soil community through consumption of bacteria and fungi, control of their populations, and release of excess N that can be utilised by other organisms (Clarholm, Bonkowski, and Griffiths, 2007; Coleman, 1994; Gao, Karlsson, Geisen, Kowalchuk, and Jousset, 2019). This N may be preferentially targeted for uptake by AM fungi, which may be an important source of N for AM hosts (Koller, Rodriguez, Robin, Scheu, and Bonkowski, 2013). We suggest that the importance of protists in N liberation is less important in EcM systems due to the tight control of EcM on N cycling, yet protists may be important in the turnover of EcM biomass, from which N can be recycled back through the EcM symbiosis, and protists may also play an important role in EcM fungal community dynamics (Gao et al., 2019; Geisen et al., 2016). But ultimately the activity of protists may be influenced by mycorrhizal mycelium which connects soil patches of nutrients and soil moisture (Jentschke, Bonkowski, Godbold, and Scheu, 1995), which protists are sensitive to and require for movement and functioning (Geisen, Bandow, Römbke, and Bonkowski, 2014). Yet, further studies into protist communities from a mycorrhizal type perspective are warranted, especially given the respective N cycling effects associated with EcM and AM systems (Phillips et al., 2013). As protists have been found to be more sensitive to N addition compared to other soil microbes in agricultural systems (Zhao et al., 2019), it remains to be investigated whether such effects of N availability on protist communities may occur in forest settings across an EcM to AM dominance gradient.

The presence of earthworms also plays an important role in C and nutrient dynamics in tree-mycorrhizal systems, by reducing soil organic layer thickness, altering bulk density, and mixing organic matter with mineral soils across soil horizons (Filser et al., 2016; Frelich et al., 2006; Van Groenigen et al., 2014). Aside from climate, the presence and activity of earthworms is driven mostly by the availability of high-quality litter (De Wandeler et al., 2018; Szlavecz et al., 2018), and impeded by low pH (Phillips et al., 2019). Earthworms can be grouped into three functionally distinct groups according to their burrowing behaviours. Burrowing anecic and endogeic worms are associated with mull formation in forest soils, whereas, in mor soils usually only epigeic (surface-living earthworms) are found (Bouché, 1977; Satchell, 1983). While not directly explored from a mycorrhizal type perspective, across temperate and boreal forests earthworm biomass, species richness and the occurrence of epigeic earthworms have been found to be lowest in forests with a greater evergreen (EcM) gymnosperm fraction and highest in forests with a greater deciduous (AM) angiosperm fraction (De Wandeler et al., 2018), largely consistent with the effects of lower pH on earthworms. Consequently, at least in certain temperate forests, the dominant feeding source of earthworms may also vary between EcM- and AM-dominated systems, with epigeic and anecic fresh litter feeders dominating in younger (AM-dominated) systems and endogeic soil organic matter feeders dominating in older (EcM-dominated) systems (Szlavecz et al., 2018). The role and distribution of earthworms in tropical forests is more complex to interpret from an EcM and AM system perspective.

Mycorrhizal interactions with N-transforming microbes

Bacteria are the most abundant and diverse free-living organisms in soils acting as key N-fixing microbes, nitrifiers, and denitrifiers (Lladó et al., 2017; López-Mondéjar et al., 2018). Archaea are also widely distributed in soils and include members who play potentially important roles in soil N cycling as ammonia-oxidizing archaea (AOA) (Bates et al., 2011; Cavicchioli, 2011). The contrasting N dynamics of EcM and AM systems is largely owing to their interactions with microbes involved in N fixation and subsequent transformations, as mycorrhizal fungi lack the ability to fix atmospheric N or carry out nitrification.

Both EcM and AM fungi interact with N-fixing bacteria, which can provide a substantial amount of N input to these systems (Pastor and Binkley, 1998; Son, 2001). N-fixing tree symbioses occur in both EcM and AM systems but are most abundant in tropical AM systems (Steidinger et al., 2019). Yet rhizobial N-fixing trees in tropical forests tend to be insensitive to soil N availability, and more facultative in their relationship with their N-fixing symbionts (Vitousek et al., 2002), while actinorhizal temperate and boreal N-fixing trees are more sensitive to soil N availability with a more obligatory relationship with their N-fixing symbionts, which are more crucial for plant N acquisition (Menge, Lichstein, and Ángeles-Pérez, 2014; Vitousek, Menge, Reed, and Cleveland, 2013). The success of actinorhizal N-fixing trees, that grow quickly at early successional stages and are later outcompeted by non-fixing trees (Liao & Menge, 2016), is likely related to the relative proportion of EcM to AM trees. AM systems may have greater turnover of canopy trees and gap creation with heterogeneity in successional stages suitable for the establishment of shade intolerant actinorhizal N-fixing trees, compared to monodominant EcM systems (Tedersoo, Bahram, & Zobel, 2020). AM trees also likely depend more on symbiotic N fixation for their nutrient economies, due to a looser control on N dynamics and reliance on other organisms for N liberation, including a potentially higher reliance on atmospherically fixed N especially in N-limited ecosystems (Averill et al., 2019; Bagyaraj, 1990; Barea, Azcon, and Azcón-Aguilar, 1992). However, it should be noted that boreal forests dominated by EcM gymnosperms have a significant moss component, where moss-cyanobacterial associations may be responsible for a significant input of N into these systems, which can be cycled through the EcM symbiosis, however this N is potentially only released into the soil slowly or after disturbances (Carleton and Read, 1991; Rousk, Jones, and DeLuca, 2013).

The contribution of free-living N-fixing bacteria in the soil to overall N fixation tends to be smaller compared to symbiotic N fixation and is less explored across biomes and across mycorrhizal types, however, there seems to be little difference between gymnosperm and angiosperm forests in this respect (Reed, Cleveland, and Townsend, 2011; Son, 2001). This N can be a significant input into forests with few symbiotic N-fixing bacteria such as boreal and temperate forests, and in evergreen compared to deciduous forests (Reed et al., 2011). AM systems stand to benefit more from the activity of free-living N-fixing bacteria in soils. Yet, the more extensive EcM mycelium is associated with greater moisture and soluble C sources compared to the bulk soil, and may provide good habitat for free-living bacteria who require high-quality soluble C in order to undertake N fixation, although at the same time decreased pH in the ectomycorrhizosphere may inhibit N fixation (Smercina, Evans, Friesen, and Tiemann, 2019). Both EcM and AM trees host non-nodulating endophytic N-fixing bacteria, which may not only play important roles in N acquisition but also in the establishment and maintenance of the mycorrhizal symbiosis (Aghai et al., 2019; Oses, Frank, Valenzuela, and Rodríguez, 2018).

While N fixation is important for N dynamics, subsequent nitrification is dependent on the activity of both ammonia-oxidizing archaea (AOA) and ammonia-oxidizing bacteria (AOB), and then nitrite-oxidizing bacteria (NOB) to complete the nitrification process (Stempfhuber et al., 2017). AOA are thought to dominate in nutrient-poor and acidic soils and are outcompeted by AOB with increasing N availability (Bates et al., 2011; Di et al., 2009; Xiang, He, He, Myrold, and Chu, 2017). Thus, it is expected that AOB would dominate ammonia-oxidation in AM systems, compared to the dominance of AOA in EcM systems. Overall, nitrification tends to be lower in EcM systems compared to AM systems (Lin et al., 2017), due to enhanced competition by EcM fungi for N with nitrifying prokaryotes (Tatsumi, Taniguchi, Du, Yamanaka, and Tateno, 2019), and a potential mismatch between ammonia-oxidizing microbes and nitrite-oxidizing microbes in EcM systems, particularly under EcM gymnosperm trees, who may even inhibit the activity of AOA despite often being associated with low pH conditions (Isobe et al., 2012;

Stempfhuber et al., 2017; Stopnišek et al., 2010). It is tempting to speculate that in AM systems more so than in EcM systems, AOB and NOB may form a symbiosis enhancing the nitrification process (Daims, Lücker, and Wagner, 2016), facilitated by higher N availability and pH values (Averill et al., 2019; Lin et al., 2017; Tedersoo and Bahram, 2019). While general patterns of soil N cycling and the contribution of different organisms remain unresolved across different forest biomes, mycorrhizal and tree types, the conservative N economy of EcM systems and the open N economy of AM systems are seen as the defining contrasting functional and ecological trait between the two, as shown mainly in temperate forests (Averill et al., 2019; Lin et al., 2017; Phillips et al., 2013), and interactions with N-transforming microbes likely play a large role in these differences.

EcM-AM interactions

Another important and often overlooked interaction is between EcM and AM fungi, because they often coexist in various ecosystems and even on the same tree individual (Kubisch, Hertel, and Leuschner, 2016; Teste, Jones, & Dickie, 2019; Toju, Sato, & Tanabe, 2014). AM systems may facilitate the establishment and survival of EcM trees, while EcM systems may impede the establishment and survival of AM trees (Kadowaki et al., 2018; Tedersoo, Bahram, & Zobel, 2020). Furthermore, the mycelium of AM and EcM fungi may co-occur in the same niche or occur via spatial separation in the soil profile (Moyersoen, Fitter, and Alexander, 1998; Teste, Jones, & Dickie, 2019). In addition, increasing evidence shows that when growing together on the same root system, AM and EcM may have a synergistic effect on plant-soil functioning, which seems to be driven by extreme environmental fluctuations such as soil moisture, nutrient availability, and temperature, where EcM may dominate colonization under mesic conditions and AM under extreme soil moisture conditions, and high temperatures and nutrient availability (Teste, Jones, & Dickie, 2019). Yet little is known about the actual physical and chemical interactions between the mycelia of EcM and AM fungi when in the vicinity of one another, with obvious difficulties in exploring this. Greater antagonisms may exist within guilds between functionally equivalent taxa as opposed to between EcM and AM fungi, due to competition for colonization sites, ultimately regulated by the host's attempt to balance C and nutrient budgets

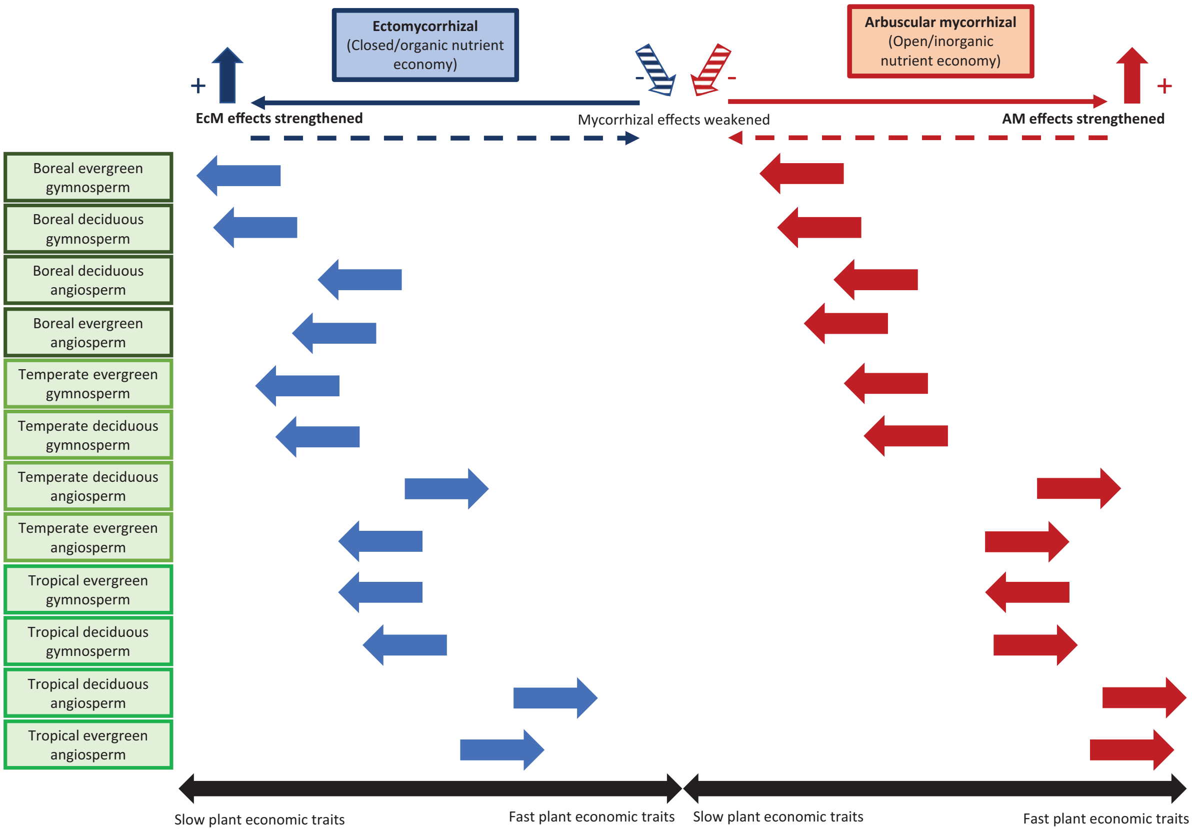

Fig. 1. Conceptual diagram exploring the relative trade-offs between strengthening and weakening effects on the closed and open nutrient economies of EcM and AM systems by different tree functional trait and forest biome combinations. The position and direction of arrows of the different tree/biome combinations is relative to their suggested balance between strengthening or neutralizing/weakening effects on EcM- or AM- associated nutrient dynamics and where these combinations sit on the plant economic trait spectrum.

(Bogar et al., 2019; Hortal et al., 2017; Smith and Smith, 2012).

Mycorrhizal fungi select for distinct soil communities

Overall, the EcM symbiosis represents a trade-off between conservative nutrient acquisition and flexibility, with EcM trees tending towards collaboration in nutrient acquisition, while the AM symbiosis represents a flexible and rapid nutrient acquisition over security trade-off, with AM trees tending towards ‘do it yourself’ nutrient uptake but also engaging in collaboration (Averill et al., 2019: Bergmann et al., 2020). These trade-offs may be further exacerbated due to different tree types and also different climatic biomes, where the combination of EcM with gymnosperms in boreal forests represents the extreme of slow plant economic traits and the combination of AM with angiosperms in tropical forests represents the extreme of fast plant economic traits (Fig. 1) (Augusto et al., 2015; Bond, 1989; Phillips et al., 2013; Vitousek, 1982). Within biomes and tree types, the greatest difference is likely between evergreen EcM trees and deciduous AM trees (Fig. 1) (Angst et al., 2019; Augusto et al., 2015; Dawud et al., 2017; Vesterdal, Clarke, Sigurdsson, and Gundersen, 2013; Zhang et al., 2018).

Using this framework, we hypothesize that EcM systems exert a selective pressure for a less functionally redundant soil community and attempt to maintain low pH and high C/N conditions to tightly control N cycling and maintain the dominance of their hosts (Cheeke et al., 2017; Tedersoo and Bahram, 2019; Tedersoo, Bahram, & Zobel, 2020). That is, EcM fungi dominate the soil environment enhanced by functional variation between EcM types (Chen, Koide, and Eissenstat, 2018; Zak et al., 2019), while saprotrophs and pathogens may be supressed and less functionally diverse. In addition, N-transforming microbes as well as predators and grazers may also be functionally less diverse (Fig. 2) (Averill and Hawkes, 2016; Chen et al., 2019; De Wandeler et al., 2018; Moore et al., 2015). Thus, EcM systems may experience less temporal soil community turnover, have reduced functional redundancy within the soil community, and place a direct selective pressure on beneficial organisms (Fig. 2) (Deveau et al., 2016; Frey−Klett et al., 2005), representing a more tight and closed nutrient acquisition strategy within the holobiont.

By contrast, AM systems with more homogenous functional variation within AM fungi (Chagnon, Bradley, Maherali, and Klironomos, 2013), nevertheless, may facilitate greater multifunctionality within the soil community in

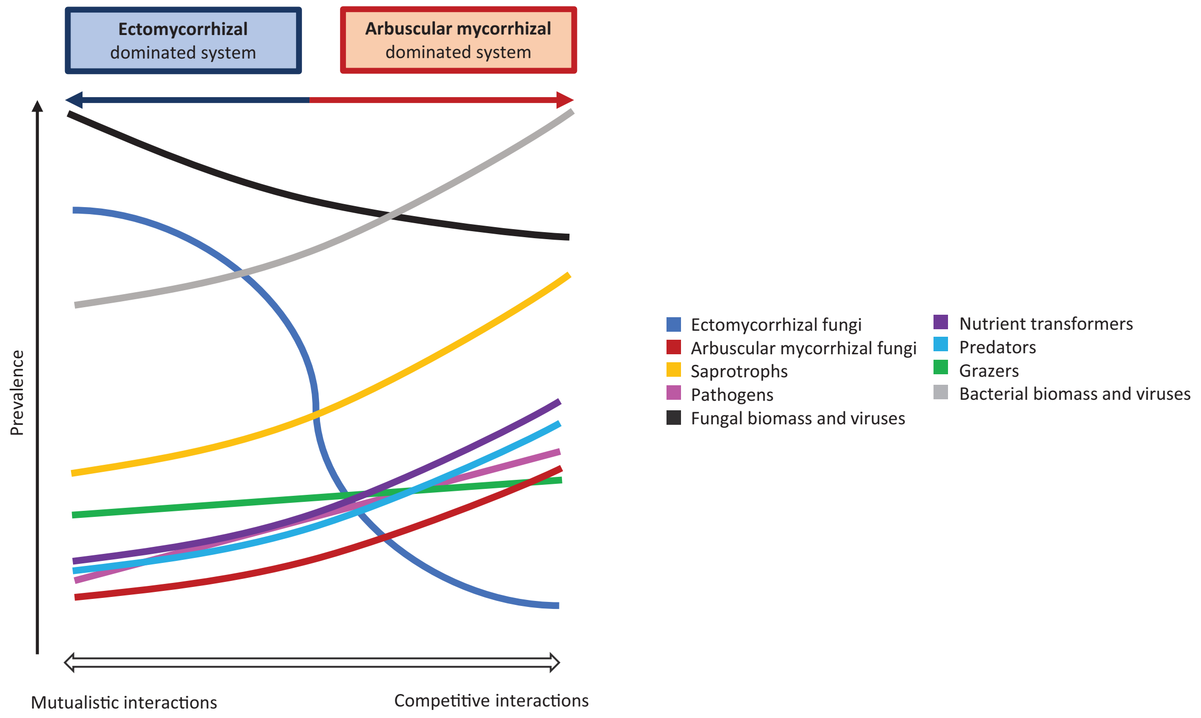

Fig. 2. Conceptual diagram exploring the relative prevalence of different soil organism groups as a system goes from EcM host dominance to AM host dominance, and in accordance from more mutualistic interactions to more competitive interactions. In EcM systems compared to AM systems, fungal biomass and viruses are greater than bacterial biomass and associated viruses, EcM fungi are the dominant soil guild, saprotrophs, nutrient transformers, predators, pathogens, and AM fungi are all less prevalent and potentially suppressed, while those that are present are likely to have more neutral or beneficial interactions with EcM trees and fungi, compared to more competitive and antagonistic interactions with AM trees and fungi.

general (Fig. 2) (Battini, Cristani, Giovannetti, and Agnolucci, 2016; Rillig, 2004). The associated soil communities will experience a greater range of pH and C/N conditions, and a looser N cycle (Averill et al., 2019; Phillips et al., 2013), and may also be more functionally redundant (Banerjee et al., 2016), with less capacity for organisms to reach monodominance both below and above ground (Rillig, 2004; Tedersoo, Bahram, & Zobel, 2020; Yang, Wagg, Veresoglou, Hempel, and Rillig, 2018). They are thus representing an open and loose nutrient acquisition strategy and a holobiont strategy, which involves highly precise nutrient foraging by AM fungi to supplement more passive plant nutrient uptake in a highly competitive soil environment rather than an overall control on nutrient cycling (Chen et al., 2018; Phillips et al., 2013). This has obvious implications for C and nutrient dynamics under global environmental change.

Future directions

We have put forward that AM and EcM systems may vary greatly in their effects on soil communities and ecosystem functioning. Hence there is a strong need to study AM and EcM systems across biomes, tree types, and edaphic gradients in order to get a more complete picture of these systems and their functioning. Specifically, further research is needed to untangle mycorrhizal type effects from environmental filtering, and whether in fact different mycorrhizal systems have the capacity to reinforce environmental controls on nutrient dynamics by actively manipulating the biotic and abiotic environment in their zone of influence. One approach to do so is to study these contrasting mycorrhizal types together in controlled environmental settings such as mesocosms, greenhouse experiments, or at least under the same edaphic conditions such as in common garden experiments. In addition, there continues to be a need for field-based studies, especially in mixed or neighboring EcM and AM systems in underrepresented regions such as tropical forests, temperate forests of the southern hemisphere, tree line ecotones, and boreal forests where some sparse occurrences of AM-forming trees occur. We further call upon researchers studying any processes and organism groups (both above and belowground) in forests to consider the presence and relative dominance of AM and EcM trees to help further understand these systems. The ease of this is facilitated by a recent plant mycorrhizal status database (Soudzilovskaia et al., 2020). We also recommend researchers studying soil processes in EcM and AM systems to study multiple soil organism groups simultaneously, something that will be facilitated by constantly improving molecular methods and cross-disciplinary collaborations (Baldrian, 2019). In line with assigning trees with a mycorrhizal status, there is also a need to continue to consider the presence of mycorrhizal associations by assessing colonization and biomass measurements or proxies of these (Soudzilovskaia et al., 2015), as well as considering the contribution of and further exploring the ecology of different functional types within mycorrhizal guilds. Finally, there continues to be the need to incorporate EcM and AM system dynamics into models predicting terrestrial processes and environmental change.

Declaration of Competing Interest

None.

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BOX 2. EcM and AM systems under environmental change

EcM and AM systems may respond differently to environmental change, such as accelerated climate change, due to their unique C and nutrient dynamics driven by interactions between a greater ecosystem with trees, their mycorrhizal symbionts, and the entire soil community (Cheeke *et al.*, 2017). Warming, changing precipitation patterns, and alterations to N availability stand to benefit AM systems more than EcM systems, due to a more flexible nutrient acquisition strategy and a lower C cost for the host (Soudzilovskaia *et al.*, 2015; Jo et al., 2019; Pugnaire et al., 2019; Steidinger *et al.*, 2019), and as we propose here due to greater functional redundancy. Dual EcM-AM trees may also become increasingly more common due to their ability to colonize new areas and function under a wider variety of fluctuating environmental conditions (Gerz et al., 2018; Teste *et al.*, 2019; Moyano et al., 2020). Recent research has shown EcM systems to experience greater negative alterations to their functioning compared to AM systems under environmental change, including enhanced decomposition of SOM (Kumar et al., 2020), decreased EcM tree performance (Fernandez et al., 2017; Wheeler et al., 2017; Averill et al., 2018; Jo *et al.*, 2019; DeForest and Snell, 2020), and decreased prevalence and colonization by EcM fungi (Kilpeläinen et al., 2017; Boeraeve et al., 2019). Within EcM fungi as a guild there may be a shift in dominance to short contact types that are less C-demanding and form less extensive external mycelia, and thereby reducing the overall presence of EcM fungi in the soil (Fernandez et al., 2017; León−Sánchez et al., 2018), hinting at reduced functional redundancy. These results point towards AM systems potentially benefiting more from environmental change in many cases compared to EcM systems which may be inhibited, in line with their opposing open and closed nutrient acquisition strategies, differing C costs for their hosts, and proposed contrasting functional properties of their soil communities.

References

Agerer, R. (2001). Exploration types of ectomycorrhizae. *Mycorrhiza*, *11*(2), 107–114.

Aghai, M. M., Khan, Z., Stoda, A. M., Sher, A. W., Ettl, G. J., & Doty, S. L. (2019). The effect of microbial endophyte consortia on Pseudotsuga menziesii and Thuja plicata survival, growth, and physiology across edaphic gradients. *Frontiers in Microbiology*, *10*, 1353.

Angst, G., Mueller, K. E., Eissenstat, D. M., Trumbore, S., Freeman, K. H., Hobbie, S. E., & Mueller, C. W. (2019). Soil organic carbon stability in forests: Distinct effects of tree species identity and traits. *Global Change Biology*, *25*(4), 1529–1546.

Anslan, S., Bahram, M., & Tedersoo, L. (2018). Seasonal and annual variation in fungal communities associated with epigeic springtails (Collembola spp.) in boreal forests. *Soil Biology and Biochemistry*, *116*, 245–252.

Antunes, P. M., & Koyama, A. (2017). Mycorrhizas as nutrient and energy pumps of soil food webs: Multitrophic interactions and feedbacks. *Mycorrhizal mediation of soil* (pp. 149−173). Elsevier.

Augusto, L., De Schrijver, A., Vesterdal, L., Smolander, A., Prescott, C., & Ranger, J. (2015). Influences of evergreen gymnosperm and deciduous angiosperm tree species on the functioning of temperate and boreal forests. *Biological Reviews*, *90* (2), 444–466.

Averill, C., Turner, B. L., & Finzi, A. C. (2014). Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature*, *505*(7484), 543–545.

Averill, C., & Hawkes, C. V. (2016). Ectomycorrhizal fungi slow soil carbon cycling. *Ecology Letters*, *19*(8), 937–947.

Averill, C., Dietze, M. C., & Bhatnagar, J. M. (2018). Continental−scale nitrogen pollution is shifting forest mycorrhizal associations and soil carbon stocks. *Global Change Biology*, *24* (10), 4544–4553.

Averill, C., Bhatnagar, J. M., Dietze, M. C., Pearse, W. D., & Kivlin, S. N. (2019). Global imprint of mycorrhizal fungi on whole-plant nutrient economics. *Proceedings of the National Academy of Sciences*, *116*(46), 23163–23168.

Awad, A., Majcherczyk, A., Schall, P., Schröter, K., Schöning, I., Schrumpf, M., & Seidel, D. (2019). Ectomycorrhizal and saprotrophic soil fungal biomass are driven by different factors and vary among broadleaf and coniferous temperate forests. *Soil Biology and Biochemistry*, *131*, 9–18.

Bagyaraj, D. J. (1990). Biological interactions between VA mycorrhizal fungi and other beneficial soil organisms. *Current Trends in Mycorrhizal Research*, 237–241.

Bahram, M., Hildebrand, F., Forslund, S. K., Anderson, J. L., Soudzilovskaia, N. A., Bodegom, P. M., & Huerta-Cepas, J. (2018). Structure and function of the global topsoil microbiome. *Nature*, *560*(7717), 233–237.

Bahram, M., Netherway, T., Hildebrand, F., Pritsch, K., Drenkhan, R., Loit, K., & Tedersoo, L. (2020). Plant nutrient−acquisition strategies drive topsoil microbiome structure and function. *New Phytologist*, *227*(4), 1189–1199.

Baldrian, P. (2017). Forest microbiome: Diversity, complexity and dynamics. *FEMS Microbiology Reviews*, *41*(2), 109–130.

Baldrian, P. (2019). The known and the unknown in soil microbial ecology. *FEMS Microbiology Ecology*, *95*(2), fiz005.

Banerjee, S., Kirkby, C. A., Schmutter, D., Bissett, A., Kirkegaard, J. A., & Richardson, A. E. (2016). Network analysis reveals functional redundancy and keystone taxa amongst bacterial and fungal communities during organic matter decomposition in an arable soil. *Soil Biology and Biochemistry*, *97*, 188–198.

Barea, J. M., Azcon, R., & Azcón-Aguilar, C. (1992). 21 vesicular-arbuscular mycorrhizal fungi in nitrogen-fixing systems. *Methods in microbiology: 24* (pp. 391−416). Academic Press.

Bates, S. T., Berg-Lyons, D., Caporaso, J. G., Walters, W. A., Knight, R., & Fierer, N. (2011). Examining the global distribution of dominant archaeal populations in soil. *The ISME Journal*, *5*(5), 908–917.

Battini, F., Cristani, C., Giovannetti, M., & Agnolucci, M. (2016). Multifunctionality and diversity of culturable bacterial communities strictly associated with spores of the plant beneficial symbiont Rhizophagus intraradices. *Microbiological Research*, *183*, 68–79.

Bengtsson, J., Setälä, H., & Zheng, D. W. (1996). Food webs and nutrient cycling in soils: Interactions and positive feedbacks. In G. Polis, & K. Winemiller (Eds.), *Food webs: Patterns and processes* (pp. 30−38). Chapman & Hall.

Bennett, J. A., Maherali, H., Reinhart, K. O., Lekberg, Y., Hart, M. M., & Klironomos, J. (2017). Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science*, *355*(6321), 181–184.

Berg, G., & Smalla, K. (2009). Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. *FEMS Microbiology Ecology*, *68*(1), 1–13.

Bergmann, J., Weigelt, A., van der Plas, F., Laughlin, D. C., Kuyper, T. W., Guerrero-Ramirez, N., & Mommer, L. (2020). The fungal collaboration gradient dominates the root economics space in plants. *Science Advances*, *6*(27), eaba3756.

Bever, J. D., Mangan, S. A., & Alexander, H. M. (2015). Maintenance of plant species diversity by pathogens. *Annual Review of Ecology, Evolution, and Systematics*, *46*, 305–325.

Blodgett, J. T., Herms, D. A., & Bonello, P. (2005). Effects of fertilization on red pine defense chemistry and resistance to Sphaeropsis sapinea. *Forest Ecology and Management*, *208* (1-3), 373–382.

Boeraeve, M., Honnay, O., & Jacquemyn, H. (2019). Forest edge effects on the mycorrhizal communities of the dual-mycorrhizal tree species Alnus glutinosa (L.) Gaertn. *Science of the Total Environment*, *666*, 703–712.

Bogar, L., Peay, K., Kornfeld, A., Huggins, J., Hortal, S., Anderson, I., & Kennedy, P. (2019). Plant-mediated partner discrimination in ectomycorrhizal mutualisms. *Mycorrhiza*, *29*(2), 97–111.

Bond, W. J. (1989). The tortoise and the hare: Ecology of angiosperm dominance and gymnosperm persistence. *Biological Journal of the Linnean Society*, *36*(3), 227–249.

Bonfante, P., & Genre, A. (2010). Mechanisms underlying beneficial plant−fungus interactions in mycorrhizal symbiosis. *Nature Communications*, *1*(1), 1–11.

Bouché, M. B. (1977). Strategies lombriciennes. *Ecological Bulletins*, (25), 122–132.

Brabcová, V., Nováková, M., Davidová, A., & Baldrian, P. (2016). Dead fungal mycelium in forest soil represents a decomposition hotspot and a habitat for a specific microbial community. *New Phytologist*, *210*(4), 1369–1381.

Branzanti, M. B., Rocca, E., & Pisi, A. (1999). Effect of ectomycorrhizal fungi on chestnut ink disease. *Mycorrhiza*, *9*(2), 103–109.

Brodribb, T. J., Pittermann, J., & Coomes, D. A. (2012). Elegance versus speed: Examining the competition between conifer and angiosperm trees. *International Journal of Plant Sciences*, *173* (6), 673–694.

Brundrett, M. C., & Tedersoo, L. (2018). Evolutionary history of mycorrhizal symbioses and global host plant diversity. *New Phytologist*, *220*(4), 1108–1115.

Brzostek, E. R., Dragoni, D., Brown, Z. A., & Phillips, R. P. (2015). Mycorrhizal type determines the magnitude and direction of root−induced changes in decomposition in a temperate forest. *New Phytologist*, *206*(4), 1274–1282.

Buchkowski, R. W., Bradford, M. A., Grandy, A. S., Schmitz, O. J., & Wieder, W. R. (2017). Applying population and community ecology theory to advance understanding of belowground biogeochemistry. *Ecology Letters*, *20*(2), 231–245.

Bunn, R. A., Simpson, D. T., Bullington, L. S., Lekberg, Y., & Janos, D. P. (2019). Revisiting the 'direct mineral cycling'hypothesis: Arbuscular mycorrhizal fungi colonize leaf litter, but why? *The ISME Journal*, *13*(8), 1891–1898.

Carleton, T. J., & Read, D. J. (1991). Ectomycorrhizas and nutrient transfer in conifer−feather moss ecosystems. *Canadian Journal of Botany*, *69*(4), 778–785.

Cavicchioli, R. (2011). Archaea—Timeline of the third domain. *Nature Reviews Microbiology*, *9*(1), 51–61.

Cesarz, S., Ruess, L., Jacob, M., Jacob, A., Schaefer, M., & Scheu, S. (2013). Tree species diversity versus tree species identity: Driving forces in structuring forest food webs as indicated by soil nematodes. *Soil Biology and Biochemistry*, *62*, 36–45.

Chagnon, P. L., Bradley, R. L., Maherali, H., & Klironomos, J. N. (2013). A trait-based framework to understand life history of mycorrhizal fungi. *Trends in Plant Science*, *18*(9), 484–491.

Cheeke, T. E., Phillips, R. P., Brzostek, E. R., Rosling, A., Bever, J. D., & Fransson, P. (2017). Dominant mycorrhizal association of trees alters carbon and nutrient cycling by selecting for microbial groups with distinct enzyme function. *New Phytologist*, *214*(1), 432–442.

Chen, W., Koide, R. T., & Eissenstat, D. M. (2018). Nutrient foraging by mycorrhizas: From species functional traits to ecosystem processes. *Functional Ecology*, *32*(4), 858–869.

Chen, L., Swenson, N. G., Ji, N., Mi, X., Ren, H., Guo, L., & Ma, K. (2019). Differential soil fungus accumulation and density dependence of trees in a subtropical forest. *Science*, *366* (6461), 124–128.

Clarholm, M., Bonkowski, M., & Griffiths, B. (2007). Protozoa and other protista in soil. Modern soil microbiology,(Eds. JD van Elsas, JT Trevors, EMH Wellington). (pp. 147−175). Amsterdam: Marcel Dekker.

Clemmensen, K. E., Finlay, R. D., Dahlberg, A., Stenlid, J., Wardle, D. A., & Lindahl, B. D. (2015). Carbon sequestration is related to mycorrhizal fungal community shifts during long−term succession in boreal forests. *New Phytologist*, *205*(4), 1525–1536.

Coleman, D. C. (1994). The microbial loop concept as used in terrestrial soil ecology studies. *Microbial Ecology*, *28*(2), 245–250.

Connell, J. H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of Populations*, *298*, 312.

Connell, J. H., & Lowman, M. D. (1989). Low-diversity tropical rain forests: Some possible mechanisms for their existence. *The American Naturalist*, *134*(1), 88–119.

Corrales, A., Mangan, S. A., Turner, B. L., & Dalling, J. W. (2016). An ectomycorrhizal nitrogen economy facilitates monodominance in a neotropical forest. *Ecology Letters*, *19*(4), 383–392.

Cromack, K., Jr, Fichter, B. L., Moldenke, A. M., Entry, J. A., & Ingham, E. R. (1988). Interactions between soil animals and ectomycorrhizal fungal mats. *Agriculture, Ecosystems & Environment*, *24*(1-3), 161–168.

Crowther, T. W., Glick, H. B., Covey, K. R., Bettigole, C., Maynard, D. S., Thomas, S. M., & Tuanmu, M. N. (2015). Mapping tree density at a global scale. *Nature*, *525*(7568), 201–205.

Daims, H., Lücker, S., & Wagner, M. (2016). A new perspective on microbes formerly known as nitrite-oxidizing bacteria. *Trends in Microbiology*, *24*(9), 699–712.

Dawud, S. M., Raulund−Rasmussen, K., Ratcliffe, S., Domisch, T., Finér, L., Joly, F. X., & Vesterdal, L. (2017). Tree species functional group is a more important driver of soil properties than tree species diversity across major European forest types. *Functional Ecology*, *31*(5), 1153–1162.

DeForest, J. L., & Snell, R. S. (2020). Tree growth response to shifting soil nutrient economy depends on mycorrhizal associations. *New Phytologist*, *225*(6), 2557–2566.

Deveau, A., Antony-Babu, S., Le Tacon, F., Robin, C., Frey-Klett, P., & Uroz, S. (2016). Temporal changes of bacterial communities in the Tuber melanosporum ectomycorrhizosphere during ascocarp development. *Mycorrhiza*, *26*(5), 389–399.

De Wandeler, H., Bruelheide, H., Dawud, S. M., Dănilă, G., Domisch, T., Finér, L., & Ratcliffe, S. (2018). Tree identity rather than tree diversity drives earthworm communities in European forests. *Pedobiologia*, *67*, 16–25.

Di, H. J., Cameron, K. C., Shen, J. P., Winefield, C. S., O'callaghan, M., Bowatte, S., & He, J. Z. (2009). Nitrification driven by bacteria and not archaea in nitrogen-rich grassland soils. *Nature Geoscience*, *2*(9), 621–624.

Dickie, I. A., Koele, N., Blum, J. D., Gleason, J. D., & McGlone, M. S. (2014). Mycorrhizas in changing ecosystems. *Botany*, *92*(2), 149–160.

Dighton, J., Zapata, E. J. G., & Ruess, L. (2000). Food preferences of a fungal-feeding Aphelenchoides species. *Nematology*, *2*(2), 223–230.

Ekblad, A., Wallander, H., Godbold, D. L., Cruz, C., Johnson, D., Baldrian, P., & Kraigher, H. (2013). The production and turnover of extramatrical mycelium of ectomycorrhizal fungi in forest soils: Role in carbon cycling. *Plant and Soil*, *366*(1-2), 1–27.

Fernandez, C. W., & Kennedy, P. G. (2016). Revisiting the 'Gadgil effect': Do interguild fungal interactions control carbon cycling in forest soils? *New Phytologist*, *209*(4), 1382–1394.

Fernandez, C. W., Nguyen, N. H., Stefanski, A., Han, Y., Hobbie, S. E., Montgomery, R. A., & Kennedy, P. G. (2017). Ectomycorrhizal fungal response to warming is linked to poor host performance at the boreal−temperate ecotone. *Global Change Biology*, *23*(4), 1598–1609.

Fernandez, C. W., See, C. R., & Kennedy, P. G. (2019). Decelerated carbon cycling by ectomycorrhizal fungi is controlled by substrate quality and community composition. *New Phytologist*, *226*(2), 569–582.

Fierer, N. (2017). Embracing the unknown: Disentangling the complexities of the soil microbiome. *Nature Reviews Microbiology*, *15*(10), 579.

Filser, J., Faber, J. H., Tiunov, A. V., Brussaard, L., Frouz, J., De Deyn, G., & Wall, D. H. (2016). Soil fauna: Key to new carbon models. *SOIL*, *2*, 565–582.

Finlay, R. D., & Read, D. J. (1986). The structure and function of the vegetative mycelium of ectomycorrhizal plants: I. translocation of 14C−labelled carbon between plants interconnected by a common mycelium. *New Phytologist*, *103*(1), 143–156.

Fitter, A. H., & Garbaye, J. (1994). Interactions between mycorrhizal fungi and other soil organisms. *Plant and Soil*, *159*(1), 123–132.

Franklin, O., Näsholm, T., Högberg, P., & Högberg, M. N. (2014). Forests trapped in nitrogen limitation−an ecological market perspective on ectomycorrhizal symbiosis. *New Phytologist*, *203*(2), 657–666.

Frelich, L. E., Hale, C. M., Reich, P. B., Holdsworth, A. R., Scheu, S., Heneghan, L., & Bohlen, P. J. (2006). Earthworm invasion into previously earthworm-free temperate and boreal forests. *Biological Invasions Belowground: Earthworms as Invasive Species* (pp. 35−45). Dordrecht: Springer.

Frey, S. D. (2019). Mycorrhizal fungi as mediators of soil organic matter dynamics. *Annual Review of Ecology, Evolution, and Systematics*, *50*, 237–259.

Frey−Klett, P., Chavatte, M., Clausse, M. L., Courrier, S., Roux, C. L., Raaijmakers, J., & Garbaye, J. (2005). Ectomycorrhizal symbiosis affects functional diversity of rhizosphere fluorescent pseudomonads. *New Phytologist*, *165*(1), 317–328.

Gadgil, R. L., & Gadgil, P. D. (1971). Mycorrhiza and litter decomposition. *Nature*, *233*(5315) 133−133.

Gadgil, P. D., & Gadgil, R. L. (1975). *Suppression of litter decomposition by mycorrhizal roots of Pinus radiata*. New Zealand Forest Service.

Gao, Z., Karlsson, I., Geisen, S., Kowalchuk, G., & Jousset, A. (2019). Protists: Puppet masters of the rhizosphere microbiome. *Trends in Plant Science*, *24*(2), 165–176.

Geisen, S. (2016). The bacterial-fungal energy channel concept challenged by enormous functional versatility of soil protists. *Soil Biology and Biochemistry*, *102*, 22–25.

Geisen, S., Bandow, C., Römbke, J., & Bonkowski, M. (2014). Soil water availability strongly alters the community composition of soil protists. *Pedobiologia*, *57*(4-6), 205–213.

Geisen, S., Koller, R., Hünninghaus, M., Dumack, K., Urich, T., & Bonkowski, M. (2016). The soil food web revisited: Diverse and widespread mycophagous soil protists. *Soil Biology and Biochemistry*, *94*, 10–18.

Gerz, M., Guillermo Bueno, C., Ozinga, W. A., Zobel, M., & Moora, M. (2018). Niche differentiation and expansion of plant species are associated with mycorrhizal symbiosis. *Journal of Ecology*, *106*(1), 2.

Gilbert, S. F., Sapp, J., & Tauber, A. I. (2012). A symbiotic view of life: We have never been individuals. *The Quarterly Review of Biology*, *87*(4), 325–341.

Gill, A. L., & Finzi, A. C. (2016). Belowground carbon flux links biogeochemical cycles and resource−use efficiency at the global scale. *Ecology Letters*, *19*(12), 1419–1428.

Gower, S. T., & Richards, J. H. (1990). Larches: Deciduous conifers in an evergreen world. *BioScience*, *40*(11), 818–826.

Hodge, A. (2014). Interactions between arbuscular mycorrhizal fungi and organic material substrates. Advances in applied microbiology *(Vol: 89* (pp. 47−99). Academic Press.

Hortal, S., Plett, K. L., Plett, J. M., Cresswell, T., Johansen, M., Pendall, E., & Anderson, I. C. (2017). Role of plant−fungal nutrient trading and host control in determining the competitive success of ectomycorrhizal fungi. *The ISME Journal*, *11*(12), 2666–2676.

Horton, T. R. (2017). Spore dispersal in ectomycorrhizal fungi at fine and regional scales. *Biogeography of mycorrhizal symbiosis* (pp. 61−78). Cham: Springer.

Ingham, R. E. (1988). Interactions between nematodes and vesicular-arbuscular mycorrhizae. *Agriculture, Ecosystems & Environment*, *24*(1-3), 169–182.

Isobe, K., Koba, K., Suwa, Y., Ikutani, J., Fang, Y., Yoh, M., & Senoo, K. (2012). High abundance of ammonia-oxidizing archaea in acidified subtropical forest soils in southern China after long-term N deposition. *FEMS Microbiology Ecology*, *80* (1), 193–203.

Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *The American Naturalist*, *104*(940), 501–528.

Jentschke, G., Bonkowski, M., Godbold, D. L., & Scheu, S. (1995). Soil protozoa and forest tree growth: Non-nutritional effects and interaction with mycorrhizae. *Biology and Fertility of Soils*, *20*(4), 263–269.

Jo, I., Fei, S., Oswalt, C. M., Domke, G. M., & Phillips, R. P. (2019). Shifts in dominant tree mycorrhizal associations in response to anthropogenic impacts. *Science Advances*, *5*(4), eaav6358.

Kadowaki, K., Yamamoto, S., Sato, H., Tanabe, A. S., Hidaka, A., & Toju, H. (2018). Mycorrhizal fungi mediate the direction and strength of plant−soil feedbacks differently between arbuscular mycorrhizal and ectomycorrhizal communities. *Communications Biology*, *1*(1), 1–11.

Kaiser, C., Kilburn, M. R., Clode, P. L., Fuchslueger, L., Koranda, M., Cliff, J. B., & Murphy, D. V. (2015). Exploring the transfer of recent plant photosynthates to soil microbes: Mycorrhizal pathway vs direct root exudation. *New Phytologist*, *205*(4), 1537–1551.

Keenan, R. J., Reams, G. A., Achard, F., de Freitas, J. V., Grainger, A., & Lindquist, E. (2015). Dynamics of global forest area: Results from the FAO Global Forest Resources Assessment 2015. *Forest Ecology and Management*, *352*, 9–20.

Keller, A. B., & Phillips, R. P. (2019). Leaf litter decay rates differ between mycorrhizal groups in temperate, but not tropical, forests. *New Phytologist*, *222*(1), 556–564.

Kilpeläinen, J., Barbero-López, A., Vestberg, M., Heiskanen, J., & Lehto, T. (2017). Does severe soil drought have after-effects on arbuscular and ectomycorrhizal root colonisation and plant nutrition? *Plant and Soil*, *418*(1-2), 377–386.

Kimura, M., Jia, Z. J., Nakayama, N., & Asakawa, S. (2008). Ecology of viruses in soils: Past, present and future perspectives. *Soil Science and Plant Nutrition*, *54*(1), 1–32.

Kivlin, S. N., Hawkes, C. V., & Treseder, K. K. (2011). Global diversity and distribution of arbuscular mycorrhizal fungi. *Soil Biology and Biochemistry*, *43*(11), 2294–2303.

Koller, R., Rodriguez, A., Robin, C., Scheu, S., & Bonkowski, M. (2013). Protozoa enhance foraging efficiency of arbuscular mycorrhizal fungi for mineral nitrogen from organic matter in soil to the benefit of host plants. *New Phytologist*, *199*(1), 203–211.

Kubisch, P., Hertel, D., & Leuschner, C. (2016). Fine root productivity and turnover of ectomycorrhizal and arbuscular mycorrhizal tree species in a temperate broad-leaved mixed forest. *Frontiers in Plant Science*, *7*, 1233.

Kumar, A., Phillips, R. P., Scheibe, A., Klink, S., & Pausch, J. (2020). Organic matter priming by invasive plants depends on dominant mycorrhizal association. *Soil Biology and Biochemistry*, *140*, 107645.

Kuzyakov, Y., Friedel, J. K., & Stahr, K. (2000). Review of mechanisms and quantification of priming effects. *Soil Biology and Biochemistry*, *32*(11-12), 1485–1498.

Kuzyakov, Y., & Mason-Jones, K. (2018). Viruses in soil: Nano-scale undead drivers of microbial life, biogeochemical turnover and ecosystem functions. *Soil Biology and Biochemistry*, *127*, 305–317.

Kyaschenko, J., Clemmensen, K. E., Karltun, E., & Lindahl, B. D. (2017). Below−ground organic matter accumulation along a boreal forest fertility gradient relates to guild interaction within fungal communities. *Ecology Letters*, *20*(12), 1546–1555.

Laliberté, E., Lambers, H., Burgess, T. I., & Wright, S. J. (2015). Phosphorus limitation, soil−borne pathogens and the coexistence of plant species in hyperdiverse forests and shrublands. *New Phytologist*, *206*(2), 507–521.

León−Sánchez, L., Nicolás, E., Goberna, M., Prieto, I., Maestre, F. T., & Querejeta, J. I. (2018). Poor plant performance under simulated climate change is linked to mycorrhizal responses in a semi−arid shrubland. *Journal of Ecology*, *106*(3), 960–976.

Lindahl, B. D., & Tunlid, A. (2015). Ectomycorrhizal fungi−potential organic matter decomposers, yet not saprotrophs. *New Phytologist*, *205*(4), 1443–1447.

Lin, G., McCormack, M. L., Ma, C., & Guo, D. (2017). Similar below−ground carbon cycling dynamics but contrasting modes of nitrogen cycling between arbuscular mycorrhizal and ectomycorrhizal forests. *New Phytologist*, *213*(3), 1440–1451.

Liao, W., & Menge, D. N. (2016). Demography of symbiotic nitrogen-fixing trees explains their rarity and successional decline in temperate forests in the United States. *PloS One*, *11*(10), e0164522.

Lin, G., Chen, Z., & Zeng, D. H. (2019). Presence of mycorrhizal fungal hyphae rather than living roots retards root litter decomposition. *Forests*, *10*(6), 502.

Liu, Y. Y., Van Dijk, A. I., De Jeu, R. A., Canadell, J. G., McCabe, M. F., Evans, J. P., & Wang, G. (2015). Recent reversal in loss of global terrestrial biomass. *Nature Climate Change*, *5*(5), 470–474.

Lladó, S., López-Mondéjar, R., & Baldrian, P. (2017). Forest soil bacteria: Diversity, involvement in ecosystem processes, and response to global change. *Microbiology and Molecular Biology Reviews*, *81*(2) e00063−16.

López-Mondéjar, R., Brabcová, V., Štursová, M., Davidová, A., Jansa, J., Cajthaml, T., & Baldrian, P. (2018). Decomposer food web in a deciduous forest shows high share of generalist microorganisms and importance of microbial biomass recycling. *The ISME Journal*, *12*(7), 1768–1778.

Mariotte, P., Mehrabi, Z., Bezemer, T. M., De Deyn, G. B., Kulmatiski, A., Drigo, B., & Kardol, P. (2018). Plant−soil feedback: Bridging natural and agricultural sciences. *Trends in Ecology & Evolution*, *33*(2), 129–142.

Martino, E., Morin, E., Grelet, G. A., Kuo, A., Kohler, A., Daghino, S., & Hainaut, M. (2018). Comparative genomics and transcriptomics depict ericoid mycorrhizal fungi as versatile saprotrophs and plant mutualists. *New Phytologist*, *217*(3), 1213–1229.

Mayor, J. R., & Henkel, T. W. (2006). Do ectomycorrhizas alter leaf−litter decomposition in monodominant tropical forests of Guyana? *New Phytologist*, *169*(3), 579–588.

Menge, D. N., Lichstein, J. W., & Ángeles-Pérez, G. (2014). Nitrogen fixation strategies can explain the latitudinal shift in nitrogen−fixing tree abundance. *Ecology*, *95*(8), 2236–2245.

Minina, E. A., Filonova, L. H., Sanchez-Vera, V., Suarez, M. F., Daniel, G., & Bozhkov, P. V. (2013). Detection and measurement of necrosis in plants. *Necrosis* (pp. 229−248). Totowa, NJ: Humana Press.

Moore, J. A., Jiang, J., Patterson, C. M., Mayes, M. A., Wang, G., & Classen, A. T. (2015). Interactions among roots, mycorrhizas and free−living microbial communities differentially impact soil carbon processes. *Journal of Ecology*, *103*(6), 1442–1453.

Moyano, J., Dickie, I. A., Rodriguez−Cabal, M. A., & Nuñez, M. A. (2020). Patterns of plant naturalization show that facultative mycorrhizal plants are more likely to succeed outside their native Eurasian ranges. *Ecography*, *43*(5), 648–659.

Moyersoen, B., Fitter, A. H., & Alexander, I. J. (1998). Spatial distribution of ectomycorrhizas and arbuscular mycorrhizas in Korup National Park rain forest, Cameroon, in relation to edaphic parameters. *The New Phytologist*, *139*(2), 311–320.

Nilsson, L. O., Giesler, R., Bååth, E., & Wallander, H. (2005). Growth and biomass of mycorrhizal mycelia in coniferous forests along short natural nutrient gradients. *New Phytologist*, *165*(2), 613–622.

Oliverio, A. M., Geisen, S., Delgado-Baquerizo, M., Maestre, F. T., Turner, B. L., & Fierer, N. (2020). The global-scale distributions of soil protists and their contributions to belowground systems. *Science Advances*, *6*(4), eaax8787.

Olsson, P. A., & Johnson, N. C. (2005). Tracking carbon from the atmosphere to the rhizosphere. *Ecology Letters*, *8*(12), 1264–1270.

Öpik, M., Vanatoa, A., Vanatoa, E., Moora, M., Davison, J., Kalwij, J. M., & Zobel, M. (2010). The online database MaarjAM reveals global and ecosystemic distribution patterns in arbuscular mycorrhizal fungi (Glomeromycota). *New Phytologist*, *188*(1), 223–241.

Öpik, M., Zobel, M., Cantero, J. J., Davison, J., Facelli, J. M., Hiiesalu, I., & Liira, J. (2013). Global sampling of plant roots expands the described molecular diversity of arbuscular mycorrhizal fungi. *Mycorrhiza*, *23*(5), 411–430.

Oses, R., Frank, A. C., Valenzuela, S., & Rodríguez, J. (2018). Nitrogen fixing endophytes in forest trees. *Endophytes of Forest Trees* (pp. 191−204). Cham: Springer.

Pastor, J., & Binkley, D. (1998). Nitrogen fixation and the mass balances of carbon and nitrogen in ecosystems. *Biogeochemistry*, *43*(1), 63–78.

Peh, K. S. H., Lewis, S. L., & Lloyd, J. (2011). Mechanisms of monodominance in diverse tropical tree−dominated systems. *Journal of Ecology*, *99*(4), 891–898.

Pepe, A., Giovannetti, M., & Sbrana, C. (2018). Lifespan and functionality of mycorrhizal fungal mycelium are uncoupled from host plant lifespan. *Scientific Reports*, *8*(1), 1–10.

Persson, L., Bengtsson, J., Menge, B. A., & Power, M. E. (1996). Productivity and consumer regulation—Concepts, patterns, and mechanisms. In G. Polis, & K. Winemiller (Eds.), *Food webs: Patterns and processes* (pp. 30−38). Chapman & Hall.

Phillips, R. P., Brzostek, E., & Midgley, M. G. (2013). The mycorrhizal-associated nutrient economy: A new framework for predicting carbon−nutrient couplings in temperate forests. *New Phytologist*, *199*(1), 41–51.

Phillips, H. R., Guerra, C. A., Bartz, M. L., Briones, M. J., Brown, G., Crowther, T. W., & Orgiazzi, A. (2019). Global distribution of earthworm diversity. *Science*, *366*(6464), 480–485.

Poulter, B., Ciais, P., Hodson, E., Lischke, H., Maignan, F., Plummer, S., & Zimmermann, N. E. (2011). Plant functional type mapping for earth system models. *Geoscientific Model Development*, *4*(4), 993–1010.

Pratama, A. A., & van Elsas, J. D. (2018). The ‘neglected’soil virome−potential role and impact. *Trends in Microbiology*, *26*(8), 649–662.

Prober, S. M., Leff, J. W., Bates, S. T., Borer, E. T., Firn, J., Harpole, W. S., & Cleland, E. E. (2015). Plant diversity predicts beta but not alpha diversity of soil microbes across grasslands worldwide. *Ecology Letters*, *18*(1), 85–95.

Pugnaire, F. I., Morillo, J. A., Peñuelas, J., Reich, P. B., Bardgett, R. D., Gaxiola, A., & Van Der Putten, W. H. (2019). Climate change effects on plant-soil feedbacks and consequences for biodiversity and functioning of terrestrial ecosystems. *Science Advances*, *5*(11), eaaz1834.

Read, D. J. (1991). Mycorrhizas in ecosystems. *Experientia*, *47*(4), 376–391.

Read, D. J., & Perez−Moreno, J. (2003). Mycorrhizas and nutrient cycling in ecosystems−a journey towards relevance? *New Phytologist*, *157*(3), 475–492.

Read, D. J., Leake, J. R., & Perez-Moreno, J. (2004). Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. *Canadian Journal of Botany*, *82* (8), 1243–1263.

Reed, S. C., Cleveland, C. C., & Townsend, A. R. (2011). Functional ecology of free-living nitrogen fixation: A contemporary perspective. *Annual Review of Ecology, Evolution, and Systematics*, *42*, 489–512.

Reich, P. B., Walters, M. B., & Ellsworth, D. S. (1997). From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences*, *94*(25), 13730–13734.

Reich, P. B. (2014). The world−wide ‘fast−slow’plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*(2), 275–301.

Rillig, M. C. (2004). Arbuscular mycorrhizae and terrestrial ecosystem processes. *Ecology letters*, *7*(8), 740–754.

Romaní, A. M., Fischer, H., Mille-Lindblom, C., & Tranvik, L. J. (2006). Interactions of bacteria and fungi on decomposing litter: Differential extracellular enzyme activities. *Ecology*, *87*(10), 2559–2569.

Rosling, A., Lindahl, B. D., Taylor, A. F., & Finlay, R. D. (2004). Mycelial growth and substrate acidification of ectomycorrhizal fungi in response to different minerals. *FEMS Microbiology Ecology*, *47*(1), 31–37.

Rousk, K., Jones, D. L., & DeLuca, T. H. (2013). Moss-cyanobacteria associations as biogenic sources of nitrogen in boreal forest ecosystems. *Frontiers in Microbiology*, *4*, 150.

Satchell, J. E. (1983). Earthworm ecology in forest soils. *Earthworm ecology* (pp. 161−170). Dordrecht: Springer.

Scharlemann, J. P. W., Tanner, E. V. J., Hiederer, R., & Kapos, V. (2014). Global soil carbon: Understanding and managing the largest terrestrial carbon pool. *Carbon Management*, *5*(1), 81–91.

Shahzad, T., Chenu, C., Genet, P., Barot, S., Perveen, N., Mougin, C., & Fontaine, S. (2015). Contribution of exudates, arbuscular mycorrhizal fungi and litter depositions to the rhizosphere priming effect induced by grassland species. *Soil Biology and Biochemistry*, *80*, 146–155.

Sheldrake, M., Rosenstock, N. P., Revillini, D., Olsson, P. A., Mangan, S., Sayer, E. J., & Tanner, E. V. (2017). Arbuscular mycorrhizal fungal community composition is altered by long−term litter removal but not litter addition in a lowland tropical forest. *New Phytologist*, *214*(1), 455–467.

Smercina, D. N., Evans, S. E., Friesen, M. L., & Tiemann, L. K. (2019). To fix or not to fix: Controls on free-living nitrogen fixation in the rhizosphere. *Applied and Environmental Microbiology*, *85*(6) e02546−18.

Smith, S. E., Smith, F. A., & Jakobsen, I. (2003). Mycorrhizal fungi can dominate phosphate supply to plants irrespective of growth responses. *Plant Physiology*, *133*(1), 16–20.

Smith, S. E., & Read, D. J. (2010). *Mycorrhizal symbiosis*. Academic Press.

Smith, S. E., & Smith, F. A. (2012). Fresh perspectives on the roles of arbuscular mycorrhizal fungi in plant nutrition and growth. *Mycologia*, *104*(1), 1–13.

Smith, G. R., & Wan, J. (2019). Resource−ratio theory predicts mycorrhizal control of litter decomposition. *New Phytologist*, *223*(3), 1595–1606.

Son, Y. (2001). Non-symbiotic nitrogen fixation in forest ecosystems. *Ecological Research*, *16*(2), 183–196.

Soudzilovskaia, N. A., Douma, J. C., Akhmetzhanova, A. A., van Bodegom, P. M., Cornwell, W. K., Moens, E. J., & Cornelissen, J. H. (2015). Global patterns of plant root colonization intensity by mycorrhizal fungi explained by climate and soil chemistry. *Global Ecology and Biogeography*, *24*(3), 371–382.

Soudzilovskaia, N. A., van Bodegom, P. M., Terrer, C., van’t Zelfde, M., McCallum, I., McCormack, M. L., & Tedersoo, L. (2019). Global mycorrhizal plant distribution linked to terrestrial carbon stocks. *Nature Communications*, *10* (1), 1–10.

Soudzilovskaia, N. A., Vaessen, S., Barcelo, M., He, J., Rahimlou, S., Abarenkov, K., & Tedersoo, L. (2020). FungalRoot: Global online database of plant mycorrhizal associations. *New Phytologist*, *227*(3), 955–966.

Staddon, P. L., Ramsey, C. B., Ostle, N., Ineson, P., & Fitter, A. H. (2003). Rapid turnover of hyphae of mycorrhizal fungi determined by AMS microanalysis of 14C. *Science*, *300* (5622), 1138–1140.

Starr, E. P., Nuccio, E. E., Pett-Ridge, J., Banfield, J. F., & Firestone, M. K. (2019). Metatranscriptomic reconstruction reveals RNA viruses with the potential to shape carbon cycling in soil. *Proceedings of the National Academy of Sciences*, *116* (51), 25900–25908.

Steidinger, B. S., Crowther, T. W., Liang, J., Van Nuland, M. E., Werner, G. D., Reich, P. B., & Herault, B. (2019). Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. *Nature*, *569*(7756), 404–408.

Stempfhuber, B., Richter-Heitmann, T., Bienek, L., Schöning, I., Schrumpf, M., Friedrich, M., & Schloter, M. (2017). Soil pH and plant diversity drive co-occurrence patterns of ammonia and nitrite oxidizer in soils from forest ecosystems. *Biology and Fertility of Soils*, *53*(6), 691–700.

Sterkenburg, E., Clemmensen, K. E., Ekblad, A., Finlay, R. D., & Lindahl, B. D. (2018). Contrasting effects of ectomycorrhizal fungi on early and late stage decomposition in a boreal forest. *The ISME Journal*, *12*(9), 2187–2197.

Stopnišek, N., Gubry-Rangin, C., Höfferle, Š., Nicol, G. W., Mandič-Mulec, I., & Prosser, J. I. (2010). Thaumarchaeal ammonia oxidation in an acidic forest peat soil is not influenced by ammonium amendment. *Applied and Environmental Microbiology*, *76*(22), 7626–7634.

Szlavecz, K., Chang, C. H., Bernard, M. J., Pitz, S. L., Xia, L., Ma, Y., & Csuzdi, C. (2018). Litter quality, dispersal and invasion drive earthworm community dynamics and forest soil development. *Oecologia*, *188*(1), 237–250.

Tatsumi, C., Taniguchi, T., Du, S., Yamanaka, N., & Tateno, R. (2019). Soil nitrogen cycling is determined by the competition between mycorrhiza and ammonia−oxidizing prokaryotes. *Ecology*, e02963.

Tedersoo, L., & Bahram, M. (2019). Mycorrhizal types differ in ecophysiology and alter plant nutrition and soil processes. *Biological Reviews*, *94*(5), 1857–1880.

Steege, Ter, H., Henkel, W., T., Helal, N., Marimon, B. S., Marimon-Junior, B. H., Huth, A., & Salomão, R. P. (2019). Rarity of monodominance in hyperdiverse Amazonian forests. *Scientific Reports*, *9*(1), 1–15.

Teste, F. P., Jones, M. D., & Dickie, I. A. (2019). Dual−mycorrhizal plants: Their ecology and relevance. *New Phytologist*, *225* (5), 1835–1851.

Teste, F. P., Kardol, P., Turner, B. L., Wardle, D. A., Zemunik, G., Renton, M., & Laliberté, E. (2017). Plant-soil feedback and the maintenance of diversity in Mediterranean-climate shrublands. *Science*, *355*(6321), 173–176.

Tedersoo, L., Bahram, M., & Zobel, M. (2020). How mycorrhizal associations drive plant population and community biology. *Science*, *367*(6480), eaba1223.

Toju, H., Sato, H., & Tanabe, A. S. (2014). Diversity and spatial structure of belowground plant−fungal symbiosis in a mixed subtropical forest of ectomycorrhizal and arbuscular mycorrhizal plants. *PloS One*, *9*(1), e86566.

Urbanová, M., Šnajdr, J., & Baldrian, P. (2015). Composition of fungal and bacterial communities in forest litter and soil is largely determined by dominant trees. *Soil Biology and Biochemistry*, *84*, 53–64.

Van Den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D. A., & Bardgett, R. D. (2019). Soil nematode abundance and functional group composition at a global scale. *Nature*, *572*(7768), 194–198.

Van Der Putten, W. H. (2000). Pathogen-driven forest diversity. *Nature*, *404*(6775), 232–233.

Van Groenigen, J. W., Lubbers, I. M., Vos, H. M., Brown, G. G., De Deyn, G. B., & Van Groenigen, K. J. (2014). Earthworms increase plant production: A meta-analysis. *Scientific Reports*, *4*, 6365.

Vašutová, M., Mleczko, P., López-García, A., Maček, I., Boros, G., Ševčík, J., & Páll-Gergely, B. (2019). Taxi drivers: The role of animals in transporting mycorrhizal fungi. *Mycorrhiza*, *29*(5), 1–22.

Vayssier-Taussat, M., Albina, E., Citti, C., Cosson, J. F., Jacques, M. A., Lebrun, M. H., & Candresse, T. (2014). Shifting the paradigm from pathogens to pathobiome: New concepts in the light of meta-omics. *Frontiers in Cellular and Infection Microbiology*, *4*, 29.

Verbruggen, E., Pena, R., Fernandez, C. W., & Soong, J. L. (2017). Mycorrhizal interactions with saprotrophs and impact on soil carbon storage. *Mycorrhizal Mediation of Soil* (pp. 441−460). Elsevier.

Vesterdal, L., Clarke, N., Sigurdsson, B. D., & Gundersen, P. (2013). Do tree species influence soil carbon stocks in temperate and boreal forests? *Forest Ecology and Management*, *309*, 4–18.

Vitousek, P. (1982). Nutrient cycling and nutrient use efficiency. *The American Naturalist*, *119*(4), 553–572.

Vitousek, P. M., Cassman, K. E. N., Cleveland, C., Crews, T., Field, C. B., Grimm, N. B., & Sprent, J. I. (2002). Towards an ecological understanding of biological nitrogen fixation. *The nitrogen cycle at regional to global scales* (pp. 1−45). Dordrecht: Springer.

Vitousek, P. M., Porder, S., Houlton, B. Z., & Chadwick, O. A. (2010). Terrestrial phosphorus limitation: Mechanisms, implications, and nitrogen−phosphorus interactions. *Ecological Applications*, *20*(1), 5–15.

Vitousek, P. M., Menge, D. N., Reed, S. C., & Cleveland, C. C. (2013). Biological nitrogen fixation: Rates, patterns and ecological controls in terrestrial ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*,(1621) 20130119.

Wall, D. H., Bradford, M. A., St. John, M. G., Trofymow, J. A., Behan−Pelletier, V., Bignell, D. E., & Wolters, V. (2008). Global decomposition experiment shows soil animal impacts on decomposition are climate−dependent. *Global Change Biology*, *14*(11), 2661–2677.

Wallander, H. (2006). External mycorrhizal mycelia: The importance of quantification in natural ecosystems. *The New Phytologist*, *171*(2), 240–242.

Wang, C., Zong, S., & Li, M. H. (2019). The Contrasting responses of mycorrhizal fungal mycelium associated with woody plants to multiple environmental factors. *Forests*, *10*(11), 973.

Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., Van Der Putten, W. H., & Wall, D. H. (2004). Ecological linkages between aboveground and belowground biota. *Science*, *304*(5677), 1629–1633.

Wheeler, J. A., Frey, S. D., & Stinson, K. A. (2017). Tree seedling responses to multiple environmental stresses: Interactive effects of soil warming, nitrogen fertilization, and plant invasion. *Forest Ecology and Management*, *403*, 44–51.

Wurzburger, N., & Hendrick, R. L. (2009). Plant litter chemistry and mycorrhizal roots promote a nitrogen feedback in a temperate forest. *Journal of Ecology*, *97*(3), 528–536.

Xiang, X., He, D., He, J. S., Myrold, D. D., & Chu, H. (2017). Ammonia-oxidizing bacteria rather than archaea respond to short-term urea amendment in an alpine grassland. *Soil Biology and Biochemistry*, *107*, 218–225.

Yang, G., Wagg, C., Veresoglou, S. D., Hempel, S., & Rillig, M. C. (2018). How soil biota drive ecosystem stability. *Trends in Plant Science*, *23*(12), 1057–1067.

Zak, D. R., Pellitier, P. T., Argiroff, W., Castillo, B., James, T. Y., Nave, L. E., & Classen, A. T. (2019). Exploring the role of ectomycorrhizal fungi in soil carbon dynamics. *New Phytologist*, *223*(1), 33–39.

Zhang, H. Y., Lü, X. T., Hartmann, H., Keller, A., Han, X. G., Trumbore, S., & Phillips, R. P. (2018). Foliar nutrient resorption differs between arbuscular mycorrhizal and ectomycorrhizal trees at local and global scales. *Global Ecology and Biogeography*, *27*(7), 875–885.

Zhao, Z. B., He, J. Z., Geisen, S., Han, L. L., Wang, J. T., Shen, J. P., & Zhang, L. M. (2019). Protist communities are more sensitive to nitrogen fertilization than other microorganisms in diverse agricultural soils. *Microbiome*, *7*(1), 33.

Zhong, L., Xiao, J., Xianzhang, P., & Qiguo, Z. (2001). Organic carbon storage in soils of tropical and subtropical China. *Water, Air, and Soil Pollution*, *129*(1-4), 45–60.