Towards understanding the impact of mycorrhizal fungal environments on the functioning of terrestrial ecosystems.

Olivier Nouwen [1*], Francois Rineau [1], Petr Kohout [2,3], Petr Baldrian [2], Nico Eisenhauer [4,5], Natalie Beenaerts [1], Sofie Thijs [1], Jaco Vangronsveld [1,6], Nadejda A. Soudzilovskaia [1]

1 Centre for Environmental Sciences, Environmental Biology, Hasselt University, Campus Diepenbeek, Agoralaan, Gebouw D, 3590 Diepenbeek, Belgium

2 Institute of Microbiology of the Czech Academy of Sciences, Videnska 1083, 14220 Prague, Czechia

3 Faculty of Science, Charles University, Albertov 6, 128 43 Prague, Czechia

4 German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstr. 4, Leipzig, 04103, Germany

5 Institute of Biology, Leipzig University, Puschstr. 4, Leipzig, 04103, Germany

6 Department of Plant Physiology and Biophysics, Institute of Biological Sciences, Maria Curie-Skłodowska University, Lublin, Poland

*corresponding author email: olivier.nouwen@uhasselt.be

Key words

Mycotron experiment, soil properties, soil biochemical cycles, arbuscular mycorrhiza, ectomycorrhiza, ericoid mycorrhiza

Abstract

Mutualistic interactions between plants and soil fungi, mycorrhizae, control carbon and nutrient fluxes in terrestrial ecosystems. Soil of ecosystems featuring a particular type of mycorrhiza exhibit specific properties across multiple dimensions of soil functioning. The knowledge about the impacts of mycorrhizal fungi on soil functioning accumulated so far, indicates that these impacts are of major importance, yet poorly conceptualized. We propose a concept of mycorrhizal fungal environments in soil. Within this concept, we discuss knowledge gaps related to understanding and quantification of mycorrhizal fungal impacts. We propose an experimental framework to address these gaps in a quantitative manner, and present the field experiment “Mycotron”, where we established vegetation series featuring three mycorrhizal types - Ericoid (ERM), Ecto- (ECM) and Arbuscular mycorrhiza (AM), to quantitatively assess mycorrhizal fungal impacts on soil functioning. The experimental treatments entail manipulations in dominance level of vegetation of three pure mycorrhizal types (AM, ECM, ERM) in standardized soil conditions. This experiment constitutes a unique testbed to quantitatively assess the impacts of distinct mycorrhizal fungal environments on a large variety of ecosystem functions. Our approach aids the quantification of microbiota and plant-microbial interaction impacts on soil biochemical cycles.

Introduction

Mycorrhiza, their interactions, functioning, and diversity

Mycorrhizae are mutualistic relationships between plants and soil fungi featured by almost all terrestrial plant species (Brundrett, 1991; Smith & Read, 2008). This relationship enables plants to increase uptake of water (Ruth et al., 2011) and nutrients, such as phosphorus,

nitrogen, and micronutrients (Smith & Read, 2008). In exchange, plants supply fungi with photosynthates. This mutualistic relationship does not only affect the nutrition of the plants and fungi, but also governs many important soil functions, as mycorrhizae contribute to weathering of mineral nutrients, influence soil carbon sequestration, protect the plant from biotic and abiotic stressors, decrease soil erosion, and promote soil aggregation (Genre et al., 2020). It has been suggested that the magnitude of the impact of mycorrhizae on ecosystem functions, especially on processes related to carbon sequestration, is comparable to these of changing climatic conditions (Steidinger et al., 2019; Huang, van Bodegom, Viskari, et al., 2022a).

Depending on the fungal and plant partner species involved, and on the morphology and physiology of their interactions, mycorrhizal symbioses are categorized into four mycorrhizal types. Arbuscular mycorrhizae (AM) are most abundant, occurring in 72% of flowering and vascular plants (Brundrett, 2009; Brundrett & Tedersoo, 2018; Soudzilovskaia et al., 2020), and geographically most wide-spread (Soudzilovskaia et al., 2019). Arbuscular mycorrhiza fungi (AMF) are also taxonomically monophyletic(Brundrett & Tedersoo, 2018). In contrast, ectomycorrhizal fungi (ECMF) and ericoid mycorrhizal fungi (ERMF) are polyphyletic and form symbiosis with approximately 2% and 1.5% of plant species, respectively(Brundrett, 2009; Wang et al., 2010; Field et al., 2015; Brundrett & Tedersoo, 2018; Soudzilovskaia et al., 2020). Geographically AM plants are most abundant, and contribute 240 GT carbon in aboveground biomass, while the contribution of ECM and ERM plants constitutes 100 and 7 GT, respectively (for comparison, non-mycorrhizal pants contribute 29 GT carbon in terrestrial aboveground biomass) (Soudzilovskaia, et al, 2020).

Distinct mycorrhizae also have distinct root colonization strategies. Fungal hyphae of AM and ERM grow intracellular in plant roots, and form plant-fungal nutrient exchange structures inside roots. Ectomycorrhizal fungi do not grow into plant cells, but form a mycelial cover (mantle) around plant root tips, and form a so called ‘Hartig net’ in the extracellular space of rhizodermis and root cortex, where exchange of nutrients and carbon takes place. Ectomycorrhizal fungi often also form an extensive extramatrical mycelium in soil. Apart from differences in morphology, mycorrhizal types also have distinct nutrient acquisition strategies. Arbuscular mycorrhizal fungi, predominantly scavenge for inorganic soil nutrients (Read & Perez-Moreno, 2003a; Smith & Read, 2008). Arbuscular mycorrhizal fungi mostly provide plants with phosphorus and water, while ERMF and ECMF enable plant uptake of most micro- and macro-nutrients, including nitrogen (Read & Perez-Moreno, 2003a; Smith & Read, 2008).

Together, this variability in forms of mycorrhizal associations and functionalities related to carbon and nutrient transfer between plants and fungi, enables a large spectrum of impacts of mycorrhizas on the functioning of soil. Broadly, mycorrhizal impacts on soil processes could be summarized as “direct” and “indirect” effects (Rillig, 2004). The “direct” effects are associated with the functioning of mycorrhizal fungi. The “indirect” effects are associated with the mycorrhizal fungal contribution to plant nutrition, and therewith, the impacts on plant fitness affecting plant biomass and arguably plant eco-physiological traits (Averill et al., 2019; Cornelissen et al., 2001). The latter link, however, has been argued to be solely driven by taxonomical relatedness of ECM plant species (Koele et al., 2012). Among the multiple facets of mycorrhizal impacts on ecosystems, especially the “direct” mechanisms of mycorrhizal impacts of soil processes (i.e. mechanisms through which mycorrhizal fungi govern soil biogeochemical cycles) remain poorly understood.

Direct mycorrhizal fungal impacts on soil biogeochemical cycling

There is a growing evidence that mycorrhizae affect soil biogeochemical cycles, with the magnitude of impacts likely being comparable or even exceeding these of abiotic conditions (van der Heijden et al., 2015). By enabling an interface for direct nutrient exchange between

plants and soil, mycorrhizae affect individual aspects of soil element cycles through an entire suite of partly interlinked mechanisms.

Carbon and nutrient cycles

There are three major pathways of direct mycorrhizal fungal impacts on soil carbon and nutrient cycles (Frey, 2019; Soudzilovskaia et al., 2015)(Figure 1): (1) forming a carbon pool in mycorrhizal mycelium; (2) affecting release of carbon components from roots through root exudation; (3) mediating community composition and activity of saprotrophic organisms that enable soil organic matter decomposition.

(1) Mycorrhizal mycelial carbon pool

Plant allocation of photosynthetically fixed carbon into a network of mycorrhizal fungal mycelium constitutes the channel of direct transmission of carbon into the soil. Depending on mycorrhizal type and environment, mycorrhizas account for 20-30% of the microbial biomass in soils (Leake et al., 2004), which in itself constitutes a considerable soil carbon pool. The build-up process of the mycorrhizal mycelial carbon pool in the soil is regulated through three processes, with the magnitude having been shown to differ between mycorrhizal types. These processes are: (i) the flux of the fresh photosynthetically fixed carbon from plants to mycorrhizal fungal partners, (ii) the life span of fungi in soil, and (iii) the process of decomposition of dead mycelium of mycorrhizal fungi.

The flux of fresh photosynthetically fixed carbon from plants to mycorrhizal fungal partners is likely to be largest for ECM and / or ERM symbioses, with the AM fungal network receiving comparatively lower fraction of plant carbon (Soudzilovskaia et al., 2015). The magnitude of this flux at global scale levels remains largely unknown, with the estimations differing from allocation of a few percent of newly plant-fixed carbon into AM networks, to the values of above 20% for ECM and ERM (Leake et al., 2004).

Elevated atmospheric CO_2 conditions also increase carbon allocation to the roots (Sadowsky & Schortemeyer, 1997), and to mycorrhizal fungi (Staddon, 1998). Allocation of carbon into mycorrhiza and plant benefits of mycorrhizal colonization by specific types of mycorrhizal fungi, in the conditions of elevated CO_2, depend on nutrient availability in the soil (Godbold et al., 2014; Terrer et al., 2016), with the ecosystem response patterns ranging from ultimate carbon allocation into plant aboveground biomass to allocation into roots and/or mycorrhizal fungi (Terrer et al., 2021).

The next parameter shaping the mycorrhizal fungal carbon pools in ecosystems is the lifespan of mycorrhizal fungi. Little is known about it, with a handful of estimations available till now, suggesting that AMF have a considerably lower lifespan compared to ECMF, and virtually no data is available for ERMF. It has been reported that extraradical mycelium of AMF species can survive 5 to 6 days after severing the mycelium (Staddon et al., 2003) in sterile conditions, while in natural environments, this is likely to be accelerated due to the presence of mycelia grazers and damage caused by environmental stressors. However, recently it has been demonstrated that depending on the fungal species and distance from hyphae to the root, AMF could last up to 5 months, even if host plant shoots have been removed, thus suggesting that the survival of the extraradical mycelium of AMF is highly variable (Pepe et al., 2018). These reports, however, report survival of obligatory biotrophic AMF which does not reflect the true lifespan and turnover rate in standard environments. For both AMF, and ECMF the lifespan is likely species specific. While many ECMF have a life span of ca. 120 days, the species *Cenococcum geophilum* can have a lifespan of 831 days (Fernandez et al., 2013). Moreover, the lifespan of ECMF may depend on soil nutrient availability. The addition of N to soil have been shown to increase the lifespan of ECM, depending on the morphotype (Kou et al., 2017).

The decomposition rate of distinct guilds of mycorrhizal fungi also likely differs. Till now, only data on decomposition rates of ECMF has been available, suggesting that despite the considerable interspecific variation (Brundrett & Tedersoo, 2018), on average 80% of fungal necromass is lost within 2-8 weeks (Ryan et al., 2020). Recent research has demonstrated that the chemical composition of AMF and ECMF differs fundamentally in the aspects controlling organic matter decomposability (Huang, van Bodegom, Declerck, et al., 2022). Yet, further research on chemical composition of fungi that belong to distinct mycorrhizal guilds is needed, especially for ERMF.

Little is known about mycelial fungal traits underpinning fungal decomposition rate. The ratio of melanin:nitrogen has been suggested to be a key factor controlling decomposition of ECMF and ERMF (Fernandez & Koide, 2014; Koide & Malcolm, 2009; See et al., 2021), with melanin being the most recalcitrant fungal tissue component, and nitrogen concentrations being positively correlated to fungal decomposability (Berg, 2000; Koide & Malcolm, 2009).

(2) Release of carbon components from roots

Mycorrhizal fungi affect soil carbon pools through the release of fungal exudates and by affecting processes of root exudation (Keller et al., 2021a). Distinct mycorrhizal types affect the direct rhizosphere environments of plants, enabling the critically important mediation of root exudation, which makes mycorrhizae key determinants of soil rhizosphere processes (Leake et al., 2004; Lin et al., 2017; Keller et al., 2021b; Tedersoo et al., 2021). Two pathways are active here:

First, mycorrhizal fungi, to some extent, have control over the root exudates released into the rhizosphere, as they are utilizing the majority of this photosynthate from the plant roots (Kaiser et al., 2015; Leake et al., 2004). Therewith, mycorrhizal fungi increase the belowground allocation of carbon. It has been shown that plants inoculated with ECMF have more photosynthate buildup in the roots in comparison with non-mycorrhizal plants (Wu et al., 2002). Exudates that are not taken up by the mycorrhizal fungi become available to the other soil microorganisms associated with mycorrhizal hyphae (Kaiser et al., 2015).

It has been suggested that when mycorrhizal fungi approach a nutrient rich spot, plant hosts increase the labile carbon transport to the fungus to stimulate decomposition of organic matter by the hyphae associated saprotrophic microorganisms in the soil, making more nutrients available (Badri & Vivanco, 2009; Farrar et al., 2003; Kaiser et al., 2015). However, this interplay, the degree of efficiency at which labile carbon is used and transformed by mycorrhiza, and how this differs between mycorrhizal types, remains poorly understood.

Additionally, AMF, ECMF, and ERMF themselves secrete many carbon-rich compounds (Keller et al., 2021a). For ECMF and ERMF, these constitute components such as oxalate and chelators, which cause the liberation of micronutrients through mineral weathering, increasing their availability for plant uptake (Landeweert et al., 2001; Phillips et al., 2013). These carbon-rich compounds, such as oxalate, exuded by the fungi can further be used as a carbon source by bacteria in the rhizosphere (Sun et al., 2019). AMF can produce glomalin, which changes the soil properties in their direct environment, promoting soil aggregation, and contributing to soil carbon storage (Singh et al., 2013). Moreover, AMF-driven glomalin supply in the soil is correlated to the amount of photosynthate allocated to the plant (Taylor et al., 2009).

Fungi of distinct mycorrhizal types have different extracellular enzymatic properties which also alter their direct soil environment. Ectomycorrhizal and ERM fungi can produce hydrolytic and oxidative extracellular enzymes, such as lignases, cellulases, and polyphenol oxidases, that decompose organic matter (Read & Perez-Moreno, 2003b) and contribute to the degradation of plant material (Read & Perez-Moreno, 2003a). AM lack enzymes that are capable of

breaking down complex organic matter in their environment, but they may also produce enzymes, such as acid phosphatase for nutrient acquisition purposes (Read & Perez-Moreno, 2003a). Besides the components related to nutrient uptake, fungi release a large group of secondary compounds, such as metabolites, that have a hormonal, excretory, or antibiotic role, and at the same time constitute a contribution to soil carbon pools.

The ultimate suits of compounds released into the soil by mycorrhizal fungi differ between AMF, ECMF, and ERMF. For enzymes, these differences between mycorrhizal types are relatively well understood, they are related to the capacity of fungal enzymes to break down soil organic matter (Tedersoo & Bahram, 2019). Arbuscular mycorrhizal fungi lack saprotrophic capacities and therefore take up more mobile inorganic nutrient forms, hence their preferred uptake of inorganic nitrogen and phosphorus (Phillips et al., 2013). Since ECM and ERM have more extensive saprotrophic capacities, they have the ability to break down more complex materials, enabling them to mine nutrients from more recalcitrant sources, and to take up nutrients in their organic form.

The release of carbon-rich exudates from plant and fungal components can cause an overall ecosystem carbon loss, as the metabolism of these compounds induces the release of CO_2 by other decomposing microorganisms (Talbot et al., 2008).

(3) Activity of mycorrhizal fungi mediates soil microbial communities

Mycorrhizal fungi mediate the activity of soil microbial communities. Although mycorrhizal fungi obtain carbon from plants and not from soil organic matter, they release enzymes to break down complex organic molecules in order to take up nutrients. These breakdown products are further decomposed by other microorganisms (Talbot et al., 2008). On the other hand, carbon-rich molecules excreted by mycorrhizal fungi attract microorganisms as well. Therewith, mycorrhizal fungi mediate the decomposition environment of plant litter, forming associative networks with bacteria by shaping their environment (Odriozola et al., 2021).

By taking up nutrients from soil, mycorrhizal fungi compete for nutrients with saprotrophic microorganisms. The most known phenomenon related to this mechanism is a lower rate of soil organic matter decomposition in the presence of ECMF, resulting in a larger amount of carbon to be sequestered in the soil, known as the Gadgil effect (Gadgil & Gadgil, 1971). This effect has been proposed to be caused by a number of underlying mechanisms, such as the competition for nitrogen with saprotrophic microorganisms (Fernandez & Kennedy, 2016a). As ECMF obtain carbon from plants, their nitrogen scavenging activity is limited by availability of carbon-related resources, compared to saprotrophic fungi and to bacteria. By taking up nitrogen selectively and more efficiently than saprotrophic organisms, mycorrhizal fungi increase the carbon to nitrogen ratio of soil organic matter. Furthermore, ECM can also produce antagonistic chemical compounds, such as volatile organic compounds, anti-microbial, and anti-fungal compounds that suppress, and limit the activity of other saprotrophic microorganisms (Garrido et al., 1982; Kope & Fortin, 1990; Krywolap & Casida Jr., 1964). Also, being less limited in carbon in comparison to their saprotrophic counterparts, ECMF are capable of allocating more resources to produce these antagonistic compounds (Fernandez & Kennedy, 2016a). Finally, ECMF may also tap into the biomass of living saprotrophs using those as a source of nutrients, and therewith suppressing the decomposition of litter (Fernandez & Kennedy, 2016b). However, due to the complexity of the soil organic matter decomposition process, a lot of inconsistent results have been obtained around this topic, where in some cases the presence of ECM did not lower the decomposition rate but accelerated it (Fernandez & Kennedy, 2016a). This can be attributed to the context-dependent characteristics of mycorrhizal fungi, where different outcomes are observed depending on the biotic and abiotic conditions.

Another way in which mycorrhizal fungi may affect the community composition of microorganisms is by causing the release of decomposition products, that alter the pH of their direct environment. A change in pH can alter the bacterial community composition (Johnston et al., 2019; Kielak et al., 2016). Finally, mycorrhizal fungi, may also physically affect activity of microorganisms. Mycelial networks may even fill or form bridges in soil air gaps, facilitating bacterial movement and access to new microhabitats. (Nazir et al., 2014).

Because of the differences in enzyme production and exudation, ECMF, which produce oxalate, are able to enrich their environment with bacteria. Oxalate-rich soils feature higher abundances of nitrogen-fixing bacteria. The exudation of oxalate by ECMF attracts specific functional groups of bacteria for oxalate degradation (Sun et al., 2019).

Mycorrhizae impacts on mineral weathering and micronutrient availability

Mineral weathering plays an important role in mediating the effects of soil acidification by freeing bioavailable elements acting as a buffer, which influence the ability of the plant to overcome natural stresses. Ectomycorrhizal fungi can increase the micronutrient availability in soils, as they are able to exude substances that are capable of breaking down minerals. This mineral weathering allows mineral P and other micronutrients, such as calcium and magnesium, to become accessible for plant uptake, thereby increasing soil fertility (van Schöll et al., 2008). The scale of micronutrient mining is specific to the species of mycorrhizal fungi (van Schöll et al., 2008). Although this phenomenon has been observed in ECMF, the capacities for mineral weathering remains unknown for ERMF. Arbuscular mycorrhizal fungi are believed not to excrete mineral weathering agents, such as organic acids and chelators, and therefore, their contribution to mineral weathering is considered to be less effective than that of ECM and ERM. However, phenomena, such as tunneling, i.e. the formation of hyphae-shaped microscopic tunnel-like structures on mineral substrates (Smits, 2006), observed during mineral weathering can also be found in AM forests, where ECMF are absent. This suggests that the excretion of organic acids of AMF may either be overlooked, due to saprotrophic microorganisms in their environment, or a result of combined acidification attributed to the release of biotic agents in the rhizosphere (Koele et al., 2014).

The effects of mycorrhizae on soil acidity and associated toxicity

Mycorrhizal fungi affect soil acidity in a number of ways, by producing and releasing organic acids, by interactions with bacteria and other microorganisms, and by the process of mineral weathering itself (Finlay, 1995). Soil acidification increases the solubility of iron and aluminum (Al), and this increased solubility causes leaching from the soil, which in turn strongly affects plant nutrient uptake. Moreover, high levels of soluble Al negatively impact plant growth and physiology. Even though soil acidification may negatively influence mycorrhizal infections by influencing the allocation of carbon to the mycorrhizal fungi, and affecting the uptake of other minerals, like magnesium and calcium (Finlay, 1995; van Schöll et al., 2008), it helps plants to overcome these adverse conditions (Finlay, 1995).

Both ECMF and AMF increase plant access to nutrients, mitigating therewith the toxicity of acidic environments. Seedlings colonized with ECMF obtain a relatively higher nutrition than non-mycorrhizal seedlings in elevated metal conditions(Ahonen-Jonnarth et al., 2003). Hyphae on the root tip block the main binding sites for Al, diminishing its uptake. Moreover, Al is accumulated in mycelium, and organic acids, which act as a chelating agent, are produced so that Al remains sequestered internally or externally (Eldhuset et al., 2007; Machuca et al., 2007).

AMF, likewise, are able to detoxify Al in the rhizosphere by immobilizing it in fungal cell vacuoles or even binding it into the cell wall. AM fungal associations may even increase the

release of root exudates which bind to Al limiting its toxic effect (Seguel et al., 2013). However, likewise ECMF, the effects of AMF on Al toxicity vary between species of AMF (Seguel et al., 2013).

Mycorrhizal fungal environment – new framework embracing mycorrhizal fungal impacts on soil processes

There exists a unanimous consensus that mycorrhizal fungi strongly affect fundamental soil processes, and it has been suggested that soil processes are to a large extend determined by the mycorrhizal types dominating in an ecosystem, with AMF and ECMF imposing contrasting impacts on the majority of soil processes (Phillips et al., 2013; Soudzilovskaia et al., 2015; Leake et al., 2004; Read & Perez-Moreno, 2003).

However, in the last decade, we started to gain evidence that this view is likely to be superficial. To date, the differences between impacts of distinct mycorrhizal fungal guilds on soil processes remain poorly understood and contradicting evidence has been accumulated in regard to virtually each of the aspects of similar or differential impacts of distinct mycorrhizal fungal guilds on soil processes (Table 1). The most striking contradictions and uncertainties are manifested across the following domains: (i) Impacts of individual mycorrhizal fungal guilds on soil carbon differ between the tropics and temperate zones (Barceló et al., 2022; Fernandez & Kennedy, 2016a), which suggests that key aspects of the mechanisms attributed to mycorrhiza might be underpinned by other mechanisms of ecosystem functioning than mycorrhizas, or they are underpinned by complex interactions of mycorrhizal fungal guilds with climatic conditions; (ii) Contribution of different mycorrhizal fungal guilds to carbon transfer and to processes taking place in distinct soil carbon pools (e.g. fresh plant litter, mycorrhizal fungal biomass, and soil organic matter at distinct depth levels) seems to differ (Cheeke et al., 2017; Frey, 2019), while we are still very far from understanding the full complexity of these exact patterns; (iii) Mechanisms underpinning the influences of ECMF and of ERMF on soil processes are likely to differ a lot (Lindahl et al., 2002), while many studies consider these two fungal guilds as a joint pool (e.g. (Averill et al., 2014; Ward et al., 2022). This possibly leads to conceptual failures in framing theories about the nature of impacts of distinct mycorrhizal guilds, specifically about the role of ECMF in ecosystem functioning. Finally, very little is known about (iv) the contribution of processes associated with distinct mycorrhizal fungal guilds in the formation of carbon pools of different stability levels (particulate organic matter, mineral-associated organic matter), while there is a growing evidence that these contributions might differ as well (Cotrufo et al., 2019; Huang, van Bodegom, Viskari, et al., 2022b).

Thus, while the impacts of mycorrhiza on soil functioning are manifold and significant, the complex suits of mechanisms underlying these impacts are poorly understood. To enable progressing in understanding these mechanisms, and conceptualizing their contribution to soil biodiversity and biochemical properties, we propose a framework of *Mycorrhizal Fungal Environment (MyFE).* The MyFE represents the entire (yet possibly poorly understood) suit of mechanisms imposed by individual mycorrhizal fungal guilds on soil processes, shaping soil biodiversity and soil biochemical cycles into AMF, ECMF, or ERMF-typical soil environments. Embracing this concept allows progressing in research of mycorrhizal ecology, by recognizing the existence of the phenomenon of differential impacts of mycorrhizal fungal guilds, while accepting the fact that this phenomenon is underpinned by a multidimensional suite of underlying mechanisms, each of which is yet poorly understood. Importantly, MyFE created by a given mycorrhizal guild is not necessarily enabled by individual fungal mechanisms affecting soil processes in the same direction. These directions could be opposite and partially compensate each other. For instance, while ECMF constitute larger standing biomass in soil than AMF (and therewith positively contribute to soil carbon (Soudzilovskaia et al., 2015), root

exudates of ECM plants contribute less to soil carbon than root exudates of AM plants (Keller et al., 2021c). Embracing the MyFE framework, we elaborate the knowledge gaps in regard to the impact of mycorrhizal guilds on soil processes, and summarize them in the Table 1.

Three main factors underpin these knowledge gaps. First, plants featuring different mycorrhizal types have different growth forms: while AM plants are represented by all growth forms, the great majority of ECM plants are trees and shrubs, and the ERM plants are typically small to large shrubs (Soudzilovskaia et al., 2020). Consequently, experimental studies comparing ecosystem impacts of distinct mycorrhizal types are typically conducted with trees (e.g. Ferlian et al., 2018; Phillips et al., 2013), and are either limited to planted tree seedlings (and have to account for the fact that the build-up and activities of mycorrhizal fungal communities associated with seedlings do not fully represent those associated with mature trees), or such studies are conducted in long-existing vegetation stands which do not feature exactly the same soils, and therewith do not allow fully conclusive disentangling effects of mycorrhiza and inherent effects of soil properties. Second, natural ecosystems rarely represent one singe mycorrhizal type. Rather, we deal with a certain level of dominance of plants featuring one mycorrhizal type (for instance 80% of plant biomass is formed by AM plants), and additional impacts of other mycorrhizal types (for instance 10% of plant biomass is ECM plants and 10% is ERM plants). Considering such communities as “purely AM” is too simplistic, while estimating the additional impacts of ECMF and ERMF based on the aboveground biomass of ECM and ERM plants is impossible. Next, most information regarding the effect of mycorrhiza on biogeochemical cycling has been obtained for AM and ECM. Knowledge on the impacts of ERM plants on soil processes is extremely scarce, despite the fact that ERM plants play important roles in a number of natural ecosystems, such as tundra, boreal forests, heathland, and Mediterranean and South-African shrublands (Tedersoo, 2017).

The way forward

The proposed experimental framework, MyFE principally enables testing the concept of mycorrhizal fungal environment in a quantitative manner. To alleviate the confounding impacts of differences in soil types and history, an experimental setup to test MyFE should constitute a common garden build up with plant species of different mycorrhizal types on the same soil type. To enable comparison of impacts on ecosystem functioning between fungi of all three prominent mycorrhizal types (AM, ECM and ERM), plant hosts of all three types should be included into the experiment. In order to eliminate possible confounding effects associated with plant species choice, the experiment should employ adult plants, of the same growth form, and similar eco-physiological traits. Finally, to enable quantification of mycorrhizal impacts, gradients of domination of mycorrhizal types should be provided.

Mycotron – mycorrhizal diversity gradient experiment

As a proof of concept, we established a long-term experimental field at National Park Hoge Kempen (NPHK). The study site is located at Terhills in Maasmechelen, Belgium (51°00'05.2"N 5°42'05.6"E), located next to the Field Research Centre of Hasselt University. The experiment is situated on sandy soil at an altitude of 37,5 m a.s.l., and is characterized by an average yearly temperature of 10.9°C, and yearly average precipitation of 799 mm. The site is located on a former grassland. In May 2022, the site was again cleaned up form vegetation and organic matter which had formed on the top of the sand. Subsequently, the plot was rotor-milled and levelled before the establishment of the experiment. After homogenization, a 10 cm of sod cut collected from protected heathland in NPHK was added to each subplot. After the sod cut was put on the soil, it was covered with black tarp (water permeability: 151/m^2S), in order to prevent growth of weed featuring mycorrhizal types not planned to appear in the plots (Ferlian et al., 2018), and 60 subplots of 2.5 m x 2.5 m with a

margin of 2 m in between was established (Figure 2). The entire study site has the size of 33.5 m by 42.5 m.

We aimed to enable comparison of the three most abundant mycorrhizal types, ERM, ECM, and AM for soil impacts. We selected three plant species per each of the three mycorrhizal types (Table 2). Plant species were chosen to differ as little as possible in eco-physiological traits, besides the mycorrhiza type. All selected plant species are adult evergreen shrubs, similar in size (20-30 cm high), and having small narrow- to needle-shaped leaves.

Plants, featuring developed mycorrhiza, and pre-grown in the same type of soil, were purchased from a commercial provider. On each plot, 36 plant individuals were planted with 40 cm spacing to leave sufficient space for growth and implementing tools for future experimentation (Figure 3). All the plants were planted bare rooted. To ensure the survival of the plants, aboveground biomass of all plants was pruned ca. 30% to enable the root system, which was slightly damaged through planting to support the amount of biomass.

Different plant species were combined in different proportions to establish a gradient of mycorrhizal dominance, spanning 0% - 33% - 66% - 100% dominance of each mycorrhizal type (Figure 2). In this manner, the following conditions were created: pure mycorrhizal types (100% ERM, 100% ECM, 100% AM), dual mixtures with one dominantly present (66%/33% ratio), and plots with all types combined evenly (33%/33%/33%), each condition occurring 6 times throughout the experiment (Appendix 1).

Conclusion and outlook

Our overview of current knowledge gaps in regard to functioning of mycorrhizal fungi highlights the large uncertainties related to direct (sensu (Rillig, 2004)) contribution of fungi of distinct mycorrhizal guilds to biochemical cycles. The proposed framework of mycorrhizal fungal environment, MyFE, allowed us to identify the critical aspects that need to be covered in experimental assessments of the mechanisms of mycorrhizal fungi impact soil processes, and yielded a set of criteria which we strive to fulfill in the design of the Mycotron experiment. While this experiment could not cover a complete set of the knowledge gaps identified in this paper, it provides a comprehensive array of possible analyses, and experimental set-ups aimed to solve a large set of urgent research questions around mycorrhizal impacts on soil carbon and nutrient cycling, as well as on soil ecosystem responses to abiotic stresses. Below, we discuss a set of important analyses that we aim to conduct in this experiment. Furthermore, the experimental design may inspire the set-up of complementary experiments at other locations and soil conditions, to study the context-dependency of MyFE effects on ecosystem functioning.

Transfer of carbon form plant to soil via mycorrhizal fungi

In the first years after establishment, the Mycotron experiment allows direct comparative analysis of the turnover rate and lifespan of AMF, ECMF, and ERMF. All plants are initially planted into the same soil. Therefore, in the beginning, when soil has not yet been seriously affected by fungal activities, all fungi will be subjected to very similar abiotic conditions, eliminating the confounding impacts of differences in soil properties. The use of low state plants (shrubs) in the experiment allows isotopic labelling of individual plants, to trace carbon transfer form plants to fungi, in standardized conditions. This provides the opportunity to determine the carbon flux integrated into the biomass of fungi of different mycorrhizal types. Subsequently, the life span of individual fungal species could be assessed.

Further, the isotopic labelling technique allows examining root exudation in plants that belong to distinct mycorrhizal guilds. This allows assessments of a fractionation of carbon flow between mycorrhizal fungi and exudates, and determining the carbon costs and carbon efficiency of different mycorrhizal fungal types, independently of soil conditions.

Processes of organic matter decomposition and incorporation of carbon into mineral associated organic matter

The question to what extent dominance of fungi of distinct mycorrhizal types affect decomposition of soil organic matter, compared to soil abiotic parameters, is among the most puzzling issues in mycorrhizal research. The Mycotron experiment creates an ideal set up for the execution of various litter transplantation experiments of e.g. plant leaf, plant root, and fungal litter, among different mycorrhizal environments, that will provide insights into the impacts of mycorrhizal fungal types on soil organic matter decomposition processes. Further, soil trenching can easily be implemented on the plots to control the access of mycorrhizal fungi to litter transplants, adding another level of control, and allowing assessment of mechanisms associated with the Gadgil effect (Fernandez & Kennedy, 2016a). Finally, initial equal soil conditions allow the assessment of the mechanisms that form minerally associated organic matter in the context of MEMS theory (Cotrufo et al., 2013, 2015). Hereto, methods similar to that proposed by Sokol and Bradford (Sokol & Bradford, 2019) could be applied.

Mycorrhiza mediation of the soil microbiome and soil animal communities

To assess bacterial, fungal, and soil animal communities associated with different types of mycorrhiza, microbiome, and soil invertebrate community analyses could be applied to soil samples collected at the Mycotron experimental plots. Also, in this case the results will elucidate impacts of mycorrhizal fungi per se and not confounding impacts of soil.

Mineral weathering, acidity and metal toxicity

By the manual addition of minerals, mineral weathering processes, such as tunneling in rocks and the exudation of weathering agents, can be investigated in our experiment. With carbon tracing methods of amino sugars (Klink et al., 2022), the mycorrhizal origin of organic acids responsible for mineral weathering can be recalled as well.

Environmental stressors, such as drought or metal toxicity, can also be simulated on the experimental plots, and the physiological responses (e.g. changes in gene expression, mycorrhiza morphology, plant yield) of mycorrhizal fungi can be investigated accordingly.

Exclusive assessments of the role of ericoid mycorrhiza in soil ecosystem functioning

Till now, the great majority of assessments of mycorrhizal fungal impact on soil processes have been limited to comparisons of AMF- and ECMF-dominated systems, with ecosystems dominated by ECMF often including some ERM vegetation, which is often common in forests dominated by ECM trees. Besides the rare occurrence of a purely ERM-dominated ecosystems, the predominant shrub life form of ericoid mycorrhizal plants constitutes another obstacle to comparison of ERMF impacts on soil processes to these of AMF and of ECMF, which is typically done in tree stands (e.g. Ferlian et al., 2018; Phillips et al., 2013). According to the best of our knowledge, the Mycotron is the first common garden experiment that includes explicit experimentation with ERM plants and fungi in purely ERM-dominated vegetation stands, as well as in pre-assembled mixtures of ERM plants with AM and with ECM plants.

Quantification of mycorrhizal fungal impacts

Controlling the level of dominance of mycorrhizal types in an ecosystem, and assessing the relationship between the abundance of plants of a given mycorrhizal type and impacts of their fungal partners on the soil processes is the next necessary step in linking the data about vegetation dynamics to mycorrhizal impacts on soil nutrient dynamics. Mycotron is the first experimental setup allowing such assessments. Furthermore, it allows investigation about the interactive effects of combinations of AM, ECM, and ERM plants in distinct proportions on the associated impacts of mycorrhizal fungi on soil properties.

Conclusion

The concept of quantitative experimental research on mycorrhizal impacts on ecosystem functioning presented here establishes a benchmark for ecological experiments aimed to quantitatively unravel the mechanisms of plant-microbial interactions. The new long-term mycorrhizal experimental garden Mycotron allows us to solve an array of knowledge gaps concerning mycorrhizal impacts on ecosystem functioning that are key to understand global relationships between the dynamics of vegetation and soil processes. The concept proposed here and the insights that will be obtained through the Mycotron experiment will broaden our understanding of fundamental ecological processes involved into the functioning of mycorrhizas, and associated ecosystem services. This is especially important now in the era of global environmental change, when humanity is in search for ecosystem restoration techniques, increasing ecosystem multifunctionality through enhanced links between soil and aboveground biodiversity.

References

Ahonen-Jonnarth, U., Goransson, A., & Finlay, R. D. (2003). Growth and nutrient uptake of ectomycorrhizal Pinus sylvestris seedlings in a natural substrate treated with elevated Al concentrations. *Tree Physiology*, *23*(3), 157–167. https://doi.org/10.1093/treephys/23.3.157

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. https://doi.org/10.1073/pnas.1906655116

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. https://doi.org/10.1038/nature12901

Badri, D. v., & Vivanco, J. M. (2009). Regulation and function of root exudates. *Plant, Cell & Environment*, *32*(6), 666–681. https://doi.org/10.1111/j.1365-3040.2009.01926.x

Barceló, M., van Bodegom, P. M., Tedersoo, L., Olsson, P. A., & Soudzilovskaia, N. A. (2022). Mycorrhizal tree impacts on topsoil biogeochemical properties in tropical forests. *Journal of Ecology*, *110*(6), 1271–1282. https://doi.org/10.1111/1365-2745.13868

Berg, B. (2000). Litter decomposition and organic matter turnover in northern forest soils. *Forest Ecology and Management*, *133*(1–2), 13–22. https://doi.org/10.1016/S0378-1127(99)00294-7

Brundrett, M. C. (2009). Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. *Plant and Soil*, *320*(1–2), 37–77. https://doi.org/10.1007/s11104-008-9877-9

Brundrett, M. C., & Tedersoo, L. (2018). Evolutionary history of mycorrhizal symbioses and global host plant diversity. *New Phytologist*, *220*(4), 1108–1115. https://doi.org/10.1111/nph.14976

Cao, T., Fang, Y., Chen, Y., Kong, X., Yang, J., Alharbi, H., Kuzyakov, Y., & Tian, X. (2022). Synergy of saprotrophs with mycorrhiza for litter decomposition and hotspot formation depends on nutrient availability in the rhizosphere. *Geoderma*, *410*, 115662. https://doi.org/10.1016/j.geoderma.2021.115662

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. https://doi.org/10.1111/nph.14343

Cornelissen, J., Aerts, R., Cerabolini, B., Werger, M., & van der Heijden, M. (2001). Carbon cycling traits of plant species are linked with mycorrhizal strategy. *Oecologia*, *129*(4), 611–619. https://doi.org/10.1007/s004420100752

Cotrufo, M. F., Ranalli, M. G., Haddix, M. L., Six, J., & Lugato, E. (2019). Soil carbon storage informed by particulate and mineral-associated organic matter. *Nature Geoscience*, *12*(12), 989–994. https://doi.org/10.1038/s41561-019-0484-6

Cotrufo, M. F., Soong, J. L., Horton, A. J., Campbell, E. E., Haddix, M. L., Wall, D. H., & Parton, W. J. (2015). Formation of soil organic matter via biochemical and physical pathways of litter mass loss. *Nature Geoscience*, *8*(10), 776–779. https://doi.org/10.1038/ngeo2520

Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Denef, K., & Paul, E. (2013). The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? *Global Change Biology*, *19*(4), 988–995. https://doi.org/10.1111/gcb.12113

Eldhuset, T. D., Swensen, B., Wickstrøm, T., & Wollebæk, G. (2007). Organic acids in root exudates from *Picea abies* seedlings influenced by mycorrhiza and aluminum. *Journal of Plant Nutrition and Soil Science*, *170*(5), 645–648. https://doi.org/10.1002/jpln.200700005

Farrar, J., Hawes, M., Jones Davey, & Lindow, S. (2003). HOW ROOTS CONTROL THE FLUX OF CARBON TO THE RHIZOSPHERE. *Ecological Society of America*, *4*(84), 827–837.

Ferlian, O., Cesarz, S., Craven, D., Hines, J., Barry, K. E., Bruelheide, H., Buscot, F., Haider, S., Heklau, H., Herrmann, S., Kühn, P., Pruschitzki, U., Schädler, M., Wagg, C., Weigelt, A., Wubet, T., & Eisenhauer, N. (2018). Mycorrhiza in tree diversity–ecosystem function relationships: conceptual framework and experimental implementation. *Ecosphere*, *9*(5). https://doi.org/10.1002/ecs2.2226

Fernandez, C. W., & Kennedy, P. G. (2016a). Revisiting the 'Gadgil effect': do interguild fungal interactions control carbon cycling in forest soils? *New Phytologist*, *209*(4), 1382–1394. https://doi.org/10.1111/nph.13648

Fernandez, C. W., & Kennedy, P. G. (2016b). Revisiting the 'Gadgil effect': do interguild fungal interactions control carbon cycling in forest soils? *New Phytologist*, *209*(4), 1382–1394. https://doi.org/10.1111/nph.13648

Fernandez, C. W., & Koide, R. T. (2014). Initial melanin and nitrogen concentrations control the decomposition of ectomycorrhizal fungal litter. *Soil Biology and Biochemistry*, *77*, 150–157. https://doi.org/10.1016/j.soilbio.2014.06.026

Fernandez, C. W., McCormack, M. L., Hill, J. M., Pritchard, S. G., & Koide, R. T. (2013). On the persistence of Cenococcum geophilum ectomycorrhizas and its implications for forest carbon and nutrient cycles. *Soil Biology and Biochemistry*, *65*, 141–143. https://doi.org/10.1016/j.soilbio.2013.05.022

Fernández, N., Knoblochová, T., Kohout, P., Janoušková, M., Cajthaml, T., Frouz, J., & Rydlová, J. (2022). Asymmetric Interaction Between Two Mycorrhizal Fungal Guilds and Consequences for the Establishment of Their Host Plants. *Frontiers in Plant Science*, *13*. https://doi.org/10.3389/fpls.2022.873204

Finlay, R. D. (1995). Interactions between Soil Acidification, Plant Growth and Nutrient Uptake in Ectomycorrhizal Associations of Forest Trees. *Ecological Bulletins*, *44*, 197–214.

Frey, S. D. (2019). Mycorrhizal Fungi as Mediators of Soil Organic Matter Dynamics. *Annual Review of Ecology, Evolution, and Systematics*, *50*(1), 237–259. https://doi.org/10.1146/annurev-ecolsys-110617-062331

Gadgil, R. L., & Gadgil, P. D. (1971). Mycorrhiza and Litter Decomposition. *Nature*, *233*(5315), 133–133. https://doi.org/10.1038/233133a0

Garrido, N., Becerra, J., Marticorena, C., Oehrens, E., Silva, M., & Horak, E. (1982). Antibiotic properties of ectomycorrhizae and saprophytic fungi growing on Pinus radiata D. Don I. *Mycopathologia*, *77*(2), 93–98. https://doi.org/10.1007/BF00437390

Genre, A., Lanfranco, L., Perotto, S., & Bonfante, P. (2020). Unique and common traits in mycorrhizal symbioses. *Nature Reviews Microbiology*, *18*(11), 649–660. https://doi.org/10.1038/s41579-020-0402-3

Godbold, D., Tullus, A., Kupper, P., Sõber, J., Ostonen, I., Godbold, J. A., Lukac, M., Ahmed, I. U., & Smith, A. R. (2014). Elevated atmospheric CO2 and humidity delay leaf fall in Betula pendula, but not in Alnus glutinosa or Populus tremula × tremuloides. *Annals of Forest Science*, *71*(8), 831–842. https://doi.org/10.1007/s13595-014-0382-4

Heijden, M. G. A., Martin, F. M., Selosse, M., & Sanders, I. R. (2015). Mycorrhizal ecology and evolution: the past, the present, and the future. *New Phytologist*, *205*(4), 1406–1423. https://doi.org/10.1111/nph.13288

Huang, W., van Bodegom, P. M., Declerck, S., Heinonsalo, J., Cosme, M., Viskari, T., Liski, J., & Soudzilovskaia, N. A. (2022). Mycelium chemistry differs markedly between ectomycorrhizal and arbuscular mycorrhizal fungi. *Communications Biology*, *5*(1), 398. https://doi.org/10.1038/s42003-022-03341-9

Huang, W., van Bodegom, P. M., Viskari, T., Liski, J., & Soudzilovskaia, N. A. (2022a). Implementation of mycorrhizal mechanisms into soil carbon model improves the prediction of long-term processes of plant litter decomposition. *Biogeosciences*, *19*(5), 1469–1490. https://doi.org/10.5194/bg-19-1469-2022

Huang, W., van Bodegom, P. M., Viskari, T., Liski, J., & Soudzilovskaia, N. A. (2022b). Implementation of mycorrhizal mechanisms into soil carbon model improves the prediction of long-term processes of plant litter decomposition. *Biogeosciences*, *19*(5), 1469–1490. https://doi.org/10.5194/bg-19-1469-2022

Johnston, S. R., Hiscox, J., Savoury, M., Boddy, L., & Weightman, A. J. (2019). Highly competitive fungi manipulate bacterial communities in decomposing beech wood (*Fagus sylvatica*). *FEMS Microbiology Ecology*, *95*(2). https://doi.org/10.1093/femsec/fiy225

Kaiser, C., Kilburn, M. R., Clode, P. L., Fuchslueger, L., Koranda, M., Cliff, J. B., Solaiman, Z. M., & 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. https://doi.org/10.1111/nph.13138

Keller, A. B., Brzostek, E. R., Craig, M. E., Fisher, J. B., & Phillips, R. P. (2021a). Root-derived inputs are major contributors to soil carbon in temperate forests, but vary by mycorrhizal type. *Ecology Letters*, *24*(4), 626–635. https://doi.org/10.1111/ele.13651

Keller, A. B., Brzostek, E. R., Craig, M. E., Fisher, J. B., & Phillips, R. P. (2021b). Root-derived inputs are major contributors to soil carbon in temperate forests, but vary by mycorrhizal type. *Ecology Letters*, *24*(4), 626–635. https://doi.org/10.1111/ele.13651

Keller, A. B., Brzostek, E. R., Craig, M. E., Fisher, J. B., & Phillips, R. P. (2021c). Root-derived inputs are major contributors to soil carbon in temperate forests, but vary by mycorrhizal type. *Ecology Letters*, *24*(4), 626–635. https://doi.org/10.1111/ele.13651

Khouja, H. R., Abbà, S., Lacercat-Didier, L., Daghino, S., Doillon, D., Richaud, P., Martino, E., Vallino, M., Perotto, S., Chalot, M., & Blaudez, D. (2013). OmZnT1 and OmFET, two metal transporters from the metal-tolerant strain Zn of the ericoid mycorrhizal fungus Oidiodendron maius, confer zinc tolerance in yeast. *Fungal Genetics and Biology*, *52*, 53–64. https://doi.org/10.1016/j.fgb.2012.11.004

Kielak, A. M., Scheublin, T. R., Mendes, L. W., van Veen, J. A., & Kuramae, E. E. (2016). Bacterial Community Succession in Pine-Wood Decomposition. *Frontiers in Microbiology*, *7*. https://doi.org/10.3389/fmicb.2016.00231

Klink, S., Keller, A. B., Wild, A. J., Baumert, V. L., Gube, M., Lehndorff, E., Meyer, N., Mueller, C. W., Phillips, R. P., & Pausch, J. (2022). Stable isotopes reveal that fungal residues contribute more to mineral-associated organic matter pools than plant residues. *Soil Biology and Biochemistry*, *168*, 108634. https://doi.org/10.1016/j.soilbio.2022.108634

Koele, N., Dickie, I. A., Blum, J. D., Gleason, J. D., & de Graaf, L. (2014). Ecological significance of mineral weathering in ectomycorrhizal and arbuscular mycorrhizal ecosystems from a field-based comparison. *Soil Biology and Biochemistry*, *69*, 63–70. https://doi.org/10.1016/j.soilbio.2013.10.041

Koele, N., Dickie, I. A., Oleksyn, J., Richardson, S. J., & Reich, P. B. (2012). No globally consistent effect of ectomycorrhizal status on foliar traits. *New Phytologist*, *196*(3), 845–852. https://doi.org/10.1111/j.1469-8137.2012.04297.x

Koide, R. T., & Malcolm, G. M. (2009). N concentration controls decomposition rates of different strains of ectomycorrhizal fungi. *Fungal Ecology*, *2*(4), 197–202. https://doi.org/10.1016/j.funeco.2009.06.001

Kope, H. H., & Fortin, J. A. (1990). Antifungal activity in culture filtrates of the ectomycorrhizal fungus *Pisolithus tinctorius*. *Canadian Journal of Botany*, *68*(6), 1254–1259. https://doi.org/10.1139/b90-159

Kou, L., McCormack, M. L., Chen, W., Guo, D., Wang, H., Gao, W., Yang, H., & Li, S. (2017). Nitrogen ion form and spatio-temporal variation in root distribution mediate nitrogen effects on lifespan of ectomycorrhizal roots. *Plant and Soil*, *411*(1–2), 261–273. https://doi.org/10.1007/s11104-016-3018-7

Krywolap, G. N., & Casida Jr., L. E. (1964). AN ANTIBIOTIC PRODUCED BY THE MYCORRHIZAL FUNGUS CENOCOCCUM GRANIFORME. *Canadian Journal of Microbiology*, *10*(3), 365–370. https://doi.org/10.1139/m64-049

Landeweert, R., Hoffland, E., Finlay, R. D., Kuyper, T. W., & van Breemen, N. (2001). Linking plants to rocks: ectomycorrhizal fungi mobilize nutrients from minerals. *Trends in Ecology & Evolution*, *16*(5), 248–254. https://doi.org/10.1016/S0169-5347(01)02122-X

Leake, J., Johnson, D., Donnelly, D., Muckle, G., Boddy, L., & Read, D. (2004). Networks of power and influence: the role of mycorrhizal mycelium in controlling plant communities and agroecosystem functioning. *Canadian Journal of Botany*, *82*(8), 1016–1045. https://doi.org/10.1139/b04-060

Lindahl, B. O., Taylor, A. F. S., & Finlay, R. D. (2002). Defining nutritional constraints on carbon cycling in boreal forests – towards a less `phytocentric' perspective. *Plant and Soil*, *242*(1), 123–135. https://doi.org/10.1023/A:1019650226585

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. https://doi.org/10.1111/nph.14206

Machuca, A., Pereira, G., Aguiar, A., & Milagres, A. M. F. (2007). Metal-chelating compounds produced by ectomycorrhizal fungi collected from pine plantations. *Letters in Applied Microbiology*, *44*(1), 7–12. https://doi.org/10.1111/j.1472-765X.2006.02046.x

Martino, E., Franco, B., Piccoli, G., Stocchi, V., & Perotto, S. (2002). Influence of zinc ions on protein secretion in a heavy metal tolerant strain of the ericoid mycorrhizal fungas Oidiodendron maius. *Molecular and Cellular Biochemistry*, *231*(1/2), 179–185. https://doi.org/10.1023/A:1014485420186

Martino, E., Turnau, K., Girlanda, M., Bonfante, P., & Perotto, S. (2000). Ericoid mycorrhizal fungi from heavy metal polluted soils: their identification and growth in the presence of zinc ions. *Mycological Research*, *104*(3), 338–344. https://doi.org/10.1017/S0953756299001252

Nazir, R., Tazetdinova, D. I., & van Elsas, J. D. (2014). Burkholderia terrae BS001 migrates proficiently with diverse fungal hosts through soil and provides protection from antifungal agents. *Frontiers in Microbiology*, *5*. https://doi.org/10.3389/fmicb.2014.00598

Odriozola, I., Abrego, N., TlÁskal, V., ZrůstovÁ, P., Morais, D., Větrovský, T., Ovaskainen, O., & Baldrian, P. (2021). Fungal Communities Are Important Determinants of Bacterial Community Composition in Deadwood. *MSystems*, *6*(1). https://doi.org/10.1128/mSystems.01017-20

Pepe, A., Giovannetti, M., & Sbrana, C. (2018). Lifespan and functionality of mycorrhizal fungal mycelium are uncoupled from host plant lifespan. *Scientific Reports*, *8*(1), 10235. https://doi.org/10.1038/s41598-018-28354-5

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. https://doi.org/10.1111/nph.12221

Read, D. J., & Perez-Moreno, J. (2003a). Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? *New Phytologist*, *157*(3), 475–492. https://doi.org/10.1046/j.1469-8137.2003.00704.x

Read, D. J., & Perez-Moreno, J. (2003b). Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? *New Phytologist*, *157*(3), 475–492. https://doi.org/10.1046/j.1469-8137.2003.00704.x

Rillig, M. C. (2004). Arbuscular mycorrhizae and terrestrial ecosystem processes. *Ecology Letters*, *7*(8), 740–754. https://doi.org/10.1111/j.1461-0248.2004.00620.x

Ruth, B., Khalvati, M., & Schmidhalter, U. (2011). Quantification of mycorrhizal water uptake via high-resolution on-line water content sensors. *Plant and Soil*, *342*(1–2), 459–468. https://doi.org/10.1007/s11104-010-0709-3

Ryan, M. E., Schreiner, K. M., Swenson, J. T., Gagne, J., & Kennedy, P. G. (2020). Rapid changes in the chemical composition of degrading ectomycorrhizal fungal necromass. *Fungal Ecology*, *45*, 100922. https://doi.org/10.1016/j.funeco.2020.100922

Sadowsky, M., & Schortemeyer, M. (1997). Soil microbial responses to increased concentrations of atmospheric CO2. *Global Change Biology*, *3*(3), 217–224. https://doi.org/10.1046/j.1365-2486.1997.00078.x

See, C. R., Fernandez, C. W., Conley, A. M., DeLancey, L. C., Heckman, K. A., Kennedy, P. G., & Hobbie, S. E. (2021). Distinct carbon fractions drive a generalisable two-pool model of fungal necromass decomposition. *Functional Ecology*, *35*(3), 796–806. https://doi.org/10.1111/1365-2435.13728

Seguel, A., Cumming, J. R., Klugh-Stewart, K., Cornejo, P., & Borie, F. (2013). The role of arbuscular mycorrhizas in decreasing aluminium phytotoxicity in acidic soils: a review. *Mycorrhiza*, *23*(3), 167–183. https://doi.org/10.1007/s00572-013-0479-x

669 Singavarapu, B., Beugnon, R., Bruelheide, H., Cesarz, S., Du, J., Eisenhauer, N., Guo, L., Nawaz, A., Wang, Y.,
670 Xue, K., & Wubet, T. (2022). Tree mycorrhizal type and tree diversity shape the forest soil microbiota.
671 *Environmental Microbiology*, *24*(9), 4236–4255. https://doi.org/10.1111/1462-2920.15690

672 Singh, P. K., Singh, M., & Tripathi, B. N. (2013). Glomalin: an arbuscular mycorrhizal fungal soil protein.
673 *Protoplasma*, *250*(3), 663–669. https://doi.org/10.1007/s00709-012-0453-z

674 Smith, S. E., & Read, D. J. (2008). *Mycorrhizal Symbiosis* (3rd ed., Vol. 1). Academic Press.

675 Smits, M. (2006). Mineral tunelling by fungi. In *Fungi in biogeochemical cycles* (pp. 641–679). Cambridge
676 University Press.

677 Sokol, N. W., & Bradford, M. A. (2019). Microbial formation of stable soil carbon is more efficient from
678 belowground than aboveground input. *Nature Geoscience*, *12*(1), 46–53. https://doi.org/10.1038/s41561-
679 018-0258-6

680 Soudzilovskaia, N. A., Douma, J. C., Akhmetzhanova, A. A., van Bodegom, P. M., Cornwell, W. K., Moens, E. J.,
681 Treseder, K. K., Tibbett, M., Wang, Y.-P., & Cornelissen, J. H. C. (2015). Global patterns of plant root
682 colonization intensity by mycorrhizal fungi explained by climate and soil chemistry. *Global Ecology and*
683 *Biogeography*, *24*(3), 371–382. https://doi.org/10.1111/geb.12272

684 Soudzilovskaia, N. A., Vaessen, S., Barcelo, M., He, J., Rahimlou, S., Abarenkov, K., Brundrett, M. C., Gomes, S.
685 I. F., Merckx, V., & Tedersoo, L. (2020). FungalRoot: global online database of plant mycorrhizal
686 associations. *New Phytologist*, *227*(3), 955–966. https://doi.org/10.1111/nph.16569

687 Soudzilovskaia, N. A., van Bodegom, P. M., Terrer, C., Zelfde, M. van't, McCallum, I., Luke McCormack, M.,
688 Fisher, J. B., Brundrett, M. C., de Sá, N. C., & Tedersoo, L. (2019). Global mycorrhizal plant distribution
689 linked to terrestrial carbon stocks. *Nature Communications*, *10*(1), 5077. https://doi.org/10.1038/s41467-
690 019-13019-2

691 Staddon, P. (1998). Does elevated atmospheric carbon dioxide affect arbuscular mycorrhizas? *Trends in Ecology*
692 *& Evolution*, *13*(11), 455–458. https://doi.org/10.1016/S0169-5347(98)01493-1

693 Staddon, P. L., Ramsey, C. B., Ostle, N., Ineson, P., & Fitter, A. H. (2003). Rapid Turnover of Hyphae of
694 Mycorrhizal Fungi Determined by AMS Microanalysis of ^{14}C. *Science*, *300*(5622), 1138–1140.
695 https://doi.org/10.1126/science.1084269

696 Steidinger, B. S., Crowther, T. W., Liang, J., van Nuland, M. E., Werner, G. D. A., Reich, P. B., Nabuurs, G. J.,
697 de-Miguel, S., Zhou, M., Picard, N., Herault, B., Zhao, X., Zhang, C., Routh, D., & Peay, K. G. (2019).
698 Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. *Nature*,
699 *569*(7756), 404–408. https://doi.org/10.1038/s41586-019-1128-0

700 Sun, Q., Li, J., Finlay, R. D., & Lian, B. (2019). Oxalotrophic bacterial assemblages in the ectomycorrhizosphere
701 of forest trees and their effects on oxalate degradation and carbon fixation potential. *Chemical Geology*,
702 *514*, 54–64. https://doi.org/10.1016/j.chemgeo.2019.03.023

703 Talbot, J. M., Allison, S. D., & Treseder, K. K. (2008). Decomposers in disguise: mycorrhizal fungi as regulators of
704 soil C dynamics in ecosystems under global change. *Functional Ecology*, *22*(6), 955–963.
705 https://doi.org/10.1111/j.1365-2435.2008.01402.x

706 Taylor, L. L., Leake, J. R., Quirk, J., Hardy, K., Banwarts, S. A., & Beerling, D. J. (2009). Biological weathering
707 and the long-term carbon cycle: integrating mycorrhizal evolution and function into the current paradigm.
708 *Geobiology*, *7*(2), 171–191. https://doi.org/10.1111/j.1472-4669.2009.00194.x

709 Tedersoo, L. (2017). Biogeography of Ericoid Mycorrhiza. In L. Tedersoo (Ed.), *Biogeography of Mycorrhizal*
710 *Symbiosis* (Vol. 230). Springer.

711 Tedersoo, L., & Bahram, M. (2019). Mycorrhizal types differ in ecophysiology and alter plant nutrition and soil
712 processes. *Biological Reviews*, *94*(5), 1857–1880. https://doi.org/10.1111/brv.12538

713 Tedersoo, L., Bahram, M., Põlme, S., Kõljalg, U., Yorou, N. S., Wijesundera, R., Ruiz, L. V., Vasco-Palacios, A.
714 M., Thu, P. Q., Suija, A., Smith, M. E., Sharp, C., Saluveer, E., Saitta, A., Rosas, M., Riit, T., Ratkowsky, D.,
715 Pritsch, K., Põldmaa, K., … Abarenkov, K. (2014). Global diversity and geography of soil fungi. *Science*,
716 *346*(6213). https://doi.org/10.1126/science.1256688

717 Tedersoo, L., Mikryukov, V., Anslan, S., Bahram, M., Khalid, A. N., Corrales, A., Agan, A., Vasco-Palacios, A.-M.,
718 Saitta, A., Antonelli, A., Rinaldi, A. C., Verbeken, A., Sulistyo, B. P., Tamgnoue, B., Furneaux, B., Ritter, C.

D., Nyamukondiwa, C., Sharp, C., Marín, C., … Abarenkov, K. (2021). The Global Soil Mycobiome consortium dataset for boosting fungal diversity research. *Fungal Diversity*, *111*(1), 573–588. https://doi.org/10.1007/s13225-021-00493-7

Terrer, C., Phillips, R. P., Hungate, B. A., Rosende, J., Pett-Ridge, J., Craig, M. E., van Groenigen, K. J., Keenan, T. F., Sulman, B. N., Stocker, B. D., Reich, P. B., Pellegrini, A. F. A., Pendall, E., Zhang, H., Evans, R. D., Carrillo, Y., Fisher, J. B., van Sundert, K., Vicca, S., & Jackson, R. B. (2021). A trade-off between plant and soil carbon storage under elevated CO2. *Nature*, *591*(7851), 599–603. https://doi.org/10.1038/s41586-021-03306-8

Terrer, C., Vicca, S., Hungate, B. A., Phillips, R. P., & Prentice, I. C. (2016). Mycorrhizal association as a primary control of the CO_2 fertilization effect. *Science*, *353*(6294), 72–74. https://doi.org/10.1126/science.aaf4610

van Schöll, L., Kuyper, T. W., Smits, M. M., Landeweert, R., Hoffland, E., & Breemen, N. van. (2008). Rock-eating mycorrhizas: their role in plant nutrition and biogeochemical cycles. *Plant and Soil*, *303*(1–2), 35–47. https://doi.org/10.1007/s11104-007-9513-0

Ward, E. B., Duguid, M. C., Kuebbing, S. E., Lendemer, J. C., & Bradford, M. A. (2022). The functional role of ericoid mycorrhizal plants and fungi on carbon and nitrogen dynamics in forests. *New Phytologist*, *235*(5), 1701–1718. https://doi.org/10.1111/nph.18307

Wei, X., Zhang, W., Zulfiqar, F., Zhang, C., & Chen, J. (2022). Ericoid mycorrhizal fungi as biostimulants for improving propagation and production of ericaceous plants. *Frontiers in Plant Science*, *13*. https://doi.org/10.3389/fpls.2022.1027390

Wu, B., Nara, K., & Hogetsu, T. (2002). Spatiotemporal transfer of carbon-14-labelled photosynthate from ectomycorrhizal Pinus densiflora seedlings to extraradical mycelia. *Mycorrhiza*, *12*(2), 83–88. https://doi.org/10.1007/s00572-001-0157-2

Figure and Table captions

Figure 1: *A schematic overview of the flow of carbon from atmosphere to soil as affected by ECMF (Blue), ERMF (green), AMF (red).*

Figure 2: (a) Schematic overview of the experimental plots. The experimental design entails ten distinct mycorrhizal conditions, each replicated six times. (b) Air photograph of the experimental site.

Figure 3: A schematic overview of plant locations in Mycotron experimental plots. Each plot holds a total amount of 36 plant individual. Plants are planted 40 cm apart from each other. Plot margins are 25 com. Different colors can be attributed to different plant species, species 1 (red), species 2 (yellow), and species 3 (blue).

Table 1: The current knowledge gaps in regard to impacts of main mycorrhizal fungal guilds, AMF, ECMF, and ERMF on soil processes.

Table 2: The plant species used in the experiment and their respective mycorrhizal types

Figure 1

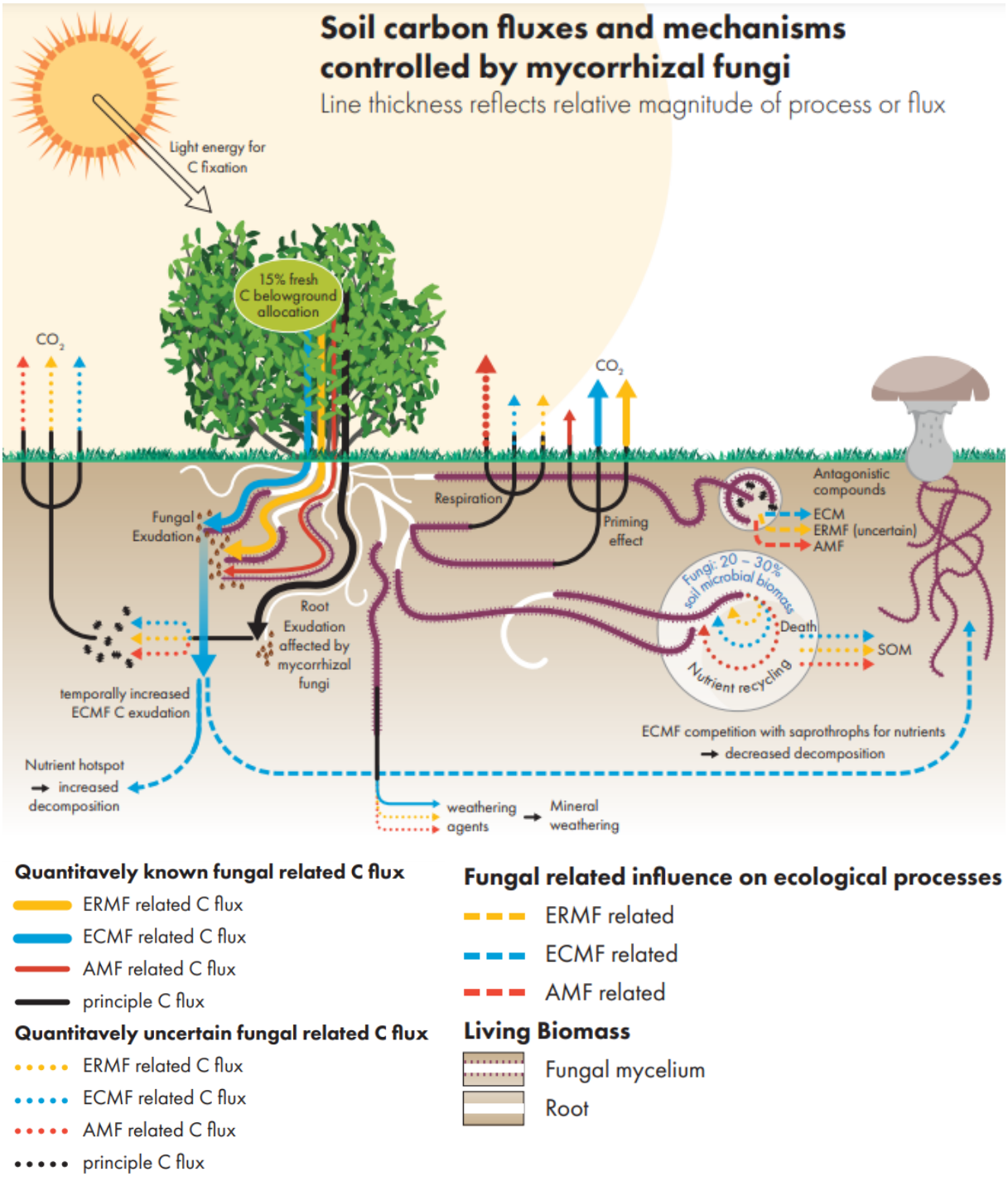
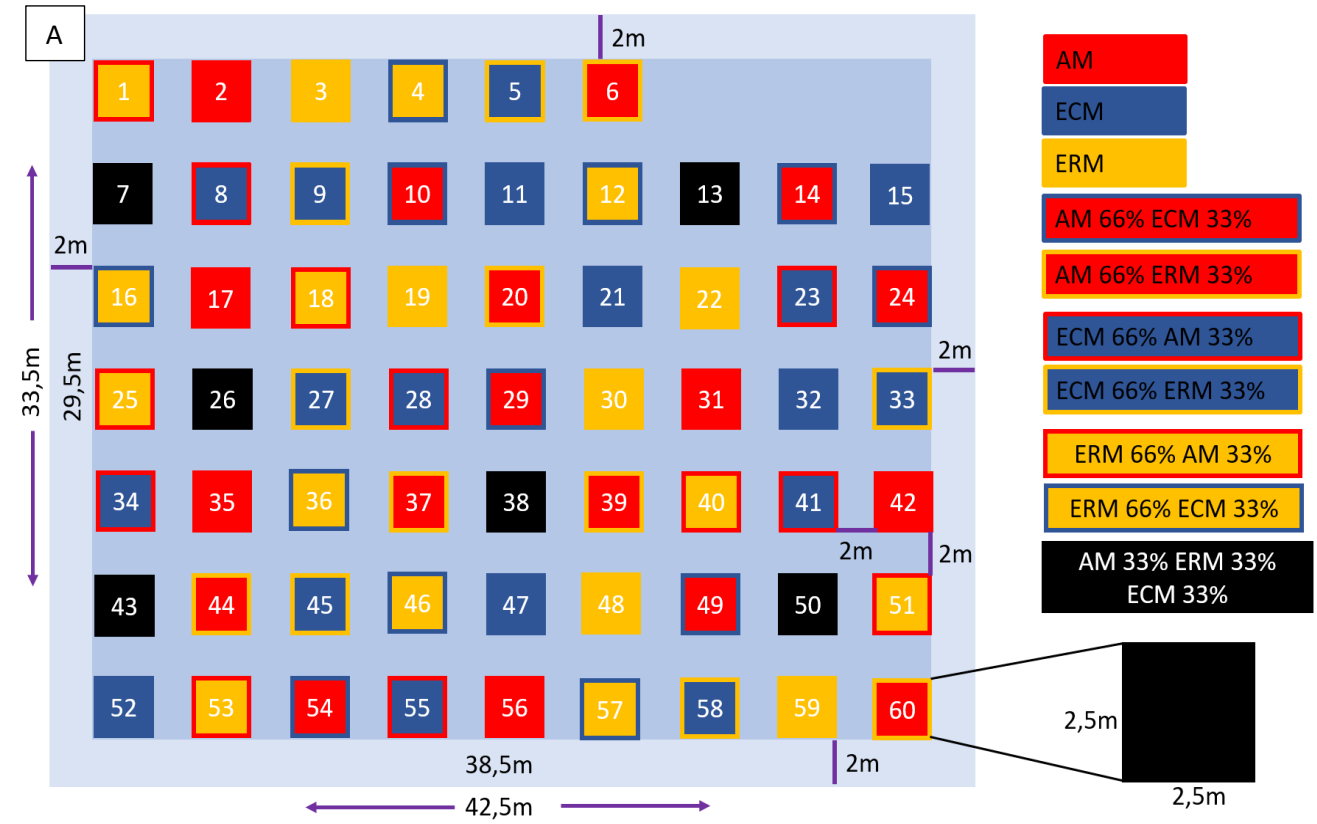
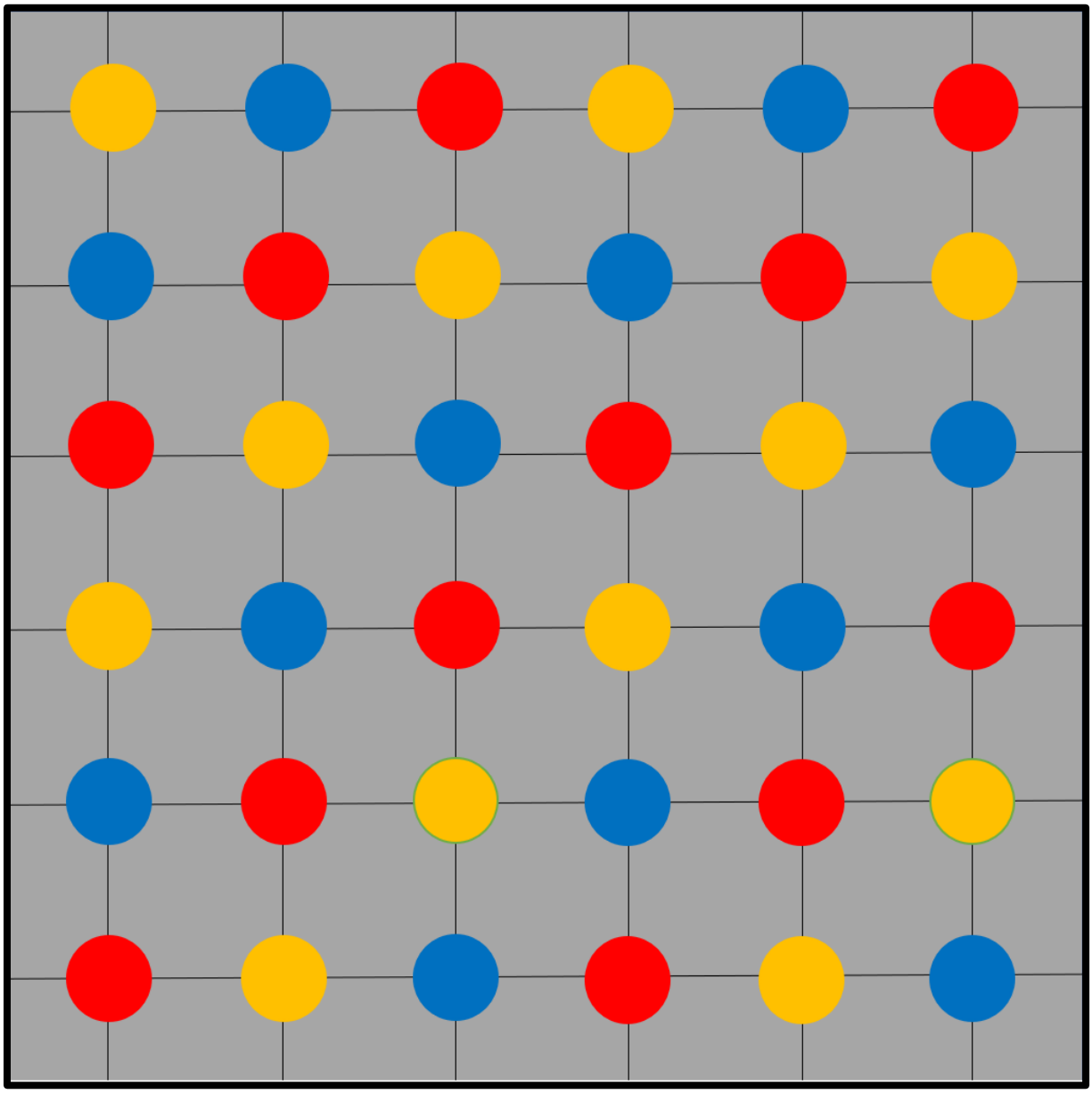

Soil carbon fluxes and mechanisms controlled by mycorrhizal fungi
Line thickness reflects relative magnitude of process or flux
Light energy for C fixation
15% fresh C belowground allocation
CO_2
CO_2
Fungal Exudation
Respiration
Priming effect
Antagonistic compounds
ECM
ERMF (uncertain)
AMF
Fungi: 20 – 30% soil microbial biomass
Death
SOM
Nutrient recycling
Root Exudation affected by mycorrhizal fungi
temporally increased ECMF C exudation
ECMF competition with saprothrophs for nutrients
→ decreased decomposition
Nutrient hotspot
→ increased decomposition
weathering agents
Mineral weathering
Quantitavely known fungal related C flux
ERMF related C flux
ECMF related C flux
AMF related C flux
principle C flux
Quantitavely uncertain fungal related C flux
ERMF related C flux
ECMF related C flux
AMF related C flux
principle C flux
Fungal related influence on ecological processes
ERMF related
ECMF related
AMF related
Living Biomass
Fungal mycelium
Root

Figure 2


A
2m
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
2m
16
17
18
19
20
21
22
23
24
33,5m
29,5m
2m
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
2m
2m
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
38,5m
2m
42,5m
AM
ECM
ERM
AM 66% ECM 33%
AM 66% ERM 33%
ECM 66% AM 33%
ECM 66% ERM 33%
ERM 66% AM 33%
ERM 66% ECM 33%
AM 33% ERM 33% ECM 33%
2,5m
2,5m


B

Figure 3



Tables

Table 1: The current knowledge gaps in regard to impacts of main mycorrhizal fungal guilds, AMF, ECMF, and ERMF on soil processes.

Mechanism 1 – Mycorrhizal mycelial carbon pool	
How much carbon from fresh photosynthates is allocated to mycorrhizal fungi, and how much seeps directly into the soil?	It is known that ECM and ERM plants transfer more carbon to the mycorrhizal fungal partner than their AM counterparts (Soudzilovskaia et al., 2015). However, it remains unclear what the magnitude of photosynthate allocation is to the fungal component across these mycorrhizal types in the same environmental setting. Moreover, we lack information on how this carbon is processed or transformed and exuded back into the soil. It is neither known at what efficiency this carbon is being used, nor how this differs across the mycorrhizal types.
What is the lifespan of AMF, ECMF, and ERMF?	Contradictions are found in reports on the overall lifespan of AMF and ECMF (Fernandez et al., 2013; Pepe et al., 2018; Staddon et al., 2003). This can be attributed to the variations in approaches (e.g. hyphae survival after plant shoot removal), which elucidates the survival of fungi without plants rather than lifespan of a hyphae in ambient conditions. There is no comparable data about the lifespan of different guilds of mycorrhizal fungi on intact hosts, and the rate at which hyphae lose viability and are renewed under non-stress conditions.
What is the production rate and turnover rate of AM, ECM, and ERM extraradical fungal biomass?	
What are the decomposition rates of AM, ERM, and ECM extraradical fungal biomass?	According to the best of our knowledge, thus far only a handful of studies addressed the differences between the chemical composition of AMF and ECMF (e.g. (Huang, van Bodegom, Declerck, et al., 2022). It is known that molecules, such as melanin, control the decomposition rate of mycorrhizal necromass (Fernandez & Koide, 2014). However, our knowledge about decomposition of mycorrhizal fungal necromass is limited to assessments of ECMF, while hardly any knowledge exists about decomposition of extraradical (going beyond roots) hyphae of AMF and ERMF. Thus, the question which chemical compounds, besides melanin, influence the rate of decomposition of these fungi remains open. Moreover, it is also unknown which microorganisms perform decomposition of the mycorrhizal fungal necromass. It is unlikely that this is similar between different types of mycorrhiza, as their chemical
Which guilds/functional groups are responsible for the decomposition of mycorrhizal necromass?	
Which compounds of mycorrhizal fungal biomass are persistent to decomposition? Which soil organic matter pools does the mycorrhizal necromass contribute to?	

	composition and microbiomes are not the same.
Mechanism 2 – Release of carbon components from roots	
What are the decomposition rates of soil organic matter in environments dominated by AMF, ECMF, and ERMF?	The decomposition rate of different sources of organic matter in different mycorrhizal environments remains unknown. To date there are a lot of inconsistencies in results obtained so far because of a context-dependent behavior of mycorrhiza (Fernandez & Kennedy, 2016a). Therefore, it remains difficult to determine processes, such as the decomposition of soil organic matter and respiration rates, in comparable ways of the three mycorrhizal types.
What are the respiration rates of AMF, ECMF, and ERMF?	
What is the scale of the Gadgil effect of ERMF?	The Gadgil effect has been intensively studied in ECM, but it has never been investigated in ERMF environments (Fernandez & Kennedy, 2016a), while given the enzymatic mechanisms possessed by ERMF, one could expect an effect similar to Gadgil effect in ERMF-dominated environments.
What is the mechanism of priming imposed by AMF, ECMF, and ERMF?	It remains unclear how the different types of mycorrhizal fungi contribute to microbial priming mechanisms.
What are the mechanisms of enhances/antagonistic decomposition with the nutrient interplay?	The interplay between mechanisms that enhance the decomposition rate in presence of mycorrhizal fungi and mechanisms that antagonize this process remain unclear (Fernandez & Kennedy, 2016a).
What are the underlying antagonistic mechanisms by which mycorrhizal fungi suppress saprotrophs in their environment, observed in the Gadgil effect?	The degree at which different mycorrhiza lower the organic matter decomposition rate in can be attributed to several underlying mechanisms (Fernandez & Kennedy, 2016a). However, it is unclear whether some of these mechanisms are species specific, and whether they significantly differ between mycorrhizal types.
Mechanism 3 – Activity of mycorrhizal fungi mediates composition of soil microbial communities	
What are specific interguild interactions between ERMF, ECMF, and AMF?	Little is known about how mycorrhizal fungi of different types can interact with fungi of other mycorrhizal types, and whether fungal type combinations have a synergistic or cumulative effect on biogeochemical cycling(Fernández et al., 2022; Ward et al., 2022).
How is photosynthate passed through the mycorrhiza into the soil to prime the environment?	It is known that mycorrhizal fungi exude labile carbon that prime nearby saprotrophic organisms (Cao et al., 2022), and that they

	create specific decomposition environments for bacteria in close vicinity to the mycorrhizal fungi (Odriozola et al., 2021). But to what degree are carbon-rich molecules that are emitted by mycorrhizal fungi are used by the bacteria? For which purposes is this carbon used?
What are the guild-specific interactions of AMF, ECMF and ERMF with microbial communities?	Despite some knowledge gained (Singavarapu et al., 2022), still little is known about the interactions of mycorrhizal fungi with the bacteria in their direct environment, or how they mediate the composition of microbial communities. Especially the data on the impacts of ERMF is lacking. Because the eco-physiological characteristics (e.g. enzyme production, exudation) of ERMF are more similar to those of ECMF, would this also be reflected in their interactions with bacteria?
The effects of mycorrhizae on mineral weathering, soil acidity, and associated toxicity	
How do different types of mycorrhiza alleviate environmental stressors, such as soil acidity and associated toxicity?	Large differences in mineral weathering capacity and mechanisms (mostly enzyme production) have already been established between AMF and ECMF. ECMF has a much higher capacity for mineral weathering than AMF (Taylor et al., 2009). ERMF that produce similar weathering agents to ECMF have been shown to have comparable weathering abilities to ECMF (van Schöll et al., 2008). ERMF are prevalent in acidic soils and often encounter heavy metals, so they are more interesting to investigate in this setting. However, knowledge about their tolerance to acidity and metals is studied in limited species (Martino et al., 2000, 2002; Khouja et al., 2013), but general knowledge on their MyFE is lacking (Wei et al., 2022).
How do ERM plants thrive in acidic soils?	
How do ERM contribute to the mineral weathering?	
What is the effect of elevated metal toxicity on AMF, ECMF, and ERMF?	

Table 2: The plant species used in the experiment and their respective mycorrhizal types

Mycorrhizal type	Plant species
AM	*Juniperus communis*
	Cotoneaster dammeri
	Hypericum calycinum
ECM	*Dryas octopetala*
	Helianthemum nummularium
	Halimium umbellatum
ERM	*Calluna vulgaris*
	Erica cinerea 'Pallas'
	Vaccinium vitis-idaea

Appendix 1: An overview of experimental conditions of each plot, and plants used.

Plot number	condition	Mycorrhizal type	Plant species
1	66% ERM 33% AM	AM	*Cotoneaster dammeri*
		ERM	*Erica cinerea*
		ERM	*Vaccinium vitis-idaea*
2	100%AM	AM	*Cotoneaster dammeri*
		AM	*Hypericum calycinum*
		AM	*Juniperus communis*
3	100% ERM	ERM	*Calluna vulgaris*
		ERM	*Erica cinerea*
		ERM	*Vaccinium vitis-idaea*
4	66%ERM 33%ECM	ECM	*Dryas octopetala*
		ERM	*Calluna Vulgaris*
		ERM	*Vaccinium vitis-idaea*
5	66%ECM 33%ERM	ECM	*Dryas octopetala*
		ECM	*Helianthemum nummularium*
		ERM	*Calluna vulgaris*
6	66% AM 33% ERM	AM	*Hypericum calycinum*
		AM	*Juniperus communis*
		ERM	*Vaccinium vitis-idaea*
7	33% AM 33% ECM 33% ERM	AM	*Juniperus communis*
		ECM	*Dryas octopetala*
		ERM	*Calluna vulgaris*
8	66% ECM 33% AM	AM	*Juniperus communis*
		ECM	*Halimium umbellatum*
		ECM	*Helianthemum nummularium*
9	66% ECM 33% ERM	ECM	*Dryas octopetala*
		ECM	*Halimium umbetlatum*
		ERM	*Vaccinium vitis-idaea*
10	66% AM 33% ECM	AM	*Juniperus communis*
		AM	*Hypericum calycinum*
		ECM	*Helianthemum nummularium*
11	100% ECM	ECM	*Dryas octopetala*
		ECM	*Halimium umbellatum*
		ECM	*Helianthemum nummularium*
12	66%ERM 33%ECM	ECM	*Dryas octopetala*
		ERM	*Erica cinerea*
		ERM	*Vaccinium vitis-idaea*
13	33%AM 33% ECM 33% ERM	AM	*Cotoneaster dammeri*
		ECM	*Halimium umbellatum*
		ERM	*Erica cinerea*
14	66% AM 33% ECM	AM	*Cotoneaster dammeri*
		AM	*Juniperus communis*
		ECM	*Halimium umbellatum*
15	100% ECM	ECM	*Dryas octopetala*
		ECM	*Halimium umbellatum*
		ECM	*Helianthemum nummularium*
16	66% ERM 33% ECM	ECM	*Helianthemum nummularium*
		ERM	*Calluna vulgaris*
		ERM	*Erica cinerea*
17	100%AM	AM	*Cotoneaster dammeri*

		AM	*Hypericum calycinum*
		AM	*Juniperus communis*
18	66% ERM 33% AM	AM	*Hypericum calycinum*
		ERM	*Calluna vulgaris*
		ERM	*Erica cinerea*
19	100% ERM	ERM	*Calluna vulgaris*
		ERM	*Erica cinerea*
		ERM	*Vaccinium vitis-idaea*
20	66% AM 33% ERM	AM	*Cotoneaster dammeri*
		AM	*Juniperus communis*
		ERM	*Calluna vulgaris*
21	100% ECM	ECM	*Dryas octopetala*
		ECM	*Halimium umbellatum*
		ECM	*Helianthemum nummularium*
22	100 % ERM	ERM	*Calluna vulgaris*
		ERM	*Erica cinerea*
		ERM	*Vaccinium vitis-idaea*
23	66% ECM 33% AM	AM	*Hypericum calycinum*
		ECM	*Halimium mbellatum*
		ECM	*Helianthemum nummularium*
24	66%AM 33%ECM	AM	*Cotoneaster dammeri*
		AM	*Hypericum calycinum*
		ECM	*Helianthemum nummularium*
25	66%ERM 33% AM	AM	*Juniperus communis*
		ERM	*Calluna vulgaris*
		ERM	*Erica cinerea*
26	33% AM 33% ECM 33% ERM	AM	*Hypericum calycinum*
		ECM	*Helianthemum nummularium*
		ERM	*Vaccinium vitis-idaea*
27	66% ECM 33% ERM	ECM	*Halimium umbellatum*
		ECM	*Helianthemum nummularium*
		ERM	*Erica cinerea*
28	66% ECM 33% AM	AM	*Cotoneaster dammeri*
		ECM	*Dryas octopetala*
		ECM	*Helianthemm*
29	66% AM 33% ECM	AM	*Cotoneaster dammeri*
		AM	*Hypericum calycinum*
		ECM	*Dryas octopetala*
30	100% ERM	ERM	*Calluna vulgaris*
		ERM	*Erica cinerea*
		ERM	*Vaccinium vitis-idaea*
31	100% AM	AM	*Cotoneaster dammeri*
		AM	*Hypericum calycinum*
		AM	*Juniperus communis*
32	100% ECM	ECM	*Dryas octopetala*
		ECM	*Halimium umbellatum*
		ECM	*Helianthemum nummularium*
33	66% ECM 33% ERM	ECM	*Dryas octopetala*
		ECM	*Halimium umbellatum*
		ERM	*Erica cinerea*
34	66% ECM 33% AM	AM	*Juniperus communis*
		ECM	*Dryas octopetala*
		ECM	*Halimium umbellatum*

35	100% AM	AM	*Cotoneaster dammeri*
		AM	*Hypericum calycinum*
		AM	*Juniperus communis*
36	66% ERM 33% ECM	ECM	*Halimium umbellatum*
		ERM	*Erica cinereal*
		ERM	*Vaccinium vitis-idaea*
37	66% AM 33% ERM	AM	*Cotoneaster dammeri*
		AM	*Hypericum calycinum*
		ERM	*Calluna vulgaris*
38	33% AM 33% ECM 33% ERM	AM	*Cotoneaster dammeri*
		ECM	*Dryas octopetala*
		ERM	*Vaccinium vitis-idaea*
39	66% AM 33% ERM	AM	*Hypericum calycinum*
		AM	*Juniperus communis*
		ERM	*Erica cinerea*
40	66% ERM 33% AM	AM	*Cotoneaster dammeri*
		ERM	*Calluna vulgaris*
		ERM	*Vaccinium vitis-idaea*
41	66%ECM 33% AM	AM	*Cotoneaster dammeri*
		ECM	*Dryas octopetala*
		ECM	*Halimium umbetllatum*
42	100% AM	AM	*Cotoneaster dammeri*
		AM	*Hypericum calycinum*
		AM	*Juniperus communis*
43	33% AM 33% ECM 33% ERM	AM	*Juniperus communis*
		ECM	*Helianthemum nummularium*
		ERM	*Erica cinerea*
44	66% AM 33% ERM	AM	*Cotoneaster dammeri*
		AM	*Hypericum calycinum*
		ERM	*Erica cinerea*
45	66% ECM 33% ERM	ECM	*Dryas octopetala*
		ECM	*Helianthemum nummularium*
		ERM	*Vaccinium vitis-idaea*
46	66% ERM 33% ECM	ECM	*Helianthemum nummularium*
		ERM	*Calluna vulgaris*
		ERM	*Vaccinium vitis-idaea*
47	100% ECM	ECM	*Dryas octopetala*
		ECM	*Halimium umbellatum*
		ECM	*Helianthemum nummularium*
48	100% ERM	ERM	*Calluna vulgaris*
		ERM	*Erica cinereal*
		ERM	*Vaccinium vitis-idaea*
49	66% AM 33% ECM	AM	*Cotoneaster dammeri*
		AM	*Juniperus communis*
		ECM	*Dryas octopetala*
50	33% AM 33% ECM 33% ERM	AM	*Hypericum calycinum*
		ECM	*Halimium umbellatum*
		ERM	*Calluna vulgaris*
51	66% ERM 33% AM	AM	*Juniperus communis*
		ERM	*Calluna vulgaris*
		ERM	*Vaccinium vitis-idaea*
52	100% ECM	ECM	*Dryas octopetala*
		ECM	*Halimium umbellatum*

		ECM	*Helianthemum nummularium*
53	66% ERM 33% AM	AM	*Hypericum calycinum*
		ERM	*Erica cinerea*
		ERM	*Vaccinium vitis-idaea*
54	66% AM 33% ECM	AM	*Hypericum calycinum*
		AM	*Juniperus communis*
		ECM	*Halimium umbellatum*
55	66% ECM 33% AM	AM	*Hypericum calycinum*
		ECM	*Dryas octopetala*
		ECM	*Helianthemum nummularium*
56	100% AM	AM	*Cotoneaster dammeri*
		AM	*Hypericum calycinum*
		AM	*Juniperus communis*
57	66% ERM 33% ECM	ECM	*Halimium umbellatum*
		ERM	*Calluna vulgaris*
		ERM	*Erica cinerea*
58	66% ECM 33% ERM	ECM	*Halimium umbellatum*
		ECM	*Helianthemum nummularium*
		ERM	*Calluna vulgaris*
59	100% ERM	ERM	*Calluna vulgaris*
		ERM	*Erica cinerea*
		ERM	*Vaccinium vitis-idaea*
60	66% AM 33% ERM	AM	*Cotoneaster dammeri*
		AM	*Juniperus communis*
		ERM	*Vaccinium vitis-idaea*