Modelling the role of mycorrhizal associations in soil carbon cycling: insights from global analyses of mycorrhizal vegetation

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Citation

Huang, W. (2024, April 10). *Modelling the role of mycorrhizal associations in soil carbon cycling: insights from global analyses of mycorrhizal vegetation*. Retrieved from https://hdl.handle.net/1887/3734176

CHAPTER 1

General introduction

1.1 Soil carbon cycle

Carbon is one of the key components of soil organic matter (SOM) (Lehmann & Kleber, 2015), a complex mixture of plant and animal residues in various stages of decomposition, as well as microbial biomass (Kögel-Knabner, 2002). The cycling of carbon through the soil thus is mostly related to the cycling of SOM, its inputs and its outputs. Soil carbon cycling involves a complex network of physical, chemical, and biological processes that influence the storage, transformation, and release of carbon in the soil (Rumpel & Kögel-Knabner, 2011).

The soil carbon cycle is important for maintaining soil health, soil fertility and plant productivity (Lehmann & Kleber, 2015). Additionally, storing carbon in soil can help offset greenhouse gas emissions by sequestering carbon dioxide from the atmosphere and as such is important to mitigating climate change (Lal, 2004). Understanding the mechanisms and drivers of the soil carbon cycle is therefore crucial for developing effective strategies to promote soil health, food security, and climate change mitigation (Smith *et al.*, 2008).

The soil carbon cycle is the continuous flow of carbon between the atmosphere, vegetation, and the soil (a simplified conceptual diagram including the key factors for soil carbon cycle mentioned here is presented in Figure 1.1). These flows are influenced by a variety of factors, including soil properties, microbial activities, plant productivity, as well as drivers of climate, land use, and management practices (Jobbagy & Jackson, 2000; De Deyn *et al.*, 2008; Xu *et al.*, 2016; Bhattacharyya *et al.*, 2022). These drivers influence the processes of carbon input and output, as well as soil internal processes including various biological, chemical, and physical transformations that occur within the soil (Cotrufo *et al.*, 2015). These internal processes include the conversion of one soil organic carbon pool to another (Guendehou *et al.*, 2014; Cotrufo *et al.*, 2015), ultimately shaping the dynamics of soil carbon. Soil carbon inputs include the addition of organic matter to the soil through plant litter, root exudates (Meier *et al.*, 2008), and residues of soil biota, including those of soil fauna (e.g. earthworms, insects, nematodes) and microbes (e.g. bacteria, saprotrophic fungi) (Rillig *et al.*, 2001). Carbon inputs into the soil primarily originate from plant productivity through the process of photosynthesis. A higher rate of plant productivity, driven by factors like sunlight, temperature, nutrient availability and water (Dolezal *et al.*, 2020), leads to increased carbon inputs into the soil through plant litter and root exudates (Liu *et al.*, 2022). The quality of input litter plays a crucial role in determining the rate of carbon input into the soil (Conn & Dighton, 2000; Strickland *et al.*, 2009), including its chemical composition and physical characteristics (Prescott, 2010). Soil carbon output, mostly consisting of CO_2 emissions to the atmosphere, is determined by soil internal processes and is influenced by soil properties (e.g. soil moisture, texture, pH, nutrient availability)

(Xu *et al.*, 2016; Luo *et al.*, 2019) and the activities of soil microbes (O'Connell, 1990) and mycorrhizal fungi (Gadgil & Gadgil, 1971; Brzostek *et al.*, 2015; Frey, 2019). Soil texture and structure play a crucial role in the storage and turnover of carbon in the soil. For example, soils with a higher clay content have a greater capacity to retain carbon due to the increased surface area provided by clay particles, facilitating the adherence of organic matter (Torn *et al.*, 1997). Well-aggregated soils, characterized by the arrangement of soil particles into larger clumps, promote better

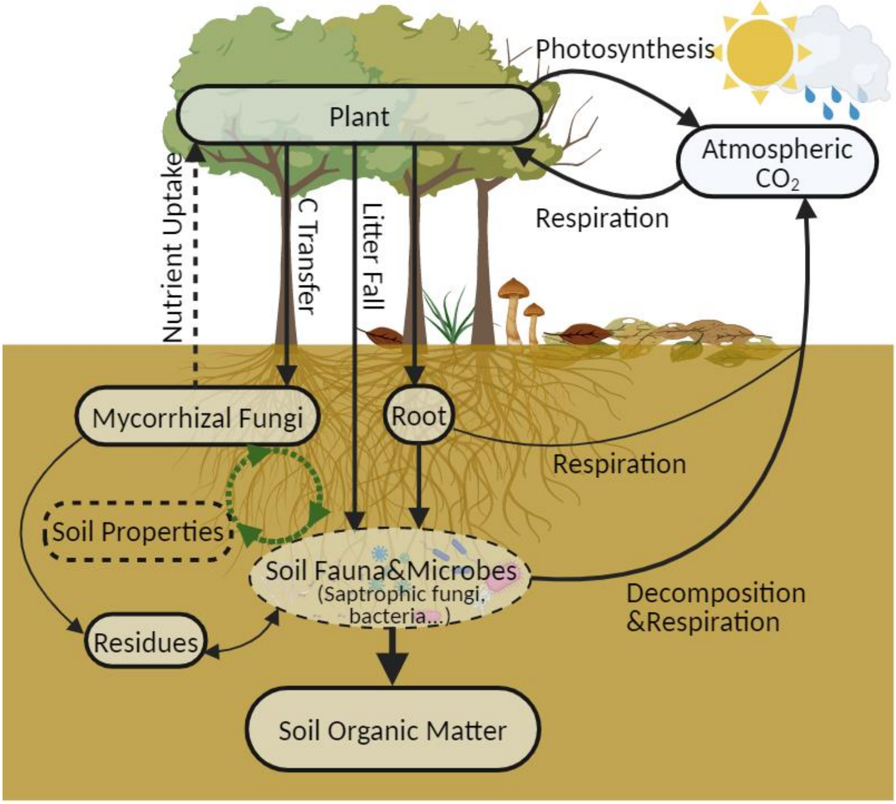

Figure 1.1 The carbon cycling process involves interactions between the atmosphere, plants, soil, and soil microbes, including mycorrhizal fungi. Black solid lines with arrows figure represent the carbon flows in this cycle. Organic materials such as plant litter, root exudates, and residues of soil biota (including mycorrhizal fungi) serve as primary inputs of soil carbon. These inputs undergo decomposition by soil fauna and microbes, transforming complex carbon compounds into simpler forms through enzymatic degradation and microbial respiration. Mycorrhizal fungi control this decomposer community, and moderate decomposition environment. Yet, although some ectomycorrhizal fungi species possess the ability to produce enzymes that break down organic matter directly, they mostly do not take up C from the organic matter. During decomposition, carbon dioxide is released into the air, and soil organic matter is mineralized. In the decomposition environment, soil properties can affect microbial activities and decomposition rates, while soil microbial activities can modify soil properties, creating feedback loops that influence decomposition rate.

pore spaces for gas exchange (Yudina *et al.*, 2022), which enables active microbial activities and enhances carbon output from the soil (Kravchenko & Guber, 2017; Kravchenko *et al.*, 2019). These soil microbial activities, including bacteria and saprotrophic fungi decomposing plant litter and other organic matter (Rousk & Frey, 2015; Müller *et al.*, 2016), release carbon dioxide back into the atmosphere through respiration.

1.2 Mycorrhiza

In recent decades, there has been growing attention to the role of mycorrhizal fungi in the soil carbon cycle and especially its involvement in those soil internal processes (Averill *et al.*, 2014; Soudzilovskaia *et al.*, 2019), with increasing research efforts aimed at understanding their interactions with other soil microorganisms (Wilkinson *et al.*, 2011; Drigo *et al.*, 2012) and their potential to promote soil carbon sequestration (Clemmensen *et al.*, 2015; Baskaran *et al.*, 2017).

Mycorrhizae are symbiotic associations between fungi and plant roots, found in most terrestrial ecosystems (Brundrett, 2009). The term “mycorrhizal fungi” refers to the fungi involved in these symbiotic associations, which form extensive networks of hyphae that can explore and exploit a larger soil volume than plant roots alone, allowing for increased nutrient uptake and transfer to the host plant (Finlay, 2008; Smith & Read, 2008). In return, the plant provides the fungi with photosynthetically fixed carbon compounds, which can be used to support fungal growth and reproduction (Wright *et al.*, 1998).

There are four main types of mycorrhizae: arbuscular mycorrhizae (AM), ectomycorrhizae (EM), ericoid mycorrhizae (ERM), and orchid mycorrhizae (Brundrett & Tedersoo, 2018). Fungi of these mycorrhizal types colonize the majority of vascular plants in terrestrial ecosystems (Smith & Read, 2008; Brundrett, 2009). These types of mycorrhizal symbioses differ in their morphology and nutrient uptake strategies, which can have important implications for plant growth, ecosystem productivity and soil biogeochemical characteristics (van der Heijden *et al.*, 1998; Rillig *et al.*, 2001).

AM and EM are the two most geographically widespread types of mycorrhizae associations (Soudzilovskaia *et al.*, 2019) that differ in ecophysiological characteristics and in the plant and fungal species that they involve (Smith & Read, 2008; Brundrett, 2009). AM form a mutualistic association with the roots of most land plants, and are prevalent in herbaceous plants, agricultural crops, and many tropical tree species. AM fungal hyphae penetrate the root cells and form branched structures, which allow for the exchange of nutrients between the plant and fungus

(Parniske, 2008; Harrison, 2012). AM fungi are obligate symbionts, meaning that they cannot survive without a host plant. They are known to play a key role in the uptake of phosphorus and other nutrients from the soil, as well as in the formation of stable soil aggregates (Smith & Smith, 2011) and can enhance plant tolerance to various environmental stresses. EM fungi form a mutualistic association with the roots of many tree species, as well as of some shrubs and herbaceous plants. EM associations are particularly common in tree species such as pines, oaks, and birches. Unlike AM fungi, they do not penetrate the root cells but instead, form a sheath around the root tips and extend their hyphae into the surrounding soil (Finlay, 2008; Martin *et al.*, 2008; Smith & Read, 2008). EM fungi are known to play a key role in plant uptake of nitrogen and other nutrients, especially in nutrient-poor soils. The extraradical mycelium of certain fungi, such as *Pisolithus tinctorius*, functions as an extension of the plant root system, significantly increasing the nutrient-absorbing surface area of roots (Rousseau *et al.*, 1992).

The distribution of mycorrhizal fungi is closely linked to the distribution of host mycorrhizal vegetation (Brundrett & Tedersoo, 2018). Mycorrhizal vegetation refers to plants that form symbiotic associations with mycorrhizal fungi and specific mycorrhizal traits provided to the plant host to colonize areas with beneficial growing conditions (Read, 1991). The global geographical distribution of mycorrhizal vegetation is influenced by factors such as climate, soil characteristics and anthropogenic influences (Tedersoo *et al.*, 2010; Barceló *et al.*, 2019; Soudzilovskaia *et al.*, 2019). EM fungi are predominantly found in temperate and boreal forests, although they also occur in some tropical and subtropical regions (Bahram *et al.*, 2012). AM fungi have a more ubiquitous distribution and are found in a wide range of ecosystems, including grasslands, agricultural fields, and forests. In nutrient-poor soils, mycorrhizal associations can confer a competitive advantage to plants by enhancing nutrient uptake, therefore, mycorrhizal vegetation is often more prevalent in ecosystems where nutrient availability is limited (Smith & Read, 2008). Additionally, disturbances of anthropogenic drivers such as land-use change, deforestation, and climate change can impact the distribution of mycorrhizal fungi and their associated vegetation (Jo *et al.*, 2019). Alterations in land use and habitat fragmentation can disrupt mycorrhizal networks and lead to changes in mycorrhizal fungi community composition (Sapsford *et al.*, 2021), which could potentially lead to variations in mycorrhizal vegetation. Climate change, including shifts in temperature and precipitation patterns, can also affect mycorrhizal associations and the distribution of mycorrhizal vegetation (Bennett & Classen, 2020).

1.3 Mycorrhiza and the soil carbon cycle

Mycorrhizae are known to play a crucial role in ecosystem functioning by influencing soil carbon cycling (Talbot *et al.*, 2008; Averill *et al.*, 2014; Soudzilovskaia *et al.*, 2019). Next to mycorrhiza, soils feature other significant pathways involved in carbon sequestration, such as bacterial activity and the decomposition of litter by soil fauna like worms and nematodes. However, despite the importance of these pathways, many of them are understood reasonably well, while the impact of mycorrhizal associations on soil carbon dynamics, and especially the role of mycorrhizal fungi, remains understudied. Therefore, this thesis primarily focuses on exploring the intricate role of mycorrhizal fungi in soil carbon cycling.

The impact of mycorrhiza on the soil carbon cycle involves various mechanisms that can be summarized into three pathways. Different types of mycorrhizae exhibit varying effects on these pathways, which might accelerate or suppress soil carbon cycling, leading to increases or decreases in the SOM pool (see Figure 1.2). These pathways are: **I**. Supporting plant nutrient uptake (e.g. N, P), leads to increased plant productivity and growth (Cornelissen *et al.*, 2001; Phillips *et al.*, 2013; Averill *et al.*, 2019) (Figure 1.2-b). This directly contributes to the litter and therewith carbon input to the soil and ultimately increases the SOM pool. Moreover, mycorrhizae can enhance plant carbon allocation to the belowground roots, thereby increasing the amount of carbon that is transferred to the soil (Högberg & Högberg, 2002; Clemmensen *et al.*, 2013). This mechanism is well-established and extensively studied; **II**. Mycorrhizae contribute to the soil carbon pool directly through the allocation of carbon fungal mycelia (Leake *et al.*, 2004; Soudzilovskaia *et al.*, 2015b), both dead and alive (Figure 1.2-c). For example, the ERM and EM fungi contribute substantially to the microbial biomass in forest soils, accounting for approximately one-third of the total microbial biomass and ranging from 700 to 900 kg ha^{-1} (Wallander *et al.*, 2001; Högberg & Högberg, 2002); **III**. Mycorrhizae can influence plant litter decomposition and organic matter formation through various mechanisms (Figure 1.2-d): a. Extracellular enzymes break down organic matter (Talbot *et al.*, 2008; Shah *et al.*, 2016). Some ectomycorrhizal fungi species possess the ability to produce enzymes that break down organic matter directly (Brzostek *et al.*, 2015), which accelerates carbon cycling, while it is not a trait shared by all mycorrhizal fungi; b. Mycorrhizae secrete a range of compounds which influence microbial community activities (Fernandez & Kennedy, 2016; Frey, 2019). While the majority of mycorrhizal fungi themselves typically do not decompose organic matter directly, they can release hyphal exudates and organic compounds into the soil that cause the ‘priming effect’ which promotes the activity of soil microorganisms (such as bacteria) involved in decomposition processes and influence the microbial community structure (Brzostek *et al.*, 2015; Zhang *et al.*, 2022). EM fungi might also suppress the activity of saprotrophic fungi involved in organic matter decomposition, through competitive interactions for resources such as carbon and nutrients, the phenomenon known as the ‘Gadgil’ effect (Gadgil & Gadgil, 1975; Fernandez & Kennedy, 2016). As a result, the decomposition of organic matter by saprotrophic fungi is reduced, leading to an accumulation of organic matter in the soil; c. Mycorrhizae modify the soil structure by influencing soil particle binding and soil aggregation (Rillig & Steinberg, 2002). These changes in soil structure could result in the deceleration of organic matter decay, leading to the stabilization and accumulation of SOM.

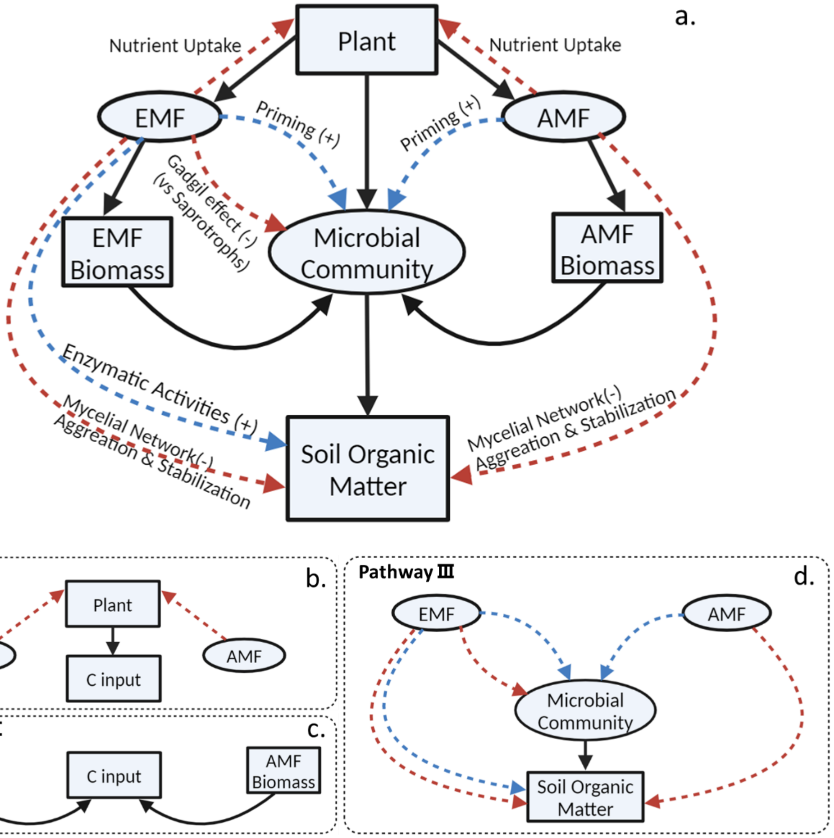

Figure 1.2 Schematic diagram illustrating the potential effects of mycorrhizal fungi on carbon cycling through different pathways. Solid arrows depict carbon flows between different carbon pools (represented by squares). Dashed arrows indicate the impact of mycorrhizae, with acceleration (+) or suppression (-) of soil carbon cycling, leading to increases (red line) or decreases (blue line) in the SOM pool. (a) Overview of potential mycorrhizal impacts on the carbon cycle; (b) **Pathway I**: Mycorrhizae support nutrient uptake to plants through mycelia, increase of plant production will ultimately increase SOM pool; (c) **Pathway II:** Mycorrhizae biomass contributes to the soil carbon pool as carbon input.

Some EMF biomass is very recalcitrant and resistant to decomposition and is thought to contribute to C storage in SOM; (d) **Pathway III:** Mycorrhizal fungi mediate soil carbon decomposition, with ectomycorrhizal fungi (EMF) and arbuscular mycorrhizal fungi (AMF) regulating the process through different mechanisms. EMF participate in organic matter decay via enzymatic degradation and can accelerate soil carbon decomposition rates by "priming" saprotrophic fungi with root and EMF exudates. Conversely, the 'Gadgil effect' of competitive interactions between EMF and saprotrophs reduces saprotrophic fungal activities, decelerating decomposition and increasing carbon input into SOM. AMF can also induce priming effects under elevated CO_2, stimulating the activity of saprotrophic microorganisms such as bacteria and fungi. The increased microbial activity can accelerate the decomposition of soil carbon in the soil. AMF and EMF can also indirectly influence soil microbial activities by mediating microbial community composition and function through interactions with root exudates. Both AMF and EMF mycelial networks contribute to soil aggregation, providing physical protection and promoting SOM stabilization.

The relationship between mycorrhizae and the soil carbon cycle is complex and depends on various factors, these factors affect the three pathways through which mycorrhiza impacts the soil carbon cycle: (1) The extent of nutrient uptake and carbon allocation by mycorrhizal fungi is influenced by mycorrhizal types (Johnson *et al.*, 2015), plant species (Treseder & Lennon, 2015), nutrient availability (Treseder & Allen, 2002), and environmental conditions (e.g., temperature, moisture) (Talbot *et al.*, 2008). One major factor is the availability of nutrients in the soil. For instance, in nutrient-poor conditions, mycorrhizae can have a particularly strong effect on nutrient uptake and plant growth, leading to increased carbon allocation into fungal mycelia (Querejeta *et al.*, 2009); (2) Mycorrhizal fungal biomass directly contributes to the soil carbon pool, which depends on the presence and abundance of mycorrhizal fungi. However, the factors influencing the turnover rates of mycorrhizal fungal biomass and carbon release are not fully understood; (3) Mycorrhizal ability to influence soil litter decomposition and organic matter formation is enabled through various mechanisms. Their ability to affect this pathway likely varies across mycorrhizal types and decomposition environments (Langley & Hungate, 2003; Tunlid *et al.*, 2016). Investigating the factors that regulate enzyme production and compound secretion, including mycorrhizal species across different mycorrhizal types, environmental conditions, and substrate availability, can help understand the extent of their impact on organic matter decomposition and soil carbon dynamics.

Among those factors, besides the external factors of the environment (nutrient availability, soil humidity etc.), the complexity of mycorrhiza itself (e.g. traits of different mycorrhizal types, mycorrhizal distribution etc.) is the key factor affecting its impact on the soil carbon cycle. Mycorrhizae can form associations with a wide range of plant species, but the extent and type of association can vary depending on the plant species and environment, resulting in varied abundances of mycorrhizal associations (Soudzilovskaia *et al.*, 2019). The distribution of mycorrhizal associations across different ecosystems influences the spatial patterns of plant productivity, nutrient availability, and carbon dynamics, ultimately impacting the soil carbon cycle at a larger scale. On the other hand, the abundance of mycorrhizal associations within a given ecosystem can determine the overall contribution of mycorrhiza to plant productivity, nutrient cycling, and subsequently, the input of organic matter into the soil locally. This, in turn, affects the soil carbon cycle and the storage and turnover of SOM.

Different mycorrhizal fungal types can have different effects on plant growth and nutrient uptake, which has consequences on regulating the soil carbon cycle (differences in Pathway I, Figure 1.2-b). EM fungi have been shown to enhance soil carbon storage, particularly in forest ecosystems (García-Palacios *et al.*, 2016; Soudzilovskaia *et al.*, 2019). This is attributed to a higher allocation of C into ectomycorrhizal fungi by EM plant hosts, compared to that of AM plant hosts, and to the capacity of EM fungi to form a sheath around the root tips and extend their hyphae into the surrounding soil creating larger mycelium than AM fungi do (Finlay, 2008; Martin *et al.*, 2008; Smith & Read, 2008). In turn, this can increase the surface area for nutrient uptake and support the transfer of carbon from plants to soil microorganisms (Clemmensen *et al.*, 2013).

Mycorrhizal types also differ in the magnitude of input of mycorrhizal biomass and extracellular compounds to soil carbon (differences in Pathway II, Figure 1.2-c). Both the amount and chemical composition of mycorrhizal biomass varies between mycorrhizal types. Mycorrhizal fungi are important C sinks of net primary production (NPP) (Kaiser *et al.*, 2015; Konvalinková *et al.*, 2017; Hawkins *et al.*, 2023), and depending on the type of mycorrhizal guilds, the annual mycelial accumulation can reach around 175–200 g C m^{-2} (Wallander *et al.*, 2001; Ouimette *et al.*, 2019). The mycelium, i.e. the network of the root-like structures (hyphae) of the fungi in the soil, varies in morphology between species. Also, the extent and the lifespan of the hyphal network differ. For instance, hyphae of EM fungi live longer compared to AM fungi (Harley, 1971; Leake *et al.*, 2004). Fungal traits facilitating a long lifespan can also potentially determine the decomposability of EM and AM fungal litter. This raised the hypothesis that dead EM hyphae are likely more recalcitrant to decomposition than AM hyphae (Langley & Hungate, 2003). The specific composition and turnover rates of mycorrhizal biomass and extracellular compounds can vary among mycorrhizal types, influencing their respective contributions to soil carbon inputs. Thus, the substantial contribution of mycorrhizal biomass to soil carbon through both mycorrhizal biomass and extracellular compounds from different mycorrhizal types may have different effects on soil carbon dynamics.

AM and EM fungi also differ in mediating litter decomposition process (differences in Pathway III, Figure 1.2-b). EM fungi are known to use different organic matter decomposition mechanisms to access organic nitrogen (Nicolás *et al.*, 2019). Some EM fungi can produce enzymes that can break down recalcitrant carbon compounds, such as lignin, which can contribute to the formation of stable soil organic matter (Courty *et al.*, 2007; Lindahl & Tunlid, 2015). While AM fungi do not break down organic materials directly, but have been shown to increase soil enzyme activities by influencing other soil microbial communities, particularly those involved in phosphorus cycling, such as acid and alkaline phosphatases (Zhang *et al.*, 2018; Etesami *et al.*, 2021). Since AM fungi are known to enhance the uptake of phosphorus and other nutrients from the soil (Wang *et al.*, 2023), they can stimulate plant growth and increase the production of root exudates that can fuel microbial activity. In addition, like EM fungi, AM fungi can also promote the formation of stable soil aggregates (Morris *et al.*, 2019), which can enhance soil structure and water retention capacity.

However, the effects of AM and EM fungi on soil biogeochemical characteristics can be complex and can vary depending on factors such as fungal species, plant species, and environmental conditions. For example, studies have shown that the effects of AM fungi on soil carbon storage can vary depending on the specific fungal species and the plant species involved (Tedersoo & Bahram, 2019). In some cases, AM fungi have been found to enhance soil carbon sequestration. Studies investigated the effects of different AM fungal species on soil carbon dynamics and found that certain species were associated with higher soil carbon stocks compared to others (Johnson *et al.*, 2015). Other studies on the influence of EM fungi on phosphorus acquisition in forests found that EM associations significantly increased phosphorus availability in the soil (Desai *et al.*, 2014; Köhler *et al.*, 2018). Understanding the effects of AM and EM fungi on soil biogeochemistry is important for developing effective strategies to enhance soil health and ecosystem productivity. Such strategies can include promoting the use of mycorrhizal fungi in sustainable agriculture and forestry practices, as well as identifying management practices that can optimize the symbiotic interactions between plants and fungi in different ecosystems.

All factors listed above have some level of importance. Understanding the effects of mycorrhiza on plant nutrient uptake, mycorrhizal abundance and turnover rates, and the production of extracellular enzymes and compounds are particularly important due to their direct influence on the pathways through which mycorrhiza impacts the soil carbon cycle. By identifying and studying these key factors, we can gain insights into the mechanisms underlying mycorrhizal contributions to soil carbon dynamics which are important to consider in modelling, and for predicting the effects of mycorrhiza on the soil carbon cycle.

1.4 Review of previous mycorrhiza research and challenges

Research on the impact of mycorrhizae on soil carbon has made significant progress over recent decades. The current body of research primarily focuses on understanding the complex interactions between mycorrhizal fungi and soil carbon cycling processes at a local or regional scale. Much of the research has been dedicated to investigating the mechanisms through which mycorrhizal fungi influence carbon allocation in plants, leading to increased plant productivity and growth (Bücking & Shachar-Hill, 2005; Smith & Smith, 2011). This results in increased litter input to the soil and enhanced carbon transfer to belowground roots (Rygiewicz & Andersen, 1994; Keller *et al.*, 2021), increasing carbon transfer to the soil (the first pathway introduced above). The direct influence of mycorrhizal fungi on soil biogeochemical pools, such as fungal mycelia as biomass input to the soil, has also been studied extensively (Rillig *et al.*, 2001; Langley & Hungate, 2003; Godbold *et al.*, 2006), and contributes to carbon storage and cycling in the soil (the second pathway). Furthermore, researchers have explored the role of mycorrhizal fungi in soil litter decomposition and organic matter formation by examining their extracellular enzyme production and compound secretion, which can influence microbial community activities (Pathway III, Figure 1.2-d) (Herman *et al.*, 2012; Nuccio *et al.*, 2013; Gui *et al.*, 2017a).

Despite these advancements, the third pathway (Pathway III, Figure 1.2-d), which investigates the mechanisms of mycorrhizal fungal mediation on soil litter decomposition and the fate of carbon, remains relatively understudied compared to the other two pathways. The processes involved in soil litter decomposition and organic matter formation are highly complex, involving multiple interacting factors, such as microbial communities and enzyme activities (Cheeke *et al.*, 2017). Assessing the impact of mycorrhizal fungi on soil carbon dynamics presents challenges due to the intricate interactions between mycorrhizal fungi and other factors, as well as the need for precise measurements in heterogeneous soil environments. Therefore, further investigations are needed to fully elucidate the mechanisms underlying mycorrhizal fungal mediation of soil litter decomposition and its influence on carbon dynamics. Particularly the mechanisms through which mycorrhizal fungi impact soil carbon at a global scale are poorly understood.

One major challenge is the lack of comprehensive data about the mycorrhizal fungi distribution and abundance patterns. Understanding the influence of mycorrhizal fungi on global soil carbon dynamics requires information on their spatial distribution and abundance across diverse ecosystems worldwide. However, obtaining such data is challenging, since mycorrhiza encompass a wide range of species with diverse ecological preferences and they reside below ground, making their study and data collection inherently challenging. Their extensive network of fine mycelia makes it difficult to directly observe and quantify their presence and abundance, especially at large scales. In many regions, systematic sampling efforts to capture mycorrhizal fungi abundance and distribution are lacking, which limits our ability to accurately estimate the impact of mycorrhizal fungi on soil carbon at a global scale. It requires specialized techniques such as molecular tools, microscopy, and DNA sequencing to measure mycorrhizal fungi (Horton & Bruns, 2001; Öpik *et al.*, 2010). These techniques are resource-intensive and may not be universally applied across all ecosystems. For example, the challenges of variations in sampling protocols, laboratory techniques, and analytical methods make it difficult to compare and synthesize data across different studies and regions. Thus, data on mycorrhizal fungi are often derived from localized studies or specific ecosystems, resulting in limited data availability, leading to a spatial bias and limited representation of global diversity (Reineke *et al.*, 2003; Johnson *et al.*, 2010).

Additionally, the complex interaction between mycorrhizal fungi and other factors, including the impact of climate, adds to the challenge of understanding the role of mycorrhizal fungi in soil carbon cycling. Soil carbon dynamics involves intricate processes that encompass mycorrhizal impact, and interactions with factors such as temperature and precipitation. These climate factors can exert significant influences on both mycorrhizal fungal activity (Bennett & Classen, 2020) and soil carbon cycling processes (Davidson & Janssens, 2006; Conant *et al.*, 2011). However, the precise nature of these interactions and their overall impact on soil carbon dynamics are not fully understood, making it difficult to accurately quantify the specific contribution of mycorrhizal fungi.

Moreover, the complexity of soil ecosystems, including the interactions between mycorrhizal fungi and other soil biota, further complicates our understanding of the role of mycorrhizal fungi in soil carbon cycling. Mycorrhizal fungi interact with various components of the soil ecosystem, including plants, other soil microorganisms, and soil physicochemical properties. Understanding the intricacies of these interactions and their collective influence on soil carbon is challenging. The complexity of these interactions requires comprehensive and integrated approaches that consider multiple factors simultaneously.

Finally, soil ecosystems exhibit spatial heterogeneity and temporal dynamics, which complicate the estimation of mycorrhizal impact on soil carbon globally. Variations in soil properties, climate, land use, and vegetation cover influence the occurrence and functioning of mycorrhizal associations (Read & Perez-Moreno, 2003; Craig *et al.*, 2018; Steidinger *et al.*, 2019), leading to spatial and temporal variability in their impact on soil carbon. Those effects on soil variations as well as other anthropogenic activities on mycorrhizal fungi and soil carbon cycling remain poorly understood (Sapsford *et al.*, 2021), highlighting the need for further research in this area.

1.5 Using modelling methods to face the challenges

Modelling is an important method for tackling the challenge of understanding the mycorrhizal impact on global soil carbon for several reasons. Considering various unknowns and uncertainties related to mycorrhizal mechanisms involved in mediating soil carbon cycling processes, modelling is ideal for hypothesis testing and knowledge integration, thus allowing researchers to evaluate different hypotheses regarding the mechanisms and processes underlying soil carbon (Shi *et al.*, 2019). By comparing model outputs with empirical observations, researchers can validate or refine their hypotheses, leading to a deeper understanding of the complex relationships involved in mycorrhizal impact on soil carbon. Models also facilitate the integration of diverse knowledge sources, such as experimental data, field observations, and theoretical frameworks, promoting interdisciplinary research and advancing our understanding of mycorrhizal contributions to soil carbon dynamics.

One major advantage of modelling is that it allows the integration of the complex interactions between mycorrhizal fungi and other components of the soil ecosystem including plants and soil microorganisms within the soil litter decomposition environment, providing a more comprehensive understanding of the mechanisms through which mycorrhizal fungi affect soil carbon (Soudzilovskaia *et al.*, 2019). It is important to note that disentangling these mechanisms from global field observations is challenging due to the tight correlation between mycorrhizal distributions and other factors such as temperature gradients (Soudzilovskaia *et al.*, 2015b; Barceló *et al.*, 2019). By incorporating these interactions into a comprehensive framework, models can simulate the dynamics of mycorrhizal associations and their influence on soil carbon cycling separately. This offers a unique opportunity to disentangle the complex interactions involved in Pathway III, where mycorrhizal fungal mediation of soil litter decomposition and carbon fate in soil remains understood poorly compared to other pathways. It allows us to assess the impact of mycorrhizal fungi on soil carbon dynamics by integrating various environmental factors and mycorrhizal properties, thereby addressing the challenge of understanding their intricate interactions in heterogeneous soil environments. Besides, the modelling approach has the capacity for scaling up findings from individual studies to larger spatial scales and global scales (Zhang *et al.*, 2013). By incorporating data from diverse ecosystems and considering the spatial heterogeneity of the distribution and abundance of mycorrhizal associations, and environmental conditions, models can provide insights into the global patterns and processes of mycorrhizal impact on soil carbon. This helps to overcome the limitations of data availability and spatial biases associated with localized studies.

Finally, modelling can be applied to predict the impact of mycorrhizal fungi on soil carbon under different scenarios, helping researchers understand how changes in environmental conditions, land use, and management practices can influence mycorrhizal impact on soil carbon globally. While it is also possible to use field climate simulation equipment to achieve such kind of simulation, this would be time and money-consuming. Using a modelling approach, by manipulating model inputs and parameters, researchers can explore different scenarios and assess the potential outcomes, aiding in the development of sustainable soil management strategies and climate change mitigation efforts.

1.6 Main research questions and objectives

This research aims to investigate how different types of mycorrhizal associations affect soil carbon cycling, explore the mechanisms underlying their impact on plant litter decomposition, and assess how these dynamics vary across different ecosystems and climatic conditions, thus enhancing our understanding of mycorrhizal ecology at a global scale. In this thesis, through the use of a modelling approach supplemented with lab experiments, to examine the role of mycorrhizae in the global carbon cycle, we seek to elucidate the complex interactions between mycorrhizal fungi, soil carbon, and environmental factors, ultimately providing insights into the implications of the current and future distributions of mycorrhizal associations for soil carbon storage in the face of global environmental change. I quantitatively explored the direct impact (fungal biomass as carbon input, Pathway II, Figure 1.2-c) and mediation effect (through influences on litter decomposition, Pathway III, Figure 1.2-d) of different types of mycorrhizal fungi on soil carbon, addressing the following research questions:

(1) How do mycorrhizal effects on soil carbon cycling vary between different types of mycorrhizal associations? (Chapter 2 and Chapter 3)

(2) How can we incorporate the mechanisms through which mycorrhizae impact plant litter decomposition in modelling? (Chapter 3)

(3) How does the impact of mycorrhizal associations on soil carbon vary across different types of ecosystems in various climates? (Chapter 4)

(4) How does global environmental change influence the distribution of mycorrhizae in the future and how could this influence the future soil carbon storage? (Chapter 5)

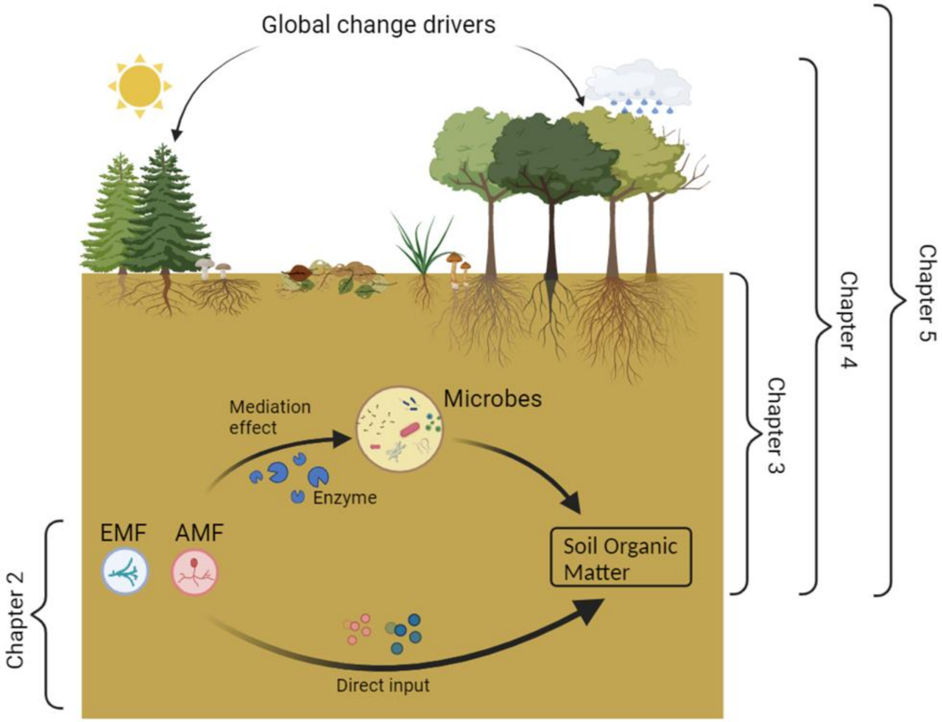

Figure 1.3 Conceptual diagram of mycorrhizal impact on soil biochemical cycles with links to each chapter.

The study is set up to provide new insights into the role of mycorrhizae in carbon sequestration to fill a critical knowledge gap in the mycorrhiza study and to identify potential strategies for mitigating climate change. In Chapter 2, the direct impact of mycorrhizae on soil carbon is investigated by examining the chemical composition of biomass from different types of mycorrhizae. Chapter 3 explores the mediation effect of mycorrhizae on the soil carbon cycle through their influence on the litter decomposition process. A well-accepted process-based soil carbon model is extended by including the mycorrhizal environment as a driver for litter decomposition, in addition to climate. In Chapter 4, this model is further applied on a global scale to compare the mycorrhizal environmental impact on litter decomposition under different climate zones. Finally, in Chapter 5, potential future variations in mycorrhizal vegetation distribution and their corresponding impact on the soil litter decomposition process are estimated under future climate and socio-economic scenarios. Figure 1.3 provides an overview of the research conceptual scheme. More details about the principal content of each chapter are explained in the next session (1.7).

1.7 Thesis outline

Chapter 1. General introduction

This thesis begins by providing a general background on soil carbon and mycorrhizal ecology, highlighting major research gaps in the area. The research goal and major research questions are also outlined in this chapter.

Chapter 2. Mycelium chemistry differs markedly between ectomycorrhizal and arbuscular mycorrhizal fungi

The question “How do the main mycorrhizal types differ in the decomposability of their mycelia’’ is central to understanding microbial contributions to the soil carbon cycle. Ecto- and arbuscular mycorrhizal fungi are the most widespread types of mycorrhizal fungi, common in all terrestrial ecosystems, and creating the dominant pool of soil microbial biomass. Yet differences in the chemical quality of these fungi that underpin the decomposability of the fungal material are unknown, due to extreme difficulties in getting sufficient amounts of fungal material of arbuscular mycorrhizal fungi. In this chapter, using in-vitro cultivation technique, I for the first time managed to cultivate ecto- and arbuscular mycorrhizal fungi in amounts sufficient to conduct chemical analysis of fungal material, and examined sixteen species of mycorrhizal fungi for chemical traits that underpin decomposability of fungal material. The outcomes of this analysis can be used as input data for mycorrhizal litter decomposition models, and also indicate that the differences in litter quality among dominant mycorrhizal types should be explicitly considered in assessments of soil carbon cycles and modelling.

Chapter 3. Implementation of mycorrhizal mechanisms into the soil carbon model improves the prediction of long-term processes of plant litter decomposition.

Although it is well established that ecosystems dominated by plants featuring ectomycorrhizae (EM) vs. arbuscular mycorrhizae (AM) exhibit distinct soil carbon dynamics, current soil carbon models do not explicitly conceptualize mycorrhizal impacts through different pathways. This chapter presents a first mechanistic model that enables examining alternative conceptualizations of mycorrhizal impacts on plant litter decomposition and the mechanistic separation of these impacts from climatic factors. It resolves the well-known problem of a tight correlation between global climate patterns and patterns of distribution of mycorrhizal vegetation, which precludes conclusive examination of mycorrhizal impacts of soil carbon dynamics. The model enables a comprehensive representation of mycorrhizal impacts on litter decomposition and effectively improves long-term predictions of decomposition dynamics.

Chapter 4. Global estimation of mycorrhizal impact on the plant litter decomposition process

Mounting evidence indicates that ecosystems dominated by plants featuring different types of mycorrhizae exhibit varied soil carbon dynamics. Yet, little is known about how distinct types of mycorrhizal environments affect global carbon cycles. This chapter focuses on the worst understood pathway of mycorrhizal impact on plant litter decomposition: mycorrhizal mediation of plant litter decomposition. Based on the new soil carbon sequestration model (Chapter 3), Yasso-Myco, which accounts for the impacts of different types of mycorrhizal vegetation on plant litter decomposition, I estimated global long-term plant litter decomposition. The study demonstrates that the variability in plant litter decomposition rate is controlled by the mycorrhizal type of dominant vegetation, which creates mycorrhizal type-specific decomposition environments. Further, it shows how the magnitude of mycorrhizal impacts differs across biomes. This chapter advances our understanding of the effects of plant-microbial interactions on the global dynamics of labile and recalcitrant soil carbon compounds. This advancement helps to reduce uncertainties in global carbon budgets, urgently needed to understand the consequences of global land-use and climate change on ecosystem functioning.

Chapter 5. Climate change and mycorrhizal-vegetation distribution impact the future soil litter decomposition process

Mycorrhizal fungi are highly sensitive to environmental change, including changes in temperature, precipitation etc. Understanding the potential changes in mycorrhizal vegetation distribution under environmental change can provide valuable insights into future ecosystem functioning. This chapter examines the changes in mycorrhizal vegetation distribution under future environmental change and analyses their corresponding impact on litter decomposition which have significant implications for global carbon cycling. It also has important implications for understanding the complex interplay between climate change and ecosystems, including the feedback that may occur between them. I used existing mycorrhizal distribution estimates and related environmental drivers to project future changes in mycorrhizal vegetation globally. Then, I quantified the impact of mycorrhizal vegetation changes on leaf litter decomposition and discussed potential cascading effects on nutrient cycling and carbon sequestration. This chapter emphasizes the importance of understanding the future evolution of mycorrhizal vegetation distribution in predicting the response of terrestrial ecosystems to global environmental change and developing effective management strategies to mitigate climate change.

Chapter 6. General discussion and conclusion

The final chapter presents an integral analysis of the knowledge obtained within my PhD research. It provides the final conclusions and proposes future steps to advance our understanding of mycorrhiza and soil systems.