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

Huang, W.

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CHAPTER 6

General discussion and conclusions

Over the past few decades, our knowledge about the role of mycorrhizae in shaping soil carbon dynamics has significantly progressed. Many studies have focused on understanding the mechanisms by which mycorrhizal fungi affect soil carbon storage and decomposition (Talbot *et al.*, 2008; Averill, 2016; Verbruggen *et al.*, 2016; Zhu *et al.*, 2018; Zhou *et al.*, 2020), and the potential consequences of changes in mycorrhizal fungal communities on carbon cycling (Clemmensen *et al.*, 2015; Fernandez & Kennedy, 2015). In these studies, researchers have employed in-situ field investigations and laboratory experiments that utilize stable isotope tracing, molecular analyses, and soil analytical techniques. Additionally, meta-analysis and modelling methods have been developed, along with biological databases (Öpik *et al.*, 2010; Brzostek *et al.*, 2014; Shi *et al.*, 2019; Soudzilovskaia *et al.*, 2019, 2020). As a result, we are now more aware of the importance of the role of mycorrhizal symbiosis in soil carbon cycling and mitigating the effects of climate change.

In this PhD study, I intend to significantly enlarge my understanding of the impacts of the major mycorrhizal types of arbuscular mycorrhizae (AM) and ectomycorrhizae (EM) on the global soil carbon cycle and the potential changes in their distribution as well as the consequences thereof under future environmental change from two perspectives: The first perspective (Chapter 2) explored their direct impact as fungal biomass input to the soil through lab experiments. The second perspective (Chapter 3, 4, and 5) investigated their impact in mediating litter decomposition through modelling.

This thesis provides insights into the role of mycorrhizal fungi in the soil carbon cycle and highlights the need to consider their impacts when assessing global soil carbon dynamics. The findings from this thesis also emphasize the importance of understanding the response of mycorrhizal fungi to environmental changes (Chapter 5), as they are highly sensitive to temperature, precipitation, and other environmental factors. Figure 6.1 illustrates the essential research components necessary for a comprehensive understanding of impact of mycorrhizal fungi on soil carbon dynamics at a global scale. The specific components addressed in this thesis are delineated in the figure and linked to each respective chapter. In the upcoming section, I will delve into the key findings of the previous chapters, elaborating on how they enhance our comprehension of mycorrhizal ecology and their implications. Additionally, I will address future research directions that can lead to a more comprehensive understanding of mycorrhizal systems.

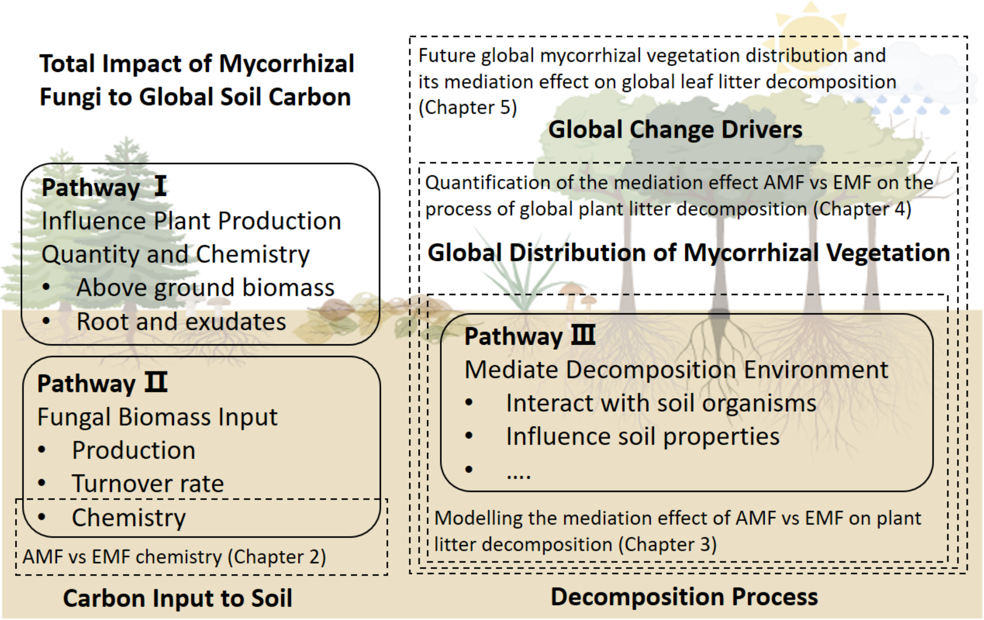

Figure 6.1 Diagram illustrating the essential research components necessary to comprehend the impact of mycorrhizal fungi on global soil carbon dynamics. Topics covered in this thesis are marked with dotted boxes.

6.1 Coupling experimental data into models

The importance of integrating experimental work into soil carbon models cannot be overstated. Experimental studies provide valuable insights into the mechanisms and processes that govern soil carbon dynamics, including leaf litter decomposition (Viskari *et al.*; Palosuo *et al.*, 2005; Järvenpää *et al.*, 2016). By incorporating experimental data into soil carbon models, we can improve the accuracy and reliability of the model predictions (Viskari *et al.*, 2020b). In the specific context of mycorrhizal impact on leaf litter decomposition, the integration of global litter decomposition data from field studies offers a comprehensive understanding of the complex interactions between mycorrhizal fungi, litter quality, and environmental factors (Chapter 3). Experimental studies provide empirical evidence of the responses of litter decomposition to varying conditions, including climate, vegetation types, and mycorrhizal associations. Such data provide crucial information for parameterizing and validating models, enhancing their ability to capture real-world processes. By comparing model predictions with experimental observations, we can assess the model's performance and identify potential areas for refinement.

Furthermore, integrating experimental work into soil carbon models allows for the exploration of specific mechanisms and feedback that may not be explicitly represented in the models. For instance, in the context of mycorrhizal impacts on leaf litter decomposition, experimental studies can elucidate the role of mycorrhizal fungi in nutrient cycling, microbial interactions, and organic matter transformations. In Chapter 3, those insights of mycorrhizal impact on litter decomposition were incorporated into models. Accounting for the different chemical compositions in litter of different mycorrhizal vegetation types enabled a more comprehensive representation of the complex processes governing litter decomposition and soil carbon dynamics. Overall, the integration of experimental work into soil carbon models bridges the gap between empirical observations and theoretical frameworks. It enhances our understanding of the underlying processes, and improves model predictions.

While soil carbon models have significantly progressed by incorporating mycorrhizal impacts, several important aspects of mycorrhiza functioning are still not captured such as root exudates, leaf litter chemical traits, and interactions with other soil organisms of mycorrhizal impact that should be explored:

(1) *Root exudates*. Mycorrhizal associations influence the composition and quantity of root exudates, which are organic compounds released by plant roots into the soil (Brzostek *et al.*, 2015; Keller *et al.*, 2021; Xu *et al.*, 2023). These exudates serve as energy sources for mycorrhizal fungi and influence nutrient uptake and microbial activity (Grayston *et al.*, 1997; Upadhyay *et al.*, 2022). Incorporating the dynamics of root exudation and its interactions with mycorrhizal fungi in models is crucial for accurately representing nutrient cycling processes. This can be done by gathering data on root exudation rates under different environmental conditions and plant species, encompassing the types and quantities of exudates produced. Existing data on mycorrhizal associations -including mycorrhizal types and their abundance- could be used to better integrate nutrient uptake and nutrient exchange under the influence of mycorrhizal fungi. Nutrient uptake can be made to depend on root exudation properties. Such properties may include variables that represent exudate production rates, their chemical composition, and how these rates vary with changing environmental factors (e.g., temperature, moisture, nutrient availability, mycorrhizal associations in the environment).

(2) *Leaf litter chemical traits affected by mycorrhiza*. Mycorrhizal fungi can alter the chemical composition of leaf litter through nutrient mobilization, enzymatic activities, and interactions with other microorganisms, hence affecting the

decomposition rates and nutrient release patterns of litter (Talbot & Treseder, 2012). In this research (Chapters 4 and 5), we assumed the same litter quality at the initial stage for our global litter decomposition analysis (i.e. using global mean leaf litter chemical composition). This assumption allowed focussing on the mediation effect of mycorrhiza on the litter decomposition process. However, models should also consider the influence of mycorrhizal associations on leaf litter chemical traits, such as lignin content, nutrient concentrations, and the availability of labile carbon sources. This could be improved in future research by considering the differences between AM and EM plant litter chemical compositions.

(3) *Interactions with other soil organisms.* Mycorrhizal fungi interact with a multitude of soil organisms, including bacteria, other fungi, and invertebrates, which can have cascading effects on nutrient cycling and carbon dynamics (Nuccio *et al.*, 2013; Gui *et al.*, 2017a). Integrating the complexity of these interactions, such as the influence of mycorrhizal associations on microbial communities and their functional diversity, is an important aspect yet to be fully captured by models. The approach presented in Chapter 3 to account for the impact of mycorrhizae on the litter decomposition process is a first attempt to approach these interactions. By including information on mycorrhizal guilds which regulate the microbial community, these interactions could be approximated and parameterised.

(4) *Mycelium chemistry*. Mycelium chemistry is among one of the most important missing aspects through which mycorrhizae contribute to the soil carbon content. Mycorrhizal fungi form extensive networks of hyphae known as mycelium, which play a crucial role in nutrient acquisition and carbon transfer (Godbold *et al.*, 2006; Fernandez *et al.*, 2016). Mycorrhizal mycelium represents a significant component of the belowground biomass in many ecosystems, as it grows and extends through the soil, and it adds to the overall biomass and carbon content of the soil (Wallander *et al.*, 2001; Högberg & Högberg, 2002). The carbon stored in mycelial biomass can become part of the soil organic carbon pool, contributing to soil carbon stocks. The chemical composition of mycelial biomass, including carbon-rich compounds such as chitin and proteins, can affect its decomposition rates, thus influencing the turnover of mycorrhizal biomass-derived carbon in the soil (Rygiewicz & Andersen, 1994; Langley & Hungate, 2003). However, the chemistry of mycelium, including its composition, enzyme activities, and interactions with organic matter, is often not explicitly considered in models. In Chapter 2, I examined the chemical composition of biomass from different types of mycorrhizae to investigate their direct impact on soil carbon. The results presented in Chapter 2 imply that differences in decomposability traits among mycorrhizal fungal guilds represent a critically

important driver of the soil C cycle, and appeals that understanding the chemical properties of mycelium is vital for accurately simulating nutrient cycling and carbon dynamics. I therefore recommend that future models take these differences into account.

So far, when it comes to modelling mycorrhizal biomass decomposition using current litter decomposition models, the models typically rely on leaf litter decomposition experimental data to train and parameterize the model (Tuomi *et al.*, 2009; Viskari *et al.*, 2020a). The decomposition models utilized in litter decomposition studies are typically parameterized using empirical observations from litter decomposition experiments and do not account for the differences in chemistry between leaf or root litter and mycelium. Therefore, current estimates of decomposition may not properly represent the differences in overall decomposition in different mycorrhizal environments (Figure 6.1).

Ideally, we would acquire experimental data from designated experiments that manipulate specific factors, such as mycelial chemistry, to parameterize their impacts on soil carbon dynamics. Moreover, long-term datasets are needed to assess the temporal variability of mycorrhizal impacts such as direct litter input to soil and their responses to environmental changes. However, such experimental data are challenging to attain due to the time and costs associated with acquiring such data, especially for the cultivation of mycorrhizal mycelium (Chapter 2).

There are several strategies that future mycorrhiza research can employ to better integrate experimental data into models. The first suggestion is to foster collaboration among researchers and encourage data-sharing initiatives (Waller *et al.*, 2018), for example, to establish partnerships between experimentalists and modellers to facilitate the exchange of data and expertise. By pooling resources and sharing data, the research community can collectively build a comprehensive dataset that can be used to parameterize and validate models. The traditional way to acquire mycorrhizal biomass for the assessment of its chemical composition used mycorrhizal samples collected from the field (Fogel & Hunt, 1983; Wallander *et al.*, 2002). Using this classical way to collect samples from the field might be an alternative to in vitro cultivation for mycelium. For example, targeted sampling campaigns specifically aimed at collecting mycorrhizal mycelium data could be designed to deal with important gaps in current data. It is crucial to identify key ecosystems or sites where mycorrhizal associations have a significant impact, and field sampling efforts should be strategically planned to collect mycelium samples and analyze their chemistry, focusing on these selected areas. This targeted approach allows researchers to optimize resources and efforts in obtaining essential mycelium data. To enhance the efficiency of studying mycorrhizal mycelium chemistry, the development and utilization of advanced analytical techniques are essential. Methods that enable rapid and cost-effective analysis of mycelium chemistry, such as spectroscopic techniques or molecular tools, should be explored and implemented. For example, the method of particle-induced x-ray emission (PIXE) combined with microscopic imaging methods has provided more accurate assessments of the chemical composition of individual mycorrhizal hyphae (Weiersbye *et al.*, 1999; Wallander *et al.*, 2002). These techniques can provide valuable data on mycelium chemistry without requiring extensive time and resources. By employing these strategies, future mycorrhiza research may overcome some of the challenges associated with acquiring mycelium chemistry data and enhance the integration of experimental data into soil carbon models.

6.2 Incorporating mechanisms of mycorrhizal impacts in soil carbon models

Incorporating mycorrhizal impacts through different pathways into soil carbon analysis is of great importance for a comprehensive understanding of soil carbon dynamics, and can help researchers gain a deeper mechanistic understanding of the processes governing soil carbon dynamics. Understanding the specific pathways through which mycorrhizae influence litter decomposition and soil carbon allows for the identification of key drivers and feedback mechanisms. This knowledge contributes to our broader understanding of ecosystem functioning and the factors that regulate carbon sequestration in soils, and provides valuable insights for identifying potential interventions or management strategies to enhance carbon storage in ecosystems. It also improves model representation, enhances parameterization, and helps to bridge knowledge gaps in soil carbon modelling. By considering the unique contributions of mycorrhizae, we can refine our predictions of soil carbon dynamics (Chapter 3), gain insights into ecosystem functioning, and inform sustainable land management practices (Leake *et al.*, 2004) aimed at promoting carbon sequestration and mitigating climate change. By considering the various pathways through which mycorrhizae influence soil carbon, we can gain a more accurate assessment of carbon sequestration potential (Soudzilovskaia *et al.*, 2015b) and better predict the response of ecosystems to environmental changes.

Despite the fact that several carbon models are already available, not all of them are suitable to incorporate a mycorrhizal component. There are several characteristics of an ideal model for incorporating mycorrhizal impacts. Below, I go over the requirements that such models should satisfy.

From the model structure point of view, the model needs to be mechanistic and integrate soil-based mechanisms with other essential drivers such as climate. A mechanistic model enables to capture of the specific mechanisms through which mycorrhizae influence plant carbon allocation, nutrient uptake, litter decomposition, and organic matter formation. The model should explicitly account for the different pathways through which mycorrhizae impact soil carbon dynamics. This includes considering the direct contributions of mycorrhizal fungi to the soil carbon pool through their fungal biomass (mycelia) (Chapter 2) and other effects via plant nutrient uptake, carbon allocation, litter input, litter decomposition (Chapter 3), and organic matter formation. Moreover, the model should consider the interactions and feedback between mycorrhizal associations and other factors that influence soil carbon dynamics such as temperature, precipitation, nutrient availability, and land management practices (Chapter 5).

The model should have sufficient spatial and temporal resolution to capture the spatial heterogeneity of mycorrhizal associations and their effects on soil carbon dynamics. The model in Chapter 3, for example, enables the representation of the variations in mycorrhizal fungal abundance, diversity, and functional traits across different ecosystems, vegetation types, and environmental conditions. Additionally, the model should be flexible and adaptable to different ecosystem types, vegetation composition, and management practices. The work presented in Chapter 4 enables the estimation of a diverse range of mycorrhizal associations in the global environment, such as AM- and EM-dominated ecosystems, and their specific functional traits.

Furthermore, the model should be parameterized and calibrated using empirical data to ensure accuracy and reliability. This entails incorporating specific measurements of mycorrhizal abundance, colonization rates, fungal traits, and their functional relationships with soil carbon dynamics. The parameterization process should be feasible and practical, considering the availability of data in different ecosystems. Then, ideally, the model should be validated against independent datasets and compared with other models and experimental studies. This validation and comparison help assess the model's performance and robustness (Chapter 3), ensuring that it accurately represents mycorrhizal impacts on soil carbon dynamics and provides reliable predictions.

Based on the abovementioned considerations, the Yasso soil carbon model (Viskari *et al.*; Liski *et al.*, 2005; Tuomi *et al.*, 2011b) was chosen for this research to incorporate mycorrhizal impacts for simulating and understanding soil carbon dynamics. Compared to other models, the Yasso model is relatively simple and easy to use, making it accessible to researchers and practitioners with varying levels of expertise. From the parameterization aspect, Yasso has been well-parameterized and validated using empirical data from various ecosystems, providing confidence in its ability to predict soil carbon dynamics which can be applied to different ecosystems and management scenarios, allowing for broad applicability (Liski *et al.*, 2005; Tuomi *et al.*, 2009, 2011a). On the other hand, the Yasso model is primarily focused on soil carbon dynamics and does not capture other aspects of ecosystem functioning or feedback with the atmosphere or vegetation.

Other models for example the CENTURY (Parton *et al.*, 1987) and RothC (Coleman & Jenkinson, 1996) which are widely used soil carbon model that simulates carbon dynamics in agricultural and forest ecosystems, offer a more comprehensive representation of soil carbon dynamics and can capture finer-scale processes. However, those models are more complex and require a substantial amount of input data, which can limit their applicability in data-scarce regions or when detailed data are not available. While Yasso may not be the simplest model in terms of the number of parameters, its key advantage lies in the fact that it primarily focuses on measurable carbon pools. These pools can be readily quantified in the field or through laboratory analysis. This makes Yasso more straightforward to apply in practice compared to models like CENTURY or RothC, which often require extensive data that may not always be readily available and require the user to choose parameter values to represent local situations. Yasso's reliance on measurable pools allows for data-driven parameterization instead. Researchers can use empirical data from specific ecosystems to fine-tune and validate the model, ensuring that it accurately represents local conditions. This reduces the risk of making predictions for the wrong reasons and enhances the model's reliability in different contexts. Its compatibility with databases of measurable carbon pools is another advantage. These databases, compiled from a wide range of sources and ecosystems, provide a rich resource for parameterization. Leveraging existing data not only saves time but also enhances the model's predictive power by drawing on a wealth of information. Also, the Millennial model takes a more mechanistic approach by incorporating a wider range of measurable carbon pools and processes of soil carbon dynamics (Abramoff *et al.*, 2018). However, its increased complexity makes it more challenging to parameterize, particularly when detailed data are scarce, and it demands more computational resources and time compared to Yasso. Acquiring such data for model input can be time-consuming and costly, making its application more limited in areas where comprehensive data are lacking. This complexity can be advantageous for detailed, process-based studies but may require more data and expertise to implement effectively for large-scale studies. Yasso provides a relatively straightforward representation of soil carbon dynamics, making it accessible for a wide range of users, including those with limited data.

6.3 Mycorrhizae as mediators of soil carbon decomposition process

In Chapter 3, the mycorrhizal mediation effect on soil carbon decomposition was examined using a proxy representing the mycorrhizal impact in the decomposition environment. We modelled the impacts of the mycorrhizal environment on plant litter decomposition as the sum of impacts caused by the predominance of AM and EM fungal types. The AM and EM fungal impacts were assumed to depend on the fungal-type-specific ability to affect the litter decomposition process and litter biomass. We assume this proxy represents intimate interactions between mycorrhiza and the decomposer microbes and the production of enzymes by the decomposer that facilitate the decomposition processes. This mediation effect can lead to either an acceleration or a deceleration of litter decomposition, depending on the specific mycorrhizal types in the environment and the chemical characteristics of the litter. This modelled mediation effect is based on the finding that some mycorrhizal associations produce enzymes that enhance litter decomposition (Courty *et al.*, 2007; Talbot *et al.*, 2008), while others may inhibit decomposition through other mechanisms such as influencing soil characteristics (Rillig & Steinberg, 2002; Smith & Smith, 2011; Morris *et al.*, 2019). Using a modelling approach, we were able to quantify those contrasting effects of mycorrhizal associations on litter decomposition and soil carbon as mediators at a global level in Chapter 4.

The findings reveal that the mycorrhizal type of the dominant vegetation plays a central role in shaping litter decomposition rates, generating mycorrhizal type-specific environments for decomposition. The recognition that mycorrhizal mediation significantly influences carbon cycling in ecosystems has far-reaching consequences. It suggests that models aiming to predict and manage soil carbon dynamics, especially in the context of climate change and land-use shifts, should incorporate the effect of mycorrhizal fungal mediation of decomposition process to better capture the complexity of carbon cycling processes. Furthermore, this research uniquely allows for the mathematical and mechanistic disentanglement of mycorrhizal impacts from other processes - a feat unattainable through traditional experimental methods or existing models. By quantifying the contributions of mycorrhizal associations to carbon cycling and elucidating their distinct mechanisms, our work provides crucial insights into the broader context of ecosystem functioning and the management of global carbon budgets. Other models can learn from this research by recognizing the importance of accounting for mycorrhizal associations in carbon models. They can incorporate mycorrhizal impacts by collecting data on specific mycorrhizal types in various ecosystems, their interactions with plant species, and their effects on litter decomposition rates. By doing so, models can provide more accurate representations of carbon dynamics, reduce uncertainties in global carbon budgets, and offer critical insights into the consequences of land-use changes and climate shifts on ecosystem functioning.

The mediation effect is only one out of the three pathways through which mycorrhiza may affect litter decomposition (Figure 1.2-d). The other two pathways include altering plant litter input (Figure 1.2-b) and the input of fungal biomass directly contributes to the soil carbon pool as carbon input (Figure 1.2-c). Ultimately, the net impact of mycorrhizae on litter decomposition and soil carbon dynamics will depend on the relative strengths and interactions of each of these pathways. In some cases, the pathways may reinforce each other, leading to a synergistic effect on decomposition rates and soil carbon turnover (Soudzilovskaia *et al.*, 2015b) (Figure 1.2-a). For example, mycorrhizae may enhance both litter production and decomposition rates, resulting in increased carbon turnover in the soil. In other cases, the pathways may cancel each other out, resulting in a net neutral effect. The specific outcome will be influenced by factors such as the composition of mycorrhizal communities, the characteristics of the litter, nutrient availability, and environmental conditions. It is important to note that the net impact of mycorrhizae on litter decomposition and soil carbon is complex and context-dependent. It may vary across ecosystems, plant communities, mycorrhizal types, and environmental conditions. Further research, including experimental studies and modelling approaches, is needed to elucidate the relative importance and interactions of these pathways and their net effect on litter decomposition and soil carbon dynamics in different ecological contexts.

Several key elements need to be considered for incorporating all three pathways through which mycorrhizal associations can influence soil carbon dynamics into a model like Yasso. Besides the mechanisms that describe how mycorrhizal associations mediate the decomposition of plant litter as presented in Chapter 2, the model should account for the influence of mycorrhizal fungi on plant litter input into the soil (Figure 1.2-b). This includes data on the types and quantities of litter produced by mycorrhizal-associated plants and how this input varies under different environmental conditions. Additionally, the model should incorporate information on how mycorrhizal fungi may modify litter chemistry, potentially making it more recalcitrant or labile. To represent the direct contribution of mycorrhizal fungi to the soil carbon pool (Figure 1.2-c), the model must incorporate factors related to fungal biomass production, turnover rates, and carbon allocation. This should include processes related to mycorrhizal mycelium, as it plays a significant role in carbon input and stabilization in soils. Accurate data on mycorrhizal fungal growth, resource allocation, and carbon sequestration potential are essential for this pathway. Incorporating all three pathways is essential for a comprehensive representation of mycorrhizal impacts on soil carbon dynamics in models. Understanding how mycorrhizal associations influence plant litter input, soil carbon decomposition processes and its biomass, allows for more accurate predictions of carbon cycling in ecosystems (Figure 6.1). Moreover, it will aid in assessing the potential effects of environmental changes, such as shifts in plant-mycorrhizal associations, on soil carbon storage and stability, which are critical considerations in the context of global carbon cycling and climate change mitigation.

6.4 The relative importance of climate vs. mycorrhiza to soil carbon decomposition

Currently, soil carbon models implicitly account for mycorrhizal impacts. For instance, models typically incorporate factors such as plant productivity and litter inputs, which are influenced by mycorrhizal associations. However, the specific mechanisms and pathways through which mycorrhizae influence soil carbon dynamics are not explicitly incorporated into most models. This implicit representation may lead to uncertainties and limitations in accurately capturing the full extent of mycorrhizal impacts (Shi *et al.*, 2019) and in differentiating the effects of climate from those of mycorrhizae.

The relative importance of climate versus mycorrhizal and other drivers in soil carbon modelling work is a complex issue. Climate factors, such as temperature and precipitation, are widely recognized as key drivers of soil carbon dynamics (Davidson & Janssens, 2006; Stockmann *et al.*, 2013). They influence factors like litter decomposition rates (Boyero *et al.*, 2011), microbial activity (García-Palacios *et al.*, 2013), and plant productivity (Nemani *et al.*, 2003) which subsequently affect soil carbon storage. Each of those factors is thus typically included as an important input in soil carbon models (Coleman & Jenkinson, 1996; Tuomi *et al.*, 2011b; Abramoff *et al.*, 2018). However, direct mycorrhizal impacts on soil carbon dynamics should not be overlooked, as they can be substantial (Averill *et al.*, 2014; Soudzilovskaia *et al.*, 2019). Mycorrhizae influence plant nutrient uptake, carbon allocation, litter quality, and microbial activities, all of which can have significant effects on soil carbon storage.

The relative importance of climate versus mycorrhizal and other drivers in soil carbon dynamics is context-dependent and can vary across ecosystems and temporal scales. Climate variables, as evidenced by studies (Davidson & Janssens, 2006; Reichstein *et al.*, 2013), play a dominant role in driving the overall variability in soil carbon dynamics, particularly in extreme environments or regions with high climate sensitivity. In other cases, the presence and activity of microbes including mycorrhizal fungi may play a more significant role, especially in nutrient-limited ecosystems or those with strong mycorrhizal-plant interactions (Smith & Read, 2008; Bardgett & van der Putten, 2014; Smith & Wan, 2019). However, it is important to recognize that climate and microbial impacts are tightly correlated, as climate directly influences microbial activity and nutrient availability in the soil (Allison & Treseder, 2008; de Vries *et al.*, 2012; Buckeridge *et al.*, 2013). Therefore, incorporating mycorrhizal effects explicitly in soil carbon models is crucial to improving the accuracy and comprehensiveness of predictions, considering the interplay between climate and microbial impacts.

The modelling work and applications presented in Chapters 3-5 significantly contribute to our understanding of the complex interplay between climate change, mycorrhizal-vegetation distribution, and soil carbon dynamics. Chapter 3 introduces the Yasso-Myco model that effectively separates the impacts of mycorrhizae from climate factors. It explicitly quantifies the impacts of mycorrhizae on the decomposition environment, distinct from the influences of climatic factors, overcoming the challenge of tight correlations between global climate patterns and mycorrhizal vegetation distribution. By comprehensively representing mycorrhizal impacts on litter decomposition, this model improves long-term predictions of decomposition dynamics. This lays the foundation for understanding the specific contributions of mycorrhizal associations to soil carbon dynamics and provides a framework for further investigations. In the original Yasso model, soil carbon pools were controlled by litter quality and climate, with climate encompassing global variations in environmental conditions. Although the original model exhibited high predictive power, particularly for short-term decomposition processes, it lacked a comprehensive consideration of microbial factors and oversimplified the role of climate, limiting the examination of future climate-induced changes in soil carbon dynamics (Pongratz *et al.*, 2018). This simplified representation of belowground processes is recognized as a significant source of uncertainty in the quantification of global terrestrial biogeochemical cycles (Trumbore, 2006; Todd-Brown *et al.*, 2013; Nyawira *et al.*, 2016; Pongratz *et al.*, 2018). Recent efforts, such as the CORPSE (Sulman et al., 2014), MIMICS (Wieder *et al.*, 2015), and Millennial (Abramoff *et al.*, 2018) models, have aimed to incorporate microbial impacts for improved representation of soil processes. Our study contributes to this growing endeavour by enabling the quantification of mycorrhizal impacts on litter decomposition processes and topsoil carbon dynamics, bridging a critical gap in modelling efforts. Compared to the original Yasso15 model, the Yasso-Myco model demonstrates reduced sensitivity to temperature variations, suggesting that previous global modelling attempts may have overestimated the influence of temperature on decomposition by neglecting mycorrhizae as a driving factor.

The work in Chapter 4 reveals that, when under the same climate condition in each type of ecosystem, the variability in plant litter decomposition rate is controlled by the mycorrhizal type of dominant vegetation which creates mycorrhizal type-specific decomposition environments. This global estimation sheds light on the effects of mycorrhizal-vegetation interactions on labile and recalcitrant soil carbon compounds, reducing uncertainties in global carbon budgets. Chapter 5 explores changes in mycorrhizal vegetation distribution under future environmental change and quantifies their impact on leaf litter decomposition. By considering the complex interplay between climate change, mycorrhizal-vegetation distribution, and soil carbon dynamics, this study provides insights into the cascading effects on nutrient cycling and carbon sequestration. By unravelling these complex relationships, the research in these chapters advances our capacity to forecast and control soil carbon dynamics amidst shifting environmental conditions. This enhanced understanding is pivotal for formulating strategies aimed at mitigating the adverse impacts of climate change on ecosystems. Ultimately, it aids in the development of evidence-based strategies for optimizing carbon sequestration, which is vital in our global efforts to combat climate change and preserve the stability of natural ecosystems.

Several areas for future research can contribute to improving soil carbon models by incorporating mycorrhizal impacts. One major focus should be to accurately quantify mycorrhizal abundance and diversity in different ecosystems. This includes developing standardized methods for assessing mycorrhizal colonization rates (Soudzilovskaia *et al.*, 2015a; Barceló *et al.*, 2023), measuring fungal biomass (Barceló *et al.*, 2020), and characterizing the functional traits of mycorrhizal fungi (Fernandez & Kennedy, 2015; Soudzilovskaia *et al.*, 2019, 2020). Incorporating this information into models can enhance their ability to capture the variability and importance of mycorrhizal impacts on soil carbon dynamics. Moreover, integrating mycorrhizal impacts into existing soil carbon models and comparing their performance with other models is a valuable research direction. Chapter 3 provided an example of integrating mycorhizal impact into the soil model carbon model Yasso. Model intercomparison studies can help to identify the strengths and weaknesses of Yasso-Myco compared to different modelling approaches and provide insights into the uncertainties associated with incorporating mycorrhizal impacts. This research can lead to the development of more robust and reliable models for predicting soil carbon dynamics considering mycorrhizal associations. Furthermore, taking Yasso as an example, current model versions normally use specific computer languages, e.g. python or R (Tuomi *et al.*, 2009; Viskari *et al.*, 2020b). Consequently, they are mostly suitable for researchers with certain knowledge and expertise backgrounds. A user-friendly interface of the model that provides clear outputs and visualization tools can better facilitate understanding and decision-making. This allows the model for a wider range of applications and will help not only researchers but also other people including land managers, and policymakers to easily input data, run simulations, and interpret results.

6.5 Social implications and conclusions

This research contributes to our understanding of mycorrhizal ecology and its role in soil carbon cycling. It addresses key knowledge gaps by investigating the chemical composition of mycorrhizal fungi, integrating mycorrhizal mechanisms into models, estimating global mycorrhizal impacts, and exploring the implications of climate change vs. mycorrhizal impacts. By doing so, it enhances our understanding of the complex interactions between mycorrhizal associations, plant-microbial interactions, and soil carbon dynamics. These findings have wide-ranging implications, including improving soil carbon models, reducing uncertainties in global carbon budgets, and informing ecosystem management strategies in the context of global land use and climate change. Overall, this research advances our knowledge of mycorrhizal ecology and its relevance for understanding ecosystem functioning.

One key outcome of this research is the development of a mechanistic model that incorporates mycorrhizal impacts on plant litter decomposition. This model represents a significant improvement over existing soil carbon models by providing a more accurate and predictive estimation of long-term carbon dynamics. By explicitly considering the influence of mycorrhizal associations, the model reduces uncertainties and enhances our understanding of the specific ways in which mycorrhizae influence soil carbon dynamics, including litter decomposition and carbon sequestration. Moreover, the research emphasizes the importance of accounting for the mycorrhizal type of dominant vegetation in estimating global plant litter decomposition rates. This insight can guide future modelling efforts and help identify environments where mycorrhizal impacts on carbon cycling are particularly significant.

The examination of changes in mycorrhizal vegetation distribution under future environmental change provides insights into the potential impacts of climate change on ecosystem functioning. This information can aid in predicting the response of terrestrial ecosystems to global environmental change and assist in the development of effective management strategies for mitigating climate change. The findings can also contribute to our understanding of the complex interplay between climate change, mycorrhizal vegetation distribution, and soil carbon dynamics. This understanding can inform policy and management decisions related to carbon cycling and carbon sequestration strategies, helping to develop more effective approaches for mitigating climate change and preserving ecosystem functioning.

In all, this research sheds light on the crucial role of mycorrhizal fungi in soil carbon cycling and their influence on the litter decomposition process. It paves the way for further investigations into the broader impacts of mycorrhizae on the carbon cycle and their interactions with other drivers of soil carbon dynamics. It also provides valuable insights for both future research endeavours and policy and management decisions aimed at addressing climate change and enhancing carbon sequestration strategies.