Global distribution patterns of mycorrhizal associations: abundance, environmental drivers and ecological impacts

Barcelo, M.

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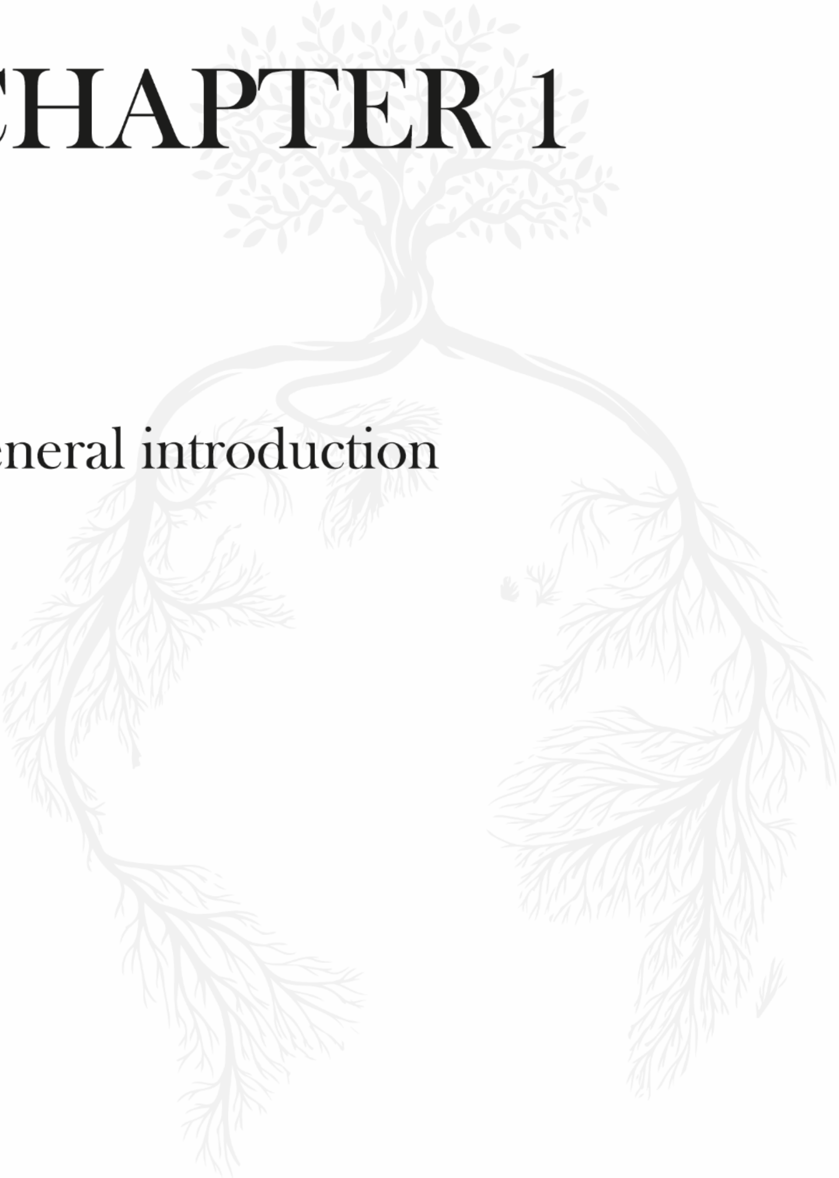
CHAPTER 1

General introduction



1.1. General Background

Mycorrhizas are symbiotic associations between soil fungi and plants. In this generally mutualistic relationship (although it can turn parasitic under certain environmental conditions (Johnson et al. 1997)), the host plant supplies photosynthetically derived carbon (C) compounds to the root-associated mycorrhizal fungi. In exchange, fungi provide soil-derived mineral nutrients (mainly phosphorus (P) and nitrogen (N)) and improve plant resistance against pathogens and environmental stress (Smith and Read 2008). Mycorrhizal fungi form associations with over 90% of the terrestrial plant species from all major lineages (except for mosses) (Wang and Qiu 2006, Pressel et al. 2014), making mycorrhizas one of the most widespread and ecologically relevant symbiotic associations on earth.

According to differences in morphology and the identity of the partners, four major types of mycorrhizas have been described: arbuscular mycorrhiza, ectomycorrhiza, ericoid mycorrhiza and orchid mycorrhiza (Brundrett and Tedersoo 2018). Among these types, arbuscular mycorrhiza (AM), ectomycorrhiza (EcM) and ericoid mycorrhiza (ErM) are the most taxonomically and geographically widespread (Brundrett 2009), being present in approximately 80% of the Earth's plant species. The majority of these plant species can form associations with only one mycorrhizal (Brundrett and Tedersoo 2018, Soudzilovskaia et al. 2020), with only a few exceptions in which the same plant species can be colonized simultaneously by AM and EcM (Brundrett and Tedersoo 2018)

Arbuscular mycorrhiza, ectomycorrhiza and ericoid mycorrhiza differ significantly in anatomy, evolutionary history and functioning (Smith and Read 2008, Brundrett and Tedersoo 2018) (Figure 1.1). The AM association is the most ancient mycorrhizal type, formed by 71% of plant species including most families of vascular plants (Brundrett and Tedersoo 2018) and fungal members of the Glomeromycota phylum (Tedersoo et al. 2018). The AM fungal development is characterized by the formation of tree-like intracellular structures called “arbuscules” that expand within cortical cells of the colonized plant (Smith and Read 2008). Arbuscules are the main structures responsible for nutrient exchange between fungal and plant partners. The EcM type is present in only 2% of the plant species but within geographically widespread and dominant families such as Pinaceae, Fagaceae, Dipterocarpaceae, Myrtaceae, and Salicaceae (Smith and Read 2008). The EcM fungal partners belong to distantly-related lineages in the phyla Ascomycota and Basidiomycota. Unlike AM, EcM fungi do not penetrate the plant cells but form a hyphal mantle that envelops the plant root tips. From the mantle, fungi grow as the hyphae that surround epidermal or cortical cells, forming the so-called "Hartig net", where the nutrient exchange takes place. The ErM association occurs between plants of the family Ericaceae and a diverse group of fungi mostly from the Ascomycota phylum. ErM fungi penetrate the plant root cells forming coils, an intracellular hyphal complex controlling nutrients exchange.

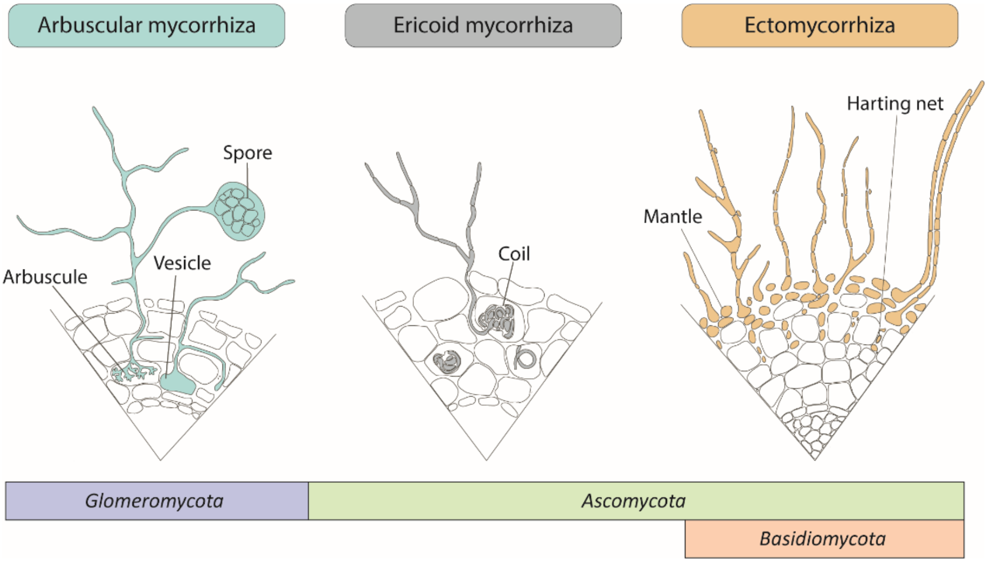


Figure 1.1: *Transversal cross-section of plant roots showing the characteristic structures of arbuscular mycorrhizal, ericoid mycorrhizal and ectomycorrhizal fungal colonization. The squares on the bottom indicate the fungal phyla that associate with each mycorrhizal type.*

1.1.1. Mycorrhizal impact on soil processes

Since mycorrhizas have been first described more than a century ago (Frank and Trappe 2005), soil biologists have focused on understanding the physiological mechanisms and the partners involved in the mycorrhizal symbiosis and its meaning for plant productivity and fitness (Marschner and Dell 1994). However, in the last decades, it has been recognized that mycorrhizal associations also play a key role in terrestrial ecosystem functioning.

Mycorrhizas can have a large impact on seedling establishment (Van Der Heijden and Horton 2009), resistance to drought (Augé 2001), heavy metals diseases, pathogens and stress (Newsham et al. 1995) and plant community composition and structure. For instance, nutrient acquisition via the mycorrhizal pathway can modify plant resource partitioning and enhance resource sharing via common mycorrhizal networks, affecting plant competitive coexistence (Bever et al. 2010).

The impacts of mycorrhizas on carbon (C) and nutrient cycling have gained more attention in the last decades. Mycorrhizal mediation of soil biogeochemical cycles involves multiple and complex pathways:

1. Mycorrhizal physicochemical weathering can directly alleviate soil micronutrient limitations. Fungal hyphae penetrate rock cracks and voids, producing enough mechanical forces to widen these fissures (Howard et al. 1991). This physical force increases the mineral area exposed to soil dissolution. Also, mycorrhizal fungi release organic acids into the soil accelerating the chemical weathering of mineral-bound micronutrients (Gadd 2007). However, most of the research on this subject has been conducted under laboratory conditions and it remains unclear whether mycorrhizal-induced weathering is relevant at the ecosystem scale (Smits and Wallander 2017).

2. Mycorrhizal fungi redistribute recently fixed C from the plant partners to the soil rhizosphere (Nottingham et al. 2013, Fernandez et al. 2016) by growing extraradical mycelium and releasing extracellular products (Schrey et al. 2015). Mycorrhizal hyphae surround soil particles, forming and stabilizing soil aggregates. The exudation of hydrophobic mycelia products acts as a binding agent, stimulating the formation of mineral–organic complexes (Rillig 2004, Leifheit et al. 2013). This mycorrhizal-mediated formation and stabilization of soil structures prevents soil erosion, and nutrient losses via leaching and protects soil organic

matter (SOM) from decomposition, which in turn, enhances C storage (Rillig and Mummey 2006).

3. After hyphal senescence, mycorrhizal fungal residues constitute a large fraction of soil microbial necromass (Leake et al. 2004, Ekblad et al. 2013, Fernandez et al. 2016). Due to its generally rapid turnover (Finlay and Clemmensen 2017), mycorrhizal necromass decomposition represents a significant flux of C and nutrients to the soil (Godbold et al. 2006). These mycorrhizal fungal materials are key components of the soil food web, feeding a wide variety of soil microorganisms such as pathogenic and saprotrophic fungi, bacteria, collembola or mites (Rousseau et al. 1996, Scheu and Folger 2004, Schneider et al. 2005, Fernandez et al. 2016), whose necromass subsequently becomes part of the SOM pool. Moreover, mycorrhizal fungal residues fixed to the mineral soil matrix have recently been recognized as playing an important role in the formation of microbially derived stable SOM pools (Wallander et al. 2011, Clemmensen et al. 2013), making mycorrhizal fungi residues particularly significant to soil C storage.

4. Another key mechanism through which mycorrhizal fungi are involved in C and nutrient cycling is their interaction with saprotrophic microbes that can result in positive or negative impacts on SOM decomposition. The release of high energy and labile products by mycorrhizal fungi accelerates saprotrophic microbial growth (Verbruggen et al. 2017), which in turn increases decomposition rates of SOM (i.e. mycorrhizal priming). The potential relevance of mycorrhizal priming effects on soil decomposition is strongly affected by soil mineral nutrient levels. Root exudates have been generally reported to have a significantly higher influence on microbial priming than mycorrhizal fungi (Shahzad et al. 2015). However, in nutrient-rich soil patches, C flows more directly from mycorrhizal fungi to decomposers than to roots, which enhances mycorrhizal role in priming decomposition (Cheng et al. 2012, Nuccio et al. 2013). On the other hand, when the growth of microbial saprotrophs is limited by low concentrations of mineral nutrients, the release of labile C by mycorrhizal fungi does not fuel microbial growth and, consequently, SOM mineralization is not boosted (Zhang et al. 2016). Soil mineral nutrient limitation can be even stimulated by mycorrhizal fungi as the

nutrient flow from fungal hyphae to the plant host reduces N and P from colonized soil patches (George et al. 1995) and causes starvation of saprotrophic microbes. This may lead to a suppression of SOM decomposition rates and ultimately to greater C sequestration in the soil. This negative interaction between mycorrhizal fungi and soil saprotrophs is known as the “Gadgil effect” (Gadgil and Gadgil 1971, Fernandez and Kennedy 2015).

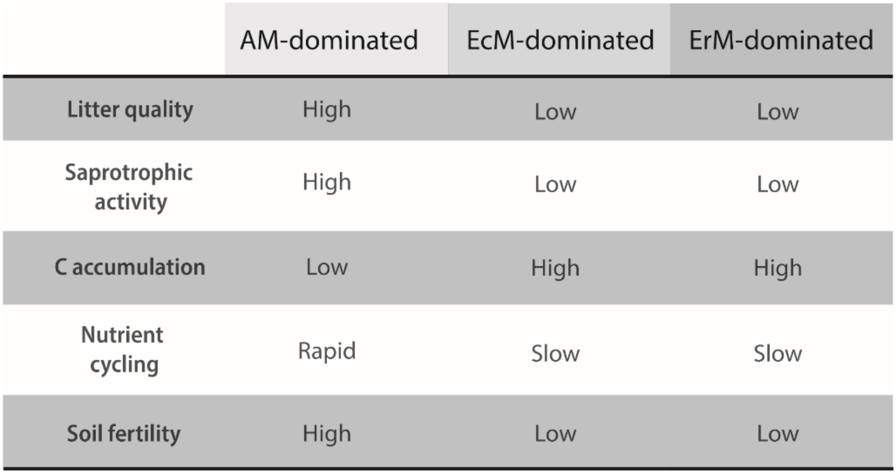
1.1.2. Differential effects of mycorrhizal types

The consequences of mycorrhizal mediation on SOM transformation processes highly depend on the dominant mycorrhizal type. This is due to the significant differences in the morphological and physiological characteristics and nutrient uptake strategies of the fungal partners (Clemmensen et al., 2015; Averill, 2016; Averill & Hawkes, 2016). The saprotrophic abilities of AM are poorly developed and rely mostly on inorganic compounds as a source of nutrients (Smith & Smith, 2011), facilitating mainly P to the plant partner. In contrast, EcM and ErM fungi are capable of breaking down organic matter through the expression of extracellular lytic enzymes (Talbot et al., 2008; Clemmensen et al., 2013; Averill & Hawkes, 2016). In the context of inorganic nutrient limitation, the greater access of EcM and ErM fungi to organic compounds can promote plant productivity by increasing N uptake, resulting in an increased C input to the soil (Orwin et al. 2011). Also, the EcM fungi removal of organic N has been shown to increase litter and soil C:N ratios (Orwin et al. 2011). Moreover, greater access to SOM makes EcM fungi compete more effectively with free-living decomposers for soil nutrients than AM fungi, and therefore Gadgil effects are more commonly reported in EcM systems (Fernandez and Kennedy 2015). Finally, EcM fungi require more C from their plant partners and have higher standing extraradical mycelium biomass and lower turnover rates than AM (Godbold et al. 2006, Ekblad et al. 2013), which results in higher inputs and longer residence time of necromass.

Finally, plants associated with distinct mycorrhizal types have been traditionally seen as possessing contrasting functional traits related to C cycling (although recent research confronts this view (Koele et al. 2012, Keller and Phillips 2019)). Plant species forming

ErM and EcM associations have been suggested to produce more recalcitrant litter and slower decay rates than plant species forming AM associations (Cornelissen et al. 2001, Hobbie 2006, Phillips et al. 2013, Midgley et al. 2015), promoting rapid C and nutrient turnover rates.

The above-mentioned specific mycorrhizal fungal and plant traits have led to the hypothesis that ecosystems dominated by EcM and ErM promote different biogeochemical syndromes than those dominated by AM (Phillips et al., 2013) (Figure 1.2). According to this hypothesis, EcM and ErM-dominated ecosystems tend to have lower SOM quality, reduced activity of saprotrophs and bacteria (Taylor et al. 2016, Cheeke et al. 2017) and lower concentrations and transformation rates of inorganic nutrients (Phillips et al. 2013, Chen et al. 2018), resulting in lower N leaching and nitrification rates (Phillips et al. 2013, Midgley et al. 2015). These ecosystem properties have been proposed to ultimately lead to higher C sequestration in EcM and ErM systems (Orwin et al. 2011, Phillips et al. 2013, Soudzilovskaia et al. 2015).



	AM-dominated	EcM-dominated	ErM-dominated
Litter quality	High	Low	Low
Saprotrophic activity	High	Low	Low
C accumulation	Low	High	High
Nutrient cycling	Rapid	Slow	Slow
Soil fertility	High	Low	Low

Figure 1.2: *Summary of the proposed main biogeochemical properties of ecosystem dominated by arbuscular mycorrhizal and ectomycorrhizal vegetation.*

1.1.3. Distribution patterns of mycorrhizas

Plants of different mycorrhizal types are known to dominate in different geographical zones. Read (1991) was the first in proposing a qualitative distribution model, where mycorrhizal vegetation was distributed along a latitudinal and longitudinal gradient, coinciding with the earth's major biomes. Read's hypothesis was primarily based on the idea of a competitive advantage that specific mycorrhizal fungal traits provide to the plant host to colonize areas with beneficial edaphic and climatic conditions. According to this hypothesis, the strong capabilities of ErM fungi to mobilize nutrients from recalcitrant organic sources and their tolerance to stress make ErM plants proliferate in very acidic and nutrient-poor soils such as heathlands. EcM trees predominate in boreal and temperate ecosystems, where mineral nutrients are trapped in the topsoil organic layer. In this context, the release of lytic enzymes by EcM fungi enhances host plants' mineral nutrition and provides a competitive advantage against other mycorrhizal types. Finally, AM associations are dominant in the mineral soil of grasslands and tropical forests where higher temperatures fuel SOM decomposition, where P is the main limiting nutrient. In these ecosystems, the ability of AM fungi to exploit soil P makes AM associations dominant.

The original Read's model presents mycorrhizal types distribution as a consequence of different climatic-driven soil properties. However, the recognition of the fact that specific mycorrhizal plant and fungal traits actively modify soil biogeochemistry suggests that mycorrhizas reinforce pristine ecosystem properties through positive soil-plant feedbacks (Averill 2016, Lin et al. 2017, Craig et al. 2018, Tedersoo and Bahram 2019). Moreover, the impacts of human-induced environmental change might be mediated by the dominant mycorrhizal type (Mohan et al. 2014, Creamer et al. 2015). The acknowledgement that mycorrhizal associations play a key role in ecosystem functioning highlights the need of making a step forward in the understanding of mycorrhizal vegetation distribution.

In recent years, data on per-site plant species occurrences and abundances have been rapidly accumulating (e.g. Liang *et al.*, 2016; rapid development of the Global Biodiversity Information Facility (GBIF, http://www.gbif.org)). This allowed the creation of several quantitative maps of mycorrhizal plant species distribution at regional scales (Menzel et al. 2016, Swaty et al. 2016, Bueno et al. 2017, Jo et al. 2019) and maps of mycorrhizal vegetation biomass distribution at global scale (Soudzilovskaia et al. 2019, Steidinger et al. 2019).

To obtain a complete picture of the distribution of mycorrhizal types and their importance as a mutualistic association, understanding the spatial distribution of both plant and fungal partners and the level of intimacy between them is essential (Soudzilovskaia et al. 2015). From a fungal perspective, mycorrhizal abundance can be characterized by two parameters: 1) abundance of extraradical mycorrhizal fungal mycelium, and 2) abundance of mycorrhizal mycelium within plant roots. Despite its direct impact on ecosystem functioning (Rillig 2004), regional and global patterns of mycorrhizal fungal mycelium abundance in the soil are unknown. On the other hand, the abundance of mycorrhizal intraradical mycelium is commonly reported in mycorrhizal literature as the proportion of roots colonized by mycorrhizal fungi (Soudzilovskaia et al. 2020). While this metric is used as an indicator of the fungal implication on above-belowground processes (Treseder 2013), it fails to inform about the actual abundance of intraradical mycelium in ecosystems. This actual abundance will also depend on the root stock capable to form associations with a given mycorrhizal fungal type. Treseder & Cross (2006) made the only biome-level estimation of AM abundance within plant roots, but it lacks spatial resolution and is based on low-accuracy databases.

1.2. Challenges in mycorrhizal research

It is a generally accepted paradigm in mycorrhizal literature, that ecosystems dominated by different mycorrhizal associations differ in key aspects of soil ecosystem functioning (van der Heijden et al. 2015). However, most of the research on this matter has been conducted in temperate forests, while much less is known about the mycorrhiza-associated impacts on biogeochemical cycles in other biomes. Especially relevant is the case of tropical forests, where despite their ecological and economical relevance, mycorrhizal studies are scarce (Corrales et al. 2018). In addition, many studies assessing mycorrhizal type impacts on ecosystem processes are restricted to a small group of plant clades and frequently do not account for phylogenic relatedness (Koele et al., 2012), which can confound impacts related to differences in specific plant traits of the species studied with direct mycorrhizal-type effects. Finally, recent studies in temperate forests argued that, when deeper soils are taken into account, general mycorrhizal-type effects can be reversed, resulting in greater C accumulation in AM-dominated stands (Lin et al. 2017, Craig et al. 2018, Zhu et al. 2018). Therefore, whether the proportion of mycorrhizal trees is a useful proxy to predict biogeochemical syndromes across different biomes and environmental gradients remains controversial (Tedersoo and Bahram 2019).

The recognized importance of mycorrhizal associations to biogeochemical cycles raises the need of gaining a quantitative understanding of mycorrhizal global distribution. The information about the biomass of mycorrhizal vegetation and fungi across ecosystems is key to quantifying the global mycorrhizal impact on ecosystem functioning and to improving model predictions of C and nutrient fluxes under future environmental scenarios. Despite the recent progress in this field (Soudzilovskaia et al. 2019, Steidinger et al. 2019), the contribution of the different driving forces (e.g. dispersal, environmental factors, edaphic characteristics, evolution) to shaping the biogeography of different types of mycorrhizal vegetation across different biomass and growth forms is not well understood.

The majority of research aiming at disentangling the distribution and role of this symbiosis in ecosystems has been carried out focusing mainly on aboveground patterns. In contrast, knowledge about patterns of mycorrhizal abundance belowground is largely incomplete. Shifting the focus towards a belowground perspective is needed to gain a better understanding of mycorrhizal impacts on ecosystems and their response to global change. Obtaining data on the abundance of mycorrhizal mycelium in the soil matrix has been largely neglected by soil scientists and it remains a challenge mainly due to current methodological difficulties in measuring fungal mycelium biomass in the soil (Leake et al., 2004). On the other hand, gaining a better understanding of fine root stocks colonized by mycorrhizal fungi has become feasible due to the release of high-resolution maps of mycorrhizal vegetation (Soudzilovskaia et al. 2019), root biomass (Spawn et al. 2020) and large plant trait databases such as FRED (Iversen et al. 2017), TRY (Kattge et al. 2011) and FungalRoot (Soudzilovskaia et al. 2020).

We are still far from a complete understanding of the quantitative relationships in the abundance of the different mycorrhizal biomass compartments. Whether, at the plant community level, the mycorrhizal fungal biomass within the plant roots relates to the biomass that expands in the soil matrix is an open question. It has been assumed that C allocation from the host plant to the fungal partner will be proportionally distributed between the intraradical and extraradical mycelium biomass (Van Aarle et al. 2002, van Aarle and Olsson 2003). But, as different mycorrhizal fungal species differ in their root vs soil C allocation strategies (Hart and Reader 2002), the correlation between root and soil biomass at the ecosystem scale will depend on the balance of different C allocation traits of the mycorrhizal fungal community. Moreover, the relationship between below- and aboveground mycorrhizal abundance patterns is also unknown. Although, at the vegetation stand level, aboveground plant biomass and the biomass of fine roots have been correlated (Li et al. 2003, Finér et al. 2011), it is not clear whether higher host plant aboveground biomass translates into higher mycorrhizal fungal biomass in roots and soils. Answering these questions will provide relevant insights into the mechanisms of C distribution from the host plant to the fungal partners and will inform about the possibility of extrapolating measurements of mycorrhizal abundance to other compartments.

1.3. Aim and research questions

This thesis aims to gain a better understanding of the distribution patterns of distinct types of mycorrhizal interactions and to identify the specific ecosystem properties that are derived from these patterns. For this, I quantitatively explored the abundance patterns of both aboveground (host plants) and belowground (roots and soil) compartments of the main mycorrhizal associations (see Figure 1.3 for a conceptual scheme). Specifically, I addressed the following research questions:

1. What are the main environmental drivers explaining the global distribution of AM, EcM and ErM host plants? (Chapter 2).

2. Do biogeochemical properties differ between AM- and EcM-dominated tropical forests? (Chapter 3).

3. What are the global distribution patterns of AM and EcM fungal abundance in plant roots? (Chapter 4).

4. Is there any relationship between the biomass of AM fungi that develops inside (i.e intraradical mycelium) and outside (i.e extraradical mycelium) the plant roots at community scale? (Chapter 5).

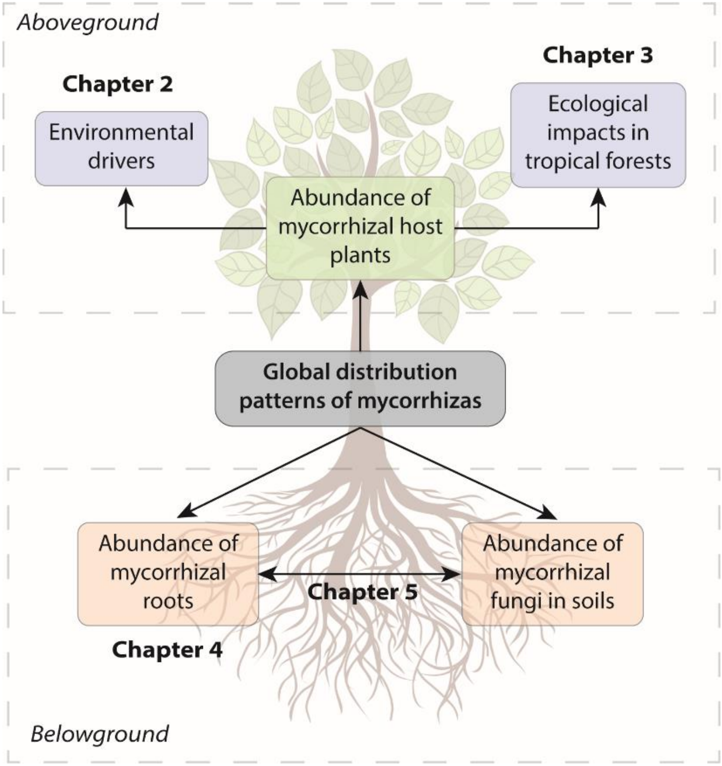


Figure 1.3: Conceptual scheme of the main chapter of the thesis.

1.4. Thesis outline

The thesis is organized in six chapters, as follows:

Chapter 1: General introduction

This chapter provides a general introduction to mycorrhizal ecology and mycorrhizal distribution patterns and identifies the major challenges and research gaps in this area. The aim of the thesis and the associated major research questions are also outlined in this chapter.

Chapter 2: Climate drives the spatial distribution of mycorrhizal host plants in terrestrial ecosystems

Understanding the link between the distribution of vegetation featuring different mycorrhizal types and environmental factors has become especially relevant for a better prediction of the ecosystem changes induced by human pressure and climatic change. This chapter aims to quantify the relative contribution of different climatic and edaphic factors in explaining the global distribution patterns of plants featuring AM, EcM and ErM mycorrhizal associations. It specifically tests the hypothesis that soil properties related to organic C content strongly influence global distribution patterns of mycorrhizas (Read 1991). The analysis is based on a gridded dataset that includes the relative abundance of distinct types of mycorrhizal vegetation (provided by Soudzilovskaia et al., 2019) and 39 different climatic and edaphic parameters.

Chapter 3: Mycorrhizal tree impacts on topsoil biogeochemical properties in tropical forests

This chapter advances our knowledge of the relationship between distinct mycorrhizal vegetation and environmental factors, focusing specifically on tropical forests. Given that these biomes have the biggest uncertainties in mycorrhizal distribution patterns and their effects on ecosystem functioning (Chapter 2), this chapter examines changes in biogeochemical proxies across a gradient from AM- to EcM-dominated tropical forests.

Chapter 4: Fine-resolution global maps of root biomass C colonized by AM and EcM fungi

Spatially explicit data on the distribution patterns of mycorrhizal abundance within plant roots is currently lacking at the global scale. This chapter provides the first high-resolution global raster maps on the fine root biomass colonized by AM and EcM fungi. To create these maps, I developed a workflow that combines multiple open-source databases of aboveground and belowground plant biomass, plot-level plant species abundance, plant traits and mycorrhizal intensity of colonization. The maps developed in this chapter serve as a basis for future examinations of mycorrhizal distribution and its environmental drivers, analysis of the influence of mycorrhizas on ecosystem processes, and the inclusion of mycorrhizal pathways on global biogeochemical models.

Chapter 5: The abundance of arbuscular mycorrhiza in soils is linked to the total length of roots colonized at ecosystem level.

Whether estimations of the mycorrhizal abundance within plant roots can be used as a proxy of mycorrhizal biomass in the soil has never been examined at ecosystem level, where different plant and fungal species coexist. In this chapter, I test the hypothesis that the total fine root length root colonized by AM fungi is correlated to extraradical AM mycelium biomass. The role of the AM fungal community composition and the different colonization strategies in the root vs soil biomass patterns was also examined.

Chapter 6: General discussion

This final chapter presents an integral analysis of the knowledge gained within my PhD dissertation. Final conclusions are drawn and future steps to advance our understanding of mycorrhizal ecology are also proposed.