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

Barcelo, M.

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GLOBAL DISTRIBUTION PATTERNS OF MYCORRHIZAL ASSOCIATIONS

Abundance, environmental drivers and ecological impacts

Milagros Barceló

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abundance, environmental drivers and ecological impacts

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

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POMOTOR

Prof. dr. P. M. van Bodegom

CO-PROMOTOR

Prof. dr. N. A. Soudzilovskaia

PROMOTIECOMMISSIE

Prof.dr. J.C. Biesmeijer

Prof.dr.ing. J.W. Erisman

Dr. S.E. Hannula

Prof.dr.ir. F.T. de Vries

Dr E. Verbruggen

To my mother

“Everything flows and nothing abides; everything gives way and nothing stays fixed.”

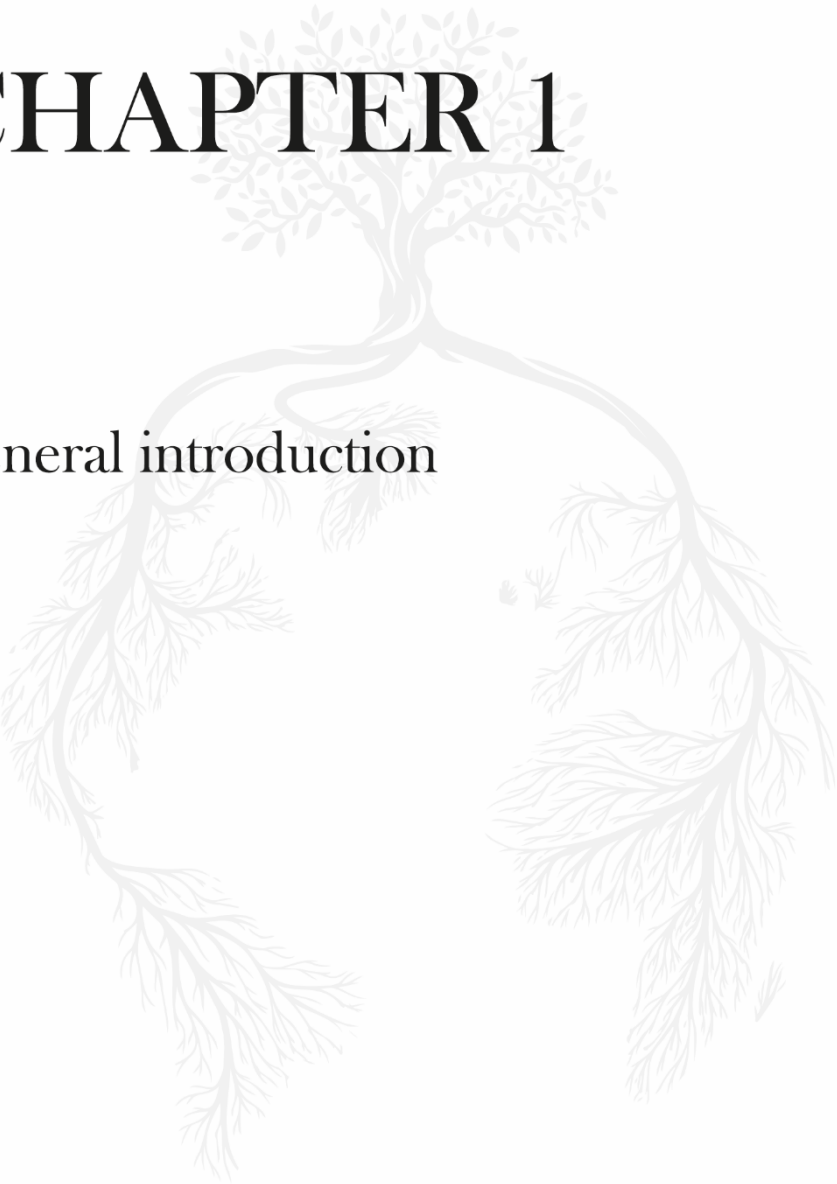
- Heraclitus -

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CHAPTER 1

General introduction



1.1. General Background

1 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.

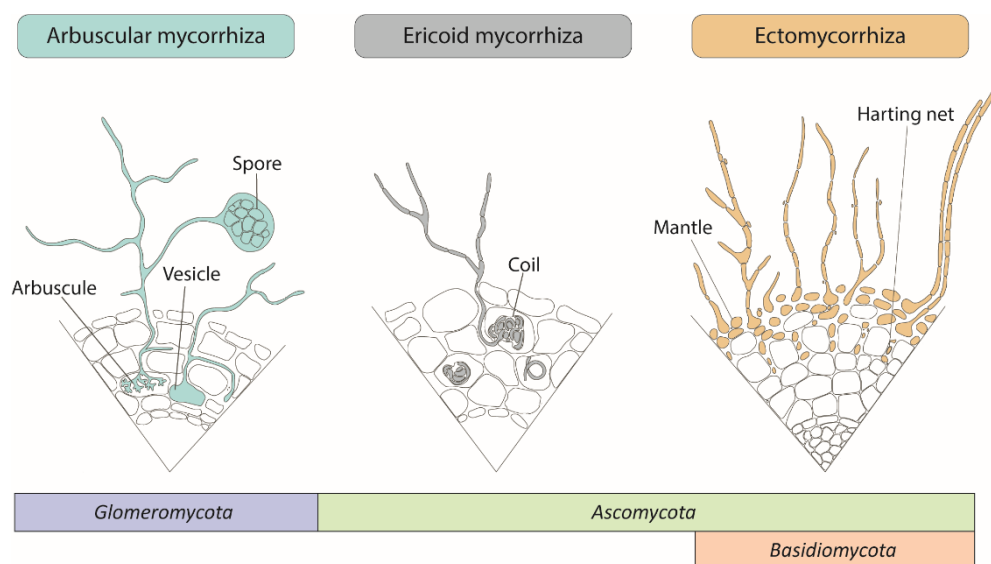


Figure 1.1: Transversal cross-section of plant roots showing the characteristic structures of arbuscular mycorrhizal, ericoid mycorrhizal and ectomycorrhizal fungal colonization. The squares on the bottom indicate the fungal phyla that associate with each mycorrhizal type.

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

1 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

1 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

1
small group of plant clades and frequently do not account for phylogenetic 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).

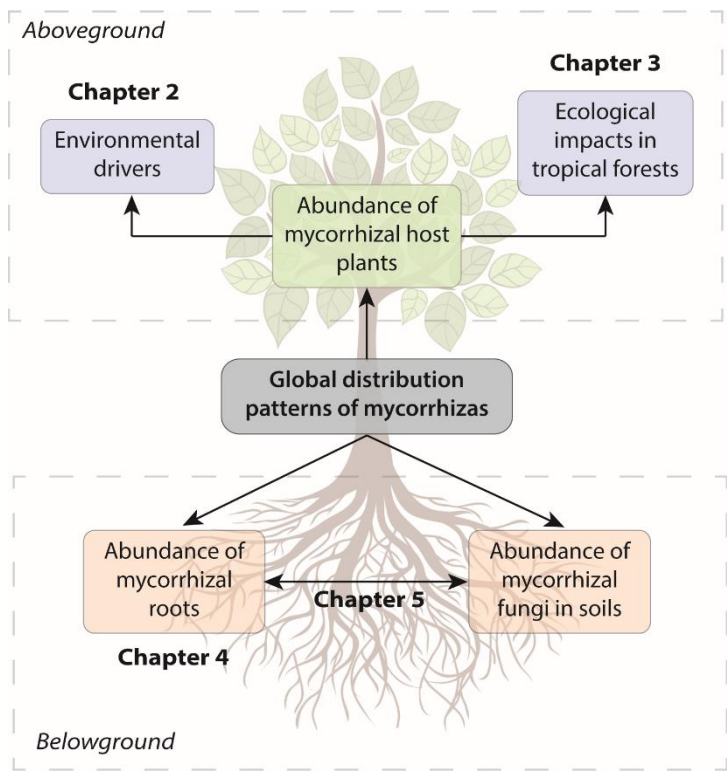


Figure 1.3: Conceptual scheme of the main chapter of the thesis.

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

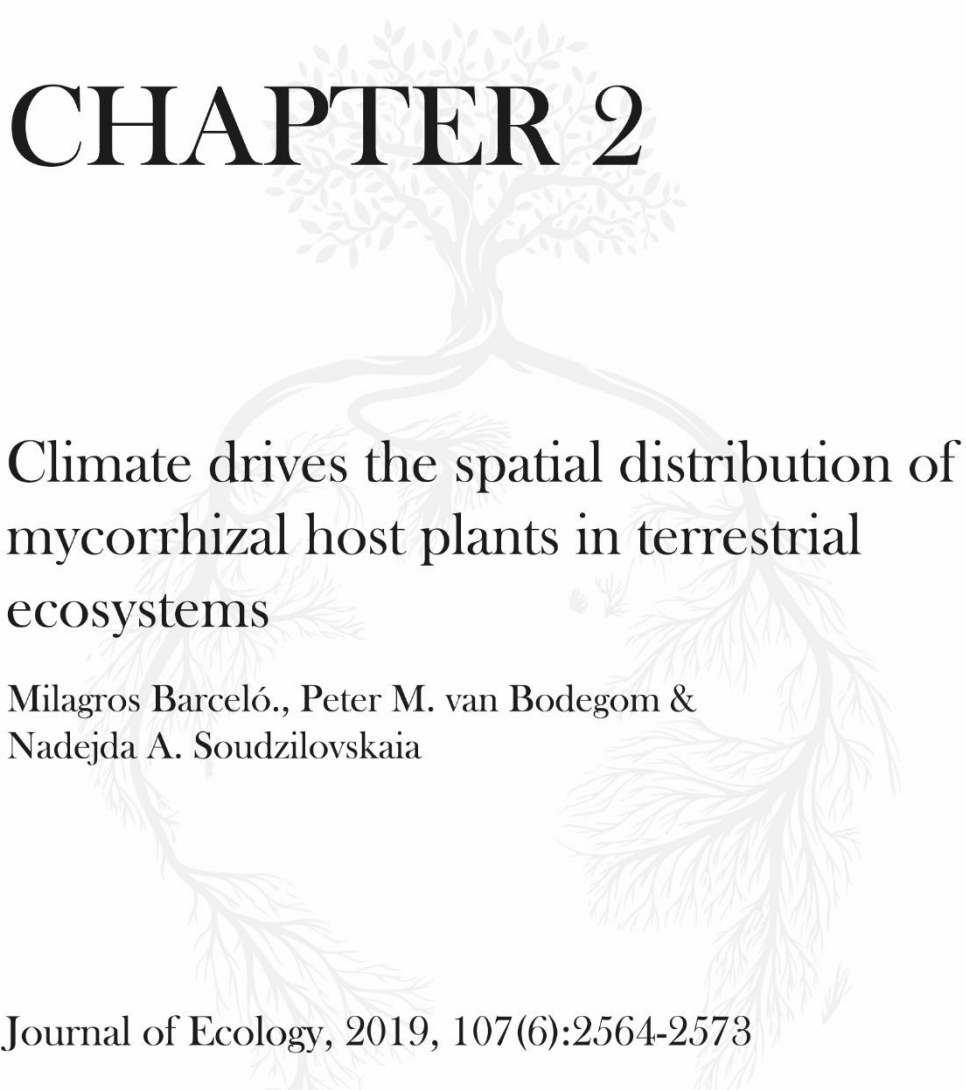
Spatially explicit data on the distribution patterns of mycorrhizal abundance within plant roots is currently lacking at the global scale. This chapter provides the first high-resolution global raster maps on the fine root biomass colonized by AM and EcM fungi. To create these maps, I developed a workflow 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.



CHAPTER 2

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

Milagros Barceló., Peter M. van Bodegom &
Nadejda A. Soudzilovskaia

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Abstract

1. Mycorrhizal associations have massive impacts on ecosystem functioning, but the mode and magnitude heavily depend on the mycorrhizal type involved. Different types of mycorrhizas are recognized to predominate under different environmental conditions. However, the respective importance of climate and soil characteristics in shaping mycorrhizal global distributions are still poorly understood.
2. We provide a quantitative and comprehensive global analysis of the main climatic and edaphic predictors of the distribution of plants featuring different mycorrhizal types. Estimates on per grid-cell relative aboveground biomass of plants holding arbuscular mycorrhiza (AM), ectomycorrhiza (EcM) and ericoid mycorrhiza (ErM) association were related to a set of 39 climatic and edaphic variables. We assessed their relationship by applying a Generalized Additive Models for Location, Scale and Shape (GAMLSS).
3. The best GAMLSS models were able to explain 55%, 41% and 46% of the variance in AM, EcM and ErM distribution, respectively. Temperature-related factors were the main predictors of distribution patterns for the three different mycorrhizal plant types. AM plants are favoured by warm climates, while EcM plants' dominance (and to some extents ErM plants too) is favoured by colder climates.
4. Synthesis: The observed lack of importance of soil drivers challenges the predominant view that mycorrhizal plants distribution mainly reflects soil type preferences – as related to its nutrient foraging strategies- of the different mycorrhizal types. Instead, our results highlight climate -and particularly temperature- as the main force shaping the distribution of AM, EcM and ErM host plants at the global scale and suggest that climate change can significantly alter the distribution of mycorrhizal host plants, with a subsequent impact on ecosystem functioning.

2.1. Introduction

Mycorrhizas are mutualistic associations between soil fungi and plants, where host plants receive mineral nutrients from fungi and, in exchange, fungi obtain photosynthetically derived carbon (C) compounds from plants (Smith and Read 2008). It is widely recognized that mycorrhizal associations play a key role in the functioning of terrestrial ecosystems, affecting plant community composition (Van der Heijden et al. 1998, Klironomos et al. 2011), soil formation and structure (Rillig and Mummey 2006, Leifheit et al. 2013), and C and nutrient cycles (Read 1991, Veresoglou et al. 2012, Phillips et al. 2013, Averill et al. 2014). However, the mode and magnitude of mycorrhizal impacts on ecosystem functioning are strongly related to the mycorrhizal type involved (Phillips et al. 2013, van der Heijden et al. 2015).

According to differences in morphology and plant and fungal taxa, seven major types of mycorrhizas are distinguished (Smith and Read 2008). Among these types, arbuscular mycorrhiza (AM), ectomycorrhiza (EcM) and ericoid mycorrhiza (ErM) are the most taxonomically and geographically widespread, being present in the majority of terrestrial biomes. It has been estimated that approximately 80% of the Earth's plant species form mycorrhizal associations with AM, EcM and ErM fungi (Brundrett and Tedersoo 2018). The majority of plant species is able to form mycorrhizal symbiosis of only one type (Wang and Qiu 2006), with only a few exceptions in which the same plant species can be colonized by two mycorrhizal fungi types (McGuire et al. 2008).

AM, EcM and ErM associations predominate under distinct edaphic and climatic conditions. This differentiation is presumed to be strongly associated to the different nutrient uptake strategies among AM, EcM and ErM fungi. For example, EcM and ErM fungi are capable of breaking down organic matter through the expression of extracellular lytic enzymes, making these associations more suitable for organic soils (Read et al. 2004). In contrast, AM saprotrophic abilities are less developed, causing AM to mostly rely on inorganic compounds as a source of nutrients, and therefore more prevalent in mineral soils (Smith and Smith 2011). Based on these insights, Read (1991) and Read and Perez-Moreno (2003) proposed a theoretical model where the

abundance of AM, EcM and ErM host plants gradually changes along a latitudinal and altitudinal gradient, driven mainly by the effects of climate on decomposition, which is ultimately reflected in the accumulation of organic C in the soil and the availability of nutrients for plants. According to this model, AM plants dominate in grasslands and tropical forests; EcM trees are abundant in temperate and boreal forests; and, finally, plants featuring ErM associations predominate in heathlands.

Since Read's first approach, only a few attempts have been made to understand quantitatively which environmental drivers explain the distribution of distinct types of mycorrhizal plants. Menzel et al. (2016) focused on AM and analysed the geographical distribution and environmental drivers of AM plants status (obligate, facultative or non-mycorrhizal) on a regional scale (Germany). Bueno et al. (2017) examined how the number of plant species featuring distinct mycorrhizal traits (type and status) varied with different climatic and soil factors at the European scale. Only recently, Steidinger et al. (2019) performed a coarse resolution (1 degree) global analysis on mycorrhizal trees distribution and its environmental drivers although focusing specifically on forest ecosystems. Despite these efforts, the contribution of the different driving forces (e.g. dispersal, climatic factors, edaphic characteristics or evolution) in shaping the biogeography of mycorrhizal vegetation of the entire plethora of plant functional types at global scale and covering all natural biomes and plant growth forms needs better understanding. Moreover, most of the previous studies were based on the number of plant species capable of forming different mycorrhizal associations, without taking the relative abundance of these species in the ecosystems into account.

A quantitative understanding of the relationships between environmental drivers and the relative abundance, in terms of biomass or plant cover, of AM, EcM and ErM host plants is important, because the relative abundance of mycorrhizal types largely underpins ecosystem functioning. Changes in relative abundance of the different mycorrhizal plant types lead to changes in C and nutrient cycling (Phillips et al. 2013, Soudzilovskaia et al. 2015), soil processes and structure (Rillig and Mummey 2006), and can even cause deeper modifications in plant community assembly (Van Der Heijden 2002). In an era of human-induced environmental changes, unravelling the relative importance of soil and climatic factors in shaping the geographical distribution

of plant species featuring different mycorrhizal types will lead to better predictions of changes in ecosystem functioning under a future climate.

Here we present the first quantitative global analysis of the role of climatic and edaphic factors in explaining the distribution patterns of the three main types of mycorrhizal plants that covers all natural biomes and includes all plant growth forms. Our analysis is based on a high resolution gridded dataset (10 arc-minutes), which includes information about 39 environmental variables and the percentage of aboveground biomass of plant species featuring AM, EcM and ErM mycorrhizal associations. Following Read's hypothesis, we expect a relatively high contribution of soil properties related to organic C content.

2.2. Methods

2.2.1. Database assembly

2.2.1.1. Distribution of biomass fractions of different mycorrhizal associations

Estimates on the relative aboveground biomass of AM, EcM and ErM mycorrhizal associations were obtained from the high-resolution 10 arc-minutes ($\sim 31.5\text{km}^2$ around the equator) gridded global maps from Soudzilovskaia et al. (2019b). An extended description of their procedure is provided in the Supplementary Information. Briefly: 1) All combinations of continents, 98 Bailey's ecological regions and 38 land cover types were considered for their mycorrhizal association. 2) The dominant species in each abovementioned combination were determined following an extensive compilation of vegetation surveys (see Supplementary Information in Soudzilovskaia et al. 2019b for a list of surveys used). 3) The mycorrhizal association of each dominant species was extracted from a large database on the presence and type of mycorrhizal colonization of vascular plant species (36,303 site records for 14,768 plant species) (complete database is available in Soudzilovskaia et al. 2019a, Supplementary Table S2.3). 4) Each dominant species was attributed to a growth form and the relative aboveground biomass of each growth form for each land cover type was estimated based on rules detailed in the Supplementary Information. 5) The fraction of biomass

of EcM, AM, ErM and non-mycorrhizal plants in each combination of ecoregion, continent and land cover type was calculated from the combination of 3. and 4. Finally, 6) Global maps were obtained by overlaying continents, ecoregions and land cover types at 10 arc-minutes and linking the results of 5. to this overlay. While these maps are composed of multiple sources of information and subjected to a number of conversion factors, their average accuracy was estimated at 80-85% (Soudzilovskaia et al. 2019).

For the purpose of the current paper, non-natural biomes (croplands and urban areas) and bare areas were excluded from the analysis to ensure reliability. This exclusion was performed using the 2015 Land Cover Initiative map developed by the European Space Agency at 300m spatial resolution (<https://www.esa-landcover-cci.org/>) as a reference. As a result, a total of 270353 gridded cells were included in the final dataset.

2.2.1.2. Climatic and edaphic factors

We assembled a dataset of climatic and edaphic variables that have been proposed to be potential drivers of mycorrhizal plants distribution at global scale (Read 1991, Smith and Read 2008). In total, our dataset includes information about 39 environmental variables (see Supplementary information, Tables S2.1 and S2.3). The inclusion of this large number of variables allowed us to evaluate the contribution of temperature, precipitation, seasonality and soil physicochemical properties to shaping the global distribution of different mycorrhizal plant types.

Climatic variables were obtained from the WorldClim database, Version2 (<http://worldclim.org/version2>; Fick and Hijmans, 2017) at 10 arc-min resolution. In total 19 bioclimatic variables were included (see Supporting Information Table S2.1). These bioclimatic variables are a combination of monthly temperatures and precipitation values. The inclusion of the 19 bioclimatic variables allowed us to determine potential correlations with seasonality or extreme and limiting environmental factors. In addition, Annual Global Potential Evapotranspiration (Global-PET) (<https://cgiarcsi.community/category/data/>; Zomer et al., 2007, Zomer et al., 2008) was added to the climatic variables due to its ecological relevance. Global-

PET was calculated according to the Hargreaves equation (Hargreaves et al. 1985) which includes mean temperature, daily temperature range and extra-terrestrial radiation.

Data on the main edaphic variables were obtained from the Harmonized World Soil Database (HWSD) (<http://dare.iiasa.ac.at/>; FAO/IIASA/ISRIC/ISS-CAS/JRC, 2012). We included in total 12 variables (see Supporting Information Table S2.2) from the soil top layer (0-30cm), which were scaled up to 10arc-minutes resolution using the mean of the raster cells as aggregation criterion.

Data on water holding capacity, Total C, Total nitrogen (N), Total phosphorus (P) and available P is not available in the HWSD database. We considered these variables to have a potential implication on mycorrhizal host plants distribution due to their high ecological relevance, and therefore we prioritized their inclusion.

Available water Capacity, Total C, Total N were obtained from the ISRIC-WISE gridded database (<https://www.isric.org/explore/wise-databases>; Batjes, 2012) at 5 by 5 arc-minutes resolution. Only the soil top layer (0-20cm) was included and scaled up to 10 arc-minutes resolution.

Phosphorus content was obtained from the gridded Global Soil Dataset for use in Earth System Models (GSDE) (<http://globalchange.bnu.edu.cn/research/soilw/>; Shangguan et al., 2014) at 30 by 30 seconds resolution. Due to the high number of missing values of the different phosphorus measurements, only data of total phosphorus and phosphorus extracted by Bray method was retained. The edaphic information on these variables was presented in eight different depth layers ranging from 0 to 2.3m. For each variable, we calculated the mean of the first four layers covering the top layer (0 – 26 cm) and aggregated it to 10-arcmin resolution.

2.2.2. Statistical analysis

As climatic variables are highly correlated (Supporting Information, Table S2.3), we applied a Principal Component Analysis (PCA) to alleviate the problematics related to the high degree of collinearity while maintaining a high degree of variance in climate

2

variables. The first two axes (PC1 and PC2) of the principal component analysis explained 79.6% of the total variance in climatic data. PC1 was mainly related to temperature variables; while PC2 incorporated mainly precipitation-related variables (Supporting Information Figure S2.1). Soil factors were examined individually due to the low explanatory power of the principal components and difficulties with the ecological interpretation of the PCA axes of the soil variables (see Supporting Information Figure S2.2).

Generalized Additive Models for Location, Scale and Shape (GAMLSS) were fitted to relate the percentage of biomass of AM, EcM and ErM plants, respectively, to the soil factors and PC1 and PC2 of the climatic factors using the “gamlss” package. A GAMLSS allows fitting flexible regression and smoothing models and relaxes the assumption of the exponential family distribution for the response variable, replacing it by a general distribution family. Models were fitted using a zero-inflated beta distribution, which is appropriate for modelling proportional data that contain a high proportion of zeros. The smooth functions of each predictor were restricted to a maximum of 3 degrees of freedom, allowing for non-linearity while detecting only general trends and avoiding overfitting issues. Assuming that different mycorrhizal plant types may vary independently to environmental drivers, EcM, AM and ErM plant distributions were modelled separately. For model simplification, interaction terms were not included.

Model selection was performed by testing competing models that included a set of variables within which each variable explained at least 5% of the data variance, had a Pearson pairwise correlations lower than 0.6 (see Supporting Information Table S2.4) and Variance Inflation Factors (VIFs) lower than 3. This procedure allowed us to select for sets of non-correlated variables with high explanatory power and to avoid including suppressive variables that would obscure the interpretation of the models. In total, we tested 18 different competing models for AM plant distribution, each of which included 8 different variables, 6 competing models for EcM plant distribution (each including 6 different variables) and 2 competing models for ErM plant distribution (each including 3 variables) (see Supplementary information Tables S2.5,

S2.6 and S2.7). For each mycorrhizal plant type, the best model was selected according to the lowest Bayesian Information Criterion (BIC).

After the best models have been selected, a further variable selection was performed. We removed non-significant variables (with p-value >0.05) and variables with low relative importance in the model. We considered that a variable had little explanatory power when the effect of removing the variable did not decrease the Pseudo R^2 (Nagelkerke 1991) with more than 1%. Finally, degrees of freedom of the smooth terms were reduced to preserve only clearly non-linear patterns.

The presence of spatial autocorrelation (SAC) in AM, EcM and ErM final model residuals was tested using Moran's I correlograms with the "sp.correlogram" function in the "spdep" package. Moran's tests confirmed the presence of SAC in the model residuals. The existence of SAC may lead to an overestimation of degrees of freedom and Type I errors may be strongly inflated (Legendre 1993). The presence of SAC can be alleviated by 1) Including spatial coordinates explicitly in the model as covariates: This can be problematic since they could covary with the environmental variables present in the model (Dormann 2007, Miller et al. 2007), which can obscure the interpretation of the relative importance of the predictors. 2) Accounting for spatial autocorrelation in model residuals: There is a wide range of methods available in the mainstream software that allow alleviating SAC in model residuals (Dormann et al. 2007). However, their implementation in the context of a zero-inflated beta distribution is still extremely limited. This problem is even increased by the large number of data points included (270353), which makes the computation of the spatial models unfeasible.

Due to these technical limitations, no correction of SAC could be applied to our global high-resolution data. However, filtering the dataset by distances where SAC is significantly reduced as they decrease exponentially with distance (see Supplementary Information Figure S2.3) demonstrated that the presence of SAC does not alter the importance of the predictors in the final models and therefore their interpretation is not biased due to the autocorrelation (more detailed information about the reduced models is provided in the Supplementary Information). As the main goal of the

models is to detect important predictors of mycorrhizal plants distribution and not to serve as a predictive tool, we further discuss the output of the model with the complete dataset.

The final models were validated by 10-fold cross-validation. A difference of less than 10% between the **RMSE** (root mean squared error) of the final models and cross-validated models was used as a criterion for model validity. Both in **AM**, **EcM** and **ErM** models, the difference was lower than 5%.

Statistical analysis was performed using **R 3.5.3** (R Core Team 2021) and gridded data was processed using **ArcGis v10.2.2**.

2.3. Results

The model selection applied to the **AM** host plant distribution retained in total 2 different climatic and soil predictors: temperature-related factors (**PC1**), and bulk density. Together, these predictors were able to explain 55% of the variance in **AM** plant distribution (as indicated by **Pseudo-R²**). **PC1** was, by far, the best single predictor, providing 44% of the total variance explained by the model. The model describes a positive logistic relation between **AM** host plant relative abundances and temperature-related factors (Figure 2.2a). These results suggest that **AM** plants dominate temperate and warm climates. Soil properties had little influence on the distribution of **AM** plants. Bulk density explained only 2% of the variance (see Table 2.1). The difference between the sum of **Pseudo-R²** of each variable (0.46) and the **Pseudo-R²** of the final model (0.55) indicates that 9% of the variance explained is shared between the two predictors.

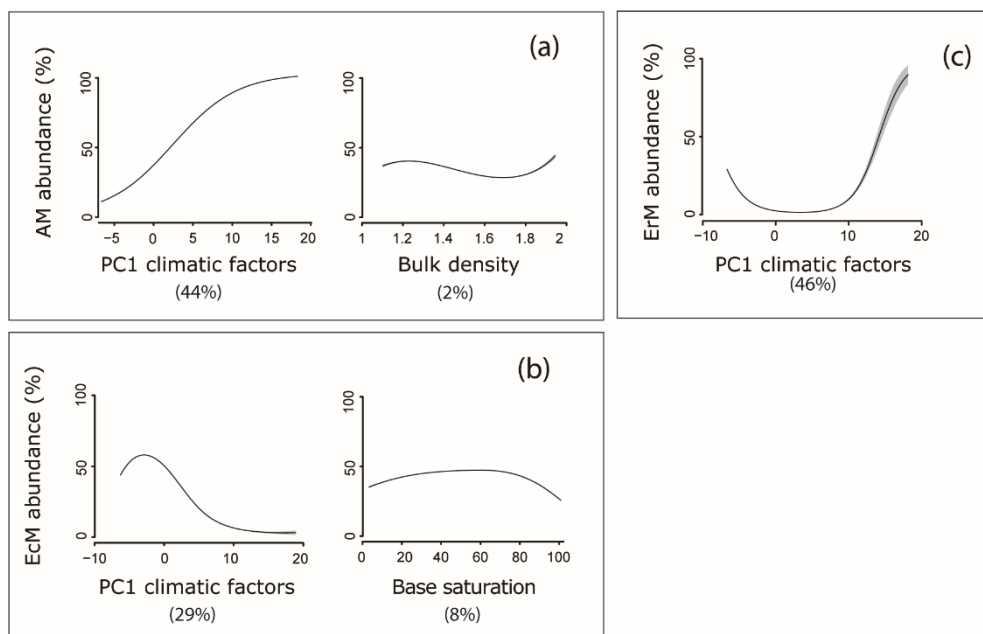


Figure 2.1: Predicted relation between AM (a), EcM (b) and ErM (c) relative abundances and the environmental factors maintained in the best models. Each relation was calculated setting the rest of the variables to the mean value. Light coloured shades represent the region within the upper and lower 95%-confidence limits. Numbers between brackets in the x-axes correspond to the individual variance explained by each factor in the models.

For the relative abundance of EcM plants, the predictors retained by the best model were temperature-related factors (PC1) and base saturation. This set of predictors explained 41% of the total variance (Table 2.1). Similar to the patterns for AM, temperature-related factors arose as the most important predictor of EcM plant distribution, explaining 29% of the variance (Table 2.1). Figure 2.2b shows that EcM plants relative abundance peaks at relatively low values of PC1, and decreases exponentially at higher PC1 values. This suggests that EcM plants dominate under cold (but not extremely cold) climates. In contrast to the AM model, soil properties played a more important role in explain EcM plants distribution. Although only base saturation remained in the final model, it was able to explain 8% of the variance. The model output shows that the dominance of EcM plants is mainly favoured by base saturation values between 40-70% (Figure 2.2b).

Table 2.1: Predictors, GAMLSS-estimated degrees of freedom (edf), t-value, p-values, Pseudo- R^2 of the final model for each mycorrhizal plant type and the Pseudo- R^2 that is attributed to each individual variable included in the final model.

	Predictor	edf	t value	p-value	Pseudo- R^2	Contribution to Pseudo- R^2 *
AM	<i>Bulk density</i>	2	-98.94	<0.001	0.55	0.02
	<i>PC1 climatic factors</i>	1	449.42	<0.001		0.44
EcM	<i>Base saturation</i>	2	-54.58	<0.001	0.41	0.08
	<i>PC1 climatic factors</i>	3	-103.51	<0.001		0.29
ErM	<i>PC1 climatic factors</i>	2	140.2	<0.001	0.46	0.46

*Due to the presence of joint effects (which refers to the shared contribution in the final model), the sum of the independent contribution of each variable to the model Pseudo- R^2 does not necessarily approximate to the Pseudo- R^2 of the final model.

For ErM plant distribution, only PC1 of climatic variables was retained in the final model, explaining 48% of the variance. Figure 2.2c indicates that ErM relative abundance is favoured by both extremely cold and warm temperatures (low and high PC1 values). However, the rapid increase in high values of PC1 had higher uncertainties associated which indicate that predictions in that temperature range are less reliable and possibly influenced by the low number of points.

Examination of the model predictions and residuals (Figure 2.1 a-f), suggests that our sets of predictors were able to capture a high degree of accuracy of the global patterns in the distribution of AM, EcM and ErM host plants.

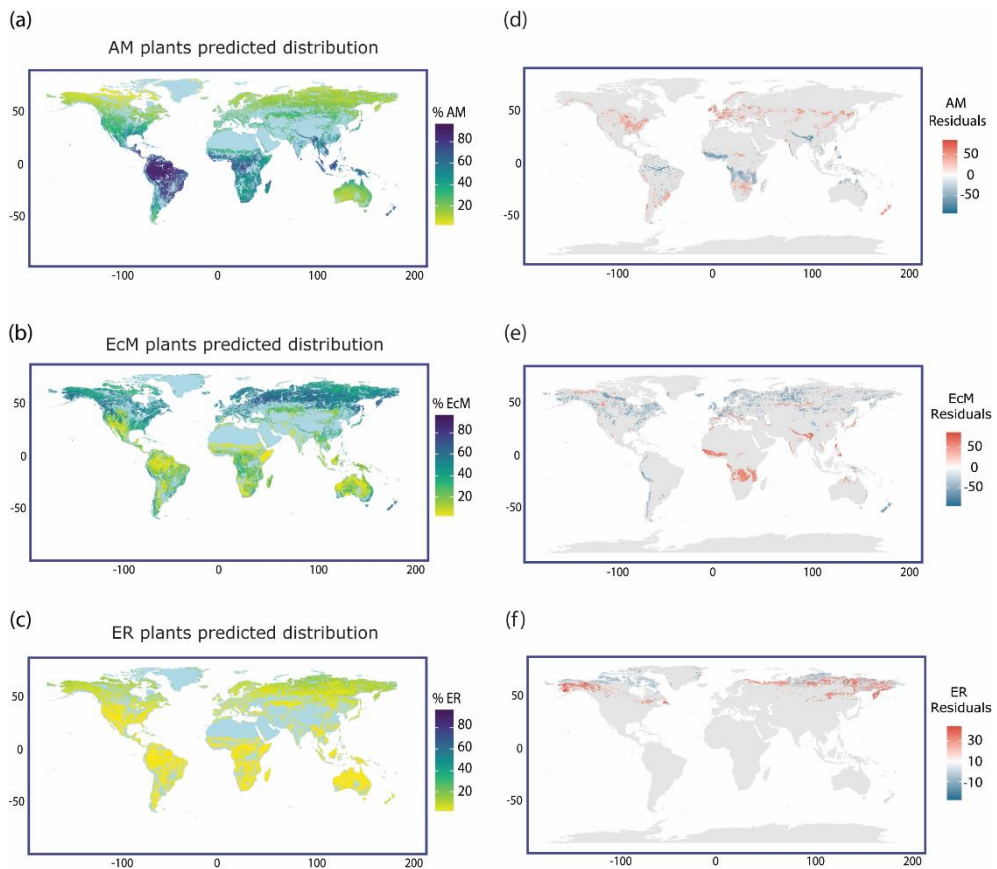


Figure. 2.2: Predicted global distribution of AM (a), EcM (b) and ErM (c) mycorrhizal host plants and prediction residuals (d-f); here only the 5% of data points with the highest residual values are depicted. Light blue areas denote non-natural biomes, bare areas or regions for which no environmental data was available. Residues are expressed as the difference between predicted and observed AM, EcM, and ErM plant relative abundances. Red points (positive values) indicate zones where the predicted plant relative abundance was overestimated by the model and blue points (negative values) indicate underestimations.

2.4. Discussion

This study is the first global data-based analysis of the environmental variables (climatic and edaphic) explaining the global distribution patterns of AM, EcM and ErM mycorrhizal plants. The fitted GAMLSS models revealed that climatic factors were

the main predictors for all mycorrhizal plant types. In contrast, soil properties played a secondary role in explaining mycorrhizal plants distribution at global scale.

The conclusion that edaphic factors do not control mycorrhizal plants distribution may be questioned based on three arguments: 1) The larger extent of unaccounted variation in soil data compared to climate may lead to an underestimation of soil importance. However, the soil data used in this analysis has been proven to be robust enough to detect association patterns with above- and below-ground plant traits at global scales (Maire et al. 2015, Freschet et al. 2017), which supports the reliability of our results. This suggests that the patterns detected within our study reflect the true set of important predictors. 2) The theoretical overlap between soil properties and climatic condition may act as a confounding factor in detecting their relative importance in our models. However, although soil properties are theoretically influenced by climate (e.g., soil organic stocks are affected by temperature regimes), their actual values result from complex interactions between climatic, geochemical and biotic conditions (Davidson and Janssens 2006, Doetterl et al. 2015). In line with this, our dataset shows that, at global scale, the principal components of climatic factors and soil properties are not highly correlated (see Supplementary Information Table S2.4), reinforcing the role of climate as a main driver of large scale distribution of mycorrhizal plants. 3) The resolution of mycorrhizal plant maps (10 arc-minutes) may not be appropriate to capture the impacts of small scale variation of soil properties and, consequently, may reduce their explanatory power in the final models. However, given that the used resolution captures the main patterns in global soil distribution (Batjes 2012) our models are likely capable of capturing global scale trends.

Thus, Read's paradigm of the latitudinal separation between AM, EcM and ErM plants being a reflection of their differential ability to take nutrient from organic sources (Read 1991, Read and Perez-Moreno 2003) is not supported by our findings. Our results also partially contradict the conclusion drawn by Steidinger et al. (2019), who as well found a strong climatic control over mycorrhizal trees distribution. Steidinger et al. (2019) related the mechanisms explaining this pattern purely to differences in decomposition rates, while they did not find a direct link with soil

physicochemical properties. Our results suggest that other mechanisms play a role, as detailed below.

2.4.1. Environmental predictors of AM plants distribution

Our results clearly highlight the impact of climate (especially temperature) on AM plant distributions. Several studies have reported temperature as an important limiting factor for the growth of AM extraradical mycelium (Rillig et al. 2002, Gavito et al. 2003, Heinemeyer and Fitter 2004). Also, a reduction of intraradical colonization has been commonly reported at temperatures lower than 15°C (Hetrick and Bloom 1984, Gavito and Azcón-Aguilar 2012). As an alternative mechanism, Veresoglou (2019) recently proposed that irradiance reduction in higher latitudes contributes to a reduction of AM fungi responsiveness, which may contribute to the detected decline of AM plant abundance in colder climates. In line with these studies, our findings suggest that the physiological restrictions of AM fungi to develop and provide benefits to its plant partner at lower temperatures might be a primarily important driver of AM plant distribution at global scale, independent of soil properties.

In contrast, soil properties were not relevant in explaining AM abundances (Table 2.1). Especially surprising is the absence of soil P impacts in the final AM best model, which contradicts the view of AM associations being a key adaptation for P uptake. This view was already challenged by previous research. For instance, Soudzilovskaia et al. (2015a) reported no significant correlation between P limitation and AM root colonization. Similarly, using a meta-analysis approach, Allison & Goldberg (2002) showed that changes in P availability do not have a consistent effect on mycorrhizal infection at plant community level. These results indicate that, although P availability influences the performance of the plant-fungi relationship at the plant species level (Treseder 2013), this does not necessarily translate into P availability driving AM distribution patterns at a global scale.

What is clear from these results is that climatic conditions are deeply affecting the global biogeography of AM associations. Therefore, the increase of global temperatures expected for next decades (IPCC 2014) can potentially modify the

distribution range of AM plants and therewith their impacts on the functioning of terrestrial ecosystems.

Although climatic and soil factors were able to explain a large part of the variability in AM plant distribution, the model predictions tended to overestimate AM abundances in tropical zones (mainly central Africa) and underestimate abundances in temperate zones (Figure 2.1a and Figure 2.1d). These mismatches may be related to the higher proportion of facultative AM plants in northern latitudes (Hempel et al. 2013, Menzel et al. 2016, Bueno et al. 2017) which suggest a differentiation in the environmental requirements between obligate and facultative AM plants. Also, the evolutionary and biogeographic history influenced by past geological and climatic episodes (such as tectonic movements, uplift of mountain ranges, climatic stability in different periods) and past human-induced changes (Kreft and Jetz 2007), may influence the global distribution patterns of mycorrhizal vegetation and their correlation with environmental factors (e.g., different phylogenetic groups may have different adaptations to similar environments which could lead to a weaker correlation with environmental factors). Recent research also suggests that the ability of certain AM fungal species to colonize leaf litter may contribute to a higher abundance of this association in organic soils (Bunn et al. 2019). Incorporating information about specific fungal functional traits and host identities will be key in future studies aimed to better understand AM plant biogeographical patterns.

2.4.2. Environmental predictors of EcM plants distribution

EcM plants relative abundance was mainly explained by temperature-related factors, but showed trends opposite to those of AM. EcM plants showed preferences for moderately cold climates, which is consistent with their greater abundance in Northern temperate and boreal zones (Soudzilovskaia et al. 2019). This climatic range possibly relates to the physiological adaptations of EcM plants present in boreal-temperate ecotones and their fungal partners to tolerate cold temperatures and frost periods (Sakai and Weiser 1973, Strimbeck et al. 2008, Kilpeläinen et al. 2016). Consequently, a temperature rise can also have serious consequences for EcM plant distributions.

Within the three mycorrhizal plant types studied, EcM plant distribution predictions by the model had the lowest accuracy. The model reflects the EcM distribution patterns in the northern hemisphere well, although with a tendency to underestimate its relative biomass; see Figure 2.1e. In contrast, EcM abundance in tropical areas is not well represented, with a clear underestimation (Figure 2.1b and Figure 2.1e). This is especially visible in certain regions of central Africa where the EcM monodominant stands cannot be predicted by climatic and soil properties. This area of the Africa continent is mainly dominated by EcM plants of the subfamily Detarioideae (family Fabaceae) (de la Estrella et al. 2017, Tedersoo 2017). These species are suggested to proliferate in nutrient-poor and acidic soils (Campbell 1996) where specific traits of ectomycorrhizal fungal communities (e.g. the ability to obtain N from organic sources) may give them advantage over AM associations (Alexander and Högberg 1986, Högberg 1986). However, our model does not support this hypothesis since differences in soil fertility were not able to explain EcM plant distribution in these areas. It is likely that a combination of specific fungal and plant traits (e.g., high host specificity, poor seed dispersal, shade tolerance) create positive feedbacks resulting in a higher proportion of EcM plant abundance in these tropical areas (Peh et al. 2011). Another potential reason of a poor predictive power of our models in tropics is the limited amount of information about EcM plants in tropical areas. Therefore the EcM distribution map is likely to have higher uncertainties in these regions.

Altogether, with respect to EcM plant abundance, our results indicate that, although climatic conditions and soil properties play an important role in explaining EcM plant distribution, other complex ecological interactions between EcM fungal communities, their host plants and other non-EcM plants may influence the biogeography of EcM associations at a global scale. Increasing the information about distribution of EcM plants in tropical areas is crucial for getting a better understanding of the biogeography of this association.

2.4.3. Environmental predictors of ErM plants distribution

The distribution of ErM plants has been traditionally associated with harsh environments, characterized by nutrient-poor and acidic soils (Read 1991). This has

2 been related to the ability of ErM fungi to produce hydrolytic and oxidative enzymes (Cairney and Burke 1998) that would increase the fitness of their symbiont in these environments. However, our results suggested that, at a global scale, the abundance of plants capable to form ErM association is influenced mainly by temperature-related factors (Table 2.1). The strong contribution of temperature to explaining the distribution of ErM plants may be a reflection of their physiological adaptations to tolerate frost events (Marian et al. 2004) and therefore to survive in extreme temperatures where other plants are unable to establish.

Unexpectedly, soil conditions were only weakly correlated to the abundance of ErM plants (Table 2.1). The fact that soil properties were not a good proxy for ErM plants abundances could indicate the complexity and heterogeneity of strategies of ErM fungi to use organic substrates as a resource of nutrients. However, little information is available about ErM fungal traits or Ericaceae niche preferences that allow a deeper exploration of these results.

2.5. Concluding remarks

Our results point at temperature-related factors as the main predictors – instead of soil properties - for the global distribution of the three most abundant mycorrhizal plant types. The observed lack of importance of soil drivers contradicts the traditional view of climate-driven soil properties, such as the rate of organic matter decomposition and nutrient availability as the ultimate mechanisms explaining the latitudinal distribution of mycorrhizal plant types (Read and Perez-Moreno 2003, Smith and Read 2008, Phillips et al. 2013, Steidinger et al. 2019). In contrast, our findings support the role of temperature as a main driving force affecting the global distribution of plant ecological strategies (Moles et al. 2014), and reinforces the view that mycorrhizal type constitutes an important part of these strategies. We suggest that the latitudinal transition between AM, EcM and ErM plants is likely to be associated with ecological mechanisms that involve direct effects of climate on plant and fungi performance and survival. In line with this hypothesis, the indirect effects of climate on decomposition and nutrient availability would play a secondary role at large scale.

Given that our results point to climate as the main force shaping the distribution of AM, EcM and ErM host plants at the global scale, and taking into account the importance of mycorrhizas on ecosystem functioning (Phillips et al. 2013), we suggest that climate change can significantly alter the distribution of mycorrhizal host plants, with subsequent impact on the functioning of terrestrial ecosystems and provisioning of associated ecosystem services. However, an accurate prediction of changes in mycorrhizal vegetation abundances under future climatic scenario will require 1) higher resolution data of mycorrhizal plants distribution and 2) higher quality soil data and 3) to increase the knowledge of mycorrhizal associations in plant species that have not been investigated yet to extend the analysis beyond the dominant species. This will allow to account for the large heterogeneity of soil properties and to evaluate the importance of smaller-scale processes that could not be considered in this work.

2.6. Acknowledgments

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2.7. Authors' contributions

MB performed modelling and wrote the first draft of the manuscript. PB and NS made substantial contributions during modelling process and revision of the manuscript.

2.8. Data Accessibility Statement

The data used in this research is compiled by joining publically available datasets:

- Mycorrhizal abundance maps:
<https://www.biorxiv.org/content/10.1101/331884v2>; DOI: 10.1101/331884
- Climatic data: WorldClim database, Version2
(<http://worldclim.org/version2>)
- Annual Global Potential Evapotranspiration (Global-PET):
<https://cgiarcsi.community/category/data/>

- Soil data:
 - Harmonized World Soil Database (HWSD): <http://dare.iiasa.ac.at/>
 - Available water Capacity, Total C, Total N: ISRIC-WISE gridded database (<https://www.isric.org/explore/wise-databases>)
 - Phosphorus content: Global Soil Dataset for use in Earth System Models (GSDE) (<http://globalchange.bnu.edu.cn/research/soilw>)

2.9. Supporting information

2.9.1. Assembly of mycorrhizal vegetation maps

Soudzilovskaia et al, 2019 constructed the maps the biomass fractions of different mycorrhizal plant types, assigning values of mycorrhizal biomass fractions to in all possible combinations of continents, 98 Bailey's ecological regions and 38 land cover types (from here onwards referred to as "combination"). The estimated fraction of each mycorrhizal type and of each growth form within each combination was based on the dominant plant species occurring in combinations, based on vegetation records (using for this purpose 1,568 sources of vegetation surveys, conducted in each combination). The maps construction process generally consisted of four steps (summary of which is provided below; for more information please consult Soudzilovskaia et al, 2019).

Step 1. Assigning mycorrhizal association to the dominant species within each combination. This information was extracted from a large database on the presence and type of mycorrhizal colonization of vascular plant species (36,303 plant species by site records) (<http://biorxiv.org/cgi/content/short/717488v1>). This information was provided by published reviews, data compilations, previously neglected or recent case studies on the type of mycorrhizal colonization (1,565 sources). By assembling the database classification of mycorrhizal type for a given species was performed following definitions of Brundrett and Tedersoo (2018) and based on the description of morphological criteria provided by the authors of a respective publication. Plant

records where the presence of intracellular arbuscules, coils or pelotons was corroborated were classified as AM, ErM or Orchid Mycorrhiza (OM), respectively. For EcM, the presence of a Hartig net or a well-developed mantle (>1 hyphal layer) was required. All plants of the families Diapensiaceae and Ericaceae were considered ErM, except for *Enkianthus* (AM), *Arbuteae*, *Pyroleae*, *Monotropeae* and *Pterosporeae* (all subtypes of EcM).

Because of multiple incorrect reports and alternative definitions for mycorrhizal types, plants were considered to belong to a given mycorrhizal type, only when this was supported by multiple independent studies and the proportion of conflicting reports was <50%. In other cases, the plant species were considered to feature a mixed type of colonization (for instance to be AM/EcM). Non-mycorrhizal species were assigned according to Brundrett, 2009 & 2017. While misdiagnosis of mycorrhizal type might be a problem in general (Bueno et al. 2019, Sun et al. 2019, Tedersoo et al. 2019) it is unlikely to have majorly affected our current analysis as the underlying maps were based on pre-dominant species only for which more consensus on mycorrhizal associations tends to exist, as such species are typically studied more extensively.

Step 2. Assigning growth form to each dominant species. This was done based on the vegetation records for each combination.

Step 3. Estimation of fractions of living biomass of each plant growth form within each combination. In these estimates, the following coefficients to translate information of plant growth forms into biomass fractions of plants were used:

- in forests that consist of two vegetation layers (trees and herbaceous/dwarf shrub understory vegetation), trees contribute 90±5% of the biomass, and the understorey vegetation comprises 5-10% of biomass;
- in forests that encompass a dense layer of shrubs, trees contribute 70±15% of the biomass, shrubs constitute 20±10% of biomass and understorey herbaceous/dwarf shrub layer constitutes 20±10%.
- In shrublands, shrubs account for 90±5% of the biomass, and herbaceous vegetation 10±5% of the biomass.

- Savannahs and forested steppes to harbor $30\pm 10\%$ of the biomass in trees, $30\pm 10\%$ of the biomass in shrubs, and the remaining biomass in herbaceous vegetation.

Step 4. Calculation of biomass fractions of mycorrhizal types and mapping those. The estimated proportion of a given mycorrhizal type per growth form was combined with the estimated growth forms biomass fractions to calculate the average biomass fraction of EcM, AM, ErM and non-mycorrhizal associations for each combination.

Finally, by overlaying the raster map of Bailey ecoregions, provided by the Oak Ridge National Laboratory Distributed Active Archive Center (10 arcmin), with the raster ESA CCI land cover dataset, spatially aggregated to 10 arcmin and a polygon map of continents, rasterized at 10 arcmin, global maps of mycorrhizal type association were created.

The maps were validated using four independent datasets: (i) forest biomass structure for Eurasia, (ii) a global dataset of forest biomass structure used for an analysis of mycorrhizal impacts on carbon vs nitrogen dynamics, (iii) estimates of mycorrhizal associations in the USA based on remote sensing, and (iv) West Australian map of mycorrhizal root abundance (Soudzilovskaia et al, 2019).

The maps of mycorrhizal vegetation have been assembled based on multiple published datasets, using a number of conversion factors. These conversions, as well as the fact that the plant species distribution data originates from multiple sources, constitute important uncertainty sources in the dataset. The average uncertainty of the biomass fractions of mycorrhizal plants per grid cell is 15-20% (Soudzilovskaia et al. 2019).

2.9.2. Environmental predictors

Table S2.1: List of bioclimatic variables included in the final dataset

Abbreviation	Meaning
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO3	Isothermality (BIO2/BIO7) (* 100)
BIO4	Temperature Seasonality (standard deviation *100)
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range (BIO5-BIO6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

Table S2.2: List of soil physicochemical properties included in the final dataset obtained from the Harmonized World Soil Database (HWSD), the ISRIC-WISE gridded database and the Global Soil Dataset for use in Earth System Models (GSDE).

Source	Soil properties	Abbreviation	Units	Original grid cell size	Comments
HWSD	Sand Fraction	Sand	% wt.	30 by 30 arc-seconds	
	Silt Fraction	Silt	% wt.	30 by 30 arc-seconds	
	Clay Fraction	Clay	% wt.	30 by 30 arc-seconds	
	Bulk density	Bulk density	kg/dm ³	30 by 30 arc-seconds	Calculated with the Equations developed by (Saxton et al. 1986)
	Reference bulk density	Ref bulk density	kg/dm ³	30 by 30 arc-seconds	SOTWIS Bulk Density estimation
	Organic carbon	Org C	% weight	30 by 30 arc-seconds	
	pH	pH	(H ₂ O) - log(H ⁺)	30 by 30 arc-seconds	pH measured in a soil-water solution
	Cation exchange capacity	Cat exc	cmol/kg	30 by 30 arc-seconds	
	Base saturation	Base sat	%	30 by 30 arc-seconds	

	Total exchangeable bases	Total exc bases	cmol/kg	30 by 30 arc-seconds	
	Calcium carbonate content	CaCO ₃	% weight	30 by 30 arc-seconds	
	Electrical conductivity	Conductivity	dS/m	30 by 30 arc-seconds	
ISRIC- WISE	Available Water Capacity	TAWC	c/m	5 by 5 arc-minutes	
	Total Carbon	Total C	g/kg	5 by 5 arc-minutes	
	Total Nitrogen	Total N	g/kg	5 by 5 arc-minutes	
	C/N ratio	C/N		5 by 5 arc-minutes	
GSDE	Bray Phosphorus	Bray P	ppm	30 by 30 arc-seconds	The amount of phosphorous using the Bray1 method
	Total Phosphorus	Total P	%	30 by 30 arc-seconds	

2.9.3. Statistical analysis

Table S2.3: Pearson correlation matrix of climatic factors. Numbers in red indicate predictors with correlation >0.6

	Evapo T	bio 1	bio 2	bio 3	bio4	bio5	bio6	bio7	bio8	bio9	bio 10	bio 11	bio 12	bio 13	bio 14	bio 15	bio 16	bio 17	bio 18	bio 19
Evapo T	1,00	0,95	0,64	0,87	-0,79	0,94	0,88	-0,71	0,82	0,87	0,94	0,90	0,14	0,26	-0,37	0,39	0,23	-0,31	-0,01	-0,12
bio1		1,00	0,42	0,91	0,89	0,88	0,97	-0,84	0,82	0,93	0,93	0,98	0,29	0,38	-0,21	0,30	0,35	-0,15	0,10	0,05
bio2			1,00	0,42	-0,21	0,66	0,27	-0,07	0,40	0,36	0,55	0,33	-0,31	-0,18	-0,56	0,43	-0,21	-0,54	0,30	0,43
bio3				1,00	-0,95	0,71	0,94	-0,90	0,71	0,86	0,75	0,95	0,42	0,50	-0,09	0,24	0,47	-0,03	0,24	0,14
bio4					1,00	-0,62	-0,96	0,98	-0,65	-0,86	-0,69	-0,96	-0,50	-0,55	0,00	-0,15	-0,52	-0,07	-0,28	-0,23
bio5						1,00	0,77	-0,54	0,78	0,83	0,98	0,79	-0,01	0,10	0,41	0,36	0,07	-0,36	0,15	0,14
bio6							1,00	-0,94	0,75	0,93	0,83	1,00	0,42	0,48	-0,07	0,20	0,45	-0,01	0,20	0,18
bio7								1,00	-0,59	-0,82	-0,62	-0,92	-0,53	-0,56	-0,07	-0,09	-0,54	-0,14	-0,31	-0,29
bio8									1,00	0,63	0,82	0,77	0,24	0,37	-0,20	0,37	0,34	-0,15	0,23	-0,12
bio9										1,00	0,86	0,93	0,25	0,31	-0,18	0,21	0,28	-0,12	0,01	0,17
bio10											1,00	0,85	0,07	0,18	-0,33	0,34	0,15	-0,29	-0,07	-0,08
bio11												1,00	0,40	0,48	-0,11	0,24	0,45	-0,05	0,19	0,14
bio12													1,00	0,94	0,60	-0,21	0,96	0,66	0,86	0,66

[illegible]

Table S2.4: Pearson correlation matrix of soil predictors and the first two principal components of climatic factors. Numbers in red indicate pairs of predictors with correlation >0.6

	Sand	Silt	Clay	Bulk density	Ref bulk density	Org C	pH	Cat exc	Base sat	Total exc bases	CaCO ₃	Conductivity	TA WC	Total C	Total N	C/N	Bray P	Total P	PC1_climatic	PC2_climatic
Sand	1,00	-0,82	-0,70	0,38	0,83	-0,22	-0,10	-0,50	-0,14	-0,47	-0,07	-0,02	-0,19	-0,11	-0,18	0,11	0,17	-0,09	-0,04	0,16
Silt		1,00	0,16	-0,33	-0,47	0,25	0,11	0,46	0,19	0,37	0,02	0,02	0,31	0,18	0,26	0,05	0,11	0,17	-0,29	-0,20
Clay			1,00	-0,24	-0,85	0,08	0,03	0,28	0,00	0,35	0,09	0,01	-0,06	-0,03	-0,02	-0,25	0,15	0,05	0,43	-0,02
Bulk density				1,00	0,29	0,81	0,23	0,67	0,15	-0,29	0,06	0,01	-0,43	-0,46	-0,40	-0,25	0,12	0,06	0,09	0,22
Ref bulk density					1,00	-0,13	-0,10	0,37	-0,11	-0,40	-0,12	-0,02	-0,02	-0,01	-0,05	0,25	0,16	0,04	-0,28	0,06
Org C						1,00	-0,26	0,82	-0,14	0,34	-0,11	-0,03	0,44	0,56	0,47	0,36	0,11	0,11	-0,18	-0,17
pH							1,00	0,06	0,87	0,54	0,57	0,14	-0,26	-0,20	-0,12	-0,46	0,19	0,32	-0,11	0,50
Cat exc								1,00	0,14	0,67	0,04	0,00	0,39	0,44	0,41	0,19	0,10	0,05	-0,22	-0,07

[illegible]

Table S2.5: Set of variables included in the 18 competing models for *AM* plant distribution and resulting *BIC* of the models. Model highlighted in yellow represents the selected model with lower *BIC*.

AM									
Model	Variables								BIC
1	Clay	Total exc bases	pH	TAWC	C/N	Bray P	Total P	PC1_climatic	-3054.7
2	Clay	Total exc bases	pH	Total C	C/N	Bray P	Total P	PC1_climatic	-3063.5
3	Clay	Total exc bases	pH	Total N	C/N	Bray P	Total P	PC1_climatic	-3107.9
4	Clay	Total exc bases	Base sat	TAWC	C/N	Bray P	Total P	PC1_climatic	-3048.2
5	Clay	Total exc bases	Base sat	Total C	C/N	Bray P	Total P	PC1_climatic	-3043.3
6	Clay	Total exc bases	Base sat	Total N	C/N	Bray P	Total P	PC1_climatic	-3078
7	Ref bulk density	Total exc bases	pH	TAWC	C/N	Bray P	Total P	PC1_climatic	-3052
8	Ref bulk density	Total exc bases	pH	Total C	C/N	Bray P	Total P	PC1_climatic	-3043.5
9	Ref bulk density	Total exc bases	pH	Total N	C/N	Bray P	Total P	PC1_climatic	-3090
10	Ref bulk density	Total exc bases	Base sat	TAWC	C/N	Bray P	Total P	PC1_climatic	-3100.4
11	Ref bulk density	Total exc bases	Base sat	Total C	C/N	Bray P	Total P	PC1_climatic	-3079.3
12	Ref bulk density	Total exc bases	Base sat	Total N	C/N	Bray P	Total P	PC1_climatic	-3116.5
13	Sand	Total exc bases	pH	TAWC	C/N	Bray P	Total P	PC1_climatic	-3029.5
14	Sand	Total exc bases	pH	Total C	C/N	Bray P	Total P	PC1_climatic	-3043.5
15	Sand	Total exc bases	pH	Total N	C/N	Bray P	Total P	PC1_climatic	-3090
16	Sand	Total exc bases	Base sat	TAWC	C/N	Bray P	Total P	PC1_climatic	-3100.4
17	Sand	Total exc bases	Base sat	Total C	C/N	Bray P	Total P	PC1_climatic	-3079.3
18	Sand	Total exc bases	Base sat	Total N	C/N	Bray P	Total P	PC1_climatic	-3116.5

Table S2.6: Set of variables included in the 6 competing models for EcM plant distribution and resulting *BIC* of the models. Model highlighted in yellow represents the selected model with lower *BIC*.

EcM							
Model	Variables						BIC
1	Ref bulk density	Total exc bases	pH	TAWC	C/N	PC1_climatic	3010.3
2	Ref bulk density	Total exc bases	pH	Total C	C/N	PC1_climatic	3155.6
3	Ref bulk density	Total exc bases	pH	Total N	C/N	PC1_climatic	3130.6
4	Ref bulk density	Total exc bases	Base sat	TAWC	C/N	PC1_climatic	2562.7
5	Ref bulk density	Total exc bases	Base sat	Total C	C/N	PC1_climatic	2608.8
6	Ref bulk density	Total exc bases	Base sat	Total N	C/N	PC1_climatic	2560.1

Table S2.7: Set of variables included in the 2 competing models for EcM plant distribution and resulting *BIC* of the models. Model highlighted in yellow represents the selected model with lower *BIC*.

ErM				
Model	Variables			BIC
1	Total C	C/N	PC1_climatic	-6086
2	Total N	C/N	PC1_climatic	-6230

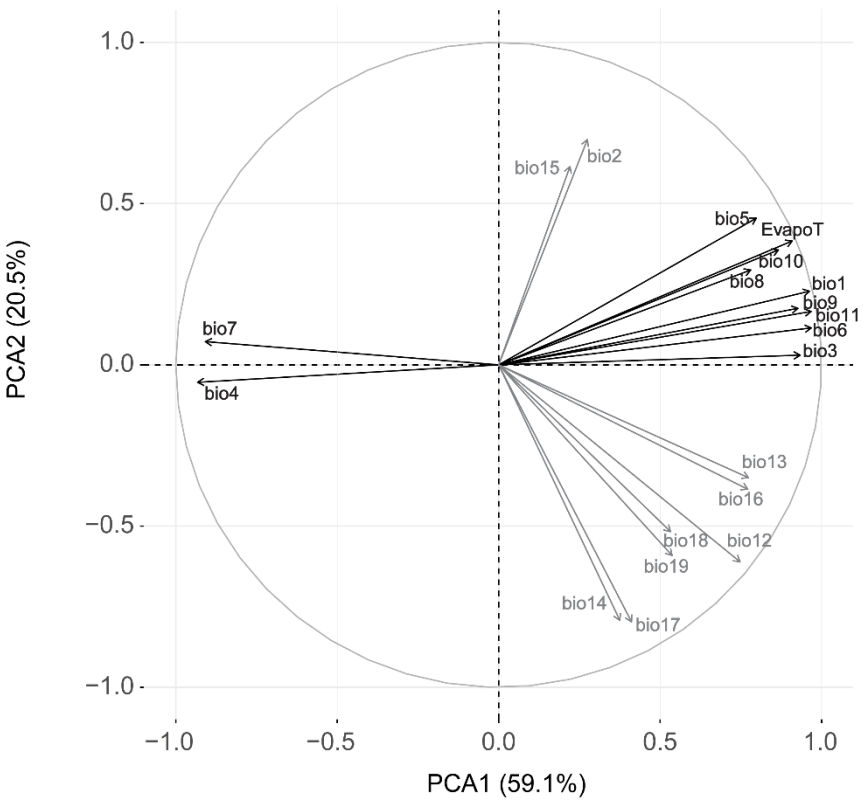


Figure S2.1: Principal component analysis ordination plot of climatic variables. Black arrows represent climatic variables mainly related to temperature factors and grey arrows represent climatic variables mainly related to precipitation factors

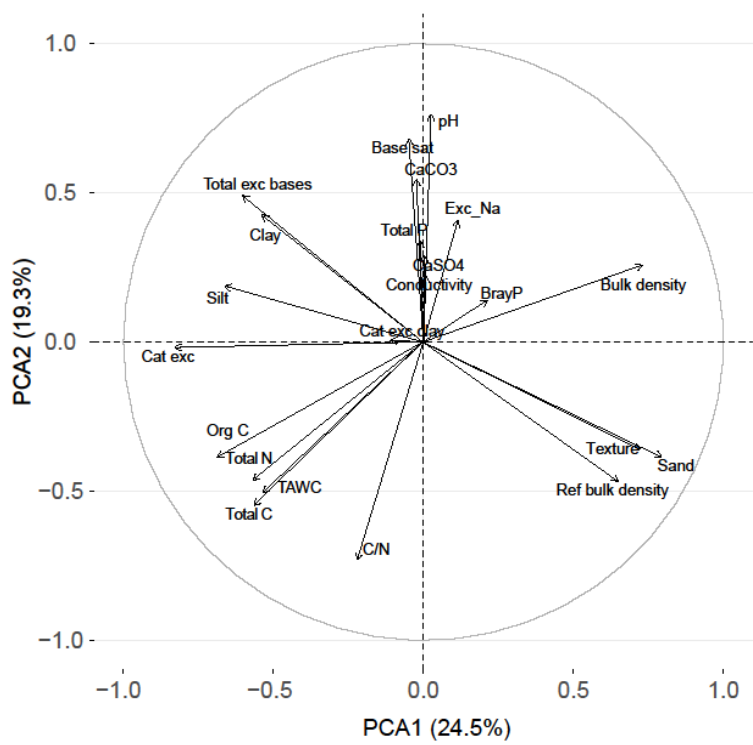


Figure S2.2: Principal component analysis ordination plot of edaphic variables.

2.9.4. Spatial autocorrelation

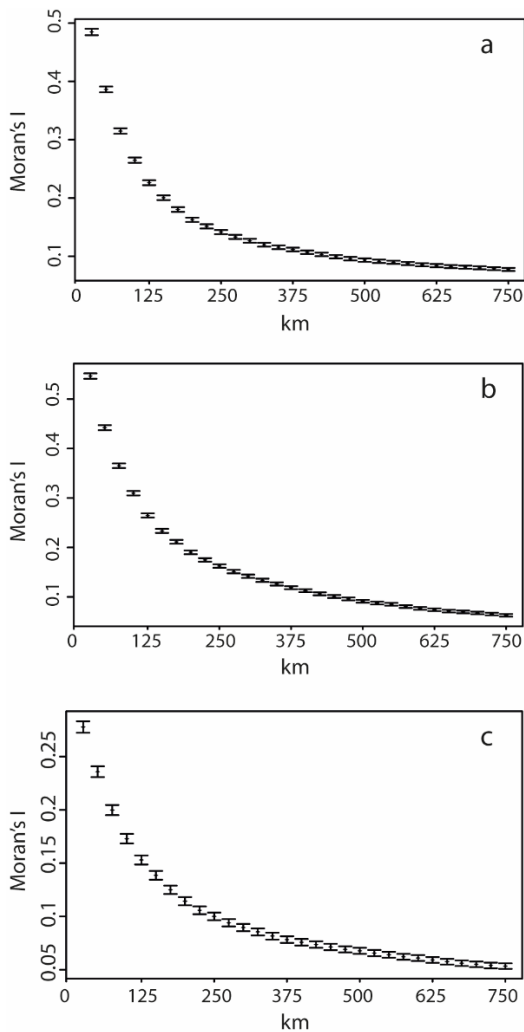


Figure S2.3: Moran's I correlogram of AM (a), EcM (b) and ErM (c) model residuals.

To evaluate whether the presence of SAC in the final model altered the final conclusion of this work, the complete dataset ($n=270353$) was subsetting according to two distance filters. In a first filter, we included only points that at least 250km apart from each other, resulting in 2337 data points. In a second filter, we included points

separated at least by 750km, resulting in 182 data points. The election of the distances is based on Moran’s I correlogram (Figure S3) and correspond to distances at which the majority vs. virtually all spatial autocorrelation had disappeared.

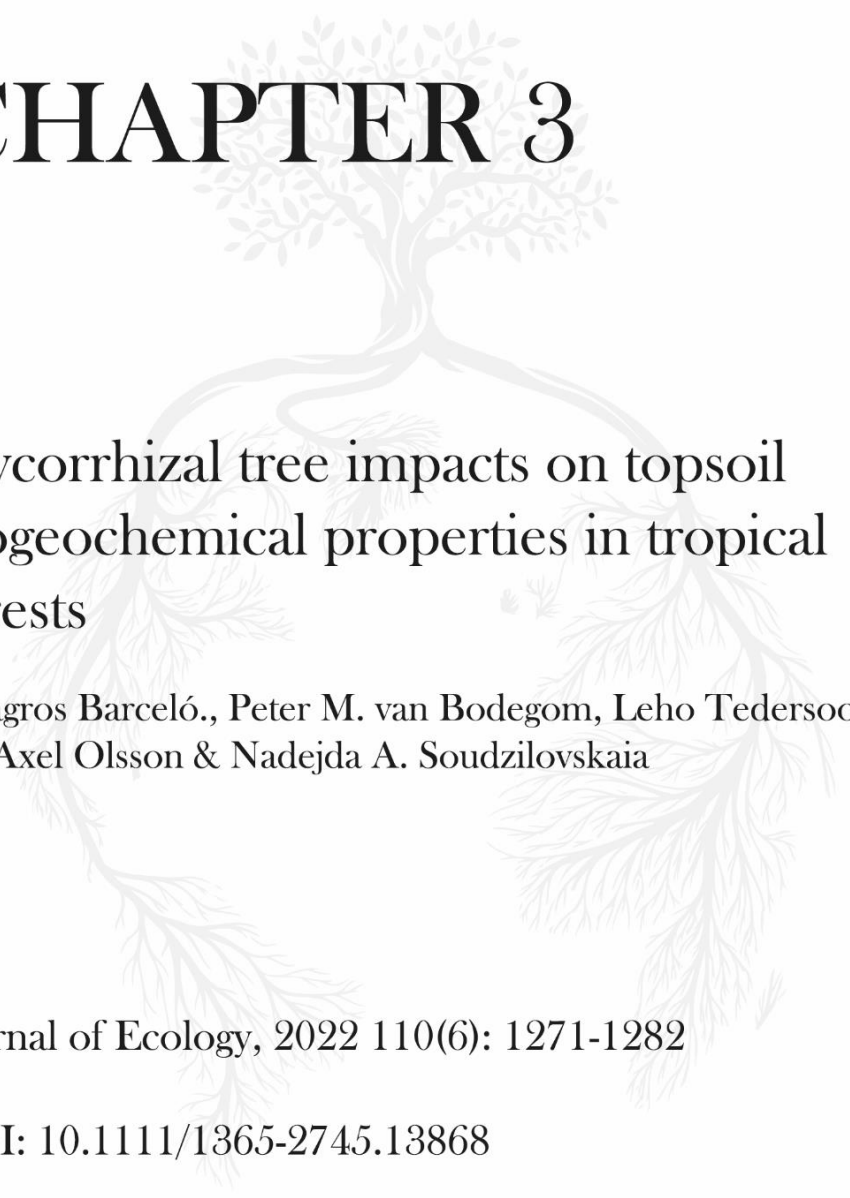
The reduced model showed that, even when the distance between points is increased, climatic variables had the highest contribution in model R^2 (see Tables S8 and S9).

Table S2.8: Predictors, GAMLSS-estimated degrees of freedom (edf), t-value, p-values, Pseudo- R^2 of the final model for each mycorrhizal plant type and the Pseudo- R^2 that is attributed to each individual variable included in the final model at a minimum distance of 250km.

	Predictor	edf	t value	p-value	Pseudo- R^2	Contribution to Pseudo- R^2 *
AM	Bulk density	2	-8.37	<0.001	0.48	0.02
	PC1 climatic factors	1	39.33	<0.001		0.38
EcM	Base saturation	2	-8.13	<0.001	0.31	0.05
	PC1 climatic factors	2	-24.6	<0.001		0.25
ErM	TOTN	2	5.99	<0.001	0.43	0.01
	PC1 climatic factors	3	-33.8	<0.001		0.37

Table S2.9: Predictors, GAMLSS-estimated degrees of freedom (edf), t-value, p-values, Pseudo- R^2 of the final model for each mycorrhizal plant type and the Pseudo- R^2 that is attributed to each individual variable included in the final model when including points at a minimum distance of 750km.

	Predictor	edf	t value	p-value	Pseudo- R^2	Contribution to Pseudo- R^2 *
AM	<i>TOTN</i>	2	-6.35	<0.001	0.43	0.03
	<i>PC1 climatic factors</i>	1	12.35	<0.001		0.35
EcM	<i>TOTN</i>	2	4.58	<0.001	0.20	0.05
	<i>PC1 climatic factors</i>	2	-8.05	<0.001		0.15
ErM	<i>PC1 climatic factors</i>	2	0.23	<0.001	0.33	0.33



CHAPTER 3

Mycorrhizal tree impacts on topsoil biogeochemical properties in tropical forests

Milagros Barceló., Peter M. van Bodegom, Leho Tedersoo,
Pål Axel Olsson & Nadejda A. Soudzilovskaia

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Abstract

1. In tropical regions, the patterns of carbon (C) and nutrient properties among ecosystems dominated by distinct mycorrhizal associations are unknown. We aim to reveal whether the dynamics differ and the ecological drivers and ecosystem functioning implications of such differences.
2. Based on a dataset of 97 tropical forest sites, we related EcM trees abundance (as a proxy for the transition from AM to EcM trees dominance) to different topsoil properties, climatic conditions, and microbial abundance proxies through Generalized Additive Models.
3. Higher abundances of EcM trees was correlated with lower topsoil concentrations of total nitrogen and C, extractable phosphorus and potassium, $\delta^{13}\text{C}$, mean annual temperature, precipitation, microbial (bacterial and fungal) biomass, and the relative abundance of saprotrophic fungi.
4. *Synthesis.* Our results reveal consistent differences in carbon and nutrient content between arbuscular mycorrhizal (AM-) and EcM-dominated vegetation across the tropical biome, pointing to lower soil fertility and lower rates of C and nutrient transformation processes in EcM-dominated forests. These patterns associate with lower topsoil C accumulation when compared to AM vegetation, which contrasts with patterns reported for temperate forests. We suggest that different mechanisms of soil organic matter accumulation explain the contrasting impacts of EcM dominance on topsoil properties of temperate and tropical biomes. Global vegetation and C models should account for the contrasting impacts of distinct mycorrhizal vegetation in different climatic zones.

3.1. Introduction

Mycorrhizal associations play a major role in the maintenance and functioning of terrestrial ecosystems. Arbuscular mycorrhiza (AM) and ectomycorrhiza (EcM) are the most taxonomically and geographically widespread mycorrhizal associations, being dominant in the majority of terrestrial biomes (Soudzilovskaia et al. 2019). It has been estimated that approximately 80% of the Earth's plant species form mycorrhizal associations with AM or EcM fungi (Brundrett and Tedersoo 2018). These two types of mycorrhizal fungi differ in physiology and morphology (Smith and Read 2008), which leads to strong differences in nutrient acquisition strategies. While EcM fungi produce exudates with extracellular lytic enzymes that can break down organic compounds (Read et al. 2004), AM fungi generally lack these saprotrophic abilities, obtaining nutrients mostly from inorganic compounds (Smith and Smith 2011).

The fundamental differences between AM and EcM fungal traits have led to the hypothesis that ecosystems dominated by EcM or AM plants have significant differences in processes of soil carbon (C) and nutrient cycling and storage (Read and Perez-Moreno 2003, Phillips et al. 2013, Brzostek et al. 2015). Consequently, this hypothesis predicts that ecosystems dominated by EcM are characterized by a slow turnover of soil organic matter, allowing the accumulation of larger pools of organic C and nitrogen (N) bound in complex recalcitrant organic molecules within the surface soils (Phillips et al. 2013, Averill and Hawkes 2016, Craig et al. 2018). These conditions select for a soil microbial community primarily dominated by ectomycorrhizal fungi with high enzymatic activity related to organic N and P liberation (Cheeke et al. 2017) and retarded activities of decomposers (Rousk and Bååth 2007). In contrast, AM-dominated systems have a rapid nutrient cycling, where labile plant litter is rapidly transformed into inorganic forms by both bacteria and saprotrophic fungi (Read 1991, Phillips et al. 2013).

Various studies examining soil biogeochemical cycles of AM- and EcM-dominated forest stands near each other suggest an active role of plant mycorrhizal types in soil carbon and nutrient cycling. However, this hypothesis has been primarily tested and corroborated in temperate forests of the northern hemisphere where AM and EcM

trees usually coexist and where data collection is generally facilitated by well-established long-term plots (Tedersoo and Bahram 2019). Extrapolations of this theory to other biomes remains controversial, especially so for tropical rainforests (Corrales et al. 2018).

Similarly to temperate forests, tropical forests feature gradients from AM to EcM-dominated forest stands (Brearley 2012, Nouhra et al. 2019, Steidinger et al. 2019). But, higher temperature and rainfall, limitation of P and other rock-derived nutrients (Camenzind et al. 2018) and hyper-diverse biological communities (Gentry 1992) make biogeochemical processes in tropical forests intrinsically different from temperate forests. Consequently, it is unclear whether this transition in plant mycorrhizal traits reflects (or promotes) changes in soil biogeochemical cycling.

A few local-scale studies have specifically addressed this issue, with contrasting results. Torti *et al.* (2001) showed that soils in a monodominant EcM forest had a lower availability of N for plants than the contiguous AM mixed forest. Along the same lines, Corrales *et al.* (2016) hypothesized that the higher abundance of the EcM tree *Oreomunnea mexicana* in a Panamanian tropical forest was linked to the depletion of available N as a result of lower mineralization rates. However, other studies in tropical biomes have not found differences in soil properties when comparing EcM-dominated plots with adjacent AM plots (Hart et al. 1989, Moyersoen et al. 1998, Henkel et al. 2002, Read et al. 2006, Peh et al. 2011). Moreover, Keller & Phillips (2019) found that, in tropical areas, AM trees and EcM trees did not differ in litter decay rates, which contradicts the patterns in temperate regions.

Altogether these studies suggest that the mechanisms that lead to the remarkable differences in soil biogeochemical cycling between AM and EcM tree stands in temperate forests may be different or may be weakened in the tropics. However, to the best of our knowledge, no study has been conducted that includes the whole tropical biome and covers the full gradient of AM to EcM tree dominance to evaluate the existence of consistent functional differences between the two mycorrhizal types. Given the ecological and economic value of tropical forests, understanding whether dominant mycorrhizal traits can be used as proxies of soil biogeochemical cycling will

lead to a better prediction of changes in carbon and nutrient cycling in the future climate, land-use changes or species introductions.

Here, we aim to evaluate changes in soil chemical and biological properties along the gradient from AM to EcM-dominated tropical systems. We base our research on a dataset containing information on topsoil properties, climatic conditions, microbial abundance, and mycorrhizal tree abundance from all four continents that contain tropical forests. Based on our analysis, we suggest a new framework explaining the role of EcM in global patterns of soil C accumulation and nutrient turnover.

3.2. Methods

3.2.1. Sample and data collection

We used 97 topsoil samples originating from a global set of soil samples presented in the study of Tedersoo *et al.* (2014). We selected all samples collected in tropical (n=83) and subtropical (latitude between 23.5° and 34°N/S; n=14) moist (mean annual precipitation (MAP)> 1500mm y⁻¹; n=8) and dry (MAP< 1500mm y⁻¹; n=89) lowland (altitude <800m; n=79) and lower montane (altitude >800m and <1500m; n=18) forests (henceforth referred to as tropical forests) (Figure 3.1). A detailed description of soil sampling can be found in Tedersoo *et al.* (2014). In short, soil samples were collected from 2500-m² plots. After removing loose debris from the forest floor, 40 topsoil cores were collected using PVC tubes (5 cm deep, 5 cm in diameter) from each of the selected plots. The soil cores included both organic and mineral horizons. These 40 soil cores were pooled, homogenised, and subsequently examined for microbial community composition and soil properties.

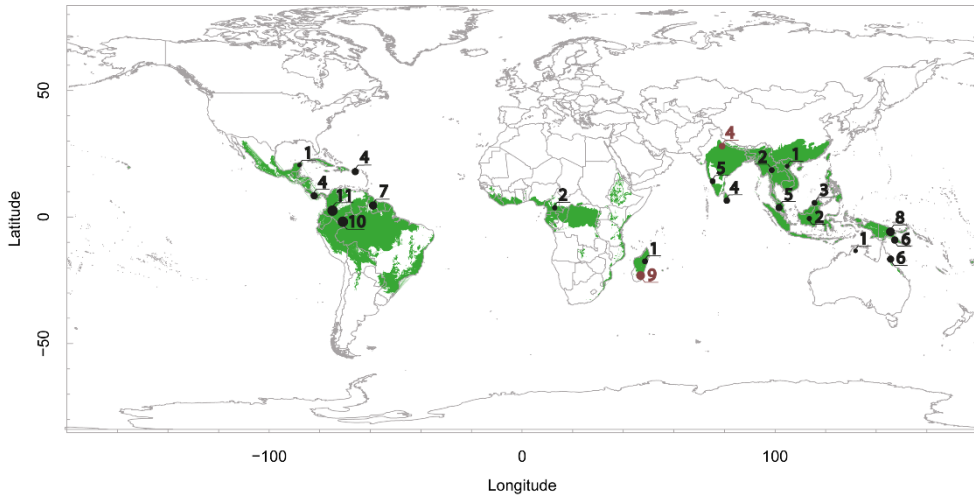


Figure 3.1: Map with the 97 independent sample locations. The green area shows the tropical and subtropical moist and dry broadleaf forest biome derived from the World Wildlife Fund (WWF) ecoregions layer (Olson et al. 2001). For better visualization, each circle indicates areas with one or more sample locations and numbers indicate the number of independent sampling locations located at each black circle. Brown circles indicate subtropical samples.

At each of the 97 plots, known EcM trees and shrubs were identified and their relative contribution to stand basal area was estimated as a proxy for EcM-associated trees abundance. Due to the low abundance of non-mycorrhizal trees and other mycorrhizal types in tropical areas (Soudzilovskaia et al. 2019, Soudzilovskaia et al. 2020), we consider all non-EcM plants as being AM hosts. Therefore, the relative abundance of EcM trees is seen as complementary to the relative abundance of AM trees (i.e. 20% coverage of EcM trees equals 80% of AM trees).

3.2.2. Soil properties and climate data

Soil chemical properties were determined as described in Tedersoo *et al.* (2012). The concentration of soil total carbon (total C), total nitrogen (total N), ammonium lactate soluble phosphorus (P), exchangeable potassium (K), calcium (Ca), and magnesium (Mg) cations were examined to assess the effect of distinct types of mycorrhizal trees on the amount and composition of soil organic matter. Additionally, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

were examined, as these reflect soil organic matter (SOM) recalcitrance (Boström et al. 2007) and mineralization rates (Houlton et al. 2006), respectively.

To control for climate in addition to soil conditions (Conant et al. 2011), we included data on the mean annual temperature (MAT) and MAP at 30 arc-seconds resolution originally retrieved from the WorldClim database (www.worldclim.org).

3.2.3. Microbial abundance

3.2.3.1. Phospholipid fatty acid (PLFA) analysis

To explore the impacts of distinct types of mycorrhizal plants on soil microbial communities, we obtained data on the abundance of the main microbial groups (fungi and bacteria) by performing a phospholipid fatty acid (PLFA) analysis. From that original batch, 34 samples could not be recovered or there was not enough material for analysis. Therefore, 63 samples were finally used for PLFA analysis. The lipid extraction from soil was performed using a one-phase mixture following Bligh & Dyer (1959) as modified by White *et al.* (1977) and Frostegård *et al.* (1991). Lipids were extracted from 1, 2, or 3 g of dried soil (depending on their SOM content) with 10 ml of Bligh & Dyer solution (CHCl₃: MeOH: citrate buffer 1:2:0.8 v/v/v). The extracted lipids were fractionated into neutral lipids, intermediate lipids, and polar lipids on pre-packed silica columns by eluting with 1.5 ml chloroform, 6 ml acetone, and 1.5 ml methanol, respectively (van Aarle and Olsson 2003). The neutral and polar lipids (containing phospholipids) were evaporated again after adding 100 µl of fatty acid methyl ester (FAME) 19:0 as internal standard. The intermediate lipids were discarded. The samples were dissolved in 1 ml toluene:methanol (1:1) and KOH in methanol (0.2 M), and incubated at 37°C for 15 min. After cooling, 2 ml of hexane:chloroform (4:1, v/v), 0.3 ml of acetic acid (1 M) and 2 ml of water were added. The upper (organic) phase obtained was transferred to a new test tube and evaporated. The samples were dissolved with 100 µl of hexane and analysed on a Hewlett Packard 6890a gas chromatograph.

The sum of the PLFA i15:0, a15:0, 15:0, i16:0, 16:1S9, i17:0, a17:0, cy17:0, 18:1 ω 7, and cy19:0 was used as a proxy of bacterial biomass (Frostegård and Bååth 1996). The amount of PLFA 18:2 ω 6 was used as a proxy of saprotrophic (and EcM) fungal biomass. The ratio 18:2 ω 6 to bacterial PLFA was used as an index of the F:B abundance ratio in the soil.

3.2.3.2. Sequencing Data

The soil fungal community was characterised using 454 pyrosequencing (Tedersoo *et al.* 2014). This data contains sequences of the ITS2 regions classified taxonomically and functionally, differentiating 12 relevant lifestyles, including arbuscular mycorrhizal, ectomycorrhizal, and saprotrophic fungi (ericoid and orchid mycorrhiza were not included). We used the total number of fungal OTUs as a proxy of the fungal richness and the relative abundance of saprotrophic fungi (calculated as the total reads of saprotrophic fungi relative to the total fungal reads) as a proxy for the abundance of saprotrophic fungi. For a detailed protocol on DNA extraction, sequencing, and bioinformatics procedures see Tedersoo *et al.* (2014).

3.2.4. Statistical analysis

A set of univariate Generalized Additive Models for Location, Scale and Shape (GAMLSS) were fitted to relate the relative abundance of EcM trees to individual soil, climatic, and microbial proxies of biogeochemical cycling using the “gamlss” package (Stasinopoulos and Rigby 2007) in R Studio. A GAMLSS approach was selected as it allows fitting flexible regression models using a beta distribution, which is appropriate for modelling continuous proportions (Douma and Weedon 2019). As the beta distribution assumes values of the response variable to be >0 and <1 while our dataset contains 0 (i.e. absences of EcM trees in the plot) and 1 (i.e. only EcM trees in the plot) values, we used the transformation $x' = \frac{x(N-1) + 0.5}{N}$ where N is the sample size (Smithson and Verkuilen 2006). The existence of non-linear relationships was explored by plotting residual vs fitted values of the univariate models. As no clear trends were detected, GAMLSS were fitted using linear predictors. Logarithmic

transformations were applied to total N, total C, P, K, Mg, and Ca to meet model assumptions. We further tested differences among tropical systems (tropical vs subtropical; moist vs dry; lowland vs lower montane) on the univariate models by including these factors as interaction terms. We did not find any influence of these distinctions on the main trends (see Supporting information Table S3.1).

To visualize the relationship between the soil properties and EcM trees abundance we also performed a Principal Component Analysis (PCA) using the “prcomp” function of R package “stats”.

To determine the importance of the selected biogeochemical drivers on explaining EcM trees abundance, we performed a multivariable model selection. The full GAMLSS model contained only a set of non-correlated climatic and soil variables (i.e. Pearson correlation <0.6 and a variance inflation factor (VIF) <3) that were significant in the univariate models. As total N and total C were highly correlated (Pearson correlation = 0.967), only total N was included in the multivariable model due to its higher univariate R^2 . Bacterial and fungal PLFA data were excluded from the multivariable model and interpreted independently, due to the high collinearity with soil C and N (see Supporting Information Table S3.2). Therefore, only MAT, MAP, Total N, C/N, $\delta^{15}\text{N}$, P, Mg, Total fungal OTUs and the relative abundance of saprotrophic fungi were included in the final model. A forward selection was performed removing non-significant variables from the model.

The presence of spatial autocorrelation (SAC) in the multivariable model residuals was tested using Moran's I test with the “morani.I” function in the “ape” package. The test confirmed the presence of SAC in the model residuals (Observed = 0.259; Expected = -0.01; P -value = 0.002) which was alleviated by explicitly including spatial coordinates in the model as a two-dimensional smooth surface (Observed = 0.059; Expected = -0.01; P -value = 0.42).

3.3. Results

3.3.1. Single variable effects on EcM trees abundance

As a first exploratory analysis, the PCA showed that distinct EcM trees abundances were separated in a multivariate space (Figure 3.2) spanned by the chemical and biological soil properties.

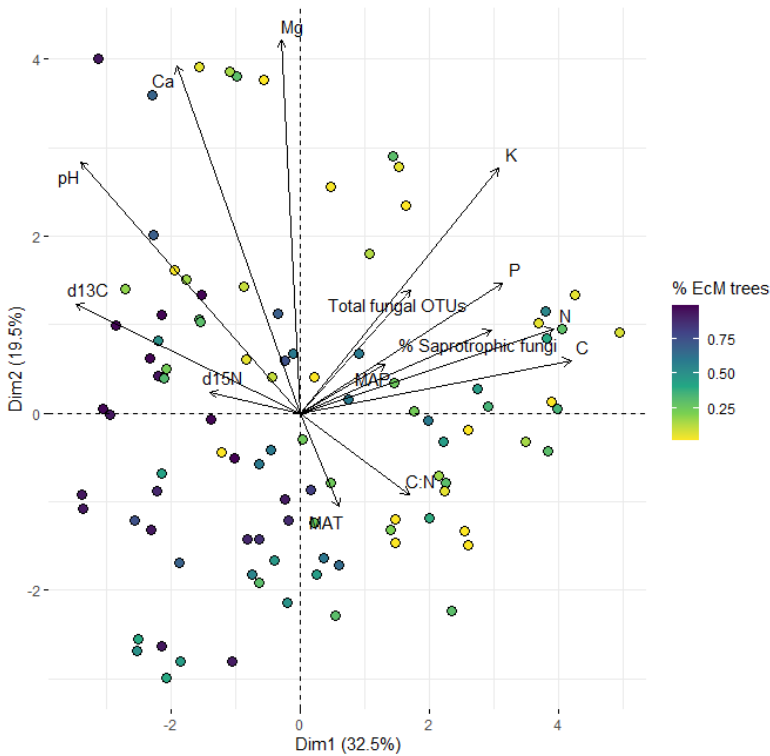


Figure 3.2: Principal components analysis (PCA) ordination plot of soil properties showing the differences in soil biogeochemistry imposed on an EcM trees abundance gradient. The vector length indicates the relative importance of the variables.

Subsequent individual GAMLSS models showed that total topsoil C and N, exchangeable P and K, MAT, and MAP decreased linearly with increasing abundance of EcM-associated trees in tropical forests (Table 3.1; Figure 3.3a-f). $\delta^{13}\text{C}$ was significantly positively related to EcM tree abundance (Figure 3.3g). Among the

predictors, topsoil total N and $\delta^{13}\text{C}$ provided the strongest models, explaining 24.1% and 22.6% of the total variance, respectively (Table 3.1).

Using the 454 sequencing data, we found that both the total number of fungal OTUs and the relative proportion of saprotrophic fungi were significantly and negatively related to the abundance of EcM trees (Table 3.1; Figure 3.3h-i).

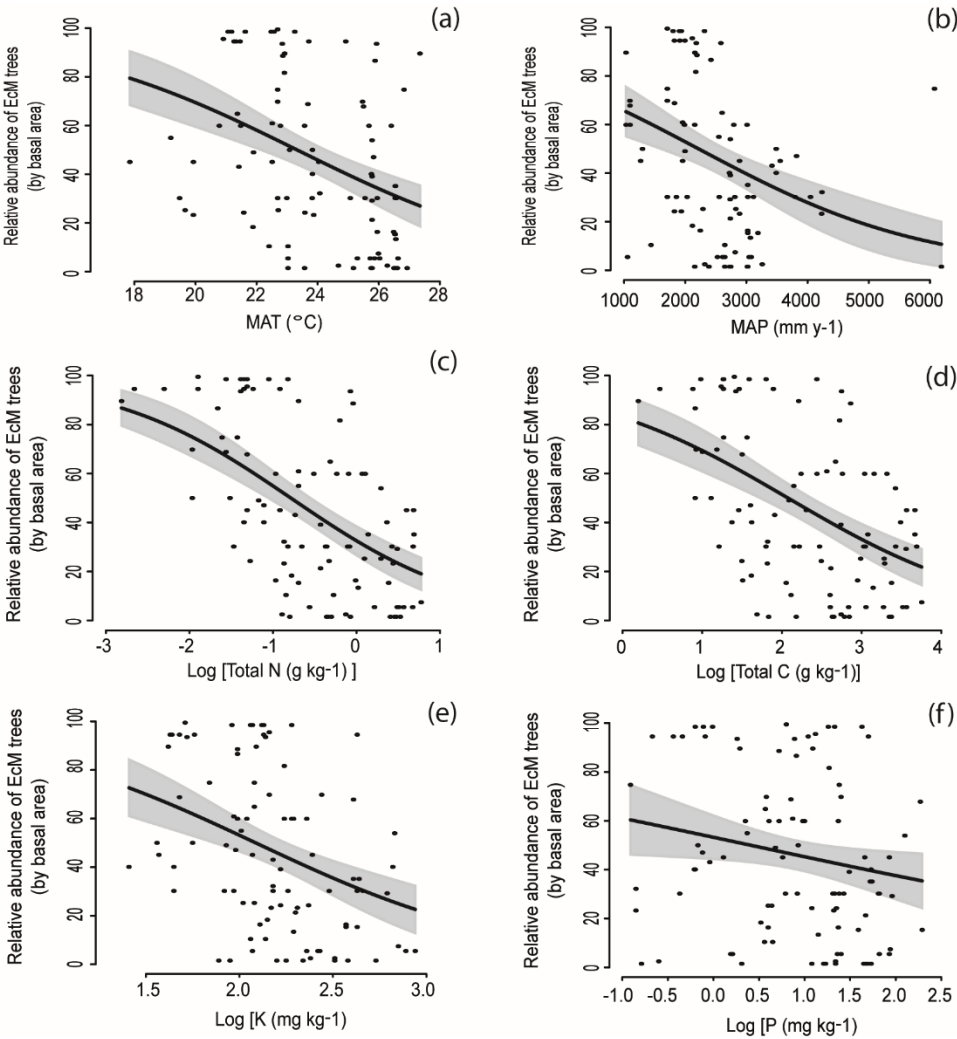
GAMLSS models of microbial abundances showed that relative EcM tree abundance was significantly (P -value < 0.05) negatively related to bacterial biomass (bacterial PLFA) (Table 3.1; Figure 3.3j). Fungal PLFA showed a marginally significant (P -value > 0.05 but < 0.1) negative relationship with EcM tree abundance, whereas F/B ratio did not show any significant relationship (Table 3.1).

Table 3.1: Regression coefficients, standard errors, t -values, P -values, and pseudo- R^2 for single variable GAMLSS models predicting EcM tree abundances based on individual soil biogeochemical proxies.

	Coefficient	Std. Error	t-value	P -value	Pseudo- R^2
MAT ($^{\circ}\text{C}$)	-0.241	0.058	-4.138	<0.001	0.159
MAP (mm y ⁻¹)	-0.0005	0.0001	-4.933	<0.001	0.121
Total N* (g kg ⁻¹)	-1.198	0.229	-5.23	<0.001	0.241
Total C* (g kg ⁻¹)	-0.052	0.011	-4.497	<0.001	0.186
C/N	0.035	0.029	1.194	0.235	0.014
C/P	-0.009	0.005	-1.784	0.08	0.042
N/P	0.024	0.013	1.862	0.07	0.04
$\delta^{15}\text{N}$ (‰)	-0.081	0.071	-1.141	0.257	0.013
$\delta^{13}\text{C}$ (‰)	0.391	0.081	4.819	<0.001	0.226
pH	0.203	0.104	1.947	0.0545	0.038
P* (mg kg ⁻¹)	-0.332	0.158	-2.105	0.0379	0.044
K* (mg kg ⁻¹)	-1.472	0.369	-3.985	<0.001	0.147
Mg* (mg kg ⁻¹)	-0.290	0.271	-1.07	0.287	0.011
Ca* (mg kg ⁻¹)	0.063	0.223	0.283	0.778	0.001
Total fungal OTUs	-0.01	0.002	-4.287	<0.001	0.17

Relative abundance of saprotrophic fungi (%)	-0.043	0.008	-5.633	<0.001	0.272
Bacterial PLFA (nmol g ⁻¹)	-0.011	0.003	-4.134	<0.001	0.235
Fungal PLFA (nmol g ⁻¹)	-0.058	0.031	-1.835	0.071	0.053
log(F/B+1)	3.683	3.482	1.058	0.294	0.017

Bold *P*-values indicate significant relations. *Variables log-transformed



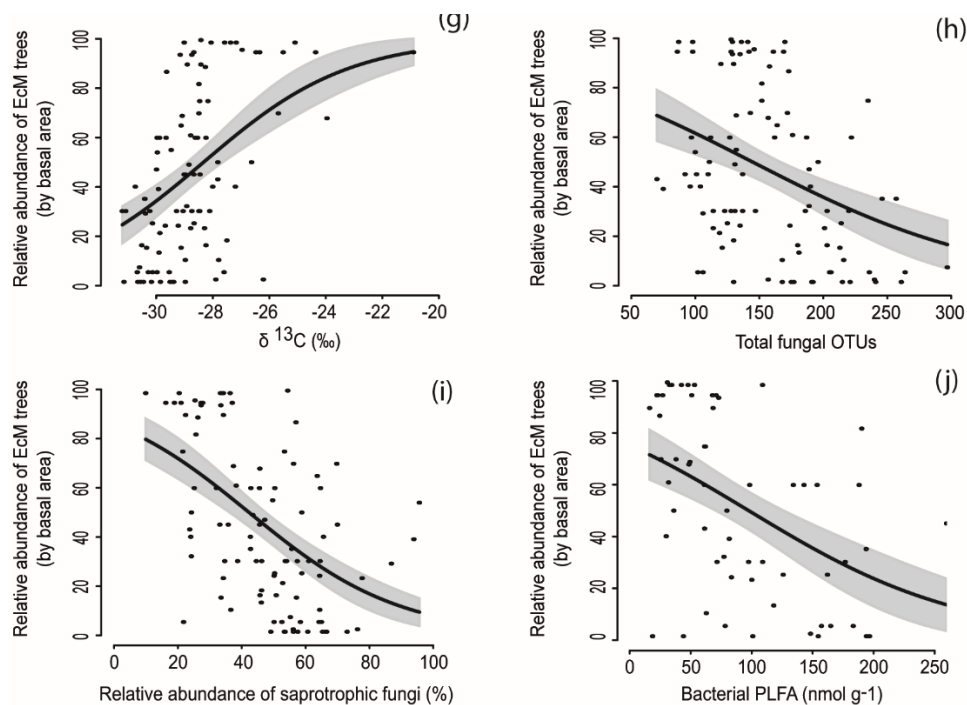


Figure 3.3: Predicted relationships between the proportion of EcM-associated trees and biogeochemical proxies in the single variable models. Each relation was calculated by setting the other variables to the mean value. Light coloured shades show the region within the 95% confidence interval.

3.3.2. Multivariable model

When all non-correlated biogeochemical proxies were included in one model, only total N, MAT, and the relative abundance of saprotrophic fungi remained in the best model (Table 3.2). Together, these three predictors explained 50% of the total variance in EcM trees abundance. When substituting total N by total C, very similar patterns with only slightly lower R^2 (0.45) were obtained. In both cases, total N and total C were the most important predictors. MAT and the relative abundance of saprotrophic fungi accounted for 12.3% and 11.6%, respectively, of the model variance.

Table 3.2: Predictors, coefficients, standard errors, *t*-values, *p*-values, and total pseudo- *R*² of the final multivariable GAMLSS model and the pseudo-*R*² that is attributed to each variable.

	Coefficient	Std. Error	t-value	<i>P</i> -value	Pseudo- <i>R</i> ²	Contribution to pseudo- <i>R</i> ^{2*}
MAT (°C)	-0.16	0.046	-3.482	<0.001	0.50	0.123
Total N (g kg⁻¹)	-0.668	0.134	-4.976	<0.001		0.186
Relative abundance of saprotrophic fungi (%)	-0.023	0.007	-3.517	<0.001		0.116

*Due to the presence of joint effects (which refers to the shared contribution in the final model), the sum of the independent contribution of each variable to the model Pseudo-*R*² does not necessarily approximate to the pseudo-*R*² of the final model.

3.4. Discussion

During the last decades, the amount of information about the mycorrhizal status of tropical plants has been growing rapidly (Brearley 2012, Corrales et al. 2018, Nouhra et al. 2019). However, the influence of distinct types of mycorrhizal associations on the ecological processes in tropical areas is still poorly understood compared to that in temperate and boreal biomes. Using a large dataset that covers the full gradient of EcM trees relative abundance, we provide the first evidence that topsoil chemistry and topsoil microbial characteristics, along with climate, are linearly related to EcM abundance across the tropical biome.

3.4.1. Biogeochemical patterns in tropical EcM forests

We found that topsoil total C and total N (two closely linked variables, see Supporting Information Table S3.2), were the main factors explaining EcM tree abundances, exhibiting a clear negative relation therewith. This suggests that in tropical forests, topsoil OM concentrations in EcM tree stands are generally lower than in AM systems. Moreover, the negative correlation found between EcM trees abundance and the concentration of extractable P and K, emphasizes the role of EcM fungi in the weathering of rock-derived nutrients (Landeweert et al. 2001, van Schöll et al. 2008) in tropical systems where these nutrients are known to be limited (Camenzind et al.

2018). Finally, the significant changes in microbial biomass and community composition of main decomposers suggest that SOM transformation rates may vary from AM to EcM dominated forests. In summary, our results reflect consistent differences associated with carbon and nutrient cycles between AM- and EcM-dominated vegetation in the tropical biome, pointing to lower soil fertility and lower C accumulation in forests dominated by EcM. Lower nutrient concentrations in EcM systems are consistent with the idea that the EcM symbiosis is an adaptation to low nutrient environments (Read 1991, Read and Perez-Moreno 2003).

The ecosystem properties that trigger these distinct biogeochemical syndromes found in the tropics remain unresolved. Here we explore several potential (non-mutually exclusive) mechanisms that are likely to explain associations between EcM trees and low nutrient and C concentrations in tropical systems:

1. **Litter quality pools:** Differential C and nutrient cycling in EcM tropical stands may be triggered by a distinct quality of the litter pool compared to AM stands (Cornelissen et al. 2001, Phillips et al. 2013). The lack of consistent relations between soil C/N ratio, F/B ratio and, pH with EcM tree abundance in our dataset does not support this hypothesis. In addition, previous studies found no differences in litter chemistry (Averill 2016, Keller and Phillips 2019) nor litter decay rates (Keller and Phillips 2019, Seyfried et al. 2021) between tropical AM and EcM plant species.
2. **SOM decomposition:** Generally, the lower C and nutrient concentrations found in EcM stands could be related to faster SOM transformation rates. However, the decrease in the total biomass of bacteria may indicate that the rate and magnitude of C and nutrient transformation processes are lower in EcM tropical forests than in AM forests. Moreover, the lower relative abundance of saprotrophic fungi in EcM-dominated plots is consistent with the so-called “Gadgil effect”, which refers to the inhibition of saprotrophic fungal activity by EcM fungi due to the competition for nutrients, resulting ultimately in reduced rates of SOM breakdown (Gadgil & Gadgil, 1971; Fernandez & Kennedy, 2015). Alternatively, topsoil SOC turnover may be enhanced by the saprotrophic abilities of EcM fungal communities (Tedersoo et al. 2014) that complement or even replace

saprotrophic communities as main decomposers (Lindahl et al. 2021). In a context of low fertility, rapid decomposition will minimize nutrient losses via leaching (Chuyong et al. 2000). Unfortunately, our dataset does not allow us to explicitly test the effect of EcM abundance on organic carbon turnover rates. The potential connections between microbial abundance and process rates should be further explored and tested.

3. **Litter inputs:** Lower topsoil C and N concentrations in EcM-dominated stands may be related to lower aboveground or belowground litter inputs. Lin et. al., 2016 found no differences in litter inputs between EcM and AM-dominated tropical stands, although this result is based on relatively few data points (n=19). Unfortunately, no relevant litter input proxy was available at sufficiently high resolution to allow testing this mechanism at the plots examined in our study.
4. **Role of N-fixing trees:** A higher proportion of N-fixing trees is expected in AM tropical stands (Veresoglou et al. 2012). This higher abundance of N-fixers has been related to an increased accumulation and stabilization of soil organic matter (Resh et al. 2002, Binkley 2005, Levy-Varon et al. 2019). Although the mechanism behind this relationship remains unclear, increased N availability may lead to greater fresh C inputs to the soil and a preferential decomposition of the newer and more labile forms of C over the older and recalcitrant forms (Resh et al. 2002). The role of facultative N-fixing trees and free-living N-fixers should be taken into consideration when testing this hypothesis.
5. **Climatic control:** The significant relationships between EcM abundance and temperature and precipitation suggest at least a partial climatic control on soil biogeochemical processes. Lower temperature and precipitation may favour the establishment of ectomycorrhizal associations through ecological mechanisms that improve the performance and survival of ectomycorrhizal plants and fungi (Barceló et al. 2019, Steidinger et al. 2019).

Further large scale research in tropical areas targeting EcM communities and their functional roles and specific ecosystem processes (e.g. litter inputs, decomposition rates and productivity) is key to disentangle the mechanisms underpinning the patterns

found in the tropics and may provide insights into the generic impacts of mycorrhizal associations on biogeochemical cycles.

3.4.2. Tropical vs temperate biogeochemical patterns across the AM–EcM transition

It is well established that, within temperate ecosystems, a higher abundance of EcM plants is generally associated with lower organic C and nutrient turnover rates (Phillips et al. 2013, Averill and Hawkes 2016). This effect has been traditionally related to ecosystem processes directly mediated by EcM fungi such as low turnover rate of extraradical mycelium (Leake et al. 2004, Olsson and Johnson 2005, Ekblad et al. 2013) or competition with other microorganisms that lower decomposition rates, reducing nitrogen availability to saprotrophic organisms (Gadgil and Gadgil 1971, Fernandez and Kennedy 2015). In temperate forests, EcM plant communities are known to have lower NPP (Read and Perez-Moreno 2003, Vargas et al. 2010, Averill et al. 2014) and more recalcitrant and acidic litter (Cornelissen et al. 2001, Phillips et al. 2013, Averill et al. 2019), contributing to slower carbon and nutrient cycling. This has led to the supposition that, in temperate ecosystems, EcM-dominated forests store more C than AM-dominated ones (Phillips et al. 2013, Averill and Hawkes 2016). Recent investigations questioned the validity of this view, suggesting that the mechanisms through which AM and EM vegetation impact biogeochemical cycling vary with soil depth (Craig et al. 2018, Jo et al. 2019). While EcM temperate stands usually accumulate more C in the upper surface soils, the pattern is reversed in deeper soils (Craig et al. 2018, Jo et al. 2019).

Until now, it was unclear if and how differences in biogeochemical cycling also prevail between AM and EcM vegetation types in tropical systems, making it impossible to generalize the impact of EcM on ecosystem functioning at global scales. Existing literature and our analyses on the upper surface soils suggest that mycorrhizal impacts of SOM might be expressed through a different set of mechanisms in the tropics than in the temperate zone. Figure 3.4 reviews the differences in topsoil biogeochemical properties in the transition from AM- to EcM-dominated vegetation in tropical and temperate forests according to existing literature and the results of our analysis.

	Temperate forests		Tropical forests	
	AM → EcM	References	AM → EcM	References
Litter input		Cornelissen et al. (2001)		Lin et al. (2016)*
Decomposition rates		Phillips et al. (2013); Keller and Phillips (2018)		Keller and Phillips (2018)
Litter quality		Cornelissen et al. (2001); Phillips et al. (2013); Averill et al. (2019)		Keller and Phillips (2018); Averill et al. (2019)
Nitrification rates		Cornelissen et al. (2001); Phillips et al. (2013); Lin et al. (2016)*		Lin et al. (2016)*
Bacterial biomass		Bahram et al. (2020)		Present study
Fungal biomass		Cheeke et al. (2017)		Present study
Fungal:Bacterial ratio		Cheeke et al. (2017); Bahram et al. (2020)		Present study
C/N		Averill et al. (2014); Lin et al. (2016)*; Cheeke et al. (2018); Zhu et al. (2018)*		Lin et al. (2016)*; Present study
C accumulation		Averill et al. (2014); Lin et al. (2016); Craig et al. (2018)*; Soudzilovskaia et al. (2019)		Present study
N accumulation		Lin et al. (2016)*; Craig et al. (2018)* but see Zhu et al. (2018)*		Present study
pH		Phillips et al. (2013)		Present study
P		Rosling et al. (2016) ⁺		Present study
K				Hall et al. (2019); Present study

*Only topsoil patterns included

⁺Local scale study

Figure 3.4: *Visualization of the differences in soil biogeochemical properties in the transition from AM to EcM-trees dominance in tropical and temperate forests according to literature data. For consistency, only analyses containing multiple sites at regional or continental scale comparisons were included. Local patterns were only included when no other relevant study was found. When different soil layers were investigated, only patterns resulting from topsoil layers were taken into account. Horizontal arrows indicate evidence of the absence of patterns. Question marks indicate that no relevant studies were found.*

We showed that in tropical forests, a higher proportion of EcM trees do not result in a build-up of C in the topsoil when compared to AM systems, contrary to temperate patterns. We hypothesize that the contrasting impacts on upper surface soils C concentrations between EcM temperate and tropical forests may be explained by distinct mechanisms through which the two biomes accumulate SOM in the upper soil layers.

Traditionally, the formation of stable SOM has been related mainly to the recalcitrant compounds in the litter that are not assimilated by decomposing microorganisms (Berg and McClaugherty 2008). Under this paradigm, slow decomposition promoted by recalcitrant litter would result in higher SOM stocks. We suggest that this is the primary mechanism acting in temperate forests where temperature constrains decomposition (Koven et al. 2017) and litter inputs are likely to be the primary source of SOM stocks in the upper soil (Liang et al. 2019). In this way, a transition from AM- to EcM-dominated forest leads to a build-up of SOM in the topsoil (Lin et al. 2017, Craig et al. 2018, Zhu et al. 2018) due to the higher recalcitrance of EcM plants litter in temperate forests (Cornelissen et al. 2001, Phillips et al. 2013) and the competition with saprotrophs (Gadgil and Gadgil 1971, Fernandez and Kennedy 2015).

In contrast, in tropical forests, the litter of EcM plants does not decay slower than AM litter (Keller and Phillips 2019) and temperature is not likely to limit saprotrophic activity. Thus, overall decay rates themselves may be less strongly limiting the final concentrations of topsoil SOM. Instead, the microbial turnover processes may be more influential. In line with this, an emerging body of research argues that microbial products fixed to the mineral soil matrix may be the primary component of stable

3

SOM (Liang and Balser 2011, Cotrufo et al. 2013, Kallenbach et al. 2016, Sokol and Bradford 2019). Consequently, conditions enhancing rates of microbial biomass growth would promote the accumulation of microbial-stabilized SOM. In this scenario, the observed higher microbial biomass of tropical AM vegetation would lead to higher topsoil C accumulation. The lack of evidence of different recalcitrance between AM and EcM litter together with the higher bacterial biomass and higher C and N concentrations found in AM-dominated plots support this hypothesis. Additionally, the higher abundance of N-fixing trees in tropical than in temperate AM-dominated ecosystems (Steidinger et al. 2019) could induce microbial growth, promoting the stabilization and accumulation of surface SOM (Binkley 2005).

Additionally, the prevalence of AM associations in sites where topsoil SOM is accumulated may be related to the importance of leaching processes in tropical forests. Contrary to temperate forests, tropical systems feature significant losses of dissolved nutrients by leaching (Montagnini and Jordan 2005). As AM fungi lack saprotrophic capabilities (Smith and Read 2008), AM associations would be favoured in locations where the soil is stabilized and losses of dissolved nutrients by leaching are minimized. In contrast, EcM fungi can access nutrients directly from organic sources (Smith and Read 2008) and can effectively immobilize nutrients through a more extensive hyphal network (Agerer 2001), and are less susceptible to leaching losses.

We suggest that using the dominant type of mycorrhizal association to predict soil biogeochemical properties based solely on patterns from the temperate zone can be misleading. Further mycorrhizal research in tropical forests explicitly testing differences in SOM cycling and accumulation between temperate and tropical forests, and accounting for differences in soils depth is needed for a better understanding of mycorrhizal effects on ecosystem functioning in different climatic zones.

3.5. Concluding remarks

Our data show that in tropical forests, EcM associations are mainly found in non-fertile soils. This reinforces the view of EcM associations being dominant in ecosystems where plant communities are nutrient-limited. However, in contrast to the patterns

observed in the temperate zone, the dominance of EcM trees does not result in an accumulation of the topsoil C. We suggest that the contrasting effect of mycorrhizal type in topsoil C concentrations between temperate and tropical biomes is related to differences in their mechanisms of SOM accumulation in the upper surface soils, which are triggered by distinct climatic and biotic conditions. Global models of vegetation dynamics and SOM pools should account for the impacts of mycorrhizal associations on soil biogeochemical processes and their associated microbial mechanisms in different climatic zones.

3.6. Acknowledgements

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3.7. Conflict of Interest

The authors declare that there is no conflict of interest.

3.8. Author contributions

M.B., N.A.S. and P.M.v.B. conceived the manuscript. P.A.O. assisted with PLFA analysis. L.T. contributed data. M.B. performed the statistical analysis and wrote the manuscript with substantial input from all the authors.

3.9. Data availability

The data that support the findings of this study are openly available in Figshare at <http://doi.org/10.6084/m9.figshare.13260227>

3.10. Supporting Information

Table S3.1: Estimates and *P*-values of univariate *GAMLSS* models including data points from only tropical or subtropical areas, dry or moist climates and lowland or lower montane locations.

	Sub-biome 1				Sub-biome 2				Sub-biome 3			
	Tropical		Subtropical		Dry		Moist		Lowland		Lower montane	
	<i>Estimate</i>	<i>P-value</i>	<i>Estimate</i>	<i>P-value</i>	<i>Estimate</i>	<i>P-value</i>	<i>Estimate</i>	<i>P-value</i>	<i>Estimate</i>	<i>P-value</i>	<i>Estimate</i>	<i>P-value</i>
MAT (°C)	-0.21	<0.001	-0.18	0.01	-0.26	<0.001	-0.25	<0.001	-0.3	<0.001	-0.33	<0.001
MAP (mm y⁻¹)	-0.0004	<0.001	0.0001	0.73	-0.002	<0.001	-0.001	<0.001	-0.0005	<0.001	-0.0005	<0.001
Total N* (g kg⁻¹)	-0.83	<0.001	-1.27	<0.001	-0.49	0.152	-0.989	<0.001	-0.94	<0.001	-0.855	<0.001
Total C* (g kg⁻¹)	-0.76	<0.001	-0.43	0.032	-0.71	0.002	-0.76	<0.001	-0.79	<0.001	-0.68	<0.001
C/N	0.02	0.53	0.06	0.05	0.04	0.32	0.03	0.23	0.03	0.23	0.3	0.28
δ15N (‰)	-0.1	0.183	-0.01	0.93	-0.05	0.672	-0.097	0.207	-0.09	0.231	-0.09	0.613
δ13C (‰)	0.37	<0.001	0.33	<0.001	0.46	<0.001	0.43	<0.001	0.39	<0.001	0.39	<0.001
pH	0.16	0.11	0.41	<0.001	0.15	0.2	0.23	0.04	0.2	0.06	0.22	0.07
P* (mg kg⁻¹)	-0.47	0.004	0.56	0.06	-0.07	0.86	-0.33	0.04	-0.35	0.03	-0.07	0.8
K* (mg kg⁻¹)	-1.46	<0.001	-0.98	0.01	-1.41	<0.001	-1.45	<0.001	-1.45	<0.001	-1.39	<0.001
Mg* (mg kg⁻¹)	-0.57	0.05	-0.07	0.79	-0.25	0.41	-0.26	0.36	-0.25	0.36	-0.22	0.5
Ca* (mg kg⁻¹)	-0.07	0.75	0.32	0.16	0.07	0.78	0.11	0.63	0.1	0.66	0.15	0.55
Total fungal OTUs	-0.01	<0.001	-0.005	0.06	-0.01	0.006	-0.01	<0.001	-0.01	<0.001	-0.01	<0.001
Relative abundance of saprotrophic fungi (%)	-0.05	<0.001	-0.02	0.008	-0.04	<0.001	-0.04	<0.001	-0.04	<0.001	-0.04	<0.001
Bacterial PLFA (nmol g⁻¹)	-0.01	<0.001	-0.005	0.2	-0.009	0.042	-0.012	<0.001	-0.012	<0.001	-0.01	0.012
Fungal PLFA (nmol g⁻¹)	-0.072	0.039	0.01	0.84	-0.04	0.5	-0.06	0.08	-0.05	0.12	-0.06	0.27
log(F/B+1)	-0.81	0.88	5.63	0.14	3.3	0.78	4.04	0.26	4.52	0.21	-1.58	0.83

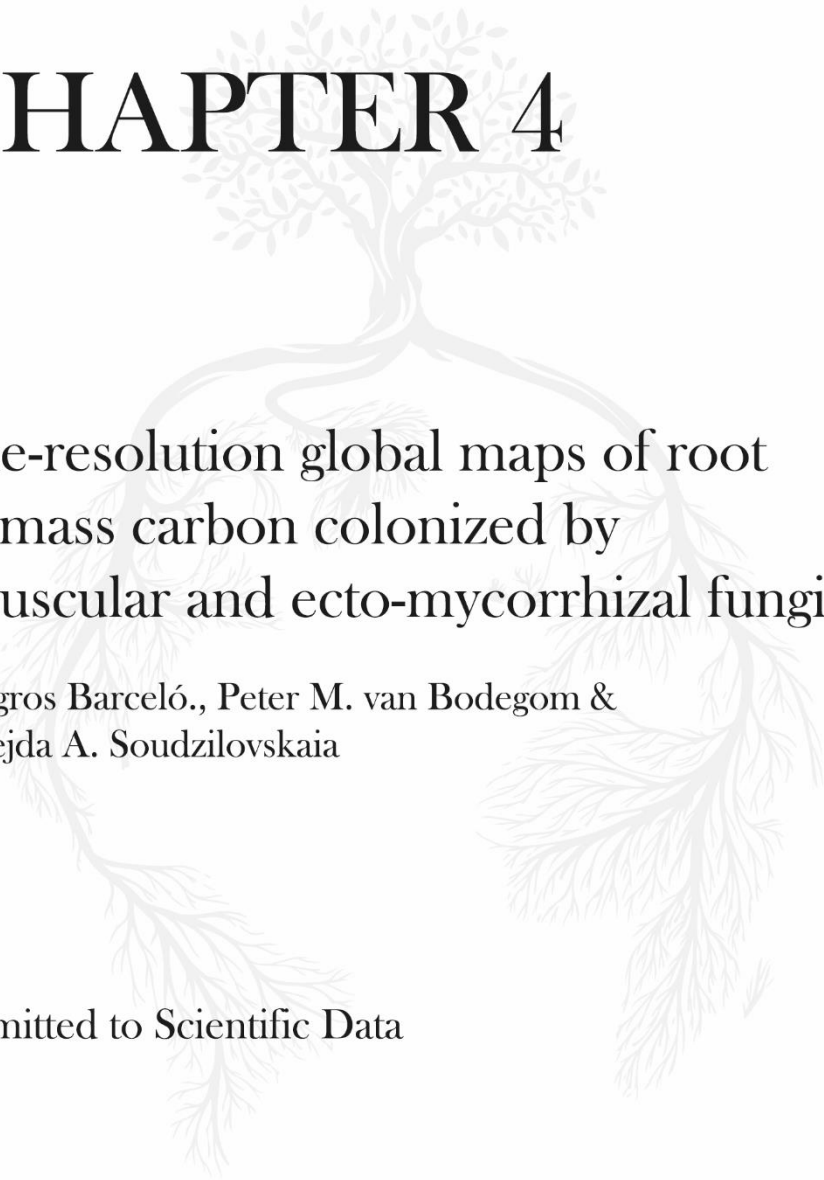
Table S3.2: Person correlation matrix of soil, climatic and microbial abundance variables.

	NPP	MAP	MAT	N	C	C/N	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	pH	LogP	LogK	LogMg	LogCa	Saprotrophs	Total fungal OTUs	Bacterial PLFA	Fungal PLFA	F/B
NPP	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MAP	0.28	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MAT	0.23	0.40	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N	0.11	0.11	0.13	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C	0.13	0.10	0.12	0.97	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-
C/N	-0.06	-0.18	-0.11	0.10	0.30	1.00	-	-	-	-	-	-	-	-	-	-	-	-
$\delta^{15}\text{N}$	0.01	0.01	0.21	-0.17	-0.29	-0.53	1.00	-	-	-	-	-	-	-	-	-	-	-
$\delta^{13}\text{C}$	-0.19	-0.32	-0.35	-0.52	-0.56	-0.15	0.24	1.00	-	-	-	-	-	-	-	-	-	-
pH	-0.17	-0.12	-0.03	-0.45	-0.55	-0.46	0.23	0.64	1.00	-	-	-	-	-	-	-	-	-
LogP	-0.02	-0.29	0.18	0.54	0.57	0.15	-0.11	-0.35	-0.35	1.00	-	-	-	-	-	-	-	-
LogK	0.03	-0.02	0.26	0.66	0.66	0.07	-0.13	-0.29	-0.13	0.64	1.00	-	-	-	-	-	-	-
LogMg	-0.41	-0.18	-0.02	0.12	0.08	-0.02	-0.14	0.23	0.57	0.17	0.42	1.00	-	-	-	-	-	-
LogCa	-0.36	-0.15	-0.04	-0.16	-0.23	-0.21	0.02	0.45	0.83	-0.07	0.19	0.82	1.00	-	-	-	-	-
Saprotrophs	-0.06	0.03	0.23	0.44	0.46	0.19	-0.12	-0.40	-0.35	0.47	0.46	0.13	-0.08	1.00	-	-	-	-
Total fungal OTUs	-0.27	0.12	0.26	0.30	0.28	0.00	0.13	-0.25	-0.12	0.18	0.37	0.22	0.04	0.28	1.00	-	-	-
Bacterial PLFA	0.20	0.04	0.03	0.86	0.85	0.07	-0.17	-0.42	-0.40	0.36	0.52	0.03	-0.16	0.30	0.18	1.00	-	-

Fungal PLFA	0.13	-0.02	0.02	0.62	0.71	0.39	-0.25	-0.37	-0.53	0.40	0.46	0.03	-0.23	0.29	0.16	0.70	1.00	-
F/B	-0.19	-0.18	-0.10	0.01	0.13	0.60	-0.19	-0.12	-0.36	0.21	0.05	0.11	-0.08	0.21	0.09	-0.02	0.54	1.00

Numbers in bold indicate pairs of variables with correlation $r > 0.6$

CHAPTER 4



Fine-resolution global maps of root
biomass carbon colonized by
arbuscular and ecto-mycorrhizal fungi

Milagros Barceló., Peter M. van Bodegom &
Nadejda A. Soudzilovskaia

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Abstract

Despite the recognized importance of mycorrhizal associations in ecosystem functioning, the actual abundance patterns of mycorrhizal fungi belowground are still unknown. This information is key for better quantification of mycorrhizal impacts on ecosystem processes and to incorporate mycorrhizal pathways into global biogeochemical models. Here we present the first high-resolution maps of fine root stocks colonized by arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM) fungi (MgC ha^{-1}). The maps were assembled by combining multiple open source databases holding information on root biomass carbon, the proportion of AM and EcM tree biomass, plot-level relative abundance of plant species and intensity of AM and EcM root colonization. We calculated root-associated AM and EcM abundance in 881 spatial units, defined as the combination of ecoregions and land cover types across six continents. The highest AM abundances are observed in the (sub-)tropics, while the highest EcM abundances occur in the taiga regions. These maps serve as a basis for future research where continuous spatial estimates of root mycorrhizal stocks are needed.

4.1. Background and summary

Mycorrhizal associations are key components of terrestrial ecosystems, influencing plant community composition (Van der Heijden et al. 1998, Klironomos et al. 2011), and soil structure (Leifheit et al. 2013) and biogeochemical fluxes (Read and Perez-Moreno 2003, Veresoglou et al. 2012, Averill et al. 2014). However, these impacts have different magnitudes and directions depending on the mycorrhizal types involved. Arbuscular mycorrhiza (AM) and ectomycorrhiza (EcM) are the most taxonomically and geographically widespread mycorrhizal associations, being present in approximately 80% of the Earth's plant species (Brundrett and Tedersoo 2018) and are known to differ in their impacts (Phillips et al. 2013, Soudzilovskaia et al. 2015).

To quantify the impacts of different mycorrhizal types in ecosystem processes and to incorporate mycorrhizal pathways into global biogeochemical models we need information about the actual abundance of mycorrhizal associations in ecosystems. As a mutualistic association between a plant and a fungus, a comprehensive understanding of mycorrhizal abundance requires taking into account the biomass of each partner and the level of intimacy between them (Soudzilovskaia et al. 2015).

Information about the relative abundance of distinct mycorrhizal host plants has been accumulating rapidly at regional (Fisher et al. 2016, Swaty et al. 2016, Bueno et al. 2017, Jo et al. 2019) and global scale (Soudzilovskaia et al. 2019, Steidinger et al. 2019) as a tool to quantify the impact of mycorrhizal types on ecosystem functioning. By contrast, current knowledge about the abundance of mycorrhizal fungi belowground is still scarce, despite its direct impact on soil ecosystem functioning.

The belowground abundance of mycorrhizal fungi comprises abundances of fungal mycelium in soil (extraradical mycelium) and in plant roots (intraradical mycelium). As the assessment of the extraradical mycelium abundance is extremely difficult due to current methodological constraints (Leake et al. 2004), this is poorly known at the regional and global scale. In contrast, the mycorrhizal abundance in plant roots is commonly reported in mycorrhizal literature (Soudzilovskaia et al. 2020) as the proportion of root length colonized by AM fungi or root tips colonized by EcM fungi.

Yet this information is typically provided for individual species and is rarely accompanied by data on the abundance of these species. While the intensity of root colonization of plant species quantifies the level of intimacy between plants and fungi, it still does not provide information about the actual abundance of intraradical mycelium of mycorrhizal fungi at the ecosystem level. For each mycorrhizal type, this parameter will ultimately depend on the total stock of fine roots capable to form given mycorrhizal associations (i.e. high colonization intensity but small root stocks will result in low total biomass of mycorrhizal fungi within plant roots).

Treseder et al. (2006) made the first quantification of total AM root stocks in different biomes. Yet, this analysis lacks spatial resolution and is based on very coarse estimations of AM plants abundance, root stocks and colonization intensity. Estimations of EcM root stocks are currently unavailable. In recent years, data on above and belowground plant abundance, and plant traits (including mycorrhizal traits) has been rapidly accumulating and compiled in open-access databases (Kattge et al. 2011, Soudzilovskaia et al. 2020, Spawn et al. 2020, Sabatini et al. 2021). The release of these global high-quality data records allows making a big step in understanding patterns of mycorrhizal abundance belowground.

Here we present the first fine-resolution map of AM and EcM abundance in roots (expressed as total carbon (C) in root biomass colonized by AM and EcM fungi). To assemble the map we combined data on root biomass C (Spawn et al. 2020), the proportion of AM and EcM tree biomass (Soudzilovskaia et al. 2019), plot-level relative abundance of plant species (Sabatini et al. 2021) and intensity of AM and EcM root colonization (Soudzilovskaia et al. 2020). As a categorisation basis to create our maps, we calculated root-associated AM and EcM abundance in 881 spatial units, defined as the combination of ecoregions and land cover types across six continents. These units are relevant to the distribution of mycorrhizal host plants (Soudzilovskaia et al. 2019) and enable higher spatial resolution than maps based upon main biome classification. The new maps presented here 1) contribute to a better understanding of mycorrhizal global patterns, and allow examining drivers of these patterns, 2) help to identify the ecosystems that are more dependent on mycorrhizas and, consequently, more likely to be affected via changes in climatic conditions due to changes in

mycorrhizal abundance, and 3) aid inferring mycorrhizal abundances in the soil matrix once the relationship between intraradical colonization and extraradical mycelium biomass (Barceló et al. 2020) has been confirmed at biome scale.

4.2. Methods

To calculate total root biomass C colonized by AM and EcM fungi, we developed a workflow that combines multiple publicly available datasets to ultimately link fine root stocks to mycorrhizal colonization estimates (Figure 4.1). These estimates were individually derived for 881 different spatial units that were constructed by combining 28 different ecoregions, 15 land cover types and six continents. In a given spatial unit, the relationship between the proportion of AM- and EcM-plants aboveground biomass and the proportion of AM- and EcM-associated root biomass depends on the prevalence of distinct growth forms. Therefore, to increase the accuracy of our estimates, calculations were made separately for woody and herbaceous vegetation and combined in the final step and subsequently mapped. Below we detail the specific methodologies we followed within the workflow and the main assumptions and uncertainties associated

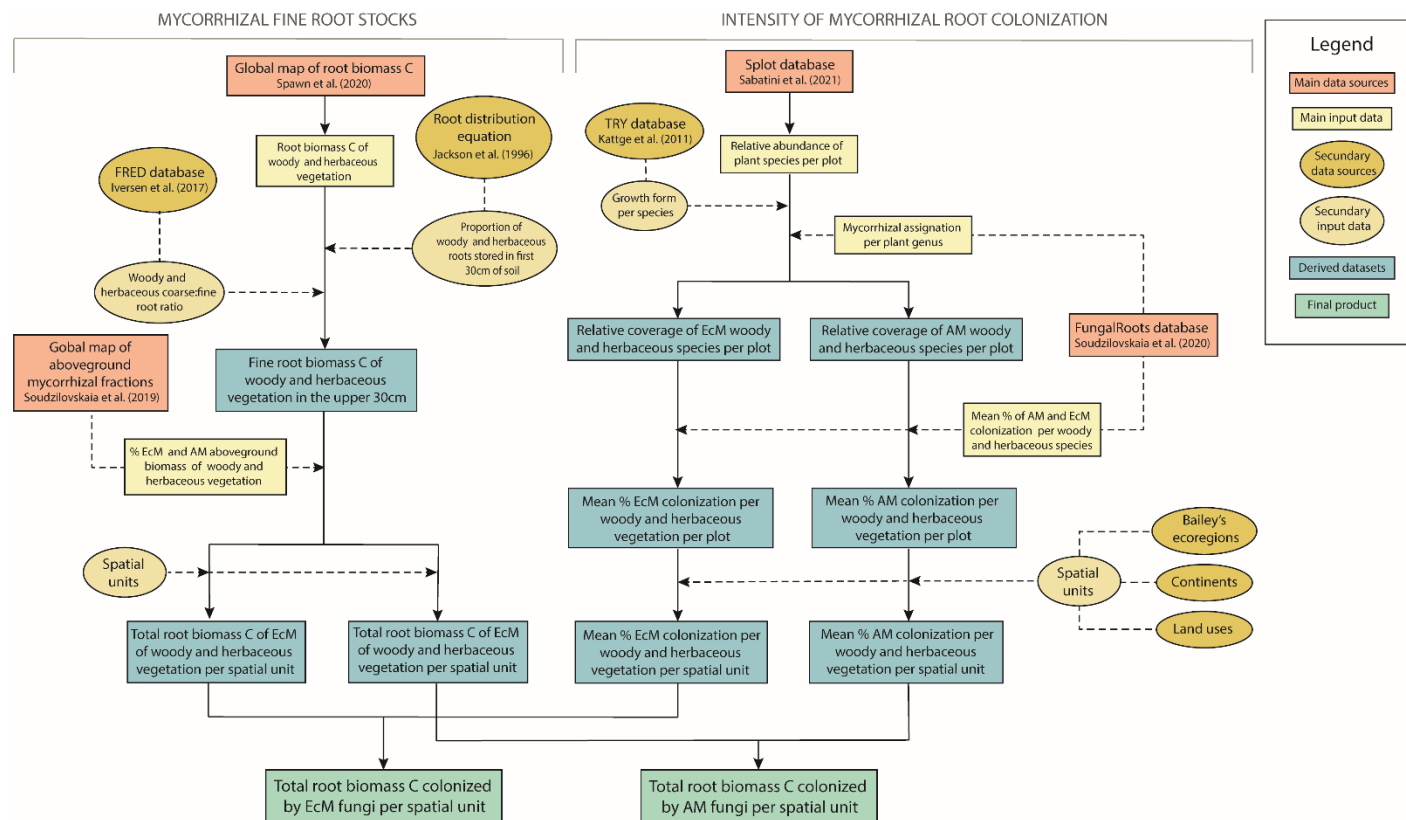


Figure 4.1: Workflow used to create maps of mycorrhizal fine root biomass carbon. The workflow consists of two main steps: 1) Estimation of total fine root stock capable to form mycorrhizal associations with AM and EcM fungi and 2) estimation of the proportion of fine roots colonized by AM and EcM fungi.

4.2.1. Definition of spatial units

As a basis for mapping mycorrhizal root abundances at a global scale, we defined spatial units based on a coarse division of Bailey's ecoregions (Bailey 2014). After removing regions of permanent ice and water bodies, we included 28 ecoregions defined according to differences in climatic regimes and elevation (see Supplementary Table S4.1). A map of Bailey's ecoregions was provided by the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL 2017) at 10 arcmin spatial resolution. Due to potential considerable differences in plant species identities, ecoregions that extended across multiple continents were split for each continent. The continent division was based upon the FAO Global Administrative Unit Layers (<http://www.fao.org/geonetwork/srv/en/>). Finally, each ecoregion-continent combination was further divided according to differences in land cover types using the 2015 Land Cover Initiative map developed by the European Space Agency at 300m spatial resolution (<https://www.esa-landcover-cci.org/>). To ensure reliability, non-natural areas (croplands and urban areas), bare areas and water bodies were discarded (Supplementary Table S4.2). In summary, a combination of 28 ecoregions, 15 land cover types and six continents were combined to define a total of 881 different spatial units (Supplementary Table S4.3). The use of ecoregion/land cover/continent combination provided a much greater resolution than using a traditional biome classification and allowed to account for human-driven transformations of vegetation, the latter based on the land cover data.

4.2.2. Mycorrhizal fine root stocks

4.2.2.1. Total root C stocks

Estimation of the total root C stock in each of the spatial units was obtained from the harmonized belowground biomass C density maps of Spawn et al. (2020). These maps are based on continental-to-global scale remote sensing data of aboveground biomass C density and land cover-specific root-to-shoot relationships to generate matching belowground biomass C maps. This product is the best up-to-date estimation of live root stock available. For subsequent steps in our workflow, we distinguished woody

and herbaceous belowground biomass C as provided by Spawn et al. (2020). As tundra belowground biomass C map was provided without growth form distinction, it was assessed following a slightly different workflow (see Section 2.2.3 for more details). To match the resolution of other input maps in the workflow, all three belowground biomass C maps were scaled up from the original spatial resolution of 10-arc seconds (approximately 300 m at the equator) to 10 arc-minutes resolution (approximately 18.5 km at the equator) using the mean location of the raster cells as aggregation criterion.

As the root biomass C maps do not distinguish between fine and coarse roots and mycorrhizal fungi colonize only the fine fractions of the roots, we considered the fine root fraction to be 88,5% and 14,1% of the total root biomass for herbaceous and woody plants, respectively. These constants represent the mean value of coarse/fine root mass ratios of herbaceous and woody plants provided by the Fine-Root Ecology Database (FRED) (<https://roots.ornl.gov/>) (Iversen et al. 2017) (Supplementary Table S4.4). Due to the non-normality of coarse/fine root mass ratios, mean values were obtained from log-transformed data and then back-transformed for inclusion into the workflow.

Finally, the belowground biomass C maps consider the whole root system, but mycorrhizal colonization occurs mainly in the upper 30 cm of the soil (Treseder and Cross 2006). Therefore, we estimated the total fine root stocks in the upper 30 cm by applying the asymptotic equation of vertical root distribution developed by Gale & Grigal (1987):

$$y = 1 - \beta^d$$

where y is the cumulative root fraction from the soil surface to depth d (cm), and β is the fitted coefficient of extension. β values of trees ($\beta=0.970$), shrubs ($\beta=0.978$) and herbs ($\beta=0.952$) were obtained from Jackson et al. (1996). A mean value was then calculated for trees and shrubs to obtain a woody vegetation β value of 0.974. As a result, we estimated that 54.6% of the total live root of woody vegetation and 77.1% of herbaceous vegetation is stored in the upper 30 cm of the soil. In combination, this

allowed deriving fine root C stocks in the upper 30 cm of woody and herbaceous vegetation.

4.2.2.2. The proportion of root stocks colonized by AM and EcM

The proportion of root stock that forms associations with AM or EcM fungi was obtained from the global maps of aboveground biomass distribution of dominant mycorrhizal type published by Soudzilovskaia et al. (2019). These maps provide the relative abundance of EcM and AM plants based on information about the biomass of grass, shrub and tree vegetation at 10arcmin resolution. To match with belowground root woody plants biomass data, proportions of AM trees and shrubs underlying the maps of Soudzilovskaia et al. (2019) were summed up to obtain the proportion of AM woody vegetation. The same was done for EcM trees and shrubs.

Our calculations are subjected to the main assumption that, within each growth form, the proportion of aboveground biomass associated with AM and EcM fungi reflects the proportional association of AM and EM fungi to belowground biomass. We tested whether root:shoot ratios were significantly different between AM and EcM woody plants (the number of EcM herbaceous plants is extremely small (Soudzilovskaia et al. 2020)). Genera were linked to growth form based on the TRY database (<https://www.try-db.org/>) (Kattge et al. 2011) and the mycorrhizal type association based on the FungalRoots database (Soudzilovskaia et al. 2020). Subsequently, it was tested whether root:shoot ratios of genera from the TRY database (<https://www.try-db.org/>) (Kattge et al. 2011) were significantly different for AM vs EcM woody plants. No statistically significant differences (ANOVA-tests p-value=0.595) were found (see Supplementary Figure S4.1)

4.2.2.3. Estimation of mycorrhizal fine root stocks

We calculated the total biomass C of fine roots that can potentially be colonized by AM or EcM fungi by multiplying the total woody and herbaceous fine root C biomass in the upper 30cm of the soil by the proportion of AM and EcM of woody and herbaceous vegetation. In the case of tundra vegetation, fine root C stocks were

multiplied by the relative abundance of AM and EcM vegetation without distinction of growth forms (for simplicity, this path was not included in Figure 4.1, but can be seen in Supplementary Figure S4.2). As tundra vegetation consists mainly of herbs and small shrubs, the distinction between woody and herbaceous vegetation is not essential in this case.

Finally, we obtained the mean value of mycorrhiza-growth from fine root C stocks in each of the defined spatial units. These resulted in six independent estimations: AM woody, AM herbaceous, EcM woody, EcM herbaceous, AM tundra and EcM tundra total fine root biomass C (see Supplementary Figure S4.3).

4.2.3. The intensity of root colonization by mycorrhizal fungi

4.2.3.1. Colonization database

The FungalRoot database is the largest up-to-date compilation of intensity of root colonization data, providing 36.303 species observations for 14.870 plant species. Colonization data was filtered to remove occurrences from non-natural conditions (i.e., from plantations, nurseries, greenhouses, pots, etc.) and data collected outside growing seasons. Records without explicit information about habitat naturalness and growing season were maintained as colonization intensity is generally recorded in the growing season of natural habitats. When the intensity of colonization occurrences was expressed in categorical levels, they were converted to percentages following the transformation methods stated in the original publications. Finally, plant species were distinguished between woody and herbaceous species using the publicly available data from TRY (<https://www.trydb.org/>) (Kattge et al. 2011). As a result, 9905 AM colonization observations of 4494 species and 521 EcM colonization observations of 201 species were used for the final calculations (Figure 4.2)

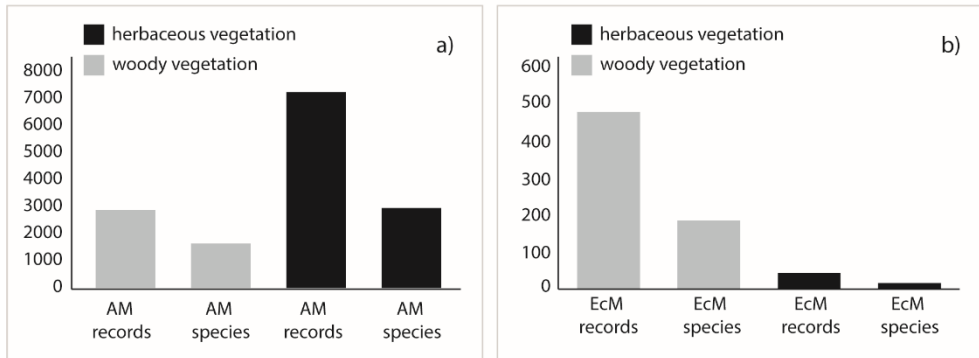


Figure 4.2: Number of AM (a) and EcM (b) herbaceous and woody plant species and total observations obtained from FungalRoot database.

The use of the mean of mycorrhizal colonization intensity per plant species is based on two main assumptions:

1. **The intensity of root colonization is a plant trait:** It is known that the intensity of mycorrhizal infections of a given plant species varies under different climatic and soil conditions (Treseder 2004, Smith and Read 2008), plant age (Javaid and Riaz 2008) and the identity of colonizing fungal species (Hart and Reader 2005). However, Soudzilovskaia et al. (2015) showed that under natural growth conditions the intraspecific variation of root mycorrhizal colonization is lower than interspecific variation, and is within the range of variations in other plant eco-physiological traits. Moreover, recent literature reported a positive correlation between root morphological traits and mycorrhizal colonization, with a strong phylogenetic signature of these correlations (Comas et al. 2014, Valverde-Barrantes et al. 2016). These findings provide support to the use of mycorrhizal root colonization of plants grown in natural conditions as a species-specific trait.
2. **The percentage of root length or root tips colonized can be translated to the percentage of biomass colonized:** intensity of root colonization is generally expressed as the proportion of root length colonized by AM fungi or proportion of root tips colonized by EcM fungi (as EcM infection is restricted to fine root tips). Coupling this data with total root biomass C stocks requires assuming that

the proportion of root length or proportion of root tips colonized is equivalent to the proportion of root biomass colonized. While for AM colonization this equivalence can be straightforward, EcM colonization can be more problematic as the number of root tips varies between tree species. However, given that root tips represent the terminal ends of a root network (Withington et al. 2006), the proportion of root tips colonized by EcM fungi can be seen as a measurement of mycorrhizal infection of the root system and translated to biomass independently of the number of root tips of each individual. Yet, it is important to stress that estimations of fine root biomass colonized by AM and EcM as provided in this paper might not be directly comparable.

4.2.3.2. *sPlot database*

The sPlotOpen database (Sabatini et al. 2021) holds information about the relative abundance of vascular plant species in 95104 different vegetation plots spanning 114 countries. In addition, sPlotOpen provides three partially overlapping resampled subsets of 50000 plots each that has been geographically and environmentally balanced to cover the highest plant species variability while avoiding rare communities. From these three available subsets, we selected the one that maximizes the number of spatial units that have at least one vegetation plot. We further checked if any empty spatial unit could be filled by including sPlot data from other resampling subsets.

Plant species in the selected subset were classified as AM and EcM according to genus-based mycorrhizal types assignments, provided in the FungalRoot database (Soudzilovskaia et al. 2020). Plant species that could not be assigned to any mycorrhizal type were excluded. Facultative AM species were not distinguished from obligated AM species, and all were considered AM species. The relative abundance of species with dual colonization was treated as 50% AM and 50% ECM. Plant species were further classified into woody and herbaceous species using the TRY database.

4.2.3.3. Estimation of the intensity of mycorrhizal colonization

The percentage of AM and EcM root biomass colonized per plant species was spatially upscaled by inferring the relative abundance of AM and EcM plant species in each plot. For each mycorrhizal-growth form and each vegetation plot, the relative abundance of plant species was determined to include only the plant species for which the information on the intensity of root colonization was available. Then, a weighted mean intensity of colonization per mycorrhizal-growth form was calculated according to the relative abundance of the species featuring that mycorrhizal-growth form in the vegetation plot. Lastly, the final intensity of colonization per spatial unit was calculated by taking the mean value of colonization across all plots within that spatial unit. These calculations are based on 38127 vegetation plots that hold colonization information, spanning 384 spatial units.

The use of vegetation plots as the main entity to estimate the relative abundance of AM and EcM plant species in each spatial unit assumes that the plant species occurrences and their relative abundances in the selected plots are representative of the total spatial unit. This is likely to be true for spatial units that are represented by a high number of plots. However, in those spatial units where the number of plots is low, certain vegetation types or plant species may be misrepresented. We addressed this issue in our uncertainty analysis. Details are provided in the Quality index maps section.

4.2.4. Final calculation and maps assembly

The fraction of total fine root C stocks that is colonized by AM and EcM fungi was estimated by multiplying fine root C stocks by the mean root colonization intensity in each spatial unit. This calculation was made separately for tundra, woody and herbaceous vegetation.

To generate raster maps based on the resulting AM and EcM fine root biomass C data, we firstly created a 10 arcmin raster map of the spatial units. To do this, we overlaid the raster map of Bailey ecoregions (10 arcmin resolution) (ORNL 2017), the

raster of ESA CCI land cover data at 300 m resolution aggregated to 10 arcmin using a nearest neighbour approach (<https://www.esa-landcover-cci.org/>) and the FAO polygon map of continents (<http://www.fao.org/geonetwork/srv/en/>), rasterized at 10 arcmin. Finally, we assigned to each pixel the corresponding biomass of fine root colonized by mycorrhiza, considering the prevailing spatial unit. Those spatial units that remained empty due to lack of vegetation plots or colonization data were filled with the mean value of the ecoregion x continent combination.

4.2.5. Quality index maps

As our workflow comprises many different data sources and the extracted data acts in distinct hierarchical levels (i.e plant species, plots or spatial unit level), providing a unified uncertainty estimation for our maps is particularly challenging. Estimates of mycorrhizal fine root C stocks are related mainly to belowground biomass C density maps and mycorrhizal aboveground biomass maps, which have associated uncertainties maps provided by the original publications. Estimates of the intensity of root colonization in each spatial unit have three main sources of uncertainties: the number of occurrences in the FungalRoot database used to calculate the mean species-level intensity of mycorrhizal colonization; the relative plant coverage in each plot that can be associated with colonization data; the number of plots used to calculate the mean intensity of colonization in each spatial unit. We provide independent quality index maps of the spatial unit average of these three sources of uncertainty. These quality index maps can be used to locate areas where our estimates have higher or lower robustness.

4.3. Data records

Maps on AM and EcM root biomass C (Figure 4.3), as well as their associated quality index maps (Figure 4.4), are available as individual raster files in tiff format. In addition, we provide herbaceous, woody and tundra AM and EcM root biomass C raster files used to construct the main product. Finally, we provide raster files of total root stocks capable to form associations with AM and EcM fungi and the intensity of AM and EcM root colonization as intermediate products. Coordinates of all raster

layers are expressed in longitude/latitude relative to the WGS84 system and the spatial resolution is 10 arc-min. These files are available through the public repository Figshare (<https://doi.org/10.6084/m9.figshare.20051249.v1>). Table 4.1 provides a summary of the available raster files.

Table 4.1: Description of the available raster layers.

Raster name	Description	Units
AM_roots_colonized	Fine root biomass carbon stocks associated with AM fungi	MgC ha ⁻¹
EcM_roots_colonized	Fine root biomass carbon stocks associated with EcM fungi	MgC ha ⁻¹
AM_herbs_roots_colonized	Herbaceous fine root biomass carbon stocks associated with AM fungi	MgC ha ⁻¹
AM_woody_roots_colonized	Woody fine root biomass carbon stocks associated with AM fungi	MgC ha ⁻¹
EcM_woody_roots_colonized	Woody fine root biomass carbon stocks associated with EcM fungi	MgC ha ⁻¹
AM_tundra_roots_colonized	Tundra fine root biomass carbon stocks associated with AM fungi	MgC ha ⁻¹
EcM_tundra_roots_colonized	Tundra fine root biomass carbon stocks associated with EcM fungi	MgC ha ⁻¹
AM_occurrences_colonization	Averaged number of occurrences in colonization database of AM species per each spatial unit	Number of occurrences
EcM_occurrences_colonization	Averaged number of occurrences in colonization database of EcM species per spatial unit	Number of occurrences
AM_rel.abundance_colonization	Mean relative abundance of AM species with colonization data per spatial unit	%
EcM_rel.abundance_colonization	Mean relative abundance of EcM species with colonization data per spatial unit	%

AM_plots	The number of plots included each spatial unit for AM calculation	Number of sPlots
EcM_plots	The number of plots included each spatial unit for EcM calculation	Number of sPlots
AM_roots	Fine root biomass C stocks that are capable to form associations with AM fungi	MgC ha ⁻¹
EcM_roots	Fine root biomass C stocks that are capable to form associations with EcM fungi	MgC ha ⁻¹
AM_intensity_colonization	The intensity of AM root colonization	%
EcM_intensity_colonization	The intensity of EcM root colonization	%

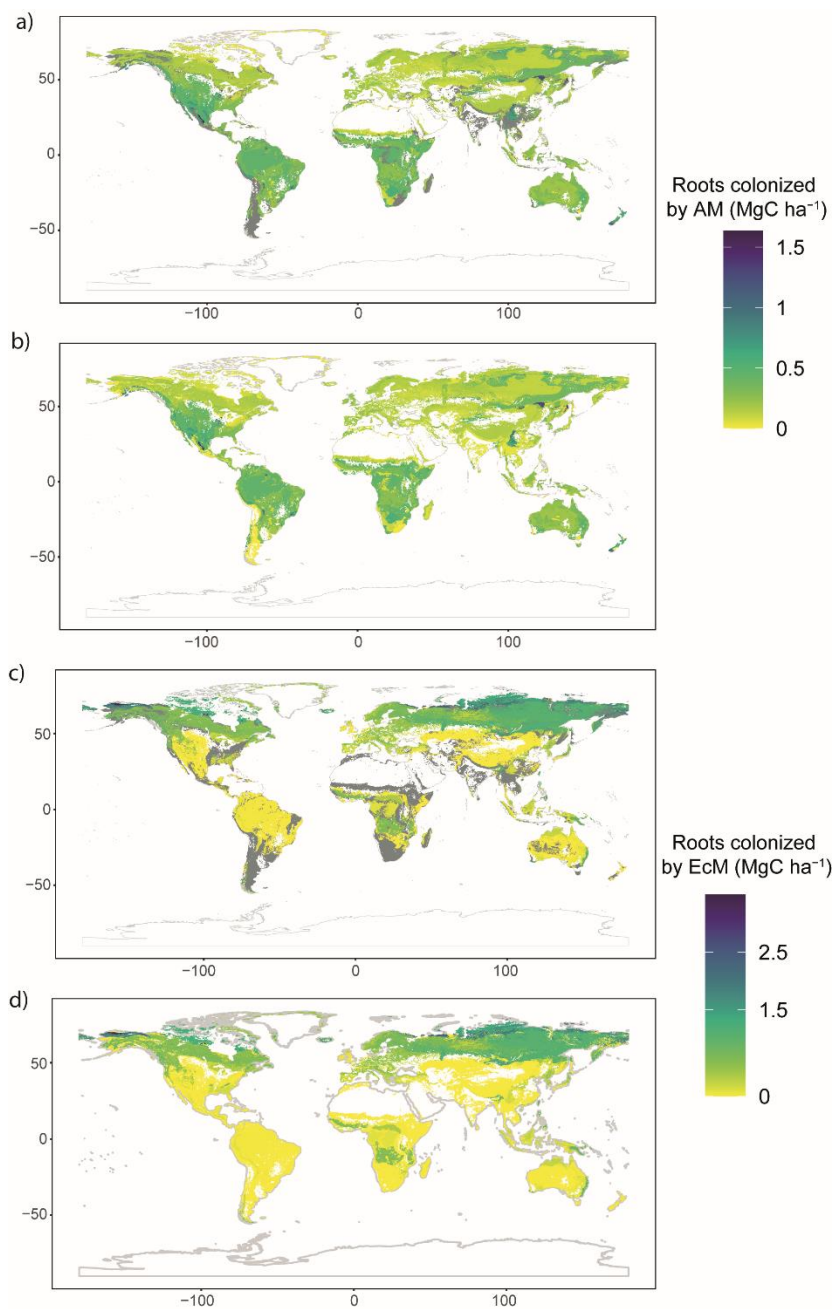


Figure 4.3: Maps of fine root biomass C colonized by AM and EcM (MgC ha^{-1}) including in grey spatial units with an absence of data (a, c) and maps with empty spatial units covered (b,d).

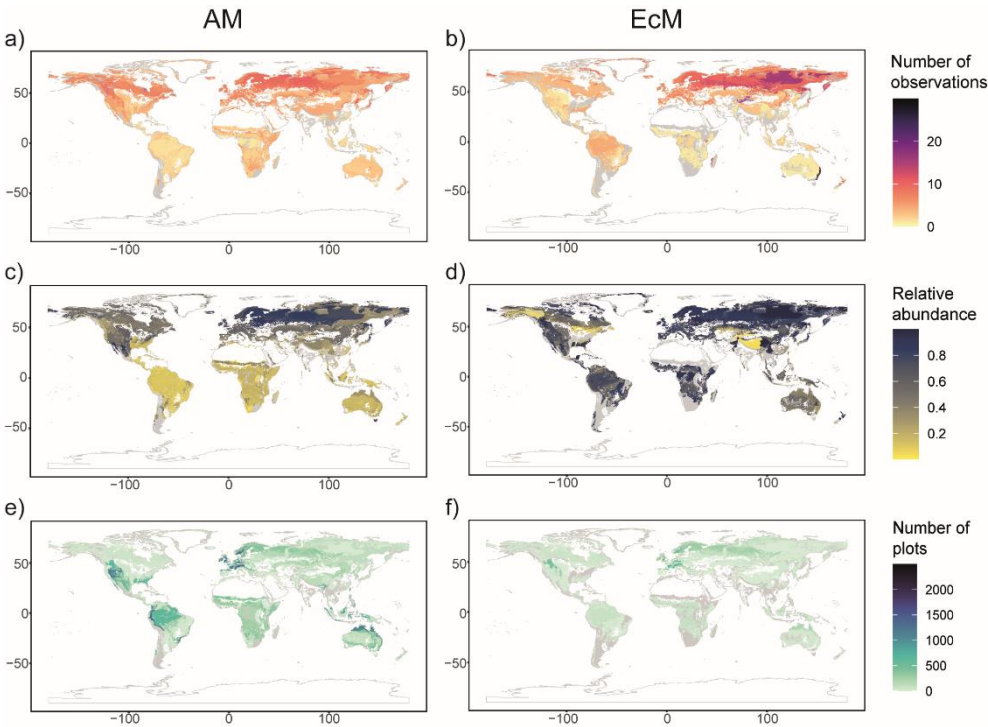


Figure 4.4: Quality index maps associated with AM and EcM total root biomass C: (a,b) The average number of occurrences in the colonization database per species in each spatial unit, (c,d) mean relative abundance of species with colonization data per spatial unit (e,f). The number of plots included in each spatial unit.

4.4. Technical Validation

Our maps are based on the combination of other maps and databases that have been previously curated and validated by the original publishers and represent the most recent and high-quality open-access information available. Through our workflow, we ensured that the introduction of errors is minimized by avoiding data that can generate biased results. Due to the lack of large-scale empirical data on belowground mycorrhizal biomass or any other similar estimation, it is not feasible to directly assess the validity of our maps.

4.5. Usage Notes

The final raster layers produced here are suitable for a broad variety of applications where continuous spatial estimates of root mycorrhizal stocks are needed. These include assessments of mycorrhizal impacts on ecosystem processes, global analyses of mycorrhizae distribution and its environmental drivers or inclusion of mycorrhizal pathways on global biogeochemical models. Additionally, the release of woody and herbaceous mycorrhizal root maps allows applications focused on specific growth forms.

Our maps are intended for continental or large scales applications. Users interested in regional or local assessments must be especially aware of the limitation and uncertainties associated with the databases used to generate the maps in the region of interest. This is particularly relevant for tropical areas that concentrate higher uncertainties and lack of data, making our estimations less robust.

Finally, it is important to note that, while our estimates can be seen as a proxy for mycorrhizal abundance within plant roots, they cannot be directly translated to intraradical (beyond roots) fungal biomass. Equations that transform root colonization into mycorrhizal fungal biomass (Toth et al. 1991) are available. However, as these formulas involve root length colonization instead of root biomass colonization, they cannot be directly applied to our estimations.

4.6. Code Availability

All mycorrhizal root biomass maps and their associated products were created in R statistical computing environment (R Core Team 2021). The code consists of five main interconnected scripts that are stored in Github repository (<https://github.com/nilimdp/Fine-resolution-global-maps-of-root-biomass-C-colonized-by-AM-and-ECM-fungi->).

1. “Spatial_units_map”: Creates raster map of spatial units
2. “Colonization_spatial_units”: Calculates the mean percentage of colonization per spatial unit

3. “Mycorrhizal_roots_biomass_stapial_unit”: Calculates mean mycorrhizal root biomass per spatial unit
4. “Final_maps”: Creates final raster maps
5. “Quality_index”: Calculates quality index per spatial unit and creates maps

4.7. Supplementary information

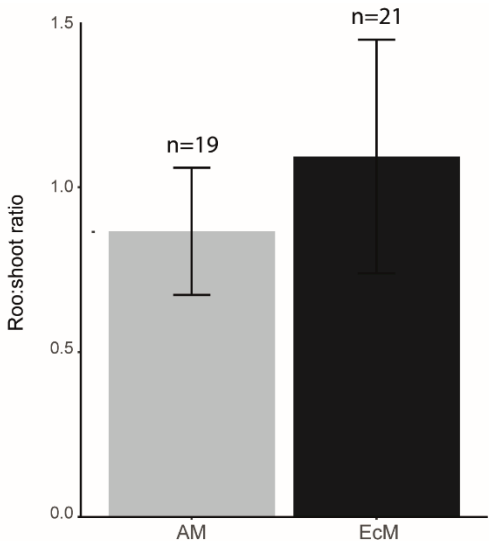


Figure S4.1: Mean and standard error of root to shoot ratios of *AM* and *EcM* woody plant species.

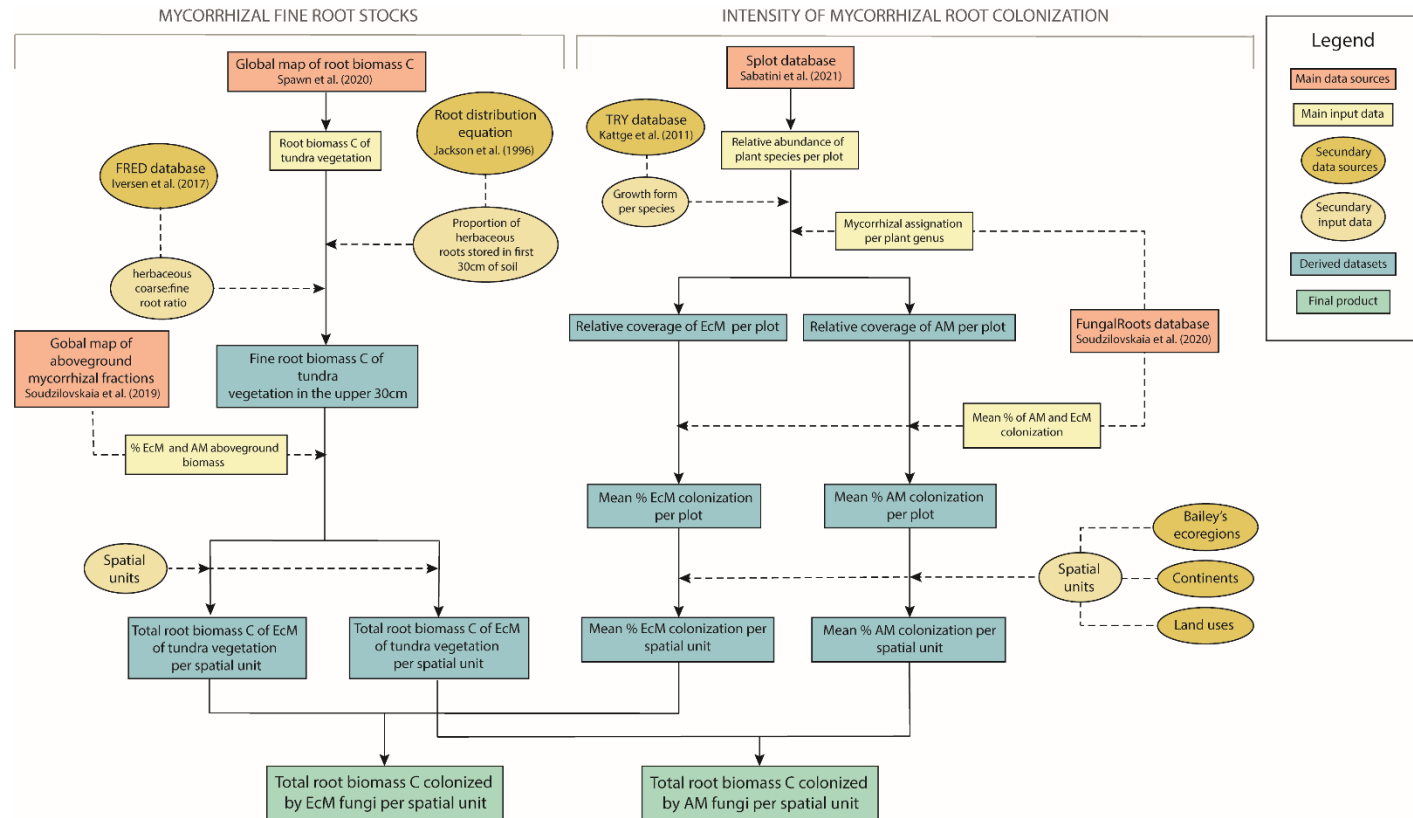


Figure S4.2: Workflow used to create mycorrhizal fine root biomass C maps specifically for tundra areas.

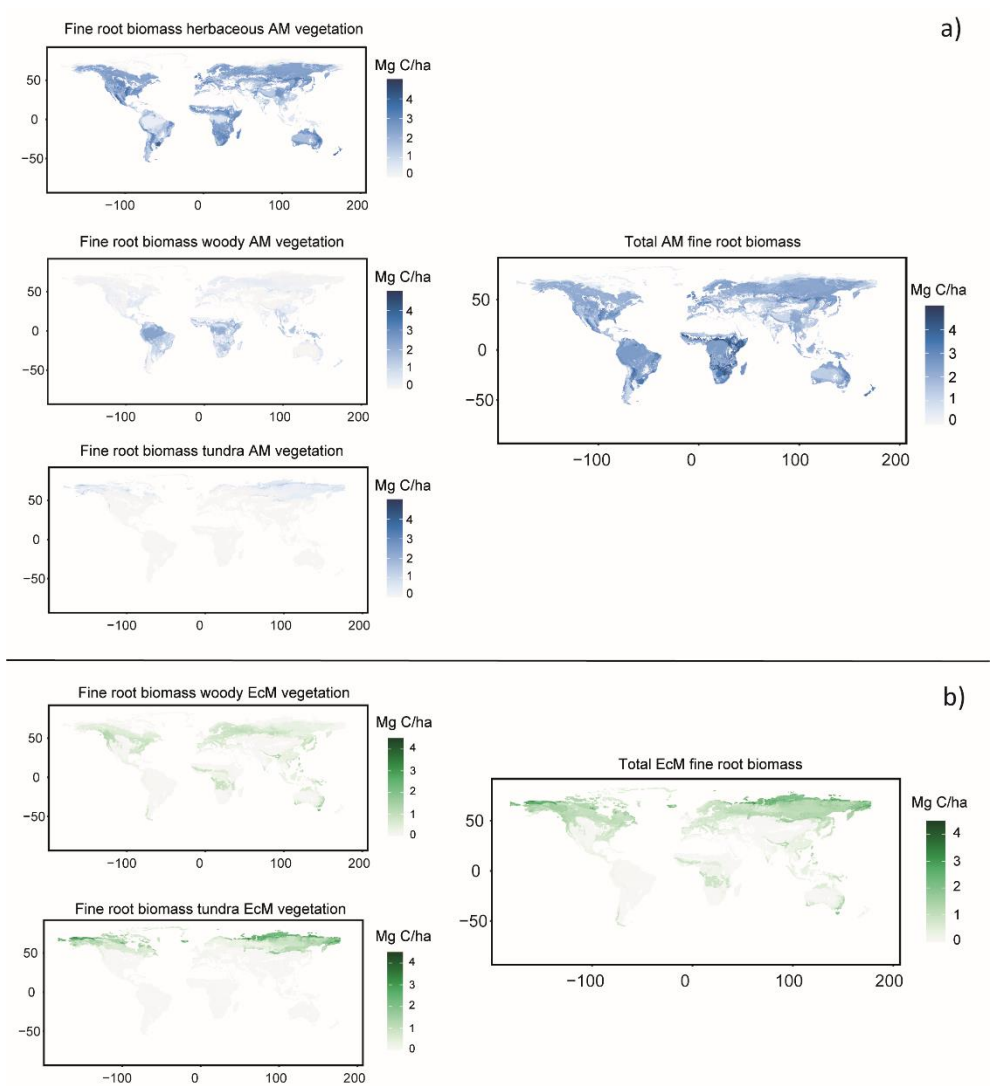


Figure S4.3: Fine root biomass stocks capable to form an association with AM (a) and EcM (b) fungi for woody, herbaceous and tundra vegetation. Final AM and EcM stock resulting from the sum of the growth form of individual maps. There were no records of fine root biomass of EcM herbaceous vegetation.

Table S4.1: Bailey ecoregions divisions and associated codes used to assemble maps of mycorrhizal root biomass

Ecoregion code and name according to Bailey (Bailey, R. G. Ecoregions. The Ecosystem Geography of the Oceans and Continents. Springer New York, 2014).			<i>Ecoregion ID used in this study</i>
<i>Original coding of Bailey ecoregions</i>	<i>Domain</i>	<i>Division</i>	
122	Polar domain	Tundra division	1
123			
124			
125			
M121		Tundra division mountain	2
M122			
131		Subarctic division	3
132			
133			
134			
135			
136			
137			
138			
M131		Subarctic division mountain	4
M132			
M133			
M134			
M135			
211		Warm continental division	5
212		Warm continental division mountain	6
M211			
M212			
M213			
221		Hot continental division	7
222			

228	Humid temperate domain		
M221		Hot continental division mountain	8
231		Subtropical division	9
M231		Subtropical division mountain	10
M232			
241		Marine division	11
242			
243			
244			
M241		Marine division mountain	12
M242			
M243			
251		Prairie division	13
252			
253			
254			
255			
M251		Prairie division mountain	14
M252			
261		Mediterranean division	15
262			
M261		Mediterranean division mountain	16
M262			
311		Tropical/subtropical steppe division	17
312			
313			
314			
315			
M312		Tropical/subtropical steppe division mountain	18
M313			
M314			
M315			

Chapter 4 – *Fine-resolution global maps of root biomass carbon colonized by arbuscular and ectomycorrhizal fungi*

321	Dry domain	Tropical/subtropical desert division	19
322			
323			
324			
325			
326			
M321		Tropical/subtropical desert division mountain	20
M322			
M323			
M324			
331		Temperate steppe division	21
332			
333			
M331		Temperate steppe division mountain	22
M332			
341		Temperate desert division	23
342			
343			
344			
345			
M341		Temperate desert division mountain	24
411	Humid tropical domain	Savanna division	25
412			
413			
414			
415			
416			
M411		Savanna division mountain	26
M412			
M413			
421		Rainforest division	27
422			
423			

424			
M421		Rainforest division mountain	28
M422			
M423			

Table S4.2: List of land cover categories within the ESA CCI Land Cover dataset, used to assemble maps of mycorrhizal root biomass. Land covers not included in the analysis are in grey. Source: ESA. CCI Land cover map 2015; <https://www.esa-landcover-cci.org/>.

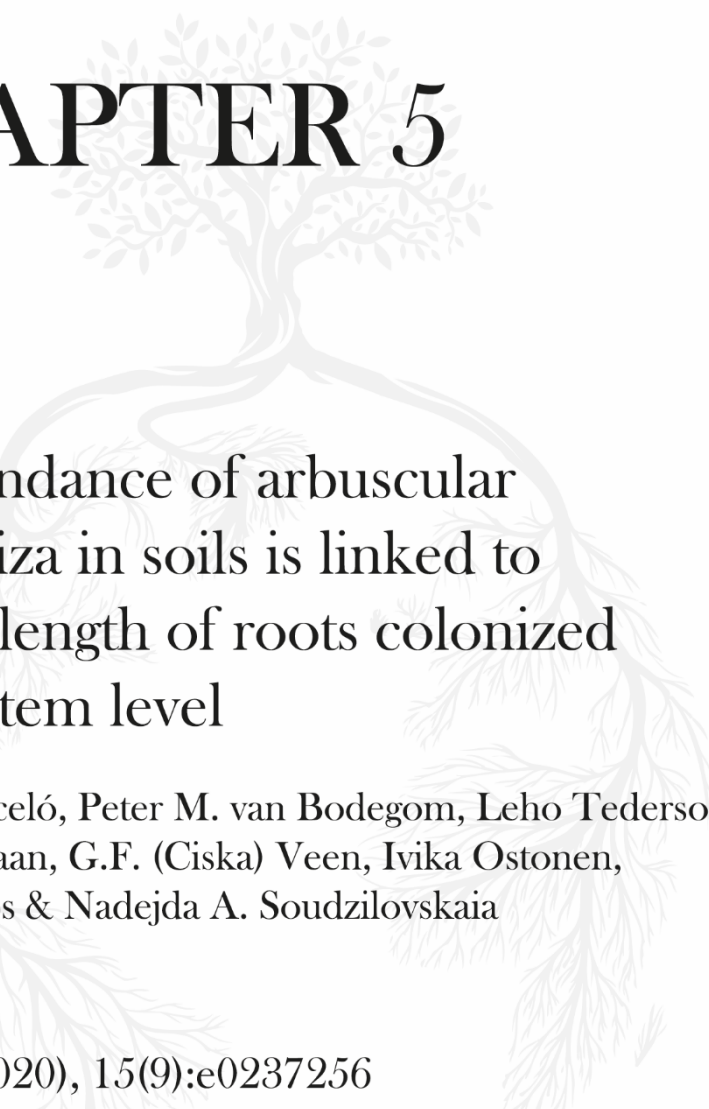
Original land cover class ID	Land cover class name
10	Cropland, rainfed
20	Cropland, irrigated or post-flooding
30	Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)
40	Mosaic natural vegetation (tree, shrub, herbaceous cover)(>50%) / cropland (< 50%)
50	Tree cover, broadleaved, evergreen, closed to open (>15%)
60	Tree cover, broadleaved, deciduous, closed to open (>15%)
70	Tree cover, needleleaved, evergreen, closed to open (> 15%-40%)
80	Tree cover, needleleaved, deciduous, closed to open (> 15%)
90	Tree cover, mixed leaf type (broadleaved and needleleaved)
100	Mosaic tree and shrub (>50%) / herbaceous cover (< 50%)
110	Mosaic herbaceous cover (>50%) / tree and shrub (<50%)
120	Shrubland
130	Grassland
140	Lichens and mosses
150	Sparse vegetation (tree, shrub, herbaceous cover)
160	Tree cover, flooded, fresh or brakish water
170	Tree cover, flooded, saline water
180	Shrub or herbaceous cover, flooded, fresh-saline or brakish water
190	Artificial surfaces and associated areas (Urban areas >50%)
200	Bare areas

201	Bare areas
202	Bare areas
210	Water bodies
220	Permanent snow and ice
0	No data (burn areas, clouds)

Table S4.3: Continent, ecoregions division and land cover category for each of the 881 defined spatial units. This table is available in Figshare (<https://doi.org/10.6084/m9.figshare.20051516.v1>).

Table S4.4: Coarse root/line root mass ratio estimations used to calculate growth-form means. This table is available in Figshare (<https://doi.org/10.6084/m9.figshare.20051516.v1>).

CHAPTER 5



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

Milagros Barceló, Peter M. van Bodegom, Leho Tedersoo, Nadja den Haan, G.F. (Ciska) Veen, Ivika Ostonen, Krijn Trimbos & Nadejda A. Soudzilovskaia

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Abstract

Arbuscular mycorrhizal fungi (AMF) strongly affect ecosystem functioning. To understand and quantify the mechanisms of this control, knowledge about the relationship between the actual abundance and community composition of AMF in the soil and in plant roots is needed. We collected soil and root samples in a natural dune grassland to test whether, across a plant community, the abundance of AMF in host roots (measured as the total length of roots colonized) is related to soil AMF abundance (using the neutral lipid fatty acids (NLFA) 16:1 ω 5 as proxy). Next-generation sequencing was used to explore the role of community composition in abundance patterns. We found a strong positive relationship between the total length of roots colonized by AMF and the amount of NLFA 16:1 ω 5 in the soil. We provide the first field-based evidence of proportional biomass allocation between intra- and extraradical AMF mycelium, at ecosystem level. We suggest that this phenomenon is made possible by compensatory colonization strategies of individual fungal species. Finally, our findings open the possibility of using AMF total root colonization as a proxy for soil AMF abundances, aiding further exploration of the AMF impacts on ecosystems functioning.

5.1. Introduction

Arbuscular mycorrhizal fungi (AMF) are widespread obligate symbionts forming associations with 85% of the vascular plant species (Brundrett and Tedersoo 2018), dominating most of the tropical forest and temperate grassland ecosystems (Read 1991, Soudzilovskaia et al. 2018). Besides the fundamental role of AMF in plant nutrition and fitness (Smith and Read 2008, Smith and Smith 2011), it is widely recognized that AMF have a substantial impact on ecosystem functioning. To understand this role, it is important to distinguish between the “intraradical mycelium”, which is the fungal biomass inside the root and the “extraradical mycelium” which is the fungal body in soil (Leake et al. 2004). While the intraradical part will likely only affect ecosystem processes indirectly through host plant nutrition and performance (Rillig 2004), the extraradical mycelium is directly related to ecosystem functioning. AMF extraradical mycelium can modify the soil microbial community structure and composition (Hodge 2000, Van Der Heijden 2002, Urcelay and Diaz 2003, Toljander et al. 2007), and enhance soil aggregation via stabilization of soil aggregates (Rillig 2004, Leifheit et al. 2013). The extraradical mycelium also acts as an active distributor of carbon (C) in the soil, feeding soil heterotrophs (Staddon et al. 2003, Pollierer et al. 2007) and stabilizing C in recalcitrant organic compounds (Treseder and Turner 2007, Sousa et al. 2012).

A comprehensive understanding of the impacts of AMF in the above-mentioned processes and the incorporation of mycorrhizal pathways into biogeochemical models requires quantitative measurements of AMF abundances in both of their functional compartments, roots and soils (Soudzilovskaia et al. 2015). Information about AMF abundances in roots (typically expressed as percentage root length colonized) is common in the literature (e.g. 19-21). In contrast, and despite their direct impact on C and nutrient cycling (Rillig 2004, Finlay 2008, Bunn et al. 2019), the abundance of AMF extraradical mycelium in natural ecosystems is rarely reported and its relation to abundances of AMF in the plant roots is poorly understood.

So far, information based on studies of single fungal isolates indicates a general increase of AMF extraradical mycelium during the process of root colonization by

5

AMF (Van Aarle et al. 2002, van Aarle and Olsson 2003). This suggests that within the same single AMF species isolate, a higher intraradical C allocation generally leads to a higher C allocation in the soil compartment. However, natural ecosystems comprise a heterogeneous network of AMF species that may have remarkable differences in the proportion of biomass they allocate inside and outside the roots (Graham et al. 1982, Hart and Reader 2002, Hart and Reader 2005). Laboratory studies demonstrate that, for instance, members of the AMF family Glomeraceae (order Glomerales) are known to have high intraradical colonization but only little expansion into the soil; members of Gigasporaceae (order Diversisporales) have the opposite colonization strategy and members of Acaulosporaceae (order Diversisporales) have low levels of both soil and root colonization (Hart and Reader 2002). Therefore, in a natural ecosystem where different AMF colonization strategies potentially coexist, whether an increase of AMF colonization in roots results in an increase of AMF mycelium in the soil is less evident and remains unsolved. Obtaining a field-based quantitative answer to this question will 1) provide important insights into the mechanisms of C and nutrient flow through mycorrhizal pathways at ecosystem level, and 2) will inform us about the feasibility of using estimates of AMF abundance in roots as a proxy of AMF soil abundance.

Here, we explore the quantitative patterns of AMF abundances in roots vs soil and the corresponding community composition in a natural dune grassland to answer the following questions: 1) is the level of colonization by AMF in the roots positively related to the abundance of AMF mycelium in the soil, within a natural ecosystem? And if so, 2) do different AMF colonization strategies influence the relationship between AMF abundance in root and soil compartments? We hypothesize that, if at the ecosystem level a single colonization strategy dominates, the proportion of biomass allocated by AMF in roots and soil compartments will remain constant, and therefore a relationship between the biomass in soil vs roots may be expected. If root and soil colonization strategies co-occur along the plant community but their intra- and extraradical relative abundances are complementary, a correlation between root and soil AMF biomass may also be expected (see Figure 5.1).

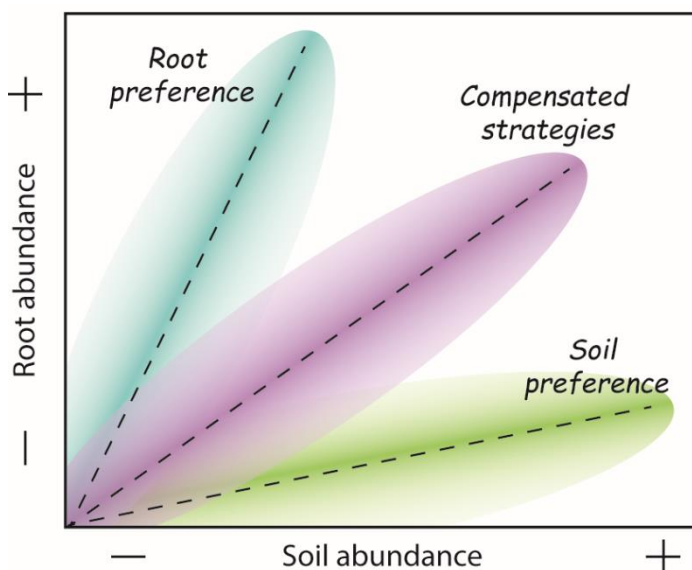


Figure 5.1: Conceptual scheme indicating possible patterns between the abundance of AMF in roots vs soil compartments. Dotted lines and coloured shapes represent three different scenarios depending on the predominance of AMF taxa with different colonization strategies. A first scenario (green shape) represents an AMF community dominated by species with preference for soil colonization. A second scenario (blue shape) represents an AMF community dominated by species with a preference for root colonization. In a third scenario (purple shape) both root and soil colonization strategies are present but their abundance tends to even out. Finally, a fourth scenario where no relationship is expected (not shown in the graph) if a) community assembly along the plant community is random (no compensated colonization strategies) or if b) the biomass allocation in root and soil of individual AMF taxa is not coupled.

5.2. Methods

5.2.1. Sample collection

Plant and soil samples were collected in May 2017 in the Kennemer Dunes National Park (52.43 N, 4.57 E), a 25 km² dune ecosystem situated along the north coast of the Netherlands. Based on a visual inspection of vegetation conditions to avoid non-mycorrhizal plants, a 350-meter-long transect was established, covering a gradient from

moist to dry soils. Such natural moisture gradient was used as a mean to ensure sampling of plant communities featuring distinct levels of AMF root colonization. This expectation is based on the fact that AMF are suppressed by high soil moisture (Miller 2000, Escudero and Mendoza 2005). Within this transect, fifteen sampling points were established. Areas with known non-mycorrhizal species were avoided.

At each sampling point, we established a circular area of approximately 3 m diameter, where five subsamples, separated from each other by at least 1 m, were collected from the topsoil layer (15 cm). These subsamples were later pooled and homogenized to obtain a total volume 1 dm³ of soil. During the collection, samples were kept frozen using dry ice to avoid degradation of organic compounds.

From each sample, soils and roots were separated by sieving. The extracted roots were carefully cleaned with tap water and weighted. Half of the root samples were preserved in 50% ethanol for AMF colonization measurements while the rest was oven-dried (35 °C, 30 h) for molecular analysis.

5.2.2. Root colonization

To estimate AMF root colonization, roots preserved in ethanol were first cut into small pieces (ca 1 cm each), cleaned with 2.5% KOH and stained by autoclaving in 5% Pelikan Blue ink (Brundrett et al. 1996). The percentage of colonization was estimated by examining vesicles, hyphae and arbuscular structures with a grid line intersect procedure (McGonigle et al. 1990). Total root length was measured with the WinRhizoTM Pro 2003b image analysis system (at 400 dpi; Regent Instruments Inc., Ville de Québec, QC, Canada). Standing root length colonized by AMF (used as a proxy of AMF abundance in roots) was calculated by multiplying the percentage of colonization and total root length per volume of soil.

5.2.3. Extraradical mycelium abundance

The abundance of AMF extraradical mycelium was measured using fatty acid analysis. The lipid extraction from 3g of freeze-dried soil was performed using a one-phase

mixture following Bligh and Dyer (Bligh and Dyer 1959) and modified by Frostegård et al (Frostegård et al. 1991). The neutral lipid fatty acid (NLFA) 16:1 ω 5 was used as a proxy for AMF abundance (Olsson 1995, Olsson and Wilhelmsson 2000).

5.2.4. AMF community structure

DNA was extracted following the protocol of Tedersoo et al (Tedersoo et al. 2014) using a PowerSoil DNA Isolation Kit (Mo Bio Laboratories, Inc., Carlsbad, CA, USA). We used 0.25 g of dried soil and 0.1 g of ground dried roots. Polymerase chain reaction (PCR) was performed using the primer pair ITS9mun/NS8a (Tedersoo and Lindahl 2016) targeting the rRNA 18S gene V9 variable region. This universal primer set was selected to cover most of the fungi including phylum *Glomeromycota* across an intron-free fragment of equal length (Nilsson et al. 2019). The PCR program consisted of 15 min incubation at 95 °C, followed by 25 cycles of 30 s at 95 °C, 30 s at 55 °C and 50 s at 72 °C. PCR products were purified using Favorgen GEL/PCR Purification Mini Kit. Amplicons were sequenced with Illumina MiSeq platform at the Estonian Genome Center.

Sequencing data were analyzed with PipeCraft (Anslan et al. 2017). To remove low-quality reads, filtering was performed with vsearch (v1.11.1) (parameters: minoverlap=15, minlength=50, E_max=1, maxambigu=0). Operational Taxonomic Units (OTU) were constructed using the UPARSE algorithm (Edgar 2013) at 97% sequence similarity threshold. Singleton clusters were removed. A post-clustering curation to OTU table was performed with LULU (Frøslev et al. 2017). Representative OTU sequences were taxonomically assigned using SILVA (release 128) database (Quast et al. 2012) with BLAST (Altschul et al. 1990) (threshold criterion $e\text{-value} < e^{-10}$). Chimera check was performed using UCHIME de novo option. No rarefaction was done because richness was unrelated to sequencing depth. The resulting OTU table was deposited in Figshare public repository (<https://doi.org/10.6084/m9.figshare.9785930.v1>).

5.2.5. Statistical analysis

The relationship between root length colonization and NLFA abundances was assessed using a linear model for vesicles, arbuscules and hyphae separately. Differences between root and soil AMF community structures were visualized using non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity using “metaMDS” function in R Package “vegan”. Root and soil community differences were tested for statistical significance using permutational multivariate analysis of variance (PERMANOVA) (“adonis” function in R Package “vegan”). PERMANOVA’s assumption of homogeneity in within-groups variability was tested using “betadisper” function in R Package “vegan”. All statistical analyses were performed using R 3.4.3 (R Core Team 2021).

5.3. Results

5.3.1. Relationship between intra-and extraradical mycelium

The linear regression models showed a significant positive relationship between the amounts of NLFA 16:1w5 in the soil and total root length colonization at the studied community (Figure 5.2). This positive relation was consistent among the different AMF structures for which colonization was measured (arbuscular, hyphae and vesicles). Root colonization by arbuscular structures showed the strongest relation with NLFA 16:1w5, followed by hyphal colonization and vesicle colonization. Despite the influence of an extremely high NLFA 16:1w5 value, the relation remained highly significant when this value was removed from the input data (see Figure S5.1-A).

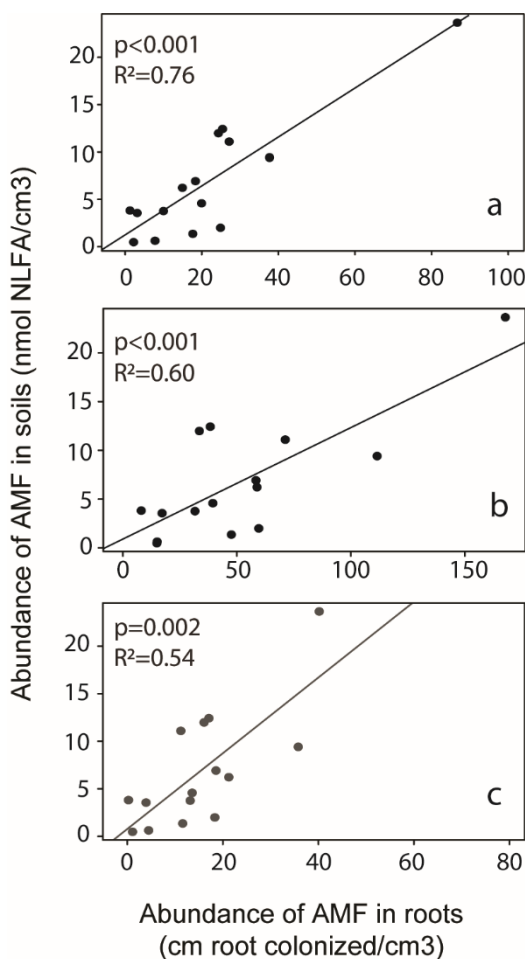


Figure 5.2: Linear relation between the AMF biomass in the soil and the total root length colonized for the three detected AMF structures. (a) arbuscules (b) hyphae and (c) vesicle. NLFA 16:1w5 was used as a proxy of the AMF biomass in the soil.

4.1.1. Community composition

Community composition analysis showed a clear dominance of members of the order Glomerales in root samples (see Figure S5.1-B). In contrast, soil samples showed a more heterogeneous composition, having in general a higher proportion of the order Diversisporales, Archaeosporales and Paraglomerales than in root samples (Figure

5.3a). Therefore, a general shift in the relative abundance of the four Glomeromycota orders can be seen between soil and plant roots. PERMANOVA analysis ratified this pattern showing significant differences ($R^2 = 0.035$, $p=0.001$) in AMF community composition between soil and roots based on OTUs' relative abundances (Figure 5.3b).

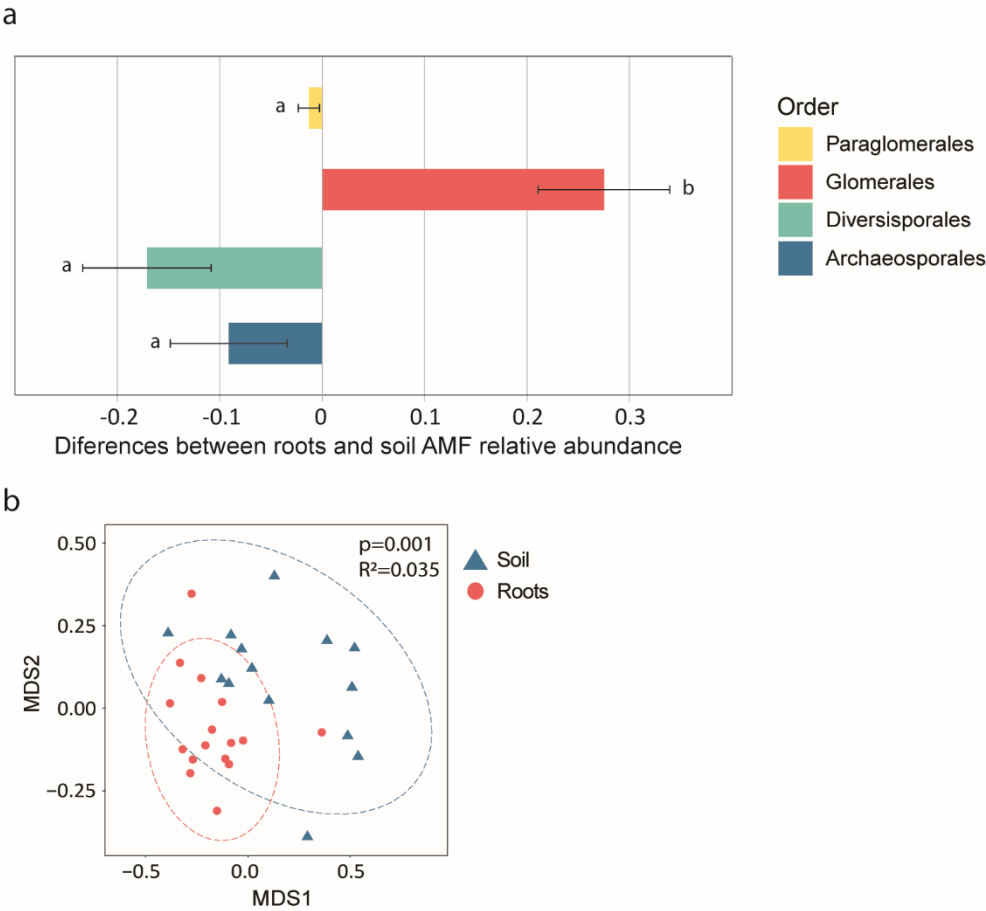


Figure 5.3: Differences in AMF community composition between root and soil samples. a) Means and standard error of the difference between the relative abundances of the AMF orders Archaeosporales, Diversisporales, Glomerales and Paraglomerales in soil and root samples. Positive values indicate that, on average, root samples had a higher relative proportion than their soil pairs, while negative values indicate the opposite trend. Different letters indicate

significant differences between orders. b) Nonmetric multidimensional scaling (NMDS) ordination plots of arbuscular mycorrhizal fungal communities present in soil and roots compartments based on relative proportions of OTUs. Ellipses delimit the 95% confidence interval around centroids

5.4. Discussion

5.4.1. Relationship between root vs soil AMF abundance

We found a strong positive relationship between the abundance of AMF in soil and the total root length colonized. Although a similar pattern has been found before in single AMF isolates (Van Aarle et al. 2002, van Aarle and Olsson 2003), our results provide the first evidence of a relationship between intra- and extraradical AMF abundance at an entire plant community level in a natural ecosystem. This suggests that, even at plant community level where different AMF species are expected, plant C allocation to the symbiotic fungi is proportionally distributed between root and soil compartments.

The strong relationship found here raises the question of whether measurements of total root colonization can be used to infer information about AMF abundance in soils or vice versa. Given the relevance of AMF for ecosystem functioning, this link is promising to gain understanding of AMF distribution in soils and roots. However, the extrapolation of the patterns found in this study to different ecosystems and environmental conditions requires caution and further testing.

Firstly, while the techniques applied here (fatty acid analysis and microscopic quantification) are widely used, they are known to induce serious biases (Vierheilig et al. 2005, Frostegård et al. 2011) that may introduce uncertainties to our results. Therefore, within the framework of this research, we have explored the possibility to use molecular quantification tools (i.e. the novel digital droplet PCR technique (Hindson et al. 2013)) as a potentially robust, accurate and rapid methodological alternative to assess AMF abundance in roots and soil. This test and its outcomes are presented in detail in the Appendix S2. In short, we have detected that the abundance of AMF in roots using ddPCR was positively related with the total root length

colonized, while using ddPCR for examining the abundance of AMF in soil was problematic, and delivered obscured results. We conclude that ddPCR techniques can already be used for the assessment of AMF abundance in roots, while the methods of using this technique for soil samples still need further development (see Appendix S2 for recommendations).

A second potential source of uncertainties is that neither the traditional nor the molecular techniques explored here can discriminate between active and dormant stages or recently dead biomass (Blagodatskaya and Kuzyakov 2013). This issue is potentially less problematic when our results are used in the context of nutrients and C cycling assessments. However, it should be considered when the assessment of ecosystem function is the main goal and differences in microbial physiological states are relevant.

5.4.2. Role of community composition

A crucial step towards further generalizations of the relationship found here is disentangling the role of AMF community composition and, specifically, the contribution of different colonization strategies (i.e. soil vs root colonizers) in affecting the relationship between root and soil abundances.

In line with the findings of several field experiments (Hempel et al. 2007, Varela-Cervero et al. 2015, Varela-Cervero et al. 2016), we found that AMF community composition differed between roots and soil compartments (Figure 5.3b). While roots were clearly dominated by members of the order Glomerales (Figure S5.1-B), their relative abundance in soil samples tended to decrease, being partially replaced by members of the order Archaeosporales and Diversisporales (Figure 5.3a). This shift in community composition between root and soil reflects, as proposed by Hart and Reader (Hart and Reader 2002), differences in colonization strategies among the main AMF groups.

Despite these differences in community composition, the ratio between AMF biomass in root and soil compartments remains relatively constant, as reflected by the strongly

significant linear relationship of soil vs roots abundance (Figure 5.2). This suggests that the second theoretical scenario presented in Figure 5.1 prevails in the studied system, indicating that co-occurring AMF species have compensatory colonization strategies, resulting in a robust relationship between soil and root abundances. The co-occurrence of different strategies may reflect an ecological specialization of co-existing AMF lineages to avoid competition for space and resources (Jansa et al. 2008, Powell et al. 2009, Maherali and Klironomos 2012). Moreover, different colonization strategies have been proposed to relate to different benefits to the plant. A more extensive extraradical mycelium is generally associated with an increase of nutrients supply to the plant (Van Der Heijden and Scheublin 2007), while a higher intensity of root colonization provides the host plant with greater protection against soil pathogens (Newsham et al. 1995). Therefore, the C flow from the host plant to their fungal partner may be distributed within different functional strategies to maximize fitness (Maherali and Klironomos 2007), which ultimately leads to coupled AMF abundances inside and outside the plant roots, even at the community level.

Even though colonization strategies seem to play an important role in assembling AMF communities, other environmental factors such as soil properties (Lekberg et al. 2007) or plant identity (Chagnon et al. 2015) can also influence AMF community composition. Within an ecosystem, the chance that higher AMF abundance in roots leads to a higher abundance in the soil will ultimately depend on the relative contribution of distinct AMF functional groups to the intra- and extra-radical biomass. Therefore, in particular conditions specific strategies may be favoured, affecting the relations found here. We tested if deviations in the AMF community mean composition of the order Divesisporales (chosen as a reference group due to its higher relative abundance in soils) were related to deviations in the relationship of AMF abundance between soil and roots (Figure S5.1-C). We found that if in a given location, the relative abundance of the order Divesisporales was higher than the community mean, the abundance of AMF in the soil was underestimated by the linear model (as indicated by positive residuals in the abundance correlation). This suggests that plant communities within which the AMF colonization strategies are not fully evened out, the relationship between intra- and extraradical may be weakened.

Further research targeting the absolute abundance of specific groups with different colonization strategies will be key to improve our understanding of AMF community assembly rules and its role in the abundance pattern of soils vs roots.

5.5. Conclusions

Our results provide the first direct evidence of a relation between AMF abundances in soils and roots at the ecosystem level, suggesting that the input from the host plant is proportionally distributed between the root-associated mycelium and the extraradical mycelium. This relationship of AMF abundances is likely to be caused by compensatory colonization strategies of individual fungal species. Specific environmental conditions may favour certain functional groups that may interfere with the coupling of AMF abundances at community level, which will demand further testing. Our findings open the possibility of using AMF intraradical abundance measurements as a proxy of extraradical abundance at a community scale. This proxy will help to estimate AMF abundance in soils, which is key towards a better understanding of terrestrial ecosystems functioning in present and future climates.

5.6. Acknowledgments

We gratefully thank Kaire Loit for her assistance in root staining procedure, Kai Ilves for her help during sample collection, Rasmus Puusepp for his assistance with sequencing and Sten Anslan for help with the bioinformatics pipeline. We acknowledge PWN institute and Hubert Kivit for permitting to sample in the Nationaal Park Zuid Kennemerland.

5.7. Supporting information

5.7.1. Appendix S1: Supplementary figures

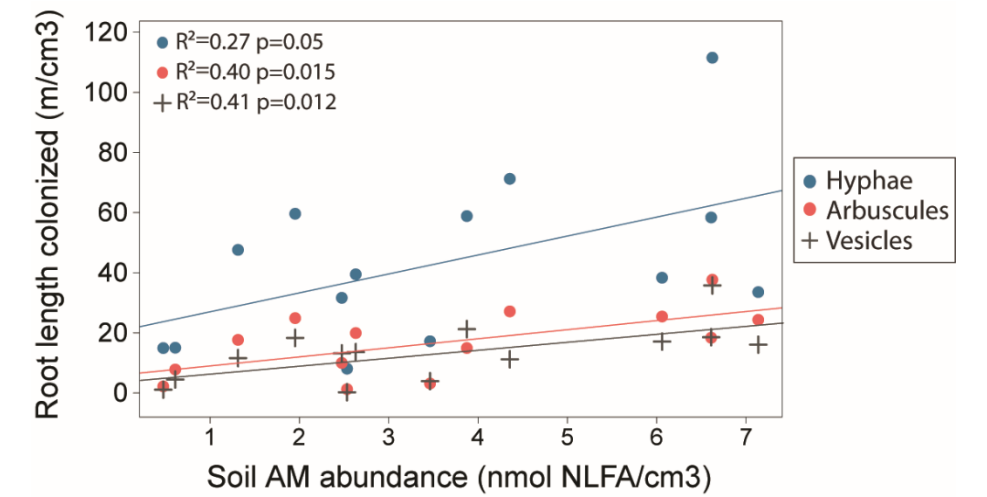


Figure S5.1-A. Linear relation between the AMF biomass in the soil and the total root length colonized for the three detected AMF structures. NLFA 16:1w5 was used as a proxy of the AMF biomass in the soil. One extreme value of NLFA (23.65 nmol/cm³) was omitted, compared to the relationship shown in Figure 5.2 in the main text, to evaluate the influence of this point on the significance of the relationship.

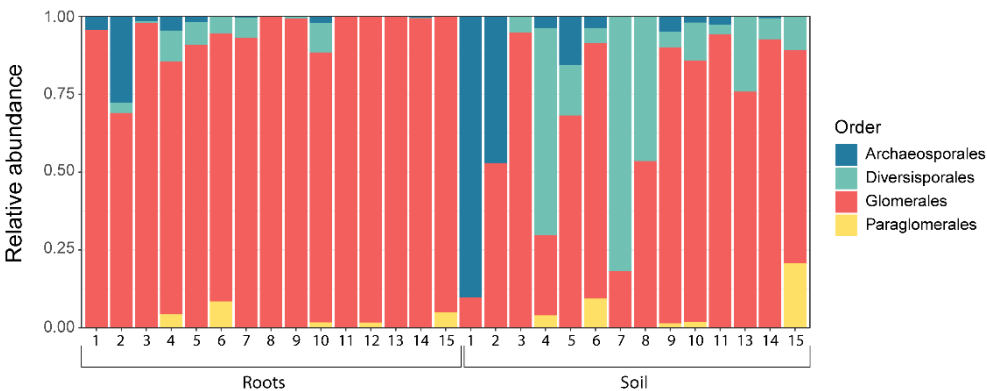


Figure S5.1-B: Relative abundance of the main AMF orders in roots and soil in each sample location.

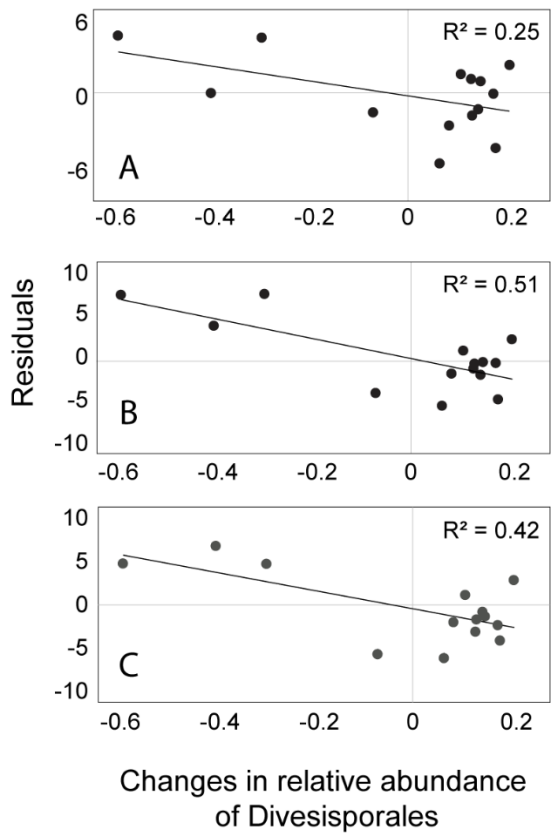


Figure S5.1-C. Linear relation between the residuals of the model on AMF abundances of soil vs roots (measured with arbuscules (A), hyphae (B) and vesicles (C) colonization) and the deviance from the mean in the relative proportion of the order *Divesisporales* between root and soil. Positive residual values indicate that the linear model underestimates AMF abundance in the soils. At those conditions, the relative abundance of *Divesisporales* tends to be lower than the mean.

5.7.2. Appendix S2: Evaluation of AMF abundance in roots and soils using digital droplet PCR (ddPCR)

As traditional method may induce considerable biases, we tested a new, potentially more reproducible technology, ddPCR.

5.7.2.1. *Methods*

Intraradical and extraradical abundance of AMF was complementarily assessed using a digital droplet PCR (ddPCR) analysis. This technique provides an absolute quantification of target DNA copy number by partitioning the PCR reaction in multiple replicates (droplets) and detecting successful DNA amplification in each replicate (Hindson et al., 2011). The ddPCR technique is more accurate and sensitive than the commonly used quantitative PCR (qPCR), especially at low DNA concentrations (Hindson et al., 2013; Yang et al., 2014; Doi et al., 2015; Nathan et al., 2015). Furthermore, the fact that ddPCR analysis does not need calibration curves nor many replicates makes it a more cost-efficient alternative to qPCR (Doi et al., 2015b; Hindson et al., 2013; Nathan et al., 2014; Yang et al., 2014).

Quantitative molecular techniques require the use of specific primers that avoid amplifying non target organisms. For this reason, we used the reverse primer AM1 (Helgason et al., 2002) and the forward AMG1F (Hewins et al., 2015) that specifically target members of the filum Glomeromycota. The final ddPCR reaction volume of 22 μ l contained 2 μ l DNA extract, 2.5 μ l 100 nM forward and reverse primers, 10 μ l Bio-Rad Evagreen Supermix (Bio-Rad, Hercules, CA, USA) and 5 μ l Milli-Q. Of this 22 μ l PCR mixture, 20 μ l were transferred onto a DG8 Biorad cartridge containing 8 wells, of which one was used for a blanc sample containing 3 μ l Milli-Q. Droplets were produced using a Bio-Rad QX-200 droplet generator with 70 μ l Bio-Rad generator oil per well. Of the resulting emulsion mixture, 40 μ L of the produced droplet mixture was pipetted into a semi skirted twintec 96-well plate and sealed using the PX1 PCR Plate Sealer (Bio-Rad). The amplification program incorporated an initial 95 °C denaturation for 5 min, followed by 35 cycles of 15 s at 95 °C, 60 s at 62 °C, and 90 s at 72 °C and a final step of 90 s at 72 °C. The samples were then analyzed with a

QX200 Droplet Reader and processed with QuantaSoft software version 1.7.4 (Bio-Rad) to obtain AMF copy number/ μl of PCR mixture. Droplets were assigned as positive or negative by thresholding based on the height of their respective fluorescence amplitude. The absolute DNA concentration was estimated from the proportion of total positive reactions and the initial concentration of the sample using a Poisson distribution. Roots and soil results were transformed to AMF copy number/ cm^3 of soil.

5.7.2.2. Results

We found a significant positive relationship between the total number of DNA copies detected by ddPCR inside the root compartment and the total root length colonization measured by microscopic identification (Figure S5.2A). In contrast, we did not find a relation between ddPCR estimation in soils and NLFA 16:1w5 values (Figure S5.2B). Concomitantly, the total number of AMF DNA copies measured inside the roots was not significantly related to the number of AMF DNA copies in soils (Figure S5.2C).

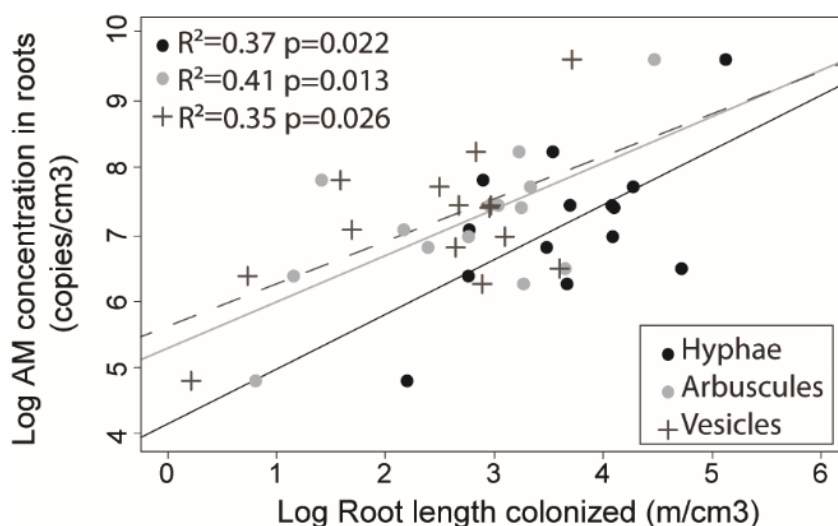


Figure S5.2-A. Linear relation between the abundance of AMF in roots measured with ddPCR and root length colonized by the three detected AMF structures (hyphae, arbuscules and vesicles).

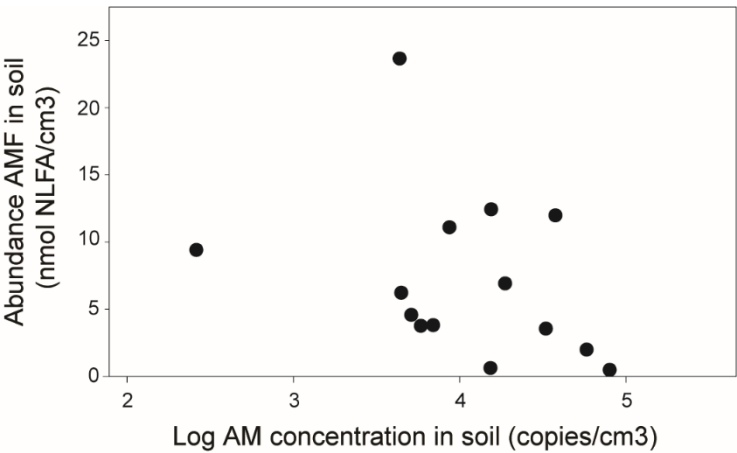


Figure S5.2-B. *Correlation between AMF abundances in soil measured with ddPRC technology and AMF abundance measured with fatty acids analysis. The total number of DNA copies detected in the samples is used as proxy of AMF abundance.*

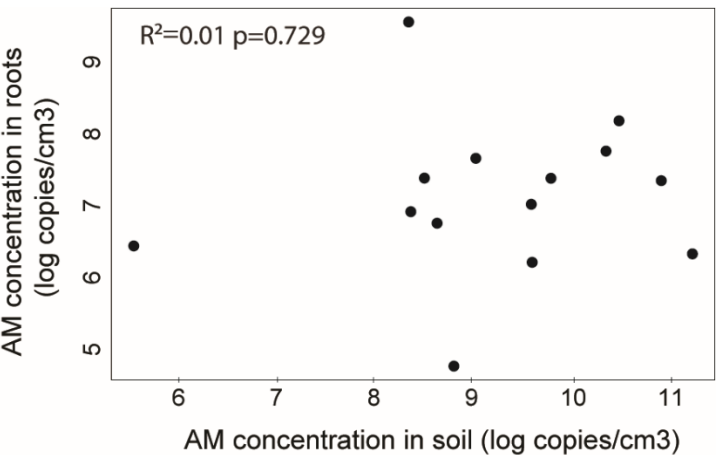


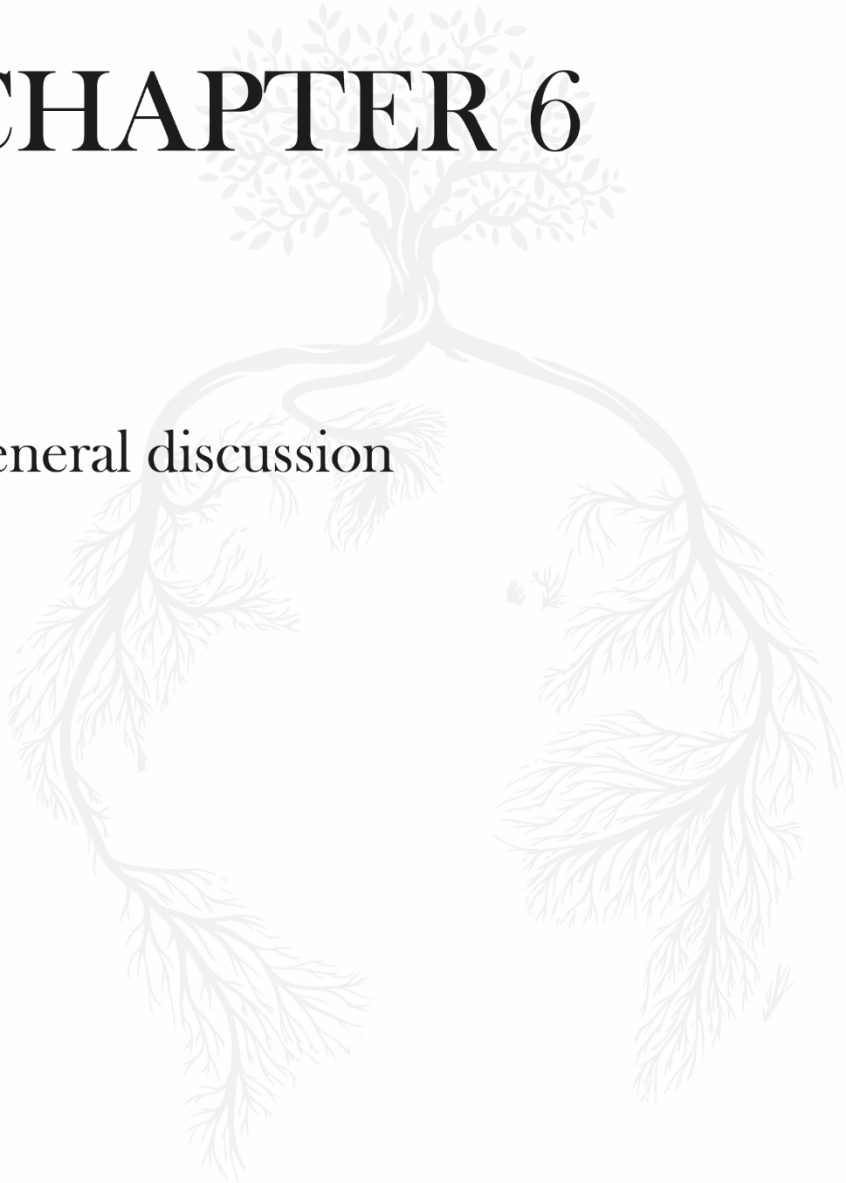
Figure S5.2-C. *The relationship between AMF abundances in soil and roots compartments using ddPRC technology. The total number of DNA copies detected in the samples is used as a proxy of AMF abundance.*

5.7.2.3. Discussion

The ddPCR technique has been shown to be a promising tool to quantify with high precision the abundance of target DNA molecules (Kim et al., 2014; Doi et al., 2015). Despite its potential, ddPCR has been rarely used in ecological research. Here, we tested the possibility to assess AMF abundance both in roots and soils using ddPCR. The abundance of AMF in roots using ddPCR was positively related with the total root length colonized (Figure S5.1). This clearly reflects the applicability of ddPCR techniques for the assessment of AMF abundance in roots. However, it seems that the higher proportion of organic compounds in soil interfered with the PCR reaction, leading to a lack of positive relation between NLFA analysis and ddPCR technique in soil samples (Figure S5.2). This interference was indicated by a much lower difference in fluorescence amplitudes between positive and negative observations in soil (even though ddPCR has been shown to be more robust to effects of organic compounds than other PCR techniques (Rački et al., 2014; Cavé et al., 2016)). Thus, the use of ddPCR for AMF quantification in soil samples requires further optimization and standardization of protocols that can mitigate the high concentration of PCR inhibitors. Possibly, inclusion of additional cleaning steps or using inhibitor removal kits such as the DNeasy PowerClean Pro Cleanup Kit (Qiagen) our protocols might yield better ddPCR results. The relatively poor performance of our ddPCR protocol in soil also seems to explain the lack of relationship between soil and root abundances when using ddPCR. Together, this implies tailor-made ddPCR protocols for soil samples are needed before it may replace the labor intensive, hard to automate and time-consuming traditional methodologies.

CHAPTER 6

General discussion



Our understanding of mycorrhizal interactions has increased substantially in the last decades (Smith and Read 2008, van der Heijden et al. 2015). The development of advanced molecular and soil analytical techniques, complex biogeochemical models and the multiplication of biological databases greatly advanced our knowledge of mycorrhizal physiology (Koltai and Kapulnik 2010), biodiversity (Kivlin et al. 2011, Tedersoo et al. 2012), evolution and ecology (van der Heijden et al. 2015). These recent findings increased our awareness of the importance of mycorrhizal symbiosis on the functioning of terrestrial ecosystems and their role as mediators of climate change impacts. However, mycorrhizas are complex interactions that involve radically different organisms (i.e. plants and fungi) and influence and connect several compartments of the earth system (i.e. lithosphere, atmosphere, biosphere) through intricate mechanisms. To add even more complexity, different mycorrhizal types differ in their ecophysiological dynamics with differential implications at ecosystem level (Tedersoo and Bahram 2019). Therefore, a complete understanding of the functioning and ecosystem implications of mycorrhizal associations remains a major challenge.

The progress of mycorrhizal research has been seriously hindered by the lack of quantitative data on the abundance of different types of mycorrhizal associations (Soudzilovskaia et al. 2017). Quantifying their abundance in ecosystems at both plant and fungal sides of the interaction is key to disentangling the role of mycorrhizas on ecosystem functioning and biogeochemical cycles (Soudzilovskaia et al. 2015). Furthermore, better knowledge about mycorrhizal distribution patterns will lead to a better evaluation of changes in mycorrhizal-mediated processes under future climate scenarios (Rillig et al. 2002).

This thesis deepens our understanding of the characteristics of large-scale distribution patterns of Arbuscular mycorrhizas (AM), Ectomycorrhizas (EcM) and Ericoid mycorrhizas (ErM) and their relationship with environmental variables. The chapters included in the thesis address this topic from an aboveground (*Chapters 2 and 3*) and belowground (*Chapters 4 and 5*) perspectives, where both plant and fungal abundances are taken into account. In *Chapter 2* I related climatic and soil factors to the global distribution of plants featuring AM, EcM and ErM associations. Here I

showed that, at the global scale, climatic factors were the primary drivers of mycorrhizal plant distribution. These findings contradict the supposed casual connection between C-related soil properties and the distribution of different mycorrhizal types at the global scale (Read 1991, Read and Perez-Moreno 2003). The results of this chapter also highlight the uncertainties that still exist in tropical areas, which relates to the lack of data on mycorrhizal distribution and information about mycorrhizal impacts on biogeochemical cycles. Concerning this major knowledge gap, I explore the relationship between climatic, edaphic and microbial community parameters and the gradient of AM to EcM-dominated tropical forests in *Chapter 3*. Contrary to previously published data on patterns in the temperate zone, the results showed that in the tropical biome, an increase of EcM trees is not related to higher topsoil C accumulation. This analysis revealed that the mycorrhizal-associated biogeochemical syndromes found in temperate and boreal zones cannot be directly extrapolated to tropical forests. In the following two chapters, I shifted the focus to the belowground part of mycorrhizal associations. In *Chapter 4* I took up the challenge of creating the first high-resolution maps of fine root biomass associated with AM and EcM fungi. These maps were assembled by creating a hierarchical workflow that relates multiple publicly available biological datasets. This chapter serves as an important foundation for future mycorrhizal research. Finally, in *Chapter 5* I explicitly assess the existence of a relationship between the biomass of AM fungi inside the plant host roots and the extraradical mycelium biomass at plant community scale. The results showed that in a natural dune plant community the abundance of AM fungi in the soil increases linearly with higher AM fungal abundance in roots. These results open the possibility of using the abundance of mycorrhizal fungi in roots as a proxy for abundance in soils.

In the following sections of this chapter, I will explore in more detail the main findings of the previous chapters and how they advance our understanding of mycorrhizal ecology and more generally, the functioning of the terrestrial ecosystem. I will also examine future research directions to be taken to gain a comprehensive and complete knowledge of mycorrhizal systems.

6.1. Drivers and impacts of mycorrhizal host plant distribution.

In recent years, our understanding of the biogeography of plants featuring different mycorrhizal types has increased significantly due to the release of high-resolution maps of the global distribution of aboveground biomass fractions of different types of mycorrhizal associations (Soudzilovskaia et al. 2019, Steidinger et al. 2019). However, the driving forces of such distribution patterns at different geographical scales and their relationship with soil biogeochemical cycles remain unsolved.

In *chapter 2*, I related the biomass fraction of AM, EcM and ErM plants from the mycorrhizal vegetation global maps published by Soudzilovskaia et. al. (2019) with a set of 39 different environmental variables, including temperature, precipitation, seasonality and soil physicochemical properties. Surprisingly, the global distributions of the three main predominant mycorrhizal types were mainly explained by temperature-related factors, while soil properties had only a marginal role. In a similar analysis but focusing only on forest ecosystems, Steidinger et. al. (2019) found also a strong climatic signal explaining the global distribution patterns of AM and EcM forests. The lack of edaphic control on mycorrhizal distribution contrasts with the current paradigm of mycorrhizal plants being globally distributed according to the capabilities of the fungal partners to exploit soil organic matter (SOM) (Read 1991, Read and Perez-Moreno 2003). While strong biogeochemical differences have been reported between AM- and EcM-dominated ecosystems at the biome level (Phillips et al. 2013, Cheeke et al. 2017, Craig et al. 2018), these are not reflected at a global scale. The results of *Chapter 2* suggest that the physiological constraints of different mycorrhizal fungi to perform at different temperature ranges might be a significant driver at global scale. In this way, AM associations would avoid low temperatures zones where AM fungal intraradical colonization (Hetrick and Bloom 1984, Gavito and Azcón-Aguilar 2012), extraradical mycelium growth (Rillig et al. 2002, Gavito et al. 2003, Heinemeyer and Fitter 2004) and fungal responsiveness (Veresoglou et al. 2019) are reduced. In contrast, EcM and ErM fungal adaptations to colder temperatures would favour the predominance of these types of mycorrhizal associations at higher latitudes. Alternatively, Steiniger et al. (2019) proposed that climatic factors controlling

mycorrhizal distributions are the same as those that control decomposition rates at global scale. Therefore, they hypothesize that distinct mycorrhizal associations are distributed globally according to differences in soil nutrient release rates. Independently on the mechanisms behind the climatic control of mycorrhizal distribution, it is clear that there are no strong mycorrhizal-associated biogeochemical syndromes at global scale.

Although the temperature-driven distribution model proposed in *Chapter 2* can explain main global trends, biome level particularities are not well captured. This is especially relevant in tropical areas. While AM is the predominant type of association across the tropical biome, EcM trees are also frequent (Brearley 2012, Nouhra et al. 2019, Steidinger et al. 2019), reaching monodominance in certain locations (Corrales et al. 2018). Therefore, even in theoretically unfavourable climatic conditions, specific local properties may enhance the relative abundance of tropical EcM symbiosis. Field measurements of mycorrhizal abundance and soil properties are scarce in tropical areas, limiting our understanding of EcM trees' ecological niche and their impact on ecosystem functioning. In *Chapter 3* I deepen the understanding of this topic by exploring the relationship between plot-level environmental variables and the relative abundance of EcM trees (used as a proxy of the AM-EcM transition). I found that an increase in EcM tree abundances was associated with lower nutrients and C content in the topsoil and a reduction in biomass and simplification of saprotrophic microbial communities. These results reinforce the view of EcM symbiosis as being an adaptation to low nutrient soils (Read and Perez-Moreno 2003). Moreover, the differences in edaphic properties suggest that distinct biogeochemical syndromes between AM and EcM systems are also present in tropical forests. However, the mechanisms that trigger these distinct biogeochemical syndromes between AM and EcM-dominated tropical forests remain unknown. Lower litter quality or litter inputs enhanced SOM decomposition or lower N-fixing symbionts in EcM- relatively to AM-dominated forests are plausible explanations for the patterns found. Further mycorrhizal research in tropical areas is needed to explore the mechanisms underpinning the patterns found in this study and to provide further insight into the mycorrhizal impacts on biogeochemical cycling.

The most intriguing result from *Chapter 3* is the lack of topsoil C accumulation in EcM tropical plots compared to AM plots, which contrasts with the patterns found in temperate forests (Phillips et al. 2013, Averill and Hawkes 2016). I hypothesized that the discrepancies between mycorrhizal-associated temperate vs tropical topsoil C accumulation patterns might relate to a more important role of microbially stabilized SOM in the topsoil C stocks of tropical forests. In AM tropical systems, higher microbial biomass production favours an increase of C accumulation in the upper soil layers. Microbial growth might be even more stimulated in AM tropical forests compared to AM temperate forests due to the higher proportion of N-fixing trees in the tropics. Additionally, AM associations in tropical areas might be favoured in soils where SOM is stabilized and nutrient losses by leaching are minimized.

Unfortunately, the nature of the dataset used in this chapter did not allow us to explore these potential mechanisms that explain the patterns found here. Future mycorrhizal research should specifically measure SOM transformation processes rates and nutrient and C stocks in different depths to disentangle the mechanisms that lead to changes in biogeochemical properties in the AM to EcM continuum in tropical forests and the differences with temperate patterns.

6.2. Patterns of mycorrhizal distributions belowground

In the last decades, the study of mycorrhizal distribution has been primarily focused on aboveground patterns. Recent research has greatly advanced our knowledge in this field, and now the biogeography of different types of mycorrhizal vegetation (Soudzilovskaia et al. 2019, Steidinger et al. 2019), as well as their environmental drivers (Steidinger *et al.*, 2019; *Chapter 2*), ecosystem impacts (e.g. Phillips *et al.*, 2013; Averill *et al.*, 2014; *Chapter 3*) and responses to global change (Talbot et al. 2008, Mohan et al. 2014) are better understood. However, when we switch our focus to belowground patterns, the picture becomes fuzzy. The evaluation of mycorrhizal fungi community composition and diversity is relatively common due to the development of molecular techniques (Tedersoo et al. 2010, Kivlin et al. 2011), in contrast, the quantification of mycorrhizal biomass in both soil and root compartments is still rare.

This lack of quantitative data makes the actual belowground abundance of mycorrhizas in ecosystems unknown.

Determining the total abundance of mycorrhizal association inside the plant root systems is methodologically challenging, as it does not only require assessing the level of intimacy between plant and fungi (i.e. root intensity of colonization) but also quantifying the standing root stocks. Only the combination of these two parameters will provide a useful metric to complete our understanding of the effect of mycorrhizas on ecosystem nutrients and C fluxes and pools (Soudzilovskaia et al. 2015). In *Chapter 4* I assembled for the first time a high-resolution global map of the abundance of mycorrhizal fungi in plant roots, expressed as the biomass of fine roots that are colonized by AM and EcM fungi. The maps are structured over 881 different spatial units that result from the combination of global ecoregions, and land cover types across six continents. The root stocks colonized by AM and EcM were calculated for each of these ecoregions, enabling a high level of spatial resolution. To assemble the maps I created a workflow that combines different publicly available datasets providing information on root biomass C (Spawn et al., 2020), the proportion of AM and EcM trees biomass (Soudzilovskaia et al., 2019), plot-level relative abundance of plant species (Sabatini et al., 2021) and intensity of AM and EcM root colonization (Soudzilovskaia et al., 2020).

It was not the goal of this chapter to provide an analysis of the ecological implications of the belowground distribution patterns revealed by these maps. Instead, I focused on creating the most accurate and high-quality product that serves as a basis for further research where estimates of root mycorrhizal stocks are needed. Including quantitative data on mycorrhizal-associated root stocks on global analysis of mycorrhizal impacts on ecosystem functioning, assessments of the mycorrhizal-mediate response to global change or global C cycling models have the potential to greatly improve our current understanding of the mycorrhizal influence on soil processes.

While *Chapter 4* provides the first steps toward a better knowledge of mycorrhizal abundance belowground, it only covers the fungal biomass that develops inside the roots of the host plants. The biomass patterns of the fungal part that extends through

the soil matrix (i.e. extraradical mycelium) remains unexplored due to the lack of quantitative data. The mycorrhizal extraradical mycelium has direct implications for soil ecosystem functioning and it is an important precursor of stable SOM (Wallander et al. 2011, Clemmensen et al. 2013). Despite its importance, the quantification of mycorrhizal fungal mycelium biomass in soils is labour- and time-consuming (Leake et al. 2004), constraining its use in mycorrhizal research. A shortcut to overcoming the lack of extraradical mycelium biomass data is to relate these parameters to intraradical abundance estimates.

A positive relationship between the intra- and extraradical AM mycelium biomass has been detected in single fungal isolates (Hart and Reader 2002), but it has never been proven at ecosystem scale. In natural plant communities, where the coexistence of different mycorrhizal species with different root vs soil C allocation strategies is expected, the extrapolation of the results found in the lab becomes less straightforward. In *Chapter 5* I found that, despite differences in community composition between soil and root compartments, the AM root and soil biomass correlation found in the lab also exists in a natural dune plant community. These results suggest that, at plant community level, different AM colonization strategies are structured in a way that the differences in the extraradical and intraradical fungal mycelium biomass get compensated. The coexistence of different AM colonization strategies may ultimately lead to maximising plant hosts' fitness by delivering different benefits to the plant. *Chapter 5* provides the first empirical proof of a correlation between root and soil AM biomass in natural ecosystems. This suggests that the maps developed in *Chapter 4* could be potentially used to infer the biomass of mycorrhizas in soil, which can have large implications for soil functioning studies. However, similar analyses in other ecosystems are needed to generate general equations that can be used in larger-scale applications.

6.3. Implications: are mycorrhizal-associated biogeochemical syndromes context-dependent?

The association between plants and mycorrhizal fungi has profoundly shaped terrestrial ecosystems, being key regulators of soil biogeochemical cycling from local

to global scale. Understanding how different mycorrhizal types distribute at different geographical scales and how they affect ecosystem functioning will not only improve our knowledge of mycorrhizal ecology but will also lead to better spatial predictions of ecosystem responses to future climate scenarios. Through the chapters of this thesis, I explored the validity of theoretical frameworks dealing with the biogeography of vegetation featuring different mycorrhizal types and their ecosystem implications as well as shedding some light on the question of how much mycorrhizal fungal biomass exists belowground.

The results presented in *Chapter 2* and *Chapter 3* suggest that the distribution of AM and EcM plants relates to a different set of environmental properties at biome and global scale (Figure 6.1). At the global scale, the distribution of different mycorrhizal types responds mainly to temperature gradients (*Chapter 2*). In contrast, within biomes where the temperature becomes more stable, the transition from AM to EcM domination is related to changes in soil biogeochemical proxies (Phillips *et al.*, 2013, *Chapter 3*). But, the magnitude and direction of these relationships are not constant across biomes (Figure 6.1), suggesting that taking the relative abundance of a given type of mycorrhizal vegetation in an ecosystem as a proxy of specific biogeochemical syndromes may be misleading without considering its specific environmental context. In temperate forests, a transition from AM to EcM tropical forests generally results in the accumulation of topsoil C, while in tropical forests the pattern is reversed, being the AM systems that are the major accumulators of topsoil C. Moreover, even within the same biomes, ecosystem impacts related to the abundance of a given type of mycorrhizal plant have been proven to be context-dependent (Kyaschenko *et al.* 2017, Fernandez *et al.* 2020). These findings imply that for more spatially explicit predictions on mycorrhizal impacts on nutrient and C cycling new theoretical frameworks need to be developed than include the interaction between specific plant and fungal traits and their soil conditions.

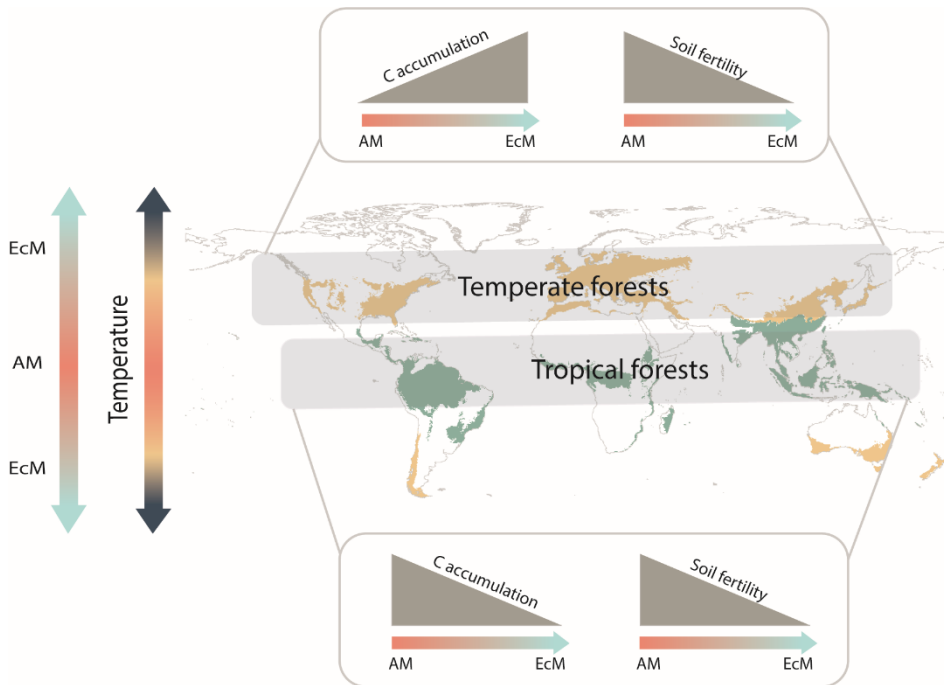


Figure 6.1: Schematic representation of the main correlations between environmental factors and EcM and AM dominance at global and biome scales. At global scale, the AM to EcM transition is driven mainly by temperature differences. While AM plants have preferences for warmer climates, EcM vegetation dominates in colder zones. At biome scales, the AM to EcM transition relates mainly to C accumulation and soil fertility. In temperate ecosystems, EcM plants dominate in low fertility soils with high topsoil C stocks. In tropical forests, the abundance of EcM vegetation is also related to low soil fertility, but low topsoil C accumulation.

It is also important to highlight that assessing mycorrhizal-mediated ecosystem processes based only on the abundance of mycorrhizal vegetation might be misrepresentative as the biomass dynamics of plant and fungal partners are not necessarily correlated. In this way, an ecosystem with a high relative abundance of a given type of mycorrhizal vegetation but low root fungal colonization might not show the same mycorrhizal impacts on ecosystem functioning as a similar ecosystem with higher levels of root colonization. Moreover, different levels of mycorrhizal root colonization can also result in different quantities of extraradical mycelium in the soil, with subsequent differential effects on ecosystem functioning processes. This issue has

been seriously undervalued in mycorrhizal research and the actual abundance of mycorrhizal fungi in roots and soils is rarely taken into consideration when assessing mycorrhizal impacts on ecosystem functioning. Improving our understanding of mycorrhizal abundance in roots is now possible thanks to the great accumulation of biological data that has been recently collected into public datasets (*Chapter 4*), allowing us to overcome methodological limitations of assessing this parameter in the field. Finally, accounting for extraradical mycorrhizal biomass is still a major challenge. Therefore, data on mycorrhizal extraradical mycelium is currently absent at global scale. Although being methodologically possible, obtaining such data will require setting up a global network that applied standardized protocols that allow within-site comparisons and global analysis. Alternatively, a correlation between soil and root biomass can be found at the species level (Hart and Reader 2002) and plant community level (*Chapter 5*), opening the possibility of inferring mycorrhizal extraradical abundances from intraradical estimates (*Chapter 4*) which avoids methodological biases of field measurements.

Taking all the chapters of this thesis together, I conclude that the current paradigms on drivers and impacts of mycorrhizal types distribution should be revised. Despite different mycorrhizal types having distinctive ecophysiological characteristics (Tedersoo and Bahram 2019), their environmental preferences and impacts on ecosystem functioning depend not only on the abundances of AM, EcM or ErM plants but are also influenced by a broader set of factors such as climatic conditions, the abundances of the fungal partners, the microbial community composition or species-specific plant and fungal traits. Acknowledging this is critical for advancing our perspectives on mycorrhizal ecology and the mechanisms behind mycorrhizal involvement in C and nutrient fluxes of terrestrial ecosystems.

6.4. Future perspectives: stepping forward from considering the AM-EcM vegetation as a binary phenomenon

In the last decades, great advances had been made in the field of mycorrhizal ecology. However, we are still scratching the surface in discerning the complex dynamics that involve this symbiotic interaction. Previous knowledge in the field has been built up

based on the premise that AM and EcM associations differ in key physiological and morphological aspects. While this binary classification has been proven useful in certain ecosystems as a predictive tool of biogeochemical processes (Phillips et al. 2013, Averill et al. 2014) or ecosystem responses to global change (Terrer et al. 2016), the observed context-dependency of mycorrhizal effects on C and nutrient dynamics makes this approach insufficient to the future progress of our knowledge.

From my perspective, the future of mycorrhizal ecology research lies in building up new frameworks that expand beyond simplistic classifications of AM vs EcM vegetation. In this sense, understanding the functional diversity of mycorrhizal fungi is critical. Even within AM and EcM fungal types, distinct taxonomic groups differ in the expression of functional traits such as nutrient mobilization capabilities (Bödeker et al. 2014, Yang et al. 2017), extraradical mycelium biomass production (Hart and Reader 2002, Weigt et al. 2012) or protection against plant pathogens (Veresoglou and Rillig 2012, Mohan et al. 2015). The relative abundance in which these functional traits appear in an ecosystem can determine the magnitude and direction of the mycorrhizal-mediated impacts on ecosystem functioning (Clemmensen et al. 2015, Fernandez et al. 2020). Therefore, understanding the abundance patterns of key mycorrhizal functional traits might be of great relevance than focusing only on traditional mycorrhizal types. This will help to solve some of the contradictions found in the mycorrhizal-associated biogeochemical syndromes framework and to improve predictions of mycorrhizal impacts on ecosystem functioning. Going in this direction will require improving our knowledge in three strategic areas of research:

1. Information about the functional diversity of mycorrhizal fungi across different taxonomic groups should be accumulated in open-access databases. Despite the development of molecular techniques, knowledge about the functional properties of mycorrhizal fungi is scarce and comprehensive functional characterization of a wide range of mycorrhizal genotypes is needed. Important progress has been made through the creation of fungal trait databases (Nguyen et al. 2016, Pölme et al. 2020), but no specific database exists that focuses specifically on mycorrhizal fungi including key functional

traits such as hyphal growth and turnover rates, biomass allocation strategy or nutrient acquisition strategy.

2. A better understanding of how distinct mycorrhizal functional traits affect ecosystem functioning is also a promising area of research. Laboratory and field experiments aiming to link mycorrhizal fungal traits with ecosystem processes will provide an important step forward in mycorrhizal ecology.
3. Quantification of community mean functional traits at different spatial scales should be encouraged. This will allow performing spatial explicit analysis on the distribution of these functional traits and their relevance for ecosystem functioning.

Hopefully, in the next years, new methodological techniques will be developed to overcome the issues identified here, allowing us to disentangle the mechanism through which mycorrhizas shape terrestrial ecosystems.

6.5. Concluding remarks

Mycorrhizas are complex interactions that profoundly affect the functioning of terrestrial ecosystems. Understanding how different mycorrhizal types distribute across different spatial scales and relate to ecosystem properties has been a major research challenge. This thesis provides valuable knowledge on the abundance, drivers and ecological implications of mycorrhizal types distribution from both fungal and plant perspectives. Despite these great advances, the future of the field depends on recognizing the complexity of mycorrhizal associations and steeping forwards from old conceptual frameworks and answering ecological questions from a broader perspective. I am sure that the coming years will bring fascinating discoveries that advance our understanding of the mechanisms that drive the biogeochemical fluxes of terrestrial ecosystems.

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Summary

Mycorrhizas are symbiotic associations between soil fungi and most vascular plant species, where the plant hosts provide carbohydrates to the associated fungi, which in exchange supply soil nutrients and water to the plant. Besides the implications of these associations for plant fitness and productivity, mycorrhizas have a profound impact on ecosystem functioning, influencing plant community composition, soil structure and soil biogeochemical cycles.

Depending on the identity of the plant and fungal partners, four mycorrhizal types have been described. Among them, arbuscular mycorrhiza (AM), ectomycorrhiza (EcM) and ericoid mycorrhiza (ErM) are the most taxonomically and geographically widespread mycorrhizal types, being present in approximately 80% of the plant species. Due to significant differences in morphology, physiology and nutrient uptake strategies of the fungal partners, the consequence of mycorrhizal mediation on ecosystem processes greatly depends on the predominant mycorrhizal types. Despite its recognized ecological relevance, quantitative information about the abundance patterns of distinct mycorrhizal plants and fungal types and their environmental drivers and ecological implications across different biomes is incomplete. This thesis quantitatively explores the aboveground and belowground abundance patterns of arbuscular mycorrhiza, ectomycorrhiza and ericoid mycorrhiza and the ecosystem properties derived from these patterns.

In Chapter 2 I assessed the climatic and edaphic factors that better predict the global distribution patterns of distinct types of mycorrhizal vegetation. Based on a gridded dataset that includes 39 soil and climatic parameters and the relative abundance of AM, EcM and ErM plants at a global scale, I showed that the distribution of mycorrhizal host plants is mainly driven by temperature-related factors. These findings contradict the predominant view that, at global scale, distinct types of mycorrhizal plants distribute according to the competitive advantage that specific mycorrhizal fungal traits provide to colonize areas with beneficial edaphic conditions. The results of this chapter highlight the role of climate as the main driving force shaping the mycorrhizal global distribution and suggest that climate change can significantly alter

the distribution of mycorrhizal host plants, with a subsequent impact on the functioning of terrestrial ecosystems.

Given the major uncertainties that exist in tropical areas regarding mycorrhizal types distribution and their environmental preferences and ecosystem impacts, Chapter 3 examines the relationship along a gradient from AM- to EcM-dominated tropical forests. Along that gradient, different topsoil properties, climatic conditions, and microbial abundance proxies were evaluated. This chapter reveals consistent differences in biogeochemical proxies between AM and EcM-dominated tropical stands, indicating lower soil fertility and lower carbon (C) and nutrient transformation rates in EcM forests. Moreover, in contrast to the patterns reported in temperate forests, EcM- dominated stands tended to accumulate less topsoil C than AM stands. A different impact of microbial residues on the formation of stable topsoil organic matter between EcM tropical and temperate forests may explain the contrasting impacts on topsoil C accumulation.

Chapter 4 focuses on the belowground mycorrhizal distribution by creating the first high-resolution global maps of fine root biomass colonized by AM and EcM fungi. This information is key for better quantification of mycorrhizal impacts on ecosystem processes and to incorporate mycorrhizal pathways into global biogeochemical models. To build these maps, I combined multiple datasets including aboveground and belowground plant biomass, plot-level plant species abundance, plant traits and mycorrhizal intensity of colonization. The maps revealed the highest AM abundances in the (sub-)tropics and the highest EcM abundances in the taiga regions. This chapter does not provide an ecological analysis of the resulting maps but serves as a basis for future research where quantitative data on mycorrhizal distribution belowground is needed.

Finally, to gain insights into the mechanisms of belowground C flow and allocation through mycorrhiza, Chapter 5 explores the existence of a relationship between the total fine root length root colonized by AM fungi and the AM extraradical mycelium at plant community level. I found that, while different colonization strategies were present in the studied AM community, the AM biomass in the soil was generally positively correlated with the AM biomass within the plant roots. I suggest that the

proportional biomass allocation between intra-and extraradical AM fungal mycelium (i.e. the AM fungal biomass that develops inside and outside the host plant roots) is made possible by compensation between different AM fungal colonization strategies to maximize plant productivity and fitness. The result of Chapter 5 opens the possibility of using AM fungal total root colonization as a proxy for soil AM fungal abundances. This proxy will help to estimate AM fungal abundance in soils, which is key to a better understanding of terrestrial ecosystems functioning in present and future climates.

Taken all together, the chapters of this thesis highlight the need of considering the specific environmental context when assessing mycorrhizal impacts on ecosystem functioning. Evaluating mycorrhizal-mediated ecosystem processes based solely on the abundance of AM, EcM and ErM plants may be misrepresentative. Specific climatic conditions, the abundances of the fungal partners, the microbial community composition or species-specific plant and fungal traits should also be taken into account. New theoretical frameworks need to be developed that allow more accurate predictions on mycorrhizal influence on biogeochemical cycles.

Samenvatting

Mycorrhiza zijn symbiotische associaties tussen bodemschimmels en de meeste vasculaire plantensoorten. De gastheren, d.w.z. de planten geven koolhydraten door aan de mycorrhizale schimmels met wie ze samenleven. In ruil daarvoor krijgt de plant bodemnutriënten en water van de schimmel. Omdat deze symbiose grote implicaties heeft voor de fitness en de productiviteit van planten, hebben mycorrhiza een aanzienlijke invloed op het functioneren van ecosystemen, de samenstelling van plantengemeenschappen, de bodemstructuur en op de biogeochemische cycli in de bodem.

Afhankelijk van de identiteit van de plant en zijn schimmelpartners, d.w.z. afhankelijk van met welke soorten we te maken hebben, kunnen we vier mycorrhizale types onderscheiden. Van deze types zijn de zogenaamde arbusculaire mycorrhiza (AM), ecto-mycorrhiza (EcM) en ericoide mycorrhiza (ErM) het meest wijdverspreid, zowel in taxonomische als in geografische zin. Samen komen zij voor in ongeveer 80% van de plantensoorten wereldwijd. Door de substantiële verschillen tussen de verschillende schimmels in termen van morfologie, fysiologie en strategie voor de opname van nutriënten, hangt de invloed van de mycorrhiza op de ecosysteemprocessen sterk af van welk mycorrhizale type dominant aanwezig is. Echter, ondanks het feit dat de ecologische relevantie algemeen erkend wordt, is kwantitatieve informatie over de verspreiding en abundantie van verschillende mycorrhizale types, hun partners, en van welke milieufactoren hun verspreiding en abundantie bepalen, incompleet. Hierdoor hebben we ook slechts beperkt inzicht in de ecologische implicaties van het verschillend voorkomen van de diverse mycorrhizale types. Dit proefschrift exploreert de patronen in bovengrondse en ondergrondse abundantie van arbusculaire mycorrhiza, ecto-mycorrhiza en ericoide mycorrhiza op een kwantitatieve manier en evalueert de verschillen in ecologische eigenschappen die daar het gevolg van zijn.

In hoofdstuk 2 heb ik onderzocht welke klimatologische en bodemcondities het best de mondiale verspreiding van verschillende mycorrhizale types verklaren. Op basis van een gerasterde dataset van 39 bodem- en klimaatvariabelen en de relatieve

abundantie van AM-, EcM- en ErM-plantensoorten op een mondiale schaal, toon ik aan dat de verspreidingen van deze plantensoorten vooral wordt bepaald door temperatuur-gerelateerde factoren. Dit resultaat contrasteert met de wijdverspreide gedachte dat, op een mondiale schaal, vooral bodemfactoren de belangrijkste aanjager zijn van de verspreiding van mycorrhizale planten. Die gedachte komt voort uit het idee dat het hebben van een andere mycorrhizaal type een ander competitief voordeel bieden voor de opname van bodemnutriënten en zo kolonisatie en vestiging mogelijk maken. De resultaten van dit hoofdstuk benadrukken echter de rol van het klimaat als belangrijkste factor voor de verschillende mondiale verspreiding van mycorrhizale types. Dit suggereert dat klimaatverandering substantieel de verspreiding van individuele mycorrhizale plantensoorten zou kunnen veranderen, met substantiële gevolgen voor het functioneren van terrestrische ecosystemen tot gevolg.

Gegeven de grote onzekerheden over de verspreiding van mycorrhizale types in de tropen, over hun milieuvorkeuren en over de ecosysteemimplicaties die dat tot gevolg heeft, onderzoek ik hoofdstuk 3 tropische bossen langs een gradiënt van een dominantie in AM tot een dominantie in EcM. Langs deze gradiënt werden de eigenschappen van de bovenste laag van de bodem, de klimatologische omstandigheden en de microbiële abundantie onderzocht. Dit hoofdstuk laat consistente verschillen in verschillende biogeochemische variabelen zien tussen de AM vs. de EcM-gedomineerde tropische bossen. In EcM-gedomineerde bossen was er een lagere bodemvruchtbaarheid, minder bodemkoolstof (C) en een lagere omzettingssnelheid van nutriënten. Bovendien, en contrasterend met patronen gerapporteerd voor bossen uit gematigde streken, accumuleerden EcM-gedomineerde bossen in de tropen minder C in de bovengrond dan AM-gedomineerde bossen. Dit verschil in C accumulatie in de bovengrond kan mogelijk verklaard worden door de andere impact die microbiële overblijfselen hebben op de vorming van stabiel bodem organische stof in tropische bossen in vergelijking met bossen in gematigde streken.

Hoofdstuk 4 concentreert zich op de ondergrondse verspreiding van mycorrhiza. In dit hoofdstuk, presenteer ik de eerste hoge-resolutie mondiale kaart van de kolonisatie van fijne wortels door AM en EcM schimmels. Deze informatie is cruciaal voor een beter begrip en kwantificering van mycorrhizale effecten op ecosysteemprocessen en

maakt het mogelijk dat mycorrhizale omzettingen worden opgenomen in mondiale biogeochemische modellen. Om deze kaarten te maken, heb ik verschillende databases gecombineerd met informatie over bovengrondse en ondergrondse plantenbiomassa, de abundantie van verschillende plantensoorten op plot niveau, planteneigenschappen en de intensiteit van kolonisatie door mycorrhizale schimmels. De kaarten laten zien dat de hoogste abundanties van het AM type voorkomt in de (sub-)tropen en de hoogste abundanties van het EcM type in de taiga regio's. Dit hoofdstuk geeft geen ecologische analyse van deze patronen, maar dient als basis voor vervolgonderzoek waarvoor kwantitatieve data van ondergrondse mycorrhizale verspreiding nodig is.

Tenslotte, om een beter inzicht te krijgen in de mechanismen van de allocatie en transport van ondergronds C, exploreert hoofdstuk 5 of er een relatie bestaat tussen de totale lengte aan fijne wortels die gekoloniseerd zijn door AM schimmels vs. de hoeveelheid mycelium (d.w.z. de biomassa aan schimmeldraden) buiten de plantenwortels. Ik vond dat - op de schaal van een plantengemeenschap - de AM biomassa in de bodem over het algemeen positief gecorreleerd was met de AM biomassa binnen de plantenwortel, ondanks dat er verschillende kolonisatiestrategieën aanwezig waren binnen de bestudeerde plantengemeenschappen. Dit suggereert dat verschillen in de allocatie van biomassa aan schimmeldraden binnen en buiten de plantenwortel, zoals die bestaan tussen verschillende kolonisatiestrategieën, onderling worden gecompenseerd om zo tot een maximale productiviteit en fitness van de planten te komen. Het resultaat van hoofdstuk 5 opent de mogelijkheid om de totale wortelkolonisatie door AM schimmels te gebruiken als benadering voor de abundantie van AM schimmels in de bodem. Schatters voor de abundantie van AM schimmels in de bodem zijn nu heel lastig te maken, maar zijn wel cruciaal voor een beter begrip van het functioneren van terrestrische ecosystemen in het huidige en een toekomstig klimaat.

Alles bij elkaar genomen onderstrepen de hoofdstukken van dit proefschrift het belang van het onderkennen van de specifieke milieucondities op de mate waarin mycorrhiza effect hebben op het functioneren van ecosystemen. Dergelijke analyses puur baseren op de abundantie van AM, EcM en ErM plantensoorten kan misleidend zijn.

Specifieke klimaatomstandigheden, de aanwezigheid van schimmelpartners, de samenstelling van de microbiële gemeenschap en van soortspecifieke planten- en schimmeleigenschappen moeten verdisconteerd worden. Nieuwe theoretische kaders moeten ontwikkeld worden om nauwkeuriger voorspellingen van de invloed van mycorrhizale symbioses op biogeochemische cycli mogelijk te maken.

Curriculum Vitae



Milagros Barceló was born on May 20th, 1988, in Mar del Plata, Argentina. In 2006 she graduated from Sant Josep Obrer high school, in Palma de Mallorca, Spain. From 2007 to 2012 she studied for her Bachelor's degree in Environmental Sciences at the Faculty of Biology of the University of Barcelona, Spain. To complete her Bachelor's final thesis, she spent one semester (2012) at Lund University (Sweden). There, she studied the impacts of different crop covers and agricultural practices on soil ecosystem services under the supervision of Dr Alwyn Williams. She pursued her Master's degree in Ecology and Environmental Restoration also at the University of Barcelona (2012-2013) with a specialization in Fundamental Ecology. During that period, she won a scholarship to collaborate with the Ecology Department on the project CARBONET (Carbon Transport and Processing in the River Network). In her MSc thesis, she assessed the effect of multiple stressors on river ecosystem functioning using the breakdown rates of wood sticks as a river functional indicator. In 2014 she moved to Australia to gain proficiency in English. In 2017, she joined the Institute of Environmental Sciences (CML) at Leiden University, the Netherlands as a PhD candidate under the supervision of Prof. Nadia Soudzilovskaia and Prof. Peter van Bodegom. Her PhD project (2017-2022) focused on investigating the global distribution patterns of different types of mycorrhizal fungi, the environmental and ecological drivers of these patterns and the implications on biogeochemical cycles.

List of Publications

Publications in peer-reviewed Journals:

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3. Barceló, M., van Bodegom, P. M., Tedersoo, L., den Haan, N., Veen, G. F., Ostonen, I., Trimbos, K. & Soudzilovskaia, N. A. (2018). Relationship between the abundance of arbuscular mycorrhiza in soils and the total length of roots colonized. State of the World's Fungi Symposium, Kew Gardens, UK. (Oral Presentation)

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