

DANIELA LEÓN VELANDIA

Mycorrhizal trait distribution  
and composition in plant communities  
under natural gradients



DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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UNIVERSITY OF TARTU

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Department of Botany, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia

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## LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications denoted in the text by the Roman numerals:

- I. Bueno, C.G., Gerz, M., Moora, M., **Leon, D.**, Gomez-Garcia, D., de Leon, D.G., Font, X., Al-Quraishy, S., Hozzein, W.N., & Zobel, M. (2021). Distribution of plant mycorrhizal traits along an elevational gradient does not fully mirror the latitudinal gradient. *Mycorrhiza*, 31(2), 149–159. <http://doi.org/10.1007/s00572-021-00891-4>
- II. **Leon, D.**, Bueno, C.G., Zobel, M., Bennett, J.A., Puglielli, G., Davison, J., Riibak, K., Pärtel, M., & Moora, M. (2022). Plant diversity but not productivity is associated with community mycorrhization in temperate grasslands. *Journal of Vegetation Science*, 33(5), 1234–1245. <http://doi.org/10.1111/jvs.13023>
- III. **Leon, D.**, Peyre, G., Zobel, M., Moora, M., Meng, Y., Diaz, M., & Bueno, C.G. (2023). Mycorrhizal symbioses in the Andean Páramo. *Mycorrhiza*, 34, 107–117. <http://doi.org/10.1007/s00572-023-01133-5>

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Author’s contribution to the publications:

Was responsible for \*\*\*, contributed substantially \*\*, contributed\*

	<b>Developing the idea</b>	<b>Collecting the data</b>	<b>Analysing the data</b>	<b>Preparing the manuscript</b>
I	*	**	**	*
II	**	***	***	***
III	***	***	***	***

# 1. INTRODUCTION

## 1.1. Background

### 1.1.1. What is symbiosis and mycorrhizal symbiosis?

The etymology of the word symbiosis derives from Greek, meaning “living together”, without any *a priori* functional connotation. The term is broadly used in biology to describe the relationship between organisms of different species that associate more or less closely (Lewin 1982). Thus, symbiosis can be understood as an association of two organisms living together in ways that can be generally classified as mutualistic (++, with both partners getting positive outcomes), parasitic (+-, with one symbiont benefiting and the other being negatively affected), or commensalistic (+0, with one benefiting and the other without apparent benefit or detriment) (Lewin 1982). Mycorrhizal symbioses are described as predominantly mutualistic relationships between plants and fungi occurring in plant roots, such that both partners benefit from the association (Smith and Read 2008). The most studied role of mycorrhiza is to enhance nutrient and water supply to the host; in exchange, fungi receive photosynthetic carbon and lipids as an energy source (Smith and Read 2008; Keymer et al. 2017). However, the benefits of mycorrhiza to host plants also include protection against pathogens (Linderman 2000; Veresoglou et al. 2012; Frew et al. 2022), herbivory resistance (Gilbert and Johnson 2017), and tolerance to abiotic stress factors, such as salinity, drought, extreme temperature, heavy metals (Varma et al. 2017; Branco et al. 2022; Singh et al. 2022). Given its trophic and non-trophic roles, mycorrhiza can have an impact on the growth and fitness of plants (Barea et al. 2002; Wang and Tang 2022; Wagg and McKenzie-Gopsill 2023) and even affect the ecosystem composition, productivity, and other characteristics, such as nutrients cycling (van der Heijden et al. 2008; Phillips et al. 2013; Tedersoo et al. 2020).

### 1.1.2. Which plants are associated with mycorrhizal symbiosis, where and why is it important?

The first mycorrhizal classification was made by Frank (1887,1891) based on whether the fungal colonization was inside the root cortical cell walls (endomycorrhiza) or outside (ectomycorrhiza) (Allen 1991; Smith and Read 2008). This classification has evolved over time with increasing information about morphological and ecological features that allow a more precise differentiation concerning the putative ecological roles of mycorrhiza in different ecosystems. Subsequently, mycorrhizal associations have been classified based on the identity of both partners and also considering the structural modifications of both partners during the association (Peterson et al. 1994). We can distinguish seven broad plant mycorrhizal types: arbuscular (AM), ecto- (ECM), ectendo- (EEM), arbutoid (ABM), monotropoid (MTM), ericoid (ERM) and orchid or orchidoid (ORM) mycorrhizal symbioses (Smith and Read 2008; Table 1). For example, AM is the only type involving non-septate fungal hyphae. In turn, ECM (*sensu stricto*) is

the only type that does not involve intracellular colonization, while EEM, ABM and MTM along with ECM can form a fungal mantle and Hartig net (Smith & Read, 2008). For this reason, EEM, ABM and MTM have been grouped and broadly considered as ECM (*sensu lato*). All these characteristics are useful for the identification and description of mycorrhiza in natural ecosystems. However, the description and definition of mycorrhizal types are unfinished tasks, as only a small percentage of plant species – around 4% of the world flora – has been explored (Meng et al. 2023). Further exploration may reveal new types or sub-types, especially among poorly explored plant taxa and areas, such as the recently described *Guapirioid* ectomycorrhiza of the *Guapira opposita* (Nyctaginaceae) family in sub/tropical areas (Furtado et al. 2023). A similar example may be seen among certain ericaceous species from the Andes that form the *Cavendishoid* mycorrhiza, which displays similarities to ericoid and ectendomycorrhiza symbioses (Setaro et al. 2006a, b; Weiß et al. 2016). This suggests that the need to study mycorrhiza is current and that novel associations could still be discovered among less explored taxa, areas and ecosystems.

**Table 1.** Characteristics of mycorrhizal types: arbuscular mycorrhizal (AM); ectomycorrhizal (ECM); ectendomycorrhizal (EEM); arbutoid mycorrhizal (ABM); monotropoid mycorrhizal (MTM); ericoid mycorrhizal (ERM); and orchid mycorrhizal (ORM), taken from Smith and Read (2008), with new updates in Red. Entries in brackets indicate rare conditions.

<b>Mycorrhizal type</b>	<b>AM</b>	<b>ECM</b>	<b>EEM</b>	<b>ABM</b>	<b>MTM</b>	<b>ERM</b>	<b>ORM</b>
Septate hyphae	–	+	+	+	+	+	+
Intracellular colonization	+	–	+	+	+	+	+
Fungal mantle	–	+	+ or –	+ or –	+	–	–
Hartig net	–	+	+	+	+	–	–
Achlorophylly	–(+)	–	–	–	+	–	+*
Fungal taxa	Glomeromycota Mucoromycota	Basidiomycota Ascomycota	Basidiomycota Ascomycota	Basidiomycota	Basidiomycota	Ascomycota Basidiomycota (Vohník et al. 2023)	Basidiomycota
Plant taxa	Bryophyta Pteridophyta Gymnospermae Angiospermae	Gymnospermae Angiospermae	Gymnospermae Angiospermae	Ericaceae (Arbutunoideae)	Monotropoideae	Ericales (Ericaceae, Diapensiaceae)	Bryophyta Orchidaceae

\*All orchids are achlorophyllous in the early seedling stages. Most orchid species are green as adults (Smith and Read 2008).

The development of mycorrhizal associations has a significant effect on processes occurring at the level of plant individuals (resource exchange, nutrient transfer, water transfer to the plant, and carbon transfer to the fungus), populations (seedling establishment, interactions between plants) and ecosystems (litter decomposition, soil formation, and aggregation). These ecological functions are differentially associated with the different mycorrhizal types, each of which has a particular ecological distribution and evolutionary history (Dheeraj et al. 2019; Tedersoo et al. 2020).

The distribution of mycorrhizal associations is affected by many different factors that can limit one or both symbiotic partners (Barceló et al. 2019; Steidinger et al. 2019). Following the most recent study of mycorrhizal symbiosis distribution (Meng *et al.*, 2023), some general features describe the distribution of each mycorrhizal type. AM associations are mainly found in low-latitude areas with warm climates, high annual mean temperatures, and solar radiation. ECM plant species occur abundantly at high latitudes with low temperatures and in acidic soils with moderate or high moisture content. ERM plants occur more frequently in cold and humid climates with low solar radiation, evapotranspiration, and acidic soils. Such conditions occur mainly in the northern hemisphere, and in the southern hemisphere only in the Andes. The current distribution data, although scarce, showed that orchids, and hence also ORM, are not so directly dependent on climatic or edaphic conditions (Meng et al. 2023). Correspondingly, the distributions of the different types of mycorrhiza are associated with different biomes and ecosystem types. Arctic tundra is predominated by ericoid; the northern coniferous forest and temperate forest by ECM; tropical rain forest and tropical seasonal forest by AM and some ECM; temperate grasslands, dry scrubs and desert by AM; tropical savannah grassland, scrub, and desert by AM; and Mediterranean vegetation by ECM, ABM, ERM and AM (Tedersoo, 2017).

According to the Smith & Read (2008) >86% of land plants potentially form at least one type of mycorrhiza. Based on the proportion of plant individuals within a species that form mycorrhiza, and whether individuals gain or lose mycorrhiza, species can be classified as obligately, facultatively and non-mycorrhizal. This mycorrhizal status indicates whether the roots of a plant species are consistently (OM), sometimes, but not always (FM) or never (NM) colonized by mycorrhizal fungi (Koide and Schreiner 1992; Smith and Read 2008; Moora 2014).

## **1.2. Characterizing mycorrhiza.**

### **1.2.1. How can mycorrhizal symbiosis in plants be measured?**

#### **Mycorrhizal traits**

Trait-based ecology is an approach that focuses on the characteristics or “traits” of organisms, which can provide insights into their roles and functions within ecosystems. Traits are measurable features that influence an organism’s performance and interactions with the environment. By examining traits such as morphology,

physiology, and phenology, researchers can predict ecological outcomes and understand how organisms contribute to ecosystem processes. This approach allows for the measurement of different organism activities and functions, providing a more comprehensive understanding of biodiversity and ecosystem functioning (Garnier et al. 2016; de Bello et al. 2021).

Mycorrhizal traits are defined as characteristics that lie at the intersection of both plant and fungal partners and are dependent on both partners (Chaudhary et al. 2020). Moora (2014) proposed four traits associated with a plant's ability to form mycorrhizal symbiosis and to respond to symbiosis: mycorrhizal type, mycorrhizal status, mycorrhizal flexibility, and mycorrhizal dependency (Moora 2014).

Chaudhary et al. (2022) proposed a more sophisticated framework, recognizing various morphological, physiological, and phenological characteristics as traits. They categorized mycorrhizal traits based on whether the variable describes predominantly the properties of fungus, plant, or symbiotic structure. On this basis, it is possible to recognize three types of traits – plant mycorrhizal traits, fungal mycorrhizal traits, and symbiotic mycorrhizal traits (Chaudhary et al. 2022).

To study how mycorrhizal symbiosis changes along environmental gradients, I adopted Moora's approach, focusing on well-defined traits that characterize key attributes of the mycorrhizal symbiosis. Moora's trait definitions enable comparisons across diverse studies and regions, contributing to a more comprehensive understanding of mycorrhizal symbiosis. The specific trait definitions proposed by Moora (2014) are outline below.

### Mycorrhizal type

This trait depends on the partner identity and the morphological and functional features of the symbiosis. I address the four most common mycorrhizal types such as arbuscular mycorrhiza (AM), ectomycorrhiza (ECM), orchid-mycorrhiza (ORM), ericoid-mycorrhiza (ERM).

### Mycorrhizal status

The mycorrhizal status of a plant is defined by whether the roots of a plant species are colonized or not by the mycorrhizal fungi: always, obligately mycorrhizal (OM); sometimes, facultatively mycorrhizal (FM) or never, non-mycorrhizal (NM).

### Mycorrhizal flexibility

Mycorrhizal flexibility describes the ability of a plant species to grow with or without mycorrhiza depending on local conditions. According to this definition, OM and NM plants are considered to be inflexible (Moora 2014). This characteristic was not considered among mycorrhizal traits in Chaudhary et al. (2022). Mycorrhizal flexibility can be considered a special case of symbiont plasticity,

defined as a variation in symbiont function within a holobiont, underpinned by various genetic, ecological, and physiological mechanisms (Zobel et al. 2024).

### Mycorrhizal dependency

Mycorrhizal dependency is used to characterize the plant response to colonization by mycorrhizal fungi (van der Heijden and Sanders 2002). Different measures such as biomass, fecundity, and growth rate (vegetative/clonal) can be used to characterize the dependency (Moora 2014).

## **1.2.2. How can mycorrhizal symbiosis in plant communities be assessed?**

If we can associate mycorrhizal trait information with the majority of species in a plant community or at least to the most representative species (abundant, frequent), we can upscale mycorrhizal measurements to the community level.

### Community Mycorrhization Index

Plant community mycorrhization can be calculated from information about the mycorrhizal type and mycorrhizal status of species in a community, accounting for their abundance in the community. Such an index provides a rough estimate of the prevalence of mycorrhizal symbiosis in the community. If mycorrhization is estimated for different communities, I may then investigate how the prevalence of mycorrhizal symbiosis in plant communities varies in relation to ecological gradients. In practical terms, (Moora 2014; Gerz et al. 2016) proposed a plant community's mycorrhization index (MI), which measures how mycorrhizal plant communities are. This measure – community-weighted mean mycorrhization – describes the proportion of plant biomass or abundance that is representative of a specific mycorrhizal type or status.

Knowledge about mycorrhizal traits provides a basis for understanding large-scale patterns in coevolution and the ecological relationships between plants, their symbiotic fungi and the environment. Studying these traits in entire plant assemblages contributes to understanding the ecological importance of mycorrhizal symbiosis in different communities and ecosystems (Moora, 2014).

## **1.3. Mycorrhizal Associations: Ecological Drivers and Plant Community Impacts**

### **1.3.1. What ecological factors drive the distribution of plant mycorrhizal traits?**

Elevation is a relevant geographic characteristic that must be considered, numerous key environmental factors and resources change rapidly along elevational gradients (Körner 2007, Rahbek et al. 2019). However, the lack of previous detailed studies about the distribution of mycorrhizal traits along elevational gradients may be related to the difficulty of obtaining information with high spatial resolution (e.g. in terms of the size of pixels or study units). For example, in the study by Bueno et al. (2017) the most detailed description of the flora was in pixels of approximately a 50 km radius. While it was one of the first studies to describe elevational trends in mycorrhizal patterns, the results were certainly limited by the imprecision of the data used. In such large study units as 50x50 km, especially in mountainous regions, elevation can vary significantly, along with other key factors driving the character of mycorrhizal symbiosis. The study by Barcelo et al. (2019), which also used large  $5 \times 5$  arcminute study units, concluded that soil conditions were not the main drivers of the occurrence and type of mycorrhizal symbiosis. This conclusion contradicts general knowledge about mycorrhizal ecology, where edaphic factors are considered crucial for the survival of mycorrhizal fungi in the soil and the establishment of mycorrhizal associations (Read 1991, Smith and Read 2008). Indeed, more recently, Meng et al. (2023) used grid cells smaller than  $1 \text{ km} \times 1 \text{ km}$  and demonstrated significant effects of edaphic factors on the distribution of mycorrhizal associations. In particular, variation in plant mycorrhizal status was better explained by both climatic and edaphic variables while plant mycorrhizal type was more phylogenetically conserved.

### **1.3.2. What is the relationship between mycorrhizal associations and key community properties, such as fertility, productivity, and diversity?**

The connections between mycorrhizal symbiosis and important plant community characteristics, such as diversity and productivity, could be assessed by using plant individual- or species-based mycorrhizal attributes (Moora 2014).

Studies scaling up plant species mycorrhizal trait information to the level of community may capture important shifts in the features of communities that are linked with mycorrhizal symbiosis (Moora 2014, Gerz et al. 2018). Plant mycorrhizal status is an effective trait that is sensitive to changes in habitat characteristics, such as soil fertility or the level of disturbance (Gerz et al. 2016, Porazinska et al. 2018). Accordingly, community mycorrhization indicates general

trends in the occurrence and character of mycorrhizal symbiosis in plant communities along ecological gradients (Moora 2014, Smith and Read 2008). Community mycorrhization, calculated as community means of mycorrhizal status weighted by plant species abundance, decreased with increasing soil fertility in temperate grasslands (Gerz et al. 2016), suggesting a less important role for mycorrhizas in fertile habitats. Furthermore, that study discovered no connection between plant diversity and community mycorrhization. By contrast, Porazinska et al. (2018) found a positive correlation between mycorrhization and diversity, with plant community richness being inversely correlated with non-mycorrhizal species abundance and positively correlated with mycorrhizal species abundance.

## 1.4. Goals

The main objective of my thesis is to characterize the structure and distribution of plant mycorrhizal traits in natural ecosystems under different climatic and edaphic conditions (I and III). I aimed to evaluate how different mycorrhizal types and the degree of mycorrhization of the whole plant community are related to plant productivity and diversity (II). While there is a clear link between mycorrhizal symbiosis and the performance of plant individuals and species, its impact on plant communities is less well understood. We know little about the distribution of these traits along major natural gradients. More detailed information about this topic would improve our understanding of the influence of mycorrhizal symbiosis on ecosystem processes. Studying the large-scale distribution of plant mycorrhizal traits in species and on the level of plant communities can therefore enhance our understanding of the role of mycorrhizal symbiosis in different ecosystems and in their main ecological processes.

Based on early research from the northern hemisphere, (Read 1991, Read and Perez-Moreno 2003) hypothesized that mycorrhizal type distribution is modulated by latitude and elevation. However, evidence of elevational changes in the occurrence and abundance of mycorrhizal types and statuses is scarce. I aimed to test this hypothesis and to describe the distributions of mycorrhizal types and statuses by examining the Pyrenean mountains range (from 400 to 3400 m.a.s.l.) and the Andean Páramo (from 2500–4000 m.a.s.l.) (I and III). I also evaluated which climatic and/or edaphic factors modulated mycorrhizal type and status distribution along these elevational gradients.

As mentioned, studying mycorrhization along elevational gradients is crucial because changes in altitude often lead to shifts in climate, soil fertility, and plant communities. These factors influence the composition and function of mycorrhizal fungi, which can affect nutrient acquisition and the structure of plant communities, contributing to varying levels of plant diversity and productivity at different elevations. As soil fertility typically decreases with elevation, plants may rely more heavily on mycorrhizal fungi, potentially fostering more intimate plant-fungal interactions (van der Heijden & Horton, 2009). Understanding these dynamics along elevational gradients also highlights the need to study mycorrhization

across productivity gradients, regardless of the specific elevational contrasting conditions. For example, it has been very poorly explored whether, in low-productivity systems, plants often depend on fungal symbiosis for nutrient acquisition, while in high-productivity environments, competition or other factors might play a larger role in structuring communities. Studying these gradients helps to elucidate the functional role of mycorrhizas in maintaining biodiversity and ecosystem stability (Tedersoo et al., 2020).

Specifically, I asked the following questions:

1. Is elevational variation consistent with latitudinal variation in the distribution of plant mycorrhizal traits in the flora along altitudinal and latitudinal gradients in the Pyrenees?
2. Is mycorrhizal trait distribution in the Andean Páramo consistent with mycorrhizal distribution theory developed in the northern hemisphere?
3. Which climatic and edaphic factors influence mycorrhizal trait distribution in the Andean Páramo?
4. How does soil fertility impact community mycorrhization?
5. How are plant productivity and diversity related to community mycorrhization?
6. Does community mycorrhization directly mediate relationships between soil fertility and plant productivity and diversity in the Estonian grasslands?

## 2. MATERIALS AND METHODS

### 2.1. Study Areas

The study areas for this thesis included the Pyrenees, Estonian temperate grasslands, and the Andean Páramo. I aimed to address the prevalence of mycorrhizal symbiosis and mycorrhizal trait distribution in plant communities and to identify and describe their edaphic and climatic drivers (I,III) and relationships with plant productivity and plant diversity (II). I studied natural and semi-natural ecosystems in Paper I, focusing on the Pyrenees mountain range, located between France and Spain. This region covers an area  $> 50,000$  square kilometers ( $\text{km}^2$ ), from the Cantabrian Sea in the west to the Mediterranean Sea in the east. The Pyrenees boast a wide elevational range, with peaks exceeding 3,000 meters above sea level (m.a.s.l.), including Aneto Peak, the highest point. The region encompasses two major biogeographic zones, with a central alpine region representing one of the southernmost alpine areas in Europe. Occurrence data of Pyrenean plant species were taken from the Pyrenean Floristic Atlas (PFA), which includes information from Spain, France, and Andorra. This atlas describes the distribution of  $> 4000$  plant species, of which  $> 600$  species are non-native, and 630 are exclusively alpine (Gómez García et al. 2020). For this study, I only considered native species.

For **paper II**, I selected 29 sites within an approximately  $800 \text{ km}^2$  region south of Tartu, Estonia ( $58.07\text{--}58.35^\circ\text{N}$ ;  $26.14\text{--}26.97^\circ\text{E}$ ), with a minimum distance of 1.2 km among sites. Plant community productivity was measured, plant richness estimated, and soil sampled at all sites, representing different positions along a steep productivity gradient ( $80\text{--}500 \text{ g/m}^2$  of shoot biomass). Data were collected from open sites within semi-natural grassland habitats. At each site, 15 adjacent subplots of  $0.5 \times 0.5 \text{ m}$ , forming an extensive site plot of  $1.5 \times 2.5 \text{ m}$ , were established during the summer of 2014. During the summer of 2015, the identity and cover of all plant species was estimated in each subplot and then averaged at the plot level.

In **paper III**, I addressed the Páramo – a Neotropical high-mountain region between the treeline and permanent snowline, located in Venezuela, Colombia, Ecuador, and Perú. The Páramo is divided into three vegetation belts. The sub-Páramo (elevation range 2800–3500) known as the ecotone from Andean forests to treeless ecosystems, is characterized by small trees and a dominance of shrubs. The mid-Páramo (elevation range 3500–4200), is characterized by non-woody communities with tall grasses and giant rosette forbs. At higher elevations  $> 4200 \text{ m}$ , the super-Páramo contains low sparse vegetation and a weakly-developed soil layer (Luteyn 1999; Peyre et al. 2018). I used VegPáramo, a vegetation database collating phytosociological relevés from 3900 georeferenced plots in Venezuela, Colombia, Ecuador, and Peru. I extracted 2646 plots from VegPáramo following data cleaning (excluding the Páramos with imprecise spatial coordinates or with incomplete taxa identification). In the plant list, there were

123 vascular plant families, 504 genera, and 2220 species (Peyre et al. 2015). The total area of the Páramo represented in the database is about 35000 km<sup>2</sup> (Peyre et al. 2021).

## 2.2. Plant mycorrhizal trait data and community mycorrhization

### 2.2.1. Mycorrhizal traits

Two plant mycorrhizal traits were considered: plant mycorrhizal type and plant mycorrhizal status. There were assigned three plant mycorrhizal types in paper I: arbuscular mycorrhizal (AM), ectomycorrhizal (ECM), and ericoid mycorrhizal (ERM), given the scarcity of species for orchid (ORM) mycorrhizal symbiosis. In papers II and III, I used four plant mycorrhizal types: AM, ECM, ERM, and ORM. Plant mycorrhizal statuses were identified as follows: obligately mycorrhizal (OM), where plants are always colonized by mycorrhizal fungi, facultatively mycorrhizal (FM), where plants are sometimes colonized, and non-mycorrhizal (NM), where plants are never colonized (Smith and Read 2008; Moora 2014).

Data about plant mycorrhizal traits were gathered during literature searches and from empirical research on field-collected plant species. I consulted data on plant mycorrhizal traits from publications by Soudzilovskaia et al. (2020), Gerz et al. (2018), Bueno et al. (2017), and Hempel et al. (2013). In order to supplement the data for papers I and II, species-specific literature searches were conducted to collect mycorrhizal information about the most prevalent plant species that previously lacked information. To provide good representation of the prominent species in the Pyrenees, there was sampled four of the most abundant species lacking mycorrhizal information: *Genista scorpius*, *Festuca eskia*, *Festuca gautieri*, and *Echinopartum horridum*. Except for *Genista* and *Echinopartum*, for which I gathered the roots of five individuals from one population, I collected roots from ten individuals per species in two populations. In paper II, there was no available mycorrhizal information in the literature for three abundant plant species (*Carex ornithopoda*, *Medicago x varia*, and *Melampyrum nemorosum*). I collected 15 individual root samples in the Pyrenees and at some study sites for the Estonian grasslands (spring and summer of 2018) – five at each of the three sites. To assess plant mycorrhizal traits, approximately 1 gram of young roots was taken from each plant's root system. The root samples were stained using the methodology of Dalpé and Séguin (2013). Colonization percentages were measured, and fungal structures were identified using the grid line-intersect approach (Newman 1966, Tennant 1975). The results are detailed in supporting information Table S2 and Figure S1 (paper II).

In Papers I and II, mycorrhizal trait data were provided at the species level. In Paper I, information was available for 1626 out of a total of 3015 Pyrenean plant species, representing approximately 53.9% of the flora. Meanwhile, in Paper II,

data were recorded for 162 vascular plant species in the 29 assessed sites. Of these plant species, 140 (86.4%) could be assigned mycorrhizal type and status information. In Paper III, the literature covered only 11.9% of the Páramo species (254 out of 2135), resulting in limited information regarding the mycorrhizal traits of these species. For this reason, mycorrhizal data at the genus level were used (Bueno et al. 2019). To avoid potentially inaccurate extrapolations at the family or order levels, genus-level trait information was calculated based on known species-level data (Bueno et al. 2019, 2021b). By utilizing genus-based information, the coverage of mycorrhizal trait information for the Páramo vegetation plots increased to 73.2%, representing 366 out of 500 genera. Utilizing all available empirical mycorrhizal data for each plant species within every genus, mycorrhizal assignments were established at the genus level (Wang and Qiu, 2006, Akhmetzhanova et al. 2012, Hempel et al. 2013, Bueno et al. 2017, 2019, Soudzilovskaia et al. 2020). For each genus, there was determined the most prevalent (and therefore typical) mycorrhizal traits (see Appendix 1 (paper III)). Prior to data compilation, a thorough examination of empirical data sources was conducted to mitigate biases stemming from misidentification errors (Brundrett and Tedersoo 2018, Bueno et al. 2019, 2021a).

### 2.2.2. Community mycorrhizal measurements

I computed community mycorrhization indexes (MI and AMI; the latter representing mycorrhization specifically of arbuscular mycorrhizal plant species) (Moora 2014, Gerz et al. 2016). For Paper II and the MI in Paper III, I employed these indexes to evaluate community mycorrhization for each plot. Initially, each plant species within the plot was assigned a unique mycorrhizal type and status, based on available empirical mycorrhizal data for each species (Bueno et al. 2019). Calculating community mycorrhization indexes involved estimating a mycorrhizal status coefficient for each plant species. This coefficient, determined by the ratio of observed mycorrhizal plant individuals to the total number of observations per species, ranges from 0 (indicating no mycorrhizal association) to 1 (indicating full mycorrhization) (Moora 2014, Gerz et al. 2016). The weighted average of plant species' mycorrhizal status coefficients ( $m_{sc}$ ) within a plot, considering the relative cover of each species, was utilized to compute the mycorrhization indices.

$$(A)MI = \ln \left( \frac{\sum(p_i \times m_{sc_i})}{1 - \sum(p_i \times m_{sc_i})} \right)$$

In this equation,  $p_i$  represents the proportional cover of species  $i$  within each plot, and  $m_{sc_i}$  denotes the numerical coefficient representing the quantitative version of the mycorrhizal status of species  $i$  (Gerz et al. 2016). Detailed examples of community mycorrhization calculations can be found in Moora (2014) and Gerz et al. (2016).

To determine mycorrhizal status, I utilized the latest at the time version of the empirical mycorrhizal database available (Bueno et al. 2017; see supporting information, Table S1 in Paper II).

### **2.3. Edaphic and climatic drivers**

In Paper I, based on the BioClim database (<https://www.worldclim.org/data/bioclim.html>), I examined four climatic variables characterizing the level and variation of temperature (mean annual temperature, MAT, and isothermality, ISO) and precipitation (annual precipitation, APP, and precipitation annual range, ARP) (Appendix S3, paper I). Isothermality (ISO) quantifies the magnitude of day-to-night temperature oscillations relative to the summer-to-winter (annual) oscillations, while the precipitation annual range (ARP) indicates annual variation in total precipitation between the wettest and the driest months. To characterize edaphic conditions, I used estimates of soil pH, cation exchange capacity (CEC), and total soil nitrogen content (N) from the World Soil Information database ([www.soilgrids.org](http://www.soilgrids.org)) (Appendix S3, paper I).

In Paper II, I characterized soil abiotic factors by analyzing soil data collected from the field. Soil samples were pooled from three individual soil subsamples ( $10 \times 10 \times 10$  cm) per site, from the area immediately surrounding each plot. Samples were analyzed for total nitrogen and organic carbon, extractable phosphorus and extractable potassium, using standard analyses, developed at the Estonian University of Life Sciences (Bennett et al. 2016).

In Paper III, I explored 46 edaphic factors from the global change (<https://data.globalchange.gov/>) and soil grids (<https://www.isric.org/explore/soilgrids>) databases (Appendix 2, paper III). These data are available as digital raster maps with a spatial resolution of a  $10 \times 10$  km grid. I extracted environmental data for each plot using the geographical coordinates of the relevés and the “extract” function from the “raster” R package (Hijmans 2023). Collinearity and multicollinearity were assessed, with thresholds of Pearson correlation  $< 0.6$  and VIF  $< 3$ ; (Zuur et al. 2010) used to select the following variables for further analysis: 1) edaphic: cation exchange capacity, which measures soil retention of positively charged ions (CEC), pH (measured with water), total soil N (N), total soil P (P), and total soil C. 2) Climatic: mean annual temperature (MAT), mean diurnal range (MDR), mean annual precipitation (MAP) and precipitation seasonality (PPS).

### **2.4. Estimates of plant diversity and productivity**

For paper II, I use the data published by Bennett et al. (2016) where the quantification of plant productivity entailed the assessment of shoot, root, and leaf litter biomass within two  $0.1 \times 1.0$  m plots at each site. The community composition of vascular plants was evaluated during the period spanning late June to early

July 2015, utilizing  $0.5 \times 0.5$  m subplots. Subsequently, species richness was computed for each site by enumerating the number of plant species identified across all subplots.

## 2.5. Statistical analyses

Data selection, collinearity, multicollinearity and further analyses.

To address potential collinearity (high correlation between pairs of variables) and multicollinearity (high correlation among multiple factors), there were retained variables with a Pearson correlation coefficient  $< 0.6$  and a variance inflation factor (VIF)  $< 3$  among edaphic and climatic variables in all papers (Zuur et al. 2009).

Paper I examined climatic and edaphic variables. Four climatic variables describing temperature (mean annual temperature, MAT, and isothermality, ISO) and precipitation (annual precipitation, APP, and precipitation annual range, ARP) were explored (BioClim database). Edaphic variables included soil pH, cation exchange capacity (CEC), and total soil nitrogen content (N) (soilgrids). High collinearity and multicollinearity were detected between APP and MAT, as well as pH and N. Given the direct relationship between precipitation and temperature in elevational gradients (Körner 2003), APP was excluded from further analyses.

Given that I was specifically interested in two highly collinear variables (pH and soil N), I explored the unique and combined effects of pH and N in two parallel models. There was considered that pH can decrease when organic matter accumulates at high elevations, containing large amount of organically bound nitrogen, as rates of decomposition and mineralization also decrease (Kielland et al. 2007). Thus, when pH is accounted within the effect of total soil N, the remaining effect of N will indicate its unique effect, irrespective of soil pH. Therefore, I ran a model where N was replaced by its residuals after removing the effect of pH [hereafter soil N(r)], and *vice versa*, to estimate the unique and combined effects of pH.

In paper I, given the high correlation between climate and topography (elevation, slope, and aspect), and the fact that topography plays a major role in configuring climatic and edaphic conditions for plants in the mountain environment (Körner 2003), I explored in parallel the climatic and topographic relationships with plant mycorrhizal traits (Fig. 1).

Paper II, collinearity issues were not found either in the GLM or the path analysis.

Paper III, involved the analysis of 46 edaphic and climatic variables (Supplementary Material Appendix 2). After collinearity and multicollinearity tests, the following variables were selected for further analysis:

Edaphic: cation exchange capacity (CEC), pH, total soil nitrogen (N), total soil phosphorus (P), and total soil carbon (C)

Climatic: mean annual temperature (MAT), mean diurnal range (MDR), mean annual precipitation (MAP), and precipitation seasonality (PPS)

### 2.5.1. Modelling approaches

In paper I, there was used generalized linear models (GLM) with binomial error distributions and logit link functions, to analyze the effect of climatic and edaphic factors on the predominance of plant mycorrhizal traits along the Pyrenean elevation range. I modelled each plant mycorrhizal type and status (AM, ECM, ERM, and NM for mycorrhizal types and OM and FM for mycorrhizal statuses), as a binary response.

Response variables were estimated as the proportion of species with a particular trait value in relation to the other values for that trait (either type or status). The total number of species was not the same for types and statuses, as types included all species including NM plants, while status (in this case OM and FM) did not include NM plant species (as NM patterns were already described in the type analysis). I used model averaging, based on the top 95% of models (Burnham and Anderson 2002). Residual spatial autocorrelation (SAC) was estimated by using Moran's spline correlograms and corrected by subsampling at 20 m distance, were no spatial autocorrelation was found.

To test the influence of soil fertility on plant community arbuscular mycorrhization (AMI), I used the same model averaging approach using binomial GLMs. The full models were built with AMI as the response variable and soil N, P and K, as well as soil moisture and pH as predictor variables. All predictors were standardized before modelling to avoid scaling issues (Burnham and Anderson 2002). Soil P was log-transformed to avoid modelling with a skewed P distribution due to the presence of two extreme values.

Generalized linear models (GLMs) were employed to assess the impact of arbuscular mycorrhization index (AMI) on plant productivity and richness. Plant productivity and richness were response variables, while AMI was the predictor. A Gaussian GLM was fitted for plant productivity due to normally distributed and homoscedastic residuals. Conversely, a negative binomial GLM with a log link function was used for richness.

In paper II, a model averaging approach was adopted to examine soil fertility's influence on plant community AMI. This method relied on the average of top-performing GLMs, identified by a 95% confidence interval of deviance explained (Delta AIC). Soil nitrogen (N), phosphorus (P), potassium (K), moisture, and pH were considered as predictors in the full models, with AMI as the response. To address scaling issues, all predictors were standardized (Burnham & Anderson, 2002). Given the presence of extreme values, soil P was log-transformed. Model assumptions (homoscedasticity and normality) were visually inspected and confirmed (Zuur et al., 2009). Collinearity diagnostics (Pearson correlation, VIF) indicated no issues among variables ( $r < 0.6$ ,  $VIF < 3$ ; Zuur et al. 2009) in either the GLMs or subsequent path analysis

In paper III, I aimed to assess the effect of elevational and environmental (climatic and edaphic) gradients on the representation of mycorrhizal traits among the plant communities of the Páramo. Because elevation is highly correlated with

several key environmental variables, I analysed them in parallel to fully understand the patterns of both groups of factors. Given that I found a predominant linear predictor-response relationship (Appendix 3), all analyses were performed using generalised linear models (GLMs) with zero- and one-inflated beta distributions to fit the proportional response variables (Rigby et al. 2019). I worked with this distribution due to the nature of data, which contained a large number of zeros and to match the data with the error-distribution. The mycorrhizal traits considered were mycorrhizal type (AM, ECM, ERM, ORM) and status (OM, FM, and NM). In addition, there was estimated the effect of elevation and environmental variables on community mycorrhization (MI) in the same plant communities, using the skew exponential power (SEP) distribution, which best fitted our data (Rigby et al. 2019).

**Table 2.** Summary of GLMs

	<b>Response variables</b>	<b>Distribution</b>	<b>Model averaged?</b>	<b>Collinearity issues?</b>	<b>Spatial autocorrelation?</b>
Paper I	Plant mycorrhizal traits	Binomial error	Yes	APP and MAT pH and N	Significant residuals SAC was corrected
Paper II	AMI () Plant productivity Richness	Negative binomial error	Yes	No	Not applicable
Paper III	Plant mycorrhizal traits	Zero and one inflated beta distribution (type and status) Binomial (ORM)	Yes	No	No

The analyses for the three papers were performed using R (R 3.5.4 (R Core Team 2019); (R x64 4.1.2)). The packages used for paper I were: Spacemaker (Dray et al. 2009), Packfor (Dray et al. 2020) and MuMIn (Barton 2020) R packages. For paper II: *MUMIn* package ; *MASS* package (Venables and Ripley 2002). For paper III: *gamlss* (Rigby et al. 2023) R package for zero- and one-inflated beta GLMs and skew exponential power GLMs, *CarData* (Fox and Weisberg 2019) and *Car* (Fox and Weisberg 2019) packages, *MuMIn* R package, and *coefplot* (Lander 2018) R package.

For papers I and III, I accounted for the uncertainty of variable selection in our environmental models using a model averaging approach based on the average of the best models ( $\Delta AIC < 7$ ; AIC, Akaike information criterion) (Burnham et al. 2011). I estimated variable importance as the frequency of variable occurrence in the selected models.

For paper III, I analysed spatial autocorrelation in the residuals of all models using Moran's correlograms and spatial residual plots. I did not find strong spatial autocorrelation patterns in the model residuals (Appendix 5).

### **Path analysis**

In Paper II, path analysis was employed to examine direct and indirect relationships among plant productivity, richness, soil fertility, and AMI (Arbuscular Mycorrhizal Index). Path analysis is particularly valuable in community-scale studies, allowing the differentiation of direct and indirect effects of predictors (Shipley 2016). The theoretical model, grounded in prior knowledge, hypothesized that soil nitrogen (as a proxy for fertility) would directly influence AMI due to potential inhibitory effects on mycorrhizal colonization. This, in turn, would indirectly affect plant richness and community productivity. The R package lavaan (Rosseel 2012) was used to build and test the model, considering robust standard errors and a Monte Carlo method due to the relatively small sample size ( $n = 28$ ). The tested model was not rejected ( $\chi^2 = 5.734$ ;  $p$ -value = 0.125) and was robust to multivariate non-normality, although the Monte Carlo simulation was only marginally non-significant ( $p = 0.062$ ). Further testing using the psem function in the R package piecewiseSEM (Lefcheck 2016) revealed an unaccounted link between nitrogen and total biomass, leading to the formulation of a new model that was considered definitive as no other d-separation claim was significant.

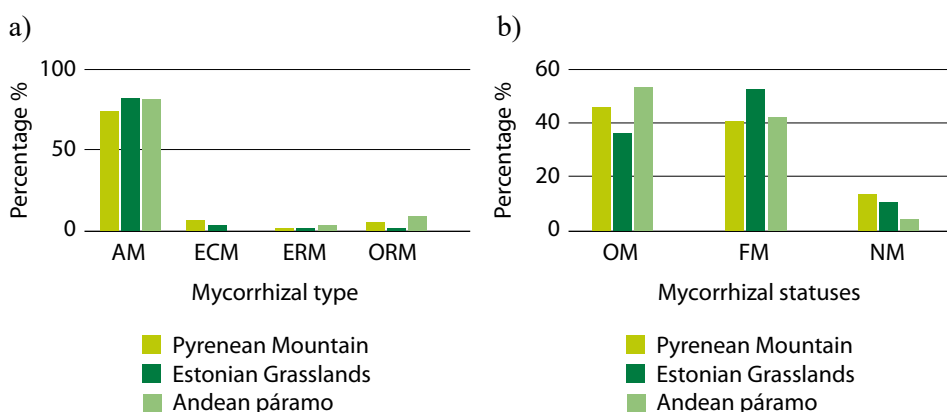
### **Ordination approaches**

To analyse the relationship between dominant plants, diversity and AMI (paper III), there was used non-metric multidimensional scaling analysis (NMDS), and I fit plant richness and AMI gradients using the function envfit, while NMDS analysis was performed using the function metaMDS, both from the R package vegan (Oksanen et al. 2019). Selection of abundant plants followed the dominance candidate index (DCI) with a criterion of  $DCI > 0.2$  (Avolio et al. 2019).

### 3. RESULTS

#### 3.1. Variation of mycorrhizal traits among the study areas

I addressed the distribution of two plant mycorrhizal traits: mycorrhizal type and mycorrhizal status. AM was the dominant mycorrhizal type in all three different study systems and regions addressed (Spanish Pyrenees, Estonian grasslands, and Andean Páramo). For the European ecosystems, AM was followed by ECM, ORM, and ERM; meanwhile, in the Andean Páramo, AM was followed by ORM, ERM, and ECM (Figure 1a). The distribution pattern of plants with different mycorrhizal statuses was similar for mountain ecosystems (Pyrenean mountain and Andean Páramo), where the majority of plants were obligately mycorrhizal (OM), followed by facultatively mycorrhizal (FM) and non-mycorrhizal (NM). By contrast, plants with FM status dominated in Estonian grasslands, followed by OM and NM (Figure 1b.).



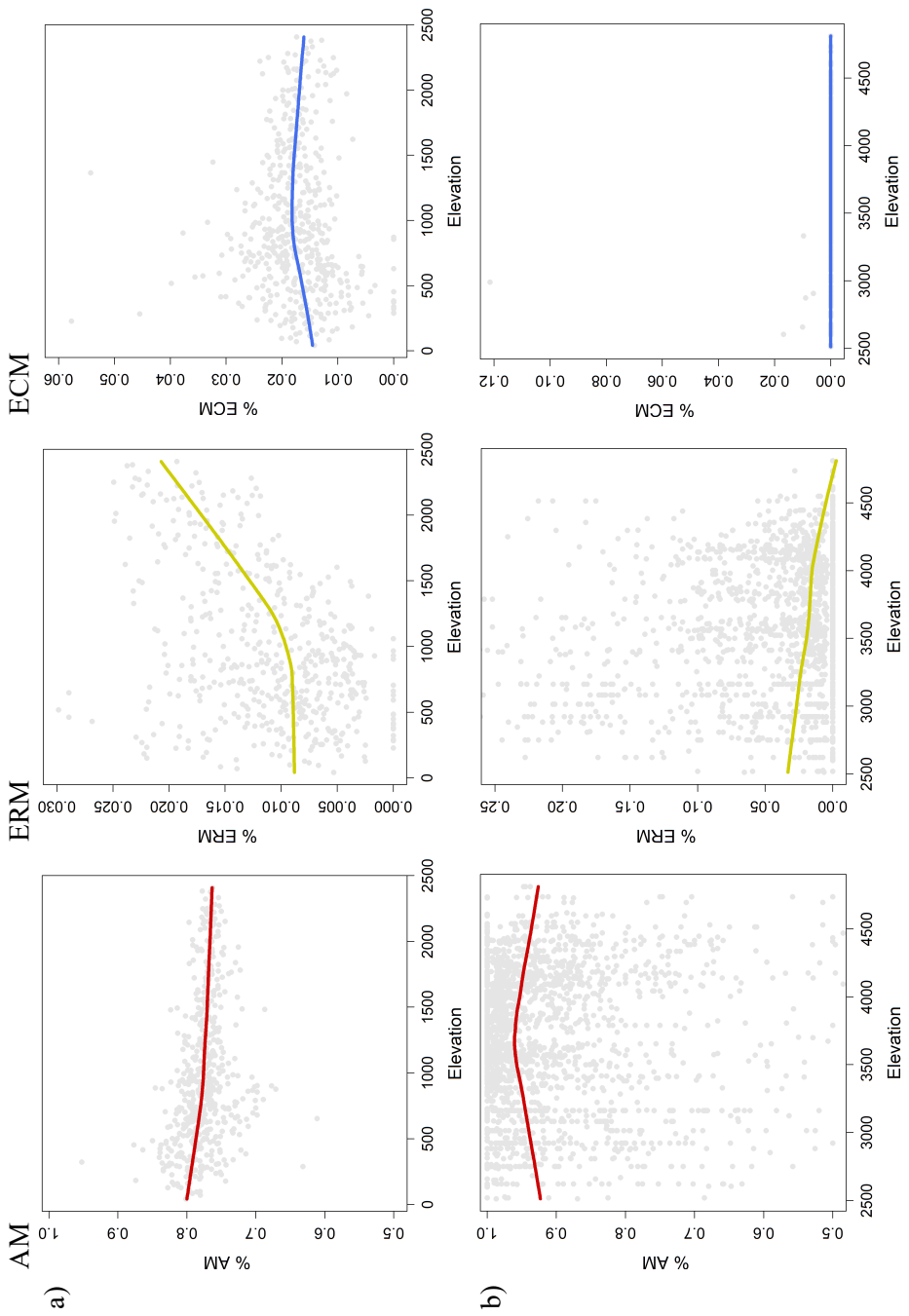
**Figure 1.** Distribution of the proportion of plant mycorrhizal types (a) and statuses (b) over three different natural ecosystems. AM, arbuscular mycorrhizal; ECM, ectomycorrhizal; ERM, ericoid-mycorrhizal; ORM, orchid-mycorrhizal; OM, obligately mycorrhizal; FM, facultatively mycorrhizal; and, NM, non-mycorrhizal.

#### 3.2. Distribution of mycorrhizal traits along two different altitudinal gradients

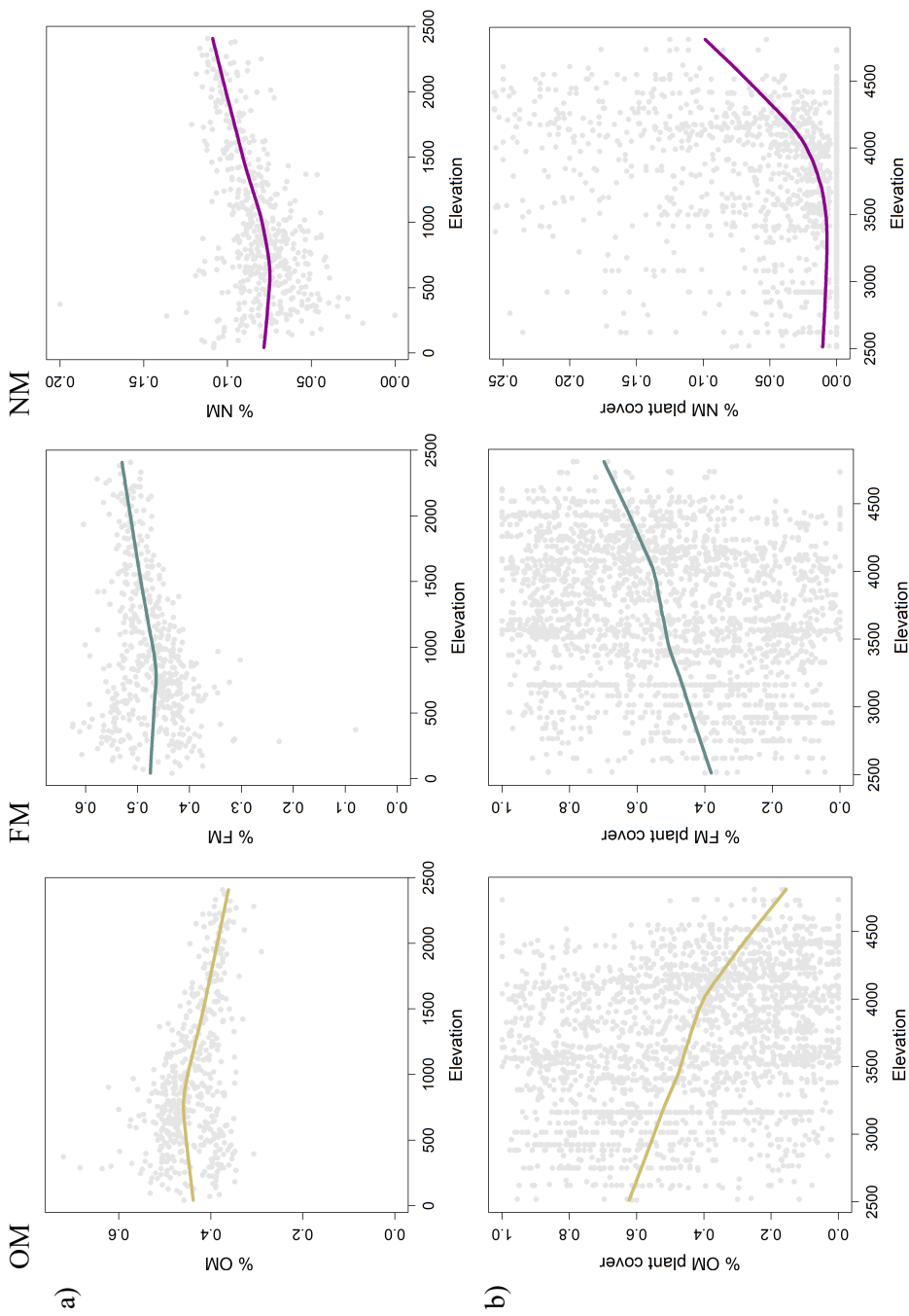
There was evaluated the distribution of plant mycorrhizal traits in two different mountain ranges. The Pyrenean mountain has an elevation range from lowland up to >2.500 m.a.s.l., and the Andean Páramo study area spans from about 2500 m.a.s.l., to 4500 m.a.s.l. There was found that mycorrhizal type and status showed different distributions along the elevational gradient in both mountain ranges (Figures 2 and 3), except in AM plants, which dominated everywhere and

along the whole gradient (Figure 2). In both mountain ranges three main mycorrhizal types (AM, ERM, and ECM) were represented, while ORM was found in the Andean Páramo, but rare in the Pyrenees). The proportion of AM plants exhibited a peak at low elevations and decreased with elevation in the Pyrenees (up to <2500 m asl). In the Andean Páramo, there was a constant increase in the proportion of AM plants with elevation from 2500 to 3500 m.a.s.l., but thereafter a decrease. The share of ERM plants showed an increase with elevation until 2500 m.a.s.l., after which it decreased. In the Pyrenees, the proportion of ECM plants increased up to 1000 m asl and then decreased. However, ECM and ORM distribution in the Andean Páramo showed no clear pattern. Finally, the proportion of NM plants increases along the altitudinal gradient.

I also addressed the relative proportions of plant mycorrhizal statuses along elevational gradients (Fig. 3a and 3b). The share of OM plant species was highest in the lowlands and declined with elevation. The proportion of FM plant species followed the opposite pattern; as elevation increased, the proportion of FM plants also increased.



**Figure 2.** The proportion of species of different plant mycorrhizal types per grid cell in the Pyrenean mountain (a), and among plant communities in the Andean Páramo (b) and the relationships with elevation. Lines represent fitted curves from loess regressions.

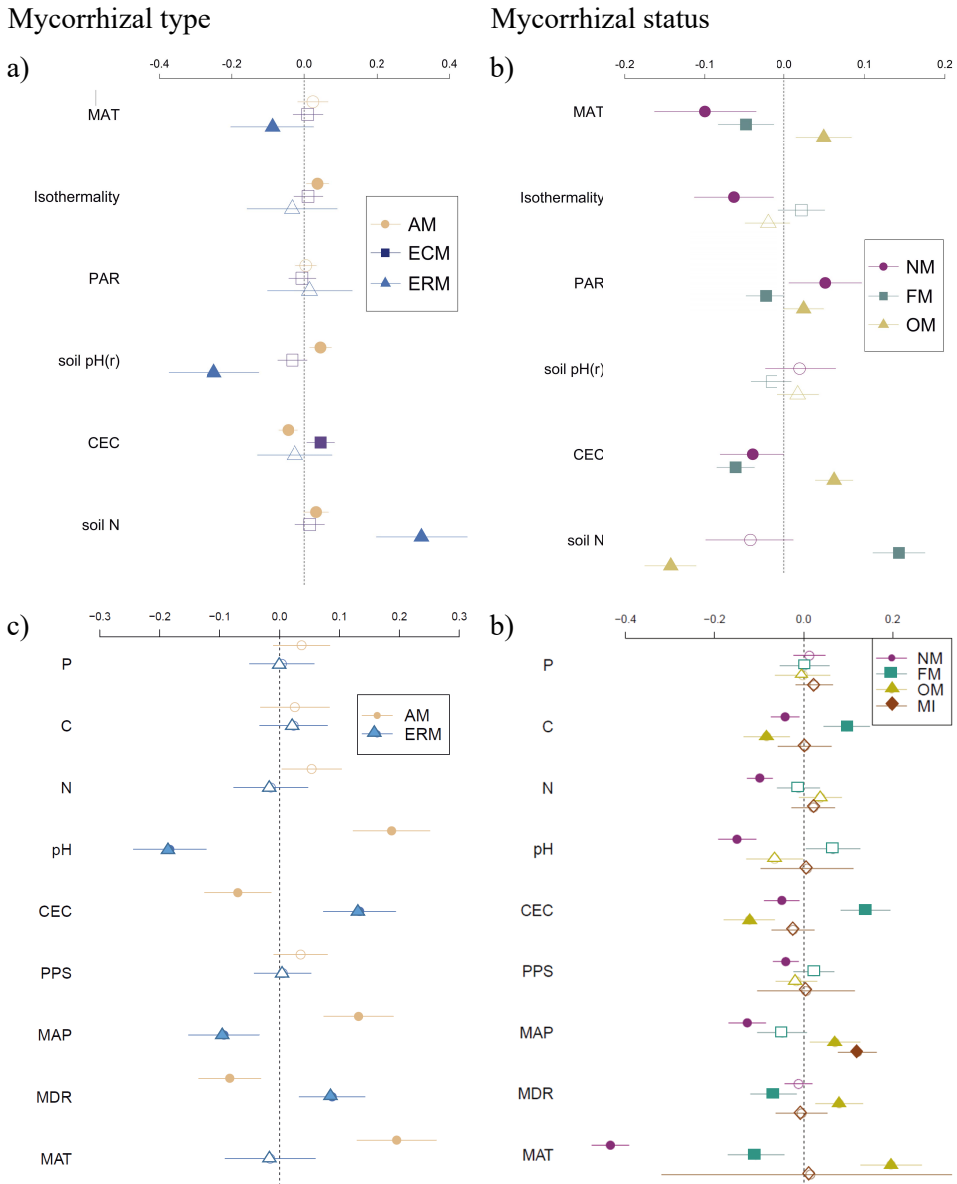


**Figure 3.** Distribution of species within plant mycorrhizal statuses per grid cell in the Pyrenean mountain (a), and among plant communities in the Andean Páramo (b) and their relationships with elevation. Lines represent fitted curves from loess regressions.

### 3.3. Drivers of the distribution of mycorrhizal traits

There was found that some climatic and edaphic variables were consistently linked to the prevalence of mycorrhizal plants in different geographic and environmental settings. The influence of temperature, soil pH, and cation exchange capacity (CEC) was similar in different mountain ranges. Temperature, represented by isothermality (ISO) in the Pyrenean study, and by mean annual temperature (MAT) in the Andean Páramo study, was positively related to the share of AM plants. Soil pH exhibited a negative relationship with the share of ERM plants, and CEC showed a negative relationship with the share of AM plants in both studies. In the Pyrenees, there was a positive correlation between the proportion of AM plant species and temperature variability (ISO), and soil N(r). Greater soil CEC was mostly correlated with higher proportions of ECM plant species (Fig. 4a). Distributions of ERM and NM were similar, showing the effects of multiple factors. For the Andean Páramo, the most important variables explaining the distribution and abundance of AM and ERM types were mean diurnal range of temperature (MDR), mean annual precipitation (MAP), soil pH, and CEC, while MAT was only significant for AM types (Figure 4c). The proportion of AM plants correlated positively with MAP, pH, and MAT and negatively with MDR and CEC. The proportion of ERM plants exhibited a positive correlation with CEC and MDR and a negative correlation with pH and MAP (Figure 4c).

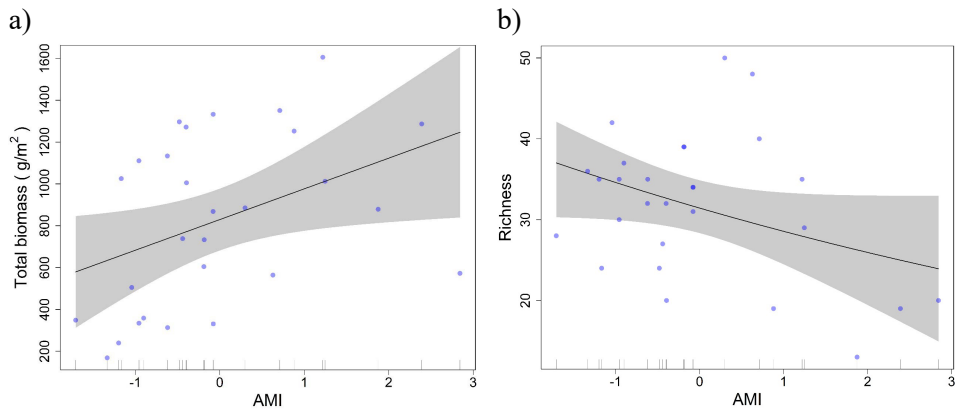
For all statuses, MAT was the most significant climatic predictor. In the Pyrenean study, the proportion of NM plant species was positively correlated with precipitation variability (ARP) and negatively correlated with MAT and ISO. High MAT, ARP, and soil CEC were linked with high proportions of OM plant species (Fig. 4b). In the Andean Páramo, MDR, CEC, and total soil C were predictors of OM and FM, whereas MAP, pH, and total soil N were predictors of NM (Figure 5b). There was a negative correlation between the share of NM plants and MAT, pH, MAP, N, CEC, C, and PPS. The percentage of FM plants was negatively correlated with MAT and MDR and a positively with C and CEC. In contrast to CEC and C, the share of OM plants was positively correlated with MAT, MDR, and MAP. Lastly, there was a positive correlation between MAP and the mycorrhization index (Figure 5d).



**Figure 4.** Forest plots indicate the effects of climatic and edaphic variables on the percentage of plant mycorrhizal types (in the Pyrenean Mountains) and abundances (in the Andean Páramo). Coefficient estimates (dots) and the respective 95% confidence intervals (whiskers), derived from regression averaged models. AM, arbuscular mycorrhizal; ECM, ectomycorrhizal; ERM, ericoid mycorrhizal; MAT, mean annual temperature; ARP, annual range of precipitation; CEC, cation exchange capacity; P, phosphorus; C, carbon; N, nitrogen; pH; PPS, precipitation seasonality; MAP, mean annual precipitation; and, MDR, mean diurnal range. Full dots indicate confidence intervals that do not include zero.

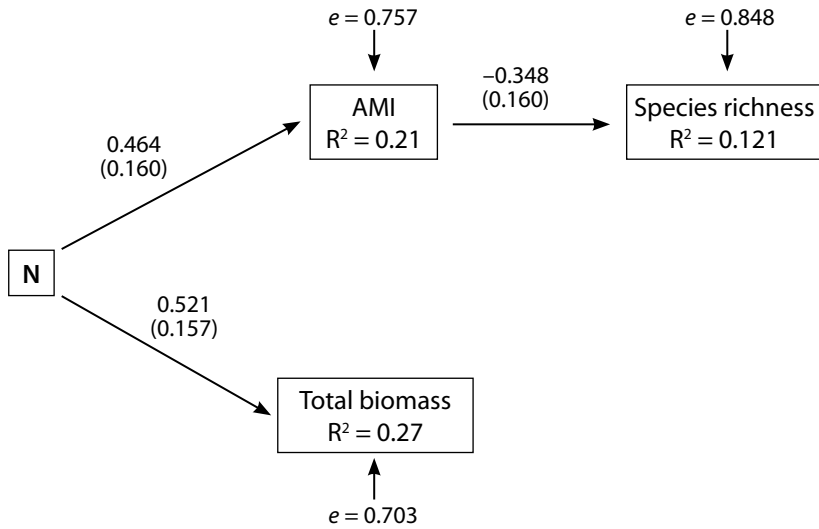
### 3.4. Effect of mycorrhizal symbiosis on plant productivity and diversity

The prevalence of mycorrhizal symbiosis in the plant communities of Estonian grasslands (vegetation units were 30x30 m) was assessed by relating the arbuscular mycorrhization index (AMI) with total standing aboveground biomass as a proxy of primary productivity, and with plant richness, as a diversity measurement. AMI was significantly positively correlated with productivity. (Figure 5a;  $F = 5.19$ ,  $P = 0.031$ ) and negatively with richness (Figure 5b;  $F = 4.13$ ,  $P = 0.042$ ).



**Figure 5.** Relationships between arbuscular mycorrhization index (AMI) and a) total biomass (plant productivity) and b) plant species richness (diversity).

Total biomass and AMI were significantly related with soil N, and negatively with species richness. Regarding AMI, total biomass, and species richness, the path analysis model explained 21%, 27%, and 12% of the variance, respectively (Figure 6). Overall, path analysis revealed a clear relationship between plant diversity and AMI, as well as a direct correlation between soil fertility and productivity (Figure 6).



**Figure 6.** Path analysis model describing possible causal links between fertility, productivity, AMI, and species richness. For endogenous variables, path coefficients, their standard errors, residual variances ( $e$ ), and the percentage of variance explained ( $R^2$ ) are displayed. In Table S3 (supplementary material paper II), model statistics are displayed. N is the overall nitrogen concentration of the soil; AMI is the arbuscular mycorrhization index.

## 4. DISCUSSION

### 4.1. Variation of mycorrhizal traits among the study areas

In nature, the occurrence and abundance of different mycorrhizal types are linked to particular climatic and edaphic conditions where selection has favored the emergence of a certain set of traits (Read 1991). Knowledge of the environmental drivers of the distribution of plant species with different mycorrhizal types and statuses can be used to forecast the effects of global change and learn more about how ecosystems work (Phillips et al. 2013; Tedersoo and Bahram 2019). However, well-documented empirical information about the drivers of plant mycorrhizal trait distribution in natural ecosystems is rather limited.

Earlier work generalized available information about the geographic distribution of mycorrhizal types and suggested that it follows a regular latitudinal pattern from the tropics to the poles. Arbuscular mycorrhizal plants (AM) predominate in lower latitude ecosystems like subtropical and tropical forests, and temperate and Mediterranean grasslands. ECM and ERM plants, which predominate in the boreal and tundra (particularly ERM) biomes, eventually replace AM plants if environmental conditions are colder and wetter, which slow down soil mineralization (Read 1991, Read and Perez-Moreno 2003, Read et al. 2004). A study by Steidinger et al. (2019) showed that climate variables, in particular, climatically-controlled variation in the rate of decomposition, are the primary drivers of the global distribution of major mycorrhizal types.

At the same time, there are regional peculiarities in the representation of mycorrhizal types and statuses in plant communities experiencing similar environmental conditions. For instance, ORM species were more abundant and ECM species less abundant in our study area in the Andes than in the Pyrenees. This probably results from a different biogeographical history, but the concrete processes underlying patchy distribution of certain mycorrhizal types require further analysis.

Our data showed that the distribution of plant mycorrhizal traits such as mycorrhizal type and status in the ecosystems of two different continents exhibited different patterns. The overall pattern of mycorrhizal type distribution in the European ecosystems was that the highest frequency and abundance was exhibited by AM, followed by ECM, ORM, and ERM. Meanwhile, for the Andean Páramo, AM was also the most common type, but was followed by ORM, ERM, and lastly ECM. Regarding plant mycorrhizal status, most mycorrhizal plants were obligately mycorrhizal (OM) in both mountain areas, followed by facultative mycorrhizal (FM) and non-mycorrhizal (NM) plants. By contrast, in the lowland Nordic grassland ecosystem, most mycorrhizal plants were FM, followed by OM and NM.

It is also possible to categorize plant species according to their mycorrhizal flexibility, depending on whether they keep their mycorrhizal status constant, being either mycorrhizal or nonmycorrhizal all the time, or whether they are able

to up- and downregulate their mycorrhiza and thus exhibit both mycorrhizal and nonmycorrhizal status, depending on local conditions (Moora 2014). ECM, ERM, ORM, OM arbuscular mycorrhizal and NM plant species can be classified as non-flexible, and FM arbuscular mycorrhizal species as flexible. Our data revealed the highest share of flexible plant species in Nordic grasslands. Similarly, Bueno et al (2017) found that the share of flexible species in European local flora increased towards higher latitudes. However, the geographic distribution of mycorrhizal flexibility has seldom been addressed, and the mechanisms underlying this pattern remain to be disentangled.

## **4.2. Distribution of mycorrhizal traits along two different altitudinal gradients**

Our current understanding about the geographic distribution of mycorrhizal types is that there is a regular elevational pattern, including a shift in dominance from arbuscular mycorrhizal (AM) to ectomycorrhizal (ECM) and ericoid mycorrhizal (ERM) plants with increasing elevation (Read 1991, Read and Perez-Moreno 2003, Read et al. 2004). However, our findings from the Andean Páramo ecosystem and those from the Pyrenees Mountain revealed contrasting elevational patterns in the representation of mycorrhizal types. In the Páramo, AM showed not strong changes, only a slight unimodal trend with subtle decrease after 2500 m, while the Pyrenees showed a consistent decrease at higher elevations.

Studies in the South Ecuadorian Andes (Haug et al. 2019) and the Qinling Mountains (Zhang et al. 2021) support the persistence of AM plants at higher elevations. This pattern contrasts with some previous research suggesting a decrease in AM plants with increasing elevation (Tibbett and Cairney 2007). One reason for such a difference might be the slower decrease of the temperature along altitudinal gradients in tropical regions compared to high-latitude mountains (Kotlínek et al. 2017, Hiiesalu et al. 2023). Some previous research also suggests that Páramo AM plants, along with their fungal partners, possess adaptations that enable them to function effectively at high altitudes (Pellissier et al. 2013). Further research is needed to explore these potential adaptations, which may involve physiological changes in the AM symbiosis that go beyond nutrient exchange, such as enhanced cold stress tolerance (Devi et al. 2019).

Our Páramo study also observed a decline in ERM and, to a lesser extent, AM plants above 3500 meters above sea level (m asl). This aligns with the overall limits on plant growth imposed by harsh climatic conditions at high elevations (Sklenář and Ramsay 2001, Peyre et al. 2018). Additionally, water limitation at higher elevations in the Páramo could restrict ERM plants, while Ericaceae species in the central Andes are typically associated with lower elevations (Luteyn 2002).

Indeed, in the Andean Páramo, most ERM plants were primarily found within the lower Páramo range (2500–3000 m asl). There was observed a decrease in ericoid mycorrhizal (ERM) plants along the Páramo elevation gradient above the

2500–3000 masl zone. Meanwhile, in the Pyrenean Mountains, I recorded a significant increase in ERM plants to 2500 masl. Consequently, the zone around 2500 masl seems to represent optimal conditions for ERM plants. Previous Páramo research aligns with this observation, as Ericales, the plant family most commonly associated with ERM symbiosis, is typically found in the understory of cool, moist montane forests near the transition to the sub-Páramo (Luteyn 2002). While some Ericales species extend into the sub-Páramo (3200–3600 m asl) (Luteyn 2002, Pabón Caicedo et al. 2002, Stevens et al. 2004), harsher conditions at higher elevations likely favor non-mycorrhizal (NM) plant strategies, potentially explaining the observed decrease in ERM presence (Kytöviita 2005).

In contrast to the Andes, the Pyrenees exhibit a pattern more consistent with latitudinal trends described by (Bueno et al. 2017). AM dominance decreased with elevation, while ECM presence peaked at mid-elevations (around 1000 m asl). Comparisons with other studies, however, show that regional variations also exist within Eurasia. The Ural Mountains show a less pronounced decrease in AM dominance compared to the Pyrenees, possibly due to the Urals' lower elevation range or historical grazing favoring AM plants in the Pyrenees (García-Ruíz and Valero-Garcés 1998, Körner 2003, Sizonenko et al. 2020). Additionally, historical factors like glaciation in northern Europe and forest logging in the Pyrenees might have influenced the distribution of NM, ERM, and FM plants at higher elevations.

Former studies have revealed different trends in plant mycorrhizal status with increasing elevation. In a pan-European study, Bueno et al. (2017) recorded a decrease in the share of FM plants along the elevational gradient. This pattern emerged mostly due to the trend observed in the Alps. However, we found the opposite pattern for the Pyrenean Mountain and the Andean Páramo where the proportion of FM plant species increases, while OM plant species decrease along the altitudinal gradient. One possible reason why plants with a flexible relationship with mycorrhizal fungi (FM) become more common at higher elevations, and those entirely reliant on this beneficial partnership (OM) become less frequent, might be the potential scarcity of proper symbiotic fungal partners at high elevations (Hiiesalu et al. 2023) which favors plant species that are capable of persisting temporarily without mycorrhiza. The question of why a similar trend is not apparent in the Alps also needs further study.

Above 4000 meters, NM plants become more abundant. There are several potential explanations for the success of non-mycorrhizal (NM) plants in harsh environments of high altitudes (and latitudes). It may reflect the poor performance of mycorrhizal fungi in these conditions, becoming a drain on plant resources rather than a benefit (Tibbett and Cairney 2007). An alternative explanation is that NM plants thrive in high-latitude, and consequently also high-altitude, ecosystems, where nitrogen is primarily found in organic forms, with the help of dark septate endophytes (Newsham et al. 2009). Some plants can even directly absorb organic nitrogen through specialized structures like proteoid roots (Shane et al. 2006; Kielland et al. 2007) or exploit temporary or localized nitrogen sources (McKane

et al. 2002). However, further research is needed to definitively identify the specific mechanisms that allow NM plants to successfully perform in cold climates.

The shift in plant community-level mycorrhizal reliance with increasing elevation, reflecting the shares of different mycorrhizal types and statuses in plant communities, has potentially significant implications for the ecology of high-mountain plants. Mycorrhizal associations may play a crucial role in the survival and success of these plants up to mid-elevations, and changes in the availability of mycorrhizal fungi with elevation can have a substantial impact on plant communities in these altitudes. At higher altitudes, the significance of mycorrhiza seems to decrease as the proportion of FM and NM plant species in the community increases. Both the lack of proper fungal partners (Hiiesalu et al. 2023), and low efficiency of mycorrhizal symbiosis at high altitudes (Tibbett and Cairney 2007) could underlie this trend.

However, it is also important to acknowledge limitations in our understanding of mycorrhizal plant distribution. The accuracy of our conclusions is ultimately dependent on the availability of comprehensive data on plant mycorrhizal traits, and this data is still scarce for many regions of the world.

### **4.3. Edaphic and Climatic drivers on the distribution of plant mycorrhizal traits**

The influence of environmental factors on the distribution of plant mycorrhizal associations differed between the Pyrenees and the Andean Páramo. In the Pyrenees, climatic factors significantly impacted the distribution of arbuscular mycorrhizal (AM), ectomycorrhizal (ECM), and especially non-mycorrhizal (NM) plant species, while having little effect on ericoid mycorrhizal (ERM) species. Edaphic factors influenced the distribution of AM, ECM, and ERM plants, but that of NM plants to a lesser extent. In the Andean Páramo, the pattern of AM distribution was similar to that described in Bueno et al. (2017) – the proportion of AM species increased with mean annual temperature and decreased with diurnal temperature variation. Climatic factors such as temperature and precipitation, and edaphic factors such as pH or CEC, had contrasting effects on AM and ERM plants in the Andes.

The occurrence of NM plants in the Pyrenees was positively associated with cold conditions, but not with soil factors. This result is in accordance with Barceló et al. (2019) who studied the global distribution of mycorrhizal types and only found the climate to be an important driver. However, the Andean data showed that NM plants were more common in drier habitats, as well as acidic, nitrogen-poor and carbon-rich soils. Large scale studies may sometimes overlook the effect of edaphic factors if they use data with a coarser spatial scale than the fine scales over which edaphic variables often vary (Pearson and Dawson 2003). In order to better understand the role of edaphic factors, empirical soil data collected from

exactly those sites where the vegetation data came from, and not extrapolated soil data, should be used in future studies.

Previous studies, including Bueno et al. (2017), Bonfante and Genre (2008), and Barceló et al. (2019), have associated ericoid mycorrhizal (ERM) plants with colder climates. The observed discrepancies in ERM distribution reported by different studies might be explained by regional differences in altitudinal environmental gradients. The sub-Páramo experiences warmer temperatures compared to the typical thermal range encountered at similar altitudes in European mountains. Additionally, precipitation patterns differ. While plants in European mountains experience increasing precipitation with elevation, Páramo plants face water limitation at high altitudes (Pérez 1991). This aligns with the natural habitat of Ericaceae in the Andes, which thrives in cool and moist environments between 1000 and 3000 meters above sea level (Luteyn 2002, Setaro et al. 2006a). Although some Ericaceae species are found in the superPáramo (Sklenář and Balslev 2005), the harsher conditions likely fall outside the optimal range for many Ericaceae species. Additionally, soil characteristics like pH and cation exchange capacity (CEC) played a role. AM plants were more frequent in high pH and low CEC soils, while ERM plants were most abundant in low pH soils. Last but not least, current and historical grazing regimes may influence the distribution of ERM plants, especially in Europe where many alpine areas have historically been used as pastures (Janssen et al. 2018).

While the Páramo harbors several endemic orchid mycorrhizal (ORM) species (Lehmann 2010), their overall low abundance limited our ability to detect clear patterns in their distribution. Similarly, I only identified three plant species belonging to ECM genera within the VegPáramo database plots. This scarcity aligns with observations by Corrales et al. (2018) who reported a patchy and regionally variable abundance of ECM plants in the tropics. Further dedicated studies are necessary to comprehensively document the occurrence and distribution of ECM plants in tropical mountain ranges like the Andes.

These studies in the Pyrenean Mountains and the Andean Páramo highlight the complex and dynamic nature of plant mycorrhizal associations in mountain ecosystems. While some general trends emerge, such as the increase in FM plants with elevation, regional variations and adaptations of plant-fungal partnerships also become evident. Further research focusing on specific regions and exploring potential physiological adaptations within AM symbioses will broaden our understanding of how these vital relationships respond to environmental changes including climate change.

It is important to acknowledge limitations in our understanding of mycorrhizal plant distributions. The accuracy of these observations is ultimately dependent on the availability of comprehensive data on plant mycorrhizal traits. These findings highlight the importance of considering geographical context, such as latitude, temperature range, and precipitation regimes, when studying the distribution of plant mycorrhizal types along elevation gradients.

#### **4.4. Relationship between community mycorrhization and soil fertility**

There was evaluated the relationships between plant mycorrhizal status (measured by the Arbuscular Mycorrhization Index – AMI), soil fertility, and plant community characteristics (productivity and diversity) in Estonian temperate grasslands. Our findings challenged some existing assumptions about mycorrhizal symbiosis (Bever et al. 2010, 2012, van der Heijden et al. 2015).

Concerning the relationship between AMI and Soil Fertility, in contrast to our initial hypothesis, I observed a positive correlation between soil nitrogen (N) and community mycorrhization. This is inconsistent with the assumption that mycorrhizal fungi would be less important in fertile environments (Hempel et al. 2013). The observed positive correlation between AMI and soil N requires deeper exploration. Nutrient stoichiometry between plants and fungi appears to play a key role (Johnson et al. 2014). In N-deficient environments, plants and fungi might compete for N, reducing the benefit of the mycorrhizal partnership (Johnson et al. 2010, Hodge et al. 2010). However, when N is readily available, it could satisfy the fungal N requirement, allowing them to provide a greater benefit to plants, especially regarding phosphorus (P) uptake. This aligns with the “Law of the Minimum” concept (Johnson et al. 2014). Interestingly, no direct link was found between AMI and plant community productivity. Along a steep productivity gradient, mycorrhizal symbiosis may influence productivity in the nutrient-limited end, while at fertile conditions it plays (Treseder 2004).

Our study also acknowledged limitations and areas for further research. Future studies should consider the type of nutrient (N vs P), fertilization methods, and their application context when evaluating effects on mycorrhizal colonization (Liu et al. 2012, Camenzind et al. 2014, Wang et al. 2018). Additionally, investigating the influence of other unmeasured soil properties, such as aluminum or calcium content, on nutrient availability for plants and fungi in general, could provide valuable insights (Penn and Camberato 2019).

Overall, this study sheds light on the complex interplay between plant mycorrhizal colonization, soil fertility and plant community dynamics. It highlights the importance of considering nutrient stoichiometry and potential interactions with other soil organisms in future research to develop a more comprehensive understanding of mycorrhizal symbiosis in different ecological contexts.

I also addressed the relationship between Arbuscular Mycorrhization Index (AMI) – a proxy of the reliance on mycorrhiza of the whole plant community – and plant species richness in temperate grasslands. Our findings challenged the expectation that higher AMI would promote greater plant diversity. Contrary to theoretical predictions (Hart et al. 2003, Bever et al. 2010), our results revealed a negative association between community mycorrhization and plant richness. This suggests that under certain circumstances, arbuscular mycorrhizal symbiosis might not contribute to the development of diverse plant communities. A possible explanation could be related to the strong mycorrhizal dependency of potential

dominants (Tedersoo et al. 2020). These species may exert strong competitive effect on their non-mycorrhizal or less-mycorrhizal neighbors (Chomicki et al. 2019). This could explain the observed association of high AMI with low richness.

Our findings align with studies suggesting that competitive plants benefit more from mycorrhizal associations compared to stress-tolerant or ruderal species (Betekhtina and Veselkin 2011, Hempel et al. 2013). This contradicts the notion that competitive plants are less reliant on mycorrhizal symbiosis due to their inherent acquisitive strategies (Grime 2001).

Further research is needed to fully understand the complex relationship between the presence and abundance of mycorrhiza in plant communities and plant richness. Exploring how community mycorrhization interacts with other plant functional traits and fungal characteristics could provide valuable insights.

Overall, this study highlights the need to move beyond theoretical predictions and empirically explore the multifaceted effects of mycorrhizal symbiosis on plant communities. The observed negative correlation between AMI and richness suggests that mycorrhizal symbiosis can influence plant community assembly through mechanisms related to competition and resource acquisition strategies.

## 5. CONCLUSIONS AND FURTHER PERSPECTIVES

In the Pyrenean Mountains, altitudinal variation in mycorrhizal type abundance resembled latitudinal trends. Climate and soil factors jointly influenced the distribution of AM and ECM plant species, while the occurrence of NM plants was primarily associated with colder temperatures, and the occurrence of ERM plants was associated with low soil pH. This highlights the distinct environmental drivers for different mycorrhizal types.

The Andean Páramo presented a contrasting pattern. AM plants dominated the entire elevational gradient, whereas ERM plants were most abundant at lower altitudes. This deviation from trends seen elsewhere suggests that specificities of the Andean ecosystem, such as drier conditions, might influence mycorrhizal prevalence at high altitudes.

In the Estonian grasslands, highly fertile soils harbored high community mycorrhization but low plant richness. This suggests that fertile environments might favor both mycorrhizal plants and fungi, potentially promoting dominant mycorrhizal plant species through competitive advantages.

Several key areas warrant further investigation to improve our understanding of the distribution and dynamics of plant mycorrhizal traits in natural ecosystems.

Although the current global distribution of mycorrhizal types generally tracks environmental gradients, there are examples of uneven representation of mycorrhizal types and statuses in different geographic regions, despite the presence of similar environments. Future research should address the regional patchiness in the distribution of plant mycorrhizal types and disentangle possible mechanisms underlying these patterns. By increasing the geographic scope of mycorrhizal studies it should be possible to build a more comprehensive picture of how mycorrhizal associations interact with environmental gradients and influence plant community structure and diversity across diverse natural ecosystems.

There is a need to improve our understanding of the Negative AMI-Richness Link. Future studies should address the mechanisms underlying the observed negative relationship between community mycorrhization and plant richness. Exploring the role of mycorrhiza in modulating plant competition via enhanced resource acquisition and protection from pathogens is crucial.

In particular, non-nutritional benefits of mycorrhizal symbiosis have received little attention. Research should compare potential non-nutritional benefits of mycorrhizal symbiosis for dominant and subordinate plant species, both in low- and high-fertility environments. Understanding how mycorrhizal fungi contribute to plant fitness in ways besides beyond nutrient acquisition could provide valuable insights.

## SUMMARY

Mycorrhizal symbiosis is a crucial association between fungi and plant roots that significantly impacts plant individuals, communities, and ecosystems. This study investigates how geographic, environmental and edaphic drivers influence the distribution of plant mycorrhizal traits (type, and status) along elevational and local soil fertility gradients. There was addressed plant mycorrhizal types including arbuscular mycorrhizal (AM), ectomycorrhizal (ECM), and ericoid mycorrhizal (ERM) and plant mycorrhizal statuses including obligately mycorrhizal (OM), facultatively mycorrhizal (FM), and non-mycorrhizal (NM).

I analyzed data from the Pyrenean Mountain range and the Andean Páramo, revealing contrasting patterns compared to what was expected based on current empirical evidence from temperate regions. While AM dominance persisted throughout the Páramo gradient, the Pyrenees displayed a slight decrease in AM with elevation and a peak in ECM at mid-elevations. In the Andean Páramo, ERM plants were most abundant at the lowest elevations. Notably, non-mycorrhizal (NM) plants thrived at higher elevations in both regions.

Across both mountain ranges, patterns of plant mycorrhizal status mirrored the elevational gradient. The prevalence of facultatively mycorrhizal plants increased, while obligately mycorrhizal plants declined, with elevation. Notably, above 4,000 meters, plants altogether lacking mycorrhizal association (non-mycorrhizal) became more common.

Additionally, I explored the relationship between community mycorrhization and plant community properties in temperate grasslands. Our findings suggest a positive correlation between soil fertility (particularly nitrogen) and the prevalence of mycorrhizal symbiosis (arbuscular mycorrhization index, AMI). Interestingly, while both community productivity and AMI increased with soil fertility, plant diversity exhibited a negative relationship with AMI. Path analysis revealed that AMI mediates the link between soil nitrogen and plant diversity, potentially by promoting dominant plant species within the community.

In conclusion, this study highlights the diverse roles of mycorrhizal symbiosis across scales. Mycorrhizal distribution patterns vary geographically, and community mycorrhization can influence plant community composition by modulating diversity alongside soil fertility gradients. These findings emphasize the need to consider mycorrhizal symbiosis when interpreting plant ecology at various scales.

**Keywords:** Mycorrhizal types, Mycorrhizal status, Elevation gradient, Plant community, Mycorrhizal symbiosis, Plant diversity, Soil fertility.

## KOKKUVÕTE

### Mükoriisete tunnuste jaotus taimekooslustes ja selle muutus piki looduslike gradiente

Taimedega elavad sümbioosis seened, mis moodustavad koos taimejuurega seenjuure ehk mükoriisa. Mükoriisset sümbioosi on mitut tüüpi. Neist levinuim on arbuskulaarne mükoriisa (AM), mille puhul seenpartneriks on mikroskoopilised krohmseedid ning taimpartneriteks enamik maismaa taimeliike, aga ka mõned veetaimede liigid. Arbuskulaarne mükoriisa on oluline sümbioos pea kõigis – looduslikes ja inimõjulistes – maismaaökosüsteemides, erandiks on üksnes äärmuslikult külmad, kuivad ning häiritud elupaigad. Parasvöötmes leiame AM-seeni pea kõigi rohttaimede juurtes ning vähemal määral põõsastel ja puudel, troopikametsade puud seevastu on valdavalt AM-seentega kooselulised. AM-seened elavad ja seega ka moodustavad eoseid mullas ning seeneriigi standardi järgi on neil väga suured eosed (30–700 µm). Seetõttu võiks eeldada, et nad on halvemad levijad kui muud mikroobid. Sellest hoolimata on enamik AM-seeneliike levinud globaalselt: samu liike võib kohata nii Aasias, Ameerikas kui ka Austraalias. Teiseks enamlevinud mükoriisa tüübiks on ektomükoriisa, mida moodustavad seened kuuluvad kandseente, aga harvematel juhtudel samuti kottseente hulka. Enamikus moodustavad ektomükoriissed seened mükoriisa puudega. Ektomükoriisa on domineerivaks tüübiks borealsetes okas- ja segametsades, aga paiguti ka ekvatoriaalsetes vihmametsades. Erikoidne mükoriisa moodustub kanarbikulaadsete seltsi taimeliikide ja kottseente koostöös ja orhoidne mükoriisa moodustub käpaliste sugukonna taimeliikide ning kandseente või erijuhul kottseente vahel.

Mükoriisne sümbioos on kooselu seente ja taimejuurte vahel, mis mõjutab oluliselt mitte ainult taimeisendeid, vaid ka terveid taimekooslusi ja ökosüsteeme. Mükoriisa olemasolu või puudumine, aga samuti taimega assotsieerunud mükoriisse seenekoosluse liigiline koosseis mõjutab taime võimet taluda keskkonnamõjusi ja panna vastu nii abiootilisele kui biootilisele stressile. Taimeliikide erinev sõltuvus mükoriisast võib olla oluliseks faktoriks, mis määrab taimevaheliste suhete tasakaalu ning mõjutab seeläbi ka taimekoosluste liigirikkust. Näiteks võib arbuskulaarne mükoriisa soodustada suhteliselt rohkem selliseid taimeliike, mis on nõrga konkurentsivõimega ning millised jääksid ilma mükoriisa toeta konkurentsias alla tugevamatele liikidele. Samas võib ektomükoriisa soodustada peremeestaime dominantse tänu oma efektiivsele talitusele ja sellest tulenevale positiivsele tagasisidemele.

Käesolevas töös vaadeldakse taimeliikide mükoriisseid tunnuseid, mis iseloomustavad taime ja mükoriisete seente sümbioosi struktuuri ja talitust. Üks oluline ja laialt kasutatav kategooriline tunnus ongi mükoriisa tüüp. Teise kategoorilise tunnuseks võib välja tuua mükoriisse staatuse, mis iseloomustab seda, kui tihe on seos taime ja seente vahel. Osa taimeliike on praktiliselt alati sümbioosis

mükoriisete seentega (obligatsiooniga mükoriisid), teised on sümbioosis vahetevahel, kuid mitte alati (fakultatiivselt mükoriisid). Samuti on taimeliike, mis ei moodustagi mükoriisat – neid võib nimetada mittemükoriisiks. Lisaks võib taimede ja mükoriisete seente sümbioosi iseloomustada kvantitatiivselt. Taime sõltuvust mükoriisast iseloomustab näiteks eksperimentaalselt määratav kasvuvastus, kus võrreldakse taime biomassi või muid tunnuseid kasvamisel koos mükoriisaseentega ja ilma. Taime mükoriisasõltuvust võib kaudselt iseloomustada ka keskmine juurte mükoriisise kolonisatsiooni määr. Oluline võib olla ka see, kui plastiline on taim suhetes mükoriisete seentega. Teataval määral võib taime plastilisust suhetes mükoriisaseentega iseloomustada juurte kolonisatsiooni varieerumine erinevate kasvukohtade vahel.

Käesolevas töös uuriti, kuidas geograafilised, kliimatilised ja edaafilised tegurid mõjutavad taimede mükoriisete tunnuste (tüüp ja staatus) jaotumist piki absoluutkõrguse gradienti mäestikes, aga samuti piki lokaalset mullaviljakuse gradienti. Töös käsitleti valdavalt kolme peamist mükoriisatüüpi: arbuskulaarne mükoriisa (AM), ektomükoriisa (ECM) ja erikoidne mükoriisa (ERM). Samuti käsitlesime kolme mükoriisese staatuse tüüpi: obligatsiooniga mükoriisid (OM), fakultatiivselt mükoriisid (FM) ja mittemükoriisid taimed (NM).

Mükoriisete tunnuste varieerumist piki absoluutkõrguse gradienti analüüsisime Pürenee mäeaheliku ja Andide Páramo taimekoosluste näitel. Pürenee puhul hõlmasid uurimisalad nii metsavööndi kui alpiinsete rohumaate kooslusi. Páramo taimekoosluste all mõistetakse aga Andides metsapiirist kõrgemal asuvaid kooslusi. Mõnikord nimetatakse Páramot ka Andide alpiinseks tundraks. Meie tulemused näitasid, et kontrastid mükoriisete tüüpide ja staatuste esindatuses kõrgusvööndite vahel olid väiksemad, kui senise info põhjal oleks võinud eeldada. Kui AM tüüpi domineerimine oli Páramo taimekooslustele iseloomulik praktiliselt kogu kõrgusgradienti ulatuses, siis Pürenees ilmnisid piki kõrgusgradienti AM tüüpi osakaalu langus ja sellega paralleelselt ECM tüüpi osakaalu tõus maksimumiga keskmiste kõrgustel. Andide Páramos esines ERM tüüp kõige rohkem madalamatel kõrgustel (ca 2500 m) ja edasi selle osakaal langes, Pürenees aga ERM tüüpi osakaal tõusis piki kõrgusgradienti, ulatudes kõrguseni 2500 m. Seega ERM osakaalu erinev trend tuleneb eelkõige mäestike erinevast kõrgusest. Mittemükoriisete taimede osakaal kasvas mõlemas mäestikis absoluutkõrguse tõustes, mis olemasolevaid kirjandusandmeid arvestades oli oodatav trend. Mõlemas mäestikis suurenes absoluutkõrguse kasvades fakultatiivselt mükoriisete taimede osakaal ja vähenes obligatsiooniga mükoriisete taimede osakaal. Ilmselt ei toimi mükoriisa suurte absoluutkõrguste karmides tingimustes alati efektiivselt ja taimedel võib energaetiliselt olla kasulikum piirata mükoriisete kolonisatsiooni juurtes. Selleks on eelkõige võimelised fakultatiivselt mükoriisid taimeliigid. Seni oli erineva mükoriisese staatusega taimede leviku kohta piki absoluutkõrguse gradienti infot vähe – tulevased uurimused peavad näitama, kui üldine meie poolt kirjeldatud trend on.

Saamaks täpsemat ülevaadet mükoriisete tunnuste esinemisest taimekoosluse tasemel, uurisime lisaks absoluutkõrguse gradiendile ka produktiivsusgradienti, pöörates tähelepanu produktiivsuse muutustele lokaalses skaalas. Konkreetselt

uurisime taimekoosluse mükoriissuse (erineva mükoriisse staatusega liikide esindatust kirjeldav indeks) ja muude taimekoosluse parameetrite (maapealne biomass, mida võib pidada kasvukoha produktiivsuse mõõduks; liigirikkus) ja mullaparameetrite vahelist seost parasvöötme rohumaadel Eestis. Tulemused näitasid positiivse korrelatsiooni olemasolu mullaviljakuse (eriti lämmastikusisalduse) ja koosluse mükoriissuse vahel – viimast mõõdeti arbuskulaarse mükoriissuse indeksi abil (AMI). Huvitaval kombel kasvasid nii maapealne biomass kui ka koosluse mükoriissus mullaviljakuse kasvades, samas kui liigirikkus vähenes. See tulemus ei ole kooskõlas tavapärase ootusega, mille kohaselt peaksid taimed olema mükoriissemad tingimustes, kus muld on vähem viljakas ja mükoriisne sümbioos aitab toidupuudust leevendada. Samas kui viljakates tingimustes peaks mükoriissus vähenema, sest toitaineid on võimalik kätte saada ka ilma mükoriisa kaasabita. Antud juhul aga ei mõõdetud otseselt juure mükoriisset kolonisatsiooni, mis tõenäoliselt käitus ülalkirjeldatud viisil, vaid iseloomustati obligaatselt ja fakultatiivselt mükoriisete taimede, ning mittemükoriisete taimede, osakaalu koosluses. Antud juhul domineerisid viljakates tingimustes taime-liigid, mis on obligaatselt mükoriisid ja see muutis koosluse mükoriissuse ja mullaviljakuse seose just selliseks, nagu ülal kirjeldatud.

Kokkuvõttes võib öelda, et käesolev töö näitab taimekoosluse mükoriisete tunnuste erisuunalist muutumist piki geograafilisi ja ökoloogilisi gradiente. Mükoriisatüüpide ja staatuste osakaalud kooslustes erinevad piirkonniti. See on seotud ühelt poolt piirkondade erineva biogeograafilise ajalooga, millest sõltub erinevate mükoriisete tunnustega taimeliikide esindatus regioonis. Teisalt iseloomustavad regioone ka unikaalsed keskkonnatingimused. Näiteks sama kõrgusvööndi temperatuur ja sademete määr võivad erinevates mäestikes drastiliselt erineda. Taimekoosluste mükoriissus kujuneb olemasoleva liigifondi põhjal, mükoriisa tüüp ja mükoriisne staatus mõjutavad kujunevate taimekoosluste liigilist koosseisu ja struktuuri tihti suuremal määral, kui seda seni on ette kujutatud.

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\* \* \*

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## **PUBLICATIONS**

## CURRICULUM VITAE

Name: Daniela Leon Velandia  
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### Education:

2017–2024 PhD studies in Botany and Ecology, University of Tartu  
2013–2015 MSc in Biological Sciences, Pontifical Xaverian University  
2001–2007 BSc in Microbiology, Pontifical Xaverian University  
1995–2000 Jose Celestino Mutis School

### Institutions and position held:

#### Senior Agricultural Professional

Agencia Nacional de Tierras – UAF, Bogotá, Colombia

January – December 2023

Provided professional services to guide the calculation of the family agricultural unit (UAF) by homogeneous physical units in prioritized municipalities.

Leveraged agricultural productive technical expertise to support the National Land Agency's objectives.

#### Researcher

Amazonian Institute of Scientific Research – SINCHI, Bogotá, Colombia (2015–2017)

Conducted research on arbuscular mycorrhizal fungi using molecular techniques and bioinformatics analysis.

Studied microbial communities in Amazonian soils using next-generation sequencing (NGS) techniques.

Supported research on bacterial and arbuscular mycorrhizal fungal communities in Amazonian soils.

Employed qPCR and NGS techniques for community analysis and quantification. Coordinated and executed field, laboratory, and data analysis activities for the Soils component.

Developed and adjusted project plans.

### Languages:

Spanish (mother tongue), English (good).

### Scientific publications:

- Leon, D.**, Peyre, G., Zobel, M., Moora, M., Meng, Y., Diaz, M., & Bueno, C. G. (2023). Mycorrhizal symbioses in the Andean paramo. *Mycorrhiza*, 1–11. <https://doi.org/10.1007/s00572-023-01133-5>
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- Pena-Venegas C, **Leon D** & Bueno C.G. (2022). Arbuscular Mycorrhizal Fungi in the Colombian Amazon: A Historical Review. 10.1007/978-3-031-12994-0\_4.
- Bueno CG, Gerz M, Moora M, **Leon D**, Gomez-Garcia D, de Leon DG, et al. Distribution of plant mycorrhizal traits along an elevational gradient does not fully mirror the latitudinal gradient. *Mycorrhiza* [Internet]. 2021;31(2):149–59. Available from: <https://doi.org/10.1007/s00572-020-01012-3>
- Bueno CG, Davison J, **Leon D**, Meng Y, Öpik M, Zobel M, et al. Towards a consistent benchmark for plant mycorrhizal association databases. *New Phytol* [Internet]. 2021 Aug;231(3):913–6. Available from: <https://onlinelibrary.wiley.com/doi/10.1111/nph.17417>
- Bueno G, Gerz M, Moora M, **Leon D**, García D, García de León D, Castell X, Al-Quraishy S, Hozzein W & Zobel M. (2021). Distribution of plant mycorrhizal traits along an elevational gradient does not fully mirror the latitudinal gradient. *Mycorrhiza*. 31. 10.1007/s00572-020-01012-3.
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- Davison J, García de León D, Zobel M, Moora M, Bueno C.G., Barceló M, Gerz M, **Leon D**, Meng Y, Pillar V, Sepp S, Soudzilovskaia N, Tedersoo L, Vaessen S, Vahter T, Winck B, Opik M. (2020). Plant functional groups associate with distinct arbuscular mycorrhizal fungal communities. *New Phytologist*. 226. 10.1111/nph.16423.
- Bueno C.G., Aldrich-Wolfe L, Chaudhary B, Gerz M, Helgason T, Hoeksema J, Klironomos J, Lekberg Y, **Leon D**, Maherali H, Opik M, Zobel M, Moora M. (2019). Misdiagnosis and uncritical use of plant mycorrhizal data are not the only elephants in the room. *New Phytologist*. 224. 10.1111/nph.15976.

### Conference presentations:

- III International Symposium of the Mycorrhizal Symbiosis in South America. Leticia, Colombia, 24 August to 2 September 2023. Oral Presentation “Mycorrhizal symbioses in the Andean páramo”.
- ICOM 10 International conference on Mycorrhiza : Mycorrhiza for sustainable World. Merida, Mexico, 30 June – 5 July 2019. Oral Presentation “Changes in plant community mycorrhization along a productivity gradient in temperate grasslands in Estonia”.

**Other activities:**

Co-advisor of Daniel Sarmiento's undergraduate thesis titled "Characterization of floristic and mycorrhizal traits of dominant plants in mixed páramo grasslands in the Páramo de Guerrero, Cundinamarca, Colombia," presented in 2020 for the degree of Environmental Engineer.

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#### Põllumajanduse vanemspetsialist

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Pakuti professionaalseid teenuseid, et suunata perekonna põllumajandusüksuse (UAF) arvutamist homogeensete füüsiliste üksuste kaupa prioriteetsetes omavalitsustes.

Kasutas Maa-ameti eesmärkide toetamiseks põllumajandustootmise tehnilisi teadmisi.

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Amazonase teadusuuringute instituut – SINCHI, Bogotá, Colombia (2015–2017)

Viinud läbi uurimistööd arbuskulaarsete mükoriisaseente kohta, kasutades molekulaartehnikaid ja bioinformaatika analüüsi.

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- Leon, D.**, Peyre, G., Zobel, M., Moora, M., Meng, Y., Diaz, M., & Bueno, C. G. (2023). Mycorrhizal symbioses in the Andean paramo. *Mycorrhiza*, 1–11. <https://doi.org/10.1007/s00572-023-01133-5>
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### Konverentsiettekanded:

- III Rahvusvaheline Mükoriisa Sümpoosium Lõuna-Ameerikas. Leticia, Colombia, 24. august – 2. september 2023. Suuline ettekanne “Mükorissed sümbioosid Andide paramos”.
- ICOM 10 Rahvusvaheline mükorisia konverents: Mükoriisa jätkusuutlikule maailmale. Merida, Mehiko, 30. juuni – 5. juuli 2019. Suuline ettekanne “Taimekoosluse mükoriseerimise muutused produktiivsuse gradiendil Eesti rohu- maal”.

**Muu teaduslik tegevus:**

Kaasjuhendaja Daniel Sarmiento bakalaureusetööle pealkirjaga “Valitsevate taimede floristilised ja mükoriissed tunnused paramo rohumaadel Guerrero paramos, Cundinamarca, Colombia”, esitatud 2020. aastal keskkonnainseneri kraadi saamiseks.

Kaasjuhendaja Daniela Díazi magistritööle pealkirjaga “Mükoriisa leviku modelleerimine Colombia paramos” keskkonnainseneri kraadi saamiseks.

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