

YIMING MENG

Plant mycorrhizal type and
status in the global flora



DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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UNIVERSITY OF TARTU

Press

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

Dissertation was accepted for the commencement of the degree of *Doctor philosophiae* in Plant Ecology and Ecophysiology at the University of Tartu on August 30th, 2024 by the Scientific Council of the Institute of Ecology and Earth Sciences, University of Tartu.

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Commencement

November 8th, 2024, at 10:15 AM in Room 127, J. Liivi 2, Tartu.

Publication of this thesis is granted by the Institute of Ecology and Earth Sciences, University of Tartu.

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ISSN 1024-6479 (print)

ISBN 978-9916-27-659-4 (print)

ISSN 2806-2140 (pdf)

ISBN 978-9916-27-660-0 (pdf)

University of Tartu Press

<http://www.tyk.ee/>

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- I **Meng Y**, Davison J, Clarke JT, Zobel M, Gerz M, Moora M, Öpik M, Bueno CG. Environmental modulation of plant mycorrhizal traits in the global flora. *Ecol Lett* 2023;26(11):1862-1876.
- II León D, Peyre G, Zobel M, Moora M, **Meng Y**, Diaz M, Bueno CG. Mycorrhizal symbioses in the Andean paramo. *Mycorrhiza* 2024;34(1):107–117.
- III **Meng Y**, Bueno CG, Öpik M, Moora M, Zobel M, Davison J. How can we best predict plant mycorrhizal types and statuses worldwide. *Manuscript*.
- IV Koorem K, Sepp SK, Bueno CG, Davison J, Liu S, **Meng Y**, Semchenko M, Vasar M, Zobel M, Moora M. Plant mycorrhizal status indicates partner selectivity in arbuscular mycorrhizal networks. *Manuscript*.
- V Davison J, García de León D, Zobel M, Moora M, Bueno CG, Barceló M, Gerz M, León D, **Meng Y**, Pillar VD, Sepp SK, Soudzilovskaia NA, Tedersoo L, Vaessen S, Vahter T, Winck B, Öpik M. Plant functional groups associate with distinct arbuscular mycorrhizal fungal communities. *New Phytol* 2020;226(4):1117-1128.

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Author's contribution to the publications:

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

	Original idea	Study design	Data collection	Analysis and interpretation	Manuscript writing
I	***	**	***	***	***
II	*	*	**	**	*
III	***	***	***	***	***
IV	**	*	**	-	*
V	*	*	**	-	*

ABBREVIATIONS

Acronyms

- AM** arbuscular mycorrhizal. 10, 11, 13–15, 17, 19–26, 28–30, 32, 34–39
- C** carbon. 11, 27, 34, 36
- CEC** cation exchange capacity. 26, 27, 34
- CS** competitor and stress-tolerator (nonruderal). 23, 30
- CSR** competitor, stress-tolerator, ruderal. 15, 17, 23, 29, 30, 36, 40
- ECM** ecto-mycorrhizal. 10, 11, 19, 24–26, 28, 29, 34, 35
- ERM** ericoid mycorrhizal. 10, 11, 19, 24–29, 32, 34, 35, 38
- FM** facultatively mycorrhizal. 10, 11, 13, 14, 19, 21, 23–30, 32–39
- GBIF** Global Biodiversity Information Facility. 19, 38
- MAP** mean annual precipitation. 26, 27
- MAT** mean annual temperature. 11, 26, 27, 33
- MI** mycorrhization index. 20, 26, 27
- N** nitrogen. 17, 21, 23, 27, 40
- NM** non-mycorrhizal. 10, 11, 13, 19, 21, 23–29, 34, 35, 39
- OM** obligately mycorrhizal. 10, 11, 14, 19, 23–29, 32, 34–37, 39
- ORM** orchid mycorrhizal. 10, 19, 20, 24–27, 29, 32
- R** ruderal. 23, 30
- RF** random forest. 20, 25
- ROC AUC** receiver operating characteristic - area under curve. 7, 21, 27, 28
- SSU** small subunit. 22
- VT** virtual taxon. 22, 23
- XGboost** extreme gradient boosting. 21, 27

1. INTRODUCTION

Mycorrhizal symbiosis represents a mostly mutualistic association between plants and root-inhabiting soil fungi, wherein photosynthetically-derived carbon is exchanged for fungal-acquired soil nutrients, facilitating enhanced nutrient acquisition and stress tolerance in plants (Smith and Read, 2008). The interaction involves an estimated 80% of plant species and plays a critical role in the structure and functioning of many ecosystems (Brundrett, 2009; Johnson et al., 1997; Smith and Read, 2008; van der Heijden et al., 2008, 2015).

Fossil evidence suggests that the first mycorrhizal partners of terrestrial plants were arbuscular mycorrhizal fungi from the phyla Glomeromycota and Mucoromycota (van der Heijden et al., 2015). During the course of evolution, alternative symbiotic associations emerged with fungi from the phyla Ascomycota and Basidiomycota, coinciding with the emergence of the Orchidaceae, Ericaceae, and certain gymnosperms among plants (Genre et al., 2020; Ramírez et al., 2007; Strullu-Derrien et al., 2018). Currently, four major types of mycorrhizal association are recognized: arbuscular (AM), ecto- (ECM), ericoid (ERM) and orchid (ORM) mycorrhiza (Smith and Read, 2008). Each type exhibits distinct evolutionary history and morphological adaptations. Plants that consistently engage in one or more of these associations are categorized as obligately mycorrhizal (OM). Other plants have evolved strategies to either mitigate environmental stresses independently of fungal partners, acquire nutrients through specialized root systems, or selectively disengage from mycorrhizal relationships when the costs outweigh the benefits. These plants are classified as facultatively mycorrhizal (FM) if they sometimes form mycorrhizal associations or non-mycorrhizal (NM) if they never engage in mycorrhizal symbiosis (Moora, 2014; Smith and Read, 2008). Understanding which plants form specific types of mycorrhizal associations and their mycorrhizal status is crucial for elucidating the ecological roles of both the plants and their fungal partners. This knowledge allows us to explore the role of mycorrhizas within and across plant communities, ecosystems, and biogeographical regions (Moora, 2014; Tedersoo, 2017). Additionally, it provides a framework for explaining plant species distributions and their responses to environmental gradients (Bueno et al., 2017; Davison et al., 2015), which is essential for predicting how plant communities might shift in response to changing environmental conditions. While this framework for understanding the diversity of plant mycorrhizal characteristics is well established, we still lack the ability to precisely explain and predict the occurrence of these characteristics among the global flora, and our understanding of how plant-fungal associations vary within and among OM and FM plants remains limited.

1.1. The expression of plant mycorrhizal type and status worldwide

Theoretical frameworks proposed by Read (1991) and Read and Perez-Moreno (2003) suggest that the distribution of different plant mycorrhizal types along latitudinal and altitudinal gradients is influenced by climatic conditions, which affect the accumulation of soil organic C and the availability of different nutrient forms. In Europe, the AM type predominantly thrives in grasslands, forests, and shrublands at lower latitudes, characterized by higher mean annual temperatures (MAT), neutral to alkaline soil pH, and increased net primary productivity (Bueno et al., 2017). The prevalence of AM species decreases with rising latitude and elevation, where colder, acidic, and less fertile conditions favor ECM and ERM types. ERM species dominate in high-latitude forests and mountainous regions, particularly in extremely acidic, nutrient-poor soils typical of heathlands and regions rich in organic matter. Their dominance increases with latitude but not necessarily with elevation (Bueno et al., 2017). Globally, it is predicted that AM plants peak in tropical and sub-tropical regions, while ECM types flourish in high latitudes of both the northern and southern hemispheres (Barceló et al., 2019; Steidinger et al., 2019).

OM plants, which are entirely reliant on symbiotic relationships with mycorrhizal fungi, display more specialized niche requirements and narrower niche widths (Gerz et al., 2016). In Europe, OM plants are more commonly observed at lower latitudes, higher elevations, and higher MAT (Bueno et al., 2017). By contrast, FM plants exhibit a high degree of ecological adaptability, enabling them to occupy more habitats and exhibit broad distributions across various environmental gradients (Clavel et al., 2021; Gerz et al., 2018; Pyšek et al., 2019), and may have greater selectivity with respect to their fungal partners (Sepp et al., 2019). NM plants are capable of thriving without mycorrhizal symbiosis (Brundrett, 2009; Lambers and Teste, 2013) and are believed to be found in highly disturbed environments or extreme conditions, such as very cold climates or soils that are highly acidic or deficient in phosphorus (Brundrett, 2009). However, NM plants may not strictly adhere to this pattern. For instance, in the extremely poor soils of Mediterranean habitats in Western Australia and South Africa, soil gradients can influence the presence of cluster roots — a key adaptation in NM plants that enhances nutrient acquisition in low-phosphorus soils (Lambers et al., 2011). This suggests that, in addition to environmental disturbances and extremes, nutrient strategies or other unknown factors may play a crucial role in shaping NM plant distributions.

While certain regional patterns in the distribution of plant mycorrhizal types and statuses have been established, there remain substantial gaps in our understanding of how these distributions are driven by the environment at the global scale. A primary limitation is the scarcity of empirical data about plant mycorrhizal type and status at the species level. For instance, among global studies, Steidinger et al. (2019) limited their research to trees, estimating the abundance

of different plant mycorrhizal types by extrapolating within genera. Similarly, Delavaux et al. (2019) extrapolated plant mycorrhizal status information within families. Barceló et al. (2019) focused on dominant species from approximately 1,550 communities, mostly woody species, to approximate the composition of terrestrial ecosystems. The use of dominant vegetation-level data and/or taxonomic extrapolation may overlook key adaptive processes and lead to discrepancies between predicted and observed distributions of mycorrhizal type and status. Furthermore, while these previous global studies have shown that plant mycorrhizal type and status vary with geographical and environmental conditions, the resolution of available vegetation and environmental data (> 100x100 km grid cells) limits the conclusions that can be drawn about potential drivers of plant mycorrhizal type and status that vary at fine scales (e.g. some soil characteristics). Moreover, significant sampling gaps exist in biodiverse areas, particularly within the southern hemisphere (Mujica et al., 2024). This scarcity of data leads to a reliance on extrapolations from studies conducted in other regions, which may not accurately represent conditions in specific locations, leading to potential inaccuracies in understanding and predicting mycorrhizal distributions under different environmental conditions (Bueno et al., 2019). Filling these geographical gaps ideally requires fine-scale empirical studies *in situ*, but may also be improved by a more detailed understanding of the environmental and phylogenetic dynamics driving the expression of mycorrhizal characteristics among plants worldwide. In other words, to fully grasp how and why plants form different types of mycorrhiza and exhibit varying levels of dependency on them across different regions of the world, we need to consider the interactions in their contemporary environmental context as well as the evolutionary histories that shape the relationships.

While previous studies have focused on geographical variation in vegetation characteristics, an entirely different approach for determining mycorrhizal type and status distribution is to assess the expression of these traits at the level of individual plant species. Taking this focus would allow us to assess the degree to which these traits are phylogenetically conserved and how environmental drivers interact with phylogenetic and biogeographic factors to determine the distribution and prevalence of different mycorrhizal types and statuses. Thus, it would allow us to test the assumption that present-day mycorrhizal associations are largely the result of ancient evolutionary events and position them instead as potentially dynamic traits that may be responsive to contemporary environmental pressures.

1.2. Prediction of plant mycorrhizal type and status

Despite the critical role of mycorrhizal associations in plant ecology and evolution, information about mycorrhizal type and status is documented for only about 4% of the world's flora (Soudzilovskaia et al., 2020). Current methods for predicting these types and statuses often rely on extrapolating observations from known to unstudied species within specific plant taxa, such as genera, families, or or-

ders (Bueno et al., 2019; Tedersoo, 2017). While this approach allows for broad generalizations about mycorrhizal characteristics, it assumes strong and consistent phylogenetic conservatism within these taxa and may neglect the potential variability or evolution of mycorrhizal types and statuses in response to changing environmental conditions (Osborne et al., 2018). Additionally, rigid taxonomic extrapolation can oversimplify the continuous and complex nature of evolution, as well as varying degrees of phylogenetic signal across different traits and trait levels. These limitations are evident in Europe, where the mismatch between predicted and observed mycorrhizal types and statuses is significant — 91% for FM, 45% for NM, and 16% for AM plant species (Bueno et al., 2019). In understudied ecosystems, such as those in the global south, where direct observations are limited, this mismatch could be even more pronounced, underscoring the need for refined predictive approaches for plant mycorrhizal type and status (Corrales et al., 2018; Mujica et al., 2024).

Phylogeny provides an alternative, far more detailed, representation of evolutionary relationships, compared with taxonomic ranks, and the wide availability of plant phylogenetic information (e.g., Jin and Qian (2019, 2022)) suggests that it could be a viable alternative for predicting mycorrhizal type and status among unstudied plant species. Besides evolutionary relationships, environmental conditions exert selective pressures that shape the functional adaptations of both plants and their mycorrhizal partners (Smith and Read, 2008), suggesting that data about plant-environmental associations could also enhance the accuracy of plant mycorrhizal predictions. Finally, significant correlations exist between above- and below-ground traits, including mycorrhizal characteristics Weigelt et al. (2021). For example, plants that depend on mycorrhizal fungi for nutrient acquisition can afford to invest less in root biomass while still meeting their nutritional needs (Bergmann et al., 2020). This positions mycorrhizal symbiosis as a crucial component of the whole-plant economic spectrum; and, as a corollary of this, it suggests that mycorrhizal characteristics may be predictable on the basis of other plant traits. However, it is important to note that the coordination between above- and below-ground plant traits remains a topic of debate, with some studies questioning the extent and consistency of these relationships (Bueno et al., 2023; Carmona et al., 2021). Additionally, the lack of comprehensive empirical data, particularly global below-ground traits, further complicates this picture (Bergmann et al., 2020; Carmona et al., 2021). Putting this together, a predictive framework that integrates plant phylogeny, environmental conditions, and plant above and belowground traits holds the potential to improve our ability to forecast plant mycorrhizal type and status. However, no attempt has previously been made to employ such an approach.

1.3. Partner selectivity in arbuscular mycorrhizal networks

Interactions between plants and fungi in AM networks are characterized by a degree of partner selectivity, where plants and fungi both exhibit preferences for specific symbiotic partners. This selectivity is influenced by factors such as relative resource abundance, environmental conditions, the history of past interactions and the evolutionary history of the plant and fungal partners (Ji and Bever, 2016; Neuenkamp et al., 2021; Veresoglou and Rillig, 2014; Werner and Kiers, 2015a,b). While earlier work has shed light on patterns of partner selection, the extent to which the strength and specificity of plant-fungal associations vary in relation to plant characteristics remains largely unclear.

Plant mycorrhizal status describes the propensity of a plant species to form mycorrhizal associations. FM status indicates that plant species form variable associations with mycorrhizal fungi, but this may theoretically occur at the level of plant individuals, between individuals within populations, or between populations (Zobel et al., 2024). Meanwhile, OM plants may theoretically still exhibit variable associations with mycorrhizal fungi to the extent that the identity of associating fungi change. Emerging evidence suggests that FM plants possess a greater filtering ability, allowing them to preferentially select optimal AM fungal partners (Sepp et al., 2019). However, there remains a lack of detailed information about how mycorrhizal colonization and associated fungal communities vary among plants of different status, and how this interacts with environmental factors, such as soil nutrient content.

Interaction network topology, which describes the structural organization of interactions within a network, provides insight into the causes and consequences of mycorrhizal network architecture (Chagnon et al., 2012). Indices such as normalized degree, resource range, species strength, and nestedness rank reflect key aspects of species interactions, broadly describing positioning along a gradient of generalism vs. specialism, and roles in maintaining network connectivity and function (Alarcón et al., 2008; Bascompte et al., 2006; Dormann et al., 2009; Poisot et al., 2012). Investigating how these network topology indices vary between plants of different mycorrhizal status, along environmental gradients, and in relation to measures of fungal colonization, can reveal how plants with different mycorrhizal characteristics differ in terms of symbiotic specialization. Thus, the network of host plants to regulate the occurrence and extent of the symbiosis may be a crucial asset underlying plant species success (Zobel et al., 2024). A more detailed understanding of what mycorrhizal statuses entails could also improve the general framework for explaining and predicting plant mycorrhizal characteristics.

1.4. Dynamics of arbuscular mycorrhizal fungal communities across plant functional groups

As introduced in Section 1.3, the relationship between plants and AM fungi is not strictly species-specific, with empirical evidence demonstrating a degree of selectivity in associations between fungal taxa and plant species. There is fragmentary information about how certain functionally-similar plant species associate with particular fungal taxa. For example, previous research has explored differences in the AM fungal communities that associate with different plant growth forms (e.g., forbs, grasses, and woody plants), forest specialist and generalist species, and shade-avoidant and shade-tolerant species (Davison et al., 2011; Koorem et al., 2017; López-García et al., 2017; Öpik et al., 2009; Sepp et al., 2019; Vandenkoornhuyse et al., 2002). Additionally, AM fungal colonization has been observed to differ between plants with different photosynthetic pathways (e.g., C₃ vs. C₄) and CSR (competitor, stress-tolerator, ruderal) strategy types (Betekhtina and Veselkin, 2011; Grman, 2012); and theoretical studies have suggested that stress-tolerant plants may preferentially associate with AM fungi adapted to conditions of low biomass or turnover (Chagnon et al., 2013, 2015). A recent study also proposed that the gradient of collaboration between plants and AM fungi (i.e., a spectrum where plants either engage in self-sufficient soil exploration through high specific root length or outsource nutrient acquisition by investing carbon into mycorrhizal partners (Bergmann et al., 2020)) varies between plant functional groups, with various plant traits influencing the response of plants to AM fungi (Romero et al., 2023). However, these studies often involved comparisons of small numbers of plant species. There has yet to be a large-scale, systematic effort to empirically investigate how the diversity and composition of associated AM fungal communities vary among plants with different ecological strategies. Additionally, the influence of plant mycorrhizal status on associated AM fungal communities remain largely unexplored (Gerz et al., 2018; Guillen-Otero et al., 2024; Neuenkamp et al., 2018). In summary, previous studies have provided valuable insights into plant-AM fungal interactions. However, these relatively small scale studies often lack the breadth needed to capture the full variability in mycorrhizal interactions across different species, environments, and ecological contexts. This limitation can lead to an incomplete or biased understanding of how mycorrhizal associations function. Thus, there is a clear need for more extensive and integrative research efforts. Studies incorporating larger, more diverse datasets are needed to robustly test hypotheses regarding the selectivity and specificity of AM fungal communities across plant functional groups.

1.5. Objectives of the thesis

This thesis aims to explain and predict plant mycorrhizal types and statuses among plant species globally, and to examine the extent to which mycorrhizal types and

statuses relate to other plant characteristics and positioning in ecological networks.

Reflecting the knowledge gaps covered in Section 1.1, the following questions are addressed in **Papers I and II**:

1. To what degree are plant mycorrhizal types and statuses phylogenetically conserved?
2. How does the share of different plant mycorrhizal types and statuses vary globally?
3. To what extent do environmental and plant phylogenetic variables alone or in combination explain the mycorrhizal types and statuses exhibited by plant species in the global flora, and which environmental drivers are associated with the different mycorrhizal states?
4. In an understudied area, the Andean paramo, what is the distribution of plants of different mycorrhizal types and mycorrhizal statuses along elevation and environmental gradients?

To address these questions, information on plant mycorrhizal types and statuses worldwide, with a specific focus on the Andean paramo, hereafter “paramo”, was compiled. **Paper I** assesses phylogenetic conservatism and the environmental modulation of plant mycorrhizal types and statuses in the global flora. Phylogenetic trees for plants of different mycorrhizal types and statuses were constructed, and the phylogenetic signal for each mycorrhizal type and status was calculated. Global distributions of plant mycorrhizal types and statuses were mapped, and variance partitioning was conducted to identify the roles of plant phylogeny and associated environmental factors in shaping plant mycorrhizal type and status expression. Important environmental variables were also identified. **Paper II** examines the distribution and environmental drivers of plant mycorrhizal types and statuses along the paramo’s elevational gradient. The proportion of each mycorrhizal type and status was calculated in each plot, and climatic and edaphic drivers of the distributions of plant types and statuses were identified.

Reflecting the knowledge gap covered in Section 1.2, the following question is addressed in **Paper III**:

5. Are plant mycorrhizal types and statuses better predicted by various plant taxonomic ranks or by plant phylogeny, and does integrating data about plant environmental associations and traits improve predictions based on taxonomic or phylogenetic information alone?

To address this question, a comparison was made between the effectiveness of using taxonomic, phylogenetic, trait, and environmental data in predicting plant mycorrhizal types and statuses. This involved integrating data from plant taxonomy, phylogeny, and environmental associations obtained in **Paper I**, along with other data describing plant above and belowground traits, to assess the potential for improving predictive accuracy through data integration.

Reflecting the knowledge gap covered in Section 1.3, the following question is addressed in **Paper IV**:

6. Do plant species with different mycorrhizal statuses exhibit variations in AM fungal colonization and network topology?

To answer this, a fungal perspective was adopted by investigating Estonian plant species of differing mycorrhizal statuses in different environments. Roots and rhizosphere soil of target plant species were collected to measure AM fungal colonization and to analyze AM fungal communities in roots and soil. Species-level indices within the plant-AM fungal taxon network were calculated to examine network interactions.

Reflecting the knowledge gap covered in Section 1.4, the following question is addressed in **Paper V**:

7. How do plant characteristics, including mycorrhizal statuses as well as growth forms, photosynthetic pathways, CSR strategies, and N-fixing statuses, influence the diversity and composition of associated AM fungal communities?

To address this, a re-analysis of several published data sets was conducted to determine how root-associating AM fungal communities vary among plants with different characteristics.

Fig. 1 provides a conceptual summary of the papers included in this thesis.

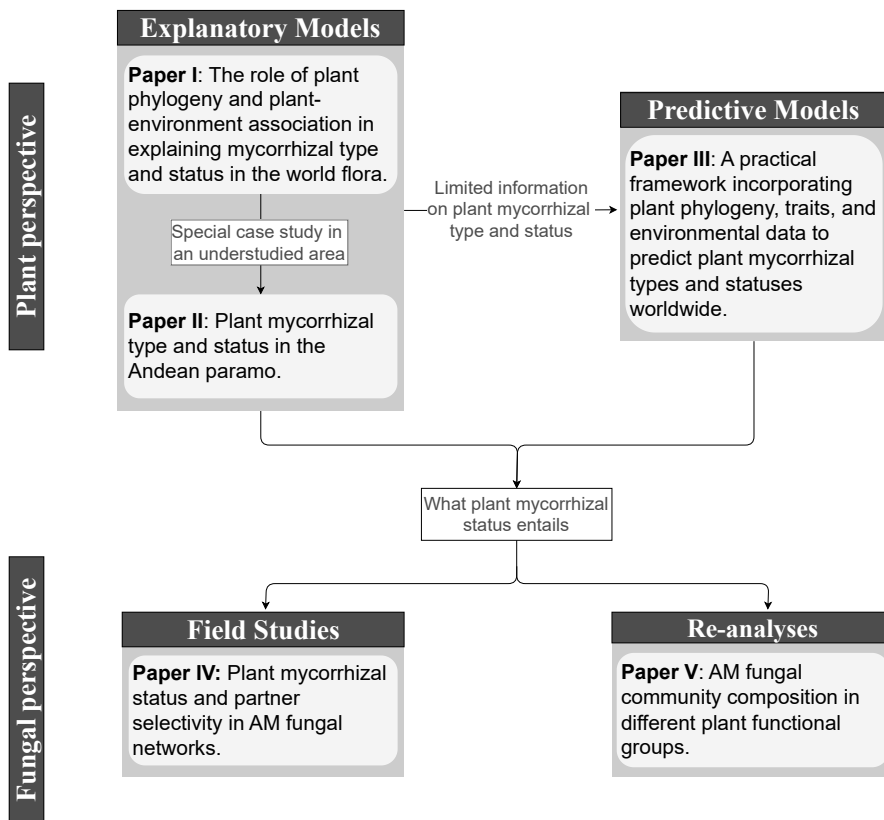


Figure 1. Conceptual summary of the papers included in this thesis. The boxes illustrate the key objectives of each paper.

2. MATERIAL AND METHODS

2.1. Plant mycorrhizal type and status list and plant species occurrences

2.1.1. Plant mycorrhizal type and status list

Data on plant mycorrhizal types and statuses were compiled from the latest literature, including studies by Harley and Harley (1987, 1990), Wang and Qiu (2006), Hempel et al. (2013), Bueno et al. (2017), Gerz et al. (2018), and Soudzilovskaia et al. (2020). Four plant mycorrhizal types (AM, ECM, ERM, and ORM) and three mycorrhizal statuses (OM, FM, and NM) were distinguished. A total of 14,722 plant taxa at the species level were classified, including 710 dual mycorrhizal species (AM + ECM), which were grouped with ECM species for further analysis due to apparent niche similarities and ongoing controversy regarding the definition (Brundrett, 2021b; Teste et al., 2020).

For the paramo study (**Paper II**), data on mycorrhizal traits were notably scarce, covering only 9.18% of paramo species (**Paper II**). Consequently, genus-level trait information was estimated from available species-level data, avoiding less precise family- or order-level extrapolations (Akhmetzhanova et al., 2012; Bueno et al., 2017, 2019; Hempel et al., 2013; Soudzilovskaia et al., 2020; Wang and Qiu, 2006).

2.1.2. Global species occurrence data

For global analyses (**Paper I** and **III**), plant species occurrence records were retrieved from the Global Biodiversity Information Facility (GBIF) for 13,479 species that were present in both the standardised GBIF species list and the mycorrhizal type and status species list. Data were intersected with a global grid of 30 arc-seconds (approximately 1 km) resolution, and species presence or absence was recorded in each grid cell. A sensitivity analysis indicated that sampling ≥ 20 grid cells yielded representative environmental parameter estimates (**Paper I**, online supplementary Appendix S1), resulting in a dataset of 62,540,387 records for 11,770 species that were present in ≥ 20 grid cells. Environmental associations were approximated by intersecting the distribution data for each species with a raster stack of 54 environmental data layers (see Supporting Information). For each intersection of species and environmental layer, the mean value and standard deviation was recorded, providing independent variables for explanatory and predictive modelling.

2.1.3. Andean paramo vegetation database

For the paramo study (**Paper II**), the VegParamo database provided data from 3,900 georeferenced phytosociological plots (Peyre et al., 2015). After cleaning, 2,646 plots remained, each representing a distinct phytosociological unit. Only

plots with geographic coordinates were retained, allowing association with environmental variables. Phytosociological relevés included species lists with cover categories based on van der Maarel (2007). Overall, the dataset included 123 families, 504 genera, and 2,220 species, and covered approximately 35,000 km² of the paramo. For quantitative analysis, 2,342 plots with comprehensive mycorrhizal trait coverage (> 60% plant cover) were selected, and cover categories were converted to percentages following van der Maarel's method (2007).

2.2. Plant phylogeny and plant-environment associations

A phylogenetic tree of the 11,770 species from Section 2.1.2 was constructed to examine phylogenetic signal in mycorrhizal traits using the δ statistic (Borges et al., 2019) (**Paper I**) and to provide explanatory and predictive variables for modelling mycorrhizal traits (**Paper I** and **III**). Variation in mycorrhizal types and statuses was modeled using random forests (RF), with traits treated as binary response variables (e.g., AM vs. non-AM) (**Paper I**). Multi-level classifications assessed trait responses to phylogenetic and environmental factors. The BorutaPy algorithm was used to identify significant features (Kursa and Rudnicki, 2010). RF analyses were conducted with phylogenetic and environmental eigenvectors both separately and combined. Model accuracy was estimated using out-of-bag (OOB) errors, and variance partitioning based on these errors quantified the unique and shared contributions of phylogeny and environment to explaining trait variation. All raw environmental predictors were included in an additional RF analysis to assess the importance of individual environmental variables. Phylogenetic vectors were included in a final RF model to evaluate potential shifts in the relative importance of environmental predictors (Fig. 1 of **Paper I**).

For the paramo study (**Paper II**), the proportion of each mycorrhizal type and status per plot was calculated based on species abundances. The mycorrhization index (MI) was determined by averaging plant species mycorrhizal status coefficients (msc), which were weighted by abundance and logit-transformed. These coefficients, ranging from 0 (non-mycorrhizal) to 1 (fully mycorrhizal), were calculated based on the ratio of "mycorrhizal" observations to total observations within each genus, following a similar approach previously used at the species level (Gerz et al., 2016, 2018; Moora, 2014). Environmental data were extracted following the approach described in Section 2.1.2. The influence of elevational and environmental gradients on mycorrhizal type and status was analyzed using Generalized Linear Models with appropriate distributions, including zero- and one-inflated beta distributions and a binomial distribution for ORM plants. Environmental impacts on MI were modeled using the skew exponential power distribution (Rigby et al., 2019).

2.3. Predictive models of plant mycorrhizal type and status

For **Paper III**, data on plant mycorrhizal type and status, and phylogenetic and environmental factors were sourced from **Paper I** for 11,770 plant species. Trait data, including six aboveground traits (plant height, leaf area, specific leaf area, leaf nitrogen (N) concentration, specific stem density, and seed mass) and four belowground traits (root diameter, specific root length, root N concentration, and root tissue density), were obtained from Carmona et al. (2021). These traits were selected due to their comprehensive coverage across species and their representation of significant plant variability (Bergmann et al., 2020; Bueno et al., 2023; Carmona et al., 2021; Díaz et al., 2016). Three datasets were compiled, each containing full environmental and plant phylogenetic and taxonomic data, but with different levels of plant trait data completeness, 1) Core Dataset (320 species): complete trait data, 2) Intermediate Dataset (1,441 species): partial trait data; species with at least one aboveground and one belowground trait, with missing traits in this dataset imputed, and 3) Full Dataset (all 11,770 species): no trait data.

Models were developed to predict mycorrhizal types and statuses using combinations of predictor variables tailored to each dataset. Since phylogenetic and taxonomic variables are alternative representations of evolutionary relationships, they were not included together in the same models. The Extreme Gradient Boosting (XGboost) classifier, which is noted for its robust performance in classification tasks (Chen and Guestrin, 2016), was employed. Mycorrhizal types and statuses were converted into binary classifications for each trait level (e.g., AM vs non-AM). Relevant environmental variables were identified using Boruta feature selection (Kursa and Rudnicki, 2010). Parameters in the XGboost algorithm were adjusted to account for the significantly imbalanced classes.

Stratified 5-fold cross-validation was utilized, ensuring that each fold was representative of the overall class distribution. Hyperparameter optimization was conducted in two stages using Optuna (Akiba et al., 2019): initially, a broad search identified promising hyperparameter spaces, followed by refined searches to pinpoint optimal values.

Model performance was evaluated on a separate test set, using metrics including the Receiver Operating Characteristic - Area Under Curve (ROC AUC) score, accuracy, and F1 score.

2.4. Plant mycorrhizal status and partner selectivity in AM fungal networks

For **Paper IV**, sampling was conducted during the mid-2020 growing season. Roots and rhizosphere soil were collected from three distinct sites for each of 19 plant species representing five families. Species were selected to include all mycorrhizal statuses (acrshortom, FM, and NM), as assigned according to Section

2.1.1, using the colonization approach described by Bueno et al. (2021). Site selection was informed by expert opinion to ensure the representation of varied growing conditions for each species. Sampling was carried out across a diverse range of habitats in Estonia. All sampled species, except for *Lupinus polyphyllus* Lindl., are native to Estonia. Each site yielded samples from three individuals per species, resulting in 171 samples of both root and soil for subsequent analyses.

AM fungal colonization was quantified using the magnified grid-line intersection method after staining fine roots with trypan blue, recording hyphae, vesicles, arbuscules, and coils under a microscope (McGonigle et al., 1990). DNA extractions from roots and soils were performed using commercial kits, with AM fungal community composition assessed by sequencing the small subunit (SSU) rRNA gene with the WANDA (Dumbrell et al., 2011) and AML2 (Lee et al., 2008) primers on an Illumina MiSeq platform. Sequencing reads were processed with the gDAT pipeline (Vasar et al., 2021) and analyzed for chimeric sequences and sequence quality. Identified sequences were matched to virtual taxa (VTs; phylogenetically-defined molecular taxa) from the MaarjAM database (Öpik et al., 2010). Unmatched sequences were further analyzed to identify potentially novel AM fungal taxa. Only samples yielding sequences from both soil and root samples were included in further analyses.

Variability in AM fungal colonization was assessed within each plant species or population using the coefficient of variation. Richness and diversity of AM fungal communities were determined using extrapolated taxon richness and Shannon diversity, based on Hellinger-transformed matrices of fungal abundance. A phylogenetic tree of AM fungal VT was built using BEAST 2.5 (Bouckaert and Drummond, 2017) and phylogenetic distances were calculated to evaluate covariation between root and soil AM fungal communities. Multivariate linear regressions were conducted to account for variations in soil chemistry. Species-level indices within the plant-AM fungal taxon network were calculated to analyze network interactions. Spatial and chemical variations were incorporated into models using principal coordinates of neighbourhood matrix and principal components analysis, respectively.

All dependent variables were analyzed at individual, population, and species scales using linear mixed-effects models to explore the effects of mycorrhizal status and AM fungal colonization. Model significances were tested, and differences among variable levels were assessed using Tukey's HSD post hoc test.

2.5. AM fungal communities across plant functional groups

For **Paper V**, 14 datasets employing similar sampling and molecular techniques to investigate AM fungi in plant roots were collated. These datasets used 454-sequencing of the SSU rRNA gene. Raw sequencing data were reprocessed to ensure consistency across studies. Sequencing reads were retained based on stringent criteria: an average quality score greater than 25, correct barcode and forward

primer sequences with allowance for one mismatch, and a minimum length of 199 base pairs. Chimeras were identified and excluded using UCHIME, with remaining reads matched against VTs from the MaarjAM database (Öpik et al., 2010) using a sequence similarity threshold of at least 97% and a BLAST e-value of less than $1e-50$.

Plant species were classified according to their mycorrhizal status (OM, FM, and NM), as outlined in Section 2.1.1. Additional functional groupings, including CSR strategies (simplified to ruderal (R) and nonruderal (CS)) and photosynthetic pathways (C_3 or C_4), were sourced from the TRY and Bioflor databases (Kattge et al., 2011; Klotz et al., 2002). N-fixing status was derived from Tedersoo et al. (2018). Functional group membership included 180 forbs, 57 grasses, 57 woody plants; 125 C_3 , 25 C_4 plants; 6 ruderal, 33 nonruderal; 58 FM, 170 OM; 277 non-N-fixing, and 20 N-fixing species. Putatively ruderal AM fungal VT were identified as those that contain representative species from described AM species grown in culture (Ohsowski et al., 2014).

Distance-based redundancy analysis (db-RDA) was used to explore variation in fungal community composition in relation to growth form, photosynthetic pathway, CSR strategy, mycorrhizal status, and N-fixation capability. Presence-absence data used Sørensen distances, while abundance data used Bray-Curtis distances. Phylogenetic beta diversity was assessed using a phylogenetic tree of VTs (taken from Davison et al. (2018)) and calculation of mean pairwise distances (MPD), weighted by VT abundance for abundance analyses. Linear mixed models were used to evaluate differences in AM fungal alpha and beta diversity, incorporating sampling location and plant species as random effects to control for spatial auto-correlation, confirmed via spatial variograms. Indicator species analysis was used to identify VTs disproportionately associating with particular plant groups. Phylogenetic correlograms were used to display correlations in indicator values relative to VTs phylogenetic relatedness, and Mantel's r was calculated to measure multivariate correlations, with confidence intervals established through bootstrapping ($n = 500$).

3. RESULTS

3.1. Global and Paramo patterns of plant mycorrhizal type and status

3.1.1. Phylogenetic conservatism in plant mycorrhizal type and statuses

Phylogenetic signal was higher for plant mycorrhizal types ($\delta = 6.7$, **Paper I**) than for statuses ($\delta = 3.2$, Fig. 2a). Signal was highest for ORM and ERM types, intermediate for ECM type and lowest for AM type (**Paper I**); FM status had lower signal than OM or NM status (Fig. 2a).

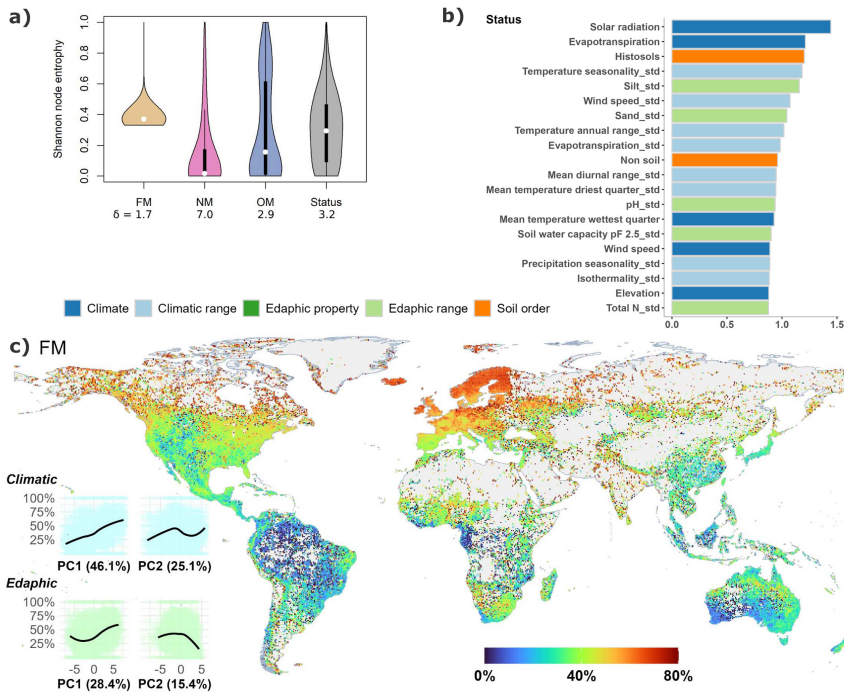


Figure 2. Phylogenetic conservatism and environmental associations of plants with different mycorrhizal statuses. a) Phylogenetic signal of plant species with different mycorrhizal statuses (Shannon entropy [on the y axis] and delta statistics [below bars] are shown), b) the most important environment variables in random forest models explaining mycorrhizal status, c) global map showing the distribution of FM plants in the global flora and relationships with climatic and edaphic gradients (inset scatterplots). Adapted from **Paper I** Figs. 2, 3 and 4.

3.1.2. Plant phylogeny and plant-environment associations explain variation in plant mycorrhizal type and status

RF classification and variance partitioning demonstrated that plant phylogeny accounted for a substantial portion of the variability in mycorrhizal type (41.2%), while there was a smaller contribution from environmental conditions (7.6%, **Paper I**). For mycorrhizal status, both phylogenetic and environmental variables explained similar fractions of variation (14.4% and 13.6%, respectively, **Paper I**).

3.1.3. Plant mycorrhizal type and status expression

AM plant species occurred worldwide but particularly in low-latitude regions, favoring warm climates with moderate precipitation and alkaline soils that maintained intermediate moisture and nutrient levels. By contrast, ECM species were more prevalent at higher latitudes, particularly in forest ecosystems of the eastern United States, Asia, parts of central and eastern Africa, Australia, and the southern cone of South America. ECM plants were typically found in cooler, acidic environments with high soil moisture and nutrient content. ERM species, primarily from the Ericaceae family, were common in cold, humid climates and moderately fertile soils, conditions that prevailed in northern high latitudes and the southern Andes. ORM species, for which we mostly had data from temperate to tundra zones, showed less clear environmental preferences, probably due to limited data, particularly the lack of tropical orchids (**Paper I**).

NM plants were frequently found at higher northern latitudes and to a lesser degree also at higher elevations, but not exclusively. Thus, while they overall thrived in colder, arid conditions without a strong correlation with specific soil types, they also peaked in tropical dry regions in Australia, Africa and Central America (**Paper I**). FM and OM plants exhibited distinct geographical and environmental patterns. OM plants predominated near the equator in nutrient-poor soils and tropical rainy climates, while FM plants were less prevalent under these conditions (Fig. 2c). Table 1 summarizes hotspots of mycorrhizal type and status abundance worldwide and characteristic plant taxa.

In the RF models developed to classify plant mycorrhizal types, both edaphic and climatic variables emerged as important predictors. Out of the top 20 predictors, 11 were related to soil characteristics and 9 to climatic conditions. Soil texture, especially sand content, and variability in soil pH were identified as the most influential edaphic factors. Additionally, climatic variability, including the standard deviation of isothermality and precipitation during the warmest month, played a significant role (**Paper I**). For classifying plant mycorrhizal status, climatic variables, including solar radiation and evapotranspiration, were consistently strong predictors. Variations in temperature, wind, and evapotranspiration also significantly influenced mycorrhizal status predictions. Beyond climatic factors, Histosols — soils predominantly composed of organic materials — and variability in soil texture and pH were notably important (Fig. 2b). **Paper I** also

Table 1. Hotspots of mycorrhizal type and status abundance worldwide and characteristic plant taxa. See **Paper I** for maps of mycorrhizal type and status abundance. Note that hotspots are not defined for AM, due to the generally abundant distribution of this trait, and for ORM due to the lack of data. Adapted from **Paper I** online supplementary Table S1.

	Hotspots of plant mycorrhizal type / status	Plant taxa
ECM	Northern hemisphere	<i>Pinus, Abies, Quercus</i>
	Eastern North America	<i>Carya</i>
	Southern Asia	<i>Alnus, Castanopsis</i>
	Central and Eastern Africa	Fabaceae including <i>Afzelia</i> and <i>Brachystegia</i>
	Australia	<i>Eucalyptus, Nothofagus, and Acacia</i>
	South America	<i>Nothofagus</i>
ERM	High latitudes	Ericaceae, <i>Diapensia lapponica</i> (circumboreal), <i>Schizocodon soldanelloides</i> (exclusive from Japan), <i>Escallonia pulverulenta</i> (mainly in South America)
NM	North America	Cyperaceae, Brassicaceae, and Juncaceae
	Central America	Polypodiaceae, Aspleniaceae, and Bromeliaceae
	Southern Africa	Crassulaceae, Amaranthaceae, and the endemic genus <i>Protea</i>
FM	Australia	Proteaceae, Droseraceae, and Cyperaceae
	Northern high latitudes	Poaceae, Cyperaceae, Fabaceae, and Asteraceae
OM	Central Africa	Malvaceae and Fabaceae
	Australia	<i>Eucalyptus</i> and <i>Acacia</i>

identified important environmental variables for each plant mycorrhizal type and status.

3.1.4. Distribution of mycorrhizal type and status in the Andean paramo

AM plants were the dominant mycorrhizal type across all elevations in the paramo (Fig. 3a). ERM plants decreased as elevation increased (Fig. 3b). There were no clear trends in the abundance of ECM or ORM plants with elevation (**Paper II**). NM plants were relatively consistent in abundance up to 3,500 m, after which their abundance increased (Fig. 3c). The abundance of FM plants increased with elevation (Fig. 3d), while the abundance of OM) plants decreased (Fig. 3e). MI peaked at 3,500 m and was lower at both higher and lower elevations (**Paper II**).

Several climatic and edaphic factors were associated with the abundance of mycorrhizal plants. The most important factors for AM and ERM plants were mean diurnal range (MDR), MAP, pH, and cation exchange capacity (CEC) (**Paper II**). The abundance of AM plants was positively correlated with MAT, MAP, and pH, and negatively correlated with MDR and CEC. The abundance of ERM plants was positively correlated with CEC and MDR, and negatively correlated with MAP and pH (**Paper II**).

For mycorrhizal statuses, the most important climatic and edaphic factor was

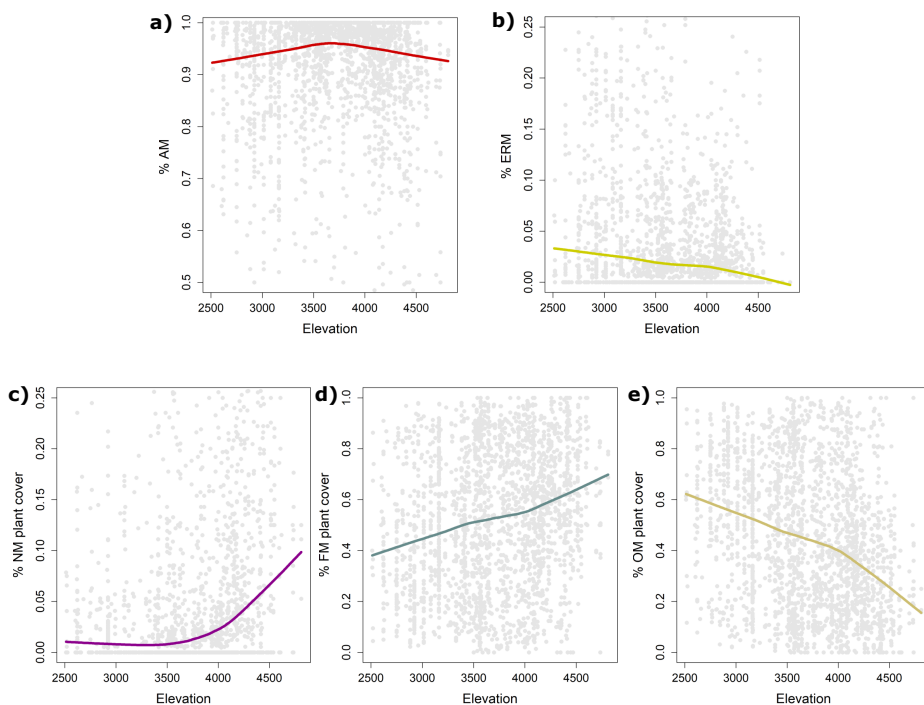


Figure 3. Elevational representation (% cover) of different mycorrhizal types and statuses among plant communities in the paramo. Lines represent fitted curves from loess regressions. Adapted from **Paper II** Figs. 1 and 2.

MAT. The abundance of NM plants was negatively correlated with MAT, MAP, pH, soil N, CEC, soil C, and precipitation seasonality. The abundance of FM plants was positively correlated with C and CEC, and negatively correlated with MAT and MDR. The abundance of OM plants was positively correlated with MAT, MAP and MDR, and negatively correlated with CEC and C. Finally, MI was positively correlated with MAP (**Paper II**).

3.2. Prediction of plant mycorrhizal type and status

XGboost models based on plant phylogeny generally outperformed those based on plant taxonomy in predicting plant mycorrhizal type and status (Fig. 4). For ERM and ORM types, taxonomic models performed comparably or slightly better. Both phylogenetic and the best taxonomic models showed high accuracy in predicting mycorrhizal types, with ROC AUC scores typically > 0.8 for top models. By contrast, models predicting statuses generally had ROC AUC scores < 0.75 (Fig. 4). Prediction accuracy varied between taxonomic levels and datasets.

In both the Core and Intermediate Datasets, models incorporating plant traits

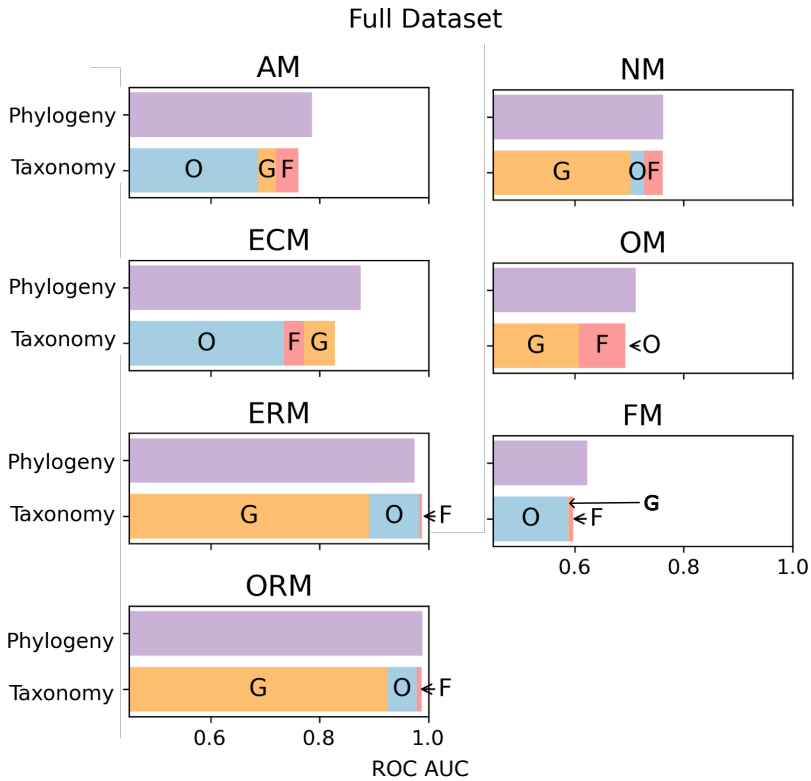


Figure 4. Predictive accuracy (ROC AUC scores) for plant mycorrhizal types and statuses using models based on plant taxonomy and phylogeny in the Full Dataset (11,770 species). O - order, F - family, G - genus. Stacked bars represent increasing ROC AUC with different taxonomic levels. Adapted from **Paper III** Fig. 2.

and/or environmental variables alongside taxonomy or phylogeny achieved the highest predictive accuracy, with phylogeny-based models outperforming taxonomy-based models in accuracy and consistency (**Paper III**). For AM and ECM types, models combining taxonomy or phylogeny with aboveground plant traits and environmental variables showed the highest accuracy. In the Intermediate Dataset, genus-level taxonomy or phylogeny alone was more effective for predicting AM type, and genus-level taxonomy alone provided better predictions of ECM type. For ERM type, all models incorporating either taxonomy or phylogeny achieved ROC AUC values > 0.85 . For NM status, taxonomy alone offered strong predictions, with minimal improvement from adding environmental variables or plant traits. However, phylogenetic models incorporating both aboveground and belowground traits showed the highest accuracy. Models including environmental variables showed good predictive accuracy for FM and OM statuses, with the best results from integrating traits into environmental models.

In the Full Dataset, phylogeny-based models consistently exhibited high and

stable predictive accuracy, particularly when combined with environmental variables (**Paper III**). Predictive accuracy varied across taxonomic ranks for AM and ECM types but remained high for ERM and ORM types. For NM status, taxonomy alone provided strong predictions, with slight improvements from adding environmental variables to phylogeny. Integrating taxonomy with environmental variables improved predictions for OM and FM statuses. A decision tree to guide prediction of plant mycorrhizal type and status is provided in **Paper III**.

3.3. Dynamics of AM fungi in relation to plant mycorrhizal status

Fungal colonization did not differ between FM (0.41 ± 0.03) and OM (0.38 ± 0.05) plants (**Paper IV**). AM fungal richness in the soil was twice that in plant roots. However, there were no differences in the richness or Shannon diversity of AM fungal communities associated with plant species of different mycorrhizal status. The richness of AM fungi in roots was, however, positively correlated with the population-level mean hyphal colonization % of the plant roots (**Paper IV**). There were no significant differences between plants of different mycorrhizal status in the intraspecific beta diversity of AM fungal communities. According to Procrustes analysis, host plants of different mycorrhizal status did not significantly differ in the strength of correlation between AM fungal communities in roots and bulk soil.

Regarding plant species level network indices, plants with different mycorrhizal statuses significantly differed in nestedness rank, normalized degree, resource range, and species strength (**Paper IV**). FM plant species had a significantly higher nestedness rank (Fig. 5a) and significantly lower species strength (Fig. 5d) than OM plant species. FM and putatively NM species had a significantly lower normalized degree (Fig. 5b) and higher resource range (Fig. 5c) than OM species.

3.4. Composition of AM fungal communities in plant functional groups

The composition of AM fungal communities varied among plants with different growth forms, photosynthetic pathways, CSR strategies, mycorrhizal statuses, and N-fixing statuses. The richest AM fungal communities were found in association with grasses (21.5 ± 0.6) and non-ruderal plants (18.6 ± 0.6) (**Paper V**). Phylogenetic alpha diversity was highest among forbs. There were no significant differences in Shannon diversity or abundance-weighted phylogenetic diversity between plant groups.

Beta diversity, both presence/absence and abundance-weighted, was higher among OM and ruderal plant species (**Paper V**). C_4 plants exhibited the highest beta diversity based on presence/absence data. Phylogenetic beta diversity

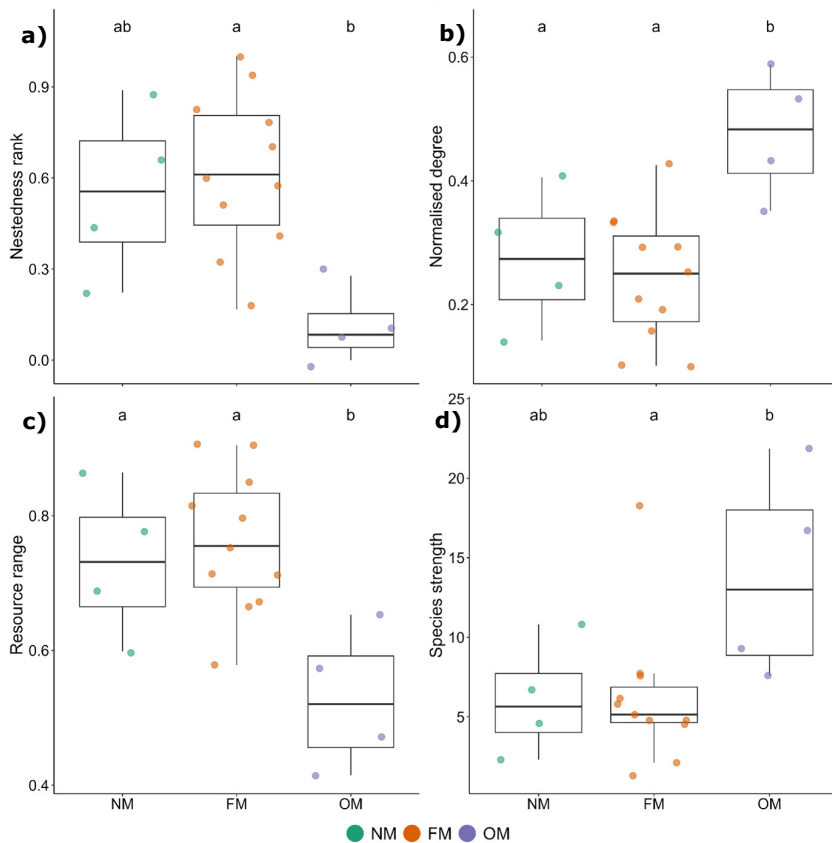


Figure 5. Parameters of networks describing AM fungal communities associating with plants of different mycorrhizal status: a) nestedness rank, b) normalised degree, c) resource range, d) species strength. Adapted from **Paper IV** Fig. 3.

differed in relation to growth form (presence/absence), photosynthetic pathway, CSR strategy (abundance), and N-fixing status (abundance), with diversity highest in forbs, C₃, ruderal, and non-N-fixing plants.

The proportion of ruderal taxa in AM fungal communities varied by growth form, photosynthetic pathway (abundance-weighted), and CSR strategy (presence/absence), with more ruderal taxa associating with forbs, C₃, and ruderal plants (**Paper V**). However, these differences were not significant once effects attributable to correlated functional groupings were accounted for (**Paper V**).

Significant indicator taxa were identified for all plant ecological groups, with highest numbers identified for woody, C₄, and FM plants. Positive phylogenetic correlation was found among indicator values for growth form and mycorrhizal status (Fig. 6).

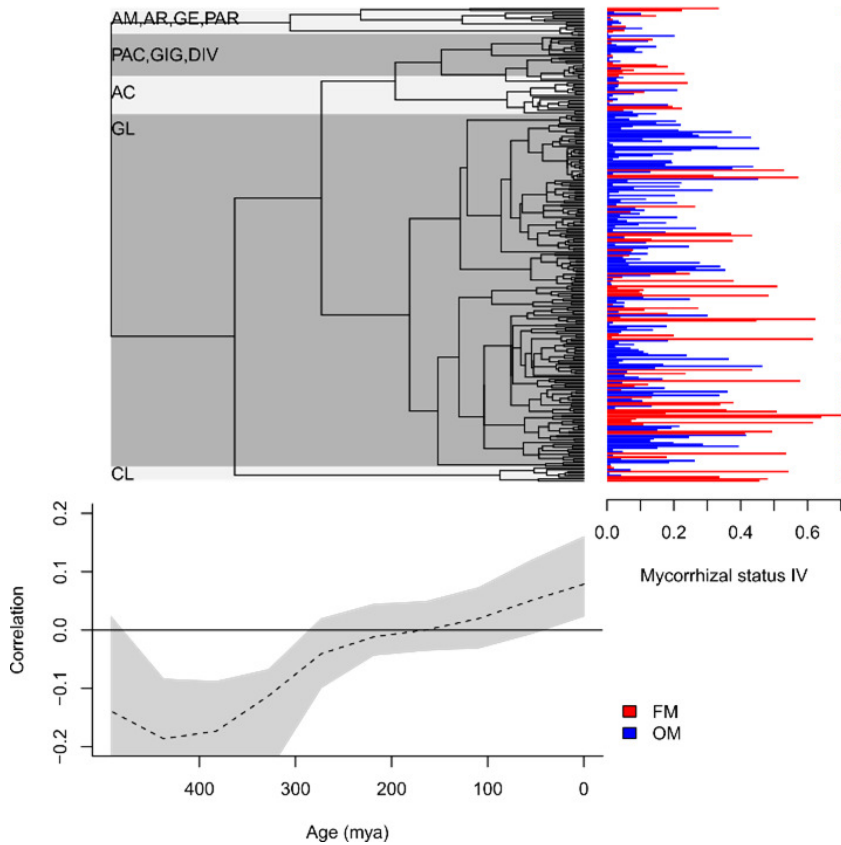


Figure 6. Phylogenetic correlogram showing correlation between fungal taxa in relation to their indicator values for plants of different mycorrhizal status. The top-left panel shows the AM fungal phylogeny; the line-plot in the top-right shows indicator values for different groups, with significant indicator values indicated with a dot at the right-hand side; the bottom panel shows estimated correlation (dashed line) and 95% confidence envelope. AC, Acaulosporaceae; AMB, Ambisporaceae; AR, Archaeosporaceae; CL, Claroideoglomeraceae; DIV, Diversisporaceae; GIG, Gigasporaceae; GL, Glomeraceae; PAC, Pacisporaceae; PAR, Paraglomeraceae. Adapted from **Paper V** Fig. 6b.

4. DISCUSSION

Mycorrhizal symbiosis plays a key role in ecosystems, meaning that it is critical to understand the characteristics of both plant and fungal partner groups and their interactions. From a plant perspective, this thesis demonstrates that plant evolutionary history and plant-environment interactions shape the expression of plant mycorrhizal types and statuses. Reflecting this complexity, detailed investigation of a previously unstudied high-elevation region in the Andean paramo showed that the elevational distribution patterns of mycorrhizal types differ from those observed in temperate northern-hemisphere ecosystems. Furthermore, for over 95% of the global flora, information about plant mycorrhizal types and statuses is lacking, underscoring the need for an accurate and broadly applicable predictive approach. This thesis showed that phylogenetic models, particularly those enriched with plant trait and environmental data, outperformed taxonomic models in predicting mycorrhizal types and statuses. From a fungal perspective, investigation of Estonian plant species in different environments revealed that both facultatively (FM) and obligately (OM) mycorrhizal plants exhibited comparable colonization levels, but that FM plants were markedly more selective in their AM fungal associations. This was supported by a re-analysis of existing AM fungal community data, which revealed significant variation in the composition and diversity of the communities associating with different plant functional groups, including plants of different mycorrhizal statuses.

4.1. Expression of plant mycorrhizal type and status

4.1.1. Plant phylogeny

Among the studied fraction of the global flora, phylogenetic signal is stronger for plant mycorrhizal type than for mycorrhizal status, indicating that mycorrhizal type is more conserved, i.e., less likely to switch during plant evolution than mycorrhizal status (**Paper I**). This pattern may reflect historical environmental conditions that imposed greater selective pressure on mycorrhizal status than on type. Alternatively, plant mycorrhizal types, which require multiple adaptations in both plant and fungal partners, may be subject to greater evolutionary inertia; that is, there are genetic, developmental, and behavioral constraints that limit the ability of plants to switch mycorrhizal types. The particularly high phylogenetic signal for ERM and ORM types, which are relatively recent evolutionary innovations (Brundrett and Tedersoo, 2018), indicates that these specialized associations have remained especially stable within their respective plant lineages. By contrast, mycorrhizal status, which reflects symbiotic flexibility primarily on the part of the plant (Zobel et al., 2024), may be less constrained.

Indeed, it is commonly assumed that plant mycorrhizal types are strongly phylogenetically conserved, allowing predictions of types based on taxonomy (Brun-

drett and Tedersoo, 2018; Brundrett, 2009). However, empirical testing has not fully supported taxonomic extrapolation at the family or genus level, challenging the assumption of phylogenetic conservatism within low taxonomic ranks (Bueno et al., 2019). Despite the observation of relatively strong conservatism among mycorrhizal types, plant lineages have transitioned between both mycorrhizal types and statuses (Strullu-Derrien et al., 2018). Among 162 plant families with more than ten studied species in **Paper I**, only two exhibited a single level for both mycorrhizal type and status (Calophyllaceae and Putranjivaceae, **Paper I** Appendix S3), underscoring the limitations of using plant taxonomy to infer mycorrhizal type and status of unknown species. Correspondingly, **Paper III** demonstrated the superior performance of phylogenetic models over taxonomic models, suggesting that while phylogenetic conservatism may be strong, it may be complex and inconsistent with particular taxonomic ranks.

4.1.2. Plant-environment associations

The fitness associated with different mycorrhizal types and statuses is likely context-dependent, influenced by climatic and edaphic conditions which drive long-term co-adaptation of plant-microbe symbioses (Freschet et al., 2017; Joswig et al., 2022; Trugman et al., 2019). For mycorrhizal status, environmental characteristics explained a higher proportion of variation, particularly for FM status, while phylogeny was secondary (**Paper I**). This suggests that independence from mycorrhiza may confer advantages under specific environmental conditions, such as very fertile soils, anoxic soils or extreme cold environments lacking mycorrhizal fungi (Brundrett and Tedersoo, 2018; Brundrett, 2009; Miller et al., 1999).

Although soil conditions are expected to directly shape mycorrhizal associations (Read and Perez-Moreno, 2003; Read, 1991), few macroecological studies have shown strong links between edaphic characteristics and the distribution of plant mycorrhizal types and statuses (Barceló et al., 2019; Bueno et al., 2017; Steidinger et al., 2019). Indeed, environmental correlations with plant mycorrhizal type and status were previously assumed to predominantly reflect climate (Barceló et al., 2019). However, the use of fine-scale plant distribution and environmental data in **Papers I-III** demonstrated the underappreciated influence of soil characteristics in driving large-scale macroecological patterns and supported the theoretical framework suggesting that mycorrhizal types vary along latitudinal and elevational gradients due to climate-induced soil changes. Soil nutrient levels and stoichiometry, pH and in particular soil texture variables, such as sand, clay or silt content, which are expected to influence water retention and pore size (Querejeta, 2017; Rillig and Mummey, 2006; Weil and Brady, 2017), were revealed to be the characteristics most significantly influencing plant mycorrhizal type and status (**Paper I**).

In the paramo, climatic and edaphic factors play important roles in shaping the distributions of plant mycorrhizal types and statuses (**Paper II**). MAT emerged

as a significant predictor for mycorrhizal statuses, with higher temperatures being positively correlated with AM plant abundance and negatively with NM plant proportions. This finding aligns with the global analysis presented in this thesis, where a similar temperature-related pattern was identified (**Paper I**). However, the role of edaphic variables, such as CEC and soil C content, in influencing the distribution of FM and OM plants in the paramo (**Paper II**) stands in contrast to the global study: globally, climatic factors, particularly solar radiation and evapotranspiration, were found to be more important predictors for FM and OM statuses (Fig. 2b and **Paper I**). Contrasting results from local and global studies may reflect the habitat-specific requirements of the paramo, where the relatively dry conditions drive nutrient and water limitations (indicated by low soil CEC and organic C), potentially influencing the overall incidence of mycorrhizal symbiosis at high elevations (Schmidt et al., 2008).

4.2. Large-scale pattern in mycorrhizal associations

Earlier hypotheses posited a gradient in mycorrhizal symbiosis distribution, with AM-dominated tropical habitats in the northern hemisphere transitioning to ECM boreal forests and ERM tundra, and the southern hemisphere dominated by AM grasslands and forests, with ECM and ERM vegetation in limited areas (Read and Perez-Moreno, 2003; Read et al., 2004; Read, 1991). Global analysis in this thesis generally supports these hypotheses (**Paper I**), identifying ECM woody species hotspots in temperate forests of eastern Southern America and Asia, tropical forests of central Africa, and Australian tropical and Mediterranean areas. These findings align with tree-based estimates and predictive biomass models (Barceló et al., 2019; Braghieri et al., 2021; Steidinger et al., 2019). Mycorrhizal symbiosis decreases with latitude - potentially due to constraints on fungal diversity and symbiosis functionality (Bueno et al., 2017; Delavaux et al., 2019; Kytöviita, 2005; Tedersoo et al., 2014) - and a latitudinal gradient in FM plant species representation was recorded in this thesis (**Paper I**). Australia's unique mycorrhizal state expression, with NM and ECM hotspots and AM species coldspots, reflects its distinct biogeographical history and strategies for coping with infertile or dry soils (Brundrett, 2021a; Lambers et al., 2018).

The study conducted in the Andean paramo (**Paper II**) revealed a dominance of AM plants across all elevations, with only a slight decrease at the highest elevations. By contrast, the abundance of ERM plants decreased with increasing elevation. This finding challenges the expected pattern of AM plants being replaced by ECM and ERM plants at higher elevations, as suggested by previous hypotheses (Read and Perez-Moreno, 2003; Read, 1991). However, it partially aligns with the global analysis in **Paper I**, where a slight increase in AM dominance and a decrease in ERM plant abundance accompanied increasing elevation (**Paper I**). Similar patterns have been noted in tropical high-elevation regions, where AM plants remain prevalent (Haug et al., 2019; Zhang et al., 2021). The

stability in AM plant dominance or increase across these gradients might be attributed to the relatively stable temperatures at low latitudes, which do not reach the extreme lows observed in higher latitude regions where ECM and ERM plants tend to dominate (Hiiesalu et al., 2023; Kotilínek et al., 2017).

The distribution of mycorrhizal statuses also exhibited notable patterns along the elevational gradient of the paramo (**Paper II**). The proportion of NM plants remained relatively stable up to about 3,500 meters, after which it increased markedly at higher elevations. This pattern aligns with observations in European mountain ranges (Bueno et al., 2017), suggesting that as environmental conditions become more extreme with elevation, plants may increasingly rely on NM strategies, possibly as an adaptation to the harsher conditions where mycorrhizal networks are less effective or less prevalent (Kytöviita, 2005). However, it should be noted that in **Paper I**, NM status started to decrease slightly above 3,500m. The observed increase in the proportion of FM plants and the decrease in OM plants with increasing elevation in the Andean paramo (**Paper II**) underscore the importance of flexibility in mycorrhizal associations as a response to environmental gradients. This pattern parallels findings from the Pyrenees, where a similar trend was reported (Bueno et al., 2021) but again contrasts with the global patterns revealed in **Paper I**, where the opposite trend was observed (**Paper I**).

Differences between the findings from the paramo (**Paper II**) and global patterns (**Paper I**) might be attributable to the unique environmental conditions found in the paramo. This region is characterized by extreme elevational gradients, high soil moisture, and elevated UV radiation levels (Luteyn et al., 1999), which may amplify the influence of soil properties on plant-mycorrhizal associations. Additionally, available data for global studies, including **Paper I**, are largely derived from the Northern Hemisphere flora, potentially causing a sampling bias that overlooks less-studied but highly biodiverse and ecologically significant regions like the paramo (Mujica et al., 2024). This highlights the need for greater research attention in these understudied areas to gain a more comprehensive understanding of the expression of mycorrhizal types and statuses.

4.3. Other plant traits as predictors of plant mycorrhizal type and status

The inclusion of environmental variables and plant traits, in addition to phylogenetic information, further enhanced predictions of mycorrhizal types and especially OM and FM statuses (**Paper III**). The frequently improved predictive power of models incorporating aboveground traits highlights the interconnectedness of plant functional traits and the importance of considering the whole-plant economic spectrum when interpreting mycorrhizal associations. The strong influence of environmental variables on the prediction of OM and FM statuses further emphasizes the role of ecological factors in shaping the frequency and intensity of mycorrhizal associations. These findings have practical implications for

predicting mycorrhizal types and statuses in understudied plant species and floras. Pioneering estimates of global-scale ecosystem functioning, such as C stocks (Soudzilovskaia et al., 2019), based on plant mycorrhizal types have previously relied on taxonomic extrapolation. The finding of **Paper III** that prediction can be improved by integrating phylogenetic, environmental, and plant trait data, offers the prospect of constructing more accurate and reliable predictions, which in turn can inform political and ecosystem management decision making.

4.4. A fungal community perspective on mycorrhizal status and other plant functional groupings

Papers IV and **V** provided detailed insight into the fungal communities engaging in mycorrhizal associations. The main focus of these papers was on determining how communities of AM fungi distinguish between plants of different mycorrhizal statuses, but **Paper V** broadened this to consider other plant functional groupings. Taken together, the results of the two papers reveal a nuanced picture of how OM and FM plants differ. On one hand, there was no significant difference in AM fungal colonization (**Paper IV**) or fungal community richness (**Papers IV** and **V**) between FM and OM plants, indicating that the frequency of association does not necessarily dictate the intensity of colonization or the number of fungal partners. Nonetheless, the overall positive correlation between AM fungal richness in roots and mean hyphal colonization suggests that plants with higher colonization levels may provide a more favorable environment for a wider range of AM fungal taxa. This could be due to differences in root architecture, exudate profiles, or other plant traits that influence fungal colonization and community assembly. **Paper V** also revealed significant differences in fungal community richness among plant growth forms and CSR strategies. The higher AM fungal richness associated with grasses and non-ruderal plants may be attributed to the specific root traits and resource allocation patterns of these plant groups. Grasses, for instance, are known to invest heavily in root production, which could create a more extensive and diverse habitat for AM fungi. Non-ruderal plants, which typically occupy more stable and less disturbed environments, may also provide a more consistent and reliable source of C for their fungal partners, promoting the establishment of richer AM fungal communities. The association of putatively ruderal AM fungi with forbs and ruderal plants is an intriguing finding that warrants further investigation. Ruderal plants, which are adapted to disturbed environments, may create conditions that favor the establishment of ruderal AM fungi, which are expected to be more tolerant of environmental fluctuations and disturbances.

4.5. Fungal community composition and partner selectivity in AM fungal networks

There were differences in AM fungal community composition, both taxonomic and phylogenetic, among all different plant functional groups studied in **Paper V**. Some groups, including OM plants were characterised by higher beta diversity (**Paper V**), indicating that these groups have more variable fungal communities across different environments or locations. The differences in species turnover among plant mycorrhizal statuses may reflect either a selectivity in fungal partners, with OM plants being less selective than FM plants, or systematic variation in environmental conditions that impacts the fungal communities available to each status. However, little research attempted to distinguish these possibilities. The higher phylogenetic beta diversity among forbs, C₃ plants, ruderal plants, and non-N-fixing plants suggests that these groups may associate with a wider range of AM fungal lineages, potentially reflecting broader ecological niches and greater flexibility in symbiotic partnerships.

Empirical investigation of the dynamics of AM fungal communities about plant mycorrhizal status (**Paper IV**) revealed differences in partner selectivity that align with the measures of beta diversity in **Paper V**, and with Sepp et al. (2019). Specifically, network analyses revealed distinct patterns of partner selectivity between FM and OM plants. The higher nestedness rank and resource range of AM fungal communities associated with FM plants indicate that these plants are more selective in their choice of fungal partners. This selectivity may allow FM plants to optimize their symbiotic relationships based on the specific benefits offered by different fungal taxa. As such, selectivity may represent one facet of mycorrhizal flexibility, which also includes the possibility of temporarily persisting in the absence of mycorrhiza (i.e. facultative status). By contrast, the lower nestedness rank and higher normalized degree of AM fungal communities associated with OM plants suggest a more generalist approach to partner selection, potentially reflecting a broader range of compatible fungal partners for these plants.

The observed differences in partner selectivity between FM and OM plants have important implications for understanding the ecological and evolutionary dynamics of mycorrhizal networks. The ability of FM plants to selectively associate with specific AM fungal taxa may allow them to fine-tune their symbiotic relationships in response to environmental fluctuations or resource availability. This flexibility could contribute to their wider ecological niches and greater success in colonizing new habitats. By contrast, the generalist approach of OM plants may provide them with a broader range of potential benefits from their fungal partners, but may also make them more vulnerable to disruptions in fungal communities. While research on the origin of facultatively mycorrhizal strategies is limited, our study in the **Paper I** indicates a clear pattern: FM species are predominantly distributed in the Northern Hemisphere and are quite scarce in the Southern Hemisphere. Two related hypotheses could explain this pattern. On one hand,

the extent of land with extremely cold conditions is much greater in the Northern Hemisphere, exposing more plants to these limiting conditions for symbiosis Kytöviita (2005). On the other hand, the history of anthropogenic land modification and perturbation is also much more extensive in the Northern Hemisphere, particularly in Europe, compared to the Southern Hemisphere (Foley et al., 2005). This suggests a potential role of prolonged exposure to soil disturbances. Indeed, global analyses of invasive plant species indicate a strong relationship with disturbance (Lembrechts et al., 2016), where FM strategies appear to be particularly successful (Moyano et al., 2020; Pyšek et al., 2019). Positive phylogenetic correlation in indicator values of AM fungal taxa for different plant mycorrhizal statuses (Fig. 6) suggests that closely related AM fungal taxa tend to disproportionately associate with plants of one or the other status, indicating a degree of co-evolutionary adaptation between plants and their fungal partners.

4.6. Limitations and future directions

While this thesis offers valuable insights into the global patterns and drivers of plant mycorrhizal associations, several limitations should be acknowledged. Firstly, the empirical data on plant mycorrhizal types and statuses remain scarce, with available information covering only about 4% of the global flora (**Paper I**). This data gap is particularly pronounced in regions such as Asia, Africa, and South America, which hampers the generalizability of our findings. Furthermore, the global analysis in this thesis relied on plant occurrence records from GBIF, which, despite providing over 100 million data points for focal plant species in this thesis, is hindered by issues such as limited description of observational methods, uncertainty in coordinate precision and projection, mistakes in taxonomic classification, and potential typographical errors. These factors led to the exclusion of nearly 50% plant species occurrences from subsequent analyses, but some errors may have still persisted in the retained data. As a result, the global scope of this study remains relatively coarse, representing an initial step towards understanding these complex associations.

Secondly, the use of genus-level extrapolations for mycorrhizal type and status in the Andean paramo study (**Paper II**) introduced uncertainty into our conclusions. While this approach was necessary due to the lack of species-level data, it underscores the need for more precise data collection. Specifically, certain groups, such as ERM, deserve more attention. The Ericaceae family in the tropics, which has been sparsely explored, includes a vast number of species with diverse functional attributes, such as epiphytes. Gathering species-level information on plant mycorrhizal associations and improving the accuracy of plant occurrence records are crucial for refining our understanding across diverse taxa and geographic regions. Clearly, further exploration of plant roots, both molecularly and microscopically, especially in the Southern Hemisphere, is essential. Research consortia, such as the one currently being developed in South America (Mujica et al.,

2024), that coordinate exploration of understudied regions and fully incorporate local scientific perspectives, can be of great value in this respect.

The predictive study (**Paper III**) and study of plant functional groups (**Paper V**) encountered limitations due to the availability and quality of plant trait and functional group information. Although above- and belowground plant traits have been shown to improve the predictive accuracy of mycorrhizal types and statuses, the Core Dataset in **Paper III** used in this study included only 300 plant species with complete data for ten traits representing significant plant variability (Carmona et al., 2021). Even after imputation of missing traits, data were available for only about 1,400 plant species worldwide. This limitation significantly restricts our understanding and predictive ability in trait-based ecology. Additionally, while the XGBoost algorithm was effective for classification tasks, it has some shortcomings, particularly with imbalanced datasets. Given the dominance of AM and OM types, achieving high prediction specificity for these types remained challenging despite efforts to adjust hyperparameters and control for the imbalance. In **Paper V**, information on plant functional groups was only partially available for five groupings. Additionally, continuous trait data for plants were too sparse to analyze in the same manner as the functional groups, making it difficult to draw broad conclusions about the relationship between plant mycorrhizal type and status and functional diversity across ecosystems.

Investigation of Estonian plant species in different environments represents a pioneering effort to use a standardized sampling design to quantify variation in AM fungal communities in the roots of OM, FM, and NM plant species (**Paper IV**). However, this study is subject to several limitations that impact the interpretation of our findings. Notably, we found AM fungal colonization in some individuals across all species, including those previously classified as NM, highlighting gaps in our understanding of mycorrhizal symbioses (Cosme et al., 2018). This led to the reclassification of three out of nineteen sampled species, suggesting that mycorrhizal status may be more environmentally dependent than previously thought. While unlikely to affect large-scale patterns, such reclassifications complicate the detection of finer patterns. This result calls for a further investigation of the NM and FM statuses, particularly in light of the environmentally-driven patterns already described in this thesis (**Paper I**). The next theoretical steps could be to investigate which environmental factors affect mycorrhizal colonization, covering factors such as seasonality, availability of fungal symbionts and exposure to extreme conditions.

5. CONCLUSIONS

This thesis provides comprehensive explanatory and predictive analysis of plant mycorrhizal types and statuses in the global flora, and insight into partner selectivity in arbuscular mycorrhizal networks. The findings highlight the complex interplay between phylogenetic conservatism, environmental factors, and plant functional traits in shaping mycorrhizal associations.

The stronger phylogenetic signal observed for mycorrhizal types than for statuses indicates that mycorrhizal statuses are more responsive to contemporary environmental pressures. The dominance of arbuscular mycorrhizal plants in warmer climates and the prevalence of ectomycorrhizal plants in cooler, acidic environments underscore the importance of environmental factors in shaping the distribution of mycorrhizal types. The contrasting distribution of obligately and facultatively mycorrhizal plants along environmental gradients also highlights the advantage, in certain conditions, of mycorrhizal flexibility.

Findings from the Andean paramo revealed distinct patterns in the distribution of mycorrhizal types and statuses along the elevational gradient, emphasizing the unique ecological dynamics of this high-elevation ecosystem. The dominance of arbuscular mycorrhizal plants across all elevations and the increase in non-mycorrhizal plants at higher elevations suggest that plants in the paramo have evolved diverse strategies to cope with the harsh environmental conditions.

The development of predictive models for plant mycorrhizal type and status demonstrated the potential of integrating phylogenetic, environmental, and plant trait data to improve predictive accuracy. The superior performance of phylogenetic models compared with taxonomic models indicates that detailed evolutionary information can be key for predicting these functional traits. The inclusion of environmental variables and plant traits further enhanced predictive accuracy, particularly for obligately and facultatively mycorrhizal statuses.

The investigation of partner selectivity in arbuscular mycorrhizal networks revealed that facultatively mycorrhizal plants exhibit greater selectivity in fungal partner choice compared with obligately mycorrhizal plants. This selectivity may allow facultatively mycorrhizal plants to optimize their symbiotic relationships based on the specific benefits offered by different fungal taxa.

Analyses of arbuscular mycorrhizal fungal communities across plant functional groups revealed significant differences in community composition and diversity. Plant growth form, photosynthetic pathway, CSR strategy, mycorrhizal status, and N-fixing status all influenced the richness, diversity, and phylogenetic structure of associated fungal communities. The association of putatively ruderal arbuscular mycorrhizal fungi with forbs and ruderal plants suggests a degree of co-evolutionary adaptation between plants and their fungal partners.

Overall, this thesis contributes to our understanding of the complex interactions between plants and mycorrhizal fungi, highlighting the importance of considering both evolutionary and ecological factors in predicting and interpreting

mycorrhizal associations. The findings have implications for our understanding of the role of mycorrhizal symbiosis in plant evolution and adaptation to changing environments, which in turn is key for ecosystem management, conservation, and restoration efforts. Future research should focus on expanding our knowledge of mycorrhizal associations across diverse plant taxa and geographic regions, collecting species-level data to validate and refine our understanding of mycorrhizal associations in understudied ecosystems.

SUMMARY

Mycorrhizal symbiosis, a widespread mutualistic interaction between plants and fungi, plays a crucial role in ecosystem functioning and plant adaptation to changing environments. Plant mycorrhizal type and status are plant characteristics that respectively describe the type of mycorrhiza a plant forms and the frequency with which it forms it. This thesis provides a comprehensive analysis of the role of plant phylogeny and environmental conditions in shaping the expression of plant mycorrhizal types and statuses in the global flora. It also assesses the prevalence of types and statuses along elevational and environmental gradients in the understudied Andean paramo ecosystem. Given the lack of information on plant mycorrhizal type and status in the global flora, the thesis develops a framework for integrating phylogenetic, environmental, and plant trait data to predict plant mycorrhizal type and status among unstudied species. Additionally, the thesis investigates how plant mycorrhizal status, and other plant functional characteristics, are associated with partner selectivity in arbuscular mycorrhizal (AM) networks and the composition of AM fungal communities.

The global analysis presented in **Paper I** revealed that both phylogenetic conservatism and plant-environment associations influence the expression of plant mycorrhizal types and statuses among plants throughout the global flora. Arbuscular mycorrhizal (AM) plants dominate in warmer climates with moderate precipitation and alkaline soils, while ectomycorrhizal (ECM) plants prevail in cooler, acidic environments, and ericoid mycorrhizal (ERM) plants are common in cold, humid climates and moderately fertile soils. Non-mycorrhizal (NM) plants are mostly found at higher latitudes and altitudes, thriving in colder, arid conditions. Obligately mycorrhizal (OM) plants predominate near the equator in nutrient-poor soils and tropical rainy climates, while facultatively mycorrhizal (FM) plants are less prevalent under these conditions. While plant mycorrhizal type is more phylogenetically conserved, environmental factors, particularly soil texture, play a significant role in shaping the expression of different mycorrhizal statuses. **Paper I** also revealed significant sampling gaps in biodiverse areas. Geographical bias, particularly in Asia, Africa, and South America, represent considerable blind spots in accessible plant mycorrhizal information.

In **Paper II**, AM plants were found to dominate across all elevations in the Andean paramo, a high-altitude ecosystem in South America, while ERM plant abundance decreases with increasing elevation. NM plants increased in abundance above 4,000m, suggesting that NM status is one strategy to cope with harsh conditions. However, the abundance of FM plants also increased with elevation, while OM plants decreased, indicating the importance of flexibility in mycorrhizal associations at high elevations and, more generally, in response to environmental gradients. Temperature and soil pH were identified as key environmental factors influencing the abundance of AM and ERM plants in the paramo. These results revealed patterns that contrasted with those observed in temperate

northern-hemisphere ecosystems, suggesting that the distribution of mycorrhizal types observed in the paramo and in Europe might reflect the different ranges of the elevational gradients studied, although the specificity of local ecological conditions in the Andean mountains may also have played a role.

Current methods for predicting plant mycorrhizal types and statuses rely on extrapolations within taxonomic ranks (e.g. families, genera), from observed species to other unstudied species. However, this approach assumes strong and consistent phylogenetic conservatism of plant mycorrhizal types and statuses, and potentially overlooks trait variation and evolution. The development of predictive models for plant mycorrhizal type and status in **Paper III** demonstrated the potential of integrating phylogenetic, environmental, and plant trait data to improve the accuracy of predictive approaches. Phylogenetic models demonstrated superior predictive accuracy compared with taxonomic models; and with the wide availability of plant phylogenetic information, phylogenetic models could offer a widely-applicable improvement on taxonomic extrapolation. Incorporating plant traits, especially aboveground traits, and environmental association data further improved the performance of modeling approaches, offering a framework to optimize prediction and placing mycorrhizal characteristics in the context of the plant leaf and belowground economy and plant niche space more generally.

While this thesis generally took a plant-centred approach, by focusing on plant mycorrhizal types and statuses, it linked this with a fungal perspective by investigating the fungal communities associating with plants of different mycorrhizal statuses and other functional groups (**Papers IV** and **V**). Investigation of AM fungal communities among Estonian plant species of different mycorrhizal status (**Paper IV**) revealed that FM and OM plants exhibit similar levels of colonization. AM fungal richness in roots is positively correlated with hyphal colonization. Network analyses showed that FM plants are more selective in their choice of fungal partners compared with OM plants, suggesting that FM plants may optimize their symbiotic relationships based on the specific benefits offered by different fungal taxa.

A re-analysis of root-associating AM fungal community data comprising multiple data sets and plant functional groups (**Paper V**) revealed significant differences in community composition and diversity. Plant growth form, photosynthetic pathway, CSR (competitor, stress-tolerator, ruderal) strategy, mycorrhizal status, and N-fixing status all influence the richness, diversity, and phylogenetic structure of associated fungal communities. The association of putatively ruderal AM fungi with forbs and ruderal plants suggests a degree of co-evolutionary adaptation between plants and their fungal partners.

This thesis contributes to our understanding of the interactions between plants and mycorrhizal fungi, highlighting the importance of considering both evolutionary and ecological factors in predicting and interpreting plant-mycorrhizal associations. The findings have implications for our understanding of the role of mycorrhizal symbiosis in plant evolution and adaptation to changing environments,

which in turn is key for ecosystem management, conservation, and restoration efforts. Future research should focus on expanding our knowledge of mycorrhizal associations across diverse plant taxa and geographic regions, collecting species-level data to validate and refine our understanding of mycorrhizal associations in understudied ecosystems, and investigating the functional traits of mycorrhizal fungi and their contributions to the ecological and evolutionary dynamics of mycorrhizal networks.

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SUPPORTING INFORMATION

54 environmental variables used in this thesis:

- aridity_index: Quantifies the dryness of the environment.
- available.water: (%) Available soil water capacity up to the wilting point.
- base.satu: (%) Percentage of base saturation in the soil.
- BDRICM_M_1km_ll: (cm) Depth to bedrock (R horizon) up to 200 cm.
- BDTICM_M_1km_ll: (cm) Absolute depth to bedrock.
- bulk.ds: (kg/m³) Bulk density of the fine earth.
- CaCO₃: (% of weight, scale factor 0.01) Percentage of calcium carbonate in the soil.
- CaSO₄: (% of weight, scale factor 0.01) Percentage of gypsum in the soil.
- CEC.soilgrids: (cmol/kg) Cation exchange capacity of the soil.
- CHELSA_bio10_01 to CHELSA_bio10_19: Climate variables; temperature in °C, scale factor 0.1 and precipitation in mm. See Climatologies at high resolution for the earth's land surface areas (CHELSA) for detailed description of each variable.
- clay: (%) Weight percentage of clay particles (< 0.0002 mm) in the soil.
- coarse: (%) Volumetric percentage of coarse fragments (> 2 mm) in the soil.
- EC: (dS/m, scale factor 0.01) Electrical conductivity of the soil.
- elevation: (m) Elevation above sea level.
- Evapotranspiration: (mm/year) Annual rate of evapotranspiration.
- ex.acidity: (cmol/kg, scale factor 0.01) Exchangeable acidity in soil.
- ex.Al: (cmol/kg, scale factor 0.01) Exchangeable aluminum in soil.
- ex.Ca: (cmol/kg, scale factor 0.01) Exchangeable calcium in soil.
- ex.K: (cmol/kg, scale factor 0.01) Exchangeable potassium in soil.
- ex.Mg: (cmol/kg, scale factor 0.01) Exchangeable magnesium in soil.
- ex.Na: (cmol/kg, scale factor 0.01) Exchangeable sodium in soil.
- pH.KCl: (scale factor 0.1) Soil pH measured in a KCl solution.
- sand: (%) Weight percentage of sand particles (0.05–2 mm) in the soil.
- silt: (%) Weight percentage of silt particles (0.0002–0.05 mm) in the soil.
- total.C: (% of weight, scale factor 0.01) Total carbon content in soil.
- total.N: (% of weight, scale factor 0.01) Total nitrogen content in soil.
- total.P: (% of weight, scale factor 0.0001) Total phosphorus content in soil.
- total.S: (% of weight, scale factor 0.01) Total sulfur content in soil.
- aswc1 to aswc3: (%) Available soil water capacity at different field capacities.
- occont: (‰) Organic carbon content in soil.

- srad : ($\text{kJ m}^{-2} \text{ day}^{-1}$) Solar radiation exposure.
- vapr : (kPa) Water vapor pressure.
- wind : (m/s) Wind speed.

In this thesis, the mean and standard deviation for each variable, along with soil taxonomies, were calculated as environmental variables.

SISUKOKKUVÕTE

Taimede mükoriisatüüp ja staatus globaalses flooras

Mükoriisne sümbioos on vastastikku kasulik kooselu taimede ja seente vahel, mis on laialt levinud ning mängib olulist rolli ökosüsteemide toimimisel ja taimede kohastumisel muutuvate keskkonnatingimustega. Selle sümbiootilise suhte raames saab seenpartner peremeestaimelt süsinikühendeid, nagu suhkrud ja rasvhapped, mis on olulised tema ainevahetuseks ja kasvuks. Vastutasuks saab taim kasu seente võimest omastada mullast toitaineid, eriti fosforit ja lämmastikku, samuti paremast vastupanuvõimest erinevate abiootiliste stressitekitajate, nagu põud ja soolsus, ning biootiliste stressitekitajate, sealhulgas patogeenide suhtes. Erinevad mükoriisatüübid, millel on erinevad morfoloogilised, funktsionaalsed ja evolutsioonilised omadused, moodustuvad erinevate taimede ja seente rühmade vastastikmõjul. Kõige levinum taimede mükoriisatüüp on arbuskulaarne mükoriisa (AM). Teised taimede mükoriisatüübid, sealhulgas ektomükoriisa (ECM) ja erikoidne mükoriisa (ERM), võivad olla kohalikul või piirkondlikul arvukad ja ökoloogiliselt olulised. Taime mükoriisne staatus kirjeldab, kui sageli taime liik moodustab mükoriisat: alati (obligatsioon mükoriis taimed; OM), mõnikord (fakultatiivselt mükoriisid; FM) või mitte kunagi (mittemükoriisid; NM). Need omadused mõjutavad taimede levikut piki keskkonnagradiende, samuti nende ökoloogilist ja ökosüsteemset rolli. Siiski puudub põhjalik arusaam teguritest, mis mõjutavad erinevate taimeliikide mükoriisatüüpe ja staatuse. Käesolev doktoritöö annab põhjaliku ülevaate sellest, kuidas taimede fülogeneetiline päritolu ja keskkonnatingimused mõjutavad taimede mükoriisatüüpide ja -staatuste avaldumist maailma flooras. Lisaks analüüsi, kuidas taimede mükoriisatüüpide ja staatuste osakaal muutub piki kõrgus- ja keskkonnagradiende seni väheuuritud Andide paramo ökosüsteemis. Kuna andmeid taimede mükoriisatüüpide ja -staatuste kohta globaalses flooras on suhteliselt vähe, on antud doktoritöös esitatud meetod, kuidas ennustada puuduvaid tunnuste väärtuseid, kasutades teisi taimede tunnuseid, taimede fülogeneesi ja keskkonnatingimusi. Lisaks uuriti doktoritöös, kuidas mükoriisne staatus ja teised taimede funktsionaalsed tunnused on seotud seenpartneri valikuga arbuskulaar-mükoriissetes (AM) võrgustikes ja AM seenekoosluste koosseisuga.

Taimede mükoriissete omaduste globaalseks uurimiseks koondati uusimad ja ulatuslikumad andmed 11 770 soontaimede liigi mükoriisatüübi ja mükoriisetaatuse kohta ning seostati need fülogeneetiliste andmete ja väikeseskaalaliste (1 x 1 km) keskkonnaandmetega. Neid andmeid kasutati taimede fülogeneetilise suguluse ja keskkonnatingimuste mõju uurimiseks taimede mükoriissete seoste avaldumisele (artikkel I) ning seni uurimata taimeliikide mükoriissete omaduste ennustamiseks (artikkel III). **Artiklis I** teostatud analüüs näitas, et nii fülogeneetiline konservatism kui taimede ja keskkonnatingimuste vahelised seosed mõju-

tavad taimede mükoriisatüüpide ja -staatuste osakaalu maailma taimestik. AM taimed domineerivad soojemas mõõduka sademete hulgaga kliimas aluselisel muldadel, samas kui ECM taimed on valdavad jahedamates happelisel muldadel ja ERM taimed on tavalisemad külmas niiskes kliimas mõõdukalt viljakatel muldadel. NM taimed esinevad enamasti suurematel laiuskraadidel ja kõrgemal mägedes külmades ja kuivades tingimustes. OM taimed on valdavad ekvaatori lähedal toitainetevaestel muldadel ning troopilises niiskes kliimas, samas kui FM taimi esineb sellistes tingimustes vähem. Taimede mükoriisne staatus sõltub tugevalt keskkonnatingimustest, eriti mulla lõimisest, samas kui taimede mükoriisatüüp on fülogeneetiliselt rohkem konserveerunud. Samuti selgus **artiklis I**, et maailma liigirikaste piirkondade mükoriisatüüpide andmestik on puudulik, seda eriti Aasia, Aafrika ja Lõuna-Ameerika osas.

Andide paramo, kõrgel mägedes asuv neotroopiline piirkond, mis hõlmab osi Venezuelast, Colombiast, Ecuadorist ja Peruust, on tunnustatud kui üks maailma ainulaadsemaid bioloogilise mitmekesisuse levialasid. Siiski on selles piirkonnas väga vähe teada taimede mükoriisete seoste leviku ja mõjutegurite kohta. **Artiklis II** valiti 2 342 georeferentseeritud ala, mis asusid kõrgusvahemikus 2 500 meetrist (sub-paramo) üle 4 200 meetrini (super-paramo), et uurida taimede mükoriisatüüpide ja mükoriisse staatuse levikut ning keskkonnamõjusid piki paramo kõrgusgradienti. leidsime, et Lõuna-Ameerika kõrgmäestik paramo ökosüsteemis domineerivad kogu ulatuses AM taimed domineerisid kõigil kõrgustel Andide paramos, ning ERM taimede osakaal kahanes kõrguse kasvades. Mittemükoriisete taimede osakaal suurenes kõrgemal kui 4 000m, mis viitab sellele, et mittemükoriisne staatus on üks viisidest, kuidas taimed karmide keskkonnatingimustega toime tulevad. Samas kasvas ka FM taimede osakaal, kuid OM taimede osakaal vähenes. See viitab, et nii kõrgmägedes kui laiemalt erinevatel keskkonnagradienditel võib olla oluline ka taimede paindlikkus mükoriisat moodustada või mitte moodustada. Kõige olulisemateks keskkonnatingimusteks Andide paramos, mis mõjutasid AM ja ERM taimede osakaalu, olid temperatuur ja mulla pH. **Artiklis I** leitud mükoriisatüüpide ja -staatuste levikumuster erineb sellest, mida on seni näidatud põhjapoolkera parasvöötme ökosüsteemides. Selle põhjusteks võivad olla nii erinevused uuritud kõrgusgradiendis kui ka spetsiifilised ökoloogilised tingimused Andide mäestikis võrreldes Euroopaga.

Seni uurimata taimede mükoriisete tunnuste väärtuste ennustamiseks kasutatakse praegu meetodeid, mis tulevad mükoriisatüübi ja staatuse taimede taksonoomilise kuuluvuse ja uuritavate liikide lähisugulaste mükoriisatunnuste alusel, st sama perekonna, sugukonna või isegi seltsi taimeliigid jagavad sama mükoriisatüüpi või -staatust. Selline meetod eeldab aga, et taimede mükoriisatüüp ja staatus on tugevalt fülogeneetiliselt konserveerunud tunnused, mistõttu see meetod võib jätta arvestamata tunnuste varieeruvuse ja evolutsiooniga. **Artiklis III** arendatud mudelid ennustamaks taimede mükoriisete tunnuste väärtuseid näitasid, et taimede fülogeneesi, keskkonnatingimuste ja teiste taimetunnuste andmete integreerimine mudelitesse aitavad oluliselt parandada mudelite ennustusvõimet.

Mudelid, mis arvestasid ka fülogeneetiliste andmetega, olid oluliselt täpsemad võrreldes ainult taksonoomiapõhiste mudelitega. Arvestades taimede fülogeneetilise info täpsust ja kättesaadavust, aitab fülogeneetilise infoga arvestamine taimede mükoriisatunnuste ennustamist täpsemaks muuta. Teiste taimetunnuste, eriti maapealsete osade tunnuste kaasamine koos keskkonnatingimuste arvestamisega aitas mudelite ennustusvõimet veelgi parandada. Mitmekesise info kaasamine mudelitesse aitab parandada mudelite ennustusvõimet ning aitab siduda mükoriisideid tunnuseid taimede maapealse ja maa-aluse osa toimimise ja niširuumiga.

Peremeestaimedega seotud seente koosluse koosseis ja mitmekesisus võivad suurel määral mõjutada mükoriisete suhete edukust ja funktsionaalsust. Doktoritöös uuriti ka taimede mükoriisse staatuse ja teiste funktsionaalsete tunnuste seoseid mükoriisaseente kooslustega (**Artikkel IV** ja **V**). **Artiklis IV** uuriti AM seenekooslusi üheksateistkümnelt Eesti taimeliigi juurtes, mis on erineva mükoriisse staatusega, ja leiti, et nii FM kui OM taimede juured olid sarnasel määral mükoriisaseente poolt koloniseeritud. Rohkem koloniseeritud juurtes oli AM seente liigirikkus kõrgem võrreldes vähem koloniseeritud juurtega. Võrgustikuanalüüs tuvastas, et FM taimed olid seenpartnerite osas valivamad võrreldes OM taimedega. Sellest järeldub, et FM taimed optimeerivad mükoriisse sümbioosi moodustamist sõltuvalt sellest, millist kasu erinevad seensümbiontid taimedele pakuvad.

Suurema andmestiku põhjal näidati **artiklis V**, et taimede funktsionaalsed rühmad erinevad oma seenpartnerite koosluste koosseisu ja mitmekesisuse osas. Ülemaailmse AM seenekoosluste andmete (hõlmates 14 andmestikku ja 148 asukohta) ning taimede funktsionaalsete rühmade uus analüüs (artikkel V) tuvastas, et AM seente koosluste koosseis ja mitmekesisus erinesid oluliselt ja süstemaatiliselt erinevate taimerühmade vahel. Taimede kasvuvorm, fotosünteesiraja tüüp, CSR-strateegia (konkurentsitaluja, stressitaluja, ruderaal), mükoriisne staatus ja lämmastiku fikseerimise võime mõjutasid mükoriisaseenekoosluste liigirikkust, mitmekesisust ja fülogeneetilist struktuuri. Leitud seos oletatavalt ruderaalsete AM seente (neid, mida saab kultuuritingimustes kasvatada ja mis eeldatavasti kasvavad hästi häiritud keskkondades, sarnaselt ruderaalsete taimedega) ja rohundite ning ruderaalsete taimede vahel viitab taimede ja nende seensümbiontide vahelisele koevolutsioonile.

Käesolev doktoritöö aitab mõista taimede ja mükoriisaseente vahelisi vastastikuseid seoseid ning tõstab esile evolutsiooniliste ja ökoloogiliste tingimuste olulisuse mükoriisete seoste ennustamisel ja tõlgendamisel. Saadud tulemused rõhutavad mükoriisse sümbioosi rolli taimede evolutsioonis ja keskkonnatingimustega kohastumisel. Sellised teadmised aitavad omakorda paremini ökosüsteeme hoida, kaitsta ja taastada. Edaspidi on siiski vajalik jätkata mükoriisse sümbioosi uurimist erinevatel taimetaksonitel ning seni väheuuritud piirkondades, et paremini mõista sellise interaktsiooni toimimist ja rolli ning valideerida erinevate mudelite ennustusi. Samuti on vajalikud täiendavad teadmised mükoriisaseente funktsionaalsete tunnuste kohta ning kuidas need mõjutavad mükoriisavõrgustike ökoloogilist ja evolutsioonilist dünaamikat.

ACKNOWLEDGEMENTS

The path leading to this moment has been long and winding. First and foremost, I would like to express my sincere gratitude to Professors Feng Huyuan and Maarja Õpik. Without their support, the doors of the University of Tartu might have remained closed to me. I am deeply thankful for their belief in me and for allowing me one last retreat.

My deepest appreciation goes to my supervisors, Guille and John. I must have saved the world in a parallel universe to have been fortunate enough to meet them in this one. Because of them, for the first time, I no longer had to face the unknown alone. They were always there, always, always willing to help. Their guidance and unwavering support have been the cornerstone of my journey, both academically and personally. I offer my sincere gratitude for their dedication and mentorship in all aspects of my life.

Thank you, Maarja. Every conversation with you revealed to me just how much I had yet to learn. Thank you, Mari, Martin, and Kadri. You were like family to me in Estonia, always supportive and encouraging. Thank you, Siqiao. With you by my side, everything seemed a little easier. My heartfelt thanks to the exceptional Plant Ecology Group and the University of Tartu for giving me the opportunity to explore my interests. Oscar, Ayesh, Bruno, Slendy, Blanca, Eleonora, and Enrico, thank you for the camaraderie and the shared moments.

To my parents, who have always given me the best of themselves, and to Lisa, for a decade of cherished friendship.

This thesis represents countless sleepless nights, strands of fallen hair, silent tears, a significant computation bill from the university, and a laptop that nearly overheated and ultimately succumbed to the weight of calculations. Now, I present it to you, hoping you can perceive a glimmer of my faint perseverance within its pages.

The research presented in the thesis was funded by the European Regional Development Fund (Centre of Excellence EcolChange, Centre of Excellence Agro-CropFuture), European Union (ERC grant PlantSoilAdapt, 101044424), Estonian Research Council (PRG1065, PRG1789, PRG741, PRG1836, IUT 20-28), Ramon y Cajal fellowship (RYC2021-032533-I), Spanish Consolidation grant (CNS2023-143989), EU Horizon project ALFAwetlands, Alexander von Humboldt Foundation, the Polish National Agency for Academic Exchange (NAWA; PPN/ULM/2019/1/00248/U/00001), ERA-NET Cofund BiodivERsA3 (SoilMan), and University of Alcalá (grant number 2018-T2/BIO-10995). Additionally, ChatGPT (April 2023 version), was utilized for suggestions on Paper III XGBoost modeling and hyperparameter tuning, as well as for preparing Paper III Figure 3.

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