

MARET GERZ

The distribution and role of mycorrhizal
symbiosis in plant communities



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The distribution and role of mycorrhizal
symbiosis in plant communities



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LIST OF ORIGINAL PUBLICATIONS

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

- I **Gerz, M.**, Bueno, C.G., Zobel, M., & Moora, M. 2016. Plant community mycorrhization in temperate forests and grasslands: Relations with edaphic properties and plant diversity. *Journal of Vegetation Science* 27: 89–99.
- II Bueno, C.G., Moora, M., **Gerz, M.**, Davison, J., Öpik, M., Pärtel, M., Helm, A., Ronk, A., Kühn, I., & Zobel, M. 2017. Plant mycorrhizal status, but not type, shifts with latitude and elevation in Europe. *Global Ecology and Biogeography* 26: 690–699.
- III **Gerz, M.**, Bueno, C.G., Ozinga, W.A., Zobel, M., & Moora, M. 2018. Niche differentiation and expansion of plant species are associated with mycorrhizal symbiosis. *Journal of Ecology* 106: 254–264.
- IV **Gerz, M.**, Bueno, C.G., Ozinga, W.A., Zobel, M., & Moora, M. 2019. Responses of plant community mycorrhization to anthropogenic influence depend on the habitat and mycorrhizal type. *Oikos* 128: 1565–1575.

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Author's contribution to the publications:

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

	Developing the idea	Collecting the data	Analysing the data	Preparing the manuscript
I	**	***	***	***
II	**	**	—	**
III	***	***	***	***
IV	**	***	***	***

1. INTRODUCTION

1.1. Background

Mycorrhizal symbiosis is an ancient association between plants and root inhabiting soil fungi in which plants provide fungi with photosynthetically derived carbon in exchange for fungal acquired soil nutrients (Smith & Read 2008). In addition to nutritional benefits, plants can also gain other types of advantages from associating with mycorrhizal fungi, such as increased protection against pathogens (Albornoz et al. 2017; Delavaux et al. 2017), herbivores (Babikova et al. 2013; Frew et al. 2022) and parasitic plants (Sui et al. 2019), or tolerance to abiotic stress factors (Finlay 2004; Miransari 2010; Poudel et al. 2021; Puy et al. 2022). Forming mycorrhizal symbiosis is ubiquitous as more than 90% of plant species are currently thought to associate with mycorrhizal fungi (Brundrett & Tedersoo 2018), making the symbiosis a key player in ecosystem processes (Rillig 2004; van der Heijden et al. 2008; Bardgett et al. 2014; van der Heijden et al. 2015).

However, plants can rely on mycorrhizal symbiosis to varying degrees and can thus be considered to exhibit different mycorrhizal statuses. Obligately mycorrhizal (OM) plant species always associate with mycorrhizal fungi, facultatively mycorrhizal (FM) plant species sometimes form symbiosis with mycorrhizal fungi and sometimes do not, depending on the environmental conditions, and non-mycorrhizal (NM) plants never form mycorrhizae (Smith & Read 2008; Moora 2014). Also, mycorrhizal associations are very diverse, and several mycorrhizal types can be distinguished based on the morphology and function of the symbiosis and interacting plant and fungal partners (Smith & Read 2008), yet three of them are most abundant in ecosystems. The oldest (Strullu-Derrien et al. 2018) and most widespread mycorrhizal type is arbuscular mycorrhiza (AM). Approximately 80% of plant species from different families (Brundrett & Tedersoo 2018) form AM, with roughly only 300 described fungal morphospecies (Öpik & Davison 2016) from phylum Glomeromycota (Schüßler et al. 2001; Tedersoo et al. 2018). In arbuscular mycorrhizal symbiosis, fungi inhabit plant cortical root cells, where they usually form specialized structures called arbuscules, which are the main sites of nutrient exchange (Smith & Read 2008). Another globally important mycorrhizal type is ectomycorrhiza (EcM), which is formed by around 2% of plant species, mainly trees (Brundrett & Tedersoo 2018), and up to 20 000 fungal species from the phyla Basidio- and Ascomycota (Rinaldi et al. 2008). Ectomycorrhizal symbiosis is characterized by the presence of a thick hyphal mantle on root tips and hyphal proliferation between cortical root cells – the Hartig net – which is responsible for nutrient exchange (Smith & Read 2008). Interestingly, some plant species are also capable of forming both AM and EcM (Teste et al. 2020). Around 1% of plant species, which all belong to the Ericaceae family, form ericoid mycorrhizal symbiosis (ErM) with only a few proven fungal species mainly from the phylum Ascomycota (Perotto et al. 2018). In ErM, the

fungal hyphae also penetrate plant root cells, proliferating and forming extensive hyphal coil complexes as a nutrient exchange interface (Smith & Read 2008).

There is accumulating evidence that different mycorrhizal associations are rather the norm than the exception among plants (Cosme et al. 2018; Brundrett & Tedersoo 2018). Thus, mycorrhizal symbiosis plays a crucial role in interplant relationships (Moora & Zobel 2010; Klironomos et al. 2011; Wagg et al. 2011; Tedersoo et al. 2020), interactions between plants and other soil microbiota (Larimer et al. 2014) and many ecosystem processes (Rillig & Mummey 2006; Phillips et al. 2013; Averill et al. 2014; Bardgett et al. 2014; Leifheit et al. 2015; Frey 2019; Clemmensen et al. 2021). However, despite a considerable advancement in mycorrhizal research there are still many unknown facets to mycorrhizal symbiosis and questions in need of an answer.

1.2. Distribution of mycorrhizal symbiosis and its drivers

In order to fully appreciate the contribution of mycorrhizal symbiosis to ecosystem functioning, there is a need to understand its distribution in plant communities and at larger scales. In general, mycorrhizal symbiosis is expected to prevail in infertile soils as its main advantage to the plants is enhanced nutrient acquisition (Smith & Read 2008). Non-mycorrhizal plants, on the other hand, are thought to dominate on either very fertile soils, where nutrient uptake via the mycorrhizal pathway is not cost-effective (Johnson et al. 1997; Johnson & Graham 2013), or in very harsh conditions not suitable for mycorrhizal fungi (Brundrett 2009). The foundation of describing the biogeography of mycorrhizal associations was laid by Read (1991) who proposed the global distribution of dominant mycorrhizal types in biomes. This was based on the recognition that distinct climatic conditions and their effects on soil development have led to the selection of certain mycorrhizal types, depending on nutrient acquisition strategies of associating fungal partners (Read 1991; Read & Perez-Moreno 2003; Read et al. 2004). According to this hypothesis, arbuscular mycorrhizal plants dominate in grasslands and tropical forests at low latitudes and altitudes with higher soil pH and mean annual temperatures. These conditions favour mineral nutrient cycling (Yu et al. 2022), giving a competitive advantage to plants associated with AM fungi, which acquire nutrients mainly in the mineral form (Read & Perez-Moreno 2003). Ectomycorrhizal plants are characteristic of forests in intermediate latitudes and altitudes in which cooler temperatures contribute to litter accumulation and soil acidification (Read 1991). EcM fungi possess proteolytic capabilities and are thus capable of accessing nutrients from organic compounds (Read & Perez-Moreno 2003; Read et al. 2004). Ericoid mycorrhizal plants are expected to dominate in tundra biomes at high latitudes and altitudes (Read 1991). The acidic soils and thick humus layer in these conditions favour symbiosis with ErM fungi as they, even more so than EcM fungi, have saprotrophic abilities to enable access to nutrients in organic forms (Read & Perez-Moreno 2003; Read et al. 2004).

Identifying mycorrhizal distribution patterns together with their drivers using real-world data and quantifying the reliance of vegetation on mycorrhizal symbiosis has gradually gained more attention. The first step was made by describing plant communities based on the abundance (Barni & Siniscalco 2000) and the relative share of plant species with distinct mycorrhizal types and statuses in a species pool (Cázares et al. 2005). These have indeed provided support for the expectations that NM plants dominate fertile and disturbed habitats, while AM plants are characteristic of herbaceous plant communities and EcM and ErM plants of woody and shrubby communities. Coinciding trends have also been observed in AM and EcM root colonization levels (Piotrowski et al. 2008). However, more recent analyses at the community level also provide some contradictory results, showing that grasslands with lower fertility or higher pH are not necessarily more mycorrhizal as would be expected (Bitomský et al. 2021; Leon et al. 2022) and variation in mycorrhizal strategies within communities can be larger than between different habitats (Bitomský et al. 2021).

The accumulation of mycorrhizal trait data as well as plant distribution and environmental data has made analyses at a larger scale more feasible. One of the first attempts to analyse the distribution of mycorrhizal symbiosis at regional scale was by Swaty et al. (2016) who mapped the historical distribution of mycorrhizal types in conterminous United States. AM plants were found to dominate the area, while a big proportion of vegetation types also included plants with other mycorrhizal types (Swaty et al. 2016). More recently, conterminous USA has also been addressed regarding the relative dominance of AM and EcM trees (Jo et al. 2019). In addition, the distribution of AM plants with different mycorrhizal statuses, and NM plants have been mapped in Germany, where the share of AM plants decreased with increasing area of mixed and coniferous forests (Menzel et al. 2016), further supporting theoretical predictions. Data from the polar regions suggest that despite AM, EcM and ErM types are present in these ecosystems, the importance of NM plant species increases, and that of OM plant species decreases with increasing latitude (Newsham et al. 2009).

There is accumulating evidence that different mycorrhizal statuses and types are associated with specific edaphic and climatic conditions. Obligately mycorrhizal plants have been shown to prefer warmer and drier habitats with higher soil pH, while occurring less frequently in fertile soils (Hempel et al. 2013). On the other hand, FM and NM plants preferred high soil moisture and occurred less frequently in dry soils, while FM plants also preferred more fertile habitats (Hempel et al. 2013). Associations with AM fungi have been shown to be more common in warmer habitats with higher soil pH and lower C:N ratio (Peat & Fitter 1993; Soudzilovskaia et al. 2015; Menzel et al. 2016; Jo et al. 2019), where mineral nutrient cycling is prevalent (Phillips et al. 2013; Averill et al. 2014; Soudzilovskaia et al. 2015; Yu et al. 2022). When compared to AM symbiosis, EcM is dominant in colder and more acidic soils with higher moisture content and C:N ratio (Soudzilovskaia et al. 2015; Craig et al. 2018; Jo et al. 2019), characteristic of the organic nutrient economy (Phillips et al. 2013; Averill et al. 2014; Yu et al. 2022).

Prior to the original research papers presented in this thesis, only a few attempts had been made at mapping mycorrhizal associations and identifying the drivers, while considerable efforts have been made afterwards. Recent advances have taken mycorrhizal biogeography to global scale and provide general empirical support to the expected distributions proposed decades ago. Delavaux et al. (2019) have found that the proportion of mycorrhizal plant species decreases, while the proportion of NM plant species increases towards the poles, associated with decreasing temperature. AM plant species still dominate species pools globally (Delavaux et al. 2021), while incorporating plant abundances into the analyses highlights the importance of EcM and ErM symbiosis at higher latitudes (Steidinger et al. 2019; Barceló et al. 2019; Soudzilovskaia et al. 2019). These studies also suggest that mycorrhizal biogeography at larger scales is mainly driven by climatic factors, while edaphic factors still contribute to the observed patterns (Steidinger et al. 2019; Barceló et al. 2019).

1.3. Mycorrhizal symbiosis as a mediator of plant diversity

Plant ecology has long sought to explain patterns of plant coexistence and diversity (Tilman 1982; Chesson 2000; HilleRisLambers et al. 2012; Levine et al. 2017). Yet, mycorrhizal symbiosis has not been traditionally integrated into theories of coexistence until relatively recently (Bever et al. 2010; Klironomos et al. 2011; Tedersoo et al. 2020). It has been observed that plant communities dominated by different mycorrhizal types can vary markedly in their species richness, e.g., EcM dominated boreal forests are relatively species poor, while AM dominated grasslands and tropical rainforests can harbour extreme plant diversity (Connell & Lowman 1989; Allen et al. 1995; Toussaint et al. 2020). The observations from natural systems, together with the acknowledged importance of mycorrhizal symbiosis in plant fitness, lay the foundations for identifying the role of mycorrhizal symbiosis in patterns of plant diversity.

Mycorrhizal symbiosis can be responsible for both increases as well as decreases in plant diversity (van der Heijden 2002), and several mechanisms might underlie these patterns. One of the factors contributing to differential effects on plant diversity is the variation in plant species dependency on mycorrhizal symbiosis (Wilson & Hartnett 1998). More specifically, whether associations with mycorrhizal fungi promote or hinder plant richness is determined by the mycorrhizal dependency of the community dominants (Hartnett & Wilson 2002; O'Connor et al. 2002; Lin et al. 2015) and subordinates (Grime et al. 1987; Urcelay & Díaz 2003). The presence of mycorrhizal fungi is expected to increase plant diversity if subordinate plant species are more responsive to mycorrhizal symbiosis than dominant plant species (Grime et al. 1987; Gange et al. 1993; Lin et al. 2015). Alternatively, plant richness is hindered when community dominants are more dependent on mycorrhizal associations than subordinates (Zobel & Moora 1995; Hartnett & Wilson 1999; Hartnett & Wilson 2002; Leon et al. 2022). However, mycorrhizal symbiosis is expected to function along a mutualism-

parasitism continuum (Johnson et al. 1997; Johnson & Graham 2013), and the modification of plant coexistence by mycorrhizal symbiosis at the parasitism end of the spectrum might depend on plant species' differential resistance to negative growth effects (Mariotte et al. 2013). For example, it has been shown that in some grassland systems, the negative effect of AM fungi is more pronounced for dominant plant species than for subordinates, thus alleviating interspecific competition and promoting diversity (Mariotte et al. 2013). Plant species can also vary in their reliance on mycorrhizal symbiosis in regeneration (Hartnett et al. 1994). Combined with spatial heterogeneity in mycorrhizal infectivity in plant communities, it can lead to differential regeneration niches and thus enhanced interspecific coexistence (Hartnett & Wilson 2002). In addition, local plant diversity can also be positively related to mycorrhizal fungal diversity (van der Heijden et al. 1998; Hiiesalu et al. 2014; Nguyen et al. 2016), although this relationship is often not observed at larger scales (Toussaint et al. 2020; Fei et al. 2022).

A significant role in determining plant community diversity is also played by plant-soil feedback, resulting from plant species modifying their abiotic and biotic environment, which has further consequences on conspecific as well as heterospecific neighbours (Bever 2003; van der Putten et al. 2013; Semchenko et al. 2022). An important part of plant-soil feedback and its outcome on plant coexistence is attributable to interactions with mycorrhizal fungi (Reynolds et al. 2003; Bever et al. 2010) and depends on the mycorrhizal type (Bennett et al. 2017; Kadowaki et al. 2018). AM plant species tend to experience more negative plant-soil feedbacks as their abundance increases (Kadowaki et al. 2018), mostly as a result of an accumulation of pathogens (Bennett et al. 2017). Also, the negative density dependence can be directly caused by preferential allocation of resources to mycorrhizal fungi, which in turn benefit mostly other plant species (Bever 2002). As pathogens or mycorrhizal fungi, which promote other plant species, accumulate, the dominant plant species are adversely affected. This leads to enhanced coexistence and higher plant diversity, as often seen in grasslands and tropical forests. On the other hand, low plant diversity or even monodominance in EcM systems has been ascribed to positive plant-soil feedbacks (Connell & Lowman 1989; Laliberté et al. 2015; Kadowaki et al. 2018). EcM trees suffer less from pathogens than AM trees (Bennett et al. 2017) as EcM fungi physically ensheath young feeder roots, which leaves pathogens fewer opportunities to infect the roots (Marx 1972). Indeed, EcM tree seedlings tend to do better near conspecific trees than heterospecifics (Bennett et al. 2017; Kadowaki et al. 2018), indicating EcM fungal pathogen protection, and leading to reinforcement of lower plant diversity. However, recent evidence shows that not only the EcM tree dominance hinders plant diversity, but also the dominance of AM trees can have similar inhibiting effects (Carteron et al. 2022).

Plant coexistence and diversity have been traditionally explained by competition-driven differences in resource use, leading to niche partitioning (MacArthur & Levins 1967; Tilman 1982). However, positive interactions are more widespread in nature than previously thought and the need to include these into niche theory has been highlighted (Bruno et al. 2003; Stachowicz 2012; Bulleri et al.

2016). Mycorrhizal symbiosis could also contribute to plant niche partitioning and thus plant community diversity (Reynolds et al. 2003; Bever et al. 2010; Peay 2016; Tedersoo et al. 2020). Obligately, facultatively and non-mycorrhizal plants are shown to prevail in different environmental conditions (Peat & Fitter 1993; Hempel et al. 2013; Menzel et al. 2016), while FM plants also occupy more habitat types than plants with other mycorrhizal statuses (Hempel et al. 2013). The main benefit of mycorrhizal symbiosis is increased access to growth-limiting nutrients and enhanced stress tolerance, allowing plants to grow at lower resource levels or in harsher environments (Smith & Read 2008). This suggests niche differentiation and expansion (Bever et al. 2010) among plants with different mycorrhizal statuses. In addition, plants form several mycorrhizal types with distinct guilds of mycorrhizal fungi and grow in specific habitat conditions (Read 1991; Read & Perez-Moreno 2003). One of the underlying mechanisms could be niche partitioning mediated by different resource preferences of mycorrhizal fungi belonging to these distinct guilds (Peay 2016). Also, niche differentiation of mycorrhizal fungal species within mycorrhizal types (Dickie et al. 2002; Reynolds et al. 2003; Davison et al. 2021) could possibly contribute to resource partitioning of plant species. In addition, forming a certain mycorrhizal type could lead to wider niches compared to other types as broadly distributed fungi, such as AM fungi (Davison et al. 2015), can help plant species to occupy a larger array of habitats (Peat & Fitter 1993). Within mycorrhizal types, mycorrhizal fungal diversity could also contribute to plant niche expansion (Reynolds et al. 2003). It has been shown experimentally that mycorrhiza-mediated niche differences can indeed be important in plant coexistence as plant community diversity is promoted when plants with different mycorrhizal strategies are present (Veresoglou et al. 2018). In addition, tree diversity is highest when both AM and EcM hosts are equally abundant (Carteron et al. 2022). However, very little is still known about whether and how plant species with different mycorrhizal strategies differ in their realized niches.

1.4. The effect of anthropogenic influence on mycorrhizal symbiosis in plant communities

Anthropogenic influence is affecting ecosystems and ecosystem service provision globally (Ellis & Ramankutty 2008; Jacobson et al. 2019; Riggio et al. 2020). Human population densities and increasing land-use change relate to changes in climate, modifications in biodiversity patterns as well as ecosystem functioning (Vitousek et al. 1997; McKinney & Lockwood 1999; Grimm et al. 2008; Newbold et al. 2015). Thus, as mycorrhizal associations also play an important role in ecosystem processes (van der Heijden et al. 2015), it is essential to identify how anthropogenic influence affects these symbiotic relationships.

Human impact could potentially influence the variation in mycorrhizal symbiosis in plant communities via several mechanisms, which are not strictly independent of each other. One aspect of human pressure on ecosystems is increasing urbanization (Seto et al. 2012), which alters the physical characteristics of habitats (Foley et al. 2005). Urban areas are characterized by higher temperatures and drier, more alkaline and fertile soils (Gilbert 1991). Implications of these conditions on plant community mycorrhization could be variable: higher temperatures, increased soil pH and lower soil moisture are shown to favour mostly OM plant species (Hempel et al. 2013; Menzel et al. 2016), which could increase the prevalence of mycorrhizal symbiosis in plant communities, while the more fertile soils could give advantage to NM plant species (Johnson et al. 1997; Johnson & Graham 2013) and reduce the importance of mycorrhizal symbiosis in areas of greater human impact (Soudzilovskaia et al. 2019). In addition, cities are also very heterogenous habitats (Cadenasso et al. 2007), where a limited amount of poorly connected more natural habitat patches exist in a matrix of highly disturbed or artificial uninhabitable conditions, also functioning as a potential dispersal barrier for both plants and fungi. These conditions could favour FM plant species as they may take advantage of their wider ecological range (Hempel et al. 2013; Moora 2014) and occupy habitat patches with variable abiotic as well as biotic conditions. While urban habitats can favour plants with different mycorrhizal statuses, the association with mycorrhizal types appears more consistent. The microclimatic and edaphic properties characteristic to cities are expected to favour AM plants rather than plants with other mycorrhizal types (Hempel et al. 2013; Menzel et al. 2016). Large-scale analyses also suggest that human-induced land-use change, including urbanization, have increased AM plant abundance, while EcM and ErM plants are disproportionately negatively affected by anthropogenic impact (Swaty et al. 2016; Jo et al. 2019; Soudzilovskaia et al. 2019).

Another consequence of human activities on plant communities is the introduction of alien plant species (Pyšek 1998; Szymura et al. 2018), which alters biodiversity patterns and ecosystem processes (Ehrenfeld 2010; Yang et al. 2021). The success of alien plant species can be potentially mediated by mycorrhizal symbiosis (Marler et al. 1999; Carey et al. 2004). On one hand, it could be expected that NM or FM plant species are more successful invaders as they do not depend on the presence of a suitable symbiotic partner (Richardson et al. 2000). On the other hand, mycorrhizal symbiosis could broaden plant species' tolerance to different environmental conditions (Peay 2016), allowing them to occupy more habitats. While it has been shown that many alien plant species belong to NM plant families (Pringle et al. 2009) and some can reduce their reliance on mycorrhizal symbiosis (Seifert et al. 2009), the accumulating evidence instead suggests that mycorrhizal symbiosis confers an advantage to alien plant species (Moyano et al. 2021). Naturalized floras show a higher proportion of mycorrhizal and a lower proportion of NM plants (Delavaux et al. 2019; Delavaux et al. 2021). However, FM alien plant species are the most successful as they naturalize to a greater extent compared to OM plants (Menzel et al. 2017; Pyšek et al. 2019; Moyano et al. 2020). Regarding mycorrhizal types, plants forming AM are more

likely to be naturalized, and to a greater extent, while EcM plants are also over-represented among aliens (Pyšek et al. 2019; Delavaux et al. 2021). This pattern could be attributed to the wide spread of AM (Davison et al. 2015) and EcM fungi (Tedersoo et al. 2010) and the low specificity in AM symbiotic partner selection (Klironomos 2000). Plants with other mycorrhizal types rarely contribute to plant invasions (Pyšek et al. 2019), potentially due to high specificity between symbiotic partners (Smith & Read 2008).

The mycorrhization of plant communities can also be influenced by changes in plant species distribution, which are strongly modified by increasing human impact (Channell & Lomolino 2000; Newbold et al. 2018). In the face of anthropogenic pressure, plant species can either expand their range and be considered “winners”, or they may experience range contraction and be regarded as “losers” (Baskin 1998; McKinney & Lockwood 1999). If plant communities consist more of range contracting species, the communities could be viewed as more natural, while communities consisting more of range expanding plants are more human influenced. Indeed, it has been shown globally that anthropogenic disturbance increases the proportion of widespread “winners” and decreases narrow-ranged “losers” in plant communities (Newbold et al. 2018). Whether plant species are range expanders or contractors depends on their functional traits (McCune & Vellend 2013), yet little is known about the relationships with plant mycorrhizal traits. However, it can be expected that natural plant communities are more mycorrhizal compared to the ones experiencing anthropogenic pressure, as the range contracting plant species are often specialists with slower growth rates, reproduction and dispersal (McKinney & Lockwood 1999; Broennimann et al. 2006; Zhu et al. 2012), which are generally associated with OM woody plant species (Peat & Fitter 1993; Hempel et al. 2013; Elumeeva et al. 2018). On the contrary, range expanders characteristic of disturbed habitats tend to be generalist species (McKinney & Lockwood 1999), which are often FM (Hempel et al. 2013). In addition, range expansion also positively relates to annuality, high growth rates, fast reproduction and efficient dispersal (McKinney & Lockwood 1999; Broennimann et al. 2006) often characteristic of NM plants (Peat & Fitter 1993; Hempel et al. 2013; Elumeeva et al. 2018). However, the community-level relationships between the naturalness and mycorrhizal symbiosis in the context of plant species range modifications are still unexplored.

1.5. Objectives of the thesis

The main objective of the thesis was to increase our understanding of the distribution (**I, II, IV**) and role (**I, III**) of mycorrhizal symbiosis in plant communities. Although mycorrhizal symbiosis has been increasingly recognized as a key player in plant community dynamics and ecosystem processes, its distribution patterns are still not fully resolved. At the time of conducting the original research presented in this thesis, the information about both community-level as well as large-scale distribution of mycorrhizal symbiosis was limited. In this thesis, we aimed to

perform the first quantitative analysis to determine the variation in the prevalence of mycorrhizal symbiosis in natural vegetation types at the regional scale **(I)**. We also undertook a study to reveal the distribution patterns of mycorrhizal symbiosis at the continental scale across Europe **(II)**. In addition, we aimed to identify the drivers behind these distribution patterns at both scales **(I, II)**. As mycorrhizal symbiosis is an important factor influencing interplant relationships, we aimed to determine the associations between the prevalence of mycorrhizal symbiosis and plant diversity **(I)**. Furthermore, we also targeted the possibility that mycorrhizal symbiosis could participate in plant niche partitioning **(III)**, which is considered as a mechanism contributing to plant diversity. Mycorrhizal symbiosis is also affected by increasing anthropogenic pressure on natural plant communities, which has been identified as the main threat to biodiversity and ecosystem functioning. Therefore, we aimed to reveal the effects of human impact on the distribution of mycorrhizal symbiosis **(IV)**.

Specifically, we asked the following questions:

1. Does the prevalence of mycorrhizal symbiosis vary between temperate forests and grasslands at the regional scale in Estonia? **(I)**
2. How are plants with different mycorrhizal types and statuses distributed across continental Europe? **(II)**
3. Which edaphic and climatic variables drive the distribution patterns of mycorrhizal symbiosis at regional and continental scales? **(I, II)**
4. Is plant diversity related to the prevalence of mycorrhizal symbiosis in temperate forests and grasslands? **(I)**
5. Do plant species with distinct mycorrhizal traits differ in their realized niches? **(III)**
6. How does anthropogenic pressure, specifically urbanization, introduction of alien plant species and modifications in plant species distribution areas influence the prevalence of mycorrhizal symbiosis in plant communities? **(IV)**

Based on the knowledge summarized in the introduction of this thesis, we hypothesized that the prevalence of mycorrhizal symbiosis differs between temperate forests and grasslands in Estonia. Notably, we expected forest communities to show higher overall mycorrhization and lower arbuscular mycorrhization than grasslands, whereas grasslands were anticipated to show the opposite trend **(I)**. We also expected that plants with different mycorrhizal types and statuses show clear latitudinal patterns. Specifically, AM plants were expected to have the highest share in lower latitudes, EcM plants in intermediate latitudes and ErM plants in higher latitudes. In addition, we expected the increasing importance of NM and FM plant species in northern areas **(II)**. Regarding the drivers of mycorrhizal distribution, we predicted soil factors to be paramount, yet climatic conditions were still expected to be crucial at the continental scale **(I, II)**. Plant

community mycorrhization was anticipated to be related to plant richness: specifically, we expected mycorrhization in forests to associate with lower plant diversity, while in grasslands the opposite trend was assumed (I). We also hypothesized that mycorrhizal symbiosis plays a part in plant realized niche differentiation and expansion. Notably, while the realized optimal growing conditions of plants with different mycorrhizal statuses and types were expected to depend on specific environmental axes, the range of tolerable conditions was proposed to be highest for FM and AM plants (III). Finally, we expected human activities to influence the prevalence of mycorrhizal symbiosis in plant communities, however, due to contradictory information about specific anthropogenic impact types and mycorrhizal symbiosis, alternative effects of urbanization and introduction of alien plant species were regarded possible. More natural plant communities in terms of plant range modifications were hypothesized to be more mycorrhizal than the ones more under human influence (IV).

2. MATERIALS AND METHODS

2.1. Vegetation data

To address the variation in the prevalence of mycorrhizal symbiosis in plant communities and describe its edaphic drivers and relationships with plant diversity in **Paper I**, six forest and five grassland community types in Estonia, Northern Europe were sampled. The community types were chosen to maximally represent the variation in soil properties (soil fertility, pH and moisture): dry boreal forest, alvar forest, eutrophic boreonemoral forest, mesotrophic boreal forest, mesotrophic paludifying forest, oligotrophic paludifying forest, alvar grassland, mesic boreonemoral grassland, moist boreonemoral grassland, floodplain grassland and coastal grassland (Figs. 1 & 2; Appendix S1 in **I**). Each plant community type was represented with two sites, either sampled in summers 2012 and 2013 or for which data was retrieved from previously published research (Zobel 1989; Moora et al. 2007; Aavik et al. 2008; Koorem & Moora 2010; Neuenkamp et al. 2013). All sites from all community types were represented by ten randomly located 1 m² vegetation relevés, where all field layer vascular plant species were identified, and their percentage cover was estimated. The woody canopy cover was estimated for a larger area surrounding the field layer plots.

In **Paper II**, the distribution of plants with different mycorrhizal trait values and its drivers were assessed at the continental scale. For this, we used the most extensive plant species atlas for Europe (Kalwij et al. 2014), which incorporates data from the Atlas Flora Europaea (Jalas & Suominen 1988) and the Atlas of North European Vascular Plants (Hultén & Fries 1986) and describes plant species occurrences in 50 km × 50 km grid cells. Due to low representation, the Mediterranean areas as well as some former Soviet countries in the eastern part of Europe were excluded from the analyses (Appendix S2 in **II**).

Papers III and **IV** addressing mycorrhiza mediated niche differentiation in plant species and the effect of human influence on the prevalence of mycorrhizal symbiosis, respectively, retrieved the vegetation data from the National Dutch Vegetation Database (GIVD-ID:EU-NL-001; Schaminée et al. 2012), which covers all habitat types across the Netherlands. For both papers, stratified sampling from the database was used to ensure an adequate representation of rare habitat types. For **Paper III**, geographically representative selection of plots for each habitat type was chosen to capture maximal variability along soil fertility, moisture, pH, salinity, light availability and temperature axes (Ellenberg et al. 1992; Ozinga et al. 2005), resulting in 36 342 plots in total. In **Paper IV**, 32 268 plots were selected from five broad habitat types: woodlands (6366 plots), heathlands (1092 plots), grasslands (13 470 plots), wetlands (6137 plots) and coastal meadows (5203 plots) (Appendix 1 in **IV**).

In order to facilitate merging vegetation data with plant trait data (**II**, **III**, **IV**), plant species names were standardized using The Plant List database (<http://www.theplantlist.org>).

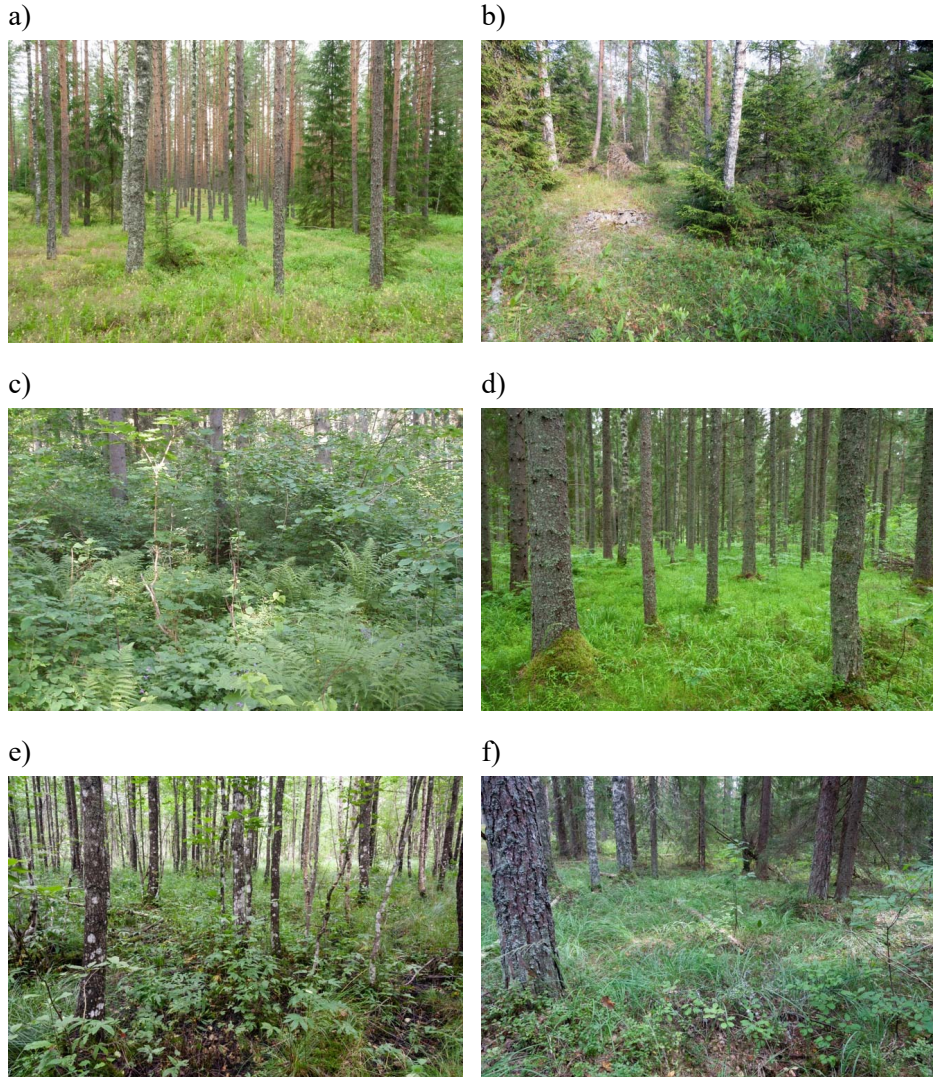


Figure 1. Photos illustrating the six forest types used in the **Paper I**, which assessed the mycorrhization of Estonian forests and grasslands: a) dry boreal forest in Mälara, Pärnumaa; b) alvar forest in Jalase, Raplamaa; c) eutrophic boreonemoral forest in Koeru, Järvamaa (Photo: M. Moora); d) mesotrophic boreal forest in Tõrvaaugu, Järvamaa; e) mesotrophic paludifying forest in Soomaa, Viljandimaa; f) oligotrophic paludifying forest in Mälara, Pärnumaa.

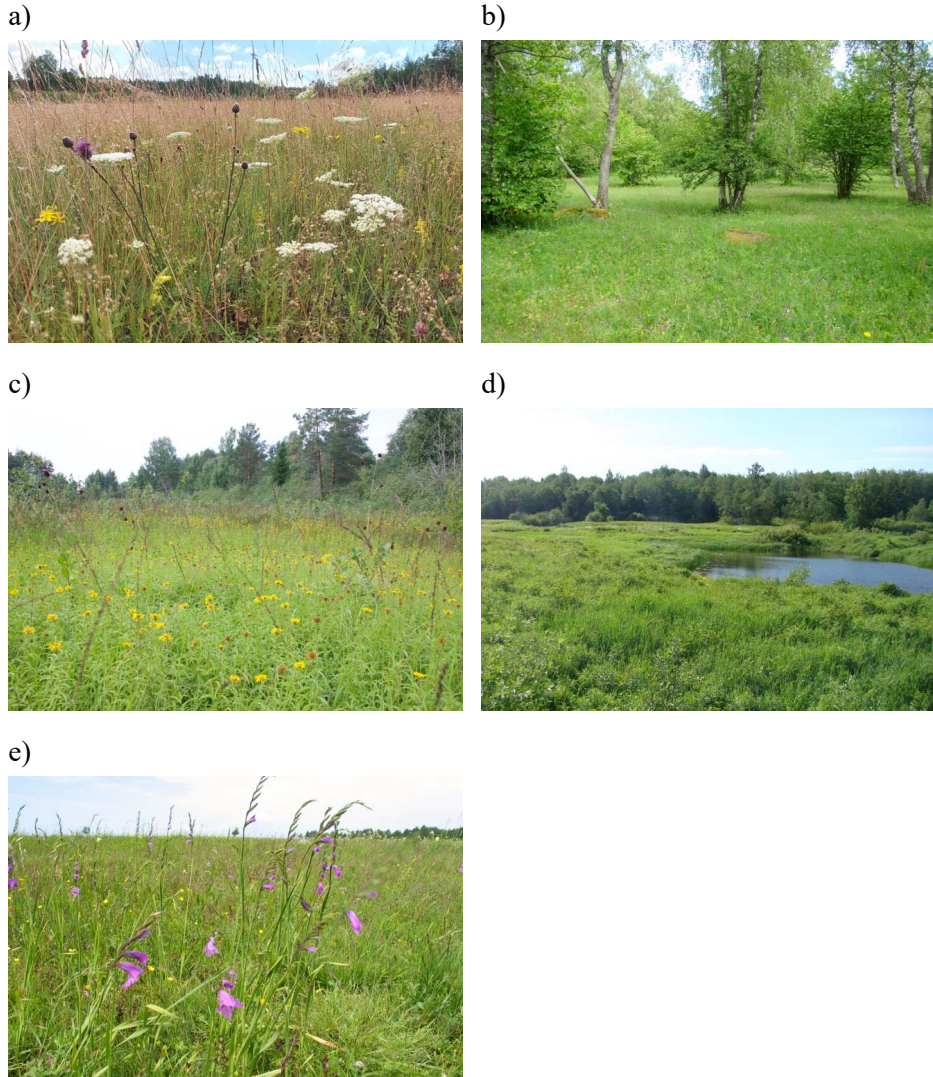


Figure 2. Photos illustrating the five grassland types used in the **Paper I**, which assessed the mycorrhization of Estonian forests and grasslands: a) alvar grassland in Sillukse, Läänemaa (Photo: K. Koorem); b) mesic boreonemoral grassland in Laelatu, Läänemaa (Photo: M. Zobel); c) moist boreonemoral grassland in Märjamaa, Raplamaa; d) floodplain grassland in Alam-Pedja, Tartumaa (Photo: M. Zobel); e) coastal grassland in Häädemeeste, Pärnumaa (Photo: K. Püssa).

2.2. Plant mycorrhizal trait data and community mycorrhization

The importance of describing underground plant functional traits and determining their effects on ecosystem processes as well as responses to environmental change are increasingly recognized (Bardgett et al. 2014; Freschet et al. 2021). In all four research papers (**I, II, III, IV**) incorporated in this thesis, plant mycorrhizal traits – mycorrhizal status, type and flexibility (Moora 2014) – were used to address various aspects of mycorrhizal symbiosis on plant distribution and diversity. Plant mycorrhizal types are distinguished based on the morphology of the symbiosis and identity of interacting plant and fungal species (Smith & Read 2008). The most common mycorrhizal types are arbuscular (AM), ecto- (EcM), ericoid (ErM) and orchid (OrM) mycorrhiza. Plant mycorrhizal status characterizes the frequency of occurrence of mycorrhizal symbiosis in plants, and based on this, plant species can be viewed as obligately mycorrhizal (OM), facultatively mycorrhizal (FM) or non-mycorrhizal (NM) (Trappe 1987; Smith & Read 2008, p. 31; Moora 2014). However, NM status of a plant species could also be viewed together with mycorrhizal types. Mycorrhizal flexibility of a plant species addresses the plant's ability to grow with or without mycorrhizal fungi. It is related to the plant species' ability to change its mycorrhizal colonization in roots (Grman 2012), depending on the environmental conditions. Inflexible plant species, such as OM and NM plants, cannot change their mycorrhizal status and are either always mycorrhizal or non-mycorrhizal, while flexible plant species, such as FM plants, could potentially regulate their mycorrhizal status.

The plant mycorrhizal trait data used in all papers (**I, II, III, IV**) was obtained from four core publications: Hempel et al. (2013), Harley & Harely (1987), Wang & Qiu (2006) and Akhmetzhanova et al. (2012). In **Paper I**, three plant species (*Festuca sabulosa* (Andersson) H.Lindb, *Geranium palustre* L., *Sagina nodosa* (L.) Fenzl) with previously unknown mycorrhizal status were empirically studied to determine the occurrence of mycorrhizal symbiosis. Six random individuals of each plant species from one location were sampled: roots were stained according to Koske & Gemma (1989), and root AM fungal colonization was determined using the magnified gridline intersect method (McGonigle et al. 1990) with 200 intersects per sample. In **Papers II** and **III**, an additional literature research was carried out to determine the mycorrhizal type and status of the most abundant plant species, which lacked relevant information. In **Paper IV**, in addition to the core references, additional information obtained for **Papers I, II** and **III** was also used. Using this data, all plant species in **Papers I, II, III** and **IV** were assigned a mycorrhizal status (OM, FM, NM) and type (AM, AM+EcM, EcM, ErM, OrM), while flexibility (flexible, inflexible) was also used in **Paper III**. In **Paper II**, NM status was analysed together with mycorrhizal types. Monotropoid and arbutoid mycorrhizal types were pooled together with EcM due to structural and functional similarities. Dual mycorrhizal (AM+EcM) plant species were assigned to either AM or EcM category in **Paper I** and **IV**, depending on the majority of

references supporting either of the types. In **Paper II**, dual mycorrhizal plants were assigned to both AM and EcM categories in single-type analyses, while OrM plants were discarded from the analyses due to very low representation. Plants with missing mycorrhizal trait data were discarded from the analyses. In **Paper II**, we also assessed the potential influence of undetected errors in the mycorrhizal trait data by introducing random errors to the dataset by replacing the mycorrhizal trait value for 20% of plant species with a randomly chosen alternative. Further analyses with this data resulted in similar results as the analyses done with the original data (Appendix S2 in **II**).

To quantify the total prevalence of mycorrhizal symbiosis and the prevalence of AM symbiosis in plant communities in **Papers I** and **IV**, we used the community mycorrhization index (MI) and arbuscular mycorrhization index (AMI) (Moora 2014). These indices are based on plant species' mycorrhizal statuses and their relative contribution to the community biomass. To calculate the mycorrhization indices, we first categorized plant species according to their mycorrhizal status, and in the case of the overall mycorrhization index, the plant species were regarded either as obligately (OM), facultatively (FM) or non-mycorrhizal (NM). In the case of arbuscular mycorrhization index, plants were first categorized by mycorrhizal type and then by status and regarded either as obligately AM, facultatively AM or never AM. The latter group in AM status included both NM plants as well as plants with other mycorrhizal types. These mycorrhizal statuses were then given a numeric coefficient from 0 to 1, with NM and non-AM statuses receiving a value of 0, and OM and obligately AM statuses a value of 1. The FM and facultatively AM statuses obtained a value in between, representing the proportion of empirical data sources describing mycorrhizal condition (as opposed to NM or non-AM condition) out of all observations. Mycorrhization indices MI and AMI were then calculated as mycorrhizal statuses of plant species weighted by their relative abundances summed together and expressed as logit functions:

$$(A)MI = \ln \frac{\sum(p_i \times M_i)}{1 - \sum(p_i \times M_i)}$$

where p_i denotes the relative cover of species i in a plot, and M_i represents the numerical coefficient of the mycorrhizal status of the plant species i .

To assess the distribution and drivers of plants with distinct mycorrhizal traits in Europe (**II**), the proportion of the number of plant species with each mycorrhizal type (AM, EcM, ErM, OrM, NM) and status (OM, FM) out of all plant species was calculated for each grid cell.

2.3. Edaphic and climatic drivers

In **Paper I**, the edaphic drivers of the prevalence of mycorrhizal symbiosis in plant communities were described using Ellenberg indicator values (Ellenberg et al. 1992). These are expert-knowledge classifications of species habitat preferences on a relative scale along several environmental axes and have shown to be good proxies for direct environmental measurements (Hill & Carey 1997; Schaffers & Sýkora 2000; Diekmann 2003; Ozinga et al. 2013). We calculated cover-weighted community mean Ellenberg values for soil fertility, pH and moisture for each plot, while plant species missing Ellenberg values were discarded from the analyses.

In **Paper II**, several climatic drivers from the Numerical Terradynamic Simulation Group and BioClim databases were considered, which describe annual trends, seasonality and extreme conditions of evapotranspiration, temperature and precipitation (Appendix S4 in **II**). After checking for collinearity and multicollinearity, four BioClim variables ($r < 0.6$, $VIF < 3$; Zuur et al. 2010) were chosen for the analyses: mean annual temperature (MAT), mean diurnal temperature range (MDR), annual precipitation (APP) and precipitation seasonality (PPS). MAT and APP provide information about annual trends, whereas MDR and PPS indicate variation in the specific drivers and thus, to a certain level, the continentality of the climate. From the World Soil Information website (Appendix S4 in **II**), data for soil pH and soil organic carbon (SOC) were obtained. However, due to high negative correlation ($r = -0.8$) only soil pH was retained in the analyses. Net primary productivity (NPP) data was obtained from the Numerical Terradynamic Simulation Group website (Appendix S4 in **II**), and after controlling for climatic variables, NPP can indicate soil fertility. Climatic, edaphic and productivity variables can be tightly related at larger scales (Brady & Weil 2010) and indeed, high correlation was evident between latitude and MAT ($r = -0.9$), pH ($r = -0.7$) and NPP ($r = -0.7$). Also, MAT and NPP ($r = 0.8$), together with MAT and pH ($r = 0.7$), were highly correlated (Appendix S4 in **II**). Therefore, to avoid multicollinearity issues in the analyses, MAT was replaced by the residuals of MAT (MATr) after controlling for the effects of pH and NPP. All variables were scaled up to 50 km \times 50 km resolution prior to conducting any analyses.

2.4. Estimates of plant diversity

In order to determine the relationships between plant community mycorrhization and plant community structure (**I**), we utilised different metrics of plant diversity. Specifically, plant species richness per plot, exponential Shannon diversity ($\exp H'$) and inverse Simpson dominance index (λ^{-1}). The two latter indices give more weight to the abundant species, while all of them still operate on species as units, allowing their easier comparison (Hill 1973). In addition, we also evaluated the equity of plant species' abundances by calculating plant community evenness (Alatalo 1981):

$$Evenness = \frac{\lambda^{-1} - 1}{\exp H' - 1}$$

where $\lambda = \sum p_i^2$ and $H' = -\sum p_i \ln p_i$ are calculated using the relative cover p of plant species i in each plot.

2.5. Niche characteristics

To target mycorrhiza-mediated niche partitioning in **Paper III**, we utilized plant species' realized niches, representing the range of environmental conditions which a species occupies in the presence of competition (Hutchinson 1957) and positive interactions (Bruno et al. 2003; Stachowicz 2012; Bulleri et al. 2016; Peay 2016). Realized niches were characterized using realized niche optima, which represent the optimal conditions of species in the presence of interspecific interactions along a given environmental axis; realized niche widths, which represent the tolerance ranges of species in the presence of interspecific interactions along a given environmental axis; and niche volume, which represents the range of conditions which a species occupies in the presence of interspecific interactions along a multitude of environmental axes (Hutchinson 1957). The realized niche characteristics were calculated using Ellenberg indicator values (Ellenberg et al. 1992) for soil fertility, pH, moisture, salinity, light and temperature, ranging from 1–9, except for salinity, which ranges from 0–9 and moisture, which ranges from 1–12. The ecological position of a vegetation plot along a specific niche axis was calculated as the mean of the indicator values of all plant species present in a given plot. Subsequently, the realized niche optimum and realized niche width of a plant species along a specific niche axis was calculated as the mean and standard deviation of the ecological positions of the vegetation plots, which were occupied by that plant species, respectively (Ozinga et al. 2013). The realized niche widths were not strongly correlated along the environmental axes ($r < 0.6$), necessitating the calculation of the realized niche volume to fully characterize the plants' realized niches. The niche volumes of plant species were calculated as a product of realized niche widths along all six environmental axes.

2.6. Estimates of anthropogenic influence

The effect of anthropogenic impact on the prevalence of mycorrhizal symbiosis in plant communities in **Paper IV** was investigated from three different aspects: increase in urbanization, introduction of alien plant species and reduction of plant community naturalness by modifications of plant species range sizes. For estimating urbanization in plant communities, we used urbanity indicator values, which characterize the affinity of plant species to cities and urban environments

(Kühn et al. 2004). According to this, plant species were classified as urbanophobic, moderately urbanophobic, urbanoneutral, moderately urbanophilic and urbanophilic. Each urbanity category of plant species was assigned a numeric coefficient ranging from 0–4. The urbanity of vegetation plots was then calculated as community weighted mean of these coefficients, using the relative cover of plant species as weights.

The extent to which plant communities are affected by species introductions, i.e., the alienness of vegetation plots, was characterized using species floristic statuses (native or alien), which were obtained from Tamis et al. (2004). Specifically, alienness was calculated as a natural log-ratio of alien plant richness in each vegetation plot (j) weighted by their relative cover:

$$\text{Alienness} = \ln \frac{(\text{richness of alien plant spp.}_j \times \text{relative cover of alien plant spp.}_j)}{(\text{richness of native plant spp.}_j \times \text{relative cover of native plant spp.}_j)}$$

Plant species can either expand (“winners”) or contract (“losers”) their range sizes as a result of human influence (McKinney & Lockwood 1999). To detect whether plant species have experienced expansion or contraction of their ranges, we estimated their distribution trends in the Netherlands by calculating the percentage of change in the occupied 1 km × 1 km grid cells from 1935 to 1999 (based on data from van der Meijden et al. 2000)). We considered a minimum of 10% change in range dynamics as a relevant change, in order to allow natural fluctuations, i.e., plant species showing decreased distribution range by at least 10% were regarded as decreasing, and plant species with increased distribution range by at least 10% were regarded as increasing, while the rest of the species were regarded stable. It can be assumed that “winning” plant species, which benefit from human activities and expand their range sizes, are more characteristic to habitats under stronger anthropogenic pressure. On the contrary, the “losing” species are more common in natural environments as they are negatively affected by human influence and experience range contraction. Therefore, naturalness, which serves as an indication of the degree of human-induced biotic homogenization, can be calculated for each vegetation plot (j) as:

$$\text{Naturalness} = \ln \left(\frac{\text{richness of plant spp. with decreasing ranges}_j \times \text{relative cover of plant spp. with decreasing ranges}_j}{\text{richness of plant spp. with increasing ranges}_j \times \text{relative cover of plant spp. with increasing ranges}_j} \right)$$

Thus, higher values of naturalness indicate weaker anthropogenic pressure, while lower naturalness values indicate stronger human impact.

2.7. Statistical analyses

To analyse the variation in plant community mycorrhization among plant community types and ecosystem types at the regional scale in Estonia (**I**), we used linear mixed-effects models (LMM) and post-hoc comparisons with Bonferroni corrections. MI and AMI were used in the models as response variables, community types (11 types) or ecosystem types (grasslands or forests) as predictors and site included as random factor. For determining the role of edaphic factors on the prevalence of mycorrhizal symbiosis in ecosystem types (**I**), LMMs were used. In grasslands, MI and AMI were included as response factors, cumulative Ellenberg soil fertility, pH and moisture as predictors and site as a random factor. In forests, however, cumulative Ellenberg soil fertility and pH were highly correlated ($r = 0.8$), thus two parallel models were calculated: 1) AMI and MI as response variables, cumulative Ellenberg soil fertility and moisture as predictors and site as a random factor, and 2) AMI and MI as response variables, cumulative Ellenberg soil pH and moisture as predictors and site as a random factor. In order to determine the climatic and edaphic factors of mycorrhizal distribution at the continental scale in Europe (**II**), we used generalized linear models (GLM) with binomial error distributions and logit link functions. Binary response variables for each mycorrhizal type (AM, EcM, ErM, NM) were formed based on the number of plant species with the specific mycorrhizal type and the number of plant species without the given mycorrhizal type. For plant mycorrhizal status (OM and FM), just one level was used to analyse the trait variation in relation to the potential drivers. Predictor variables used in the models were pH, NPP, MATr, APP, MDR and PPS, which were all standardized and model averaging approach was used to account for model uncertainty ($\Delta AIC < 7$) (Burnham & Anderson 2002). Moran's correlogram and spatial residual plots were used to detect spatial autocorrelation in the residuals of the models, and it was then accounted for by adding all models the spatial predictors from spatial eigenvector mapping (SEVM) approach (Dray et al. 2006).

We addressed the relationships between mycorrhizal symbiosis and plant diversity in forests and grasslands (**I**) using partial correlation, taking the effect of potentially confounding soil factors into account. LMMs were used to determine the effect of edaphic factors on plant community mycorrhization and plant diversity with site as a random factor. In case of plant richness, GLMMs with Poisson distribution were used. Partial correlation between the residuals of plant community mycorrhization and plant diversity models were then calculated. Additionally, we also estimated the individual and joint effects of mycorrhization and edaphic factors on plant diversity by carrying out variation partitioning using marginal R^2 (R_m^2) (Nakagawa & Schielzeth 2013). $\text{Exp}(H')$ and λ^{-1} were ln-transformed prior the analyses to meet model assumptions. To determine the associations between plant mycorrhizal traits and realized niche characteristics (**III**), we conducted univariate analyses with realized niche optima, widths and volumes along six environmental axes (soil pfertility, pH, moisture, salinity, light, temperature) as response variables and mycorrhizal status, flexibility and type as

explanatory variables, using phylogenetic least squares models (PGLS, Grafen 1989). Plant phylogeny (Durka & Michalski 2012) was incorporated into the models, together with the maximum-likelihood estimation of the phylogenetic signal Pagel's λ (Pagel 1999). To meet model assumptions, all niche volumes and salinity niche optima and widths, and pH niche width were ln-transformed prior to all and mycorrhizal type analyses, respectively.

In **Paper IV**, addressing the human influence on the distribution of mycorrhizal symbiosis, we first tested whether habitat types (woodlands, heathlands, grasslands, wetlands and coastal meadows) differ in their community mycorrhization by using linear models (LM) with Tukey post-hoc comparisons. MI and AMI were included in the models as response variables and habitat type as a predictor variable. The effects of anthropogenic variables on community mycorrhization were analysed in each habitat type separately. The associations between mycorrhization and urbanity was analysed using generalized additive models (GAM), while the relationships between mycorrhization, alienness and naturalness were determined using LMs. MI and AMI were used as response variables, and urbanity, alienness and naturalness were included in the models as predictors. The proportion of explained variance ($R^2_{adj.}$) was used to interpret the effects of habitat types and human impact variables on mycorrhization as due to the size of the dataset, the interpretation of p -values might not be biologically relevant.

The analyses were carried out using (R Core Team 2015) (<https://www.R-project.org>), while more detailed information on specific versions and used packages can be obtained from the original papers (**I, II, III, IV**). The assumptions for all models were checked visually.

3. RESULTS

3.1. Distribution of mycorrhizal symbiosis and its drivers

The prevalence of mycorrhizal symbiosis measured as plant community mycorrhization (MI) differed between plant community types ($F_{10,198} = 7.38$, $p = 0.001$; **I**). The MI was highest in oligotrophic paludifying forests and dry boreal forests, while wetlands exhibited the lowest MI (Fig. 1c in **I**). When community types were pooled into broad ecosystem types, forests showed significantly higher MI than grasslands ($F_{1,198} = 13.62$, $p = 0.001$; Fig. 1a in **I**). Arbuscular mycorrhization (AMI), too, differed between plant community types ($F_{10,198} = 6.29$, $p = 0.003$; **I**), but showed the opposite pattern: dry boreal forests exhibited the lowest AMI, whereas alvar grasslands, followed closely by other grassland types, showed the highest MI (Fig. 1d in **I**). Analysis with broad ecosystem types also showed that grasslands exhibit higher AMI than forests ($F_{1,198} = 25.58$, $p < 0.0001$; Fig. 1b in **I**). This result is supported by the fact that forests were dominated by EcM and ErM plant species, making up 69% of the community, while grasslands were dominated by AM as 79% of the community formed AM when accounting for plant species abundances (Appendix S6 in **I**). In forests, soil fertility and pH negatively influenced MI, whereas AMI was positively affected by soil reaction (Table 1 in **I**). In grasslands, soil fertility and moisture were negatively related to both MI and AMI (Table 1 in **I**).

At the regional scale, AM plant species dominated across continental Europe with an average (\pm SD) proportion of AM plant species being $75 \pm 4\%$ and ranging from 58–83% of the total plant species numbers in $50 \text{ km} \times 50 \text{ km}$ grid cells (Fig. 1a in **II**). The proportion of NM plant species was $21 \pm 2\%$ in grid cells (Fig. 1d in **II**), while EcM and ErM contributed significantly less (Fig. 1b, c in **II**). The proportion of plant species with different mycorrhizal types changed along the latitudinal gradient (Fig. 2a in **II**), but not along the elevational gradient (Fig. 2b in **II**). The share of AM plant species was highest at low latitudes, except for mountain ranges, and declined towards higher latitudes (Fig. 2a in **II**). NM plant species showed an increase along latitude but were not affected by altitude (Fig. 2d in **II**). The distribution of EcM and ErM plant species showed an increasing proportion in higher latitudes, while EcM plants were also more frequent at high elevations in low latitude mountain ranges (Fig. 2b, c in **II**). The share of AM plant species in grid cells was positively influenced by soil pH, NPP, MATr and APP, while slight negative effect of mean diurnal range (MDR) was evident (Fig. 3a in Corrigendum to **II**). EcM plant species were negatively affected by soil pH, NPP and MATr, while being positively affected by MDR, APP and PPS (Fig. 3a in Corrigendum to **II**). The proportion of ErM plants decreased with increasing soil pH, NPP, MATr and MDR, and increased with PPS (Fig. 3a in Corrigendum to **II**). NM plant species showed negative relationships with soil pH, NPP, MATr and APP (Fig. 3a in Corrigendum to **II**).

Mapping the distribution of mycorrhizal statuses in continental Europe revealed that the share of OM plant species decreased with latitude and increased with altitude, while FM plant species showed the opposite trend (Fig. 1e in Corrigendum to **II**, Fig. 1f & 2c, d in **II**). The proportion of FM plant species in grid cells was mostly higher than that of OM plant species at all latitudes but equalized at high elevations (Fig. 2c, d in **II**). The share of OM plant species was negatively affected by MATr and positively related to MDR, contrary to FM plant species (Fig. 3c in Corrigendum to **II**).

3.2. Mycorrhizal symbiosis as a mediator of plant diversity

Partial correlations between MI and plant richness revealed a negative association in forests and no relationship in grasslands (Fig. 2b, e in **I**). On the contrary, AMI exhibited a positive relationship with plant richness in forests and no relationship was evident in grasslands (Fig. 2c, f in **I**). Positive relationships between AMI, Shannon's diversity index and inverse Simpson's dominance index were found in forests but not in grasslands, while MI was not related to these diversity indices (Appendices 7, 8b–f in **I**). Neither MI nor AMI was related to plant community evenness (Appendix 9 in **I**). However, variance partitioning indicated that edaphic conditions were responsible for the bulk of explained variance, while MI and AMI explain less variance (Appendix 5 in **I**).

The results from **Paper III** indicate that plants with distinct mycorrhizal statuses and types exhibit differences in their realized niche optima (Table 1 in **III**). NM plant species had the highest, FM plants intermediate, and OM plants the lowest moisture optimum (Fig. 1b in **III**), whereas the highest temperature optimum was found for OM plants, intermediate optimum for NM and lowest optimum for FM plant species (Fig. 1f in **III**). Regarding mycorrhizal types, ErM plant species exhibited the lowest niche optima along soil fertility, soil pH and temperature axes, but together with AM and OrM plants, they showed a higher light optimum (Fig. 1a, c, f in **III**). Dual mycorrhizal plant species showed a tendency to have intermediate niche optima compared to that of AM and EcM plant species or more similar to EcM plants (Fig. 1 in **III**). Plant species with different mycorrhizal statuses, flexibility and types showed differences in realized niche widths and volumes, indicating niche expansion of mycorrhizal plants (Table 1 in **III**). FM and flexibly mycorrhizal plant species had consistently wider niches and a larger niche volume along soil moisture, soil pH, salinity and light axes (Fig. 2b, c, d, e, g in **III**). Also, flexibly mycorrhizal plant species showed wider niches along the soil fertility axis (Fig. 2a in **III**). Among OM plant species, EcM and ErM plants tended to exhibit the widest niches and largest niche volumes compared to plants with other mycorrhizal types (Fig. 2 in **III**). The niche widths and volume of dual mycorrhizal plants were intermediate to those of AM and EcM plants (Fig. 2 in **III**).

3.3. The effect of anthropogenic influence on mycorrhizal symbiosis in plant communities

The five habitat types included in the analyses – woodlands, heathlands, grasslands, wetlands and coastal meadows – differed in their community mycorrhization (MI; $F_{4, 31\ 837} = 2880.50$, $p < 0.0001$, $R^2_{(adj.)} = 0.266$; Appendix 1 Fig. A3a in **IV**) and arbuscular mycorrhization (AMI; $F_{4, 32\ 078} = 4237.60$, $p < 0.0001$, $R^2_{(adj.)} = 0.346$; Appendix 1 Fig. A3b in **IV**). MI was higher in woodlands and heathlands, where the relative abundance of OM plants was highest. In comparison, other habitat types showed lower MI with lower relative abundance of OM and higher relative abundance of FM plants (Appendix 1 Fig. A1 in **IV**). AMI was highest in grasslands and coastal meadows, which were dominated by mostly facultatively AM plant species, and lower in woodlands, heathlands and wetlands (Appendix 1 Fig. A1, A2, A3b in **IV**).

The variance in MI and AMI was markedly explained by community mean urbanity in woodlands, heathlands and grasslands, while the mycorrhization indices in wetlands and coastal meadows were less influenced by urbanity (Table 1 in **IV**). In woodlands and heathlands, urbanity negatively affected MI and positively affected AMI (Fig. 1a, b, d, e in **IV**). In grasslands, MI showed either a neutral or slightly positive relationship with MI and AMI (Fig. 1c, f in **IV**), and in wetlands increasing urbanity was related to increasing AMI (Appendix 1 Fig. A4c in **IV**). Urbanity was the most influential predictor of AMI in heathlands as it explained 73% of variance (Fig. 1e in **IV**).

The introduction of alien plant species affected MI positively and AMI negatively in woodlands and heathlands, while in grasslands and coastal meadows, only negative relationships were evident between community alienness and MI and AMI (Fig. 2, Appendix Fig. A5 in **IV**). Alienness was the strongest predictor of MI and AMI in coastal meadows, explaining up to 50.9% of the variance (Appendix 1 Fig. A5 in **IV**). In addition, alienness also explained 18.2% of variance in MI in woodlands, while in other habitat types, the explained variances in MI and AMI remained below 10% (Fig. 2 in **IV**).

Naturalness was positively related to MI and negatively related to AMI in heathlands, explaining 12.2% and 34.3% of variance, respectively. Wetlands and coastal meadows in a more natural state exhibited slightly higher MI, while human impact positively affected AMI in all habitat types but coastal meadows (Fig. 3, Appendix 1 Fig. A6 in **IV**). However, naturalness explained very little variance in MI and AMI in all other habitat types except for heathlands (Table 1 in **IV**).

4. DISCUSSION

4.1. Distribution of mycorrhizal symbiosis and its drivers

The quantitative analysis of the prevalence of mycorrhizal symbiosis using plant mycorrhizal statuses in **Paper I** revealed that the community mycorrhization at the regional scale in Estonia varied between temperate forests and grasslands and was affected by soil conditions. While the overall prevalence of mycorrhizal plants was high in forests, the abundance of arbuscular mycorrhizal symbiosis was low. The opposite pattern was observed in grasslands, which had a lower overall prevalence of mycorrhizal symbiosis compared to forests, whereas the importance of AM symbiosis was high. This result is also supported by findings in **Paper IV** where patterns in the overall importance of mycorrhizal symbiosis, as well as AM symbiosis in woodlands and grasslands in the Netherlands were similar to those detected in Estonia. The observed distribution of mycorrhizal symbiosis can be attributed to the dominant mycorrhizal types in forests and grasslands as well as the different reliance of plants on these mycorrhizal types. Temperate and boreal forests are usually characterized by lower soil pH, leading to nitrogen limitation and the accumulation of organic matter, which favours the dominance of EcM and ErM (Read & Perez-Moreno 2003; Read et al. 2004; Soudzilovskaia et al. 2015; Jo et al. 2019). Fungi forming these symbioses can access nutrients sequestered in organic forms (Lindahl & Tunlid 2015; Shah et al. 2016; Lindahl et al. 2021), while this nutrient pool is mostly directly unavailable to plants or AM fungi. In addition, EcM and ErM fungi can have inhibitory effects on AM fungal abundance (Kovacic et al. 1984; Genney et al. 2001), further contributing to the low prevalence of AM plants. The EcM and ErM types are mostly obligate for respective plant species, making temperate and boreal forests highly mycorrhizal, while the abundance of AM symbiosis remains low. Grasslands, on the other hand, are characterized by higher soil pH, leading to increased bacterial dominance (Yu et al. 2022) and thus, higher availability of mineral nutrients, which favours AM fungi (Treseder & Cross 2006; Soudzilovskaia et al. 2015) and the associated plants (Read 1991; Read & Perez-Moreno 2003). However, AM symbiosis is often a facultative association for plants (Hempel et al. 2013), reducing the overall reliance of grasslands on mycorrhizal symbiosis.

The distribution of plant mycorrhizal traits in co-occurring plant species assemblages assessed at the European scale in **Paper II** showed distinct patterns for both mycorrhizal statuses and types along the latitudinal gradient. FM plants predominated over OM plants, and the share of FM plant species increased along latitude, while that of OM plant species decreased. Also, the share of NM plant species increased towards northern areas. Our results indicate that at the European scale, the driving force of FM and OM plant distribution is the variation in temperature rather than edaphic factors, which are usually thought to be of utmost importance as the symbiotic relationship occurs in soil and is mainly of nutritional benefit (Smith & Read 2008). Similarly, global analysis by Delavaux et al. (2019)

has revealed that the proportion of mycorrhizal plant species is highest at the equator and decreases towards poles. This suggests that the importance of mycorrhizal symbiosis is lower at high latitudes where the harsh climate, which inhibits fungal growth (Kytöviita 2005; Gavito et al. 2005), seems to favour more flexible strategies or the abandonment of mycorrhizal symbiosis altogether (Kytöviita 2005). Historical adverse environmental conditions in northern areas brought about by glaciation could also be reflected by the currently observed pattern of the highest share of OM plant species in southern European mountain ranges as these areas might have served as refugia with more favourable conditions (Schönswetter et al. 2005) for OM plants.

Presented in **Paper II**, the AM symbiosis was predominant across all Europe but decreased toward northern latitudes. The second most frequent species group was NM plants, which showed an increase along latitude. The shares of EcM and ErM plants in species assemblages slightly increased with latitude, yet they remained low throughout Europe. Global analyses with plant species assemblages have also revealed similar trends that the proportion of AM plant species decreases, while that of EcM plant species increases towards poles (Delavaux et al. 2021). The latitudinal patterns in mycorrhizal type distribution are coherent with edaphic and climatic factors influencing these changes in the share of mycorrhizal types among plant species. While at regional scales, the relevant abiotic environmental variation is mostly observed in edaphic conditions, such as soil fertility, pH and moisture in **Paper I**, at the continental scale, climatic factors, especially temperature, play a crucial role. As expected, the environmental drivers impacted the share of AM plants differently compared to that of EcM and ErM plants, highlighting their contrasting ecological roles (Phillips et al. 2013). AM plants were favoured by higher temperature, soil pH and soil fertility, while the share of EcM and ErM plants was higher with lower temperatures, soil pH and soil fertility. Global analyses of mycorrhizal types also highlight the significance of climate in determining the observed patterns. Steidinger et al. (2019) have found that temperature-controlled decomposition rate determines the dominant tree mycorrhizal type: AM trees dominate in warm aseasonal conditions, which favour decomposition, whereas EcM dominance occurs in seasonally cold and dry conditions, which inhibit decomposition. As EcM fungi can access nutrients from sequestered organic forms (Lindahl & Tunlid 2015), these fungi make their hosts superior competitors over AM plants in these conditions. However, a recent analysis by Barceló et al. (2019) suggests that climate infers a direct effect on the physiologies of plants and mycorrhizal fungi, while the effect of soil on global mycorrhizal distribution is negligible. Nevertheless, the high importance of climate in determining mycorrhizal type distribution could mean that in the face of increasing global air temperatures (IPCC 2022) the importance of EcM and ErM plant species may decrease, leading to the potential loss of carbon stocks stored in soil (De Deyn et al. 2008; Soudzilovskaia et al. 2019).

Although clear patterns exist, we did not observe the relative change in mycorrhizal type dominance along the latitudinal gradient as was expected based on Read's hypothesized distribution of mycorrhizal types in different ecosystems

(Read 1991). However, more recent work has allowed global analyses of plant mycorrhizal trait distribution together with incorporating dominant plant species' biomass (Steidinger et al. 2019; Soudzilovskaia et al. 2019). These studies indicate that if plant abundance is considered, the dominant mycorrhizal type indeed shifts along latitude as lower latitudes are dominated by AM plants, while higher latitudes become dominated by EcM plants (Soudzilovskaia et al. 2019). Similar shift in the dominance has also been observed globally for trees, where northern hemisphere high latitudes show higher total tree basal area for EcM than for AM trees, and the opposite pattern is seen in low latitude tropical forests (Steidinger et al. 2019). However, both approaches of analysing mycorrhizal type distribution – either incorporating plant biomass or not – reveal that the expected change to the dominance of ErM plant species (Read 1991; Read & Perez-Moreno 2003; Read et al. 2004) at high latitudes is not evident. Tundra ecosystems are usually thought to be dominated by ericoid plants, but the vegetation often renders to be more heterogenous. The results from **Paper II**, which uses species assemblage data, indicate that tundra ecosystems harbour a considerable share of AM and NM plant species. Indeed, even though AM symbiosis originates from the tropics (Bonfante & Genre 2008) and has affinity to more favourable conditions, AM plants can still tolerate cold conditions (Kytöviita 2005; Tibbett & Cairney 2007), access organically bound nutrients to some extent (Hodge & Fitter 2010) or prime the decomposition of organic matter (Bunn et al. 2019), making AM plant species more common in tundra ecosystems than expected. However, when biomass is also considered, EcM plants seem to dominate, similarly to temperate and boreal forests, yet a relatively substantial role is played by AM and NM plants (Soudzilovskaia et al. 2019).

4.2. Mycorrhizal symbiosis as a mediator of plant diversity

Mycorrhizal symbiosis has been shown to influence plant diversity in a variety of ecosystems (van der Heijden et al. 2008; Bennett et al. 2017; Carteron et al. 2022). The results from **Paper I** also confirm that mycorrhizal associations relate to plant diversity, especially richness, while also emphasizing the importance of mycorrhizal type as well as the specific plant community type. The prevalence of mycorrhizal symbiosis was negatively related to plant richness in forests (**I**). Temperate forests are mostly dominated by obligately EcM tree storey and often possess ErM understorey, potentially due to the specific properties of associating fungal partners or positive plant-soil feedbacks. For example, EcM and ErM fungi have been shown to exhibit proteolytic enzymes (Martino et al. 2018; Lindahl et al. 2021), which allow access to organic N, while AM plants, which mostly utilize mineral N sources (Hodge et al. 2010), are at a disadvantage. However, EcM and ErM plants have considerably smaller species pools compared to AM plants (Brundrett & Tedersoo 2018), making these forests inherently less diverse as community mycorrhization increases. Conversely, plant diversity was increasing as the prevalence of arbuscular mycorrhizal symbiosis in forests

increased (I). It has been shown that in EcM-dominated temperate forests, the growth of field layer AM plants is hindered due to scarcity of fungal symbionts, while the increase in AM trees in the canopy also mediates herbaceous AM plant establishment (Newman & Reddell 1988; Veresoglou et al. 2017; Guy et al. 2022). Consistent with these results, the decrease in AM fungal inoculum leads to reductions in field layer richness (Zobel et al. 1999). The positive effects of AM symbiosis in temperate forests could potentially be ascribed to enhanced seedling recruitment (van der Heijden 2004; Koorem et al. 2012), amplification of intraspecific and balancing interspecific competition (Moora & Zobel 2010) or negative plant-soil feedback (Bever et al. 2010). Interestingly, despite much of the evidence about the relationships between mycorrhizal symbiosis and plant diversity comes from grassland studies (Grime et al. 1987; van der Heijden et al. 1998; Klironomos et al. 2011; Dostálek et al. 2013), we found no such relationship in temperate grasslands in our analyses (I). It is possible that the prevalence of mycorrhizal symbiosis measured by the mycorrhization index, which was used in our study, is more applicable for coarse-scale effects of mycorrhizal associations evident in successional systems where multiple mycorrhizal types are present (Hart et al. 2003). Instead, grasslands harbour mainly AM plants, and more fine-scale effects could be prominent (Hart et al. 2003). Indeed, partner selectivity and mycorrhizal fungal community differences have been shown for distinct grassland plant species, ecological groups and mycorrhizal statuses (Davison et al. 2011; Sepp et al. 2019; Davison et al. 2020; Neuenkamp et al. 2021), which could influence plant diversity. Furthermore, AM fungal richness (van der Heijden et al. 1998; Hiiesalu et al. 2014) and multifunctionality (Delavaux et al. 2017) may play a significant role but were not captured using our approach.

However, although our results, together with previous findings, suggest that AM increases plant diversity, it has been shown that AM tree dominance in forests relates negatively to plant diversity. Indeed, plant diversity has been found to be highest in forests where AM and EcM trees coexisted at approximately equal shares (Carteron et al. 2022). This also indicates the potential role of niche partitioning in plant diversity. In our study, we found that plants with different mycorrhizal types and statuses showed niche differentiation and preferred different environmental conditions, as reflected by their distinct niche optima (III), highlighting the importance of plant mycorrhizal traits when addressing plant community assembly. Given the existence of environmental heterogeneity, the highest diversity of plant species is achieved by partitioning the niches between plants with distinct mycorrhizal types and statuses. This is also supported by the study by Veresoglou and others (2018), who demonstrate that plant communities are more diverse when plants with different responsiveness to mycorrhizal symbiosis coexist as the ecological niches are better partitioned.

Plant species with distinct mycorrhizal types and statuses also diverged in terms of niche widths. Among all plants, FM plant species exhibited the widest niches, while OM and NM plants showed narrower niches (III). The flexibility of FM plants to live both with and without their fungal symbionts could be underlying the observed niche expansion (Bruno et al. 2003; Stachowicz 2012; Peay

2016). It allows them to benefit from fungal colonization and successfully compete in conditions where mycorrhizal symbionts are abundant. At the same time, they can also grow in conditions, which are not conducive for mycorrhizal fungi (Titus & Moral 1998; Cázares et al. 2005), eliminating the competition from OM plants. This renders them habitat generalists, compared to more specialized OM and NM plant species, and could give them an advantage in temporally or spatially heterogeneous habitats. Such plants could be favoured by the changing climate, or they can be effective invaders of new localities (Goodwin 1992). Wide niches are often associated with wide geographical distribution (Slatyer et al. 2013), also supported by Hempel et al. (2013) who found that FM plants indeed show the widest geographical and habitat range in Europe. Furthermore, FM plants have been shown to be globally more effective at naturalizing, especially perennial plant species (Pyšek et al. 2019). Interestingly, among OM plant species, ErM and EcM plants exhibited the largest niche expansion, contrary to AM plant species, which instead were expected to show the widest niches as they are globally widely distributed (III). However, ericoid mycorrhizal plants can grow in a variety of habitats, which can be either cold or warm, wet or dry and with high or low light availabilities (Kohout 2017), pointing towards wide niches. EcM plants could have wide realized niches due to multiple reasons. Although EcM is formed by a relatively low number of plant species, the estimated EcM fungal richness is considerably higher than that of AM or ErM fungi (van der Heijden et al. 2015), allowing for higher functional diversity. Additionally, EcM fungal communities within a single host plant roots are more species rich than AM fungal communities (Bahram et al. 2011; Saks et al. 2014), potentially underlying wider niches of EcM plants. Also, EcM trees may benefit from common mycorrhizal networks, helping seedlings to overcome poor light conditions and protecting against pathogens as indicated by frequent observations of positive plant-soil feedback (van der Heijden & Horton 2009; Simard 2009; Bennett et al. 2017; Teste et al. 2017). However, the way how plant niche widths in the context of mycorrhizal types and statuses is directly associated with plant community diversity remains to be explored.

4.3. The effect of anthropogenic influence on mycorrhizal symbiosis in plant communities

The human population continuously increases, intensifying the anthropogenic impact on natural ecosystems. The results from **Paper IV** reveal that the prevalence of mycorrhizal symbiosis in different habitat types is indeed heavily affected by human impact. However, not all forms of anthropogenic impact have the same outcome on mycorrhizal symbiosis. In fact, the effect depends on the specific characteristics of human impact as well as the habitat and dominant mycorrhizal type (IV). Urbanization was related to decreasing community mycorrhization, while the importance of AM symbiosis in plant communities increased (IV).

More recent evidence also suggests similar trends as human population density has been associated with decreasing proportion of EcM and ErM plant species, while the proportion of AM plants has increased (Delavaux et al. 2021). Additionally, N deposition, which is especially prominent near urban areas (Bettez & Groffman 2013), has been shown to favour AM tree dominance at the expense of EcM dominance (Jo et al. 2019). Also, as the overall soil fertility increases, it might not be cost-effective for plants to engage in mycorrhizal symbiosis as fungal aid in macronutrient acquisition is no longer crucial (Johnson et al. 1997; Johnson & Graham 2013), leading to the prevalence of either NM or FM plants and thus lower importance of mycorrhizal symbiosis. These patterns are further supported by the analyses of soil microbiota, revealing reduced relevance of mutualists, especially EcM fungi, and enhanced importance of pathogens in urban soils (Delgado-Baquerizo et al. 2021) and in conditions of N and P fertilization (Lekberg et al. 2021). Interestingly, although increased soil fertility can reduce AM fungal abundance (Egerton-Warburton & Allen 2000, Bainard et al. 2011) and these fungi are commonly thought to be dispersal limited due to their large hypogeous spores (Smith & Read 2008), it has been shown that urban soils still harbour abundant propagules (Chaudhary et al. 2019) as human activities can liberate them into the air, facilitating their dispersal (Chaudhary et al. 2020) and allowing the increase in the prevalence of AM symbiosis in urban areas.

Conversely to urbanity, the introduction of alien plant species increased the prevalence of mycorrhizal symbiosis and reduced that of AM (**IV**). So far, the evidence regarding mycorrhizal traits of alien plant species has been ambiguous, reporting both reduced dependence (Pringle et al. 2009) as well as increased dependence (Hempel et al. 2013; Menzel et al. 2017; Moyano et al. 2021) on mycorrhizal symbiosis. More recent evidence points towards the latter, while also indicating the importance of facultatively mycorrhizal status for plants. It has been shown that mycorrhizal plants represent the majority of naturalized plant species, and especially FM, but also OM plants have higher naturalization success than NM plants (Pyšek et al. 2019; Moyano et al. 2020). Although AM plants have shown higher naturalization success (Pyšek et al. 2019; Moyano et al. 2020), our results indicate the importance of EcM plants among aliens as opposed to AM plants (**IV**). Indeed, woodlands can be prone to plant invasions (Wagner et al. 2017) with species often belonging to obligately EcM tree genera such as *Pinus*, *Picea*, *Abies* or *Populus* (Vellinga et al. 2009) introduced for forestry, while AM is still inhibited by organic nutrient cycling. Furthermore, with increasing eutrophication, these trees could also disperse to heathlands, given the existence of fungal symbionts (Collier & Bidartondo 2009).

Human-induced biotic homogenization, however, had only effects on the prevalence of mycorrhizal symbiosis in heathlands but not in other ecosystem types (**IV**). As expected, heathlands in a more natural state were more mycorrhizal in general but less arbuscular mycorrhizal due to the higher share of obligately ericoid mycorrhizal plant species. Ericoid plant species, however, could exhibit range contraction due to warming climate in combination with human-induced physical disturbance and N deposition, which affect either plants directly

or the associated ericoid mycorrhizal fungi (Olofsson et al. 2001; Newton et al. 2009; Hazard et al. 2014; Van Geel et al. 2020; Vesala et al. 2021). For the other ecosystems, it could be possible that gradients in naturalness were not extensive enough to capture changes in mycorrhization as the Netherlands has been under strong human influence for centuries, and the completely natural end of the gradient can be underrepresented.

Interestingly, not all habitat types responded similarly to human impact as the effect on community mycorrhization was more profound in woodlands and heathlands, while grasslands were less responsive (**IV**). Our results are also in concordance with the findings of Swaty et al. (2016) and Soudzilovskaia et al. (2019) who showed a large negative effect of anthropogenic influence on EcM-dominated vegetation, while the biomass of AM and NM plants in Europe has increased (Soudzilovskaia et al. 2019). It is possible that forest-dwelling EcM and ErM plants, which are obligately mycorrhizal, are more sensitive to anthropogenic impact due to their narrower niches (**III**), while facultatively AM grassland plants exhibit broad niches, allowing them to tolerate a wide range of conditions (Hempel et al. 2013) brought about by human disturbance. Additionally, grasslands could be less affected due to their long management history in Europe (Hejcman et al. 2013), which has allowed plants and their symbiotic fungi to co-evolve in these specific conditions. On the other hand, human impact in woodlands is of more recent origin and highly destructive (Roberts et al. 2018), exerting notable pressure on slowly regenerating EcM tree species and thus reducing the prevalence of mycorrhizal symbiosis. Hence, woodlands and heathlands could be especially susceptible to anthropogenic impact, and the decline of these habitat types might be mediated by mycorrhizal symbiosis.

5. CONCLUSIONS

The results presented in this thesis show that mycorrhizal symbiosis is widely distributed and plays a significant role in plant communities. We also found that the prevalence of mycorrhizal symbiosis across different geographic scales is affected by environmental conditions. However, the environment can be considerably changed by different human activities, potentially leading to altered distribution of mycorrhizal symbiosis and thus, significant changes in ecosystem functioning. Specifically, we found that:

1. At the regional scale, the prevalence of mycorrhizal symbiosis differs between temperate forests and grasslands in Estonia. Forests exhibited higher overall mycorrhization but lower arbuscular mycorrhization, while grasslands had lower overall but higher arbuscular mycorrhization. The most mycorrhizal plant communities were oligotrophic paludifying forests and dry boreal forests, whereas floodplain meadows relied the least on mycorrhizal symbiosis. Mesic grasslands, especially alvar grasslands, exhibited the highest arbuscular mycorrhization, while dry boreal forests had the lowest prevalence of AM symbiosis (I).

2. Plants with different mycorrhizal types and statuses exhibit a distinct distribution pattern along latitude at larger geographical scales. Our results showed that the share of AM plants in European flora is consistently higher than that of plants with other mycorrhizal types, although declining with increasing latitude. Also, the proportion of NM plant species was consistently high throughout the studied area of Europe, yet still increasing towards northern areas. The share of EcM and ErM plants increased with latitude, but contrary to our expectations, their share remained lower than that of AM plant species even at the highest latitudes. Regarding mycorrhizal statuses, FM plant species dominated in all of Europe, with their proportion further increasing and that of OM plant species decreasing with latitude. However, altitudinal patterns were only evident for mycorrhizal statuses as the proportion of OM plant species increased and FM plant species decreased with altitude (II).

3. We found that both edaphic and climatic factors are important drivers of the distribution patterns of mycorrhizal symbiosis (I, II). At the regional scale, soil fertility and pH were the main drivers of the prevalence of mycorrhizal symbiosis in forests, while in grasslands, soil fertility and soil moisture had more pronounced effects. In forests, the overall mycorrhization was negatively affected by soil fertility and pH, while arbuscular mycorrhization was favoured by pH. In grasslands, soil fertility and soil moisture had an adverse effect on both community mycorrhization as well as arbuscular mycorrhization (I). At the continental scale, the share of AM plants was favoured by higher pH, soil fertility and temperature, while these factors negatively influenced the proportion of EcM,

ErM and NM plant species. Also, higher variation in precipitation and temperatures indicating continentality favoured mostly EcM plant species. Temperature was also identified as the main driver of the distribution of mycorrhizal statuses of plant species (II).

4. Plant diversity is related to the prevalence of mycorrhizal symbiosis in temperate forests but not in grasslands. Specifically, we found that more mycorrhizal forests have lower plant species richness than forests with lower mycorrhization. Conversely, arbuscular mycorrhization in temperate forests is associated with higher plant richness. The observed absence between the prevalence of mycorrhizal symbiosis and plant diversity in temperate grasslands could indicate that the community mycorrhization indices used in our study work best on broad scales, where several mycorrhizal types are present and are less effective in comparing conditions with only a single mycorrhizal type, and where more fine-scale effects have the prominent role (I).

5. We found that plants with different mycorrhizal statuses, types and flexibility differ in their realized niches. Niche optima differed among plants with different mycorrhizal statuses and types, indicating niche partitioning, but specific optima depended on the environmental gradient. Our study also revealed that mycorrhizal symbiosis plays a role in plant niche expansion. FM and flexibly mycorrhizal plants consistently exhibited wider realized niches than OM or NM, and inflexible plant species, respectively. Unexpectedly, among OM plants, EcM and ErM plant species and not AM plant species showed the widest realized niches (III).

6. Our research shows that anthropogenic pressure alters plant community mycorrhization, but the effect depends on the specific type of human influence, the plant community type and the prevalent mycorrhizal type. Specifically, urbanization decreases the prevalence of mycorrhizal symbiosis in forests and heathlands, while the reliance on arbuscular mycorrhizal symbiosis increases. The introduction of alien plant species, however, showed the opposite results. In addition, heathlands, which were more affected by human-induced biotic homogenization measured using plant species' range size modifications, were less mycorrhizal and more arbuscular mycorrhizal than the ones with increased anthropogenic effects (IV).

SUMMARY

Mycorrhizal symbiosis – an ancient mutualistic relationship between most vascular plants and soil inhabiting fungi – is ubiquitous in terrestrial ecosystems. However, plants associate with mycorrhizal fungi to various degrees and hence, they can be regarded either as obligately (OM), facultatively (FM) or non-mycorrhizal (NM). In addition, among mycorrhizal associations, three most common mycorrhizal types at the ecosystem level – arbuscular (AM), ecto (EcM)- and ericoid mycorrhizal (ErM) symbiosis – can be distinguished. In general, mycorrhizal symbiosis is the main means of plant nutrition, provides protection against different abiotic and biotic stressors, making mycorrhizal associations a key player in nutrient cycling and ecosystem functioning. Due to the pronounced effects on inter-plant relationships, mycorrhizal symbiosis can also influence plant diversity, either via differential growth effects on plant species, plant-soil feedbacks or by mediating plant niche partitioning. However, due to ever-increasing anthropogenic pressure on natural communities, the patterns of mycorrhizal distribution and thus, also plant diversity and ecosystem functioning, can be a subject to change. Therefore, the need to understand the distribution of mycorrhizal symbiosis, its drivers and the role played in plant diversity, together with the effect of human influence on these associations, is essential.

Based on observations and theoretical knowledge, it has been proposed decades ago that soil conditions determine the dominance of different mycorrhizal types in biomes as AM symbiosis dominates in grasslands and tropical rainforests, EcM is prevalent in temperate and boreal forests, and ErM symbiosis prevails in tundra ecosystems. However, the accumulation of plant mycorrhizal trait data alongside with environmental data has only recently enabled empirical research on mycorrhizal ecology at larger scales. In this thesis, we used plant functional trait data, vegetation surveys, plant distribution data, large-scale environmental data and information on anthropogenic impact to reveal the distribution patterns and the role of mycorrhizal symbiosis in plant communities at the regional scale in Estonia and the Netherlands, and at the continental scale in Europe. At the regional scale in Estonia, we found that the prevalence of mycorrhizal symbiosis and AM symbiosis in temperate forests and grasslands in Estonia differed markedly. Forests exhibited higher overall and lower arbuscular mycorrhization, while grasslands showed the opposite pattern. Oligotrophic paludifying forests were detected as the most mycorrhizal, while floodplain meadows were the least mycorrhizal among the investigated forest and grassland communities. On the other hand, mesic grasslands were the most arbuscular mycorrhizal and dry boreal forests the least arbuscular mycorrhizal plant communities. These patterns of the prevalence of mycorrhizal symbiosis were found to be driven by edaphic factors, mainly by soil fertility and pH in forests, and by soil fertility and moisture in grasslands (I). At the continental scale, our study revealed that plants with distinct mycorrhizal types and statuses are differentially distributed along the latitudinal gradient. Specifically, the share of AM plants was consistently higher than that

of plants with other mycorrhizal types, although decreasing in higher latitudes. We also found that the share of NM plants is remarkably high and increases towards higher latitudes in Europe. The share of EcM and ErM plant species was low throughout Europe, despite slightly increasing with latitude. Regarding mycorrhizal statuses, the share of FM plant species in Europe was consistently higher than the share of OM plant species, and it further increased with latitude and decreased with altitude. At the European scale, both edaphic and climatic factors drive the distribution of mycorrhizal symbiosis. Specifically, higher mean annual temperature, soil pH and soil fertility favour AM plants, while EcM and ErM plants preferred the opposite conditions. Higher variation in temperature and precipitation was found to benefit the distribution of EcM plants. Variation in air temperature was also the main driver of the distribution of plant mycorrhizal statuses (II).

Mycorrhizal symbiosis is increasingly considered as one of the determinants of plant diversity. In this thesis, we show, using empirical data, that plant richness is associated with the prevalence of mycorrhizal symbiosis as well as arbuscular mycorrhizal symbiosis in Estonian temperate and boreal forests but not in grasslands. Our findings suggest that more mycorrhizal forests harbour lower plant richness, whereas arbuscular-mycorrhization favours plant diversity (I). The absence of such relationship in grasslands possibly indicates that more fine-scale processes could be at play. One of the mechanisms how mycorrhizal symbiosis can potentially mediate plant diversity is by means of plant niche partitioning. Our analysis indeed shows for the first time that plants differing in their mycorrhizal types and statuses exhibit also differences in their realized niches. Niche differentiation was indicated by distinct realized niche optima of plants with different mycorrhizal statuses and types, but it depended on the environmental gradient. In addition, we also found evidence for mycorrhiza-mediated niche expansion as FM and flexibly mycorrhizal plant species consistently exhibited wider niches compared to either OM or NM plants. Surprisingly, among OM plant species, EcM and ErM plants, as opposed to AM plants, showed the largest niche expansion (III). Our results indicate that mutualistic interactions such as mycorrhizal symbiosis, which have thus far been largely neglected from niche-based explanations of plant diversity, play an important role in plant communities.

Human impact is currently posing an enormous threat on natural ecosystems. In this thesis, we show that the anthropogenic influence has also an effect on the prevalence of mycorrhizal symbiosis in plant communities. However, the effect depends on the specific type of human impact, the plant community type and the dominant mycorrhizal type. Specifically, the study based on the vegetation changes in the Netherlands showed that increasing urbanization brought about by increasing human populations, decreases the mycorrhization of forests and heathlands. At the same time, however, the dependence on arbuscular mycorrhization increases. On the contrary, the introduction of alien plant species in forests and heathlands was associated with increasing prevalence of mycorrhization and decreasing arbuscular mycorrhization, potentially due to woody plant species introduced for forestry as the demand for timber increases. We also found that

biotic homogenization, measured using plant species' range size modifications, alters mostly the mycorrhization patterns in heathlands as more human impacted heathlands were less mycorrhizal and more arbuscular mycorrhizal compared to more natural communities (IV). These findings suggest that forests and heathlands, which play a crucial role in the retention of organically bound carbon, could be disproportionately affected by the environmental change and thus, consequent changes in biogeochemical cycling could occur.

In conclusion, the results presented in this thesis empirically show the widespread distribution of different mycorrhizal types and statuses at the regional as well as continental scale in Europe and shed light on the edaphic and climatic drivers of these distribution patterns. In addition, the thesis also demonstrates the important role that mycorrhizal symbiosis plays in mediating plant coexistence and diversity. Last, but not least, the results highlight that human induced environmental and land-use change has the potential to alter the distribution of mycorrhizal symbiosis in certain plant communities and thus, may influence ecosystem functioning.

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SUMMARY IN ESTONIAN

Mükoriisse sümbioosi levik ja roll taimekooslustes

Mükoriisne sümbioos – vastastikku kasulik kooselu soontaimede ja mullaseente vahel – on maismaaökosüsteemides laialt levinud, kuna hinnanguliselt elab mükoriisaseentega koos koguni kuni 90% taimeliikidest. Taimi võib nende erineva mükoriisuse alusel jaotada kolmeks suuremaks rühmaks, iseloomustades nende erinevat mükoriisest staatust: obligaatselt mükoriissed (OM), fakultatiivselt mükoriissed (FM) ja mittemükoriissed (NM) taimed. Obligaatselt mükoriisete taimede juurtes elavad alati mükoriisaseened, fakultatiivselt mükoriissed taimed võivad elada nii koos mükoriisaseentega kui ka ilma nendeta, sõltuvalt keskkonnatingimustest, ning mittemükoriissed taimed ei seostu kunagi mükoriisaseentega. Samuti eristatakse erinevaid mükoriisatüüpe sõltuvalt seenjuure morfoloogiast ja taim- ning seenpartneri taksonoomiast. Ökosüsteemide seisukohalt on laia leviku tõttu olulisemad kolm peamist mükoriisatüüpi: arbuskulaarne mükoriisa (AM), ektomükoriisa (EcM) ja erikoidne mükoriisa (ErM). Mükoriisaseened aitavad taimedel omastada suure osa eluks vajalikke toitaineid ja kaitsevad neid erinevate abiootiliste (põud, raskemetallide sisaldus mullas) ja biootiliste (herbivooria, parasiitsed taimed) stressifaktorite eest, saades neilt vastu süsinikuühendeid. Selline mõlemale poolele kasulik kooselu taimede kui primaarproduktentide ja seensümbiontide vahel on ökosüsteemide toimimise seisukohalt äärmiselt oluline. Näiteks mängib mükoriisne sümbioos rolli taimekoosluste mitmekesisuse kujunemisel, kuna mõjutab taimedevahelisi suhteid läbi taimeliikide erinevate kasvuvastuste, taimede ja mulla vahelise tagasiside tõttu ning mõjutades taimede ressursi- ja elupaiganõudlust. Looduslikud ökosüsteemid aga seisavad silmitsi üha intensiivistuva inimtegevuse ja maakasutuse muutustega, mis tähendab, et ka mükoriisse sümbioosi levik ning koos sellega ka taimede mitmekesisus ja ökosüsteemide toimimine võivad muutuda. Seetõttu vajame põhjalikku arusaama sellest, kuidas mükoriisne kooselu taimede ja seente vahel on taimekooslustes levinud ja millised keskkonnategurid seda mõjutavad, kuidas see mõjutab taimede elurikkust ning milliseid muutusi toob kaasa inimtegevus.

Teoreetiliste teadmiste põhjal on juba mitu aastakümnet tagasi arvatud, et erinevate mükoriisatüüpide leviku ökosüsteemides määravad mullatingimused ning sellest lähtuvalt domineerib arbuskulaarne mükoriisa rohumaadel ja troopilistes vihmametsades, ektomükoriisa on valdav parasvöötme ja boreaalsetes metsades ning erikoidne mükoriisa on peamiselt levinud tundraökosüsteemides. Üha enam on kogutud andmeid taimede funktsionaalsete tunnuste, sh mükoriisuse tunnuste, ja keskkonnatingimuste kohta, mis võimaldavad lõpuks teoreetilisi teadmisi mükoriisse sümbioosi leviku ja selle mõjutajate kohta empiiriliselt uurida ka suuremal geograafilisel skaalal kui seni võimalik. Käesolevas doktoritöös kasutasime taimede funktsionaalseid tunnuseid, taimkatte analüüsi, taimede levikuinfot ja suureskaalalisi keskkonnatingimuste andmeid, et uurida mükoriisse sümbioosi levikut ja rolli Eesti ja Hollandi taimekooslustes ning laiemalt Euroopas.

Selleks, et tuvastada mükoriissuse osatähtsust Eesti taimkattes, uurisime kuue metsakoosluse – palumetsad, loometsad, salumetsad, laanemetsad, soostuvad metsad ja rabastuvad metsad – ja viie rohumaakoosluse – loopealsed, parasiinised pärisaruniidud, niisked pärisaruniidud, lamminiidud ja rannaniidud – taimestiku andmeid koos taimeliikide mükoriissuse tunnustega. Metsade ja rohumaade kvantitatiivne analüüs tuvastas, et nii üldine mükoriisse sümbioosi osatähtsus kui ka spetsiifilisemalt arbuskulaar-mükoriisse sümbioosi osatähtsus nendes ökosüsteemides erineb oluliselt. Metsades on mükoriisse sümbioosi osatähtsus kõrgem kui rohumaadel, samas kui arbuskulaarse mükoriisa osatähtsus on metsades väiksem. Seevastu rohumaadel esines vastupidine seos. Vaadeldud mustrid on seletatavad metsades ja rohumaadel domineerivate mükoriisatüüpide erinevustega. Metsades on valdav ektomükoriisatüüp, mis taimede seisukohalt on obligaatne sümbioos, muutes metsad tugevalt mükoriisseks. Rohumaadel kasvavad taimed moodustavad aga enamasti arbuskulaarset mükoriisatüüpi, mis on taimede jaoks tihti fakultatiivne, tehes need kooslused tervikuna vähem mükoriisseteks. Uuritud taimekooslustest osutusid kõige mükoriissemateks rabastuvad metsad ja palumetsad ning kõige madalam mükoriisse sümbioosi osatähtsus leiti lamminiitudel. Arbuskulaar-mükoriisne sümbioos oli levinuim erinevatel parasiinisketel rohumaatüüpidel, kuid oli madalaima osatähtsusega palumetsades. Uuringu tulemused näitavad, et selliste levikumustrite taga on erinevused mullatingimustes. Kõrgem mullaviljakus ja pH olid seotud madalama metsade mükoriisusega, ent samal ajal soosis mulla kõrgem pH arbuskulaar-mükoriisust. Rohumaade mükoriisust ning spetsiifilisemalt ka arbuskulaar-mükoriisust soodustasid madalam mullaviljakus ja -niiskus (I).

Doktoritöö raames tehtud suuremat osa Euroopast hõlmavas uuringus selgus, et erinevatel mükoriisatüüpidel ja -staatustel on piki laiuskraadi erinev levikumuster. AM taimede osakaal oli Euroopas kõrgem kui teistel mükoriisatüüpidel, kuigi vähenes põhjapoolsematel aladel. Samuti selgus, et mittemükoriisste taimeliikide osakaal Euroopa taimestikis on üllatuslikult kõrge ning kasvab põhjapoolsetel aladel veelgi. Ekto- ja erikoidset mükoriisat moodustavate taimeliikide osakaal oli kogu Euroopas madal ning kuigi see tõusis piki laiuskraadi, ei ületanud siiski AM taimede osakaalu ka kõige põhjapoolsematel aladel. Mükoriisete staatuste levikumustreid uurides selgus, et fakultatiivselt mükoriisete taimede osakaal ületab obligaatset mükoriisete taimede osakaalu kogu uuritud alal ning nende taimede olulisus taimestikis suureneb piki laiuskraadi, kuid kahaneb kõrguse kasvades. Obligaatset mükoriisete taimed näitasid see-eest vastupidist levikumustrit. Taimede mükoriisuse tunnuste levikumustrite peamiste mõjutajatena tuvastasime nii mulla- kui kliimatilised faktorid. Kõrgem aastane keskmine temperatuur, mulla pH ja mullaviljakus soosisid AM taimeliike, samal ajal kui EcM ja ErM taimeliigid eelistasid madalamat õhutemperatuuri, mulla pH-d ja mullaviljakust. Lisaks selgus, et EcM taimeliike soosis suurem aastane sademete hulk ning temperatuuri ja sademete hulga suurem varieeruvus. Hoolimata sellest, et mükoriisaseentega kooselu peamine kasu taimedele seisneb tõhusamas toitainete omastamises, leidsime, et ei mullaviljakus ega teised mullatingimused

ei ole siiski peamised obligaatselt ja fakultatiivselt mükoriisete taimede levikumustrite määravad suurel geograafilisel skaalal Euroopas. Erinevate mükoriisete staatustega taimede levikumustreid mõjutasid hoopis peamiselt temperatuuriga seotud faktorid, eriti aga kuude keskmine õhutemperatuuride amplituud, mis iseloomustab kliima kontinentaalsust. Obligaatselt mükoriisete taimede osakaal oli suurem kontinentaalsema kliimaga aladel, samal ajal kui fakultatiivselt mükoriisid taimed eelistasid väiksemat õhutemperatuuri varieeruvust (II).

Mükoriisne sümbioos mängib olulist rolli ka taimekoosluste mitmekesisuse kujunemisel. Käesoleva doktoritöö empiirilistel andmetel põhinevad tulemused näitavad, et taimede liigirikkus Eesti parasvöötme ja boreaalsetes metsades on seotud nii üldise mükoriisse sümbioosi osatähtsusega kui ka arbuskulaarse mükoriisa osatähtsusega nendes taimekooslustes. Leidsime, et mükoriissemates metsades on madalam taimede liigirikkus kui vähem mükoriissetes metsades, samas kui kõrgem arbuskulaarne mükoriisus soosis taimede liigirikust. Sarnast seost ei ilmnenud aga rohumaadel, kus taimede mitmekesisuse mustrid võivad olla kujunenud väiksemaskaalaliste protsesside (sümbioosipartnerite valiku eelistus, erinevused AM seenekoosluste mitmekesisuses ja multifunktsionaalsuses) tulemusel (I). Üks viis, kuidas mükoriisne sümbioos võib taimekoosluste mitmekesisust mõjutada, on taimeliikide ressursi- ja elupaiganõudluste muutmine ehk osalemine taimede niššide diferentseerumisel. Meie tulemused näitavad, et erineva mükoriisse staatuse ja tüübiga taimed erinevad oma ressursi- ja elupaiganõudlustes. Niššide diferentseerumisele viitavad erinevate mükoriisete staatuste ja tüüpidega taimede erinevad nišioptimumid, kuid olulist rolli mängis uuritav keskkonnagradiend. Näiteks leidsime, et mittemükoriisid taimed kasvavad enim suhteliselt kõrgema mullaniiskuse tingimustes, obligaatselt mükoriisid taimed kuivemates tingimustes ning fakultatiivselt mükoriisid taimed eelistasid vahepealset mullaniiskust. Ainult obligaatselt mükoriisid taimi analüüsides selgus, et erikoidset mükoriisat moodustavad taimed eristusid selgelt oma ressursi- ja elupaiganõudluste optimumtingimuste osas teisi mükoriisatüüpe moodustavatest taimedest, eelistades toitainevaesemaid ja madalama pH-ga muldasid ning madalamat õhutemperatuuri. Arbuskulaar- ja ektomükoriisete taimede optimaalsed kasvutingimused olid teataval määral sarnased, kuid ektomükoriisid taimed kaldusid siiski eelistama vahepealseid tingimusi võrreldes arbuskulaar- ja erikoidset mükoriisat moodustavate taimedega. Lisaks leidsime kinnitust, et mükoriisne sümbioos võib laiendada taimede nišše: fakultatiivselt mükoriisid taimed võivad kasvada erinevatel ressursi- ja elukohatingimustel võrreldes obligaatselt ja mittemükoriisete taimedega. Kui vaadata ainult OM taimi, siis üllatavalt olid kõige laiemad nišid EcM ja ErM taimedel, mitte kõige laiemalt levinud AM taimedel. Võib eeldada, et AM taimede laia leviku üheks põhjuseks on selle mükoriisatüübi fakultatiivne iseloom taimede jaoks (III). Meie tulemused viitavad, et mükoriisne sümbioos on oluline taimede niššide diferentseerumisel ning tuleks seetõttu kaasata ka ressursi- ja elupaiganõudluste erinevustel põhinevatesse taimede koosseksisteerimise teooriatesse.

Kasvav inimtegevus mõjutab üha enam looduslikke ökosüsteeme. Käesolevas doktoritöös uurisimegi ühe teemana, kuidas inimtegevus mõjutab mükoriisse

sümbioosi osatähtsust taimekooslustes. Hollandi taimkatte muutuste põhjal tehtud uuringu tulemuste põhjal saab üldistavalt järeldada, et inimtegevus avaldab mõju taimekoosluste mükoriisusele, kuid mõju sõltub konkreetsest inimtegevuse tüübist, taimekooslusest ning valdavast mükoriisatüübist. Täpsemalt näitasime, et linnastumine kahandab metsade ja nõmmede mükoriisust, kuid samal ajal suurendab nende koosluste arbuskulaar-mükoriisust. Linnastumine on seotud suurema mullaviljakuse, kõrgema mulla pH ja kõrgema õhutemperatuuriga, mis nii käesolevas doktoritöös kui ka varasemates uuringutes on näidatud just AM taimedele sobivate keskkonnatingimustena. Lisaks on eeldatav, et inimtegevusest tulenev surve puuliikidele, mis on enamasti obligaatset mükoriisid, on tugevam ning aeglase elukäigu tõttu ka pikaajalisem kui rohtsetele arbuskulaar-mükoriisetele taimedele. Võõrliikide introducteerimine mõjutas metsade ja nõmmede mükoriisust linnastumisega võrreldes vastupidiselt: enamate võõrliikidega kooslused olid mükoriisemad, aga väiksema AM osatähtsusega. Sellise seose tõenäoliseks põhjuseks võib pidada üha suureneva puidunõudluse tõttu introducteeritavate obligaatset ektomükoriisid puuliike, tõstes taimekoosluste mükoriisust. Lisaks leidsime, et taimeliikide levikuareaalide muutuste põhjal hinnatav potentsiaalselt inimtegevuse tõttu toimuv taimkatte ühtlustumine mõjutab peamiselt nõmmekoosluste mükoriisust. Inimtegevuse kasv vähendas nõmmekoosluste mükoriisust ja suurendas arbuskulaar-mükoriisust võrreldes looduslikumas seisus olevate kooslustega (IV). Doktoritöös esitatud tulemused näitavad, et inimtegevus mõjutab eriti oluliselt nii metsa- kui nõmmekooste mükoriisust, võides tuua kaasa ka muutusi aineringetes, kuna just need kooslused on olulised orgaanilise süsiniku säilitajad.

Kokkuvõttes, käesolev doktoritöö kinnitas empiiriliste andmete põhjal mükoriisse sümbioosi – erinevate mükoriisatüüpide ja mükoriisete staatuste – laia levikut nii väiksemal skaalal erinevates taimekooslustes kui ka kontinentaalsel skaalal Euroopas ning tuvastas mükoriisse sümbioosi levikumustreid määravad mulla- ja keskkonnatingimused. Lisaks näitasime, et mükoriisne sümbioos mängib olulist rolli nii taimede kooseksisteerimisel kui ka taimekoosluste mitmekesisuse kujundamisel. Tulemustest ilmnes, et ka inimtegevusest tulenevad muutused keskkonnatingimustes ja maakasutuses võivad muuta mükoriisse sümbioosi levikumustreid taimekooslustes ning seega omada mõju ökosüsteemide toimimisele.

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PUBLICATIONS

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