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Mycorrhizal fungal diversity along altitudinal gradients

Diverzita mykorhiznch hub podel vškovch gradient

**Bachelor's thesis**

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Ráda bych poděkovala svému školiteli Mgr. Petru Kohoutovi, Ph.D. za pomoc, vstřícnost a cenné rady během psaní této práce. Můj velký dík patří i mé rodině a přátelům za podporu a trpělivost.

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Podpis



# Abstrakt

Mykorhizní symbióza je nedílnou součástí všech terestrických ekosystémů a jedná se o nejrozšířenější mutualistický vztah na světě. Nicméně, naše znalosti týkající se diverzity mykorhizních hub podél výškových gradientů jsou značně omezené. Většina dosavadních výzkumů poukazuje na snižování diverzity mykorhizních hub s rostoucí nadmořskou výškou nebo jejich nejvyšší diverzitu ve středních nadmořských výškách, což odpovídá obecným trendům, které byly pozorovány u makroorganismů podél výškových gradientů. Nižší diverzita mykorhizních hub ve vyšších nadmořských výškách může mít v některých oblastech velký vliv na hostitelské rostliny, které kvůli globálnímu oteplování migrují vzhůru. Pochopení změn v distribuci mykorhizních hub podél výškových gradientů nám tedy umožní lépe předpovědět vliv klimatických změn na mykorhizní houby i hostitelské rostliny. Abychom rozšířili své znalosti ohledně diverzity mykorhizních hub, je nezbytné prohloubit naše porozumění faktorům, které podél výškových gradientů formují odpovědi mykorhizních hub.

**Klíčová slova:** mykorhizní houby, výškové gradienty, diverzita, druhová bohatost, klimatická změna

# Abstract

Mycorrhizal symbiosis is an integral component of all terrestrial ecosystems and the most widespread mutualistic association in the world. Nevertheless, our current knowledge regarding diversity patterns of mycorrhizal fungi along altitudinal gradients is considerably limited. Published studies to date suggest either a decrease in mycorrhizal fungal diversity with increasing elevation or a hump-shaped pattern, similar to the general altitudinal diversity patterns that have been observed in macroorganisms. Lower mycorrhizal fungal diversity at higher elevations in some regions may significantly impact host plants migrating upward due to global warming. Therefore, insights into the shifts in mycorrhizal fungal distribution along elevational gradients can provide better predictions of future effects of climate change on mycorrhizal fungi and host plants. In order to advance our knowledge of mycorrhizal fungal diversity, it is crucial to deepen our understanding of the factors that shape mycorrhizal fungal responses along altitudinal gradients.

**Keywords:** mycorrhizal fungi, altitudinal gradients, diversity, species richness, climate change



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# List of Abbreviations

**AM** Arbuscular mycorrhiza

**AMF** Arbuscular mycorrhizal fungi/fungal

**CAR** Natural rocky rupestrian fields

**CRR** Rocky rupestrian field in the regeneration stage

**EcM** Ectomycorrhiza

**EcMF** Ectomycorrhizal fungi/fungal

**ENDF** Endophytic fungi/fungal

**ErM** Ericoid mycorrhiza

**ErMF** Ericoid mycorrhizal fungi/fungal

**GAF** Gallery forests

**GRA** Natural grasslands

**HAC** High-altitude *cerrado* savannas

**IPCC** Intergovernmental Panel on Climate Change

**ITS** Internal transcribed spacer

**MDE** Mid-domain effect

**OTU** Operational taxonomic unit

**PLFA** Phospholipid fatty acid



# Introduction

Mycorrhizal symbiosis represents a mutualistic relationship between fungi and the roots of vascular plants. The association is based on a nutrient exchange, increased water intake and defense against pathogens provided by the fungus on the one hand, and provision of organic compounds, products of photosynthesis, by the plant on the other. Fungal mycelium increases the soil volume available for plants by creating mycorrhizosphere, extending the reach for more nutrients and affecting the surrounding soil environment with extraradical hyphae.

It is estimated that up to 90 % of vascular plants and thousands of fungal species exhibit this type of symbiosis among all terrestrial ecosystems, making mycorrhiza one of the most widespread symbiotic interactions in the world. Since mycorrhizal associations are a common characteristic among vascular plants, it might be considered as an evolutionary adaptation, which helped plants conquer the terrestrial world, suggesting the first appearance of mycorrhiza 400-460 million years ago [1].

Based on the anatomy and morphology of the root colonization, mycorrhizas can be categorized into two major groups - endomycorrhiza, in which the fungus penetrates the plant cell wall and ectomycorrhiza, where the fungus colonizes root surface and intercellular space of rhizodermis and cortex. Endomycorrhizas are further divided into three types – arbuscular, ericoid, and orchid mycorrhiza, based on the fungal and plant interacting species and the morphological as well as anatomical changes they undergo.

Arbuscular mycorrhiza is by far the most widespread type of endomycorrhiza present in approximately 70 % of plant species, including grasses and some deciduous trees. Fungi involved in this symbiosis belong exclusively to the Glomeromycota division. Glomeromycota species are crucial for increased phosphorus intake allowing host plants to survive in nutrient-poor environments, whereas fungi are supplied by lipid precursors. Although there are plant lineages that do not form arbuscular mycorrhiza (e.g., Chenopodiaceae, Brassicaceae, Caryophyllaceae), all vascular plant species carry genes necessary for AM functioning, because the last common ancestor of all vascular plants formed the mycorrhizal symbiosis [1]. Geographically, arbuscular mycorrhiza is most widespread in tropical and subtropical forests as well as temperate grasslands.

Boreal and temperate forests are dominated mainly by ectomycorrhiza, the second most common mycorrhizal type. These ecosystems are particularly characterized by nitrogen limitation, which grows with increasing distance from the equator. Symbionts are woody plants, mostly conifers, and fungi from the phyla Basidiomycota, Ascomycota, or Zygomycota. However, some plant species have been found able to form both

ectomycorrhiza as well as arbuscular mycorrhiza (e.g., *Salix*, *Populus*, *Alnus*) [1]. Ectomycorrhiza has developed over sixty-six times during evolution as a one-way process [2]. The evolution of this association is tightly connected to that of the host plants, especially the Pinaceae family [3].

As we move to higher latitudes, the environment rapidly becomes nutrient-poor with a decreasing soil pH, especially in tundra and taiga biomes. To survive in such inhospitable conditions, Ericaceae plants have developed a mutualistic association with fungi from the Ascomycota (Helotiales) and Basidiomycota (Sebacinales) phylum. Fungi not only supply the plants with nitrogen and phosphorus but also protect them from toxic heavy metals. There are also less common mycorrhizal types such as orchid mycorrhiza or monotropoid mycorrhiza. However, the main focus of this thesis will be on the first three types mentioned above.

Aside from biotic interactions, the distribution of plant and fungal species can also be largely affected by abiotic environmental conditions. Climate, the primary factor impacting diversity along altitudinal gradients, changes similarly as it does across latitude. With increasing elevation, there is a significant linear decrease in temperature as well as land area and an increase in atmospheric pressure and precipitation. Another crucial determinant of vegetation composition is nutrient availability, which also varies with elevation. Consequently, high-elevation areas are usually colonized by shrubs and grasslands with distinctive root-shoot ratios resulting in low aboveground biomass and a highly developed underground root system to reach all available nutrients. Undoubtedly, the importance of mountainous regions is immense as they play a key role in carbon storage and host a high species diversity.

Tropical mountain ecosystems are unique in terms of species richness and endemism. It is estimated that approximately 87 % of the global terrestrial diversity of vertebrate species, including amphibians, birds, and mammals, is located in mountainous regions [4]. Moreover, many of the species are endemic to these regions. For example, The Northern Andes host roughly 45000 plant species, of which about 44 % are endemic to this region [5]. Other so-called hyper-diverse tropical mountain regions include the Sichuan/Yunnan mountains of Asia, the East African Highlands, and the mountains of Papua New Guinea [6]. Mountainous areas of temperate and arctic zones, on the other hand, are relatively low in species diversity [4].

However, in terms of general diversity patterns, there is a contradiction between latitudinal and altitudinal gradients. As opposed to latitudinal gradients, where the highest diversity is located in the tropical areas, altitudinal gradient patterns of macroorganisms mainly follow the so-called hump-shaped pattern, with diversity peaking at mid-elevations [7].

The primary focus of biologists has always been on studying biogeographical patterns of macroorganisms, for an obvious reason: they are noticeable and can be easily studied. However, microorganisms are a crucial component of our ecosystems, particularly in establishing underground environments which can subsequently enhance aboveground diversity. Mycorrhizal fungi, specifically, are essential in determining and altering soil characteristics affecting plants directly, for example, through increased water and nutrient intake.

Due to all the aforementioned facts, I have chosen mycorrhizal fungal diversity as the topic for my bachelor's thesis. The main objective of this thesis is to determine the factors as well as so-called confounding factors that influence mycorrhizal fungal diversity along altitudinal gradients. To achieve this, I will describe how altitude impacts the three main mycorrhizal types, arbuscular mycorrhiza, ericoid mycorrhiza, and ectomycorrhiza, in terms of fungal species richness, diversity and community composition in the first part of my thesis. Furthermore, I will mention some confounding factors, abiotic and biotic, driving diversity patterns alongside altitude. In the second part, I will briefly highlight the significance of mycorrhizal fungal distribution along altitudinal gradients in predicting future ecosystem responses to climate change. Lastly, I will propose a direction for further research, as much in the area of mycorrhizal fungal diversity and biogeography remains unknown and needs to be discovered for an in-depth comprehension of global ecosystem processes.



# 1. Shifts in mycorrhizal fungal diversity along altitudinal gradients

Elevational gradients represent complex environments where various abiotic and biotic factors undergo substantial shifts within a relatively small spatial scale. However, many variables covary with elevation, impeding the distinction between their effects on the ecosystem. Such variables include, for example, temperature, precipitation, soil pH, or soil mineral nutrient contents.

Many studies show that among environmental factors, temperature and land area have the most significant impact on organisms across altitudinal gradients. An increase in elevation is associated with a significant decrease in the land area availability resulting in a lower abundance of organisms. Mountains in different regions of the world are topographically very distinct and their land-area reduction rate varies. For example, the land area above the tree line in the Andes is reduced by 50 % after less than 200 m of elevational increase and by 90 % after additional 600 m of elevation. In contrast, the land area in the Himalayas is reduced by half after 600 m of elevational increase above the tree line, suggesting a more gradual land reduction. [8]

Temperature is a crucial factor for many ecosystem processes, including photosynthesis, decomposition, and nutrient mineralization rates [9]. As mentioned above, temperature decreases with increasing elevation, approximately by 0.6 °C per 100 m [10], causing a decline in the rate of these processes as well. The increasing elevation is therefore associated with a decrease in soil fertility and litter quality, leading to a higher root biomass allocation [11] and an inevitable establishment of different mutualistic symbioses with soil biota. Moreover, plant communities inhabiting higher altitudes with such stressful conditions have also adapted, for example, via a pronounced decrease in aboveground biomass and a slower growth rate [12], which has been well observed along the tree line [13].

Additionally, different plant communities tend to express facilitating behavior patterns towards each other in harsh conditions, which also occur in high elevations [14]. In contrast, lower elevations promote negative interactions between aboveground communities, specifically competitive behavior [14]. There is a similar facilitating pattern among belowground communities, for example, cooperative interactions between some ectomycorrhizal fungi and their tree symbionts at high elevations [15].

Geographical constraints are yet another type of environmental factors influencing the distributional patterns of belowground communities. The so-called mid-domain effect

(MDE) [16] demonstrates that if we run a simulation based on a random placing of ranges of different species within a defined geographical area (domain), these ranges will have a higher probability of overlapping towards the middle of the domain [17].

Throughout this thesis, the main focus will be on mycorrhizal fungal community shifts along elevational gradients and how they affect fungal species richness, meaning the number of species present, and fungal diversity, meaning both the species richness and species evenness. The majority of published studies regarding soil biota responses to altitudinal gradients to date is focused on temperate regions at local scales. Nonetheless, I will also evaluate studies depicting belowground community responses to elevational gradients in tropical regions as well as larger-scale analyses. As previously mentioned, there are significant differences between tropical and temperate mountains, especially in regard to biodiversity [4]. For that reason, each mycorrhizal type and its fungal diversity patterns will be divided geographically into temperate and tropical regions.

## **1.1 Arbuscular mycorrhiza**

As noted above, arbuscular mycorrhiza (AM) is the most common mycorrhizal type. It is predominant along the equatorial belt, mainly in tropical and sub-tropical forests and temperate grasslands. AMF supply plants with phosphorus, which otherwise the scarcity thereof would be limiting for their plant growth in these regions. Because of the significant role AM plays in ecosystem processes, it is crucial to understand mycorrhizal fungal responses to elevation and how it affects aboveground as well as other belowground communities and the ecosystem as a whole. Comprehending these responses to elevation will also allow us to better predict future shifts in AMF communities caused by ongoing global changes.

### **1.1.1 AMF in temperate regions**

The temperate geographical zone is divided into the north and south temperate zone and demarcated by the 23.5° and 66.5° north and south latitudes. Temperate regions experience significant seasonal changes throughout the year in comparison with the tropics, setting the mean temperature range between -3 °C and 18 °C during the coldest month of the year [18]. Based on the Köppen climate classification system [18], temperate regions in this thesis will also include dry-winter humid subtropical climate represented by the first case study in Tibet [19].



Belowground community responses to elevation, fungi, in particular, are very inconsistent across many studies. However, it is possible to identify common patterns among these responses. For example, there appears to be a negative correlation between elevation and AMF species richness in temperate regions [19, 20].

A study carried out in southeast Tibet on Segrila Mountain across a single elevational gradient of 1990-4648 m a.s.l. indicated an apparent negative correlation with altitude in almost all aspects. Not only species richness but also AMF spore density and colonization, including the frequency and intensity of colonization, showed a decreasing trend with increasing elevation. Nevertheless, AMF diversity did not display any noticeable change across the elevational gradient. [19]

Based on spore counts and spore morphology, the study determined fungal spore density as well as fungal species richness and diversity. 72.2 % of all 45 plant families detected were colonized by AMF. The intensity of colonization peaked at the lowest elevation (1990 m a.s.l.), and the frequency of colonization was highest from the lowest up to intermediate elevations (1990-3043 m a.s.l.). The highest abundance of spores was also at lower elevations, declining significantly after reaching 3043 m a.s.l. AMF species richness exhibited decreasing tendencies at higher elevations as well; in contrast, fungal diversity was consistent across the altitudinal gradient (Figure 1.1). Considering the frequency and relative abundance of AMF species, Glomeraceae family dominated across all sites, Acaulosporaceae being the second most abundant. [19]

The results suggest that the AMF community composition on Segrila Mountain is driven by different abiotic and biotic factors. For example, a correlation was found between spore density and soil pH, soil organic matter, respectively. However, due to many covarying factors present, including temperature, moisture, plant community composition, or soil properties, it remains unclear how belowground communities respond to individual variables. [19]

The second study, based on the same methodology and carried out in the Qinling Mountains, another renowned species richness hotspot in China, revealed similar patterns. The root and soil samples were collected at the highest peak, Mount Taibai. The experimental range was also large, extending from 1050 to 3750 m a.s.l. across a total of 19 elevational belts within a single altitudinal gradient. The mean annual temperature positively correlated with  $\alpha$ -diversity and AMF species richness, hence decreasing significantly with increasing altitude. As opposed to the prior study, AMF colonization rates and spore density values reached their maximum at the intermediate elevations, around 2000 m a.s.l. Additionally, due to the increasing heterogeneity of the encompassing environment with elevation, there was a significant rise in  $\beta$ -diversity. [20]

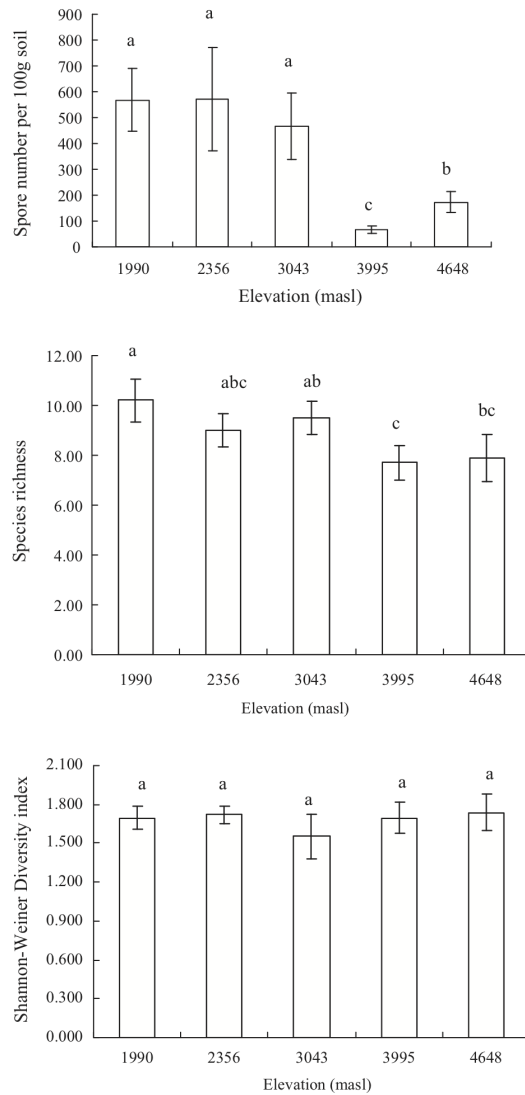


Figure 1.1: “AM fungal spore number, species richness and Shannon-Weiner index at different altitudes.” [19]

A variation of the AMF community composition, including relative abundance and occurrence frequency, was demonstrated across all of the studied elevation sites. Despite the highest number of species belonging to the Glomeraceae family, the most abundant genus was *Acaulospora*, from the Acaulosporaceae family, with the relative abundance of 58.2 % and the occurrence frequency of 100 %. Other genera present along the entire gradient were for example *Claroideoglossum* as well as *Funneliformis* (Table 1.1). [20]

Plant community composition differed among the studied elevational belts as well. Lower elevations were composed of host plants associating with AM fungi and intermediate elevations dominated by non-host plants, which resulted in colonized roots originally from understory grasses. Lastly, the higher elevational sites were colonized mainly by grasses; in other words, AM host plants. [20]

Genus	Relative abundance (%)	Occurrence frequency (%)
<i>Acaulospora</i>	58.244	100.00
<i>Claroideoglomus</i>	11.579	100.00
<i>Diversispora</i>	0.526	31.58
<i>Funneliformis</i>	9.156	100.00
<i>Gigaspora</i>	0.446	26.32
<i>Glomus</i>	18.556	98.68
<i>Paraglomus</i>	0.059	6.58
<i>Racocetra</i>	0.048	5.26
<i>Rhizophagus</i>	0.936	25.00
<i>Sclerocystis</i>	0.090	6.58
<i>Scutellospora</i>	0.313	13.16
<i>Septoglomus</i>	0.047	5.26

Table 1.1: “Relative abundance and occurrence frequency of arbuscular mycorrhizal fungal genera presented in soil samples collected from Mt. Taibai of the Qinling Mountains.” [20]

The study discovered that soil parameters exhibited minimal effect on the overall AMF diversity, with the only exception of soil phosphorus, which negatively correlated with AMF colonization. On the other hand, climate variables, such as mean annual temperature, had a major impact on  $\alpha$ - and  $\beta$ -diversity as well as AMF species richness. Therefore, it was concluded that AMF community composition along the slope of Mount Taibai was mainly influenced by environmental factors, elevation variation, and host plant communities. [20]

The final study regarding AMF diversity examined central European meadows, namely, in the Czech Republic. Although this thesis primarily examines larger-scale elevational gradients, the altitudinal range presented in this research was only from 159 to 784 m a.s.l. Nevertheless, this study was carried out on an exceptionally large regional scale and took into account many variables, providing an elaborate survey on different environmental characteristics influencing the AMF community composition. The Czech Republic is a particularly well-suited area for such research owing to its notable geographical as well as climatic heterogeneity. [21]

The main objective of this survey was to map AMF community responses across temperate meadows, natural as well as managed grasslands, to habitat, geography, and climate. 80 sites were selected within the borders of the Czech Republic to obtain representative samples of different environmental conditions. The methodology presented in this study was based on sequencing the highly genetically variable ITS 2 region of the ribosomal DNA operon of AMF acquired from soil samples. [21]

Soil pH was considered as the most significant habitat parameter in the findings of this study. Geography likewise exhibited a considerable effect on AMF community composition, highlighting both altitude and latitude as important factors in this research

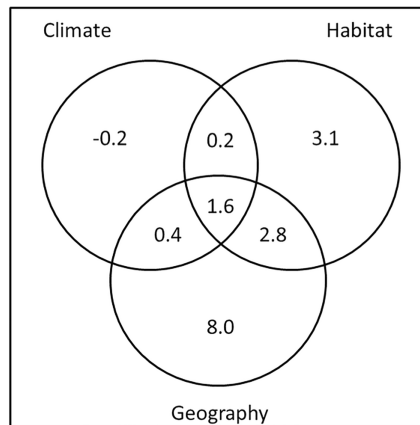


Figure 1.2: “Venn diagram illustrating the partitioning of the total explained variation (%) in soil arbuscular mycorrhizal communities across the Czech Republic among three groups of predictors (climate, habitat, and geography). The negative value is an artifact of the method and should be regarded as zero.” [21]

(Figure 1.2). Additionally, the spatial distance between sampling sites also proved to be a relevant factor in the AMF community structuring. Even though climate is generally considered a key factor, this survey did not register any significant effect (Figure 1.2), presumably due to the scarcity of collected climatic data. [21]

The most frequent genus was *Glomus* sp., occurring in 95 % of soil samples. Other abundant AMF genera found across sampling sites were *Septoglomus*, *Paraglomus*, *Funneliformis*, *Dominikia* and *Archaeospora*. This survey also detected associations between certain AMF species and environmental factors. For example, *Septoglomus* and *Paraglomus* exhibited a positive and negative correlation with pH, respectively. In addition, all identified genera exerted either positive or negative correlation with altitude. Nonetheless, a larger altitudinal gradient would be necessary for these results to be conclusive. [21]

### 1.1.2 AMF in tropical regions

The tropics are located between latitudes 23.5°N and 23.5°S and defined as the geographical zone with a minimal mean annual temperature of 18 °C and high precipitation [18]. In contrast to the temperate zone, the tropics generally see less of a seasonal variation throughout the year, allowing species to develop a narrower range of physiological tolerances [22]. Tropical mountains are complex ecosystems comprising of many different climate types with abrupt transitions [4], occasionally resulting in the formation of rare climatic conditions [23]. This is well illustrated in the tropical montane cloud forest, which is characterized by a permanent cloud cover at specific elevations.

The first research [24] on the AMF diversity in tropical ecosystems referred in this thesis, was executed on a single altitudinal gradient ranging from 800 to 1400 m a.s.l. within Brazilian rupestrian grasslands. Due to its unique microclimatic and soil variations, this ecoregion is characterized by a rocky landscape with mainly shrub or herbaceous vegetation, as well as different soil types, notably quartz and sandstone [24]. Such considerable environmental heterogeneity has resulted in a high degree of biodiversity as well as endemism [25]. The primary focus of this study was to determine what influences the variation in AMF communities, spore density, and species richness across an elevational gradient, based on AMF spore survey [24]. Sampling sites were located in the southern part of the Espinhaço Range, specifically in the Serra do Cipó [24].

Sampled soils were generally sandy, acidic, and nutrient-poor. Several soil properties, such as organic matter, fine sand, amount of aluminum, and soil acidity, positively correlated with altitude. The highest values of AMF spore density were discovered at intermediate levels (1100 m a.s.l.), presumably due to lower levels of phosphorus and high aluminum values, which resulted in a stress-induced increased production of AMF propagules. Additionally, the research findings suggested that AMF density was influenced by common AMF species, which were also present at intermediate levels. Furthermore, alterations in soil characteristics, such as organic matter, also affected AMF distribution along the gradient to a certain extent. [24]

Along with AMF spore density, the AMF species richness also peaked at middle elevations. The most abundant genera, namely *Acaulospora* with 14 species and *Glomus* with 10 species detected, were found across the whole gradient. *Glomus invermaium* appeared to have the highest occurrence frequency with 84 % at the majority of altitudes, *Claroideoglomus etunicatum* ranked second with 68 % and lastly, *Glomus glomerulatum* ranked third with 66 % (Figure 1.3). [24]

Another Brazilian study examined the effect of different montane habitat types on the diversity and distribution of AMF along a single elevational gradient of 1451-1958 m a.s.l. Similar to the prior study, the identification of AMF was based on spore morphology. However, in this case, the studied sites were located approximately 700 km north of Serra do Cipó in the tropical mountains of Serra das Almas. The vegetation of Serra das Almas also consists of rupestrian shrublands. The five examined habitat types included high-altitude *cerrado* savannas (HAC), natural grasslands (GRA), gallery forests (GAF), natural rocky rupestrian fields (shrublands; CAR) and rocky rupestrian field in the regeneration stage (CRR). [26]

*Glomus* with nine and *Acaulospora* with eight species recorded were identified as the most abundant genera across all sampling sites, followed by *Scutellospora* with five species. There were several significant differences in the abundance of spores among AMF genera

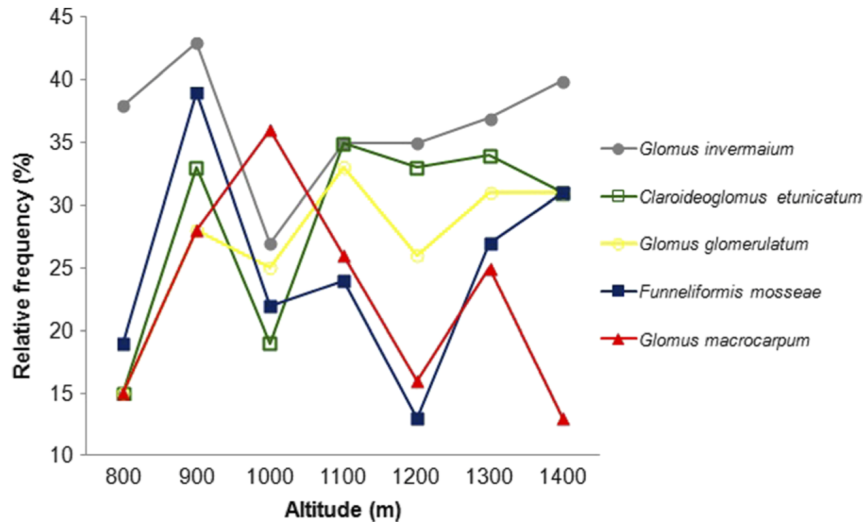


Figure 1.3: “Relative frequency of the most common AMF species in relation to the number of AMF species sampled along the altitude gradient in the rupestrian grassland complex, Serra do Cipó, Brazil. Species richness represents the number of AMF species at each sampled altitude.” [24]

regarding habitat types (Figure 1.4). For example, the abundance of *Glomus* varied among all habitat types, with the highest abundance in CAR and GAF and the lowest in CRR. Similarly, *Acaulospora* showed a peak in abundance in CAR as well; nevertheless, it decreased considerably in HAC. *Bulbospora*, on the contrary, demonstrated an exact opposite trend than the one of *Acaulospora*. However, there was no evident variation among habitat types in the average AMF species richness and diversity. Moreover, there was a considerable shift in the AMF community composition between the habitats of CAR and CRR, as well as between CRR and GAF. [26]

Despite the initially proposed hypothesis that AMF communities change in different habitat types, the only significant variation observed was between natural rupestrian fields, rupestrian fields in the regeneration stage, and gallery forests, hence confirming this hypothesis only partially. Nevertheless, there was a considerable correlation of soil variables with the AMF community structuring, in particular its silt and coarse sand contents as well as soil texture. [26]

Variations in AMF species composition along altitudinal gradients were also investigated in the Southern Ecuadorian Andes. The experimental range was considerably more extensive than in the previous study, from an elevation of 1000 up to 4000 m a.s.l. across six study sites with 646 samples of mycorrhizal fungi. In this case, sampling locations were spread across four elevational belts consisting of dissimilar vegetation types. [27]

Unlike the previously presented studies, the species determination, in this case, was based on the analyses of fungal OTUs, which showed a significant shift in the AMF community

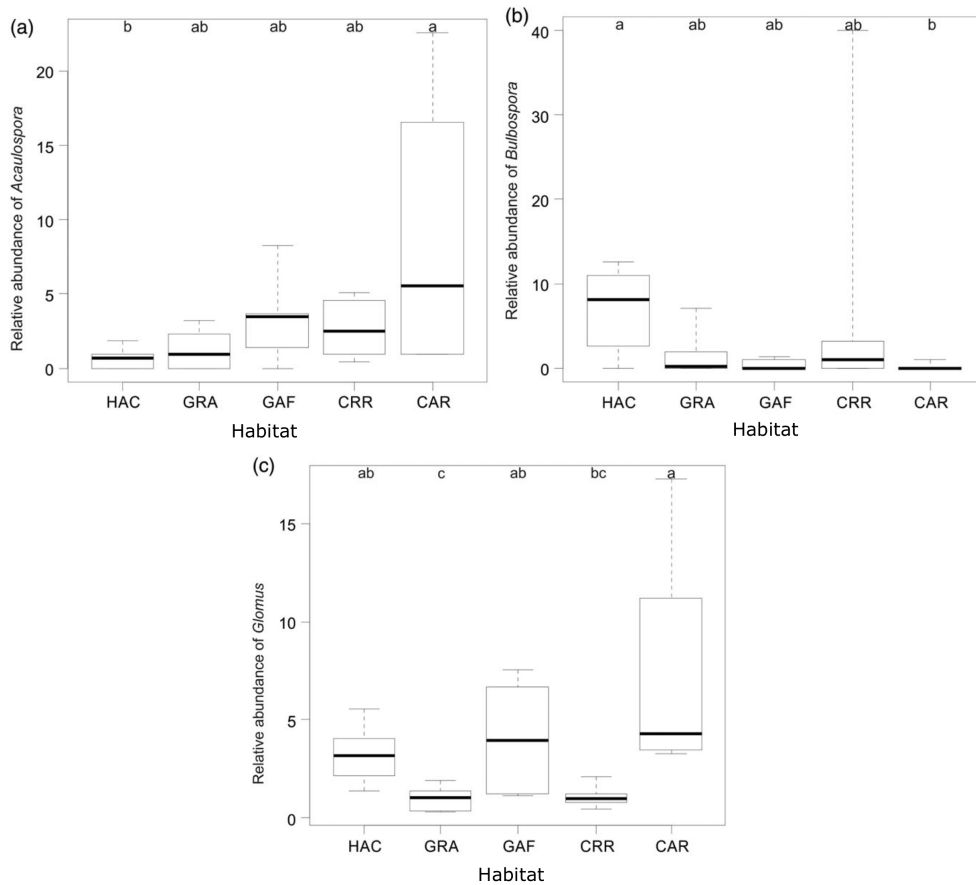


Figure 1.4: “Relative abundance of the Glomeromycota genera (%) *Acaulospora* (a), *Bulbospora* (b) and *Glomus* (c) in HAC (high-altitude *cerrado*), GRA (grassland), GAF (gallery forest), CRR (*campo rupestre* in regeneration) and CAR (*campo rupestre*) habitats, in the Serra das Almas, Bahia, in Northeast Brazil. Means followed by the same letter do not differ statistically by the Tukey test at 5% probability. Interquartile range (box), median (line inside the box) and lower-upper values (whiskers) are shown.” [26]

composition between the elevation of 2000 and 3000 m a.s.l. (Figure 1.5). Lower altitudes were dominated by Glomeraceae, specifically by the most abundant genus *Glomus* and higher altitudes by Acaulosporaceae, namely by the genus *Acaulospora*. [27]

This noteworthy shift in AMF community dominance at such elevation was unexpected. The authors of the study assumed that the main shift in AMF community composition would occur between the elevations 3000 and 4000 m a.s.l. since this is where forest vegetation is being replaced by shrub-like páramo [27]. Nevertheless, another study demonstrated that nitrogen additions can negatively influence the distribution of *Acaulospora* [28], which might explain the switch in AMF species dominance since nitrogen values declined with increasing elevation [27].

The selected case studies representing temperate regions showed a decreasing trend in AMF species richness and a decreasing trend or no significant change in AMF diversity

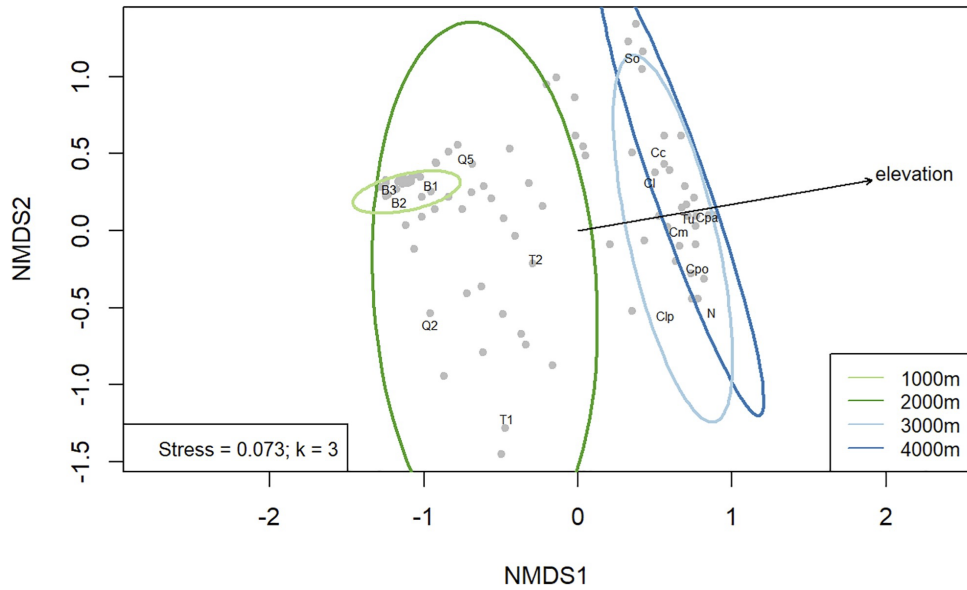


Figure 1.5: “NMDS plot for AM fungal communities. NMDS ordination showing turnover of species composition along elevational gradient. Species scores are shown as gray dots and site scores as black labels. The ellipses around data points show the 95% confidence interval for the 1000 m (light green), 2000 m (green), 3000 m (light blue) and 4000 m (blue) sites. The 1000 m and 2000 m confidence ellipses were not overlapping with the 3000 m and 4000 m ellipses, indicating significant turnover of AMF communities from 2000 m to 3000 m. Overall effect of elevation on AMF communities is supported by PERMANOVA ( $F = 2.6488$ ,  $p = 0.001$ ). Overall stress of the ordination is 0.073 with 3 dimensions ( $k = 3$ ).” [27]

with increasing elevation [19, 20]. In contrast, tropical studies in Brazil demonstrated either peak in AMF species richness at intermediate elevations [24] or no significant change across an altitudinal gradient [26]. Nevertheless, except for the Czech study, which had a small altitudinal scale, and the South Ecuadorian study, none of these research studies examined more than a single elevational gradient. Therefore, there is no conclusive evidence identifying factors that played the most significant role in shaping AMF community responses or AMF species richness changes along these gradients.

## 1.2 Ectomycorrhiza

This part of the thesis will examine the effect of altitude on the second most widespread type of mycorrhiza, called ectomycorrhiza (EcM). Since EcM is predominant in temperate, boreal forests of the Northern as well as the Southern Hemisphere, the majority of relevant research is concentrated in this particular area. EcMF specialize in supplying the host plants with nitrogen, an essential macronutrient for plant growth, which is often limiting at higher latitudes.



Even though EcMF establish mycorrhizal symbiosis with merely 2 % of all plant species [1], mainly woody plants, EcM plays a crucial role in many ecosystem processes, including decomposition, therefore enhancing nutrient availability for plants, as well as carbon sequestering [29]. It has been discovered that EcMF developed from saprotrophic fungi, explaining the origin of oxidative enzymes EcMF produce for the decomposition of soil organic matter [2]. The first part will summarize some studies regarding EcMF diversity in temperate montane ecosystems, followed by some examples from the tropics.

### 1.2.1 EcMF in temperate regions

Temperate forests are characterized by EcM plant species, including broadleaf and coniferous trees. EcM symbiosis, therefore, dominates along the altitudinal gradients of temperate regions. The local and regional patterns of EcMF diversity have been analyzed in the old-growth Hyrcanian forests of northern Iran. Three altitudinal transects near the shores of the Caspian Sea were chosen as sampling sites, namely Asalem (400-2000 m a.s.l.), Nowshahr (100-2400 m a.s.l.), and Savadkuh (400-2700 m a.s.l.). These sites are dominated by subalpine shrubs, submontane and montane deciduous trees. Based on obtained root samples from the three transects, a total of 367 EcMF species was found based on molecular analyses. [30]

The results concerning EcMF species richness variation at the regional scale were consistent with the general assumption that species richness declines with increasing altitude. However, at the local scale, a negative correlation between species richness and altitude proved to be significant both in Asalem and Nowshahr, but not in Savadkuh (Figure 1.6). As for the environmental parameters, regional-scale EcMF species richness negatively correlated with the mean annual precipitation. Yet, the mean annual temperature positively correlated with EcMF species richness at the local scale, in particular at the locations of Asalem and Nowshahr. [30]

The EcMF community composition at the regional scale was mainly structured by altitude, host species, mean annual precipitation, and geographical distance. Similarly, local-scale communities were also significantly affected by altitude and host species; however, temperature and soil nutrients emerged as more important locally. Most common EcMF species within all sampling sites discovered were *Cenococcum geophilum*, *Cortinarius* Ir1 along with Ir2, *Clavulina* Ir1, and lastly *Tomentella* Ir2. According to these findings, EcMF diversity patterns can be influenced not only by various factors along an elevational gradient, but the impact of these factors also differs among local as well as regional scales. Nevertheless, the main drivers, that is altitude, climate, and host plant communities remain constant. [30]

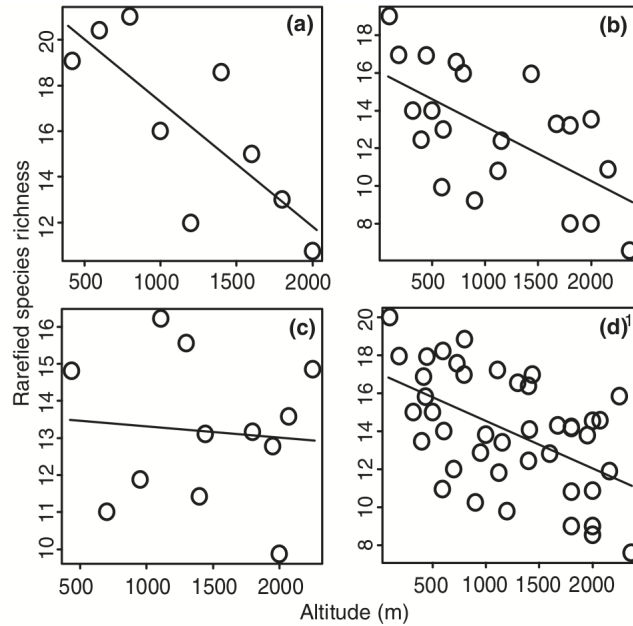


Figure 1.6: “Variation in the total species richness of plots along the altitudinal gradient in different transects and the whole region. Solid lines represent linear regression lines. (a) Asalem ( $R^2 = 0.619$ ,  $P = 0.012$ ); (b) Nowshahr ( $R^2 = 0.384$ ,  $P = 0.003$ ); (c) Savadkuh ( $R^2 = 0.008$ ,  $P = 0.780$ ); (d) whole region ( $R^2 = 0.283$ ,  $P < 0.001$ ). <sup>1</sup>Residuals of the spatial model have been used instead of species richness.” [30]

The second study was conducted in the German Bavarian Alps across a 600m long elevational gradient of Mount Iseler. In this particular research, the main objective was to determine how EcMF diversity will respond not only to elevation but also to the age of the host tree. Three sampling locations were selected across a single altitudinal gradient at 900 m, 1300 m, and 1500 m a.s.l. This analysis examined the association of EcMF with a single host, specifically Norway spruce (*Picea abies*), of two different age forms. [31]

At first, root samples were collected from 45 young (about 10 years old) and 45 old (about 70 years old) Norway spruce trees, in total. Subsequently, sequencing of the ITS region detected 1285 fungal taxa associated with the roots of Norway spruce, 89 % belonging to the Basidiomycota phylum, with the Agaricales, Atheliales, Cantharellales, Russulales, Sebaciniales, and Telephorales as the most abundant orders, followed by Ascomycota with 11 % and the Pezizales as its predominant order. Furthermore, multiple saprotrophic fungal orders were identified as well, for example, Corticiales, Hymenochaetales, and Polyporales. [31]

Findings showed that altitude affected the EcMF community composition and also suggested that various confounding abiotic and biotic factors contribute to the formation of these responses to elevation. For example, fungal members of the order *Sebaciniales* exhibited a decline in abundance with increasing elevation, which can be explained by their inclination toward mineral soils. The distribution of other taxa, such as

*Zelleromyces hispanicus* and *Cortinarius subtortus*, appeared to be limited only to middle and lower altitudes, respectively. However, different elevations did not appear to affect EcMF diversity significantly across the sampling sites. [31]

The host tree age proved to be a considerable factor as well. Older trees displayed a higher fungal diversity in the rhizosphere, presumably owing to their developed root systems and their larger biomass, allowing them to initiate a higher count of symbiotic associations. This study showed that the two factors of interest, namely altitude and host age, displayed a major effect on both the EcMF community composition and diversity in the roots of Norway spruce in the Bavarian Alps. [31]

## 1.2.2 EcMF in tropical regions

As previously mentioned, EcM is dominant in temperate regions, especially in nutrient-poor environments. As a result, little research has been done concerning EcMF diversity in tropical areas to date. Nevertheless, EcMF may predominate in soils even in tropical regions, particularly in monodominant forests consisting of EcM trees [32], which are relatively common in Africa, for example [33]. Therefore, it is essential to turn the attention towards the distribution patterns of EcMF communities in the tropics to understand their role in local ecosystem processes [32].

A study conducted in Borneo aimed to describe EcMF species richness and community composition changes along a single elevational gradient of Mount Kinabulu and to determine the role of MDE in shaping these patterns. Sampling sites were spread across the altitude of 425-4000 m a.s.l. consisting of four different forest types: lowland dipterocarp forest, montane forest, ultramafic rock forest, and granite boulder forest with a subalpine zone. EcM host trees were present along the entire experimental gradient. Except for the fungal genera of *Tomentella* and *Telephora* peaking at the lowest elevation and gradually decreasing with higher levels, EcMF species richness was highest at low and middle altitudes (1000-2000 m a.s.l.), corresponding to dipterocarp and montane forests. The restrictiveness of certain EcMF species to specific forest types suggests that the EcMF community composition was influenced by forest types as well. Due to the difference between the richness predicted by the MDE model and the observed richness, the MDE did not demonstrate any significant effect on EcMF species richness patterns along the slope of Mount Kinabalu (Figure 1.7). [34]

A large-scale survey of fungal diversity in the Andean Yungas corroborates the importance of vegetational types. Sampling was conducted across the entire latitudinal range of the Yungas of northern Argentina within an elevation of 405-2160 m a.s.l., including three forest zones represented by the piedmont, montane, and montane cloud forests.

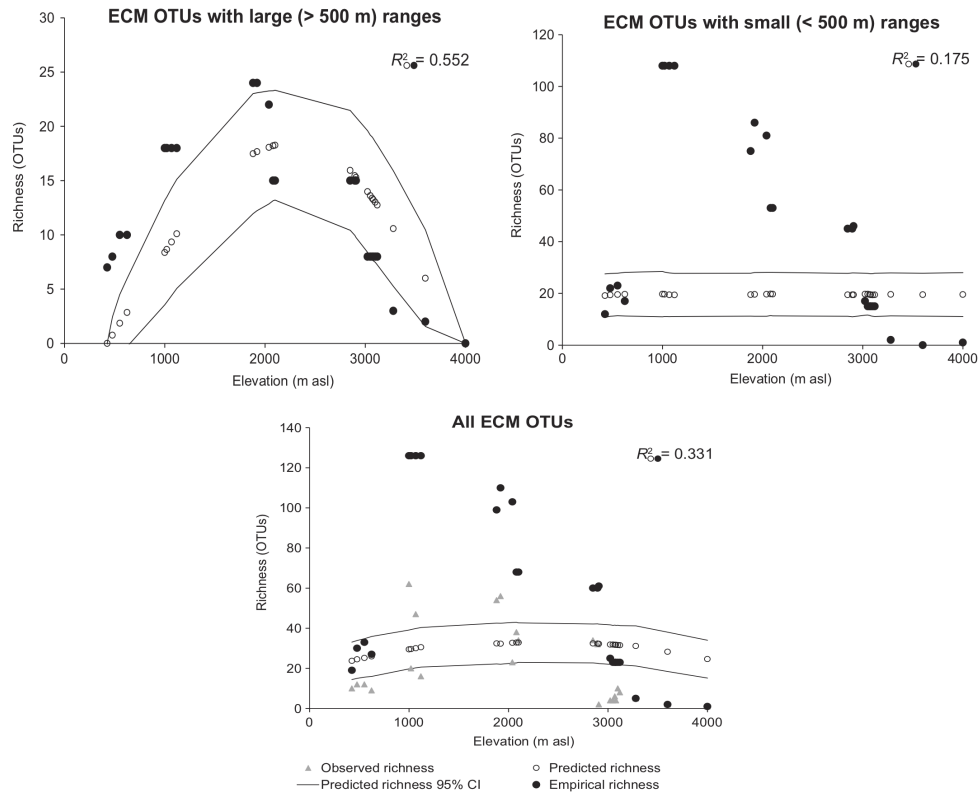


Figure 1.7: “Observed, empirical and predicted mean operational taxonomic unit (OTU) richness as a function of elevation for ectomycorrhizal (ECM) fungi. The bottom graph displays results for all OTUs, whereas the middle and the uppermost graphs show results for OTUs with empirical elevation ranges smaller and greater than 500 m, respectively. Grey triangles and closed circles indicate observed and interpolated empirical richness, respectively, for each field sampling elevation. Open circles show mean richness with 95% confidence intervals (CIs; fine lines) predicted by the mid-domain effect randomization model. The coefficient of determination for the regression of empirical on expected richness appears on each graph. m asl, m above sea level.” [34]

Once again, EcM vegetation was present at each studied gradient, although the lowest elevations were quite scarce in their numbers. Besides elevation, vegetation proved to be crucial in structuring fungal communities across the altitudinal gradient. Moreover, there was a significant inclination of different fungi to certain altitudinal forest types. In this case, the montane cloud forests (1500-3000 m a.s.l.) were the sites with the highest EcMF diversity, characterized by the EcM host dominance of *Alnus acuminata*. [35]

Furthermore, abiotic factors considerably affected fungal communities as well [35]. It is well established that EcMF prefer soils with low pH [36], which is in agreement with the results in this study since montane cloud forests, sites with the highest EcMF diversity, are acidic [35]. Apart from low pH, montane cloud forests are also represented by high nitrogen and soil organic matter contents, similarly contributing to the structuring of fungal communities [35].

Case studies in temperate mountains revealed a linear decrease in EcMF species richness with increasing altitude in Iran [30], but there was no significant difference in species richness along the altitudinal gradient of the Bavarian Alps [31]. However, EcMF species richness in tropical montane forests was highest at low to middle altitudes in Borneo [34], whereas the survey in the Andean Yungas showed a peak in EcMF diversity at the highest elevations [35]. As the study conducted in Iran compared three independent altitudinal gradients, it should be considered as the study with the highest validity from all the studies presented in this section.

### 1.3 Ericoid mycorrhiza

The last mycorrhizal type this thesis will cover is ericoid mycorrhiza (ErM), where substantial knowledge of the ErMF distribution continues to be inadequate. ErM is formed by a single plant family, specifically the Ericaceae family, which is highly diverse in the Cape Floristic Region, the Andes, and the mountains of New Guinea [37]. Yet, Ericaceae plants also represent characteristic vegetation of higher latitudes, in particular tundra and taiga biomes, as well as temperate, boreal forests understory vegetation. Little is known about the biogeography of their ErM symbionts, which are members of the Helotiales order (Ascomycota), including the most common ErMF *Rhizoscyphus ericae* aggregate [38], as well as the Sebaciniales order (Basidiomycota). However, recent studies show that some Ericaceae plants associate with endophytic fungi (ENDF) as well [39]. Furthermore, it was discovered that some ErMF species behave as root endophytes of non-ErM plants (for example, members of the Helotiales order [40]), which may provide additional information about ErMF distribution.

#### 1.3.1 ErMF in temperate regions

*Vaccinium membranaceum*, a member of the Ericaceae family, is a suitable ErM host plant for assessing how root-associated fungal communities might respond to changing altitudinal gradients, owing to its broad ecological plasticity. This question was addressed in a Canadian study conducted in the Rocky Mountains of British Columbia across four elevational zones (875-1923 m a.s.l.). Results showed significant differences in root-associated fungal communities between studied elevations, particularly between the lowest and the highest altitudinal sites. *V. membranaceum* was mainly colonized by two ENDF, namely *Cryptosporiopsis* sp. and *Phialocephala fortinii* at the lower elevations, whereas the highest sampled sites were dominated by ErMF *Rhizoscyphus ericae*. [41]

Species pairs	C-score <sup>a</sup>
<i>Cryptosporiopsis</i> – <i>Rhizoscyphus ericae</i>	136
<i>Cryptosporiopsis</i> – <i>Meliniomyces</i> sp.	88
<i>Lachnum</i> sp.– <i>Cryptosporiopsis</i>	66
<i>Neonectria radicola</i> – <i>Rhizoscyphus ericae</i>	56
<i>Meliniomyces</i> sp.– <i>Lachnum</i> sp.	50
<i>Meliniomyces</i> sp.– <i>Epacris microphylla</i> root-fungi	50
<i>Cryptosporiopsis</i> – <i>Epacris microphylla</i> root-fungi	0
<i>Cryptosporiopsis</i> – <i>Geomyces pannorum</i>	0
Standard deviation = 18.46; mean $\pm$ standard deviation = 95 % confidence interval; upper limit = 46.81; any C-score $\geq 47$ is in upper 2.5 % of distribution.	
a Mean = 9.98.	

Table 1.2: “*Vaccinium membranaceum*-associated fungal species pairs showing C-scores that represent significant distances between each pair. Species with zero distance between them, indicate that these were always found together.” [41]

Co-occurrence of some root-associated fungi in *V. membranaceum* was far more frequent than expected. For example, *Cryptosporiopsis* sp. was more likely found in the roots of *V. membranaceum* with *Geomyces pannorum*, whereas *Cryptosporiopsis* sp. never occurred with *R. ericae* (Table 1.2). In addition, the fungal colonization pattern showed to be non-random, which may be attributed to the influence of host facilitation rather than competition. Despite the varying plant and soil parameters along the altitudinal gradient, such as plant age, pH, or soil water content, there was no apparent correlation with the fungal community structure. [41]

Given the limited number of studies regarding ErMF diversity along altitudinal gradients, this work will provide an insight into ErMF diversity along a vegetation gradient instead. The differences between vegetation types were well illustrated in Scotland on two species of ericaceous shrubs, typical components of heathland and forest understory vegetation, *Calluna vulgaris*, and *Vaccinium myrtillus*. The research discovered a large fungal diversity in both species across all sampling sites. Besides varying fungal communities between *C. vulgaris* and *V. myrtillus*, the hair roots of *C. vulgaris* revealed significant differences in fungal taxa among heathland, *Pinus sylvestris* forest, and the transition zone between those two. Although the taxonomic richness was very similar in roots of both shrubs, ascomycetes (represented mainly by the *Rhizoscyphus ericae* aggregate) were overall more frequent in *C. vulgaris*. Furthermore, the results presented in this study corroborate the associations of ericaceous plants with EcM ascomycetes, in this case, with *Cenococcum geophilum*, as well as basidiomycetes. [42]

The endophytic tendencies of some ErMF in non-ericaceous plants were tested in the Bohemian Forest in the Czech Republic on the roots of Norway spruce (*Picea abies*), a typical EcM conifer. In total, about 36 % of the examined root tips contained an endophyte, *R. ericae* aggregate being the most frequent, specifically *Meliniomyces*

*variabilis*. Moreover, not only was *M. variabilis* able to colonize *Vaccinium myrtillus*, an ericaceous host; it also promoted its growth. Therefore, it was assessed that certain ErMF inhabiting environments with no available ErM plants might exploit ectomycorrhizas as their selective niches. [43]

### 1.3.2 ErMF in tropical regions

Although our current knowledge of the ErMF diversity in tropical biodiversity hotspots is lacking, one study surveyed the effect of elevation, host plants, and spatial distance in montane habitats of Papua New Guinea on the distribution of ErMF as well as ENDF. The highest peak of Papua New Guinea, Mount Wilhelm (4509 m a.s.l.), was chosen as a sampling site within a single elevation gradient of 3387-4483 m a.s.l. The effect of altitude was tested on one Ericaceae species (*Acrothamnus* sp.), while the impact of spatial distance and host species was examined on five Ericaceae species, including the Vaccinioideae, Styphelioideae, and Ericoideae subfamilies, along with one non-ericaceous species (*Hypericum* sp.) at 3600 m a.s.l. [44]

The results of this research showed no significant effect of elevation on neither ErMF nor ENDF species richness; nevertheless, it did have an impact on their community structuring. Besides being the most abundant order across all sites, the Helotiales order was also predominant at the highest elevation. Meanwhile, Sebaciniales, the second most abundant order, preferred lower altitudes. The composition of ErMF and ENDF communities was also influenced by host plant phylogenetic distance, specifically at the genus and subfamily level, respectively (Figure 1.8). However, the biogeographic origin of sampled Ericaceae plants did not contribute to the structuring of fungal communities. As for the only non-ericaceous species in this research, *Hypericum* sp. exhibited similar ErMF and ENDF communities to those of the Ericaceae species in its roots. Lastly, the effect of spatial distance was significant only for the ENDF community. [44]

While primarily highlighting the EcMF diversity in the Andean Yungas, the large-scale study described in the previous section (see EcMF in tropical regions) also analyzed other root-associated fungi, including members of the Helotiales and Sebaciniales orders. Fungal diversity of both orders peaked at the highest elevations in the montane cloud forest (1500-3000 m a.s.l.). These results applied particularly to the Helotiales, considering that certain members exhibited a preference for this vegetation type. [35]

Because research studies focusing on ErMF diversity along elevational gradients in the tropics are scarce, the final case study selected for this section assesses ErMF communities in an Australian tropical cloud forest at a single altitude of 1150 m a.s.l. Root-associated fungal communities were acquired from the hair roots of three *Rhododendron lochiaie*

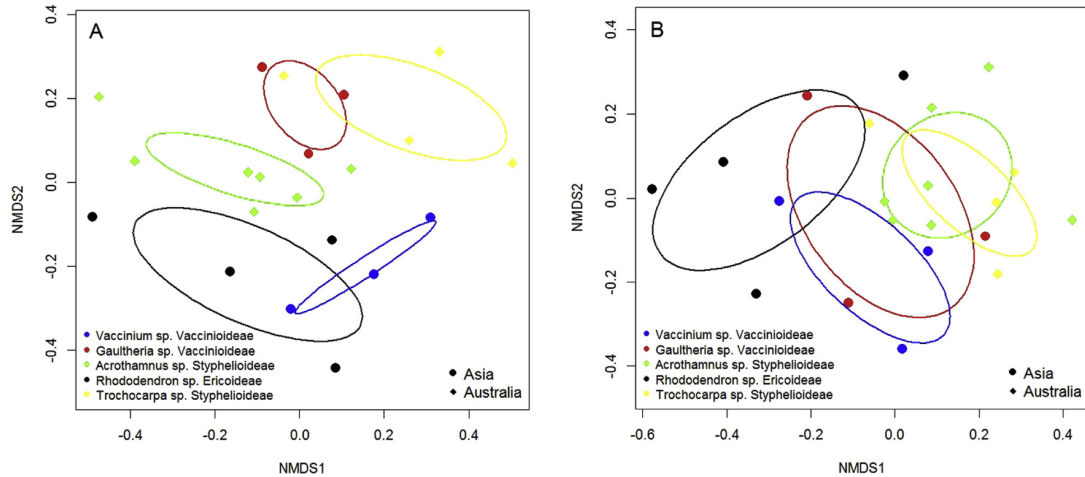


Figure 1.8: “(A) Putative ErMF and (B) ENDF community dissimilarity among the studied Ericaceae genera as revealed by non-metric multidimensional scaling (NMDS) ordination.” [44]

plants, a characteristic ericaceous shrub component of northern Australian cloud forests. The roots of *Rhododendron lochiaie* demonstrated a high fungal diversity with considerable differences in fungal communities between each sampled plant. Based on ITS sequence similarity, approximately 41-51 % of fungal isolates were identified as ErMF members of Helotiales, including isolates resembling the *Rhizoscyphus ericae* aggregate (formerly known as *Hymenoscyphus ericae* which is used in this study) as well as *Oidiiodendron maius*. The second major fungal group was the Xylariaceae order, a common tropical endophytic group. The results show a taxonomic similarity between ErMF communities in tropical and temperate habitats; nevertheless, more research is needed in this field of study, particularly in tropical areas, to gain more conclusive findings. [45]

Interestingly, case studies from both temperate and tropical zones have shown similar responses of ErMF along altitudinal gradients. Small differences were observed in ErMF species richness with increasing elevation in Canada [41] as well as Papua New Guinea [44]. Concurrently, altitudinal differences significantly affected community composition in both studies, demonstrating preferences of certain ErMF species to specific elevations [41, 44] and, moreover, to certain vegetation types, such as of the tropical montane cloud forest in the Andean Yungas [35]. Besides elevation, host plant phylogenetic distance also proved to impact the structuring of both ErMF and ENDF communities and the influence of spatial distance on ENDF communities in Papua New Guinea [44]. Nevertheless, more research is needed on ErMF diversity in the mountains, particularly in the ErMF biodiversity hotspots in the tropics.



## 2. The effect of climate change on mycorrhizal fungi

Rapid changes in the global climate represent one of the biggest issues of the present and the future. Due to anthropogenic activity, the atmospheric CO<sub>2</sub> levels keep rising, crossing the threshold of 400 ppm several years ago. Along with other greenhouse gases, such as methane, N<sub>2</sub>O, and water vapor, CO<sub>2</sub> causes a rise in the average global temperature and, consequently, a decrease in precipitation. According to the Intergovernmental Panel on Climate Change (IPCC), from 1880 to 2012, the global temperature rose by 0.85 °C, and the predictions for upcoming decades estimate a much steeper rise if no precautions are taken [46]. These changes can have a tremendous impact on ecosystems, leading to a decline in biodiversity and shifts in species distribution, especially by the migration of species to higher latitudes as well as altitudes [47].

Soils are considered to be the largest carbon sink, sequestering up to 1/3 of global carbon. Furthermore, 73 % of the world's soil carbon is stored in forests [48], and based on the latest data, the most extensive sink is located in temperate and subarctic regions of the Northern Hemisphere [49]. Since climate is one of the most important factors influencing carbon sequestration and soil carbon losses [50], changes in global climate can disrupt the carbon balance through a rise in soil temperatures and increased microbial respiration, causing a positive feedback to atmospheric CO<sub>2</sub> levels [47].

Mycorrhizal fungi are an inseparable component of soil carbon storage because of the interface they provide between the roots of plants and the pedosphere. Once plants allocate organic compounds to their symbionts, mycorrhizal fungi can either store the acquired carbon in the soil or release it back to the atmosphere through respiration. The role of mycorrhizas in carbon cycling is reinforced by the so-called Gadgil effect, a phenomenon explaining the inhibition of decomposition rates in the soil due to the competition for resources between EcMF and saprotrophic fungi, which results in an increased carbon sequestration [51]. Aside from that, ErMF contribute to the accumulation of carbon in tundra and boreal forests by forming mycelium that is highly resistant to decomposition [52]. Additionally, some EcMF and ErMF possess saprotrophic abilities, potentially participating in the decomposition of soil organic matter [53, 54].

Elevated temperature directly affects the physiology and distribution of both aboveground and belowground communities, including plants and mycorrhizal fungi, respectively [55]. On the other hand, increased CO<sub>2</sub> concentrations in the atmosphere mainly impact plants, which may respond by accelerated growth, increased photosynthesis, and productivity, affecting mycorrhizal fungi indirectly through increased carbon

allocation [56]. It has been suggested that this could lead to shifts in the composition of mycorrhizal fungal communities favoring species that will invest extra carbon in developing their long-distance mycelia for increased nutrient uptake demanded by plants [47]. Furthermore, mycorrhizal symbiosis is considered to be an important factor for facilitating plant establishment in new environments, as plants will continue to migrate upward and northward [57].

As previously mentioned, soil communities, including mycorrhizal fungi, and their interactions with plants, are crucial for ecosystem processes, such as nutrient cycling or carbon sequestration [55]. Aside from their role in plant acclimatization due to global warming, mycorrhizal fungal communities also stabilize terrestrial ecosystems by establishing mycorrhizal networks, and consequently, mycorrhizas may play a significant role in alleviating the impacts of climate change [47]. To better predict ecosystem responses to climate change along with shifts in species distribution, we must expand our knowledge of mycorrhizal fungal distribution along altitudinal gradients, since they represent a suitable proxy for such predictions.

## **2.1 Altitudinal gradients as long-term models for predicting future shifts in the composition of fungal communities**

Vegetation shifts along mountain slopes resulting in an upward expansion of treelines [58] and altered plant species distribution, including the colonization of new species, towards higher elevations are a well-known phenomenon [59]. However, it is critical to explore how these shifts will affect the above- and belowground linkages and at what rate, particularly in the mountains [60]. Besides warming-induced accelerated nutrient cycling and increased net primary productivity, shifts in vegetation may be reflected in long-term changes in soil organic matter, due to altered quantity as well as quality of plant litter [60]. Since soil organic matter is crucial in nutrient cycling, its modification could largely impact the overall functioning of ecosystems [60].

The study of altitudinal gradients represents one of the most effective methods of disentangling these plant-soil interactions. Given the abrupt climate transitions that occur along mountain slopes, it allows us to analyze long-term ecosystem responses to changing temperatures. The following Swedish study attempted to address these issues by testing shifts in soil communities, including mycorrhizal fungi, to increasing elevation as well as different vegetation types and how these changes may affect belowground community functioning, specifically soil nutrient cycling [61].

The altitudinal gradient ranged from 440 to 900 m a.s.l. with a temperature difference of 3 °C between the lowest and the highest elevations during the growing season, allowing to authentically illustrate the predicted temperature increase by the end of this century according to the IPCC [61, 62]. At each elevation, there were three distinct vegetation types comprised of heath, dominated by ericaceous shrubs, meadow, with prevailing herbaceous plants, and *Salix*-dominated vegetation, all commonly found in the subarctic [61]. Based on applying the phospholipid fatty acid (PLFA) analysis it was determined which belowground communities were present in the sampled soils [61].

According to the study, soil communities responded to increased elevation through changes in their abundance and composition. However, these responses differed with respect to each vegetation type. For example, increasing elevation in heath and meadow vegetation resulted in a decreased abundance in AMF, but *Salix*-vegetation showed an increasing abundance of AMF with increasing elevation. Moreover, plant and soil communities often demonstrated coordinated responses to environmental factors, suggesting potential linkages within above- and belowground communities. Furthermore, there were also differences in the degree of coordination among distinct soil communities across vegetation types. [61]

The linkage between above- and belowground communities was also analyzed along an altitudinal gradient of four peatlands in Switzerland. Peatland ecosystems represent a significant long-term carbon sink formed by the accumulation of plant litter in the form of peat. The expansion of ericaceous shrubs upward and northward caused by global warming may outcompete mosses of the genus *Sphagnum*, which are major contributors to the peat formation, eventually resulting in increased carbon feedback to the atmosphere. Therefore, our understanding of plant-soil interactions in these ecosystems is important. [63]

The elevation of studied sites ranged between 585 and 1885 m a.s.l. with a soil temperature difference of 5 °C. The determination of soil communities at each elevation was also based on the PLFA analysis. The results of this study showed a decrease in both the aboveground biomass of ericaceous shrubs and fungal biomass with increasing altitude, supporting the potential linkage between shifts in vegetation and soil communities. [63]

Findings of both studies suggest that different vegetation types may play an important role in regulating the effects of ongoing climate change on soil communities and, thus, the functioning of entire ecosystems [61, 63]. However, the coordinated responses between plants and soil biota may be hampered by various factors, such as different dispersal abilities, potentially disrupting above- and belowground linkages [64]. Nevertheless, more research is needed to enhance our understanding of future ecosystem responses to global warming.



# Conclusion

The case studies presented in this thesis showed very contrasting results on mycorrhizal fungal diversity along altitudinal gradients. Nevertheless, there seems to be a decreasing trend of AMF and EcMF diversity with increasing elevation in temperate studies [19, 20, 30], whereas AMF and EcMF diversity in the tropics tends to peak at either intermediate levels [24, 34] or even at the highest elevations of mountain slopes [35]. As for ErMF, both studies showed that elevation did not have any significant effect on ErMF species richness but strongly impacted the composition of ErMF community across the changing altitude within mountains [41, 44].

The general tendency of mycorrhizal fungal diversity to decline with increasing elevation in temperate regions may lead to the lower availability of suitable mycorrhizal symbionts for the host plants at higher altitudes. Consequently, the altered distribution of mycorrhizal plants due to the advancing climate change may result in the colonization of sites with low mycorrhizal fungal diversity, potentially causing greater stress for plants. Therefore, dispersal abilities of mycorrhizal fungi may determine the fate of migrating mycorrhizal plants and substantially affect the composition of plant and soil communities.

So far, there is no definitive conclusion regarding which factor is the most significant driver of the diversity of mycorrhizal fungi across these environmental gradients. To a certain extent, altitude affects mycorrhizal fungi and their distribution, either via differing climatic conditions or other abiotic and biotic factors that covary with elevation. Aside from temperature, mycorrhizal fungi can be influenced by precipitation, soil pH, nutrient availability, and the composition of plant communities. Moreover, fungal species might respond differently to each factor. For example, it was hypothesized that the low host specificity of ErMF might diminish the influence of elevation on ErMF species richness [44].

There are several ways to expand our current knowledge of mycorrhizal fungal biogeographical and diversity patterns. Firstly, it is absolutely necessary to conduct more research across separated altitudinal gradients at local as well as regional scales. This will allow us to disentangle the role of various biotic and abiotic factors associated with elevational changes on mycorrhizal fungal communities and provide validation of conclusions obtained from single altitudinal gradients. Secondly, studies should adopt uniform sampling strategies and methodological approaches. Since each study varies in its designed experiment, it is problematic to compare the presented results. Furthermore, some methods are more precise than others, such as the identification of fungal species based on molecular techniques (e.g., DNA metabarcoding) rather than fruiting body

surveys. Lastly, it is crucial to turn the attention towards tropical regions, where the number of studies still lacks, particularly regarding ErMF diversity.

In order to predict future shifts in species distribution and ecosystem responses to global warming, it is necessary to conduct more experimental studies along altitudinal gradients. There are two main time-based approaches that can be taken. Short-term experiments, for example, encompass transplanting plants to different elevations and studying their responses; however, the time-lags in some environmental processes might not be taken into account. On the other hand, long-term experiments based on observing shifts in species distribution along an altitudinal gradient spanning ten or more years might provide more accurate results.

To conclude, this thesis sheds light on how altitude drives fungal diversity patterns of three mycorrhizal types (arbuscular mycorrhiza, ectomycorrhiza, and ericoid mycorrhiza) and what environmental factors, biotic and abiotic, contribute to mycorrhizal fungal community shifts along altitudinal gradients. It also elucidates the significance of mycorrhizas in various ecosystem processes and thus the necessity for more research in the field of mycorrhizal fungal biogeography.

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