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MTA Doctoral Dissertation

From phylogeography to landscape ecology of fungi: patterns in fungal diversity and distribution at various spatial scales and their relationships with environmental factors

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1. Introduction and research aims

Microorganisms represent most of the Earth's biodiversity and play crucial roles in ecosystem processes, providing functions that ultimately sustain all life. Fungi, the focus of this dissertation, represent one of the largest groups of living organisms with key roles in the functioning of terrestrial ecosystems. The taxonomic identity, genetic diversity, distribution, and abundance of species that make up the fungal community at a given site are expected to affect the functionality of their communities, given the metabolic variability of fungal species (Read and Perez-Moreno 2003). Plant interactions with soil fungi (e.g., root symbionts, decomposers or pathogens) determine ecosystem functioning, primary productivity, and nutrient cycling in terrestrial habitats worldwide (Wardle 2002).

There still are important gaps in our knowledge regarding the factors that influence the distribution of fungal species at different spatial scales. Our understanding of how the structuring of their communities and their resilience to stress and disturbance are influenced by environmental variables is still in its infancy and the series of studies featured in this dissertation were meant to close some of these knowledge gaps. Beside environmental factors, the role of biotic interactions in fungal community composition is considered important, although more difficult to estimate and are also influenced by environmental factors and phylogeographic histories of the species involved. For example, owing to functional differences among species, species-rich mycorrhizal communities tend to promote plant diversity, plant growth and nutrient uptake from soil (van der Heijden et al. 2008). Similarly, high diversity of pathogens may also enhance plant richness by specifically suppressing dominants through the mechanism of density-dependent mortality (Bagchi et al. 2014, Comita et al. 2014). The interactions between vegetation and soil microbiome have important ramifications for below- and above-ground diversity and community dynamics of all biotic communities as well as their resilience to environmental stressors (e.g., climate change) and their ability to regenerate following disturbance (e.g., deforestation).

A large part of my scientific research in the twenty years since my first Ph.D. has been devoted to studying the roles of phylogeography, landscape heterogeneity, abiotic factors and resulting habitat diversity in explaining observed spatial patterns of diversity and composition of fungal communities using environmental DNA sequence data generated from soil samples. The research projects included in this dissertation span several biomes and are organized according to interconnected conceptual themes, such as fungal phylogeography, compositional changes of fungal communities along (meso)climatic and edaphic gradients at various spatial scales, and the responses of soil fungal communities to various aspects of climate change.

1.1. Phylogeography of arctic and boreal fungi

Until recently, microscopic organisms (both prokaryotic and eukaryotic) were presumed to have essentially global distributions, i.e. "everything is everywhere, but the environment selects" (Finlay 2002). This was based on the assumptions that populations were so large and dispersal was so effective in most microorganisms that any tendencies toward geographic isolation and speciation were swamped by gene-flow and, hence, microbes were

thought to lack detectable biogeography (Fenchel and Finlay 2004). Where geographic patterns of genetic structure were seen in microbes, the question arose as to whether it is due to selection by the habitat or historical limitations on dispersal (Martiny et al. 2006).

Fungi share some features with prokaryotic microbes: many species are unicellular and nearly all fungi disperse via single celled mitotic and/or meiotic spores. They also share many features with other eukaryotes, including discrete evolutionary lineages that are not interconnected by lateral gene transfer. A number of molecular phylogenetic studies summarized in Taylor et al. (2006) have demonstrated inter-continental genetic breaks in cosmopolitan fungal morphospecies. However, at present, our understanding of these patterns is very coarse and there are examples of fungi capable to disperse over long distances and to become established (Kärnefelt 1990, Galloway and Aptroot 1995, Brown and Hovmøller 2002, Moyersoen et al. 2003, Feuerer and Hawksworth 2007, Moncalvo and Buchanan 2008, Printzen 2008). Furthermore, although ecological attributes likely play a role in the dispersal capacities of fungal taxa, it is little known to what extent fungi inhabiting the same biome share phylogeographic patterns and whether or not there is any general trend among them.

In addition to the question of long-distance dispersal, characterizing the phylogeographic population structure of species is important to better understand their resilience towards environmental or anthropogenic stressors. Climatic changes during the Quaternary Period dramatically influenced the distribution of flora, fauna, and funga in high latitudes. During glacial maxima, plants, animals, and fungi were forced to unglaciated refugia, from which they recolonized newly exposed areas in warmer interglacial periods. Reconstruction of these historical events is of paramount importance because they had major influences on past speciation events and present population structures.

As a result of currently warming temperatures, shifts in land surface vegetation in northern high latitudes have already been observed (e.g., Chapin et al. 1995, Bret-Harte et al. 2002, Stow et al. 2004). However, possible responses of fungi to climate change and their potential roles in vegetation change are scarcely known. At circumpolar scales, the ability of fungi to cope with the changing arctic environment is likely to be related to their genetic diversity. According to basic principles of conservation genetics, populations possessing a small amount of genetic diversity are more susceptible to regional extinction during times of stress (e.g. rapid climatic change) than genetically diverse populations (Avise 2000). Another important aspect is the degree to which fungi are able to follow shifts in regional climate, colonize newly exposed, suitable habitats (e.g., following receding glaciers or advancing treelines) and to exchange genes with populations inhabiting different geographical regions. The capacity to migrate is of particular importance, because climate warming is causing a northward shift in the distribution of many arctic and boreal species, and the dispersal capabilities of individual species will greatly influence the composition of future communities, particularly in newly colonized areas (Alsos et al. 2007).

Comparative phylogeographic analyses can contribute to broader studies of ecology and evolution in at least three principle ways: (1) phylogeography can provide an evolutionary and geographical context for the species comprising ecological communities, therefore, permitting determination of historical and spatial influences on patterns of species richness and community composition (e.g. Ricklefs and Schluter 1993); (2) phylogeographic analyses can identify historically and evolutionarily independent regions that can be considered as natural

replicates from which generalizations about specific processes can be tested statistically (Bermingham and Moritz 1998); (3) an understanding of historical responses to changes in the landscape and the identification of evolutionarily isolated areas can inform conservation strategies (Moritz and Faith 1998). From the perspective of this dissertation, perhaps the most important aspect of phylogeography is that it results in differences among regional species pools, from which local communities are assembled via deterministic (e.g., niche-based) and stochastic (e.g., dispersal) processes, as detailed in the later chapters on fungal community ecology in different biomes.

1.2 Fungi in the changing Arctic

Terrestrial areas of the Arctic cover ca. 7 567 000 km^2 (appr. 5% of Earth's land surface), spread over Russia, Norway, Iceland, Greenland, Canada and the U.S.A. (Callaghan et al. 2004). Climatically, the arctic tundra is often defined as the area where the average temperature for the warmest month is below 10 °C (Walker et al. 2005), however, mean annual air temperatures varies greatly according to location, even at the same latitude. The growing season is short, varying between 3.5 to 1.5 months from the southern to the northern boundaries. The cool summers and prolonged and cold winters produce a continuous permafrost soil layer, and a snow cover that lasts for two thirds of the year (Sturm et al. 2005).

At landscape scale throughout arctic regions, the influence of topography on drainage and soil moisture is particularly strong due the presence of permafrost. Here, the effect of topography is two-fold, as it not only affects the direction of water movement in the soil, but also influences the position of permafrost and the depth of active soil layer, i.e. the upper layer that thaws seasonally. This greatly influences soil development, the composition of tundra communities, and ecosystem processes (Walker 2000). Several studies in the Arctic observed clear shifts in the composition plant and fungal communities across gradients of bioclimates, primary succession, and nitrogen (N) deposition (Bjorbækmo et al. 2010, Lilleskov et al. 2011, Blaalid et al. 2012, Fujimura and Egger 2012, Timling et al. 2012), in response to varying soil chemical properties (Siciliano et al. 2014), or amongst habitats and rhizospheres of contrasting plant species in the Arctic (Wallenstein et al. 2007, Timling et al. 2014, Shi et al. 2015).

The arctic tundra is considered a maritime biome, because appr. 80% of non-alpine tundra is located within 100 km of a coastline (Walker et al. 2005) and because arctic sea surface and sea ice cover temperature have been shown to be closely linked to adjacent land surface temperature, precipitation and primary productivity (Bhatt et al. 2010). As a result of the retreating sea ice, arctic land surface temperatures have increased and will continue to increase, causing major changes in terrestrial ecosystems (Kaufman et al. 2009).

Fungi play central roles in the functioning of terrestrial arctic ecosystems due to their roles as symbionts (e.g. mycorrhizae, endophytes, lichens) and decomposers. Almost all plants in polar and subpolar habitats are highly dependent on mutualistic relationships with mycorrhizal fungi for survival in these nutrient-poor environments. Given their intimate relationships with plants in a wide range of symbioses, the landscape-level community dynamics of fungi likely are influenced by vegetation patterns driven by topographic,

mesoclimatic and edaphic factors. In addition, fungi, through their facilitation of certain symbiotic plants, are expected to play important roles in climate-driven vegetation changes.

Warming-induced changes have already been observed in terrestrial arctic ecosystems, including higher microbial activity and resulting increased plant nitrogen (N) availability (Chapin 1983, Aerts 2006), faster C turnover in soils (Hobbie and Chapin 1998; Shaver et al. 2006), and compositional shifts in land surface vegetation (Chapin et al. 1995, Bret-Harte et al. 2002). For example, shrub cover and abundance has increased, which is expected to have positive feedbacks on ecosystem change and greater climate forcing (Sturm et al. 2001). Greater shrub size leads to increased local accumulation of snow in winter, resulting in increased soil insulation, higher winter and spring soil temperatures, and higher rates nutrient mineralization, with positive feedback on shrub growth and expansion (Sturm et al. 2005). Moreover, the expansion of shrubs lowers surface albedo and increases regional summer temperatures, providing another positive feedback to warming (Chapin et al. 2005).

While vascular plant species diversity is strongly influenced by summer temperatures, soil temperature may be important as a determining factor of soil fungal diversity, particularly in winter, when most fungal metabolic activity takes place (Nemergut et al. 2005). As such, snow depth (the thickness of the insulating layer) and its spatial distribution are expected to influence soil fungal communities at small spatial scales.

The studies included in Chapter 3 were based on samples collected in three arctic regions: in northeastern (NE) and western (W) Greenland, and in northern Alaska, the latter also used for the long-term experimental manipulation study simulating climate change.

1.3 Compositional dynamics of tropical forest fungi along elevation gradients

Tropical forests are a major reservoir of biodiversity and play important roles in global climate regulation and biogeochemical cycling. Most of microbial ecological research has focused on temperate and boreal regions, and, despite the growing number of microbial studies in the tropics, the principal mechanisms that drive microbial community composition within the tropics are poorly known. This lack of knowledge needs urgent redressing. It is crucial to understand how environmental factors, including edaphic and bioclimatic factors as well as anthropogenic impact interact to influence the structure and functioning of microbial communities in tropical forests as integral parts of these ecosystems.

Montane ecosystems generally are recognized as biodiversity hotspots as well as areas of high endemism (Lomolino 2001). Despite representing about one-eighth of the world's land area outside Antarctica, mountains harbor about one-third of all terrestrial species (Spehn et al. 2012, Antonelli 2015). Since the early scientific studies of von Humboldt, Darwin, and Wallace on mountain biota, documentation of changes in species richness and community composition have been central to ecological and biogeographic studies (Lomolino 2001, McCain and Grytnes 2010). Mountains provide unique opportunities to test various ecological hypotheses, such as those relevant to climate change, as they are characterized by gradients of abiotic factors such as temperature and available moisture (Guo et al. 2013). However, in most organismal groups, we lack answers to fundamental questions regarding diversity,

distributional patterns, and community composition in montane systems (Lomolino 2001, Guo et al. 2013, Perrigo et al. 2020).

Numerous abiotic factors that shape biological communities change more or less predictably with increasing elevation. Among these, temperature is the most predictable, with an average decrease of ca. 0.6 °C per 100 m increase in elevation (Barry 2008). In contrast, changes in precipitation along elevation gradients generally are less predictable due to complex relationships of regional climate and topography (Barry 2008). In mid- and high latitudes, precipitation tends to increase with elevation, whereas tropical mountains typically show little variation in rainfall along an elevation gradient or exhibit a moderate mid-elevation peak (McCain and Grytnes 2010). Related environmental factors vary with temperature and precipitation to determine biological productivity, including solar radiation, cloud cover, edaphic properties, as well as habitat surface area due to geometric constraints (Stevens 1992, Rosenzweig 1995). Because organisms occupy niches along elevation gradients according to their physiological requirements and their interactions with other species, changes in community structure with increasing elevation have been a focal point for ecological and evolutionary research, providing insight into spatial patterns of biodiversity and their underlying mechanisms.

Most studies of species richness along elevation gradients have focused on vascular plants and animals (e.g., Parris et al. 1992, Wood et al. 1993, Nor 2001, Cardelús et al. 2006, Ghalambor et al. 2006, Grau et al. 2007, Grytnes et al. 2008, Liew et al. 2010). Fungi represent one of the largest groups of living organisms with key roles in the functioning of ecosystems. Several studies have been conducted in mountains in temperate regions on the distribution of specific fungal functional groups along elevation gradients: phyllosphere fungi (Cordier et al. 2012, Coince et al. 2014), bryophyte-associated fungi (Davey et al. 2013), wood-inhabiting fungi (Meier et al. 2010), arbuscular mycorrhizal (AM) fungi (Gai et al. 2012), foliar endophytes (Siddique and Unterseher 2016, Bowman and Arnold 2018), and ectomycorrhizal (ECM) and other root-associated fungi (Bahram et al. 2012, Nouhra et al. 2012, Coince et al. 2014, Miyamoto et al. 2014, Javis et al. 2015, Rincón et al. 2015, Bowman and Arnold 2018, Schön et al. 2018, Truong et al. 2019, Bueno et al. 2021). On the other hand, species richness and composition of fungal communities in tropical mountains remain scarcely known. There have been a few studies on fungi along tropical elevational gradients based on sporocarps (Gómez-Hernández et al. 2012, Shearer et al. 2015, Rojas-Jimenez et al. 2016) or environmental DNA (Geml et al. 2014, Merckx et al. 2015, Geml 2017, Geml et al. 2017, Oita et al. 2021), each mostly limited to one region of interest. Despite these important advances, we still lack a synthetic view of the ways in which species richness and composition of fungal communities shift with elevation: are similar factors important for different functional guilds and for montane systems in neotropical and paleotropical forests? This gap in our knowledge seems particularly concerning because fungi are major drivers of the diversity and composition of plant communities in tropical forests (e.g., Bagchi et al. 2014) and because fungi, through their interactions with plants, contribute to ecosystem services such as the provision of clean water, food, and air (Bakker et al. 2019).

In the studies featured in Chapter, we compared community composition and richness of diverse functional groups of fungi in forest soils along elevation gradients in five tropical mountain areas: Andean Yungas in northwestern Argentina, Atlantic Forests in southern

Brazil, Central American forests in western Panama, Bornean forests in Sabah, Malaysia, and Oceanian forests in Papua New Guinea.

1.4 Landscape ecology of Pannonian forest fungi

In temperate regions, topography is among the most influential factors that drive the physical environment at the landscape level. Slope aspect in particular is well-known to affect abiotic conditions, primarily due to the amount of solar radiation per surface area, which is a function of the angle of incidence of solar radiation (McCune and Keon 2002). As a result, slopes oriented toward the Equator receive higher intensity and greater duration of solar radiation, which can be 50% higher on south-facing than on north-facing slopes in the northern hemisphere (Geiger 1965; Rosenberg et al. 1983; Gilliam et al. 2014). These contrasting energy inputs can profoundly alter mesoclimatic conditions, particularly air and upper soil temperature, which, in turn, affect relative humidity, evapotranspiration, soil moisture and edaphic processes (Fekedulegn et al. 2003). As a result, slopes with poleward (in this case, northerly) aspect generally are cool and more humid, while slopes with southerly aspect tend to be markedly warmer and drier, particularly in mid- and high latitudes (Holland and Steyn 1975; Méndez-Toribio et al. 2016). For example, Rorison et al. (1986) reported a 2.5-3 °C annual mean temperature difference recorded between adjacent north- and south-facing slopes in a British calcareous grassland, a difference roughly equivalent to that encountered in a shift of 5° in latitude or 500 m in altitude (Barry 1992).

Such aspect-related contrasts in the abiotic environment are intuitively expected to have influence on the composition of biotic communities. Indeed, the effects of aspect on vegetation are well known and clear compositional differences have been found between north- and south-facing slopes in various ecosystems, e.g., in temperate and Mediterranean forests (Whittaker 1956; Sternberg and Shoshany 2001; Gilliam et al. 2014), temperate grasslands (Rorison et al. 1986), boreal forests (Hollingsworth et al. 2006), and arctic tundra (Walker et al. 1994). On the other hand, virtually nothing is known about the influence of aspect on richness and community composition of fungi at landscape level, except two recent studies focusing on arbuscular mycorrhizal fungal richness in boreal forests and arid steppes in China (Chu et al. 2016; Liu et al. 2017). Therefore, how slope aspect affects richness and community composition of various taxonomic and functional groups of fungi remains unknown.

According to the macroecological study of Tedersoo et al. (2014), global-scale fungal diversity and distribution patterns are primarily influenced by climatic factors, mainly mean annual temperature and precipitation, followed by edaphic factors, particularly pH, and spatial patterns due to dispersal limitation. On the other hand, the coupling between vegetation and soil fungal community composition and richness appears to be much weaker, with the exception of ECM fungi (Tedersoo et al. 2014; Peay et al. 2016). Therefore, it is reasonable to hypothesize that the above-mentioned topography-driven environmental differences are expected to influence the diversity and distribution of fungal communities at landscape level as well.

Our studies featured in this chapter focus on the Pannonian biogeographic region, which is unique in Europe, partly because it is a meeting point for species characteristic of distinct

biogeographic regions, such as sub-Mediterranean, Pontic, Balkanian, continental, Atlantic, and Carpathian floristic and faunistic elements, and partly because of Pannonian endemics (Suba 1983; Vojtkó 2002; Sundseth 2009; Vojtkó et al. 2010; Fekete et al. 2016). The study region is in the Északi-középhegység (North Hungarian Mountains), which is characterized by high habitat diversity, due to the wide variety of calcareous, volcanic and igneous rocks (Pelikán 2010) and diverse topography that create a broad spectrum of edaphic and mesoclimatic conditions. This diversity of habitats allows the coexistence of sub-Mediterranean, continental, Atlantic, and Carpathian floristic and faunistic elements often in close proximity, depending on slope aspect, elevation, and geological parent material (Suba 1983; Vojtkó 2002; Vojtkó et al. 2010). With respect to macrofungi, there is a long history of sporocarp-based studies in various areas of the Északi-középhegység (Bohus and Babos 1960; Takács and Siller 1980; Rimóczi 1992, Rimóczi 1994; Tóth 1999; Siller et al. 2002; Albert and Dima 2005; Egri 2007; Pál-Fám et al. 2007; Rudolf et al. 2008; Siller 2010; Siller and Dima 2014). In addition, morphological and molecular analyses of roots colonized by ECM genera *Humaria*, *Genea*, *Tomentella*, and *Tuber* have been carried out in a well-preserved montane beech forest reserve (Kovács and Jakucs 2006; Erős-Honti et al. 2008; Jakucs et al. 2015). However, the diversity and distribution of fungi, particularly microscopic fungi, in various habitats types are still unexplored and I am not aware of any molecular study assessing the richness and community composition of fungal communities in the Pannonian forests before the two studies featured in Chapter 5.

The goals of these two DNA metabarcoding studies were to provide the first insights into the taxonomic and functional diversity of fungi in different Pannonian forest types at a landscape scale and their richness and community composition differ among forest types, which themselves are shaped by topography-driven edaphic and mesoclimatic factors. Specifically, I evaluated the effects of various topography-driven environmental factors on the richness and composition of taxonomic and functional groups of fungi in a wide range of Pannonian forest types in northern Hungary.

2. Phylogeography of arctic and boreal-temperate fungi


Figure 2.1. Arctic tundra landscape in Colesdalen, Svalbard with an ECM fungus (*Cortinarius favrei*) growing in a carpet ECM host dwarf shrubs *Salix polaris* and *Dryas octopetala*, (photos by the author).

This chapter is based upon the following publications:

Geml J**.** 2011. Coalescent analyses reveal contrasting patterns of inter-continental gene flow in arctic-alpine and boreal-temperate fungi. In: *Biogeography of microscopic organisms - Is everything small everywhere?* (Ed. Fontaneto D) Cambridge University Press, p. 177-190.

Geml J, Kauff F, Brochmann C, Lutzoni F, Laursen GA, Redhead SA, Taylor DL. 2012a. Frequent circumpolar and rare transequatorial dispersals in the lichenised agaric genus *Lichenomphalia* (Hygrophoraceae, Basidiomycota) ***Fungal Biology*** 116:388-400.

Geml J, Kauff F, Brochmann C, Taylor DL. 2010a. Surviving climate changes: High genetic diversity and transoceanic gene flow in two arctic-alpine lichens, *Flavocetraria cucullata* and *F. nivalis* (Parmeliaceae, Ascomycota) ***Journal of Biogeography*** 37:1529-1542.

Geml J, Kauff F, Laursen GA, Taylor DL. 2009a. Genetic studies point to Beringia as a biodiversity 'hotspot' for high-latitude fungi. ***Alaska Park Science*** 8: 37-41.

Geml J, Laursen GA, Herriott I, McFarland JM, Booth MG, Lennon N, Nusbaum HC, Taylor DL. 2010b. Phylogenetic and ecological analyses of soil and sporocarp DNA sequences reveal high diversity and strong habitat partitioning in the boreal ectomycorrhizal genus *Russula* Pers. (Russulales; Basidiomycota). ***New Phytologist*** 187:494-507.

Geml J, Laursen GA, O'Neill K, Nusbaum HC, Taylor DL. 2006. Beringian origins and cryptic speciation events in the Fly Agaric (*Amanita muscaria*). ***Molecular Ecology*** 15:225-239.

Geml J, Laursen GA, Taylor DL. 2008a. Molecular phylogenetic diversity assessment of arctic and boreal *Agaricus* taxa. ***Mycologia*** 100:577-589.

Geml J, Laursen GA, Timling I, McFarland JM, Booth MG, Lennon N, Nusbaum HC, Taylor DL. 2009b. Molecular phylogenetic biodiversity assessment of arctic and boreal *Lactarius* Pers. (Russulales; Basidiomycota) in Alaska, based on soil and sporocarp DNA. ***Molecular Ecology*** 18:2213-2227.

Geml J, Timling I, Robinson CH, Lennon N, Nusbaum HC, Brochmann C, Noordeloos ME, Taylor DL. 2012b. An arctic community of symbiotic fungi assembled by long-distance dispersers: phylogenetic diversity of ectomycorrhizal basidiomycetes in Svalbard based on soil and sporocarp DNA. ***Journal of Biogeography*** 39:74-88.

Geml J, Tulloss RE, Laursen GA, Sazanova NA, Taylor DL. 2008b. Evidence for strong inter- and intracontinental phylogeographic structure in *Amanita muscaria*, a wind-dispersed ectomycorrhizal basidiomycete. ***Molecular Phylogenetics and Evolution*** 48:694-701.

Geml J, Tulloss RE, Laursen GA, Sazanova NA, Taylor DL. 2010c. Phylogeographic analyses of a boreal-temperate ectomycorrhizal basidiomycete, *Amanita muscaria*, suggest forest refugia in Alaska during the Last Glacial Maximum. In: *Relict Species - Phylogeography and Conservation Biology*. (Ed. Habel J), Springer p. 173-186.

2.1. Introduction

Before diving into studying landscape-scale distribution patterns of fungi and the environmentl factors shaping it as discussed in the following chapters, I wanted to dedicate a chapter to distribution patterns of fungi at continental and regional scales that ultimately define the local species pool, from which fungal communities of all habitats on a landscape are assembled.

Studying migration in fungi, i.e. the degree to which they are able to disperse and establish in suitable habitats and to exchange genes with populations inhabiting different geographic regions, is fundamental to understand their present geographic distributions and is also relevant for climate change studies. Climatic fluctuations have repeatedly caused latitudinal shifts in the distribution of many species and dispersal capabilities of individual species have greatly influenced the community composition. An improved knowledge of migration history, dispersal capacities, and present-day genetic diversity of species is essential to better understand how species may respond to climate change.

While phylogeography of arctic and boreal plants and animals have been extensively studied (Reiss et al. 1999, Tremblay and Schoen 1999, Abbott and Comes 2003, Brunhoff et al. 2003, Fedorov et al. 2003, Flagstad and Røed 2003, Wickström et al. 2003, Alsos et al. 2005, Dalén et al. 2005, Parmesan 2006, Alsos et al. 2007, Eidesen et al. 2007, Schönswetter et al. 2007, Marthinsen et al. 2008), phylogeography of fungi in arctic and boreal regions has been lagging behind, despite their critical roles in the functioning of these nutrient-poor ecosystems (Callaghan et al. 2004, Printzen 2008). Beside the possible theoretical advancement in our knowledge regarding long-distance dispersal, studying transoceanic gene flow has practical implications in understanding the composition of past, present, and future communities during shifts in species distributions due to climatic changes. In the phylogeographic studies summarized in this chapter, we mainly focused on the circumpolar phylogeography of ectomycorrhizal (ECM) and lichenized fungi, because these two functional groups are particularly diverse and ecologically important in northern high latitudes and are dependent on mutualistic associations with photosynthetic hosts. This dependence on the presence of plant hosts in the colonized area could theoretically make long-distance dispersal and especially establishment more difficult than in free-living fungi, such as saprotrophs.

Our phylogeographic studies on arctic and boreal fungi included in this chapter can be divided into three topics:

1. Phylogeography of the boreal-temperate ECM fungus *Amanita muscaria*: a circumpolar morphological species complex made up of regionally endemic phylogenetic species;
2. Phylogenetic diversity of arctic and boreal ECM genera *Lactarius* and *Russula* in Alaska.
3. Comparative phylogeography of arctic and boreal fungi;
4. Phylogenetic diversity of ECM fungi in Svalbard: a community assembled by long-distance dispersers;

For the first topic, as a conservative test of the extent to which wind-dispersed mycorrhizal fungi may exhibit phylogeographic structure, we chose to study *Amanita*

muscaria. This species is native to temperate and boreal forest regions of the Northern Hemisphere, where it is an ECM fungus with a wide host range (Trappe 1987). Although it is most commonly associated with various birch (*Betula*), pine (*Pinus*), spruce (*Picea*), fir (*Abies*) and larch (*Larix*) species, it is known to form ECM associations with representatives of other genera, particularly when its primary hosts are rare or non-existent in a certain area. *Amanita muscaria* has traditionally been reported as a single morphospecies, although its morphological variations have been interpreted to correspond to intraspecific varieties, such as *A. m. var. muscaria*, *var. formosa*, and *var. regalis* described from Europe and *A. m. var. alba*, *A. m. var. flavivolvata*, and *A. m. var. persicina* described from North America (Jenkins, 1986). This well-known fungus was thought to have little biogeographic structure for the following reasons: 1) it is widely distributed and common throughout its range, 2) its spores are largely wind-dispersed and it produces copious above-ground fruiting bodies (mushrooms), 3) it appears to have little host-specificity as it associates with a wide variety of both coniferous and angiosperm host trees, and 4) it is considered to be an invasive species where it has been introduced in the Southern Hemisphere (Bagley and Orlovich, 2004). We generated and analyzed DNS sequences of multiple genes from herbarium specimens using phylogenetic and coalescent methods to test if phylogenetic relationships of genotypes within the *Amanita muscaria* species complex correlate with their geographic distributions and to estimate intercontinental gene flow (Geml et al. 2006, Geml et al. 2008b, Geml et al. 2009a, Geml et al. 2010c).

For the second topic, we conducted the first molecular phylogenetic assessments on two of the dominant ECM fungal genera in the boreal forests and arctic tundra of Alaska: *Lactarius* and *Russula*. ECM fungi are among the most abundant fungi in boreal ecosystems, and form obligate associations with all tree genera found in this region (e.g. *Alnus*, *Betula, Larix*, *Picea, Populus*, *Salix* etc.) (Smith and Read 1997). Such mycorrhizal associations can form on more than 95% of these trees' roots and participate in the nutrient and carbon transfer between the fungus and the host plant (Smith and Read, 1997). With the exception of the non-mycorrhizal genus *Agaricus* (Geml et al. 2008a) and the ECM *Amanita muscaria* species complex (Geml et al. 2006), species distributions, relationships to taxa in other regions, within species genetic diversity, and phylogeographic origins of boreal Alaskan fungi were, at the time of publication, and still are, very poorly known. Both genera belong to the family Russulaceae, with approximately 350 *Lactarius* and 750 *Russula* known species worldwide (Ainsworth 2008), with new species being described every year. We analyzed ITS rDNA sequences generated in a high throughput fashion from both curated sporocarp collections and soil PCR clone libraries (Geml et al. 2009b, Geml et al. 2010b). The herbarium collections were gathered from across Alaska over a 35-year period. Soil sampling for clone-library construction was carried out at various plots throughout the Bonanza Creek Long Term Ecological Research program (BNZ LTER, http://www.lter.uaf.edu/) in Interior Alaska, representing characteristic types and successional stages of the boreal forest, and along the Alaskan portion of the North American Arctic Transect (NAAT) (Walker 2000, Raynolds et al. 2008), spanning three arctic tundra subzones.

For the third topic, fungi that are widely distributed in the Northern Hemisphere and represent different taxonomical and ecological groups were chosen for the analyses to estimate transoceanic gene flow: the arctic-alpine lichens *Flavocetraria cucullata*, *Flavocetraria*

nivalis, and *Dactylina arctica*, the arctic-alpine ECM agaric *Cortinarius favrei*, the arctic-alpine lichenized agaric *Lichenomphalia umbellifera*, the temperate-boreal ECM fungi *Amanita muscaria*, *Amanita pantherina*, and *Lactarius deliciosus*, the boreal-temperate wood-rotting *Grifola frondosa*, and the temperate lichen *Trapeliopsis glaucolepidea*. Our main goal was to estimate inter-continental migration between populations of arctic-alpine and boreal-temperate fungi in the Northern Hemisphere with the purpose of gaining some insights in the possible mechanisms that play roles in the dispersal capacities of fungi. Beside the possible theoretical advancement in our knowledge regarding long-distance dispersal, the varying capacities of fungi to migrate over vast areas have practical implications in shaping the composition of past, present, and future communities during shifts in species distributions due to climatic changes.

For the fourth topic, we analyzed phylogenetic diversity of ECM fungal communities on Svalbard (Figure 2.1). The Svalbard Archipelago had been proposed as a good model system for studying long-distance dispersal in the Arctic, because of its remote location and geological history (Alsos et al. 2007). Svalbard was almost entirely glaciated during the last glacial maximum (Landvik et al. 1998). Prior to using molecular markers, it had been debated whether Svalbard's flora had survived in local refugia, but genetic studies indicate that colonization by plants occurred after the glacial retreat (Brochmann et al. 2003). This agrees with geological and climatological reconstructions that suggest an extreme ice cover that excluded the local survival of most, if not all, terrestrial plant species (Landvik et al. 1998), with paleorecords that show a sparse arctic vegetation only after 10,000 yr before present (Birks et al. 1994).

2.2. Materials and Methods

Data generation

For a case study on boreal-temperate fungal phylogeography, ninety-eight specimens of *Amanita muscaria* were collected from various geographic regions spanning the known distribution of the species complex. DNA was extracted from small samples of dried specimens using the E-Z 96 Fungal DNA Kit (Omega Bio-tek, Inc., Doraville, GA) or the DNeasy Plant Mini Kit (QIAGEN, Inc., Valencia, CA). DNA sequences were obtained for four loci: *β-tubulin* gene, translation elongation factor 1-alpha gene (*EF1-α*), nuclear large ribosomal subunit gene (LSU), and the internal transcribed spacer (ITS) + 5.8S ribosomal subunit gene region. The primers, PCR and sequencing protocols had been described previously (Geml et al. 2005). Newly generated sequences were deposited to NCBI under accession numbers DQ060871-DQ060923 and EU071826-EU072015 (Geml et al. 2006, Geml et al. 2008b).

For the phylogenetic characterization of arctic and boreal ECM fungal genera *Lactarius* and *Russula* in Alaska, we generated ITS plus partial LSU rDNA (ca. 1300 bp) sequences in a high throughput fashion from both curated sporocarp collections deposited at ALA and soil PCR clone libraries. The herbarium collections were gathered from across Interior Alaska over a 35-year period. Soil sampling for clone-library construction was carried out at various plots of the Bonanza Creek Long Term Ecological Research program (BNZ LTER) in Interior Alaska, representing multiple vegetation types and successional stages of forest development

in Interior Alaska. For example, the upland mixed forest sites, featuring white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*), and Alaska paper birch (*Betula neoalaskana*), represent a post-fire vegetation successional chronosequence on permafrost-free south-facing slopes. In contrast, the black spruce (*Picea mariana*) sites are mostly underlain by permafrost and differ with respect to parent material, hydrology, edaphic, and plant community characteristics. PCR clone libraries were generated from soil DNA extracts from the forest types and subtypes, representing different dominant plant species, stand ages and environmental conditions (Table 2.1). Methods have been described in Taylor et al. (2007). The resulting 65,000 sequences of ITS/LSU clones were subject to BLAST searches to identify *Lactarius* and *Russula* sequences. Of the total of 189 *Lactarius* and 373 *Russula* ITS sequences from soil clone libraries and herbarium specimens were chosen for phylogenetic analyses and were deposited in Genbank (*Lactarius*: EU711563-EU711723, FJ607365-FJ607394; *Russula*: EU711724-EU712096) (Geml et al. 2009b, Geml et al. 2010b). Homologous sequences of non-Alaskan specimens were downloaded from GenBank.

Table 2.1. Habitat, clone library names, plot numbers, and locations for soil samples used in the molecular phylogenetic diversity assessment of ECM fungal genera *Lactarius* and *Russula* in Alaska.

Habitat	Clone library (sampling year)	Plot number	Stand age (years)	Location
Early successional upland mixed forest	UP1 (2004) and UP4 (2005)	UP1 A	23-25	Bonanza Creek LTER, Parks Hwy
		UP1 B	23-25	Bonanza Creek LTER, Parks Hwy
		UP1 C	23-25	Bonanza Creek LTER, Parks Hwy
Mid-successional upland mixed forest	UP2 (2004) and UP5 (2005)	UP2 A	93-98	Bonanza Creek LTER, Parks Hwy
		UP2 B	93-98	Bonanza Creek LTER, Parks Hwy
		UP2 C	93-98	Bonanza Creek LTER, Parks Hwy
Late successional upland mixed forest	UP3 (2004) and UP6 (2005)	UP3 A	225-230	Bonanza Creek LTER, Parks Hwy
		UP3 B	225-230	Bonanza Creek LTER, Parks Hwy
		UP3 C	225-230	Bonanza Creek LTER, Parks Hwy
Black spruce, acidic, dry	TKN7 (2004) and TKN11 (2005)	TKN-0012	200-210	Washington Creek, Elliott Hwy.
		TKN-0122	90-100	Delta Junction, Alaskan Hwy.
		TKN-0001	95-100	Bonanza Creek LTER, Parks Hwy
Black spruce, acidic, wet	TKN8 (2004) and TKN12 (2005)	TKN-0015	170-180	Washington Creek, Elliott Hwy.
		TKN-0022	150-180	Babe Creek, Elliott Hwy.
		TKN-0109	90-104	Caribou Poker Creek Research Watershed, Steese Hwy.
Black spruce, non-acidic, dry	TKN9 (2004) and TKN13 (2005)	TKN-0039	130-190	Goldstream creek, Ballaine Rd., Fairbanks
		TKN-0123	97-100	Delta Junction, Alaskan Hwy.
		TKN-0126	120-130	Delta Junction, Alaskan Hwy.
Black spruce, non-acidic, wet	TKN10 (2004) and TKN14 (2005)	TKN-0051	68-91	UAF Arboretum, Fairbanks
		TKN-0119	280-320	Delta Junction, Alaskan Hwy.
		TKN-0040	179-216	Ballaine Rd., Fairbanks
Arctic tundra, subzone E	NA12 (2007)	HV-zonal	n/a	Happy Valley, Dalton Hwy

tussock-sedge, erect dwarf shrubs				
Arctic tundra, subzone D sedges, prostrate dwarf shrubs, lichens	NA9 and NA10 (2007)	FB-zonal	n/a	Franklin Bluffs, Dalton Hwy
Arctic tundra, subzone C bare soil, lichens, prostrate dwarf shrubs	NA 10 and NA11 (2007)	HI-zonal	n/a	Howe Island, Prudhoe Bay, Beaufort Sea

For the intercontinental gene flow project, we concentrated our efforts on the ITS region, because this locus had been useful in earlier phylogeographic studies in a variety of fungi (e.g., Shen et al. 2002; Palice and Printzen 2004; Oda et al. 2004) and because it is the most frequently sequenced fungal locus and, thus, it usually provides the greatest sample size and geographic coverage for any species. DNA sequence data analyzed in this project comprised mostly newly generated data from specimens we collected in various parts of the Arctic (e.g., in different parts of Alaska, Canada, Greenland, Russia, and Svalbard) or sampled at different herbaria (ALA, C, DAO, DUKE, H, LE, O, QFA etc.), supplemented by conspecific sequences available from GenBank. Because our main purpose was to estimate transoceanic gene flow, only species with several sequences from both Eurasian and North American samples were included (Geml et al. 2010b, Geml 2011, Geml et al 2012a). The final datasets for the individual species contained the following sequences (GenBank accession numbers): *Flavocetraria cucullata* (FJ914765-FJ914812), *Flavocetraria nivalis* (GU067685-GU067729), *Dactylina arctica* (GU981748-GU981760), *Lichenomphalia umbellifera* (AY293955-AY293961, GU810926-GU810969), *Cortinarius favrei* (DQ295071-DQ295085, AF182798, AF325575, GU234036, GU234040, GU234070, GU234087, GU234096, GU234128, GU981746-GU981747), *Amanita muscaria* (AB080777-AB080795, AB080980-AB080984, AB081294-AB081296, AB096048-AB096052, EU071889, EU071893, EU071896-EU071936), *Amanita pantherina* (AB080774-AB080776, AB080784-AB080786, AB080973-AB080978, AB096043-AB096047, AB103329, EF493269, EU525997, EU909452, GQ401354), *Grifola frondosa* (AY049091-AY049141), *Lactarius deliciosus* (AF230892, AF249283-AF249284, AY332557, DQ116886-DQ116904, EF685050-EF685059, EU423914-EU423923), and *Trapeliopsis glaucolepidea* (AY600064-AY600082).

For assessing the phylogenetic diversity of ECM fungi in Svalbard, we generated DNA sequences from sporocarps and soil samples we collected in Svalbard as well as from herbarium specimens from O (Geml et al. 2012b). Soil samples were taken in July 2007 at three sites in Brøggerhalvøya, representing different vegetation types in the vicinity of Ny-Ålesund (78°55’ N, 11°56’ E) (Table 2.2). At each site, we sampled soils from five non-sorted circles (‘frost boils’) and adjacent interboil areas. Due to the high spatial heterogeneity of soil fungal communities, we collected 20 cores, 1.8 cm in diameter and 5-10 cm deep, from each boil, and 20 cores from each interboil. Cores from the same boil or interboil were pooled and mixed, and frozen as quickly as possible, usually within 2 h of sampling. DNA was extracted separately for each frost boil and interboil, resulting in a total of 30 soil DNA extractions (from 600 cores). In addition, we generated DNA sequences from 132 curated specimens of ECM fungi

representing the following genera: *Alnicola*, *Cortinarius*, *Hebeloma*, *Inocybe*, *Laccaria*, *Lactarius*, *Leccinum*, *Russula*, *Thelephora*) collected by M.E. Noordeloos and myself and deposited at the National Herbarium of the Netherlands (L), supplemented by collections from O. Most of these samples had been collected in various areas of Svalbard, including the vicinities of Longyearbyen (Isfjorden) and Ny-Ålesund (Kongsfjorden). DNA was extracted from small samples of dried specimens using the DNeasy Plant Mini Kit (Qiagen, Valencia, CA, USA). In all sporocarp and soil samples, the entire ITS region was PCR amplified and sequenced as described in Taylor et al. (2007, 2008, 2010) and Geml et al. (2009b, 2010ab, 2012ab). For each soil DNA extract, seven replicate PCRs were performed and pooled. To minimize chimera formation, 25 PCR cycles were performed for soil samples. We utilized a molecular tagging strategy to mark PCR products from various sources with DNA tags, which can then be pooled prior to library sequencing (Taylor et al. 2008). We cloned the resulting PCR products into TOPO TA 4.0 vectors (Invitrogen, Carlsbad,CA, USA), then shipped transformed plasmids frozen to the Broad Institute of Massachusetts Institute of Technology and Harvard University, where plating, colony picking, Templiphi reactions and sequencing were carried out on automated equipment. Because of the lack of reference sequences from arctic sites in publicly available databases, we compared the Svalbard soil clone sequences with our soil sequences (D.L.T., unpublished data) generated from sites along the North American Arctic Transect (NAAT), which spans more than 1000 km from the Brooks Range in Alaska to Ellef Ringnes Island in the Canadian Arctic (Fig. 1; http://www.geobotany.uaf.edu/naat). We included 53 soil clone sequences representing 97% ITS sequence identity operational taxonomic units (OTUs) that showed highest similarity to the Svalbard sequences. Sequences were deposited in GenBank (sporocarps: GU234009-GU234165 and JF304373-JF304420; Svalbard soil clone OTUs: HQ215749-HQ215833; NAAT soil clone OTUs: JF304320-JF304372).

Table 2.2. Description of soil sampling sites near Ny-Ålesund used for the Svalbard ECM fungal study (Geml et al. 2012b).

Site	Bioclimatic subzone	Vegetation
Site 1, Outer Kongsfjord; 78°56'09.6"N, 11°48'03.7"E	B	*Salix polaris* and *Dryas octopetala* tundra with *Minuartia stricta*, *Pedicularis lanata*, *Oxyria digyna*, *Saxifraga cernua*, *Cerastium arcticum*
Site 2, Inner Kongsfjord; 78°54'44.5"N, 11°58'55.5"E	C	*Cassiope tetragona* tundra with *Racomitrium*, *Pedicularis lanata*, *Cerastium arcticum, Papaver dahlianum, Silene acaulis, Sagina nivalis, Minuartia stricta, Draba* sp.
Site 3, Outer Kongsfjord; 78°55'16.5"N, 11°51'21.9"E	B	*Salix polaris* and *Dryas octopetala* tundra with *Oxyria digyna*, *Pedicularis lanata*, *Saxifraga nivalis, Saxifraga cernua*, *Cerastium arcticum, Cochlearia officinalis, Silene acualis*

Phylogenetic analyses

Sequence data obtained for both strands of each locus were edited and assembled for each isolate using CodonCode Aligner v. 1.3.4 (CodonCode Inc., Dedham, MA). Sequence alignments were initiated using Clustal W (Thompson et al. 1997) and subsequently alignments

were subsequently refined using Muscle 3.7 (Edgar, 2004), with final manual corrections, when necessary. For each locus, analyses were conducted using the maximum-parsimony method (MP) in PAUP* 4b10 (Swofford 2000), maximum-likelihood (ML) in Garli 0.94 (Zwickl 2006), and the Bayesian method in Mr.Bayes 3.0 (Huelsenbeck and Ronquist 2001). Before combining the loci, we tested for phylogenetic conflict among the different loci (i.e. if individual gene trees significantly differed from each other) using the partition homogeneity test (PHT) with 1000 randomized datasets and heuristic searches with simple addition of sequences in PAUP*. The best-fit evolutionary model for ML and Bayesian analyses was determined for each dataset by comparing different evolutionary models with varying values of base frequencies, substitution types, α-parameter of the γ-distribution of variable sites, and proportion of invariable sites via the Akaike information criterion (AIC) using PAUP* and Modeltest 3.06 (Posada and Crandall 1998). MP analyses were carried out with the heuristic search option using the "tree bisection and reconnection" (TBR) algorithm with 100 random sequence additions to find the global optimum with MAXTREES set to 10,000 in the combined analyses. To test the stability of clades detected, the bootstrap test (Felsenstein 1985) was used with "full heuristic search". The number of replicates were 1000 and 100 for the individual and combined datasets, respectively, with the maximum number of trees saved set to 10 for each replicate. In Bayesian phylogenetic analyses, 200,000 generations were run in four chains for the single-locus, and 1,000,000 generations for the combined datasets. The chains were sampled every 100th generation. When the likelihood scores of trees sampled approached similar values, they were considered to have converged. In each run, trees after this convergence point were used to compute a majority rule consensus tree. Gaps were scored as "new state" in MP and as "missing data" in Bayesian analyses. To compare the likelihood of different tree topologies, two-tailed Kishino-Hasegawa tests were used (Kishino and Hasegawa 1989) with parsimony and likelihood settings specified beforehand. More details are provided in Geml et al. (2006, 2008b, 2010ab, 2012ab).

Detecting geographic population structure and estimating gene flow

For each locus, the number of polymorphic sites and their distribution were determined and nucleotide diversity was measured using π, the average number of nucleotide differences among sequences in a sample (Nei and Li 1979). Between phylogenetic species, divergence was measured as D_{xy}, the average number of nucleotide substitutions per site between species pairs (Nei and Kumar 2000). In addition, genetic differentiation (*Fst*) (Hudson et al. 1992), the number of fixed differences, and shared mutations were calculated for the species pairs, as were the number of positions that were polymorphic in one phylogenetic species but monomorphic in the other. Measures of variation and differentiation were performed with the computer program DnaSP v. 4.10.9 (Rozas and Rozas 1999).

For coalescent analyses, identical sequences were collapsed into haplotypes using SNAP Map (Aylor et al. 2006) after excluding insertion or deletions (indels) and infinite-sites violations. The analyses presented here assume an infinite sites model, under which a polymorphic site is caused by exactly one mutation and there can be no more than two segregating bases. Site compatibility matrices were generated from each haplotype dataset

using SNAP Clade and Matrix (Bowden et al. 2008) to examine compatibility/incompatibility among all variable sites, with any resultant incompatible sites removed from the data set. Tajima's *D* (Tajima 1989) and Fu and Li's *D** and *F** (Fu and Li, 1993) test statistics were calculated with DnaSP to test for departures from neutrality. Genetic differentiation among geographic populations was analyzed using SNAP Map, Seqtomatrix and Permtest (Hudson et al. 1992) implemented in SNAP Workbench (Price and Carbone 2005). Permtest is a nonparametric permutation method based on Monte Carlo simulations that estimates Hudson's test statistics (*KST*, *KS*, and *KT*) under the null hypothesis of no genetic differentiation. For this purpose, sequences were assigned to the geographic regions they were found. Significance was evaluated by performing 1000 permutations. If we found evidence for geographic subdivision, MDIV (Nielsen and Wakeley, 2001) was used to determine whether there was any evidence of migration between pairs of subdivided populations. MDIV implements both likelihood and Bayesian methods using Markov chain Monte Carlo (MCMC) coalescent simulations to estimate the migration rate (*M*), population mean mutation rate (*Theta*), and divergence time (*T*). Ages were measured in coalescent units of 2*N*, where *N* is the population size. This approach assumes that all populations descended from one panmictic population that may or may not have been followed by migration. For each dataset, the data were simulated assuming an infinite sites model with uniform prior. We used 2,000,000 steps in the chain for estimating the posterior probability distribution and an initial 500,000 steps to ensure that enough genealogies were simulated before approximating the posterior distribution. If MDIV showed evidence of migration, MIGRATE was used to estimate migration rates assuming equilibrium migration rates (symmetrical or asymmetrical) in the history of the populations (Beerli and Felsenstein, 2001). We applied the following specifications for the MIGRATE maximum-likelihood analyses: *M** (migration rate *m* divided by mutation rate (μ) and *Theta* generated from the F_{ST} calculation, migration model with variable *Theta*, and constant mutation rate. The numbers of immigrants per generation ($4N_em$) were calculated by multiplying *Theta* of the receiving population with the population migration rate *M**. Subsequently, we reconstructed the genealogy with the highest root probability and the ages of mutations in the sample using coalescent simulations in Genetree v. 9.0 (Griffiths and Tavaré 1994).

2.3. Results and discussion

Phylogeography of the boreal-temperate Amanita muscaria *species complex*

The distribution patterns of the phylogenetic species in the *Amanita muscaria* complex make for a good example for biogeographic endemism. We discovered that the morphologically very similar Eurasian and North American specimens of *A. muscaria* not only belong to different phylogenetic species, but there are several more phylogenetic species in this complex, whose distributions correspond to different biogeographic regions within the North American continent (Geml et al. 2006, Geml et al. 2008, Geml et al. 2010c).

Beside the two major phylogenetic clades in *A. muscaria* that correspond to North American and Eurasian populations (clades I and II in Geml et al. 2008), we found several other divergent lineages that occupy different habitats or regions in the same continent, sometimes in relative proximity. In these cases, spore dispersal is unlikely to be a limiting factor and adaptation to different ecological niches is a more parsimonious explanation. Such ecoregional diversification is particularly obvious in clade III (*A. muscaria var. regalis*) that is

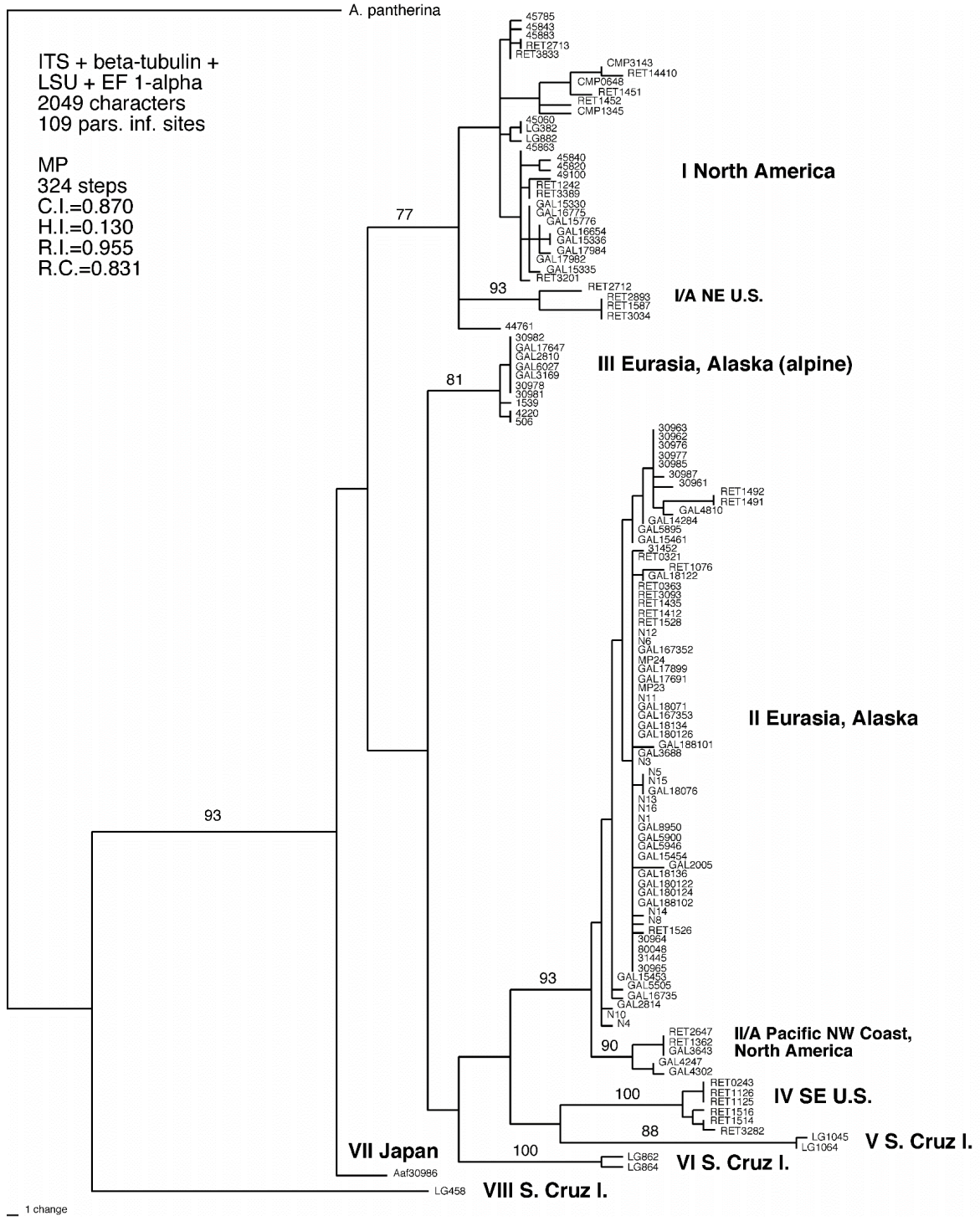


Figure 2.2. A maximum-parsimony tree of representatives of the *Amanita muscaria* species complex based on DNA sequences from four loci, with >70% bootstrap values above the branches (Geml et al. 2008b).

sympatric with the Eurasian clade II (*A. muscaria var. muscaria*) over the former's entire range, but is predominantly found above subalpine habitats and is, therefore, micro-allopatric with the boreal-temperate clade II. Also, clade IV (*A. muscaria var. persicina*) almost exclusively inhabits the mixed pine-oak-hickory forests of the southeastern U.S. and has been collected infrequently as far north as Long Island, NY. Lineages V, VI, and VIII represent formerly unknown phylogenetic species and have only been found to date on Santa Cruz Island off the coast of California (Figure 2.2).

In addition to the species-level ecoregional endemism, we found evidence for additional phylogeographic structure at the population level in clades I and II of the *Amanita muscaria* complex (Geml et al. 2010c). In clade I, coalescent analyses revealed lack of migration and considerable divergence among the four major geographic groups, i.e. 'Alaskan', 'Eastern North American', 'Western North American', and 'Mexican'. The divergence with the weakest support was that found between populations of Eastern vs. Western North America. In this case, the results were only marginally significant, and some current migration could not be ruled out. Future sampling in Canada and the northern Great Plains should provide evidence as to whether Eastern and Western North America represent one or more populations. In clade II, we found a low to intermediate level of migration among most of the geographic groups spanning Eurasia and Alaska. On the other hand, the 'Pacific Northwest North American' group (clade II/A) shows unequivocal evidence for both genetic and ecoregional isolation from

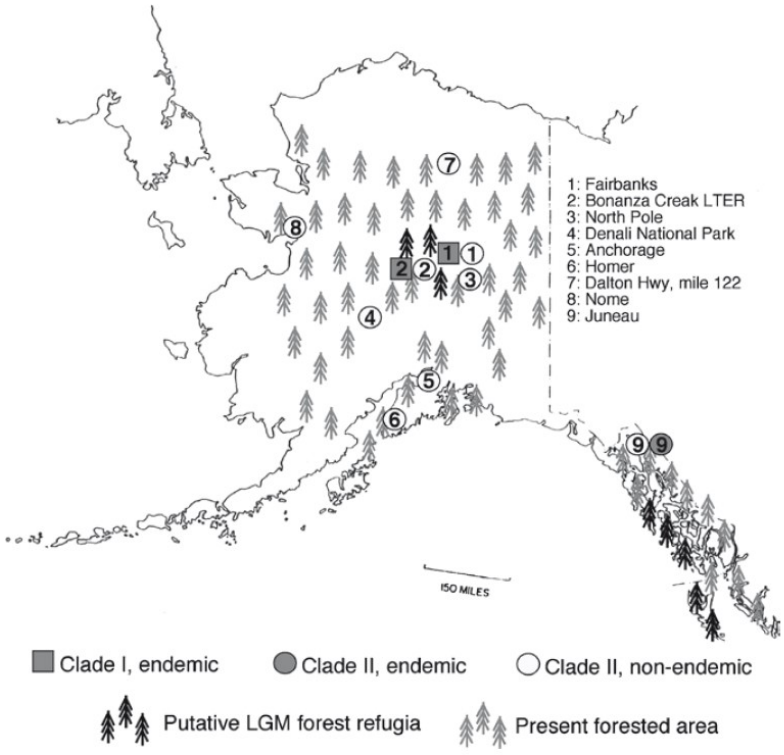


Figure 2.3. Outline map of Alaska showing the collecting locations for the 43 Alaskan specimens included in this study. Dark grey squares and circles indicate sampling localities for endemic haplotypes, while light grey circles refer to haplotypes shared between Alaska and Eurasia. Black stylized spruce drawings mark putative forest refugia during the Last Glacial Maximum (LGM) suggested by this and other studies mentioned in the discussion. Grey tree figures indicate present forested area, without making a distinction between boreal and maritime forests of Interior and Southeast Alaska, respectively (Geml et al. 2010c).

the rest of clade II. This latter group has only been found in the maritime rainforests from Washington state to southeastern Alaska along the Pacific coast of North America. Interestingly, these population-level differences support the idea that at least two independent lineages in the *Amanita muscaria* complex survived the Last Glacial Maximum in Alaskan glacial forest refugia: 1) a Clade I population in the boreal forest in Interior Alaska; and 2) the Clade II/A lineage in the maritime rainforest in Southeast Alaska and the Pacific Northwest (Figure 2.3).

The possible existence of forest refugia in Interior and Southeast Alaska is also supported by several other independent lines of evidence. For example, although previous palynological biome reconstructions suggest that Beringia was covered by arctic tundra (Edwards et al. 2000, Kaufman et al. 2004, Swanson 2003), pollen data by Brubaker et al. (2005) supports the theory that *Picea* forests were present in Eastern Beringia (i.e. Alaska), at least in small fragments restricted to habitats with favorable microclimates. The northernmost distribution of *Picea*, unlike that of *Betula* and *Populus*, is restricted, by definition, to the boreal region. Therefore, Brubaker's findings indicate the existence of the boreal forest biome in Alaska during the LGM. Similarly, Anderson et al. (2006), surveying forest stands across northwestern North America, found several chloroplast DNA haplotypes of *Picea glauca* that were unique to Alaska, suggesting local survival. Maroja et al. (2007) analyzed mitochondrial DNA sequence data from the spruce beetle (*Dendroctonus rufipennis*) and suggested that the postglacial range expansion of these beetles occurred from three refugia, one of which was in Interior Alaska. Forest refugia in Southeast Alaska are also supported by genetic studies in several different taxa. For example, this is a region with high mammalian endemism due to its fragmented landscape and complex glacial history. Even animals, as mobile as wolves, have been shown to exhibit a strong signal of independent histories for the coastal and continental populations (Weckworth et al. 2005). Also, phylogenetic studies of Fleming and Cook (2002) on ermine (*Mustela erminea*) showed that there was at least one lineage strictly endemic to Southeast Alaska that likely survived locally during the Wisconsin glaciation. Locations for such glacial refugia in Southeast Alaska have been proposed by Carrara et al. (2003) based on geological evidence.

Phylogenetic characterization of Lactarius *and* Russula *genera in Alaska*

Our results provided the first phylogenetic characterization of *Lactarius* and *Russula* genera in Alaska and revealed several unidentified clades that had not been documented previously. When comparing the number of phylogroups detected by different sampling methods, we observed that 16 (37.1%) and 13 (30.2%) of the 43 *Lactarius* phylogroups contained only sporocarp or soil clone sequences, respectively, while 14 phylogroups (32.6%) were represented by both soil and sporocarp samples (Figure 2.4). Of the 45 *Russula* phylogroups, 5 (11.1%) only contained sporocarp sequences, 29 (64.4%) only soil sequences, and 9 phylogroups (20%) contained sequences from oil and sporocarps (Figure 2.5). The mismatch between soil and sporocarp sampling is a well-known phenomenon in fungal ecology and is partly caused by the patchy distribution of ECM fungal mycelia in the soil (Horton and Bruns 2001) and the ephemeral appearance of fruitbodies.

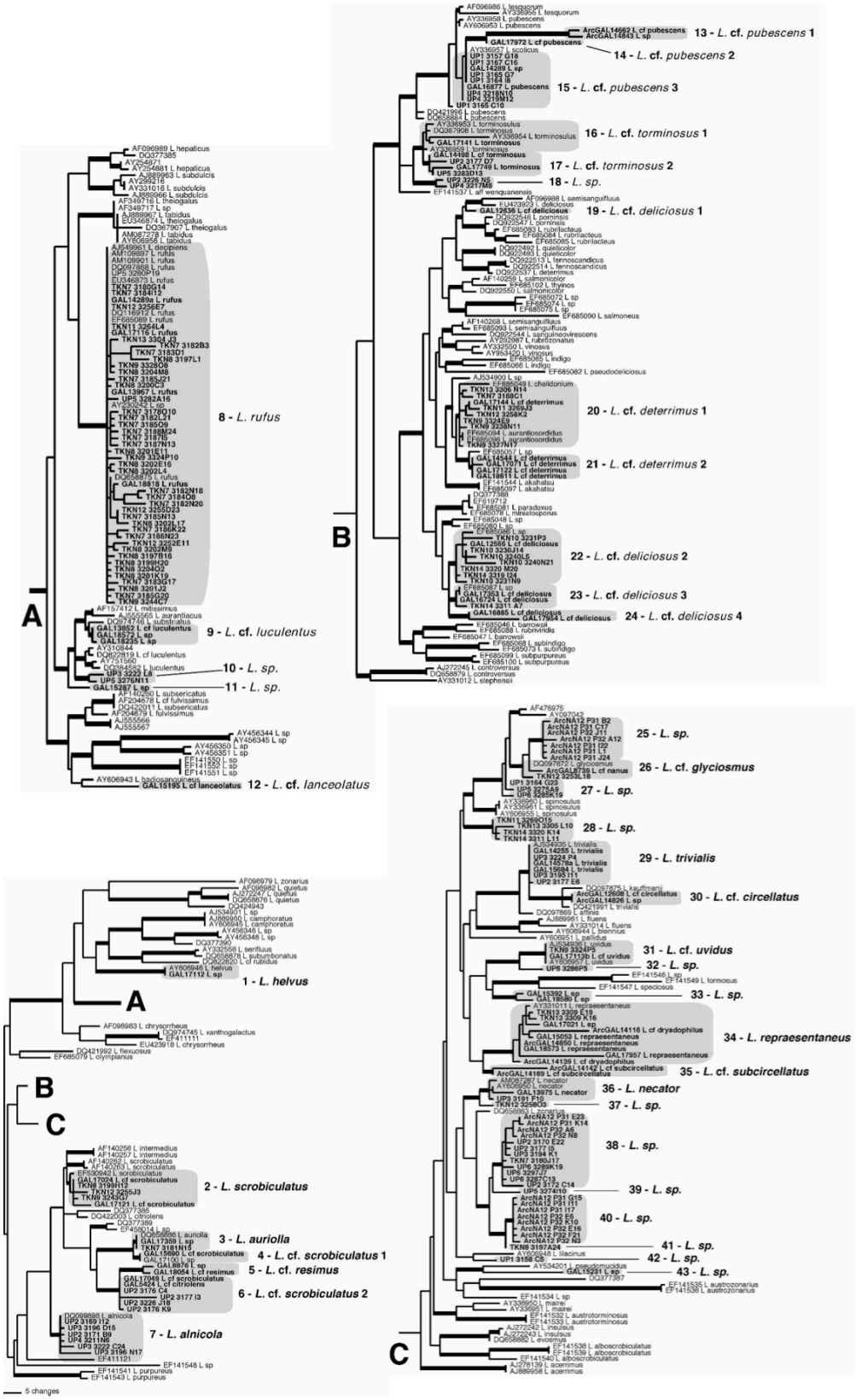


Figure 2.4. A maximum-likelihood phylogram showing the phylogenetic spread of arctic and boreal Alaskan *Lactarius* sequences (in bold) generated in this study among representatives of *Lactarius* taxa in GenBank. Sequences with GAL numbers were derived from herbarium specimens (for easier viewing, arctic and boreal specimens are labeled ArcGAL and GAL, respectively), while UP, TKN, and ArcNA sequences in bold are from soil clone libraries of upland boreal forest, lowland boreal forest, and arctic tundra, respectively. Thick branches indicate Bayesian posterior probability support ≥ 0.95. Grey boxes mark phylogroups with Alaskan sequences. GenBank sequences with no name are from environmental samples (Geml et al. 2009b).

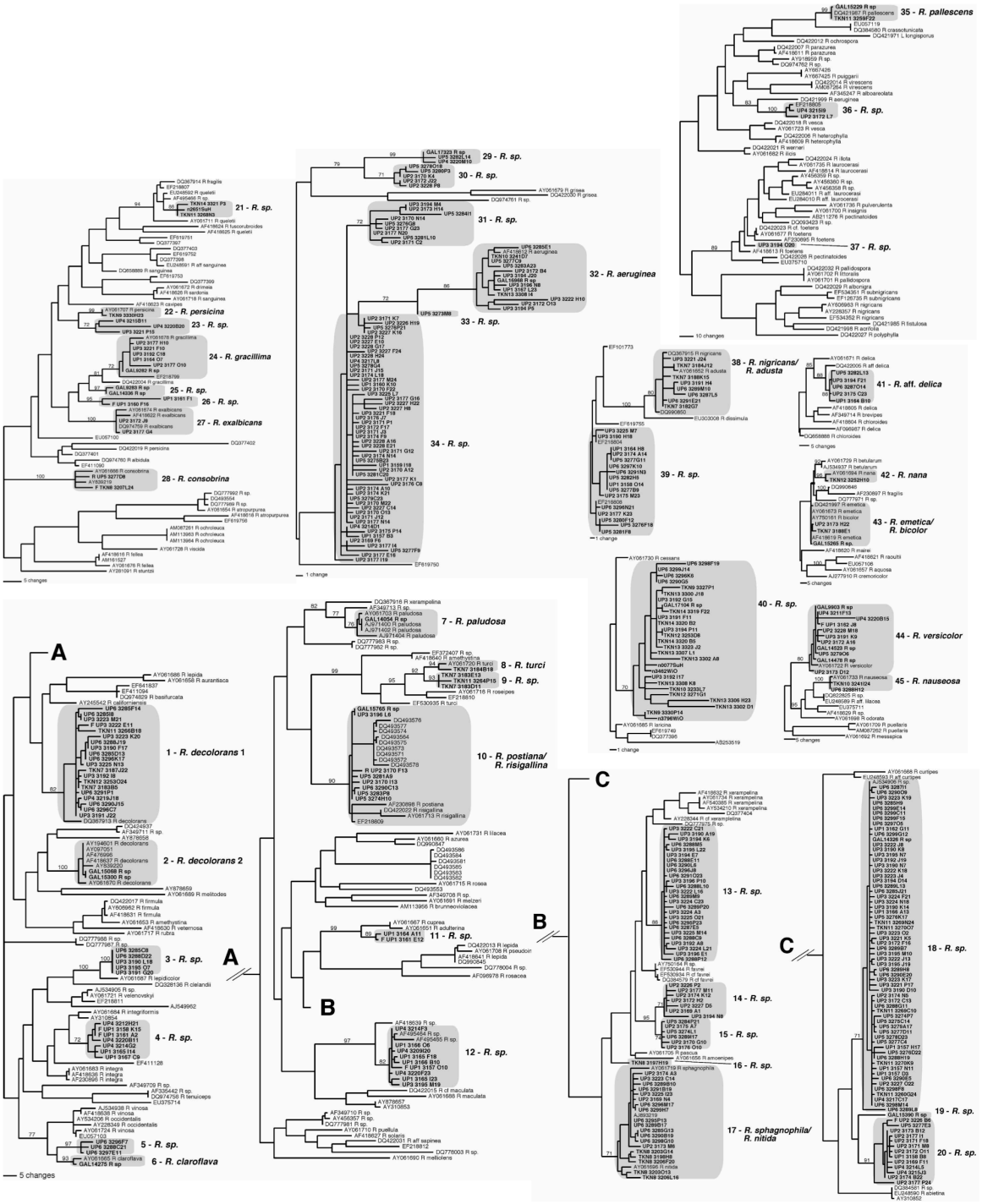


Figure 2.5. Representatives of the equally parsimonious, midpoint-rooted trees generated for all 75% similarity ITS groups, showing the phylogenetic breadth of boreal Alaskan *Russula* sequences (in bold) generated in this study among representatives of *Russula* taxa in GenBank. As the ITS region could not be aligned unambiguously across all *Russula* sequences, we grouped the ITS sequences into 75% similarity groups using Cap3 (Huang and Madan, 1999) and constructed multiple sequence alignments separately for each group. Sequences with GAL numbers were derived from herbarium specimens, while UP, TKN, and other sequences in bold are from soil clone libraries as described in Figure 2.4. >70% maximum-parsimony bootstrap values are shown for clades including Alaskan sequences. Phylogroups with bootstrap support including Alaskan taxa are indicated with grey boxes. GenBank sequences with no name are from environmental samples (Geml et al. 2010b).

In addition, even though all species for which sporocarps were sampled have to be present in the soil, diverse communities in general are characterized by a few abundant and many relatively rare species, some of which are missed by the "blind" (non-targeted) manner and non-exhaustive nature of soil sampling. Our results not only imply that combined sporocarp and soil sampling should be used for biodiversity assessments in fungi, but also suggests that the true diversity of arctic and boreal *Lactarius* and *Russula* in Alaska likely is somewhat higher than what we observed.

Based on the phylogenetic breadth of our sequences, we found most known major phylogenetic lineages of *Lactarius* and *Russula* are represented in Alaska (Geml et al. 2009ab, Geml et al. 2010b). This is in sharp contrast to the trend seen in the non-mycorrhizal saprotrophic *Agaricus*, the only other genus that has undergone a similar assessment of phylogenetic diversity, in which only a fraction of the major subgeneric groups have been found in Alaska (Geml et al. 2008a). Some of the Alaskan *Lactarius* and *Russula* OTUs clearly matched known species and some were unique with or without known close relatives. These taxa of unknown identity may or may not represent newly discovered species, the formal description of which was beyond the scope of this work. In several instances, we observed multiple closely related phylogroups of which one often contained only Alaskan sequences and its sister contained sequences from outside Alaska as well. Some of these phylogroups could represent morphologically cryptic, but phylogenetically different entities that will require a multi-locus approach to clarify. However, they do suggest some phylogeographic endemism in several lineages of both *Lactarius* and *Russula*, similar to the patterns observed in *Amanita muscaria* (Geml et al. 2008b). Also, our data indicate that the species composition of both *Lactarius* and *Russula* communities differ significantly between forest types, despite the low number of replicate sites, which indicates clear habitat preference.

Comparative phylogeography of arctic and boreal fungi

Nonparametric permutation tests, migration estimates, and genealogies generated using coalescent methods all indicate little or no transoceanic migration in boreal-temperate fungi and moderate to high inter-continental migration rates in all arctic fungi analyzed (Geml et al. 2010a, Geml et al. 2011, Geml et al. 2012a). Although values for *Theta* were comparable among all analyzed boreal-temperate and arctic-alpine species, estimates for long-distance gene flow were widely different between these two groups (Figures 2.6-2.8). In all boreal-temperate species, MDIV showed evidence for no inter-continental gene flow (M=0) and statistically significant, non-zero population divergence time (T, data not shown). On the other hand, in all arctic-alpine species, MDIV estimated moderate to high gene flow between North American and Eurasian populations and estimated no population divergence (T not significantly different from 0). MIGRATE detected bidirectional gene flow between Eurasian and North American arctic populations, such as in the ascolichens *Flavocetraria cucullata* and *F. nivalis* and in the basidiolichen *Lichenomphalia umbellifera* (Figures 2.8). Coalescent-based genealogies showed strong historical population divisions in boreal, but not in arctic species, and showed variation between and within geographical regions (Figure 2.7).

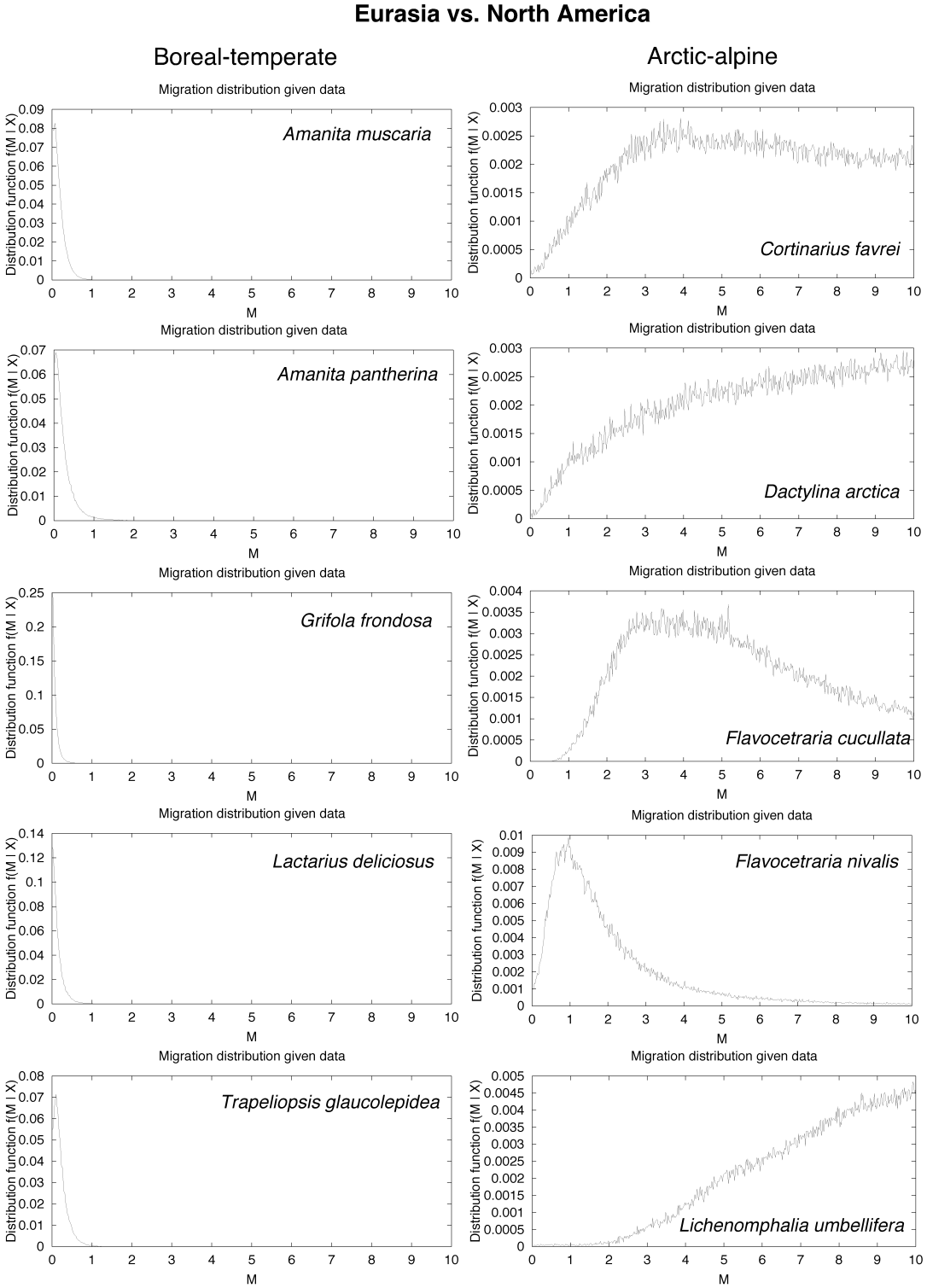


Figure 2.6. Posterior probability distributions of migration (M=2$N_e m$) estimated between transoceanic population pairs of arctic/alpine and boreal/temperate species using Markov chain Monte Carlo coalescent simulations in MDIV. For each dataset, the data were simulated assuming an infinite sites model, using 2,000,000 steps in the chain, and an initial 500,000 steps to ensure that enough genealogies were simulated before approximating the posterior distribution (Geml et al. 2011).

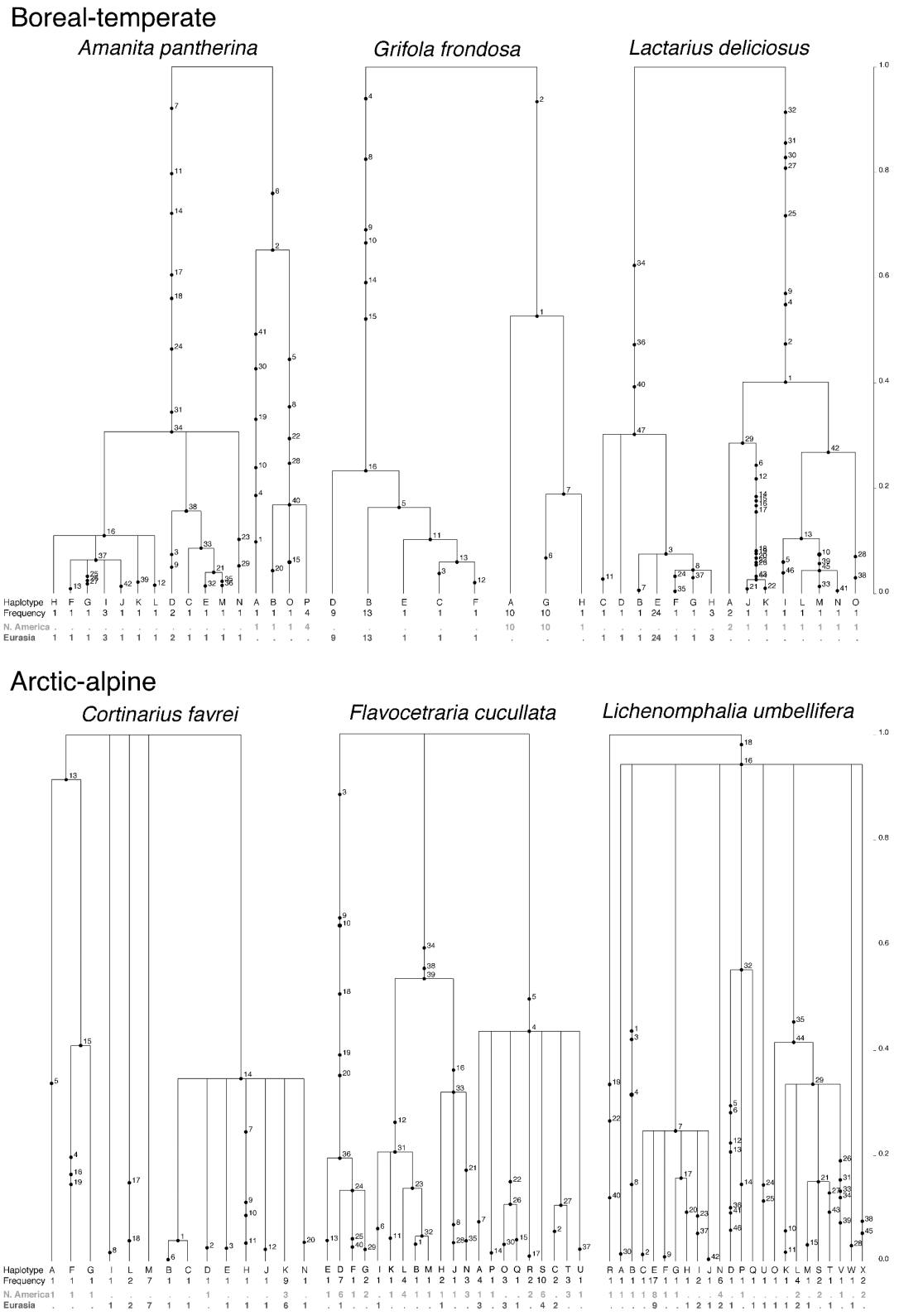


Figure 2.7. Examples of coalescent-based genealogies with the highest root probabilities showing the distribution of mutations for the ITS region. The inferred genealogies are based on 2,000,000 simulations of the coalescent. The time scale is in coalescent units of 2*N*, where *N* is the population size. Mutations and bifurcations are time ordered from the top (past) to the bottom (present). The letters and numbers below the trees designate the distinct haplotypes, their observed frequencies in total and in the different geographical regions, respectively (Geml et al. 2011).

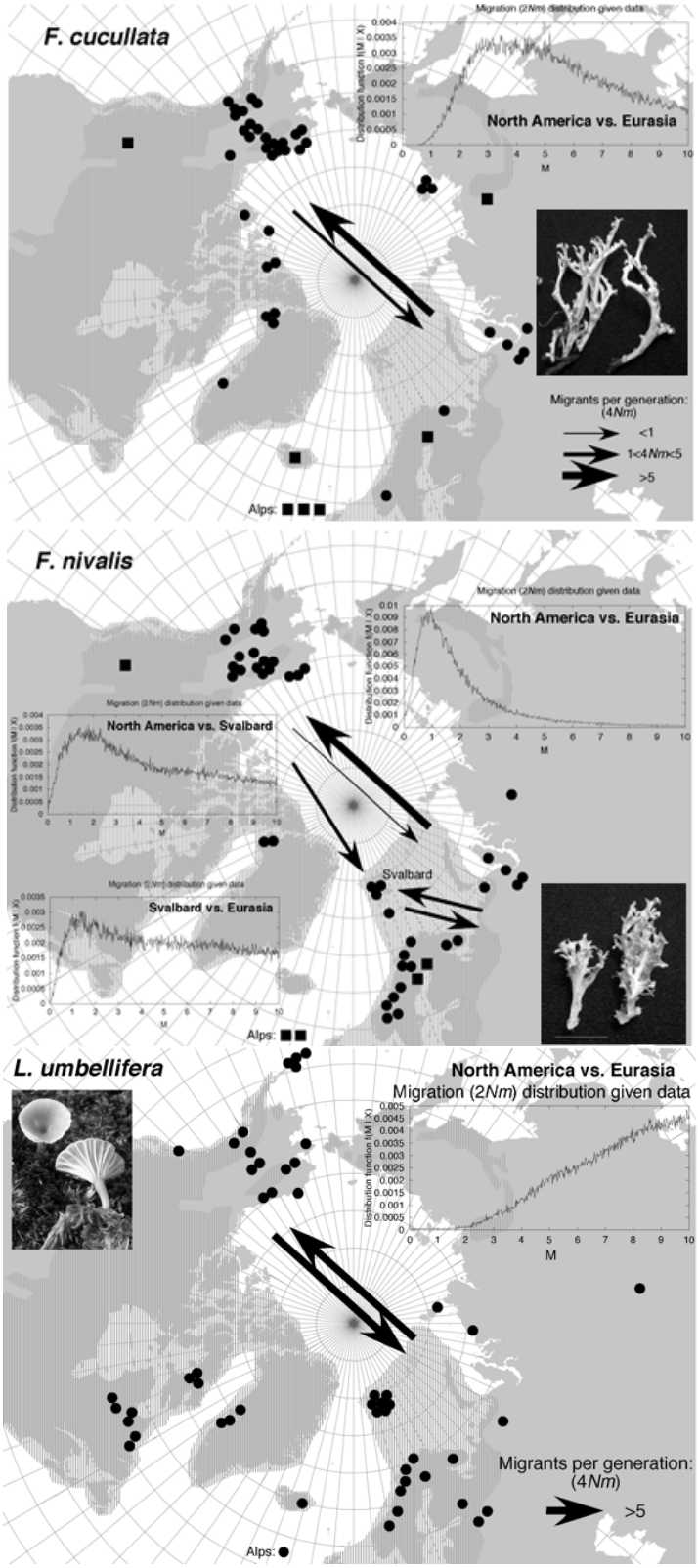


Figure 2.8. Geographic locations of sampled ascolichen *Flavocetraria cucullata* and *F. nivalis* and basidiolichen *Lichenomphalia umbellifera* populations and transoceanic migration estimates among them. Circles refer to our collected and sequenced samples, while squares refer to geographical origins of sequences from GenBank. Shading indicates areas that were glaciated during the Last Glacial Maximum. Inserts show posterior probability distributions of migration (M=$2N_em$) that were estimated between transoceanic population pairs using MCMC coalescent simulations in MDIV. Arrow thickness indicates numbers of migrants per generation ($4N_em$) to the specified direction (Geml et al. 2010a, Geml et al. 2012a).

Several other studies also reported strong intercontinental, sometimes even intracontinental, phylogeographical patterns and limited dispersal in boreal-temperate fungi, with substantial geographic endemism (Geml et al. 2008b, Bergemann et al. 2009, Geml et al. 2010c). Morphological species complexes of fungi from the Northern Hemisphere have generally been shown to include at least two major phylogenetic lineages, practically sister species, corresponding to Eurasia and North America (Shen et al. 2002, Oda et al. 2004, Geml et al. 2006, Taylor et al. 2006). Because in most studied fungi, the allopatric phylogenetic clades inhabit similar environments in different continents, this implies a phylogenetic structure that has arisen from the lack of inter-continental dispersal. All boreal-temperate species analyzed here share this pattern of no inter-continental gene flow and have distinct phylogenetic lineages corresponding to continents.

As mentioned above, the phylogeography of arctic fungi is very different from the above examples of boreal-temperate fungi and is characterized by inter-continental gene flow and no significant phylogeographic structure at circumpolar scale. This suggests that, in response to climatic fluctuations, arctic fungi have been able to migrate over large distances due to efficient long-distance dispersal capability. In addition, large and diverse populations have served as sources for such migrants, as suggested by the relatively high haplotype diversity in several arctic fungal species. The high observed genetic diversity in the Arctic indicates long-term survival at northern high latitudes, while the estimated migration rates and the no or weak geographical population structure suggest continuing long-distance gene flow between continents that has prevented pronounced genetic differentiation. Similar patterns of circumpolar genetic diversity have been detected in some other arctic organisms, for example in highly mobile animals, such as the arctic fox, *Alopex lagopus* (Dalén et al. 2005) and the snowy owl, *Bubo scandiacus* (Marthinsen et al. 2008), as well as in the arctic-alpine lineage of the bog blueberry *Vaccinium uliginosum* (Alsos et al. 2005). The dispersal capabilities af arctic fungi are also illustrated by the fact that several fungi, e.g. lichens, have bipolar distribution caused by relatively recent colonization of subantarctic regions (Geml et al. 2010a). The transequatorial dispersal is less frequent than circumpolar dispersal, but is frequent enough to result in the relatively recent divergence of southern lineages from northern ancestors. An example is the lichenized basidiomycete genus *Lichenomphalia* (Geml et al 2012a), where we detected polar divergence in two lineages with lack of current gene flow (Figures 2.9, 2.10).

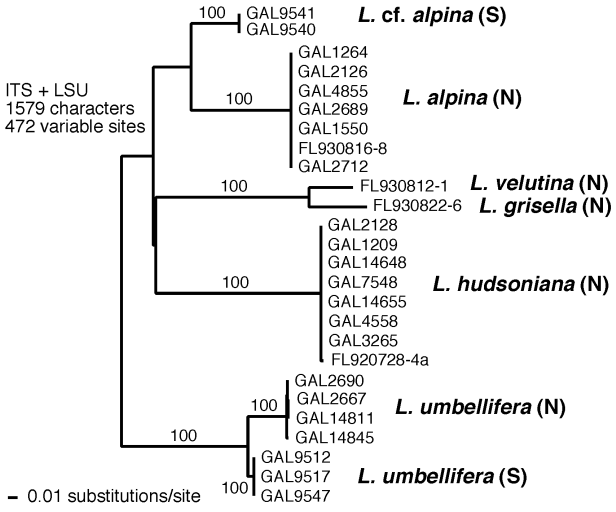


Figure 2.9. Maximum-likelihood phylogram of *Lichenomphalia* species (-lnL=5261.7163) inferred from the combined ITS+LSU rDNA dataset. The tree was rooted using *L. umbellifera* based on phylogenetic results from a study with broader taxon sampling (Lutzoni 1997). Bootstrap values greater than 70% are shown above the branches. Geographic distribution of the supported clades is marked by N (Northern Hemisphere) and S (Southern Hemisphere) (Geml et al. 2012a).

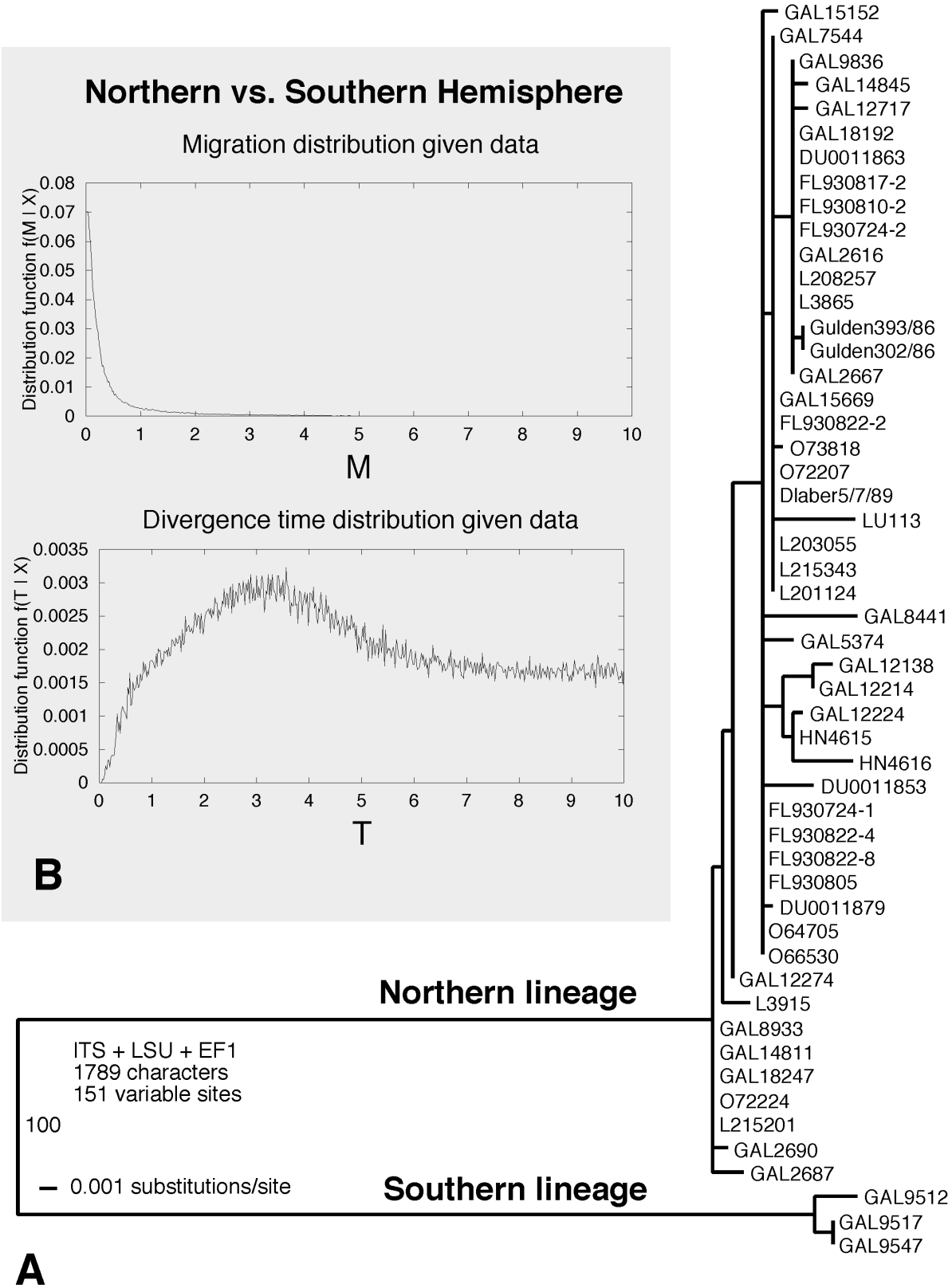


Fig. 2.10. A) Maximum-likelihood phylogram of *Lichenomphalia umbellifera* (-lnL=3387.6449) inferred from the combined ITS+LSU+EF dataset. The tree is midpoint rooted. The only bootstrap value greater than 70% is shown on the longest branch. B) Posterior probability distributions of migration ($M=2N_em$) and divergence time (T, measured in coalescent units of $2N_e$) that were estimated between northern and southern populations using Markov chain Monte Carlo coalescent simulations in MDIV. Data were simulated assuming an infinite sites model, using 2,000,000 iterations in the chain, and an initial 500,000 iterations to ensure that sufficient number of genealogies were simulated before approximating the posterior distribution (Geml et al. 2012a).

ECM fungi in Svalbard: a community assembled by long-distance dispersers

The results summarized here were first published by Geml et al. (2012b) and represented the first comprehensive analyses of ECM fungal communities in Svalbard, using combined soil and sporocarp data. Our evidence suggest that long-distance dispersal has likely played a major role in the phylogeographic history of many ECM fungi at high latitudes in the Northern Hemisphere, and our results may have implications for studies on the biodiversity, ecology and conservation of arctic fungi in general. It is very likely that many arctic fungi, particularly the widespread taxa with circumpolar distributions, have been selected for mobility during the glacial cycles, as has been suggested for plants (Brochmann and Brysting 2008). In addition, we report numerous phylogroups that were not represented previously in public databases and may or may not represent novel taxa.

Despite its geographic isolation and high arctic climate, ECM fungal communities in Svalbard are surprisingly diverse. We recovered 332 distinct non-singleton OTUs for all fungi from the Svalbard soil sequences based on 97% ITS sequence similarity. Of these, basidiomycete ECM genera contained 72 OTUs, while the total number of "soil + sporocarp" phylogroups was 109. Out of the 109 inferred phylogroups in total, we were able to identify 62 to known species or species complexes, while 47 remained unidentified (Figures 2.11, 2.12). The most diverse basidiomycete ECM genera in our samples were (with the number of soil clone OTUs and phylogroups in parentheses, respectively): *Thelephora*/*Tomentella* (30 OTUs, 30 phylogroups), *Inocybe* (17, 27), and *Cortinarius* (11, 19). Additional genera in the order of decreasing diversity were *Russula* (2, 8), *Hebeloma* (2, 7), *Lactarius* (1, 6), *Entoloma* (3, 4), *Sebacina* (3, 3), *Clavulina* (1,1), *Laccaria* (2, 2), *Leccinum* (0, 1), and *Alnicola* (1, 1). It is reassuring that we recovered in our samples most of the ECM taxa that Väre et al. (1992) had found in Svalbard using morphological techniques and the ones in the species list of Gulden and Torkelsen (1996). In addition, we report many more, e.g., a large number of species in genera (e.g. *Tomentella, Sebacina* etc.) that are entirely missing from these earlier species lists of Svalbard fungi. It is very likely that increased future sampling will result in the discovery of additional lineages, particularly in very diverse and taxonomically difficult genera, such as *Tomentella, Cortinarius,* and *Inocybe*. Because sequences generated from soil and sporocarp samples often give complementary views of phylogenetic diversity, our combined approach made it possible to detect more lineages than using either sampling method alone. In this regard, it is worth noting that fungi with presumably high biomass in the soil but with rare and/or inconspicuous sporocarps (e.g., *Sebacina*, *Thelephora*, and *Tomentella*) have been vastly underrepresented in sporocarp collections from Svalbard. This observation is in agreement with records of thelephoroid fungi from other biomes as well, where they are generally well-represented as mycorrhizae in the soil, but are underrepresented in the above-ground fruiting record (e.g., Gardes and Bruns, 1996). On the other hand, some groups with generally abundant fruiting have been found in a low number of soil clones (e.g., *Lactarius* and *Russula*). These latter taxa may be present at relatively low biomass in arctic soils, unlike what has been observed in boreal regions (Geml et al. 2009b, Geml et al. 2010b). Further studies are needed to provide a solid taxonomic context for the unidentified and potentially undescribed taxa.

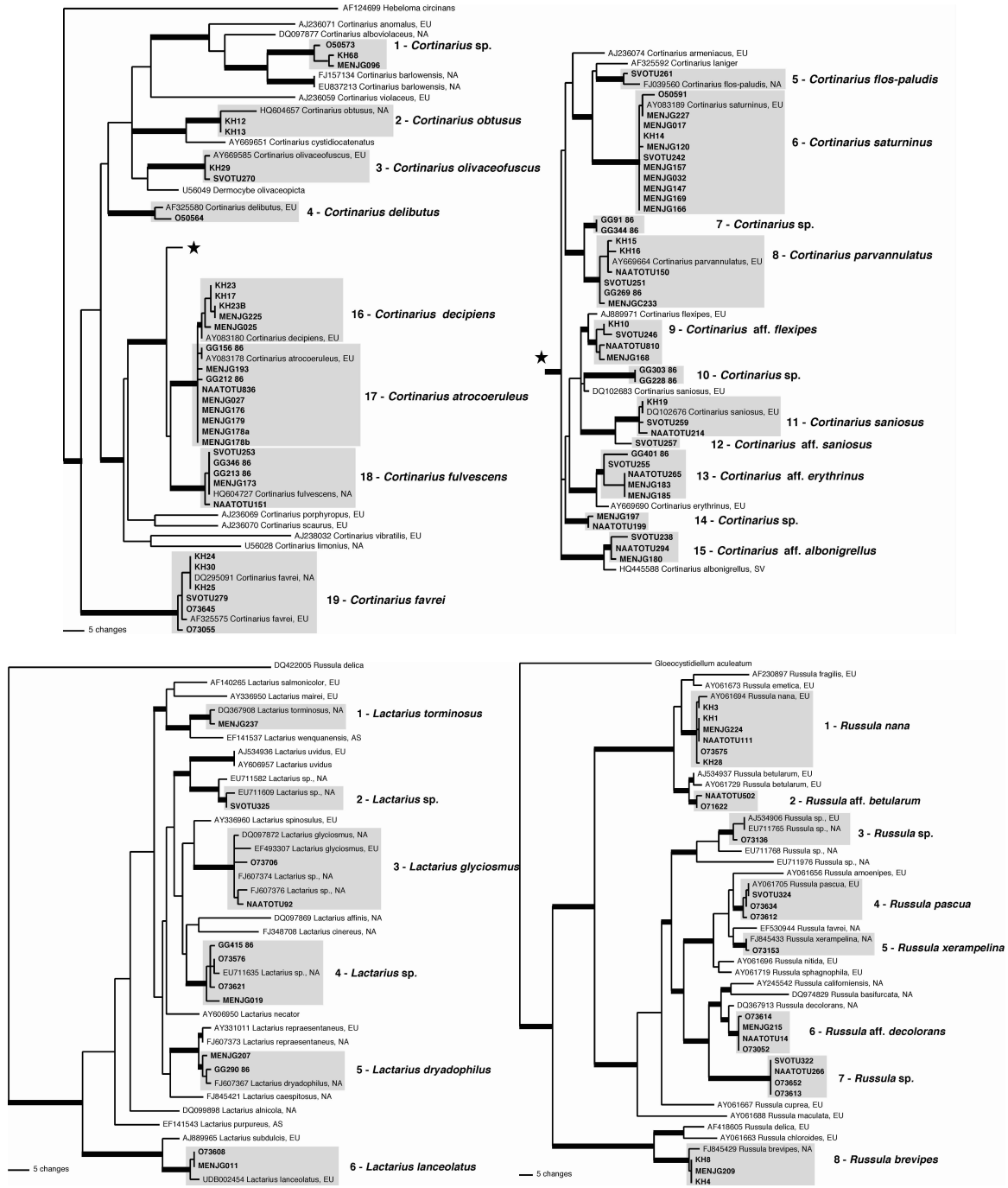


Figure 2.11. Maximum-likelihood phylogram of arctic *Cortinarius*, *Lactarius*, and *Russula* taxa inferred from ITS rDNA sequences representing soil operational taxonomic units (OTUs) and sporocarp sequences generated in our study (in bold) among representative sequences from GenBank. Sequences with MENJG, O, GG, and KH numbers were from specimens deposited at herbaria L and O. SVOTU and NAATOTU numbers refer to 97% DNA sequence similarity OTUs of soil sequences from Svalbard and the North American Arctic Transect (NAAT), respectively. GenBank sequences with no name are from unidentified environmental samples. Geographic origins of reference sequences are abbreviated as follows: SV: Svalbard, NA: North America, EU: Europe, AS: Asia, AU: Australia, and NZ: New Zealand. Branches with Bayesian posterior probability support ≥ 0.95 are thickened. Phylogroups including sequences from Svalbard are indicated with grey boxes and are putatively named based on closest relatives (Geml et al. 2012b).

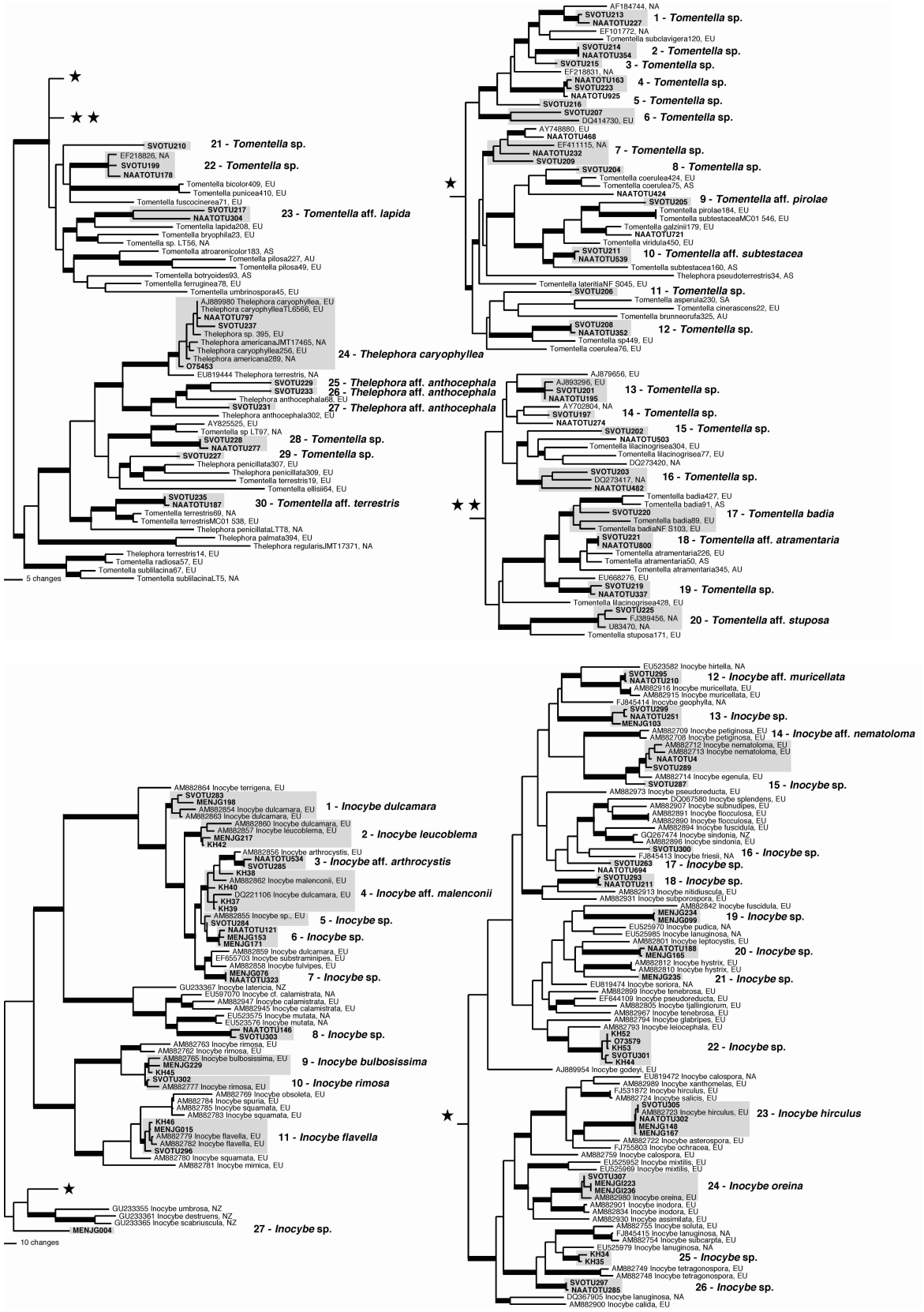


Figure 2.12. Maximum-likelihood phylogram of arctic *Tomentella*/*Thelephora* and *Inocybe* taxa inferred from the ITS rDNA datasets showing the phylogenetic spread of soil clone operational taxonomic units (OTUs) and sporocarp sequences generated in this study (in bold) among representatives of congeneric taxa in GenBank. Branches with Bayesian posterior probability support ≥ 0.95 are thickened. Phylogroups including sequences from Svalbard are indicated with grey boxes and are putatively named based on closest relatives

Considering Svalbard's geological isolation since approximately the Early Pliocene (ca. 4-5 Mya), phylogenetic patterns presented in our paper suggest that most ECM fungi in Svalbard likely have colonized the archipelago by long-distance dispersal events, as opposed to vicariance and *in situ* divergence. There are possible exceptions among taxa with no previous DNA sequence records and, thus, with unknown geographic distributions outside Svalbard. Further sampling in other arctic areas is needed to reveal whether these species are true endemics. We argue that, for most taxa, the low level of sequence divergence observed (regardless of species limits) is largely incompatible with the vicariance scenario and suggest relatively recent migration to the archipelago. Furthermore, the vegetation in Svalbard must have been very different in the mid-Pliocene (ca. 3 Mya), when the climate was 10-20°C warmer than today in the circumpolar Arctic (Salzmann et al. 2009). Although biologically unlikely, it is at least theoretically possible that Svalbard's extant ECM species were already present on the archipelago at the time of separation and that their populations remained in contact with continental populations by intermittent or continuous long-distance gene flow, which would be indistinguishable from purely postglacial gene flow. This limitation, however, is by no means crucial, as detecting recent migration between arctic areas still suggests that these ECM fungi do not depend on land routes to migrate, regardless of how long Svalbard has been inhabited by them. Overall, our data support recent long-distance dispersal of most extant species more strongly than vicariance and *in situ* speciation on the archipelago.

Thus, if we accept dispersal as the most likely explanation for the presence of a relatively diverse ECM fungal community, it is fortunate that we can further narrow down the possible time interval of (re)colonization of Svalbard by ECM fungi to the last 10,000 years, based on the fact that Svalbard was fully or almost fully glaciated in the last ice age. ECM fungi are obligate symbionts of plants (mostly woody plants). Geological evidence shows that Svalbard was completely or almost completely glaciated in the Last Glacial Maximum (LGM) and during most of the other glacial maxima. Whether or not nunatak survival occurred in some very hardy arctic plants is still a matter of debate. Recent evidence suggest that the rare arctic-alpine pioneer plant *Arenaria humifusa* may have survived in Eastern Greenland and/or Svalbard during the LGM (Westergaard et al. 2010a). Nonetheless, ECM host plants (shrubs) are among the more thermophilous species and molecular data suggest that they recolonized Svalbard postglacially (Alsos et al. 2007). In almost all ECM genera identified, we observed multiple lineages that likely have colonized Svalbard in postglacial times. On the other hand, although unlikely for most taxa, glacial survival of some ECM fungi cannot be entirely ruled out, given the possibility of nunatak survival for some arctic plants (Westergaard et al. 2010ab). It is important to note that we by no means imply that there had been no ECM fungi on Svalbard before the current interglacial. Rather, it is very likely that ECM fungi had been present in Svalbard during many previous interglacials, but they were likely wiped out repeatedly by the glaciations, and then recolonized Svalbard again and again, as it has been shown in arctic plants as well (Eidesen et al. 2007). The high current migration estimates for the only ECM species with available data suitable for coalescent analyses further support our view that long-distance dispersal is frequent in arctic ECM fungi.

Our findings for arctic ECM fungi are, therefore, in contrast with inferred transoceanic migration rates and general phylogeographic patterns seen in mid-latitude fungi, as detailed in the preceeding subsections of this chapter. Former findings have suggested that typical ECM

plant and fungus symbionts require overland routes for migration, possibly as a consequence of the obligate symbiotic habit of ECM associations (Malloch et al. 1980, Halling 2001). In theory, long-distance dispersal and establishment of either the mycorrhizal fungus or the host plant in isolation has been considered unlikely, because the simultaneous arrival of fungal spore and host plant seed are presumed to be necessary (Moyersoen et al. 2003). In addition, even for wind-dispersed ECM fungi, the vast majority (generally >95%) of basidiospores have been shown to be deposited within 5 m of the parent basidiome (e.g. Li 2005). As a result, there are numerous cases of marked ITS sequence divergence between sister lineages inhabiting different continents in various ECM species complexes in lower latitudes (e.g., Oda et al. 2004, Geml et al. 2006, Geml et al. 2008, Geml et al. 2009ab, Geml et al. 2010b). There is little or no evidence for such patterns in our data. On the contrary, the phylogenetic relationships of arctic ECM fungi present in Svalbard suggest effective transoceanic dispersal, similar to what has been found in arctic plants (Alsos et al. 2007), including ECM hosts, and in non-mycorrhizal arctic fungi (Geml et al. 2010a, Geml et al. 2011, Geml et al 2012a).

Besides the observed diversity of taxa, considering that some of the ECM fungi included in this paper have very narrow host ranges, we assume that basidiospores likely are dispersed regularly to Svalbard from remote areas. For example, *Leccinum rotundifoliae*, a circumpolar species, is specific to *Betula* hosts, of which only *B. nana*, dwarf birch, is found in Svalbard. Furthermore, the distribution of *B. nana* in Svalbard is restricted to a very few localities having particularly suitable microclimatic conditions, namely Colesdalen and Adventdalen (Alsos et al. 2002). The size of these *B. nana* populations is generally small and, unlike populations that are widespread in the circumpolar low arctic, this species apparently does not reproduce sexually in Svalbard (Alsos et al. 2003). Even if we consider that the distribution of *B. nana* may have been somewhat wider in Svalbard during the Holocene Climatic Optimum (9000 to 5000 years before present), it almost certainly remained very localized and restricted to the Isfjorden region and the reunion with its ECM symbionts (many of them occur nowhere else in Svalbard) after independent transoceanic journeys is particularly impressive.

One cannot avoid posing the question: Why do arctic-alpine fungi differ in phylogeographic trends from more southern species? The most likely explanation is that climatic changes during the Quaternary dramatically influenced the distribution of flora and fauna, particularly at higher latitudes. During glacial maxima, plants, fungi, and animals were restricted to unglaciated refugia, from which they recolonised newly exposed areas in warmer interglacial periods (Abbott and Brochmann 2003). Although climatic changes have caused some shifts in species distributions in most terrestrial habitats around the globe, changes have been the greatest at high latitudes, so were the geographic distances the species had to cover to track their ecological niche and to colonize newly available habitats following glacial retreats. It is, therefore, very likely, that many arctic fungi, particularly the keystone taxa with circumpolar distribution, have been selected for mobility during the glacial cycles, as suggested for plants (Brochmann and Brysting 2008).

Because no specialized sporocarp adaptation to arctic environments has been reported (perhaps other than smaller sporocarp size, in general), it is likely that wind dispersal is important, as is for most fungi. Wind dispersal likely is particularly effective in the Arctic because of the open landscape, strong winds, and extensive snow and ice cover, as shown for

arctic plants (Alsos et al. 2007). In this regard, the sea ice may be of particular importance for inter-continental dispersal, as it provides a dry surface bridging the continents and archipelagos. Obviously, this is an important difference to boreal-temperate species, which would need to cross greater distances of open water to reach another continent. Although such transoceanic dispersals are sometimes documented in fungi in mid-latitudes in the Southern Hemisphere (Moyersoen et al. 2003, Moncalvo and Buchanan 2008), facilitated by extremely strong and mostly unidirectional wind currents, long-distance dispersal in mid-latitudes in the Northern Hemisphere seems to be rare. Besides wind, other possible means of dispersal include spores being carried by migratory animals, driftwood, and drifting sea ice, which may also favor arctic fungi due to ocean currents and animal migrations (particularly birds) linking continents over shorter distances.

The implications of our results may not be restricted to species discussed here, but can be important for studies on the biodiversity, ecology and conservation of arctic fungi in general. Reconstruction of phylogeographical patterns of arctic organisms is of paramount importance because knowledge of both past migrational history and present-day genetic diversity are essential to improve our predictions on how arctic species and communities will respond to global change. The high genetic diversity and the efficient long-distance dispersal capability of the arctic taxa analyzed here suggest that these species, and perhaps other arctic fungi as well, will probably be able to track their potential niche in the changing Arctic.

3. Landscape ecology of fungi in the changing Arctic

Figure 3.1. ECM fungi *Amanita regalis* and unidentified *Lactarius* and *Russula* species growing among host shrubs *Arctostaphylos rubra* and *Salix glauca* in the arctic tundra near the Toolik Field Station in Alaska (photos by the author).

This chapter is based upon the following publications:

Canini F, Zucconi L, Pacelli C, Selbmann L, Onofri S, Geml J. 2019. Vegetation, pH and water content as main factors for shaping fungal richness, community composition and functional guilds distribution in soils of Western Greenland. ***Frontiers in Microbiology*** 10:2348.

Geml J, Morgado LN, Semenova TA, Welker JM, Walker MD, Smets E. 2015. Long-term warming alters richness and composition of taxonomic and functional groups of arctic fungi. ***FEMS Microbiology Ecology*** 91: doi: 10.1093/femsec/fiv095.

Geml J, Morgado LN, Semenova-Nelsen TA. 2021. Tundra type drives distinct trajectories of functional and taxonomic composition of arctic fungal communities in response to climate change -results from long-term experimental summer warming and increased snow depth. ***Frontiers in Microbiology*** 12: 490.

Geml J, Semenova TA, Morgado LN, Welker JM. 2016. Changes in composition and abundance of functional groups of arctic fungi in response to long-term summer warming. ***Biology Letters*** 12:20160503.

Grau O, Geml J, Pérez-Haase A, Ninot JM, Semenova-Nelsen TA, Peñuelas J. 2017. Abrupt changes in the composition and function of fungal communities along an environmental gradient in the High Arctic. ***Molecular Ecology*** 26:4798-4810.

Morgado LN, Geml J**.** 2020. Modifications of community structure in ectomycorrhizal arctic fungi as a consequence of global warming. In: *Mushrooms, Humans and Nature in a Changing World* (Pérez-Moreno J, Guerin-Laguette A, Flores Arzú R, Yu FQ) Springer, p. 451-472.

Morgado LN, Semenova TA, Welker JM, Walker MD, Smets E, Geml J. 2015. Summer temperature increase has distinct effects on the ectomycorrhizal fungal communities of moist tussock and dry tundra in Arctic Alaska. ***Global Change Biology*** 21:959-972.

Morgado LN, Semenova TA, Welker JM, Walker MD, Smets E, Geml J. 2016. Long-term increase in snow depth leads to compositional changes in arctic ectomycorrhizal fungal communities. ***Global Change Biology*** 22:3080-3096.

Semenova TA, Morgado LN, Welker JM, Walker MD, Smets E, Geml J. 2015. Long-term experimental warming alters community composition of ascomycetes in Alaskan moist and dry arctic tundra. ***Molecular Ecology*** 24:424-437.

Semenova TA, Morgado LN, Welker JM, Walker MD, Smets E, Geml J. 2016. Compositional and functional shifts in arctic fungal communities in response to experimentally increased snow depth. ***Soil Biology and Biochemistry*** 100:201-209.

3.1. Introduction

Fungi constitute one of the most species-rich groups of organisms in northern terrestrial ecosystems and, unlike plants and animals, do not show a latitudinal decrease in richness either globally (Tedersoo et al. 2014) or within the Arctic (Bjorbækmo et al. 2010, Timling and Taylor 2012). Arctic plants are highly dependent on mutualistic relationships with mycorrhizal fungi for survival in these nutrient-poor environments, with the exception of a few graminoid species (*Carex* spp., *Eriophorum* spp.) and herbs in the family Brassicaceae (Hobbie et al. 2009). Saprotrophic and ECM fungi are the dominant functional groups in the arctic tundra. They are essential for the functioning of northern terrestrial ecosystems and control much of the C balance (Gardes and Dahlberg 1996, Dahlberg and Bültmann 2013). ECM fungi, such as those in Figure 3.1, help vascular plants to obtain N, which is highly limiting in arctic soils (Hobbie and Hobbie 2006). Saprotrophic fungi are active primary or secondary decomposers and strongly influence C and nutrient cycles (Christiansen et al. 2016), while pathogenic fungi can cause severe diseases in plants and can greatly decrease plant biomass (Olofsson et al. 2011). Many arctic fungi form lichens, that are important primary producers (Webber 1974, Longton 1988), while also contributing to N fixation (Crittenden and Kershaw 1978), and are important food sources for several herbivores. However, the abiotic and biotic factors that determine the occurrence of these functional groups at landscape (e.g. habitat) and microhabitat scale and the link between composition and function are still poorly understood, especially for non-lichenized fungi (Dahlberg and Bültmann 2013). In this chapter, I summarized the findings of our research on abiotic drivers of arctic fungal community composition at landscape and microhabitat scales and on the responses of arctic fungi to long-term experimental increase in temperature and snow depth simulating climate change.

Regarding the first topic, our studies featured in this section investigated soil fungal communities in contrasting habitat types (e.g., snowbed, heath and fell field vegetation) that are widespread across the Arctic and are primarily distributed according to differences in soil moisture and snow depth largely driven by mesotopographic gradients and prevailing winds (Walker et al. 1999). In addition, we compared fungal communities occurring in distinct microhabitats, such as monodominant patches of dwarf shrubs *Dryas octopetala* or *Salix arctica*, and bare ground in northeastern (NE) Greenland (Grau et al. 2017) and mixed shrub vascular vegetation of *Empetrum nigrum*, *Vaccinium uliginosum*, *Betula nana*, and *Salix glauca*, biological soil crusts dominated by bryophytes and lichens, and bare ground in western (W) Greenland (Canini et al. 2019). Both *Dryas* and *Salix* are dominant ECM hosts throughout the Arctic, while *Betula* species are restricted to the Low Arctic (Walker 2000, Newsham et al. 2009, Timling et al. 2012).

We hypothesized that: 1) the differences in the composition of fungal communities would respond primarily to vegetation types driven primarily by soil moisture and pH; 2) within each habitat, composition of fungal communities would also differ among microhabitats; 3) the proportional richness of the functional groups (i.e. saprotrophic, lichenized, plant pathogenic, root endophytic, and ECM fungi) would co-vary with abiotic conditions; and 4) groups with intimate interactions with vascular plants (ECM, root endophytic, and plant pathogenic fungi) would dominate in the *Dryas* and *Salix* patches. To

our knowledge, these studies were the first to use high-throughput DNA sequencing methods to explore soil fungal communities in Greenland.

For the second topic, we compared fungal communities in long-term (18 years) experimental plots simulating climate change in the Alaska Arctic in dry and moist tundra types (Geml et al. 2015, Morgado et al. 2015, Semenova et al. 2015, Geml et al. 2016, Morgado et al. 2016, Semenova et al. 2016, Morgado and Geml 2020, Geml et al. 2021). Beside the control plots, treatments in both vegetation types included (1) ambient and experimentally increased summer air and near-surface soil temperature; (2) ambient and experimentally increased snow depth; and with (3) combined treatment of increased summer warming and increased snow depth in dry heath and moist tussock tundra. We aimed to answer (1) how composition of fungal functional groups changes in response to long-term increase in winter snow depth, summer temperature, and their combination; and (2) whether there are differences in responses between dry and moist tundra.

3.2. Materials and Methods

Data generation

The fieldwork for the first study (Grau et al. 2017) was conducted in July 2011 at Zackenberg Valley (Northeast Greenland, 74°28'N, 21°33'W). The region lies within the bioclimatic subzone C that belongs to the High Arctic, with mean July temperatures ranging from 3 to 7° C and mean annual precipitation is 250 mm (Hansen et al. 2008). We compared three different habitats along a topographic gradient on the southwestern slope of Mount Aucellabjerg that represent a decreasing gradient of snow depth: snowbed at ca. 40 m a.s.l., dry heath tundra at ca. 200 m a.s.l, and a fell field at ca. 425 m a.s.l. These differences in abiotic conditions across habitats produce a gradient of increasing environmental severity from the snowbed to the fell field (referred hereafter as the 'main gradient') and a corresponding decrease in plant cover. We selected three replicate 10 × 10 m plots in each habitat at similar elevation and aspect, separated by a few hundred meters. In each plot, we selected patches larger than 25 × 25 cm where *Dryas*, *Salix*, or bare ground clearly dominated (with >80% cover). Four soil samples were collected for each microhabitat in each plot with a 3.5-cm corer to a depth of 5 cm. The coarse litter layer was removed in the patches of *Dryas* or *Salix*, and the soil cores were centered on the base of the roots to collect soil from the rhizosphere. The four soil samples were mixed and pooled into one composite sample (n = 3 habitat types × 3 microhabitats × 3 plots = 27 composite samples in total). The samples were immediately frozen for transport to the lab and were divided into two subsamples: one was preserved in tubes with cetyltrimethyl-ammonium bromide (CTAB) for subsequent molecular analyses, and the other was used to measure pH and the contents of organic C, total N, and available phosphorus (P).

The second fieldwork in Greenland was carried out in Kobbefjord, Nuuk, West Greenland (64°08' N, 51°23' W) (Canini et al. 2019). The climate of the area was classified as Low Arctic, subzone D, with mean July air temperature of 10.7 °C and annual precipitation ranging from 838 to 1127 mm (Søndergaard et al. 2012). Sampling was carried out in July 27-31, 2017, along the NERO line vegetation transect (Bay et al. 2008), where plant compositions have been monitored for more than ten years. In total, twenty 2-m^2 plots scattered in the

landscape, representing the three habitat types: bare ground (BG), biological soil crust consisting of mosses and lichens (BSC), and vascular vegetation (VV). BG and BSC plots were generally adjacent to the vegetation and in some cases small patches were dispersed among the vegetation. In each plot, three replicates of soil samples were collected aseptically at a depth of 5 cm, after removing the top of the soil, resulting in a total of 60 samples. Samples were stored at -20 °C in sterile bags until molecular analyses.

The field sampling for the experimental warming study was undertaken in July, 2012 at the Arctic Long Term Ecological Research site at Toolik Field Station in the northern foothills of the Brooks Range, Alaska, USA (68°37' N, 149°32' W, 760 m above sea level). We sampled long-term experimental plots that are part of the circumpolar International Tundra Experiment (ITEX) network (Walker et al. 1999). The region lies within the bioclimatic subzone E, the warmest subzone of the arctic tundra and represents the Low Arctic, with mean July temperatures ranging from 9 to 12° C and annual precipitation ranging from 200 to 400 mm, of which ca. 50% of the precipitation falls as snow. (Walker et al. 2005). The two main vegetation types of the region are: dry acidic heath tundra, characterized by *Dryas octopetala*, *Salix polaris*, *Vaccinium* species and fruticose lichens, and moist acidic tussock tundra, dominated by *Betula nana*, *Salix pulchra* species, the sedge *Eriophorum vaginatum*, and several peat moss species (*Sphagnum* spp.). Detailed descriptions of the plant communities can be found in Walker et al. (1999). As a part of ITEX network, hexagonal open top chambers (OTCs) and the snow fences were established in 1994, in both the dry and moist tundra, to increase summer air and upper soil temperature and winter snow depth, respectively (Welker et al. 1997, Jones et al. 1998, Welker et al. 2000) (Figure 3.2). The OTCs have a 1 m^2 surface area, are 0.4 m high, are made of translucent fiberglass and are only placed in the plots in the snow-free period between late May and end of August (Marion et al. 1997, Walker et al. 1999), they increase the summer air and upper soil temperature by a mean daily average of 1.5 to 2 °C measured at 15 cm height and 5 cm depth, respectively, within the OTCs (Jones et al. 1998, Walker et al. 1999). Snow fences are 2.8 m tall and 60 m long, creating a ca. 60-meter leeward snow drift. The soil sampling was focused on the intermediate zone near the center of the experimental setup, corresponding to ca. 1-1.5 m winter snow depth, with 1.8 °C (±0.2) higher in winter soil temperature relative to the control. These treatments led to compositional shifts in vegetation and increases in above-ground plant biomass (Walker et al. 1999, Wahren et al. 2005, Welker et al. 2005, Walker et al. 2006, Pattison and Welker 2014). In both dry and moist tundra, we sampled five replicate plots in the summer warming and increased snow depth treatments as well as in the control plots, located adjacent to the experimental treatments. Each replicate sample consisted of five soil cores of 2 cm diameter and 20 cm depth that were thoroughly mixed and kept frozen until lyophilization. Both organic and mineral layers were included in the cores, while undecomposed litter, moss, and coarse roots were removed. In total, we sampled 150 soil cores across 30 plots of ca. 1 m^2 each, as described in detail in Geml et al. (2015, 2016, 2021), Morgado et al. (2015, 2016) and Semenova et al. (2015, 2016).

DNA work and bioinformatic analyses

In the studies featured here, genomic DNA was extracted from 0.5 g of dry soil per sample either with the Macherey-Nagel NucleoSpin® Soil kit or with the QIAGEN DNEasy

Powersoil kit, following the manufacturer's protocol. We used 1 ul of DNA template with DNA concentration normalized for all samples per study for PCR amplification of the ITS2 region (ca. 250 bp) of the nuclear ribosomal DNA repeat with primers fITS7 (Ihrmark et al. 2012) and ITS4 (White et al. 1990), as described in Geml et al. (2014). The locus of choice only differed in the NW Greenland study of Canini et al. (2020), where ITS1 was amplified using ITS1F (Gardes and Bruns 1993) and ITS2 (White et al. 1990) primers following Smith and Peay (2014). The equimolar pools of uniquely barcoded amplicons were sequenced either with paired-end (2 × 300 bp) Illumina MiSeq or with Ion Torrent using an Ion 318^{TM} Chip. We generally obtained between 30,000 and 60,000 DNA sequence reads per sample, which corresponds to an approximately 100× coverage of the expected richness of fungi per sample. Routine chemical analyses of soil samples were carried out by different commercial laboratories, as described in the publications of the various studies given below.

Bioinformatic processing of the environmental DNA sequence data included the following major steps: sorting sequences according to sample-specific tags, removing adapters and primers, quality filtering, clustering in taxonomic units and identification based on curated reference databases. DNA sequence data were demultiplexed according to samples and adapters were removed in Galaxy (https://main.g2.bx.psu.edu/root). Demultiplexed sequences were then processed with Geneious Pro 5.6 (BioMatters, New Zealand) to remove primer

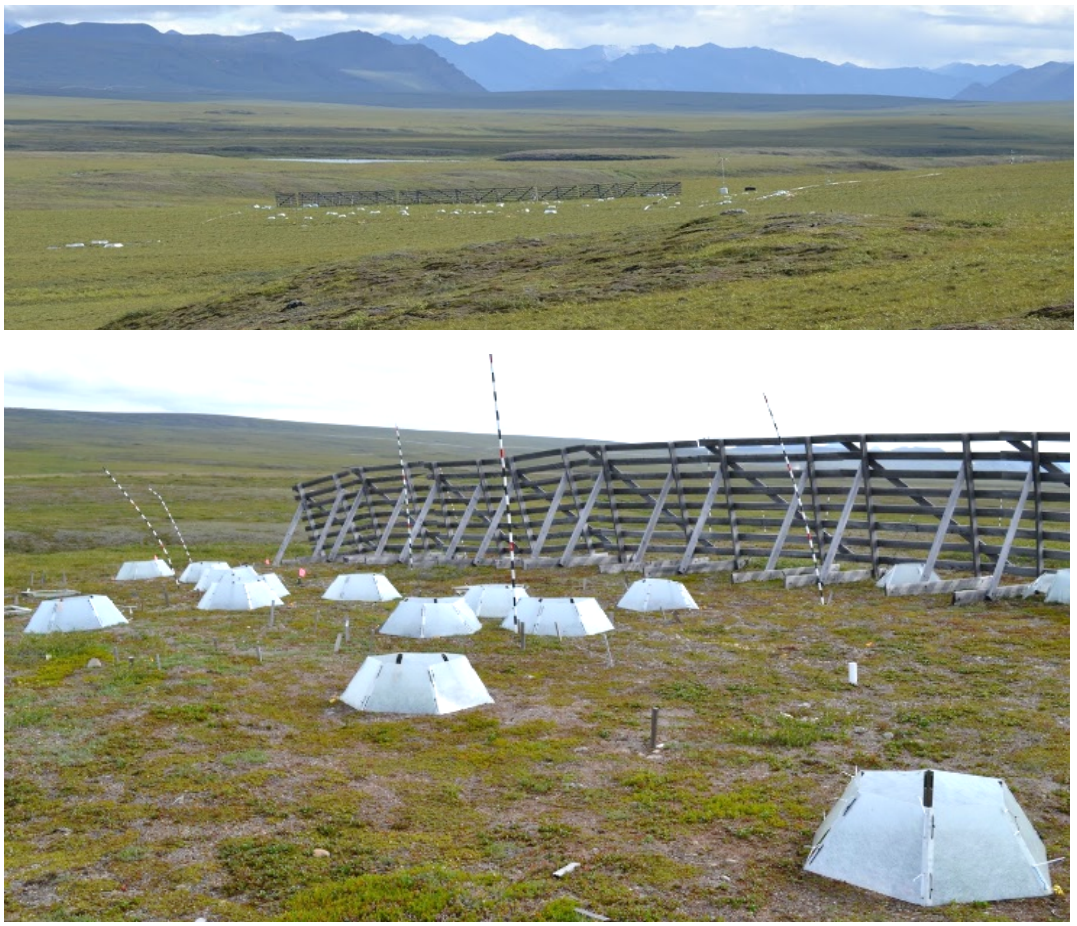


Figure 3.2. Arctic tundra landscape near the Toolik Field Station in Alaska, showing the snow fence and open top chambers on the moist (above) and dry (below) tundra (photo by the author).

sequences and to trim poor-quality ends. Quality filtering was done either with USEARCH versions 8 to 11 (Edgar 2010) or with VSEARCH versions 2.5 to 2.7 (Rognes et al. 2016) with the following settings: all sequences were truncated to 200 bp and sequences with expected error > 1 were discarded. The quality-filtered sequences were grouped into operational taxonomic units (OTUs) at 97% sequence similarity in USEARCH or VSEARCH, and global singletons and putative chimeric sequences were removed. We assigned sequences to taxonomic groups based on pairwise similarity searches against the latest version of the curated UNITE+INSD fungal ITS sequence database (unite.ut.ee), containing identified fungal sequences with assignments to Species Hypothesis groups based on dynamic similarity thresholds (Kõljalg et al. 2013). We excluded OTUs with < 80% similarity or < 150 bp pairwise alignment length to a fungal reference sequence. In the earlier studies, we assigned fungal OTUs to putative functional guilds following Tedersoo et al. (2014), supplemented by information regarding the isolation source of curated reference sequences in UNITE. Later, as more and more complete reference databases became available, we used FunGuild (Nguyen et al. 2016) and lately the FungalTraits database (Põlme et al. 2020). For the statistical analyses in each study, we only focused on the functional groups with a relatively high number of OTUs. DNA sequence data for the studies featured in this chapter are deposited in GenBank under accession numbers as individual sequences of OTUs, such as MF180633-MF182100 (NE Greenland), or as raw sequence data files grouped in Targeted Locus Studies: KCYB01000000 (W Greenland), KEOG01000000 (Alaska).

Statistical analyses

Unless otherwise noted, all statistical analyses were done in the R environment for statistical computing (R Core team 2015). The fungal community matrix was normalized (rarefied) by random subsampling to the smallest library size on a per-sample basis using the *vegan* package (Oksanen et al. 2015). We statistically compared OTU richness and relative abundance of fungal functional groups among the samples with ANOVA and Tukey's HSD test and presented these graphically as boxplots with *ggplot2* (Wickham 2016). Compositional differences among samples were visualized using non-metric multidimensional scaling (NMDS) in *vegan* with presence-absence data using the Jaccard dissimilarity and with the read-abundance data using the Bray-Curtis distance measure on the Hellinger-transformed matrices. We calculated the richness (number of OTUs) and proportional abundance (number of sequences representing a given functional group divided by the total number of sequences on a per-sample basis) of various functional groups to assess and compare their prevalence among the habitats and microhabitats. We used the *envfit* R function to fit richness, proportional abundance, and continuous environmental variables, such as edaphic properties, vegetation data etc. onto the NMDS ordinations. In order to estimate the amount of variation in fungal community composition explained by environmental variables, we explored correlations between fungal beta diversity and categorical (e.g., tundra type, experimental treatment) and continuous (e.g., edaohic properties) variables by performing PerMANOVA (adonis) with 9999 permutations. At first, for each study, we assessed correlations for each variable independently and subsequently built a combined model using the significant variables to account for relationships among them.

3.3. Results and discussion

Composition dynamics of arctic fungal communities at habitat and microhabitat scales

In the high arctic study site in NE Greenland, we found that both fungal richness and community composition were primarily driven by habitat-scale differences in abiotic conditions along the mesotopographic gradient studied (Grau et al. 2017). For example, one of the more striking patterns was that the severity of the environment, manifested by a decrease in snow depth, and water and nutrient content, was positively correlated with total fungal richness. Soil temperature during the cold season is also expected to co-vary with snow depth (Brown et al. 2000, Woo et al. 2007), with lower soil temperatures in areas with little snow accumulation (Jones et al. 1998), thereby contributing to the increase in environmental severity towards the fell field, also illustrated by the decrease in vegetation cover (Grau et al. 2017). Overall, the most hostile environment, i.e. the dry, rocky tundra of the fell field, apparently hosts the highest number of fungal species in NE Greenland (Figure 3.3). Almost half of the OTUs from the fell field (48%) were not found in the heath, nor in the snowbed (Figure 3.4), whereas the proportions of OTUs found exclusively in the heath or the snowbed were lower (20 and 25%, respectively). The number of shared OTUs was highest amongst contiguous habitat types. Grau et al. (2017) also found that richness patterns of functional groups differ greatly among habitats. The proportional richness of ECM and root endophytic fungi correlated negatively, whereas that of saprotrophic, lichenized, and plant pathogenic fungi correlated positively with elevation and, thus, increasing severity of the environment (Figure 3.3).

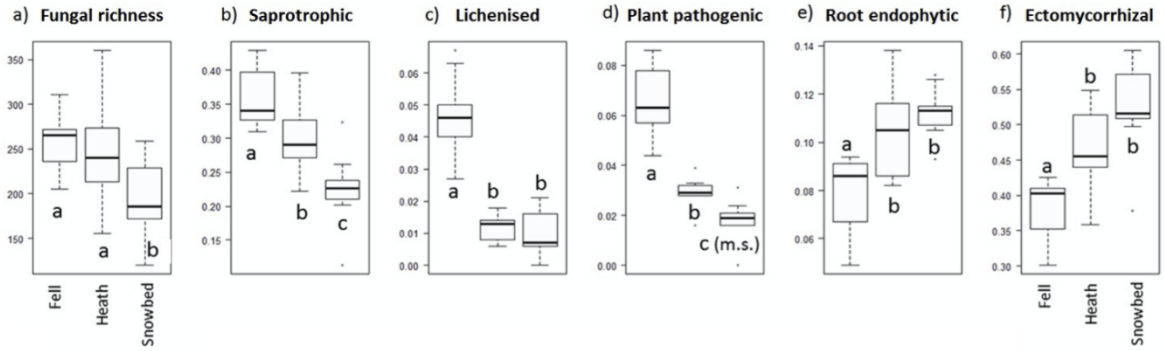


Figure 3.3. Total fungal richness and proportional richness of saprotrophic, lichenised, plant pathogenic, root endophytic, and ECM fungi in fell field, heath and snowbed habitats (a-f) in NE Greenland (Grau et al. 2017). The letters indicate significant differences.

The opposite trends of ECM and saprotrophic fungi observed are particularly noteworthy, because they constitute the two most diverse and abundant functional groups of arctic fungi that are in direct competition for nutrients (Nordin et al. 2004). ECM fungi can outcompete saprotrophic fungi by decreasing the availability of N in the soil (Leake 2002) and the resulting decrease in decomposers is expected to slow soil C respiration and increase soil C storage (Orwin et al. 2011), as demonstrated by Averill and Hawkes (2016). This mechanism could, therefore, explain the higher accumulation of soil organic C in the snowbed and the

heath (Grau et al. 2017). In contrast, competitive exclusion by mycorrhizal fungi should be less pronounced in the fell field, because the proportional richness of mycorrhizal fungi is lower. Consequently, the higher proportional richness of saprotrophic fungi could partly explain the lower accumulation of organic C in the fell field, together with the very low input of dead plant biomass in this poorly vegetated habitat (Grau et al. 2017). The increase in proportional richness of lichens towards the fell field is likely due to the decrease in vegetation cover, because lichens are easily outcompeted by dense vascular vegetation but thrive in poorly vegetated habitats (Cornelissen et al. 2001, Joly et al. 2009). The higher proportional richness of pathogenic fungi in the fell field is surprising at first glance given the low plant cover, although bryophyte diversity generally is the highest in this habitat. In addition, most plants in this hostile habitat likely are closer to their physiological limits and may be more prone to pathogenic infections (Read 2003). These functional patterns are very similar to those reported by Timling et al. (2014) along a latitudinal gradient through the Arctic, where proportional richness of saprotrophic, pathogenic, and lichenized fungi correlated negatively and that of ECM fungi correlated positively with temperature and shrub cover. Therefore, the strong influence of abiotic conditions on inferred functional patterns of soil fungal communities along the mesotopographic gradient in Grau et al. (2017) are similar to those along the more than 1500-km long arctic latitudinal gradient in Timling et al. (2014).

It is noteworthy that the fungal community in the fell field is not only the richest, but compositionally the most unique (Figures 3.4-3.6) (Grau et al. 2017), indicating that many taxa are highly adapted to the harsh conditions in this habitat. Such compositional difference between the fell field and the heath and snowbed plots is particularly pronounced in ECM and root endophytic fungi, even though the principal ECM host dwarf shrubs are also found in that habitat (Figure 3.6). Furthermore, habitat-scale filters likely drive the establishment of a further subset of the local species pool, partly selected according to their functional attributes. Geml et al. (2016) in the Alaskan Arctic and Grau et al. (2017) in NE Greenland (Figure 3.6) both observed compositional differences amongst habitats within the functional groups, indicating the contribution of niche-based processes to community assembly.

The changes in the relative importance of each functional group are closely associated with the environmental severity (Figures 3.3, 3.4). The decrease in fungal richness towards the snowbed seem to be driven at least in partly by the decrease in saprotrophic, lichenized, and plant pathogenic fungi, as also observed in low arctic tundra sites in Alaska with thick snow cover (Semenova et al. 2016, Geml et al. 2021). We found that in both Greenland and Alaska, the proportional richness values of ECM and root-associated fungi were higher in habitats with higher vegetation cover and soil moisture, such as the snowbed and heath in Greenland and the moist tussock tundra in Alaska, likely due to more favorable abiotic conditions and increased abundance of their hosts (Grau et al. 2014, 2017, Geml et al. 2021).

In the low arctic tundra of northern Alaska, tundra type (dry vs. moist) appears to be the strongest driver of the structuring of fungal communities at landscape level, explaining between 21% and 42% of the variation in community composition of the various functional groups (Geml et al. 2015, Geml et al. 2016, Geml et al. 2021). Despite the spatial proximity of the dry and moist tundra plots, the overwhelming compositional differences and numerous

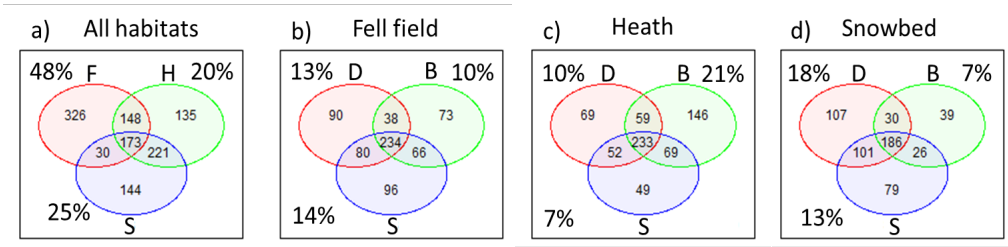


Figure 3.4. Venn diagrams of the number of OTUs from a) all habitats, b) the fell field, c) the heath, and d) the snowbed. The abbreviations in panel a represent habitat type (F - fell field; H - heath; S - snowbed), and the abbreviations in panels b-d represent microhabitat type (D - *Dryas*; S - *Salix*; B - bare ground) in each habitat (Grau et al. 2017).

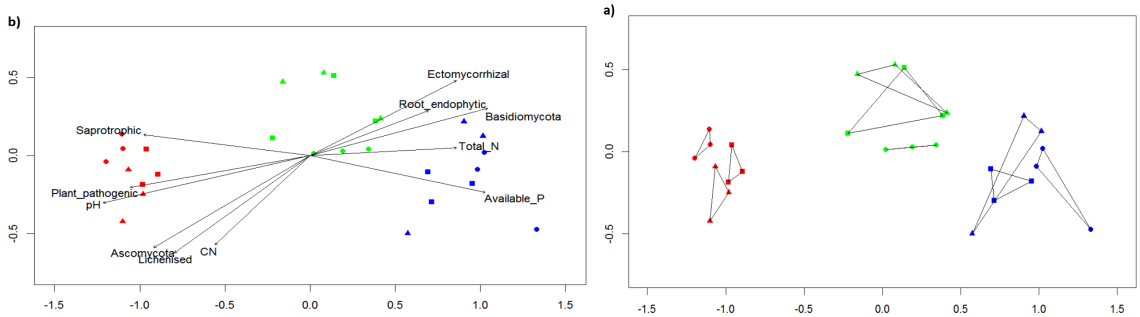


Figure 3.5. a) NMDS analysis of the presence or absence of OTUs in the sampled habitats fell-field (red), heath (green), and snowbed (blue) as well as microhabitats *Dryas* (triangles), bare ground (circle), and *Salix* (squares), with vectors of the proportional richness of fungal phyla and functional groups, and the abiotic variables with significant correlations with the NMDS axes (Grau et al. 2017).

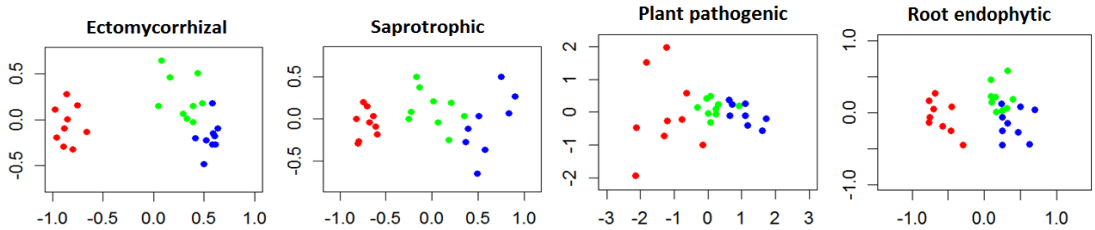


Figure 3.6. NMDS analysis of the presence or absence of OTUs in the four dominant functional groups in habitats fell field (red), heath (green), snowbed (blue) (Grau et al. 2017).

indicator OTUs suggest that many fungi appear to be sensitive to the differences in hydrology and vegetation between these tundra types (Table 3.1). However, it is worth to note that a relatively large fraction of the fungal community is shared between the dry and moist tundra and among various treatments. It is plausible that climate change and related changes in abiotic factors will favor these fungi with apparently wide niche breadth as opposed to those with narrower observed niche breadth that are restricted to a certain habitat, as discussed in the subsequent subchapter on the responses of arctic fungi to experimental manipulations simulating climate change. Because dispersal generally is not considered a limiting factor in arctic fungi (Geml et al. 2010a, Geml 2011, Geml et al. 2012ab), it is presumed that environmental filtering strongly influences fungal community composition at tundra type level.

Table 3.1. Arctic Alaskan ectomycorrhizal fungal OTUs that were significant indicators for dry or moist tundra with values of significance of association, percent sequence similarity to matching taxon and Species Hypotheses (SH in the Unite database (unite.ut.ee). This table was made based on data published by Geml et al. (2021).

OTU	**Tundra**	***p***	**%**	**Matching taxon**	**SH**
OTU853	Dry	0.001	99.5	*Atheliales sp.*	SH0142754.10FU
OTU1963	Dry	0.003	96.9	*Byssocorticiaceae sp.*	SH1004750.10FU
OTU599	Dry	0.003	98.5	*Byssocorticium sp.*	SH0858559.10FU
OTU4330	Dry	0.045	95	*Cenococcum sp.*	SH0999694.10FU
OTU1666	Dry	0.043	100	*Cenococcum sp.*	SH1037872.10FU
OTU395	Dry	0.001	89.3	*Ceratobasidiaceae sp.*	SH0987434.10FU
OTU390	Dry	0.027	99.5	*Chromosera citrinopallida*	SH0936530.10FU
OTU287	Dry	0.049	99.5	*Clavulina cinerea*	SH0858162.10FU
OTU142	Dry	0.03	98.5	*Cortinarius heterodepressus*	SH1365595.10FU
OTU132	Dry	0.002	98.5	*Cortinarius laetus*	SH1018136.10FU
OTU429	Dry	0.002	95.5	*Cortinarius pelargoniostriatulus*	SH1365768.10FU
OTU168	Dry	0.022	91.5	*Glonium stellatum*	SH0999716.10FU
OTU90	Dry	0.001	98	*Hebeloma pungens*	SH1375954.10FU
OTU297	Dry	0.045	93.5	*Inocybe nitidiuscula*	SH0998216.10FU
OTU407	Dry	0.008	100	*Inocybe sp.*	SH0902345.10FU
OTU1051	Dry	0.007	98	*Inocybe striipes*	SH0909818.10FU
OTU511	Dry	0.001	99.5	*Lactarius sp.*	SH0961083.10FU
OTU361	Dry	0.001	99.4	*Polyozellus umbrinus*	SH0881211.10FU
OTU884	Dry	0.026	98.3	*Russula aeruginea*	SH0978162.10FU
OTU3	Dry	0.001	99.5	*Russula cremicolor*	SH0882189.10FU
OTU1122	Dry	0.047	99	*Russula griseascens*	SH0944258.10FU
OTU704	Dry	0.008	98.8	*Sebacinales sp.*	SH0974378.10FU
OTU443	Dry	0.041	94.7	*Thaxterogaster microspermus*	SH1018809.10FU
OTU26	Dry	0.002	97	*Thelephoraceae sp.*	SH0125701.10FU
OTU198	Dry	0.001	100	*Tomentella sp.*	SH0917913.10FU
OTU38	Dry	0.005	100	*Tomentella sp.*	SH0918848.10FU
OTU42	Dry	0.03	94.5	*Tomentella sp.*	SH0921804.10FU
OTU586	Moist	0.001	99	*Alnicola cholea*	SH0995054.10FU
OTU220	Moist	0.02	100	*Cortinarius boreotrichus*	SH1364989.10FU
OTU996	Moist	0.003	98	*Cortinarius fragrantissimus*	SH1888270.10FU
OTU544	Moist	0.001	96	*Cortinarius fulvopaludosus*	SH1887182.10FU
OTU747	Moist	0.009	96	*Cortinarius pelargoniostriatulus*	SH1365768.10FU
OTU701	Moist	0.003	98	*Hebeloma matritense*	SH1375852.10FU
OTU530	Moist	0.001	99.5	*Hebeloma monticola*	SH1904173.10FU
OTU487	Moist	0.001	97.5	*Helotiaceae sp.*	SH0872812.10FU
OTU1483	Moist	0.001	99.4	*Helotiaceae sp.*	SH0996159.10FU
OTU1167	Moist	0.018	100	*Helotiales sp.*	SH0984773.10FU
OTU562	Moist	0.007	97.5	*Inocybe sp.*	SH0746810.10FU
OTU500	Moist	0.002	100	*Inocybe sp.*	SH0857387.10FU
OTU814	Moist	0.001	99.4	*Lactarius nanus*	SH0960786.10FU
OTU95	Moist	0.006	99	*Lactarius pseudodelicatus*	SH0960970.10FU

OTU331	Moist	0.001	100	*Lactarius vietus*	SH1333316.10FU
OTU114	Moist	0.001	100	*Russula renidens*	SH0944188.10FU
OTU81	Moist	0.001	99.5	*Russula vinososordida*	SH0957147.10FU
OTU362	Moist	0.05	99.5	*Sebacina sp.*	SH0934265.10FU
OTU454	Moist	0.023	97	*Sebacina sp.*	SH1299909.10FU
OTU285	Moist	0.001	99.5	*Thelephoraceae sp.*	SH0125578.10FU
OTU435	Moist	0.001	100	*Thelephoraceae sp.*	SH0125888.10FU
OTU677	Moist	0.012	100	*Thelephoraceae sp.*	SH0125934.10FU
OTU2866	Moist	0.004	98	*Thelephoraceae sp.*	SH0920725.10FU
OTU232	Moist	0.015	96.5	*Tomentella lapida*	SH1769657.10FU
OTU212	Moist	0.021	100	*Tomentella sp.*	SH0918802.10FU
OTU274	Moist	0.017	97.5	*Tomentella sp.*	SH0922449.10FU

In addition to habitat, the microhabitat type often also has a clear, although less strong, effect on fungal community composition and richness (Figures 3.5-3.8). In our studies in NE and W Greenland and in Alaska, we observed strong habitat and microhabitat partitioning in arctic fungi (Geml et al. 2015, 2016, Grau et al. 2017, Canini et al. 2019, Geml et al. 2021), similar to studies in Svalbard (Blaalid et al. 2014, Mundra et al. 2014) and Canada (Timling et al. 2012, 2014). These microhabitats often are less than a meter in size, e.g., patches of bare ground in the middle frost boils or a cushion of *Dryas* on a rocky fell field, and while on the surface they often have clear boundaries, these lines are less pronounced underground. Some mycelia and shrub roots likely expand beyond the patches covered by *Dryas* and *Salix*, and may have been sampled in bare ground patches. Furthermore, ECM host plants, such as *Kobresia myosuroides* and *Saxifraga oppositifolia*, often occur in bare ground patches in the sampled plots in NE Greenland (Grau et al. 2014). ECM and other root-associated fungi have shown to be surprisingly diverse in recently exposed glacier fronts in the Arctic (Blaalid et al. 2012) and in the coldest parts of the Arctic (bioclimatic subzone A) that lacks any woody species (Timling et al. 2014) and the relative importance of the above-mentioned non-woody ECM hosts to sustain ECM fungi likely is greater in those barrens. The

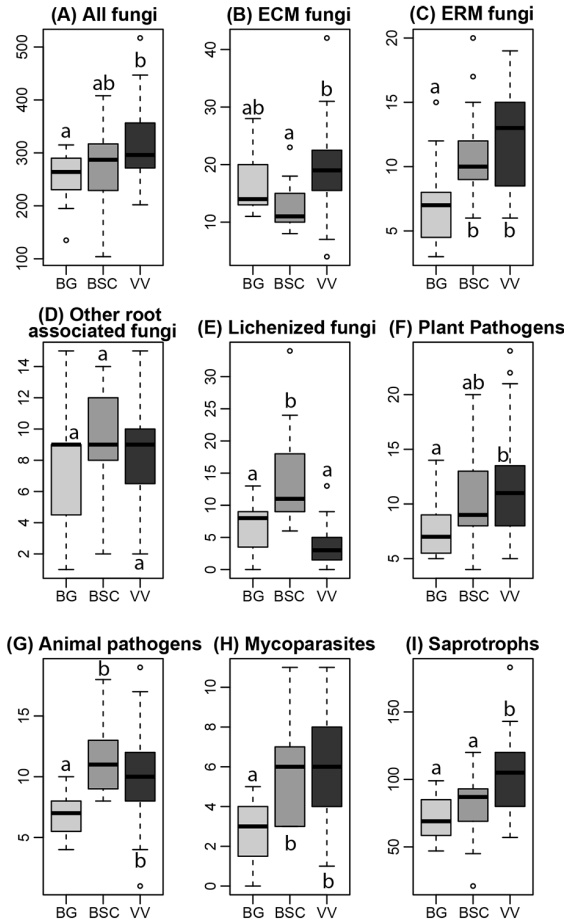


Figure 3.7. Richness of the total, ECM, ericoid mycorrhizal (ERM), other root-associated, lichenized, plant pathogenic, animal pathogenic, mycoparasites and saprotrophic fungi in bare ground (BG), biological soil crust (BSC) and vascular vegetation (VV) microhabitats in W Greenland (Canini et al. 2019). Letters indicate significant differences.

observed compositional differences among microhabitats indicate the influence of edaphic factors on the small-scale distribution of ECM fungi associated with the roots of the same host.

In our study in W Greenland (Canini et al. 2019), richness and relative abundance of ECM fungi were highest in the vegetated (VV) plots, likely due to greater diversity and abundance of their hosts (Figure 3.7). High shrub cover generally corresponds to many roots available for mycorrhizal colonization, and mycorrhizal fungi favor the development of dominant dwarf shrubs such as *Dryas* and *Salix* (Timling et al. 2012). However, both richness and relative abundance of ECM fungi were surprisingly high also in BG plots, with no significant difference compared to VV plots, being lower only in BSC samples. ECM fungi and other root-associated fungi have been shown to be highly diverse in recently exposed glacier front areas in the Arctic (Blaalid et al. 2012) in the Arctic bioclimatic subzone A, that generally lacks woody plants and is characterized by lichens, bryophytes, cyanobacteria, and scattered forbs (Timling et al. 2014). In first instance, this situation could be explained by the fact that in the earliest stages of fungal colonization and community development, stochastic processes are the main driving factors of community composition (Jumpponen 2003), favoured by the already well documented high dispersal ability of Arctic fungi (Geml et al. 2010a, Geml 2011, Geml et al. 2012b), of which ECM fungi are the main components. Some ECM sequences found in these plots could originate from spores, which could facilitate the expansion

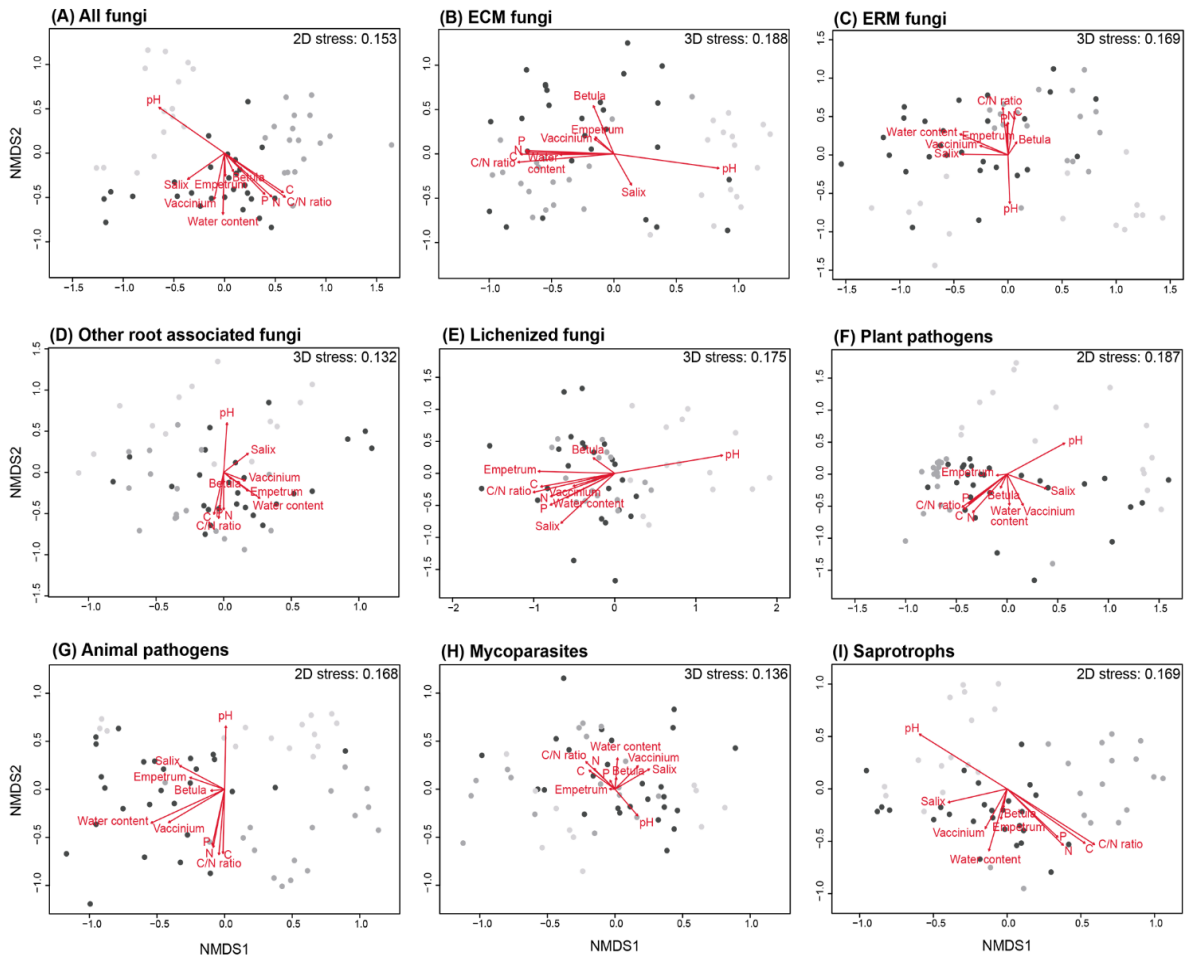


Figure 3.8. Compositional differences of fungal functional groups among microhabitats studied (light grey - bare ground, dark grey - biological soil crust, black - vascular vegetation) in W Greenland (Canini et al. 2019).

of shrubs from the surrounding areas. However, it is remarkable that the composition of ECM fungal communities in the bare grounds is well differentiated from the communities in the vegetated plots (Figure 3.8), suggesting a negligible effect of 'spore rain'. Therefore, a probable explanation for the high prevalence on ECM fungi in the BG plots is that most of them are likely associated with the roots of shrubs and other hosts growing in adjacent vegetated patches. Furthermore, the compositional differences among microhabitats likely indicate the influence of edaphic factors on the community composition of ECM fungi, associated with the root system of the same host, at small spatial scales. For example, parts of a shrub root system may grow in soils with different pH, which is expected to shape ECM community composition. Additionally, considering only fully vegetated, shrub-dominated plots, we found that pH and water content had a stronger effect on ECM community composition than shrub composition, confirming the importance of differences in edaphic conditions in shaping ECM fungal community structure at small spatial scales (Canini et al. 2019). Finally, the negative relationship between soil N content and ECM fungi richness and abundance has been repeatedly reported (Bödeker et al. 2014), which likely explains at least in part the patterns observed here, i.e. the lower abundance and richness of ECM fungi in biological soil crust plots, characterized by higher N content (Canini et al. 2019) likely driven by the abundance of lichen-symbiotic and free-living N-fixing cyanobacteria, such as *Nostoc* (Schell and Alexander 1973).

ERM fungi showed an increase in richness with increased vegetation coverage, likely due to the presence of their host species (Figure 3.7). Their diversity and, to a lesser extent, their abundance were also high in BSC plots. ERM fungi have evolved recently from saprotrophic fungi (Martino et al. 2018) and, unlike ECM fungi that, during the transition to fully mycorrhizal habit, have lost genes coding for plant cell wall-degrading enzymes (Martin et al. 2016), all ERM fungi, regardless of their taxonomic position, feature a large set of degrading enzymes, specifically those involved in the degradation of hemicelluloses, pectins, glucans and mannans. This suggests that they still are in a transitional evolutionary stage between saprotrophy and mutualism (Martino et al. 2018) and, thus, are not obligate mutualists. Therefore, ERM fungi can occur in BSC plots, where their symbiotic hosts are not present and where they can survive as saprotrophs, thanks to their ability to thrive in more limiting conditions. Among the habitats sampled in our study, ERM fungal community composition was mainly driven by edaphic variables. They are usually characteristic of acidic soils, with low nutrients availability and high content of recalcitrant compounds (Cairney and Meharg, 2003); the strong negative correlations between the richness and relative abundance of ERM fungi and soil pH confirm that. Additionally, in the VV plots, we found that despite the presence of two Ericaceae genera being significant in shaping the structure of ERM communities, the effect of the *Salix* relative abundance was stronger. This pattern may be explained by the versatile habit of ERM fungi as well because, besides being able to act as decomposers, ERM fungi can also live as endophytes in root tips of ECM plants (Bergero et al. 2000), and colonize both co-occurring ECM and non-ECM plants (Chambers et al. 2008).

Saprotrophic fungi had a higher richness and relative abundance in VV plots, accounting also for the great part of indicator OTUs with an assigned function (33.6% of the OTUs identified as indicator species for this habitat). Their greater richness and relative abundance in the vegetated plots is likely due, in part, to greater soil moisture and possibly to

an increase in plant litter biomass (Canini et al. 2019). Within the saprotrophic guild, the above increase was primarily driven by litter decomposer and wood decaying fungi (mainly basidiomycetes), as opposed to the generalist saprotrophs relying on simple sugars (mainly ascomycetes), as indicated by the relative richness values of the two phyla among the habitats.

Table 3.2. Proportion of variation in fungal community composition in W Greenland, explained by microhabitat type (categorical) and edaphic variables (continuous) calculated independently with permutational multivariate analysis of variance (Canini et al. 2019). Continuous variables that remained significant in the combined model after accounting for correlations among them are in bold.

Variables	Variance (%)	*p*	Variance (%)	*p*	Variance (%)	*p*
	All fungi		**Ectomycorrhizal fungi**		**Ericoid mycorrhizal fungi**	
Microhabitat	18.145	0.001	16.549	0.001	17.028	0.001
pH	**10.267**	**0.001**	**10.259**	**0.001**	**8.836**	**0.001**
Water content	**6.325**	**0.001**	5.634	0.001	**5.913**	**0.001**
C	7.705	0.001	8.796	0.001	6.127	0.001
N	**6.508**	**0.001**	**7.638**	**0.001**	5.227	0.002
C/N ratio	**9.315**	**0.001**	9.591	0.001	**8.198**	**0.001**
P	5.968	0.001	**7.632**	**0.001**	4.683	0.002
	Other root fungi		**Lichenized fungi**		**Plant pathogens**	
Microhabitat	14.083	0.001	11.713	0.001	20.030	0.001
pH	**9.974**	**0.001**	6.063	0.001	**14.895**	**0.001**
Water content	4.845	0.005	2.708	0.093	4.116	0.020
C	6.683	0.001	4.460	0.003	9.780	0.001
N	5.456	0.001	**3.878**	**0.006**	**7.910**	**0.001**
C/N ratio	7.673	0.001	5.285	0.002	11.346	0.001
P	5.666	0.003	3.341	0.019	7.303	0.001
	Animal pathogens		**Mycoparasites**		**Saprotrophs**	
Microhabitat	28.070	0.001	11.041	0.001	18.464	0.001
pH	**11.731**	**0.001**	6.659	0.001	**10.734**	**0.001**
Water content	12.803	0.001	4.763	0.006	6.376	0.001
C	11.712	0.001	4.601	0.012	8.624	0.001
N	10.162	0.001	4.332	0.017	**7.126**	**0.001**
C/N ratio	**13.548**	**0.001**	5.219	0.002	**10.315**	**0.001**
P	8.271	0.002	**3.987**	**0.025**	6.199	0.001

Among the edaphic parameters tested, pH tended to differ among microhabitats and correlated strongly with fungal richness and community composition (Figure 3.8, Table 3.2), as in our microhabitat study (Canini et al. 2019) and in primary successional studies at glacier fronts (Kwon et al. 2015). Soil pH is one of the strongest parameters in shaping the fungal communities across the Arctic (Timling et al. 2014) as well as worldwide (Tedersoo et al. 2014, Vétrovsky et al. 2020). The observed increase in P content with increased vegetation complexity in our W Greenland plots (Canini et al. 2019) is similar to what had been reported for a glacier foreland (Borchhardt et al. 2019), where microbial P storage increased with distance from the glacier. Despite being abundant in the topsoil of bedrock of glaciated regions due to mineral weathering (Bradley et al. 2014), P is subjected to high rates of release by leaching (Wu et al. 2015). Microbial assimilation and storage of P is fundamental for its

availability for plant colonization. The possible increasing in plant coverage could increase fungal richness and this could explain the strong positive relationship of P content and fungal richness that we found. Even being significant for community composition, in most cases P effect was not independent from other parameters. P availability is highly affected by soil pH, the main determinant of our communities. In fact, P is highly soluble at neutral pH values and becomes less available at basic and acidic pH levels. Similar effects for soil P content have been reported also for root-associated fungi in the high Arctic, making it difficult to disentangle the effects of pH from those of other edaphic factors (Fujimura and Egger 2012).

Effects of temperature and snow depth increase on arctic fungi - implications for climate change studies

A series of our studies were among the first to provide insights into the compositional dynamics of arctic fungi, highlighting their diversity, abundance, and distribution in dry and moist acidic tundra and their possible responses to warming and increased winter precipitation (Geml et al. 2015, Morgado et al. 2015, Semenova et al. 2015, Geml et al. 2016, Morgado et al. 2016, Semenova et al. 2016, Morgado and Geml 2020, Geml et al. 2021). The results show that experimental warming and increased snow depth have different effects on edaphic variables and fungal communities on dry vs. moist tundra, and that there are important differences among functional groups of fungi in how they respond to increases in summer temperatures, snow depth, and alterations in soil chemistry.

Experimental manipulations generally had weak effect on total fungal richness in dry tundra sites and a strong effect in the moist tundra, although richness differed among treatments in four of the six functional groups studied (Figure 3.9). In ECM fungi, richness was highest in the moist tundra control plots, with all warming and snow depth treatments in moist tundra showing significantly lower richness. The highest ECM richness in the dry tundra was also found in the control, but it was not significantly different from any of the experimental treatments. In plant pathogenic fungi, highest richness was observed in the S and SW treatments, although only the latter differed significantly from the control. No statistical differences were observed in the moist tundra for the same functional group. Conversely, root-associated non-mycorrhizal fungi showed highest richness in moist control plots and decreased in all treatment plots, with significant difference observed between control and the SW and S. For this functional group, richness values were uniformly low for all treatments in the dry tundra. Saprotrophic fungal richness generally did not differ among all treatments, except for the dry control and dry S pair, the latter showing highest richness of all treatments.

In addition to the differences in fungal species pools in dry and moist acidic tundra at the sampling sites (as discussed in the previous subchapter), there were also distinct responses of the dry and moist tundra fungal communities to experimental warming and increase in snow depth. This suggests that species pool and pre-disturbance environmental factors, such as site hydrology and resulting differences in vegetation structure, likely drive response trajectories of fungal communities, similar to what has been reported for plants as well (Walker et al. 2006, Pattison and Welker 2014). Geml et al. (2021) found that, in dry tundra, experimental increase in summer temperature or snow depth correlated significantly with community composition in all functional groups except root-associated fungi and wood decomposers, respectively. In

moist tundra, summer warming correlated strongly with the composition of functional groups, except in wood decomposers, while increased snow depth had weak effects, with community composition of only ECM and other root-associated fungi showing significant correlation with snow depth in the moist tundra. (Figure 3.10, Table 3.3)

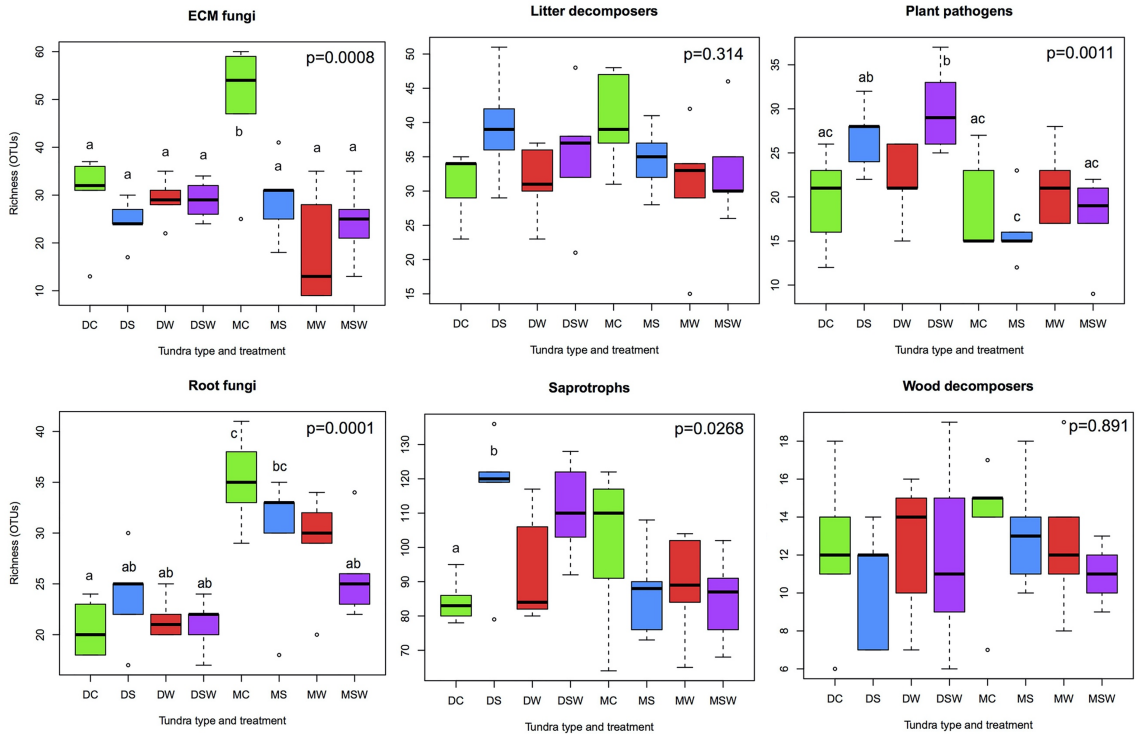


Figure 3.9. Comparisons of richness of functional groups of arctic fungi across dry and moist tundra and experimental treatments. D - dry tundra, M - moist tundra, W - summer warming, S - increased winter snow depth, WS - combined warming and snow depth treatments (Geml et al. 2021).

The strong responses in fungal communities to warming in the moist tundra agree with more pronounced plant community responses in the moist than in the dry tundra, although it is unclear to what extent compositional shifts in the fungal community drive vegetation shifts or are driven by them. In addition, differential fungal responses to warming in the dry and moist tundra likely are related to differences in natural temperature fluctuations in the dry and moist tundra. Moist tundra soils generally experience less temperature variation due to higher water content and a dense peat moss layer that buffers changes in air and surface temperature. In dry tundra, where vegetation cover generally is below 50% and soils are relatively dry, the ca. 2°C warming during the summer may represent a negligible change relative to the high variation in temperatures experienced under normal circumstances. With respect to increased snow depth, it is important to note that greater snow depth increases winter soil temperature as well as soil moisture, particularly in early summer, and these effects cannot be decoupled. The strong effect of available moisture on plant growth has repeatedly been shown in dry tundra (Jones et al. 1998, Wahren et al. 2005). Therefore, the stronger response by the community of the dry heath

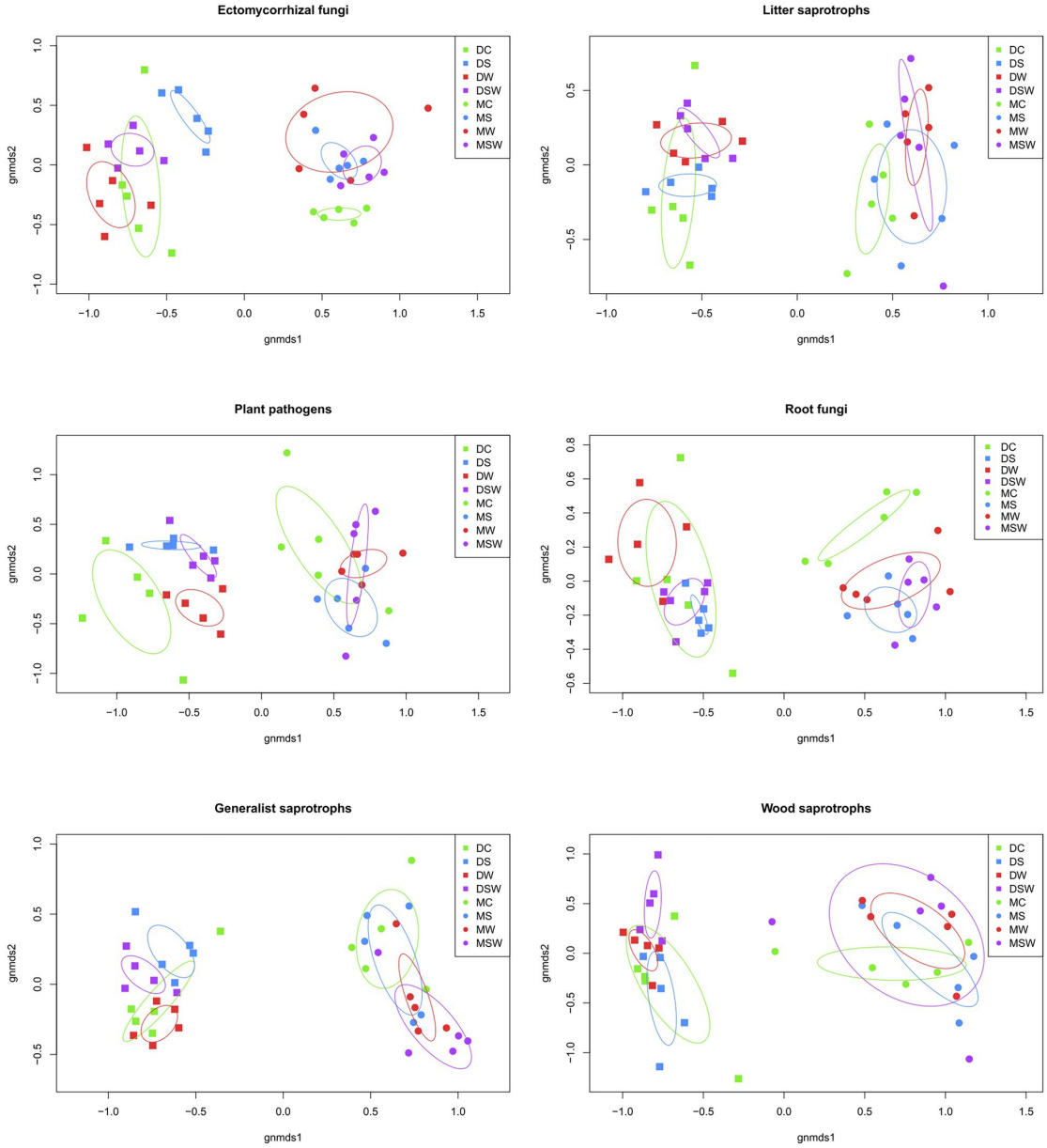


Figure 3.10. Non-metric multidimensional scaling (NMDS) ordination plots of the six most diverse functional groups of arctic fungi. For each treatment, circles indicate the standard deviation. D - dry tundra, M - moist tundra, W - summer warming, S - increased winter snow depth, WS - combined warming and snow depth treatments (Geml et al. 2021).

tundra may partly be explained by partially alleviating water stress in this habitat. In addition, S treatment plots in the dry tundra differ most from the rest in soil pH and C/N ratio (Geml et al. 2021). More precisely, these plots have the most acidic soils that contain the most decay-resistant organic matter. The fact that the richness of generalist saprotrophs was the highest in this treatment, but not their relative abundance, may indicate that the low nutrient levels favor a high diversity of relatively slow-growing saprotrophic fungi. Moist tundra soils are mostly saturated by water throughout the growing season and winter snow cover is deeper and more homogenous than in the dry tundra community, where soils tend to have little or no snow cover and low moisture content, resulting in very cold temperatures and frequent desiccations. It is noteworthy that, particularly in the dry tundra, the compositional effects of the combined SW

treatment resulted in communities that appeared to be intermediate between those of S or W only, as suggested by the NMDS results. Similarly, opposite trends in S and W treatment were also observed to some extent in richness and in soil pH and C/N ratio, though they remained mostly non-significant. This suggests that in the dry tundra, these S and W treatments may have divergent effects on the fungal communities, possibly because they alter soil moisture and soil chemical processes in opposite directions.

Table 3.3. Proportion of variation in fungal community composition explained by tundra type, experimental warming and increased snow depth calculated independently with permutational multivariate analysis of variance in dry and moist tundra communities in the Alaskan Arctic (Geml et al. 2021). Significant results are in bold. Climatic and edaphic variables that remained significant in the final composite model for each fungal group are shown with an asterisk (*)All - all fungi, ECM - ectomycorrhizal fungi, LD - litter decomposers, PP - plant pathogens, RF - non-mycorrhizal root fungi, SAP - generalist and soil saprotrophs, WD - wood decomposers.

All plots	**All**	**ECM**	**LD**	**PP**	**RF**	**SAP**	**WD**
Tundra type	**31.89***	**21.17***	**27.02***	**24.92***	**41.09***	**34.29***	**31.69***
Warming	4.03	3.98	**5.88***	4.22	2.55	4.33	3.74
Snow depth	3.74	**4.23***	3.42	3.61	3.99	4.23	2.37
pH	**5.87***	**6.01***	**5.33**	**7.62***	**6.35**	**5.56**	5.08
EC	3.04	2.95	3.59	3.62	3.4	3.03	1.88
N	3.56	2.91	4.36	3.63	3.43	4.24	2.19
C	2.77	2.62	3.55	2.97	2.61	3.27	1.65
C/N	**6.84***	**5.26**	**5.63**	**8.17***	**6.4***	**7.38***	**6.49***
Dry tundra	**All**	**ECM**	**LD**	**PP**	**RF**	**SAP**	**WD**
Warming	**9.02**	**11.11***	**11.78***	**12.54**	7.51	**9.96**	**13.72**
Snow depth	**13.78***	**10.53***	**10.34***	**19.53***	**13.61***	**19.14***	7.27
pH	**14.83***	**12.38***	**12.13***	**20.67***	**18.41***	**16.99***	**16.27**
EC	6.97	**5.84**	**8.17**	9.79	8.76	5.67	5.09
N	**8.9***	**7.45***	**8.89***	**12.97***	**14.17***	**8.61**	6.44
C	7.25	6.03	**7.97**	8.98	**10.57***	6.98	6.14
C/N	**13.89***	**10.81**	**9.4**	**15.05***	**16.91***	**17.94***	**17.2***
Moist tundra	**All**	**ECM**	**LD**	**PP**	**RF**	**SAP**	**WD**
Warming	**12.76***	7.32	**10.96**	**9.03***	**10.21***	**17.05***	7.65
Snow depth	8.09	**10.61***	6.83	7.13	**12.69***	6.73	5.15
pH	7.44	**10.09***	6.72	6.47	**10.44***	6.04	6.46
EC	**12.18***	**10.47***	**11.66***	7.59	7.52	**17.53***	8.47
N	**8.15**	7.42	**9.59**	6.65	6.03	**12.02**	6.43
C	**8.22**	7.61	**9.79**	6.67	5.86	**12.1**	6.39
C/N	6.66	5.7	5.59	5.78	6.83	8.65	5.03

ECM and non-mycorrhizal root fungi appear to be most diverse in the moist tundra, but their high richness is not coupled with high overall abundance. Their decreasing trends in richness and abundance and the strong compositional shifts in the moist tundra treatment plots, suggest that the altered abiotic conditions, and possibly the resulting differences in vegetation, are no longer suitable for many root-associated fungi that normally inhabit moist acidic tussock tundra. This is surprising, because ECM fungal richness and abundance generally correlate with host plant abundance (Tedersoo et al. 2014) and higher density and biomass of ECM

shrubs were reported in increased snow depth plots in both tundra types (Pattison and Welker 2014). Differences in nutrient scavenging capabilities among ECM fungal species under the altered conditions may explain some of the observed patterns, as changes in plant community and N dynamics had been reported to be more strongly affected by the increased snow depth in the moist than in the dry tundra (Schimel et al. 2004, Wahren et al. 2005). For example, presenting data from the S and W plots analyzed here, Morgado et al. (2015, 2016) argued that ECM fungi with exploration types adapted to labile N uptake generally showed decreasing richness under increased snow depth, while the richness of ECM fungi with exploration types adapted to acquire recalcitrant soil N were not affected by increased snow depth. Although Morgado et al. (2015, 2016) did not analyze data from the combined SW plots that are presented here, their observations, coupled with the higher C/N values observed here suggest that the capability of acquiring recalcitrant N may represent an important environmental filter for ECM fungi under increased snow depth and appear to be explain partly the lower richness and abundance of ECM fungi. Alternatively, it could partly be caused by the water-logged, likely hypoxic conditions in the SW plots in the summer (József Geml, pers. obs.). The findings presented here show that the above differences likely are at fine taxonomic scales, i.e., at species level, as most ECM genera included numerous OTUs that were specific to a habitat and others that were shared among tundra types and treatments, indicating that in most genera comprise species that represent a wide spectrum of ecological preferences and niche breadths. It is well-known that ECM fungi compete with saprotrophic fungi for water and nutrients (Orwin et al. 2011) and the decline in ECM fungi, the increased abundance of decomposers, and higher rates of decomposition with increasing summer and winter soil temperatures (as discussed below), may result in decreased C sinks in tundra soils, as plants in cold climates transfer up to 70% of their C uptake directly to ECM fungal mycelia (Clemmensen et al. 2013).

The increased relative abundance of decomposers of litter and wood in the snow addition treatments (S and SW) in moist and dry tundra, respectively, may be related to the abilities of these fungi to take advantage of more available substrate as well as more favorable conditions for enzymatic degradation. Increased quantities of litter and woody debris resulting from the greater above-ground biomass of shrubs and graminoids have been reported for these plots with increased snow depths as well as with summer warming (Hollister and Webber 2000, Wahren et al. 2005, Semenova et al. 2015) and microbial decomposition rates have been found to be greater (Sistla et al. 2013). Saprotrophic fungal activity generally is correlated with decomposition rates and CO_2 flux between the terrestrial and atmospheric pools. Therefore, an increased abundance of saprotrophic fungi may increase fungal enzymatic activity in soils, with higher rates of C mineralization and greater CO_2 emission to the atmosphere (Guhr et al. 2015). The greater aboveground plant biomass of the moist tundra treatment plots also is in agreement with the higher proportional abundance of plant pathogenic fungi that could benefit from greater host biomass. Greater snow depth increases winter soil temperature, which is expected to have positive effects on microbial decomposition. The increased abundance of generalist saprotrophs in the increased snow depth and warming plots provides further support for this idea. Overall, the observed changes in richness and abundance decomposer and other saprotrophic fungi provides proof for the conceptual framework that increased snow depth provides greater soil insulation, resulting in higher winter and spring-time soil temperatures, and increased rates of nutrient mineralization. This, in turn, favors shrub growth and expansion,

which leads to decreased albedo, increased snow trapping, and enhanced CO_2 release to the atmosphere, providing positive feedback to climate change.

Lichens showed a mixed response to warming both in terms of tundra type and lichenized fungal genera. The negative effect of warming on lichen richness in the moist plots observed by Geml et al. (2015) may be partly explained by the observed decrease in cover of shade-intolerant lichens and bryophytes and the increase in shrub size in the moist warmed plots (Walker et al. 2006), while the low abundance of erect shrubs results in little shading in the dry plots. However, strong taxon-specific responses were observed again, as OTU richness of *Cladonia* and *Shaerophorus* strongly negatively correlated with warming particularly in the dry plots, while *Agonimia*, *Peltigera*, *Verrucaria* and *Xanthoria* benefited from the increased temperatures in the dry tundra. The reindeer lichens (*Cladonia* spp.) are considered keystone components in arctic ecosystems and are the main winter food source for caribou (Dahlberg and Bültmann 2013). *Cladonia* was one of the very few fungal genera that showed consistent and strong warming-induced decline in richness in both tundra types (Geml et al. 2015) and was among indicators of the dry control plots (Table 3.4). Because the sampled tundra types represent communities with the greatest surface areas in Northern Alaska (Walker et al. 2005), the observed trend of declining lichen richness (Geml et al. 2015, Semenova et al. 2015) and cover (Walker et al. 2006) may have detrimental effects on Alaskan caribou populations, with potentially profound social implications for local people (Joly et al. 2009).

Table 3.4. Arctic Alaskan fungal OTUs that were significant indicators for a specific treatment with values of significance of association, percent sequence similarity to matching taxon and Species Hypotheses in the Unite database (unite.ut.ee), and with genus-based functional assignment following Pölme et al. 2020). This table was made based on data published by Geml et al. (2021). DC - dry tundra control, DS - dry tundra increased snow depth, DW - dry tundra summer warming, DSW - dry tundra combine snow and warming treatment, MC - moist tundra control, MS - moist tundra increased snow depth, MW - moist tundra summer warming, MSW -- moist tundra combine snow and warming treatment, ECM - ectomycorrhizal fungi, LD - litter decomposers, PP - plant pathogens, RF - non-mycorrhizal root fungi, SAP - generalist and soil saprotrophs, WD - wood decomposers.

OTU	**Treat.**	***p***	**%**	**Matching species**	**SH**	**Function**
OTU2108	DC	0.035	98.5	*Cladonia crispata*	SH0932994.10FU	LICH
OTU1835	DC	0.035	91.5	*Cladonia pyxidata*	SH0932997.10FU	LICH
OTU1556	DC	0.021	99	*Mycoblastus sanguinarius*	SH0961272.10FU	LICH
OTU1577	DC	0.033	98.5	*Parmelia fertilis*	SH0850423.10FU	LICH
OTU1922	DC	0.014	94.1	*Pertusaria coccodes*	SH0888857.10FU	LICH
OTU3634	DC	0.041	96	*Podosphaera yulii*	SH0956000.10FU	PP
OTU237	DS	0.004	100	*Archaeorhizomyces*	SH0783891.10FU	SAP
OTU414	DS	0.007	95.5	*Capronia sp.*	SH0828463.10FU	SAP
OTU576	DS	0.018	97	*Cladonia arbuscula*	SH0933203.10FU	LICH
OTU472	DS	0.004	98	*Cladophialophora*	SH0959352.10FU	SAP
OTU2935	DS	0.025	90.5	*Cortinarius idahoensis*	SH1017669.10FU	ECM
OTU132	DS	0.005	98.5	*Cortinarius laetus*	SH1018136.10FU	ECM
OTU1772	DS	0.034	99.5	*Cortinarius sordidemaculatus*	SH0986234.10FU	ECM
OTU1623	DS	0.012	96.5	*Fontanospora fusiramosa*	SH1749277.10FU	LD
OTU951	DS	0.012	99.5	*Hyaloscypha sp.*	SH0897265.10FU	LD
OTU438	DS	0.040	100	*Laetisaria sp.*	SH0970594.10FU	PP
OTU1122	DS	0.005	99	*Russula griseascens*	SH0944258.10FU	ECM

OTU4546	DS	0.030	94.6	*Sclerotinia sclerotiorum*	SH0156797.10FU	PP
OTU1017	DS	0.014	99.4	*Serendipita sp.*	SH0163592.10FU	RF
OTU400	DS	0.004	98	*Serendipita sp.*	SH0167374.10FU	RF
OTU306	DS	0.009	99.4	*Serendipita sp.*	SH0734092.10FU	RF
OTU2367	DW	0.012	96.4	*Genolevuria amylolytica*	SH0757992.10FU	SAP
OTU341	DW	0.047	97.5	*Peltigera*	SH0132237.10FU	LICH
OTU2520	DW	0.033	92	*Pezoloma ericae*	SH0897066.10FU	RF
OTU1929	DW	0.034	96	*Phaeococcomyces kinklidomatophilus*	SH0072834.10FU	SAP
OTU560	DW	0.036	95.5	*Pseudogymnoascus roseus*	SH0980625.10FU	SAP
OTU382	DW	0.030	93	*Serendipita sp.*	SH0734102.10FU	RF
OTU4839	DW	0.034	93.5	*Serendipita sp.*	SH0734287.10FU	RF
OTU38	DW	0.009	100	*Tomentella sp.*	SH0918848.10FU	ECM
OTU2479	DW	0.032	92	*Verrucaria substerilis*	SH0986067.10FU	LICH
OTU1600	DSW	0.033	98.1	*Clitopilus sp.*	SH0865672.10FU	LD
OTU148	DSW	0.035	99.5	*Cortinarius badiolatus*	SH1403482.10FU	ECM
OTU503	DSW	0.004	98.5	*Exobasidium vaccinii*	SH0934702.10FU	PP
OTU383	DSW	0.030	95.6	*Stictis sp.*	SH0021374.10FU	LICH
OTU12	DSW	0.001	96.5	*Trechispora sp.*	SH0086525.10FU	WD
OTU295	MC	0.016	94.4	*Acarospora sp.*	SH1010639.10FU	LICH
OTU263	MC	0.006	95.5	*Archaeorhizomyces sp.*	SH0927304.10FU	SAP
OTU1982	MC	0.034	99	*Atractosporocybe polaris*	SH0985147.10FU	LD
OTU767	MC	0.035	95.5	*Aureobasidium sp.*	SH0155792.10FU	SAP
OTU1453	MC	0.023	100	*Biatora pallens*	SH0895610.10FU	LICH
OTU338	MC	0.008	100	*Cadophora sp.*	SH0897492.10FU	LD
OTU204	MC	0.023	98.9	*Cladonia amaurocraea*	SH0933208.10FU	LICH
OTU1648	MC	0.001	97	*Cladonia botrytes*	SH0933156.10FU	LICH
OTU1142	MC	0.033	98.1	*Clavaria sp.*	SH0737354.10FU	SAP
OTU629	MC	0.049	94.6	*Clavaria sphagnicola*	SH0737350.10FU	SAP
OTU28	MC	0.033	100	*Cortinarius sp.*	SH0986112.10FU	ECM
OTU349	MC	0.003	100	*Cortinarius croceus*	SH1943570.10FU	ECM
OTU311	MC	0.029	98	*Cortinarius subpaleaceus*	SH0986151.10FU	ECM
OTU4100	MC	0.032	99	*Dothiorella sp.*	SH0874024.10FU	PP
OTU2665	MC	0.032	89.7	*Exophiala sp.*	SH0116027.10FU	AP
OTU2533	MC	0.043	96.5	*Genolevuria sp.*	SH0757983.10FU	SAP
OTU3093	MC	0.034	97	*Hebeloma monticola*	SH1904173.10FU	ECM
OTU1658	MC	0.006	92.6	*Hyaloscypha desmidiacea*	SH0897096.10FU	LD
OTU1233	MC	0.023	94.6	*Hysteronaevia scirpina*	SH0083074.10FU	LD
OTU1047	MC	0.001	99.5	*Inocybe catalaunica*	SH0829698.10FU	ECM
OTU1062	MC	0.032	100	*Inocybe trochili*	SH0969952.10FU	ECM
OTU329	MC	0.005	98	*Inocybe ukkoi*	SH0998227.10FU	ECM
OTU95	MC	0.008	99	*Lactarius pseudodelicatus*	SH0960970.10FU	ECM
OTU1978	MC	0.043	96.6	*Lapidomyces epipinicola*	SH0842940.10FU	SAP
OTU153	MC	0.001	99	*Linnemannia amoeboidea*	SH0777285.10FU	SAP
OTU902	MC	0.013	90.7	*Meliniomyces sp.*	SH0110884.10FU	RF
OTU495	MC	0.004	89.6	*Mniaecia gloeocapsae*	SH0008350.10FU	PP
OTU1242	MC	0.006	100	*Mortierella sp.*	SH0867664.10FU	SAP

OTU2240	MC	0.001	98.5	*Mortierella antarctica*	SH0777291.10FU	SAP
OTU1800	MC	0.023	99.4	*Mycena sp.*	SH0851569.10FU	LD
OTU606	MC	0.033	98	*Mycenella lasiosperma*	SH0961159.10FU	LD
OTU1459	MC	0.033	88.8	*Mycosphaerella sp.*	SH0072195.10FU	PP
OTU742	MC	0.034	91.6	*Phialocephala fortinii*	SH0858722.10FU	SAP
OTU661	MC	0.033	99	*Pseudoplectania lignicola*	SH0857539.10FU	LD
OTU68	MC	0.033	99.5	*Russula brevipes*	SH0100059.10FU	ECM
OTU1458	MC	0.034	98.5	*Russula gracillima*	SH0956713.10FU	ECM
OTU1853	MC	0.033	95.5	*Sakaguchia lamellibrachiae*	SH0939344.10FU	SAP
OTU904	MC	0.006	97.5	*Sebacina sp.*	SH0934249.10FU	ECM
OTU308	MC	0.006	100	*Serendipita sp.*	SH0003242.10FU	RF
OTU1671	MC	0.006	98	*Serendipita sp.*	SH0003298.10FU	RF
OTU2074	MC	0.006	99.4	*Serendipita sp.*	SH0734135.10FU	RF
OTU286	MC	0.034	100	*Serendipita sp.*	SH0734140.10FU	RF
OTU739	MC	0.034	99.4	*Serendipita sp.*	SH0734144.10FU	RF
OTU4863	MC	0.035	93.6	*Serendipita sp.*	SH0734149.10FU	RF
OTU384	MC	0.001	93.1	*Serendipita sp.*	SH0734159.10FU	RF
OTU152	MC	0.033	97	*Serendipita sp.*	SH0734171.10FU	RF
OTU696	MC	0.023	100	*Serendipita sp.*	SH0734188.10FU	RF
OTU573	MC	0.023	94.1	*Serendipita sp.*	SH0734232.10FU	RF
OTU541	MC	0.006	100	*Serendipita sp.*	SH0947181.10FU	RF
OTU219	MC	0.001	96.5	*Serendipita sp.*	SH1053489.10FU	RF
OTU151	MC	0.001	100	*Serendipita sp.*	SH1447446.10FU	RF
OTU63	MC	0.029	97.5	*Sistotrema sp.*	SH0837135.10FU	LD
OTU1738	MC	0.043	98.1	*Spirosphaera sp.*	SH1011808.10FU	LD
OTU64	MC	0.006	99	*Thelephora sp.*	SH0922499.10FU	ECM
OTU392	MC	0.032	96.5	*Tomentella sp.*	SH0125566.10FU	ECM
OTU2646	MC	0.033	97	*Tomentella sp.*	SH0126605.10FU	ECM
OTU490	MC	0.006	100	*Tomentella sp.*	SH0917872.10FU	ECM
OTU1044	MC	0.006	99	*Tomentella sp.*	SH0918799.10FU	ECM
OTU3438	MC	0.033	96.5	*Tomentella sp.*	SH0920996.10FU	ECM
OTU439	MC	0.043	96.9	*Trechispora subsphaerospora*	SH0981623.10FU	WD
OTU743	MC	0.001	88.5	*Tumularia tuberculata*	SH0878638.10FU	LD
OTU632	MC	0.006	97.5	*Xenopolyscytalum sp.*	SH1012135.10FU	LD
OTU2282	MS	0.041	93.5	*Hyaloscypha sp.*	SH0897097.10FU	LD
OTU232	MS	0.007	96.5	*Tomentella lapida*	SH1769657.10FU	ECM
OTU2770	MW	0.002	100	*Acrodontium crateriforme*	SH0842905.10FU	PP
OTU956	MW	0.041	95	*Antarctomyces pellizariae*	SH0897623.10FU	SAP
OTU893	MW	0.003	99.5	*Beauveria pseudobassiana*	SH1457879.10FU	AP
OTU1572	MW	0.032	96	*Cortinarius alboadustus*	SH1887487.10FU	ECM
OTU1112	MW	0.019	100	*Entoloma sp.*	SH0004951.10FU	LD
OTU3105	MW	0.028	100	*Fellomyces sp.*	SH0185729.10FU	SAP
OTU816	MW	0.023	98.5	*Leptodontidium sp.*	SH0001579.10FU	LD
OTU27	MW	0.035	98.1	*Leptodontidium sp.*	SH0908056.10FU	LD
OTU30	MSW	0.047	100	*Samsoniella hepiali*	SH0740181.10FU	AP

These findings and the accumulating evidence from alpine and arctic dry tundra plant communities (Welker et al. 1993, Welker et al. 1997, Lupascu et al. 2013, Sharp et al. 2013) suggest that temperature responses of microbial and plant communities likely are predicated on soil water conditions and resulting differences in productivity among tundra types. The warming-induced changes we report here are particularly notable when considering that warming-induced vegetation shifts at the same experimental site were caused by changes in the relative abundance of various plant functional groups rather than changes in richness or species composition (Wahren et al. 2005). In fungi, most of the differences in community composition among the control and warmed plots were caused by the presence of many OTUs in a particular treatment type and absence in the other, as shown by the ordinations and the indicator species analyses. It is noteworthy that the moist tundra showed both the highest OTU richness and the highest number of indicator OTUs, indicating that both summer warming and increased snow depth (i.e. winter soil warming and higher early summer water content) represent disturbance that result in the loss of a substantial amount of species from the moist tundra community (Table 3.4). While the currently prevailing view is that altered plant community composition drives fungal community change in the Arctic (Dahlberg and Bültmann 2013), we conclude that fungal community composition may change independently and that fungi may be particularly well suited to monitor early responses to environmental changes in the Arctic.

4. Compositional dynamics of tropical forest fungi along elevation gradients

Figure 4.1. Examples on tropical montane forests discussed in this chapter: a mid-elevation Andean Yungas forest in Jujuy province, Argentina (left) and a high-elevation *Leptospermum* forest on Mt. Kinabalu in Sabah (right), Malaysian Borneo (photos by the author).

This chapter is based upon the following publications:

Geml J. 2017. Altitudinal gradients in mycorrhizal symbioses - the current state of knowledge on how richness and community structure change with elevation. In: *Ecological Studies: Biogeography of Mycorrhizal Symbioses* (Ed. Tedersoo L) Springer, p. 107-123.

Geml J, Arnold AE, Semenova-Nelsen TA, Nouhra ER, Drechsler-Santos ER, Góes-Neto A, Morgado LN, Ódor P, Hegyi B, Grau O, Ibáñez A, Tedersoo L, Lutzoni F. 2022. Community dynamics of soil-borne fungal communities along elevation gradients in neotropical and paleotropical forests. ***Molecular Ecology*** 31:2044-2060.

Geml J, Morgado LN, Semenova-Nelsen TA, Schilthuizen M. 2017. Changes in richness and community composition of ectomycorrhizal fungi among altitudinal vegetation types on Mount Kinabalu in Borneo. ***New Phytologist***. 215:454-468.

Geml J, Pastor N, Fernandez L, Pacheco S, Semenova TA, Becerra AG, Wicaksono CY, Nouhra ER. 2014. Large-scale fungal diversity assessment in the Andean Yungas forests reveals strong community turnover among forest types along an altitudinal gradient. ***Molecular Ecology*** 23:2452-2472.

Merckx VSFT, Hendriks KP, Beentjes KK, Mennes CB, Becking LE, Peijnenburg KTCA, Afendy A, Arumugam N, de Boer H, Biun A, Buang MM, Chen PP, Chung AYC, Dow R, Feijen FAA, Feijen H, Feijen-van Soest C, Geml J, Geurts R, Gravendeel B, Hovenkamp P, Imbun P, Ipor I, Janssens SB, Jocqué M, Kappes H, Khoo E, Koomen P, Lens F, Majapun RJ, Morgado LN, Neupane S, Nieser N, Pereira JT, Rahman H, Sabran S, Sawang A, Schwallier RM, Shim PS, Smit H, Sol N, Spait M, Stech M, Stokvis F, Sugau JB, Suleiman M, Sumail S, Thomas DC, van Tol J, Tuh FYY, Yahya BE, Nais J, Repin R, Lakim M, Schilthuizen M. 2015. Evolution of endemism on a young tropical mountain. ***Nature*** 524, 347-350.

Nouhra E, Soteras F, Pastor N, Geml J. 2018. Richness, community composition and functional groups of Agaricomycetes along a vegetation and altitudinal gradient in the Andean Yungas of Argentina. ***Biodiversity and Conservation***.27:1849-1871.

Wicaksono CY, Aguirre Gutierrez J, Nouhra ER, Pastor N, Raes N, Pacheco S, Geml J. 2017. Contracting montane cloud forests: a case study of the Andean alder (*Alnus acuminata*) and associated fungi in the Yungas. ***Biotropica*** 49:141-152.

4.1 Introduction

In this study, we compared community composition and richness of diverse functional groups of fungi in forest soils along elevation gradients in five tropical mountain areas: Andean Yungas in northwestern Argentina, Atlantic Forests in southern Brazil, Central American forests in western Panama, Bornean forests in Sabah, Malaysia, and Oceanian forests in Papua New Guinea. Fungal richness and distribution on a global scale are strongly influenced by mean annual temperature (MAT), mean annual precipitation (MAP), soil pH, and, in the case of ECM fungi, by the diversity and abundance of host plants (Tedersoo et al. 2014, Větrovský et al. 2019). Therefore, we expected MAT, MAP, and soil pH to be the strongest drivers of fungal community structure along the sampled elevation gradients irrespective of geographic region. We also expected that elevational patterns of community structure would differ among functional groups, reflecting different environmental optima corresponding to distinct life strategies and resulting in proportional differences of functional groups in the community among elevation zones. For example, given the high turnover of plant community with increasing elevation in tropical mountains (McCain and Grytnes 2010), we expected fungi intimately associated with plants, such as ECM, plant pathogens, root-associated fungi, and wood decomposers to be affected more strongly by elevation than fungi with more indirect associations with plants, i.e. animal pathogens, mycoparasites and generalist saprotrophs.

Our hypotheses were: 1) fungal communities would show high compositional turnover within and among fungal functional groups along the elevation gradients, reflecting ecological differences among both functional and taxonomic groups; 2) there would be consistent, negative relationships between elevation and species richness of animal pathogens, plant pathogens, wood decomposers, and generalist saprotrophs due to higher host- and substrate richness at low to mid-elevations and more energy available for decomposition; 3) plant-associated functional groups, such as ectomycorrhizal (ECM), plant pathogens, root-associated fungi, and wood decomposers, would show greater community turnover along elevation gradients than those with indirect associations with plants, i.e. animal pathogens, mycoparasites and generalist saprotrophs; and that 4) elevation gradients would primarily structure fungal communities through changes in climatic factors, particularly temperature and precipitation and related changes in edaphic factors, such as soil pH and nutrient and organic matter contents.

4.2 Materials and methods

The tropical elevation gradient studies included in this capter are based on DNA sequence data generated from three Neotropical and two Paleotropical regions: subtropical Andean Yungas forests in northwestern Argentina, Atlantic forests in southern Brazil, Central American forests in Panama, Southeast Asian forests in Borneo and Oceanian forests in Papua New Guinea. Localities of the sampling sites are shown on maps corresponding to the five sampling regions (Figure 4.2). Components of these datasets have been published in Geml et al. (2014b), Tedersoo et al. (2014), Merckx et al. (2015), Geml (2017), Geml et al. (2017), Wicaksono et al. (2017), and Geml et al. (2022a).

In Argentina, the Yungas comprise tropical and subtropical humid montane forests on the eastern slopes of the Andes, which are influenced by orographic rains. Together with adjacent, seasonally dry piedmont forests, the Yungas constitute the southern limit of the Amazonian biogeographic domain (Cabrera 1976, Prado 2000). In Brazil, we focused on the Atlantic Forest biome, a world-renowned biodiversity hotspot. We sampled the southern Atlantic Forest, where at least two recognized biogeographic subregions can be found: wet coastal forests and high-elevation mixed temperate forests characterized by *Araucaria angustifolia* (Veloso 1992, Ribeiro et al. 2011, Neves et al. 2017). Panama and neighboring countries in Central and South America represent a biodiversity hotspot that is one of the richest in the world. With respect to trees alone, at least 2300 species are known to occur in Panama (Condit et al. 2011). The Caribbean side of the isthmus and the central mountains receive more than 3000 mm precipitation per year (Condit et al. 2011). From Southeast Asia to Oceania, the tallest mountains are found in Borneo and Papua New Guinea: Mt. Kinabalu (4095 masl) in Malaysian Borneo and Mt. Wilhelm (4509) in Papua New Guinea. These reach above tree line, encompassing a full elevation gradient of forests (Hope 1976, Beaman and Beaman 1990, Kitayama 1992, Beaman and Anderson 2004).

Soil samples were collected in 2011 and 2013 in Jujuy, Salta and Tucumán provinces of Argentina, in 2016 in Santa Catarina, Brazil and in Bocas del Toro, Chiriquí, Colón and Panamá provinces of Panama, in 2012 in Sabah, Malaysian Borneo, and in 2011 in the Eastern Highlands and Morobe provinces of Papua New Guinea. The sampling sites represent the entire elevation range of forests in the respective regions.

In Argentina, Brazil, and Borneo, 40 soil cores, 2 cm in diameter and ca. 20 cm deep, were taken at each sampling site (ca. 10 × 25 m) after carefully removing the litter layer. Cores were collected ca. 2 m from each other to minimize the probability of sampling the same genet repeatedly. In Panama, 10 soil cores of the above dimensions were collected in each site (ca. 4 × 5 m). In Papua New Guinea, 40 soil samples were taken from a circular area of ca. 2500 m^2 (for details, see Tedersoo et al. 2014). Soil cores taken at a given site were pooled, resulting in a composite soil sample for each site. For samples collected in Argentina, Brazil, and Panama, ca. 20 g of each sample was kept frozen until lyophilization ca. 2 weeks later. For samples collected in Borneo, and Papua New Guinea, the more remote location and lack of lab equipment in the field led us to air-dry samples immediately at 25-35 °C. Because differences field preservation of soils is expected to have limited effect on the fungal community composition (Castaño et al. 2016; Delavaux et al. 2020), we regard the dataset as being representative for each sampled area. However, because of the differences in sampling design and field preservation, we conservatively chose to conduct statistical analyses for each region separately. We consider the total number of OTUs to be of relatively marginal importance, as our main goal was to observe and compare trends in richness and community composition among elevation zones and regions.

For the newly generated data from Brazil, Panama, and Borneo, we used the same protocol used previously for the Argentinian samples, which are described in detail in Geml et al. (2014b). Namely, genomic DNA was extracted from 0.5 g of dry soil from each sample with the NucleoSpin® soil kit (Macherey-Nagel Gmbh and Co., Düren, Germany) according to manufacturer's protocol. For each sample, two independent DNA extractions were carried out and the extracts were pooled. We used 1 ul of DNA template with DNA concentration

normalized for all samples from that region and followed the PCR and sequencing methodology in Geml et al. (2014b). The ITS2 region (ca. 250 bp) of the nuclear ribosomal DNA repeat was amplified via PCR with primers fITS7 (Ihrmark et al. 2012) and ITS4 (White et al. 1990). The ITS4 primer was labelled with sample-specific Multiplex Identification DNA-tags (MIDs). The amplicon libraries were normalized for the quantity of DNA and were sequenced at Naturalis Biodiversity Center (Naturalis) with an Ion 318^{TM} Chip and an Ion Torrent Personal Genome Machine (Life Technologies, Guilford, CT, U.S.A.). Chemical analyses of soil samples from Argentina, Borneo, and Papua New Guinea were carried out as described in Geml et al. (2014b), Geml et al. (2017), and Tedersoo et al. (2014), respectively. Samples from Brazil and Panama were analysed by the Empresa de Pesquisa Agropecuária e Extensão Rural de Santa Catarina and the Instituto de Investigación Agropecuaria de Panamá, respectively. Climate data were obtained from the WorldClim database (www.worldclim.org) based on the geographic coordinates of the sampling sites.

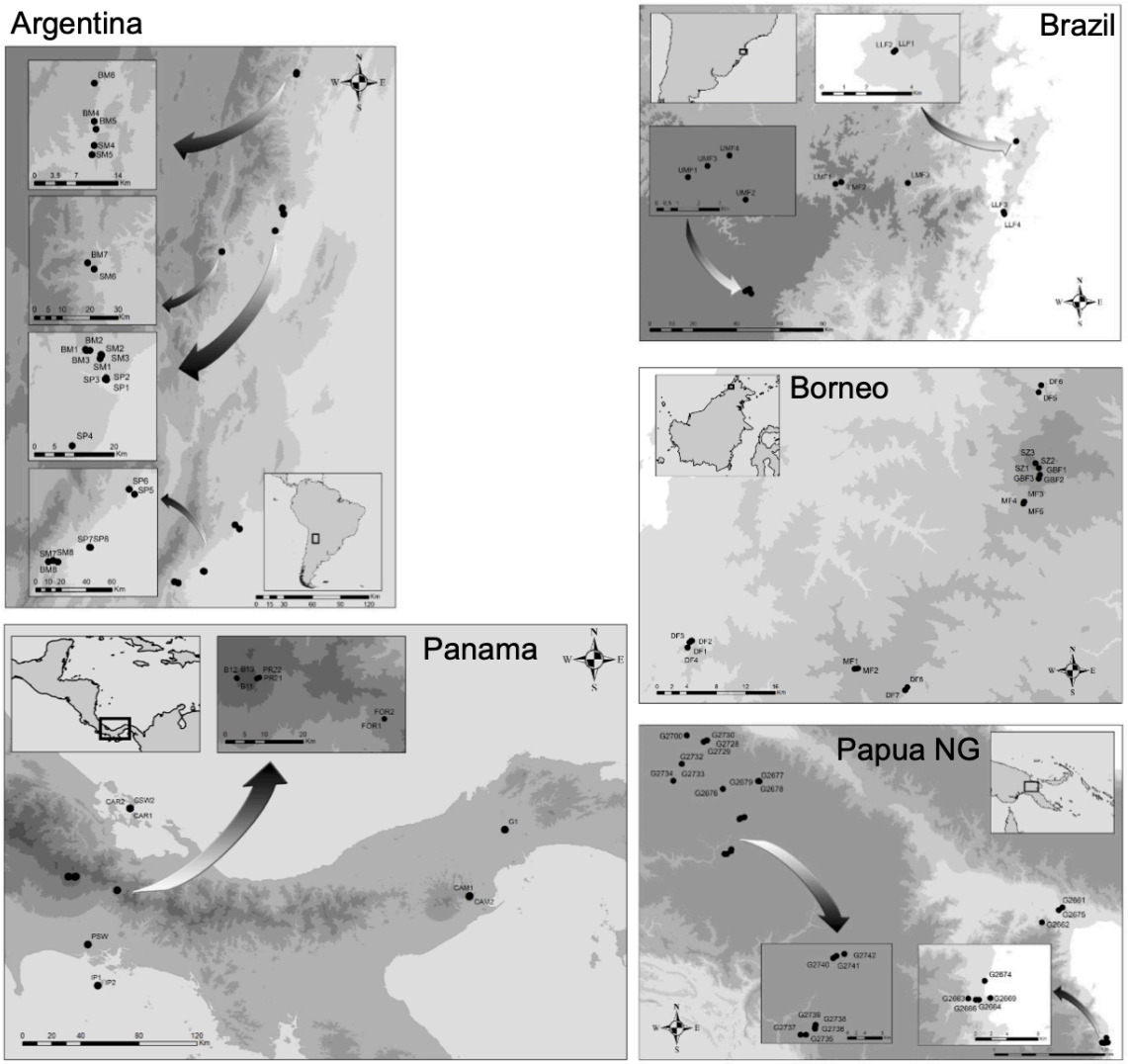


Figure 4.2. Maps of the sampling sites of tropical lowland and montane forests in the five study regions: northwestern Argentina, central Panama, southeastern Brazil, northern Borneo and eastern Papua New Guinea. Geographic coordinates, elevation and environmental parameters of sampling sites are described in detail in Geml et al. (2022a).

Bioinformatics

Sequences were sorted according to samples and adapters (identification tags) were removed in Galaxy (https://main.g2.bx.psu.edu/root). Primer sequences were removed and poor-quality ends were trimmed based on a 0.02 error probability limit in Geneious Pro 5.6.1 (BioMatters, New Zealand). Sequences were filtered with USEARCH v.8.0 (Edgar 2010) with the following settings: all sequences were truncated to 200 bp and sequences with expected error > 1 were discarded. For each sample, identical sequences were collapsed into unique sequence types while preserving their counts. The quality-filtered sequences from all samples were grouped into operational taxonomic units (OTUs) at 97% sequence similarity in USEARCH, and global singletons and putative chimeric sequences were removed. We assigned sequences to taxonomic groups based on pairwise similarity searches against the curated UNITE+INSD fungal ITS sequence database, containing identified fungal sequences with assignments to Species Hypothesis groups based on dynamic similarity thresholds (Kõljalg et al. 2013). We excluded OTUs with < 80% similarity or < 150 bp pairwise alignment length to a fungal reference sequence. To minimize artifactual OTUs that may have been generated during the molecular work, in subsequent analyses we only included OTUs that occurred in at least two samples.

We assigned fungal OTUs to putative functional guilds using the curated FungalTraits database (Põlme et al. 2020). We recognize the limitations of functional inference based on partial ITS sequences, and here use these guilds as hypothetical functional groups. For the statistical analyses, we only focused on the functional groups with a relatively high number of OTUs. Although arbuscular mycorrhizal (AM) fungi are ecologically important in tropical forests as symbiotic partners of most trees as well as diverse non-woody plants, we were only able to analyze their composition in three regions, because their number of OTUs were too low for comparison in data from Brazil and Papua New Guinea. This may partly be caused by primer bias or by the above-mentioned sampling differences among regions. Overall, functional assignments were made for 66.76% ± 6.2% of fungal OTUs obtained in our study. The quality-filtered dataset contained 8720, 2828, 4498, 7829, and 4305 fungal OTUs in the samples from Argentina, Brazil, Panama, Borneo, and Papua New Guinea, of which 5917, 1698, 2896, 5078, and 3301 OTUs were assigned to functional groups, respectively. Sequence data corresponding to the study regions have been deposited at DDBJ/EMBL/GenBank as Targeted Locus Study projects under accessions KDPX00000000 (Argentina), KEXW00000000 (Brazil), KDPY00000000 (Borneo), and KDPZ00000000 (Panama). The versions described in this paper are the first versions, i.e. KDPX01000000, KEXW01000000, KDPY01000000, and KDPZ01000000, respectively. The OTU sequences for the Papua New Guinea samples can be downloaded from Tedersoo et al. (2014).

Statistical analyses

All analyses were done in R 3.6.3 statistical environment (R Core Team 2020). For each biogeographic region, we normalized the OTU table for subsequent analyses by rarefying the number of high-quality fungal sequences per sample to the smallest library size in that region (14,241 reads for the Argentinian Yungas, 7442 for Brazil, 2000 for Panama, 24,812 for

Borneo, and 1441 for Papua New Guinea). Rarefying data, while sometimes problematic in microbial surveys (McMurdie and Holmes 2014), was appropriate in this case because our analyses do not center on comparing relative abundance of OTUs among regions. In each geographic region, OTU richness, proportional richness, and proportional abundance of functional groups were tested for correlation with elevation using quadratic regressions.

To compare community composition along the sampled elevation gradients, we used the *vegan* package (Oksanen et al. 2015) to run global nonmetric multidimensional scaling (GNMDS) ordinations on the Hellinger-transformed abundance table and a secondary matrix containing environmental variables mentioned above. Ordinations were run separately for functional groups as well as for all fungi in each geographic region with the *metaMDS* function, which uses several random starts to find a stable solution. Data were subjected to 999 iterations per run with Bray-Curtis distance measure. Pearson correlation coefficient (r) values and statistical significance between environmental variables and fungal community composition were calculated with the *envfit* function, and vectors of variables with statistically significant correlations were plotted in ordinations. Environmental variables included were MAT, MAP, soil pH, soil organic matter content (OM), soil nitrogen content (N), soil carbon and nitrogen ratio (C/N), and soil phosphorus content (P). We plotted isolines of elevation on the GNMDS ordinations with the *ordisurf* function.

We estimated the relative importance of environmental (continuous) variables as sources of variation in fungal community composition by permutational multivariate analysis of variance (PERMANOVA) for all fungi and each functional group with the *adonis* function in *vegan*. Statistical tests of the equality variances via the *betadisper* function indicated no significant difference in multivariate homogeneity of group dispersions in any region. To account for correlations among environmental variables, we performed a forward selection of parameters, including only significant environmental variables in the final model. In addition, we used partial Mantel tests in *vegan* to differentiate the effects of spatial distance and abiotic environmental variables, standardized with the *scale* function, on community composition.

To better understand the roles of replacement (i.e. the substitution of a species by a different one) and nestedness (where a poor community is the strict subset of a richer one) in community dynamics along the elevation gradients, we used Sørensen dissimilarity as total beta diversity and estimated the replacement (Simpson dissimilarity) and nestedness components based on presence/absence data using the *betapart* R package (Baselga and Orme 2012). Relationships between replacement, nestedness and total beta diversity and pairwise differences in elevation were explored with quadratic regressions.

To identify pantropical trends shared among neotropical and paleotropical montane regions, relationships between the richness of the main fungal groups (all fungi, ECM fungi, plant pathogens, saprotrophs, and wood decomposers; treated as response variables) and environmental variables were explored by general linear mixed models (Zuur et al. 2009). The explanatory variables available for all sites were MAT, MAP, pH, OM, N, and C/N. In all models, Gaussian error structure was assumed for the response variables. To fulfill the normality condition of the model residuals, some response variables were transformed (logarithmic for ECM fungi, square-root for saprotrophs and wood decomposers). All environmental variables were standardized for zero mean and variance before the analysis. Elevation was excluded from the environmental variables because it was correlated strongly

with MAT in the total dataset (r = -0.88). For all other environmental variables, the absolute values of the intercorrelations were lower than 0.6 (Table S2). Because the main purpose was to identify common trends among regions, we treated region as a random factor. Scatterplots between the response and environmental variables were checked before model selection. In the full model, all environmental variables, their second order component (if the scatterplots showed unimodal response), and first-order interactions were included. Model selection was based on backward elimination using deviance analysis (Faraway 2005, Faraway 2006). The importance of variables was analyzed by type-II analysis of variance using Wald Chi2 test of the *anova* function of the *car* package (Fox and Weisberg 2019). All models were implemented in the *lme4* package (Bates et al. 2015). Pseudo-coefficients of determination of the fixed effects (marginal effects) were calculated with the *MuMIn* package (Barton 2019). Normality and homoscedasticity of the model residuals were verified visually.

4.3. Results and discussion

Fungal biodiversity in tropical forests remains little known, and opportunities to compare data from similar guilds across diverse tropical forests at local and global scales are rare. Our results show that composition of the total fungal community in soil, as well as that of all functional groups, is strongly structured according to elevation in both the Neo- and Paleotropics (Geml 2017, Geml et al. 2014b, Merckx et al. 2015, Wicaksono et al. 2017, Nouhra et al. 2018, Geml et al. 2022a). Contrary to vascular plants, where forests at low- to mid-elevations typically harbor more tree species than montane forests (Aiba and Kitayama 1999, Brown et al. 2001, McCain and Grytnes 2010), we did not find substantial differences in soil fungal richness along the elevation gradients in most sampled regions. The lack of a strong elevational pattern in fungal richness is similar to the lack of latitudinal differences in fungal richness on a global scale (Větrovský et al. 2019). Panama was the only exception, where the mid-elevation peak in fungal richness is concordant with vascular plant richness in Central American mountains (Cardelús et al. 2006, Prada et al. 2017).

Overall, in all functional groups and in all regions, compositional structure appears to be driven by elevation and the resulting environmental filtering according to contrasting climatic and edaphic conditions, and associated differences in plant communities. Our data suggest that generally a 700-800 m of elevation difference results in a high turnover of soil fungal communities, indicating that most fungi prefer a certain elevation zone along these gradients. This may be explained by the fact that organisms at a given elevation in the tropics are subjected to a lower variation in temperature than organisms in temperate mountains and are more likely to have a relatively narrow elevation range (Janzen 1967).

Environmental drivers of community composition

Variation in fungal community composition and richness as a function of elevation is mediated by abiotic and biotic factors driven either directly or indirectly by differences in temperature, which strongly influences relative humidity, soil moisture, and soil chemical processes. In our studies based on multiple elevation gradients in the Neotropics and

Paleotropics (Geml et al. 2014, Geml et al. 2017, Geml et al. 2022a), biotic environmental variables correlated with elevation to a varying degree in the sampled regions. As expected, MAT was correlated negatively with elevation in all regions. In addition to MAT, soil pH and soil organic matter (OM) showed consistent elevational trends across biogeographic regions: with increasing elevation, soil pH generally decreased and OM increased. Consequently, forests found at different elevations have distinct mesoclimatic and edaphic conditions.

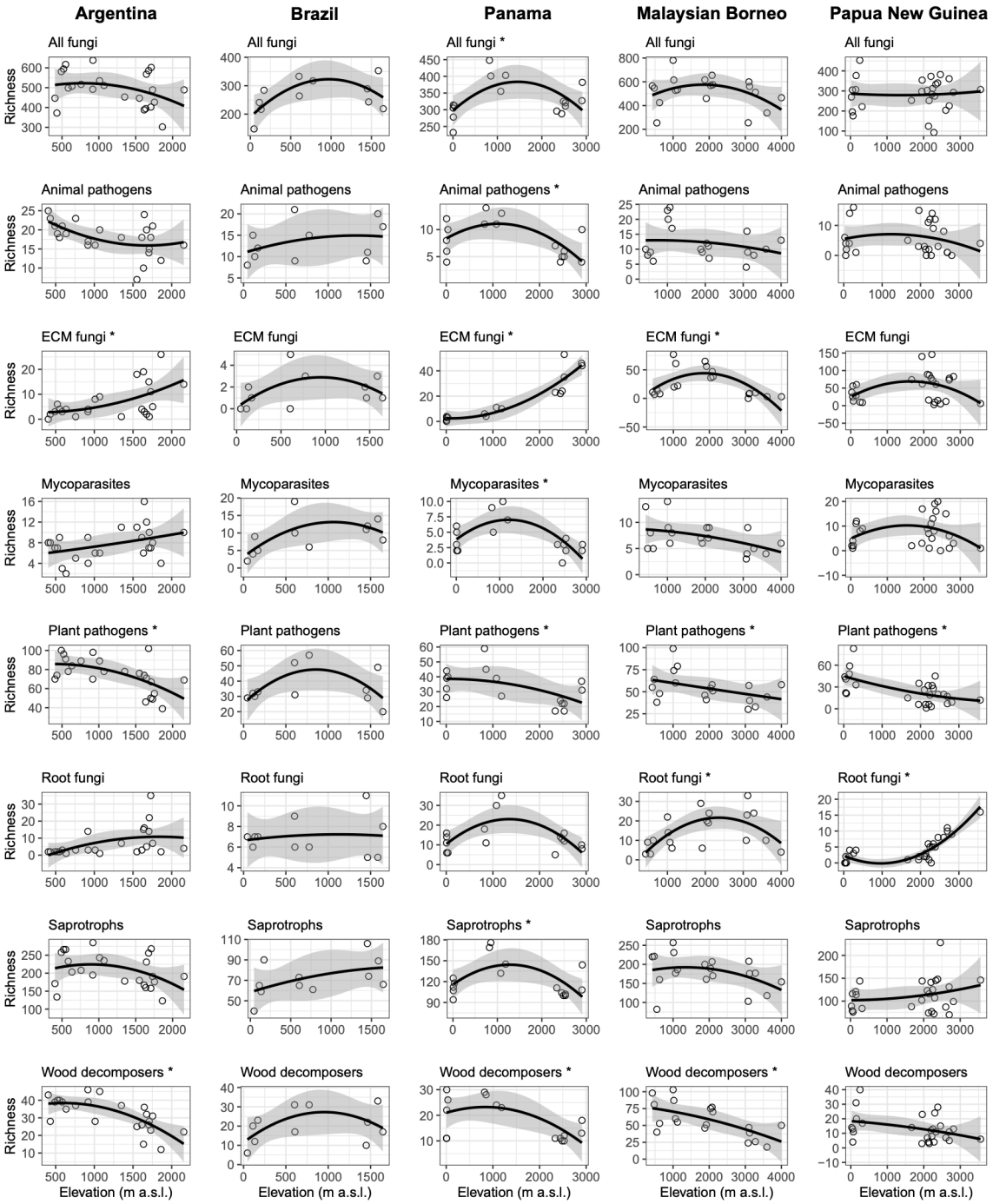


Figure 4.3. Quadratic regressions of elevation and richness of functional groups in the five sampled tropical montane regions, with 95% confidence intervals indicated by grey shading (Geml et al. 2022a). Significant relationships are marked with asterisk (*).

Moreover, high-elevation habitats generally cover smaller areas than lower elevation ones and habitat area often is correlated positively with species richness in many taxonomic groups (Gotelli 1998). However, for fungi, the decreasing habitat area with increasing elevation does not seem to offer a satisfying explanation for the richness patterns observed in our study: total fungal richness was generally similar along the elevation gradients, even though lowland forests cover much larger areas than montane forests. While some functional groups decreased in richness with increasing elevation, other groups increased (as discussed below).

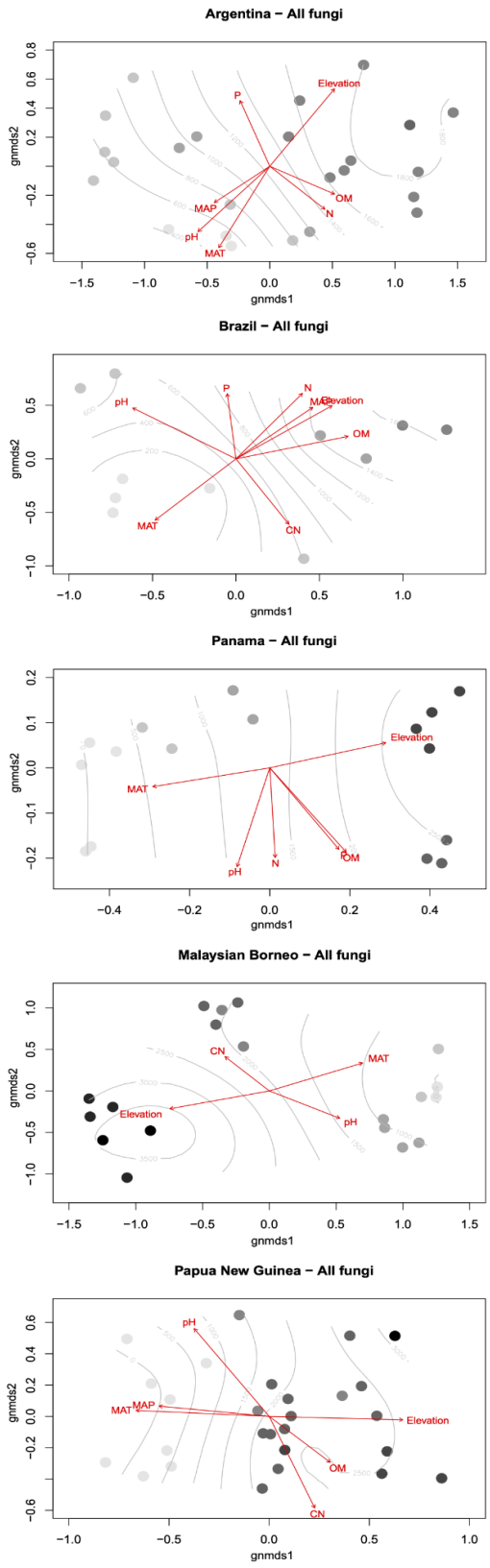
Thus, it appears that climatic and edaphic factors, as well as composition of biological communities, are far more influential drivers of fungal richness in mountains than habitat area alone. Overall, total fungal richness is weakly explained by the studied abiotic variables (R^2=0.025) in the pantropical GLMM analyses, with only pH showing a significant, but weak, positive effect on richness (Geml et al. 2022a). However, richness values of specific functional groups (ECM fungi, plant pathogens and wood decomposers) tend to correlate more strongly with environmental variables, particularly pH and MAT. For example, in our study, ECM fungal richness showed significant negative correlation with pH and with the interaction of MAT and N content. Similarly, plant pathogen richness was most strongly explained by pH, with additional positive effects of MAT. Richness of saprotrophs showed strong positive correlation with the interaction of pH and OM. Wood decomposer richness showed a strong unimodal response with MAT, with additional positive responses to pH and OM, and a negative response to N. These findings mostly confirm the importance of soil pH and MAT as drivers of fungal diversity and community composition as observed previously in our global-scale study (Tedersoo et al. 2014), except for MAP. Despite MAP being the most influential climatic predictors of fungal richness and community composition on a global scale, MAP did not contribute significantly to any final model explaining richness in our elevation gradient study.

Table 4.1. Compositional variation (%) of all fungi and the that of the major functional groups explained by environmental variables calculated independently with permutational multivariate analysis of variance, based on the fungal community matrix used for NMDS. Significant results are in bold. Climatic and edaphic variables that remained significant in the final composite model (without elevation) for each fungal group are indicated by asterisk (*). Abbreviations are ARG: Argentina, BRA: Brazil, PAN: Panama, BOR: Borneo, PNG: Papua New Guinea, AP: animal pathogen, ECM: ectomycorrhizal, MP: mycoparasite, PP: plant pathogen, RF: root endophyte, SAP: generalist saprotroph, WD: wood decomposer (Geml et al. 2022a).

ARG	**All**	**AP**	**ECM**	**MP**	**PP**	**RF**	**SAP**	**WD**
Forest type	**18.19**	**26.49**	**17.79**	**12.15**	**20.63**	**12.82**	**17.66**	**17.86**
elevation	**19.91**	**24.72**	**15.01**	**12.37**	**17.26**	**9.76**	**15.84**	**15.31**
MAT	**15.97***	**22.85**	**11.95**	**11.80***	**15.77**	**8.48***	**14.04**	**13.82***
MAP	**13.18**	**24.39***	**12.90***	**14.86***	**17.47***	**7.83**	**15.21***	**12.95***
pH	**18.56***	**16.48**	**12.03**	**8.57**	**11.97**	**6.91**	**11.40**	**12.10**
OM	**13.29**	**10.04**	6.44	5.69	6.93	3.51	**7.49**	6.21
N	**12.72**	**11.15**	7.07	6.59	**7.78**	3.56	**8.01**	**6.71**
C/N	4.52	5.12	5.10	5.74	5.34	3.88	5.31	4.88
P	**9.41**	**10.67**	5.80	6.59	**7.37**	3.64	**7.26**	5.44
BRA	**All**	**AP**	**ECM**	**MP**	**PP**	**RF**	**SAP**	**WD**
Forest type	**24.51**	**24.05**	**15.07**	**34.82**	**31.18**	18.04	**23.19**	**17.67**
elevation	**24.98**	**24.86**	**14.35**	**35.01**	**32.15**	18.02	**24.31**	**18.13**

MAT	**23.94***	**22.93**	**15.23**	**35.34***	**30.02***	15.28	**22.06***	**17.41***
MAP	**21.68**	**19.69**	**15.87***	**32.24**	**26.99**	14.92	**19.29**	**15.83***
pH	**22.42***	**25.04**	11.17	**28.63**	**22.98**	**30.37**	**26.09***	**15.07**
OM	**22.15**	**23.44**	11.87	**32.49***	**28.27***	**25.52**	**22.92***	**17.66***
N	**19.95**	**19.32**	12.17	**33.98**	**24.55***	12.31	**19.04**	**15.71**
C/N	15.06	12.51	10.34	17.57	15.69	**31.22***	**17.35**	11.75
P	13.56	10.14	12.08	**28.36**	12.47	10.29	14.28	11.38
PAN	**All**	**AP**	**ECM**	**MP**	**PP**	**RF**	**SAP**	**WD**
Forest type	**19.96**	**31.54**	**13.48**	**18.67**	**22.63**	**13.01**	**21.25**	**16.84**
elevation	**20.32**	**32.53**	**13.96**	**21.58**	**23.38**	**13.63**	**21.44**	**17.20**
MAT	**20.31***	**33.17***	**14.09***	**22.72***	**23.50***	**13.69***	**21.47***	**17.07***
MAP	**11.11**	11.84	7.34	13.44	**11.21**	8.92	**10.99**	**10.34**
pH	**12.03**	**14.40**	9.42	13.33	**11.66**	**10.57**	**12.63**	9.11
OM	**17.65**	**23.94**	**13.54**	**18.50**	**20.36**	**13.42***	**18.48**	**15.87**
N	8.32	5.30	8.60	5.58	7.61	8.87	8.79	8.17
C/N	8.04	10.78	7.80	8.04	7.96	7.01	8.54	8.31
P	**16.17**	**27.56**	**12.01**	**21.99**	**17.84**	**12.11***	**16.11**	**13.81**
BOR	**All**	**AP**	**ECM**	**MP**	**PP**	**RF**	**SAP**	**WD**
Forest type	**20.31**	**32.58**	**15.32**	**24.51**	**25.01**	**15.73**	**21.27**	**15.97**
elevation	**19.38**	**31.55**	**15.03**	**24.32**	**23.37**	**13.72**	**20.54**	**14.77**
MAT	**19.11***	**32.12***	**15.40***	**23.08***	**23.20***	**12.94***	**20.09***	**14.32***
MAP	6.91	6.43	6.67	6.06	6.55	7.66	7.23	5.89
pH	**14.32***	**14.02**	**10.06**	**15.14**	**15.66**	**13.86***	**15.36**	**13.28**
OM	8.18	5.99	**8.59***	**13.16**	7.61	**9.15***	8.51	6.79
N	7.34	6.36	7.69	7.54	7.25	**9.07**	7.69	5.71
C/N	**10.64**	9.77	8.19	**15.75**	**10.53**	**12.68**	**11.01**	**9.97**
PNG	**All**	**AP**	**ECM**	**MP**	**PP**	**RF**	**SAP**	**WD**
Forest type	**9.31**	5.43	**7.34**	**10.39**	**10.47**	**8.19**	**9.16**	**6.71**
elevation	**10.04**	**7.53**	**7.38**	**8.92**	**11.76**	**8.29**	**10.25**	**6.96**
MAT	**9.91***	**7.31**	**7.33***	**9.16***	**11.55***	**8.22***	**10.11***	**6.96***
MAP	**8.82**	5.95	**7.91***	**7.03**	**9.61**	**7.46**	**9.14***	**6.59**
pH	**7.18***	**8.17**	**5.91**	**9.15***	**7.24***	**6.13***	**7.18***	**4.88***
OM	4.69	5.71	4.06	4.67	**6.58**	4.82	4.39	3.82
N	4.78	5.47	3.75	3.59	**6.88***	4.08	4.59	4.04
C/N	**6.96***	**9.31***	**6.48***	**10.52***	**6.72**	**6.39***	**6.79***	4.34

Our results from multivariate analyses reveal that MAT and pH, are the most influential drivers of fungal community composition across elevational gradients in neotropical and paleotropical regions, while the roles of other variables seem to be more region dependent (Geml et al. 2022a). MAT and pH tend to explain the greatest variation in the community composition in most functional groups of fungi and remain significant contributors in combined models in each region when correlation among parameters is accounted for (Table 4.1). MAT always and pH often correlate with elevation, yet, in the PERMANOVA analyses, both remained significant in the combined model in four of the five regions, highlighting their complementarity in explaining fungal community composition. In addition, MAP, C/N, OM, and P explain significant proportions of variation of fungal community structure in the combined models in some regions, although their contributions differ among geographic



regions and functional groups. We also found that spatial autocorrelation in fungal community composition generally was not significant in the sampled regions structure when abiotic variables were accounted for in partial Mantel tests, implying that environmental filtering rather than dispersal limitation drives the observed compositional patterns within a certain region.

Soil pH plays an important role in shaping belowground fungal communities at both regional and global scales (e.g., Porter et al. 1987, Coughlan et al. 2000, Lauber et al. 2008, Rousk et al. 2010, Geml et al. 2014ab, Tedersoo et al. 2014, Glassman et al. 2017, Geml 2019, Geml et al. 2022ab). Because many fungal species have a relatively wide pH optimum (e.g., Wheeler et al. 1991, Nevarez et al. 2009), it is likely that the observed correlation of pH with community composition is mainly indirect, e.g., by altering nutrient availability and competitive interactions among soil fungi, bacteria (Rousk et al. 2010) and other soil biota. In all regions, we observed some decrease in pH and increase in OM with elevation, and it is difficult to disentangle their effects from that of MAT. However, along with MAT, pH remained significant in explaining compositional differences of total fungal communities in four of the five sampled regions, and OM contributed significantly to the combined model for some unctional groups in three regions (Table 1), indicating some additional effects of OM on community composition (Geml et al. 2022a). The effect of pH on richness appears to be similarly strong: it is the only environmental variable that is correlated significantly with total fungal richness at a pantropical scale, and with significant contribution to explain community composition in the combined models in all four major functional

Figure 4.4. Global non-metric multidimensional scaling (GNMDS) ordination plots of fungal communities in the sampled regions based on Hellinger-transformed data, with elevation displayed as isolines. Vectors of environmental variables with significant correlation with ordination axes are displayed. The darker the circle, the higher the elevation of the site is (Geml et al. 2022a). Abbreviations: MAT - mean annual temperature, MAP - mean annual precipitation, pH - soil pH, OM - soil organic matter content, N - soil nitrogen content, P - soil phosphorus content, and CN - carbon to nitrogen ratio.

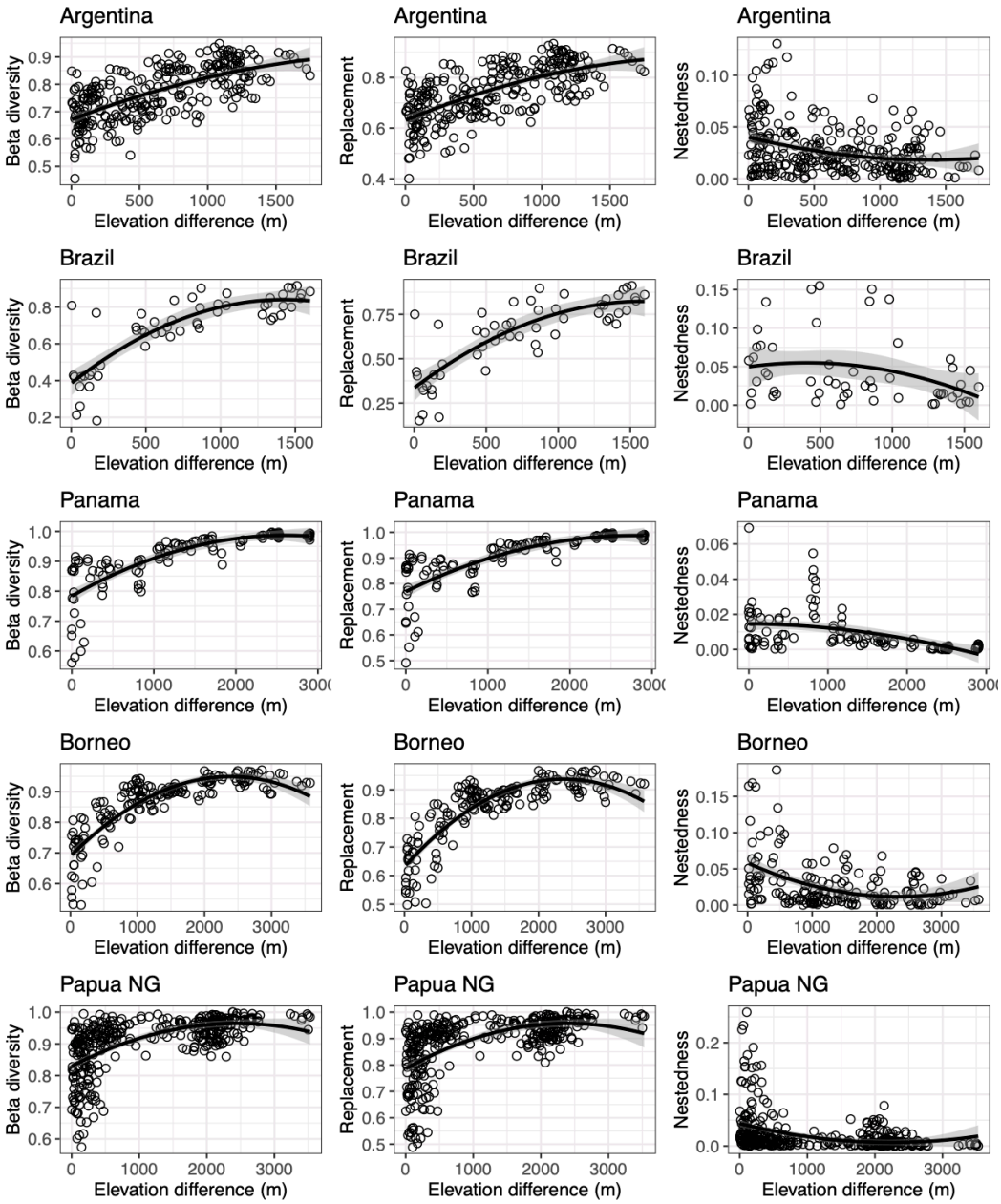


Figure 4.5. Correlation of total beta diversity and its replacement and nestedness components of fungal communities with pairwise differences in elevation among the sites, with 95% confidence intervals indicated by grey shading. All relationships, except that of nestedness in Brazil, are significant (Geml et al. 2022a)

groups. The relatively weak correlation of pH with total fungal richness seems to be explained by its negative correlation with ECM fungi, which counterbalanced the positive relationship with plant pathogens, saprotrophs, and wood decomposers. With respect to saprotrophs, the positive effect of the significant interaction between pH and OM on richness suggests that saprotrophs may benefit more from the available organic carbon under less acidic conditions. This may partly be explained by lower levels of competition with ECM fungi for nutrient acquisition, i.e. "the Gadgil effect" (Gadgil and Gadgil 1971, Fernandez and Kennedy 2016), given the observed negative relationship between pH and ECM fungal richness. While the negative effect of available N on ECM fungal richness is well known (Lilleskov et al. 2002), in our analyses it was only evident at lower elevations, where saprotrophic fungi tend to be the most diverse and most abundant, as shown by the strongly significant negative effect of the

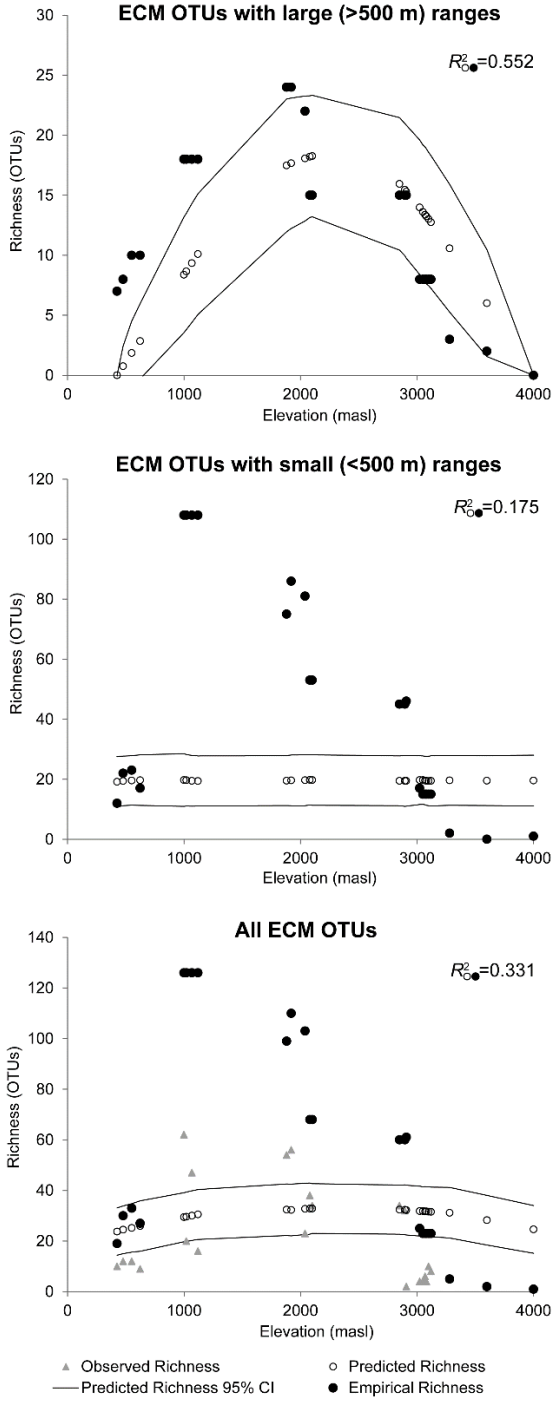
interaction between MAT and N on ECM richness. Overall, our observations suggest that despite the correlation with elevation, pH, N, and OM play important roles in shaping fungal communities in tropical mountains in ways that are not explained by MAT.

Elevational dynamics of fungal functional groups

In contrast to richness patterns of the total fungal community, richness of functional groups often vary significantly along tropical elevation gradients (Geml et al. 2014b, Geml et al. 2022a) (Figure 4.3). Overall, the emerging trend is that fungi with different life strategies are favored by different environmental conditions. Even in functional groups with no significant differences in richness over the elevational gradients studied here, we observed strong differences in composition as a function of elevation. Similar elevational differences in richness and composition also have been observed in various functional groups of plants and animals (Cardelús et al. 2006, McCain 2009, McCain and Grytnes 2010, Guo et al. 2013).

All studied functional groups of fungi tend to exhibit significant differences in community composition along tropical elevation gradients (Geml et al. 2014b, Geml 2017, Gem et al. 2017, Geml et al. 2022a) (Table 4.1). With regard to the components of beta diversity, replacement generally accounts for most of the observed beta diversity, with nestedness being negligible (generally < 0.1 Bray-Curtis distance) in all regions (Figure 4.5). Consequently, replacement values show significant positive relationships with pairwise differences in elevation in all regions. Interestingly, our results show that high replacement values are already reached at less than 1000 m difference in elevation, which indicates that the elevation range of most tropical montane fungi is relatively narrow. Conversely, nestedness is low even within the same elevation zone and decreases with increasing difference in elevation (Geml et al. 2022a). The richness of plant pathogens and wood decomposers generally is correlated negatively with elevation, ECM fungi and non-mycorrhizal root-associated fungi tend to be most diverse in mid- to high elevations, while richness of animal pathogens, mycoparasites and generalist saprotrophs show smaller elevational differences (Geml et al. 2014b, Geml 2017, Gem et al. 2017, Geml et al. 2022a). Statistical tests of the mid-domain effect on the ECM fungi in the Borneo dataset indicated that the observed mid-elevation peak in richness was not caused by the geometric overlap of elevational distribution ranges, but likely by particularly favorable conditions at mid-elevation, e.g., diversity and abundance of host trees, high relative humidity, and accumulation of litter layer (Figure 4.6, Geml et al. 2017). This also confirms that most fungi seem to inhabit relatively narrow elevation ranges, which results in high replacement rate along elevation gradients. The observed greater elevational differences in richness in plant-associated fungi compared to non-plant-associated guilds are consistent with expectations based on richness patterns of their hosts. On the other hand, at pantropical scales, elevational community turnover in plant-associated fungi is not higher than turnover in free-living functional groups, likely because compositional turnover along elevation gradients already is high in all functional groups. This confirms the driving role of abiotic factors in fungal community composition (Figure 4.7, Table 4.1), with a somewhat lesser contribution from vegetation.

With respect to ECM fungi in tropical mountains, the patterns reported here differ from those observed in temperate mountains, where ECM fungal richness tends to decrease monotonically with increasing elevation (Bahram et al. 2012, Nouhra et al. 2012, but see Bowman and Arnold 2018). Based on our work and on previous studies on tree communities of the sampled tropical forests (e.g., Aiba and Kitayama 1999, Malizia et al. 2012), ECM fungal richness appears to mirror host richness and abundance along tropical elevation gradients. This confirms the positive relationships found between the diversity and distribution of ECM fungi and of their host plants at global scale (Tedersoo et al. 2014).



The coupling of ECM fungi and their host trees also results in important differences in the elevational patterns of ECM fungi between the Neotropics and Paleotropics. In the neotropical mountain ranges from Mexico to Argentina, high-elevation forests tend to harbor the highest density of trees that form ectomycorrhizal associations, e.g., *Alnus acuminata* as the principal ECM host in the Yungas in Argentina, and *Alnus acuminata* and several *Quercus* spp. in the mountains of southern Costa Rica and northern Panama (Malizia et al. 2012, Kappelle 2016, Wicaksono et al. 2017, Nouhra et al. 2018). These findings agree with sporocarp-based studies in other areas of the wet Neotropics that reported highest richness of ECM fungi in montane forests (Mueller et al. 2006, Gómez-Hernández et al. 2012). We showed, that in Andean forests, the role of *Alnus* in maintaining ECM fungal community is so important that a warming-driven decrease in its distribution range could result in a 25-50% loss of habitat for montane ECM fungi by 2050 (Wicaksono et al. 2017).

Figure 4.6. Observed, empirical, and predicted mean operational taxonomic unit (OTU) richness as a function of elevation for ectomycorrhizal fungi in Borneo for all OTUs and for OTUs with empirical elevation ranges smaller and greater than 500 m. Empirical richness was calculated as interpolated richness, based on the assumption that each OTU inhabited all sampling sites between its lowest and highest recorded occurrences regardless of records at intermediate sites. Grey triangles and solid circles indicate observed and interpolated empirical richness, respectively, for each field sampling elevation. Open circles show mean richness with 95% confidence intervals (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 (Geml et al. 2017).

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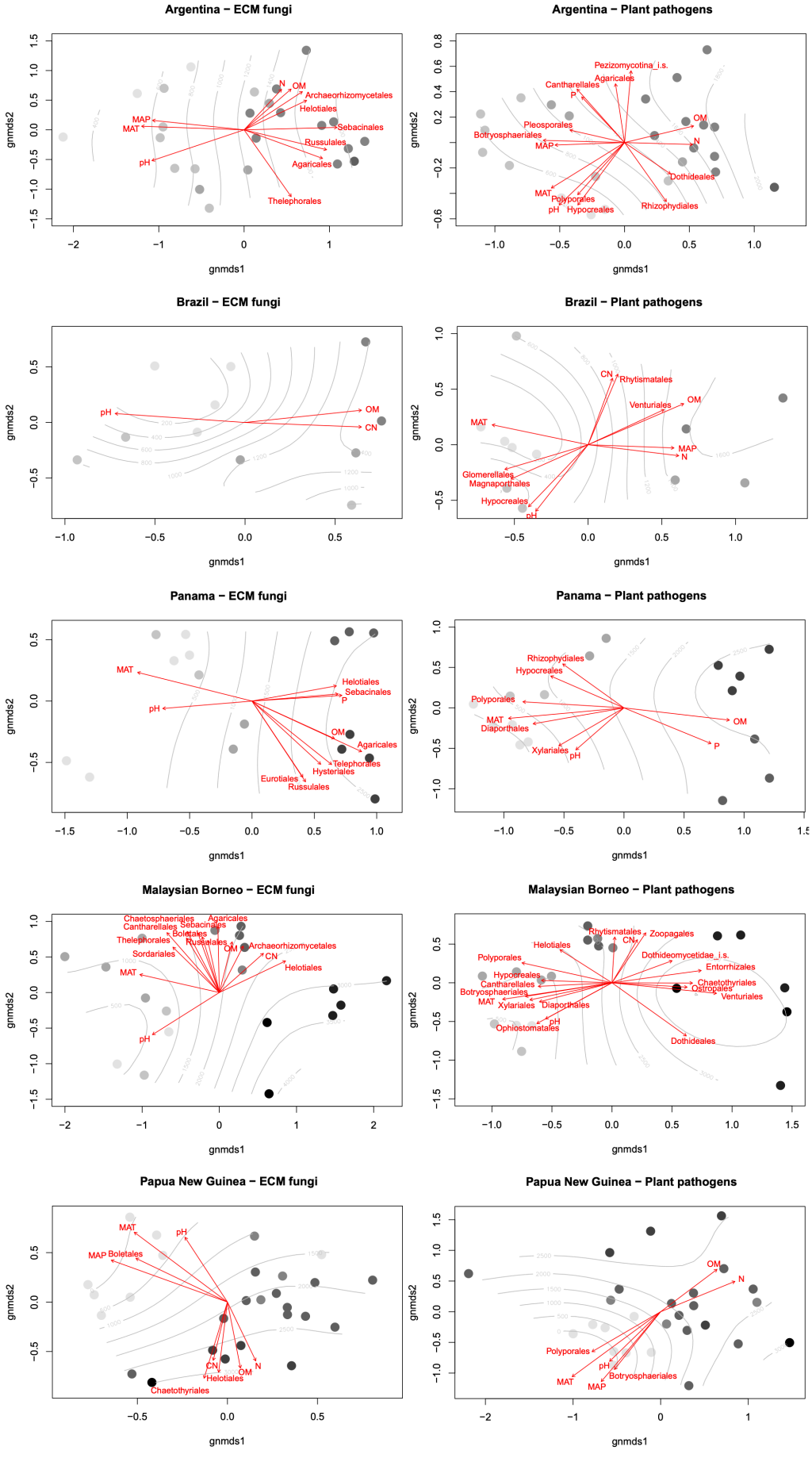
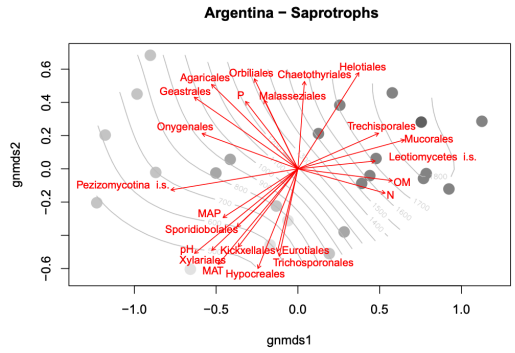
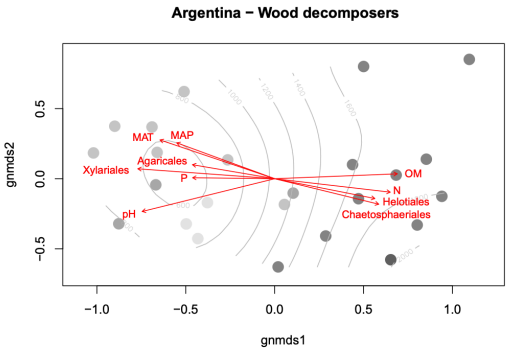
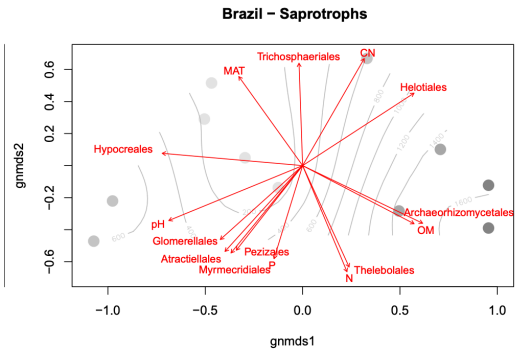



Argentina – Saprotrophs
gnmds1
gnmds2
Helotiales
Agaricales
Orbiliales
Chaetothyriales
Geastrales
P
Malasseziales
Onygenales
Trechisporales
Mucorales
Leotiomycetes i.s.
Pezizomycotina i.s.
OM
N
MAP
Sporidiobolales
pH
Kickxellales
Eurotiales
Xylariales
Trichosporonales
MAT
Hypocreales


Argentina – Wood decomposers
gnmds1
gnmds2
MAT
MAP
Agaricales
Xylariales
P
OM
N
Helotiales
Chaetosphaeriales
pH


Brazil – Saprotrophs
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gnmds2
Trichosphaeriales
CN
MAT
Helotiales
Hypocreales
Archaeorhizomycetales
OM
pH
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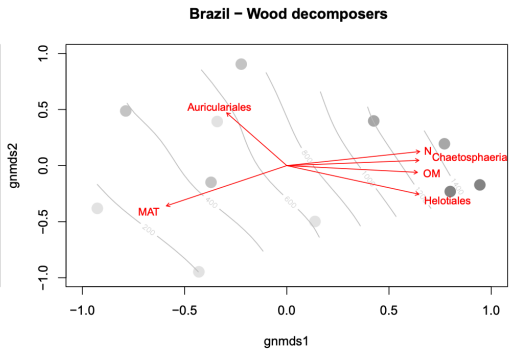
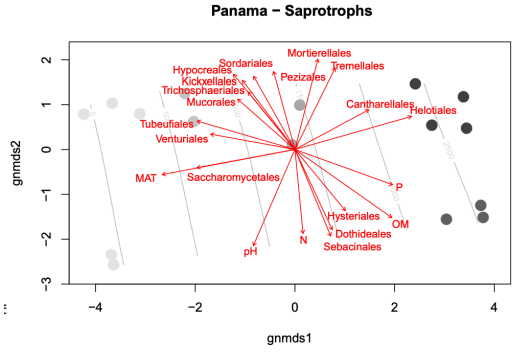
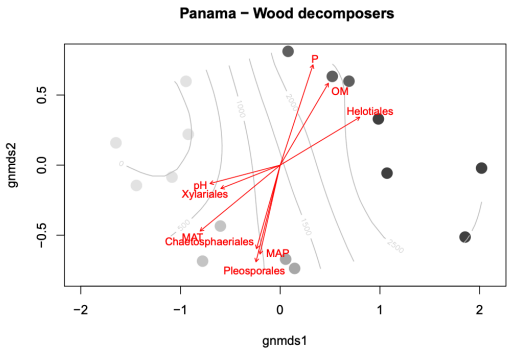
Pezizales
Atractiellales
P
Myrmecridiales
N
Thelebolales


Brazil – Wood decomposers
gnmds1
gnmds2
Auriculariales
N
Chaetosphaeria
OM
Helotiales
MAT


Panama – Saprotrophs
gnmds1
gnmds2
Mortierellales
Sordariales
Hypocreales
Pezizales
Tremellales
Kickxellales
Trichosphaeriales
Mucorales
Cantharellales
Helotiales
Tubeufiales
Venturiales
MAT
Saccharomycetales
P
Hysteriales
OM
N
Dothideales
pH
Sebacinales


Panama – Wood decomposers
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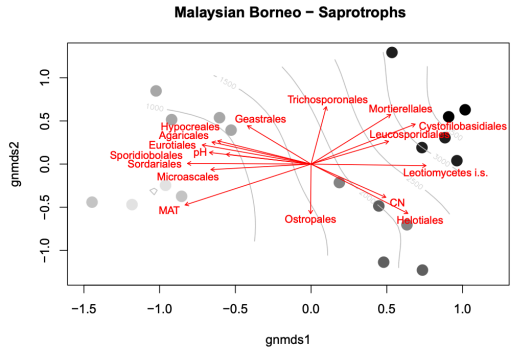
gnmds2
P
OM
Helotiales
pH
Xylariales
MAT
Chaetosphaeriales
MAP
Pleosporales


Malaysian Borneo – Saprotrophs
gnmds1
gnmds2
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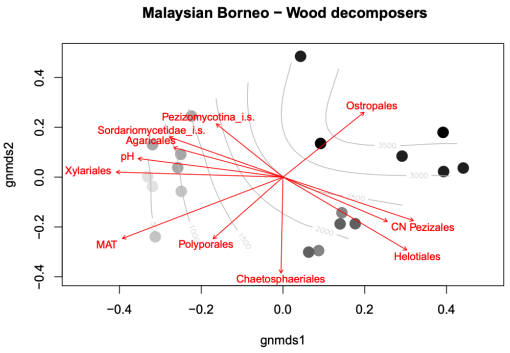
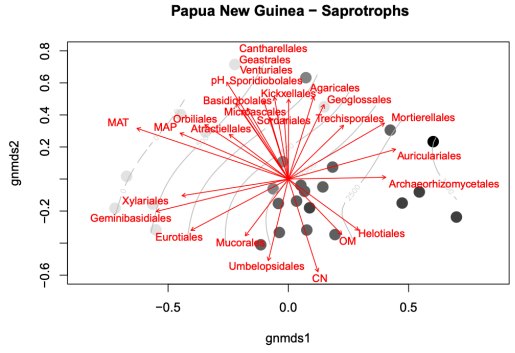
Mortierellales
Geastrales
Cystofilobasidiales
Hypocreales
Agaricales
Leucosporidiales
Eurotiales
pH
Sporidiobolales
Sordariales
Leotiomycetes i.s.
Microascales
MAT
CN
Ostropales
Helotiales


Malaysian Borneo – Wood decomposers
gnmds1
gnmds2
Ostropales
Pezizomycotina i.s.
Sordariomycetidae i.s.
Agaricales
pH
Xylariales
CN Pezizales
MAT
Polyporales
Helotiales
Chaetosphaeriales


Papua New Guinea – Saprotrophs
gnmds1
gnmds2
Cantharellales
Geastrales
Venturiales
pH
Sporidiobolales
Agaricales
Kickxellales
Basidiobolales
Geoglossales
Microascales
MAT
MAP
Orbiliales
Atractiellales
Sordariales
Trechisporales
Mortierellales
Auriculariales
Archaeorhizomycetales
Xylariales
Geminibasidiales
Eurotiales
Mucorales
OM
Helotiales
Umbelopsidales
CN

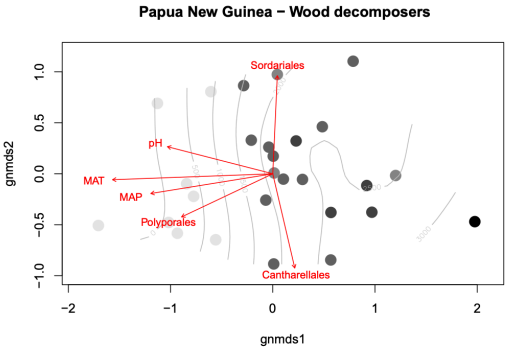

Papua New Guinea – Wood decomposers
gnmds1
gnmds2
Sordariales
pH
MAT
MAP
Polyporales
Cantharellales

Figure 4.7. Global non-metric multidimensional scaling (GNMDS) ordination plots of fungal functional groups in the sampled regions based on Hellinger-transformed data, with elevation displayed as isolines. Vectors of environmental variables and taxonomic orders with significant correlation with ordination axes are displayed (Geml et al. 2022a). The darker the circle, the higher the elevation of the site is. Abbreviations are as explained in Figure 4.4.

The Atlantic Forests are different because they lack these ECM tree genera of northern origin, and native ECM trees and shrubs are relatively rare (Sulzbacher et al. 2013, Vanegas-León et al. 2019). These differences in diversity and abundance of ECM hosts likely drive the differences in proportional richness and abundance of ECM fungi, which can reach 10% and 30% in Panama, 5 and 10% in Argentina, compared to 1 and 2% in Brazil, respectively.

In Borneo, density and richness of ECM trees are high in low- and mid-elevational forests, particularly Dipterocarpaceae and Fagaceae, respectively, tend to decline with further increase in elevation (Aiba and Kitayama 1999, Geml et al. 2017). However, in some instances, inhospitable soil type, such as ultramafic (serpentine) soils can result in exceptions from this general trend. At some high-elevation areas of Mt. Kinabalu, ECM host *Leptospermum recurvum* (Myrtaceae) tends to be dominant in ultramafic soils, occurring in much lower abundance on granite (Aiba and Kitayama 1999). In Papua New Guinea, ECM trees are relatively diverse and abundant throughout the elevation gradient, representing Dipterocarpaceae, Fagaceae, Nothofagaceae, Myrtaceae, and Gnetaceae among others (Hope 1976).

Richness of plant pathogenic and wood decomposer fungi often correlates positively with temperature (Gómez-Hernández et al. 2012, Tedersoo et al. 2014). In our study, richness (both proportional and absolute) of wood decomposers, and to some extent plant pathogenic fungi, was predictably higher at lower elevations and correlated positively with MAT. However, saprotrophs did not show a consistent elevational pattern and lacked any significant relationship with MAT in the pantropical analysis. In all regions, the lowest proportional richness of saprotrophs always coincided with the highest proportional richness of ECM fungi, possibly partly because of "the Gadgil effect" mentioned above. We note that some of the fungi identified under the functional guilds of plant pathogens and saprotrophs may prove to be endophytes, raising an interesting direction for future study and highlighting an ongoing challenge with estimating functional modes based on barcode sequences alone. Our work suggests that given the ecological and phylogenetic overlap of endophytic, saprotrophic, and pathogenic taxa in terms of ITS sequences, endophytes will broadly follow the patterns described here. Another recent study of our (Oita et al. 2021) confirms these expectations, highlighting the importance of climate (MAT and MAP) and seasonality in shaping leaf endophyte communities across an elevation gradient in Panama.

Regardless of differences in richness, the strong community structure as a function of elevation is consistent with habitat specificity and elevational turnover of species within functional guilds. We observed several consistent patterns regarding the distribution of taxonomic groups across functional guilds, suggesting a certain level of phylogenetic conservatism with respect to environmental niches (Geml et al. 2014b, Geml et al. 2022a) (Figure 4.6). For example, the consistently higher richness of Sordariomycetes, particularly Hypocreales, Sordariales and Xylariales, at lower elevations is apparent in various functional

groups and agrees with higher host and substrate diversity for these fungi, which include plant pathogens as well as saprotrophs. Unlike in boreal and many temperate forests, Sordariomycetes (including common orders such as Chaetosphaeriales, Diaporthales, Glomerellales, Hypocreales, Sordariales, and Xylariales) are the dominant class of plant endophytic fungi in tropical lowland forests (Arnold and Lutzoni 2007, Oita et al. 2021), in agreement with their prevalence in soil at low elevations. In a similar manner, the higher richness of Leotiomycetes, particularly Helotiales, at high elevations is apparent in several functional groups, such as root-associated fungi, plant pathogens, saprotrophs, and wood decomposers. Helotiales appear to be the most diverse order of ascomycetes in arctic tundra ecosystems (Semenova et al. 2015), and the above trend confirms that many Helotiales taxa thrive in relatively colder climates. The fact that habitat preference can be observed at the level of taxonomic ranks, often irrespective of functional guild, suggests shared physiological constraints and environmental optimum for certain phylogenetic lineages of fungi.

Our studies (Geml et al. 2014b, Geml et al. 2017, Geml et al. 2022a) were the first to compare community composition of fungi along elevation gradients in the Neotropics, Paleotropics, and at pantropical scales, respectively. Climate, particularly temperature, and soil pH appear to be the driving factors shaping the distribution of fungi along elevational gradients in a variety of ways, e.g., by affecting microbial processes (e.g., decomposition), vegetation, nutrient availability, and other edaphic factors, and by altering species interaction dynamics. Montane forests are among the most vulnerable terrestrial ecosystems to climate change and warming will undoubtedly affect fungal communities in these ecosystems. Given the contrasting habitat preferences of several taxonomic groups and the possible functional differences among them within the broad functional guilds, future communities at a given site may differ considerably from current ones not only in composition, but also in functionality. Habitat specificity exhibited by many fungi offers possibilities for monitoring and habitat characterization, and we advocate incorporating fungi in biodiversity assessments and conservation efforts. With the accumulating spatial data points for fungal taxa from metabarcoding studies, it will soon be possible to determine the climatic niches and model the suitable habitats for many fungi.

5. Landscape ecology of Pannonian forest fungi

Figure 5.1. Old-growth montane beech forest (*Aconito-Fagetum*) in the Bükk Mountains in northern Hungary, with representatives of ECM fungal genera *Craterellus*, *Lactarius*, *Amanita*, and *Clavulina* found in the study region (photos by the author).

This chapter is based upon the following publications:

Geml J. 2019. Soil fungal communities reflect aspect-driven environmental structuring and vegetation types in a Pannonian forest landscape. ***Fungal Ecology*** 39:63-79.

Geml J, Leal CM, Nagy R, Sulyok J. 2022. Abiotic environmental factors drive the diversity, compositional dynamics and habitat preference of ectomycorrhizal fungi in Pannonian forest types. ***Frontiers in Microbiology*** 13:1007935.

5.1 Introduction

Topography and the physico-chemical properties of soil are among the most influential landscape-level drivers of biological communities in terrestrial ecosystems. With respect to topography, elevation and slope aspect are of particular importance, because they directly influence mesoclimatic conditions that, together with the geological history of the given site, drive several soil chemical processes and can limit the primary productivity and the establishment of species depending on their ecological niches (Rosenberg et al. 1983, Rorison et al. 1986, McCune and Keon 2002 Fekedulegn et al. 2003, Geml et al. 2014ab, Gilliam et al. 2014). Despite differences in latitudinal trends in diversity, plants and fungi generally show similar levels of community structuring among biomes, biogeographic regions and landscape-level habitat types (Geml et al. 2014b, Tedersoo et al. 2014, Geml et al. 2017, Větrovský et al. 2019, Adamo et al. 2021; Boekhout et al. 2021, Geml et al. 2022ab). According to macroecological studies of Tedersoo et al. (2014) and Větrovský et al. (2019), fungal diversity and distribution at global scales primarily are driven by climatic factors, e.g., mean annual temperature and precipitation, edaphic factors, particularly pH, as well as by dispersal limitation. There is less information on the landscape-level compositional dynamics of soil fungi, but the emerging trend from the handful of published studies is that fungal community composition at landscape scale are driven mostly by the same environmental factors as at global scales, namely soil pH, temperature, available moisture, with the influence of individual nutrients often being dependent on habitat type (Baldrian 2017; Grau et al. 2017; Geml et al. 2014ab; Adamo et al. 2021; Geml et al. 2021).

The region of study is in the Északi-középhegység (North Hungarian Mountains). The geology of the region is complex, with numerous types of Paleozoic, Mesozoic, and Cenozoic calcareous, volcanic, and igneous rocks appearing near the surface as a mosaic (Pelikán 2010). Due to this geological and topographic complexity that creates a broad spectrum of edaphic and mesoclimatic conditions, the region is characterized by high habitat diversity. This is particularly true for the Bükk Mountains, as indicated by the high number of coenological vegetation types, including numerous forest and grassland communities distributed along temperature, moisture, and pH gradients (Suba 1983; Vojtkó 2002; Vojtkó et al. 2010).

The two studies included differ in spatial as well as mycological scopes: the small-scale landscape-level study of (Geml 2019) investigated the effect of slope aspect on soil fungal communities comprising various functional groups in a pair of Jurassic limestone hills, while the our later study (Geml et al. 2022b) characterized ECM fungal communities in eleven Pannonian forest types, representing elevation, moisture as well as pH gradients, distributed throughout the western half of the Bükk mountains.

We hypothesized that fungal community composition would differ significantly among Pannonian forest types differing in mesoclimatic and edaphic conditions, due to niche processes, such as environmental filtering (Hypothesis 1). Temperature, available moisture and pH, are well known drivers of fungal community composition at various spatial scales (Geml et al. 2014ab, Tedersoo et al. 2014, Kutszegi et al. 2015, Baldrian 2017, Glassman et al. 2017, Rosinger et al. 2018, Aučina et al. 2019, Větrovský et al. 2019). Based on these and other global and regional studies, and because many dominant tree genera are distributed along a wide range of forest types, we expected that the diversity and distribution of fungi at landscape-

scale would strongly be influenced by the above-mentioned abiotic factors that themselves are strongly driven by topography, primarily by elevation and slope aspect. Although the effect of slope aspect on fungal community composition had not been specifically tested before my study (Geml 2019), there is accumulating knowledge regarding the richness and composition of fungal communities among habitat types in different regions. At the landscape level, most studies report comparable fungal richness values, but also substantial compositional turnover among habitats with different mesoclimatic and/or edaphic conditions (e.g., Geml et al. 2014ab, Timling et al. 2014, Grau et al. 2017). Therefore, while aspect was not expected to affect total fungal richness, we hypothesized that fungal community composition would differ significantly between north- and south-facing slopes due to environmental filtering according to contrasting environmental conditions, i.e. community turnover will be greater among sites with different aspects than among sites of similar aspect (Hypothesis 2). Moreover, we expected differences in habitat preference among taxonomic and functional groups of fungi, as well as among congeneric species, due to differences in life strategies and in their physiological optima with respect to soil moisture and soil pH that likely influence their competitive abilities (Hypothesis 3).

5.2 Materials and methods

Study region and sampling sites

The focal area of the studies in this chapter is in the Mátra and Bükk mountains in the central region of the North Hungarian Mountains. At lower elevations, the climate is subcontinental with mean January and July temperatures of ca. -3°C and 20°C, respectively, and mean annual precipitation of ca. 550-580 mm, while at high elevations (i.e. above 750 m a.s.l.), mean annual temperature and precipitation values are 4-5 °C lower and 200-250 mm higher, respectively (Tóth 1983, Horváth and Gaálová 2007). Zonal forest types include Pannonian-Balkanic turkey oak - sessile oak forests (*Quercetum petraeae-cerris*) characteristic of gentle slopes at low elevations (200-450 m a.s.l.), Pannonian sessile oak - hornbeam forests (*Carici pilosae-Carpinetum*) in mesic, submontane (400-600 m a.s.l.) settings on gentle slopes and at valley bottoms, submontane beech forests (*Melittio-Fagetum*) on north-facing slopes at mid-elevation (400-750 m a.s.l.), and montane beech forests (*Aconito-Fagetum*) in near horizontal settings and on gentle north-facing slopes above 750 m a.s.l. In addition to these zonal vegetation types, there several topographic forest types spanning temperature and moisture gradients. In the sampled region, these include thermophilous downy oak forests (*Corno-Quercetum pubescentis*) on shallow and rocky soil on steep (> 20°) south-facing slopes with particularly warm and dry mesoclimate, dry to mesic limestone oak forests (*Seslerio-Quercetum*) on shallow, rocky soil of steep southern slopes at high elevations, mesic limestone beech forests (*Seslerio-Fagetum*) on shallow, rocky soil on northern and eastern slopes at mid- to high elevations, mesic linden-whitebeam rock forests (*Tilio-Sorbetum*) on shallow, rocky soils, on steep northern or eastern slopes, mesic linden-ash rock forests (*Tilio-Fraxinetum*) on wind-swept mountain tops, and acidophilous oak (*Luzulo-Quercetum* or *Genisto tinctoriae-*

Quercetum) and beech forests (*Luzulo-Fagetum*), both on dry to mesic, acidic, shallow soils at elevations below and above 500 m a.s.l., respectively (Vojtkó 2002, Borhidi 2003, Vojtkó et al. 2010, Bölöni et al. 2011). Photos and a brief ecological summary of the forest types are shown in Figure 5.1 and Table 5.1, respectively. Geographic coordinates and environmental data of the 62 sampling sites can be found in Geml et al. (2022).

Table 5.1. Pannonian forest types investigated in this chapter with the main habitat characteristics and soil sampling localities.

Coenological forest type	Code	Habitat characteristics	Elevation range (m a.s.l.)
Zonal forest types			
Quercetum petraeae-cerris	Qpc	mesic to dry turkey oak - sessile oak forest in colline zone	250-400
Carici pilosae-Carpinetum	CpC	mesophilous sessile oak - hornbeam forest in submontane zone and in valleys	400-600
Melittio-Fagetum	MF	mesic submontane beech forest	400-750
Aconito-Fagetum	AF	mesic montane beech forest	above 750
Edaphic forest types			
Seslerio-Quercetum	SQ	mesic to dry oak forest on shallow, rocky, non-acidic soils	400-700
Seslerio-Fagetum	SF	mesic beech forest on shallow, rocky, non-acidic soils, on northern or eastern slopes	above 500
Luzulo-Quercetum or *Genisto tinctoriae-Quercetum*	LQ	dry to mesic sessile oak forest on acidic soils	250-500
Luzulo-Fagetum	LF	dry to mesic beech forest on rocky, acidic soils	above 500
Topographic forest types			
Corno-Quercetum pubescentis	CQ	dry, thermophilous downy oak forest on steep, south-facing slopes and shallow, rocky soils	250-500
Tilio-Sorbetum	TS	mesic whitebeam - linden forest on shallow, rocky soils, on steep northern or eastern slopes	above 500
Tilio-Fraxinetum	TF	mesic ash - linden forest on shallow, rocky soils, on mountain tops	above 500

The sampling sites for the first study on the effect of slope aspect on fungal communities were in the valley of the Tarna creek situated between the Mátra and the Bükk mountains in northern Hungary (Figure 5.2). The area is characterized by rolling hills of low elevations (200-400 m a.s.l.), mostly covered with secondary forests. Within the purposefully small study area, I sampled various Pannonian forest types that are consistently formed in relatively specific environmental conditions that are mostly influenced by topography, particularly slope aspect (Vojtkó 2002, Borhidi 2003, Vojtkó et al. 2010, Bölöni et al. 2011). These vegetation types included: downy oak forests (*Corno-Quercetum pubescentis*), Pannonian-Balkanic turkey oak - sessile oak forests (*Quercetum petraeae-cerris*), Pannonian sessile oak - hornbeam forests (*Carici pilosae-Carpinetum*), and submontane beech forests (*Melittio-Fagetum*), representing a slope aspect-driven gradient in soil moisture and temperature.

Figure 5.2. Representative sampling sites of the Pannonian forest types studied (photos by József Sulyok, BNPI)

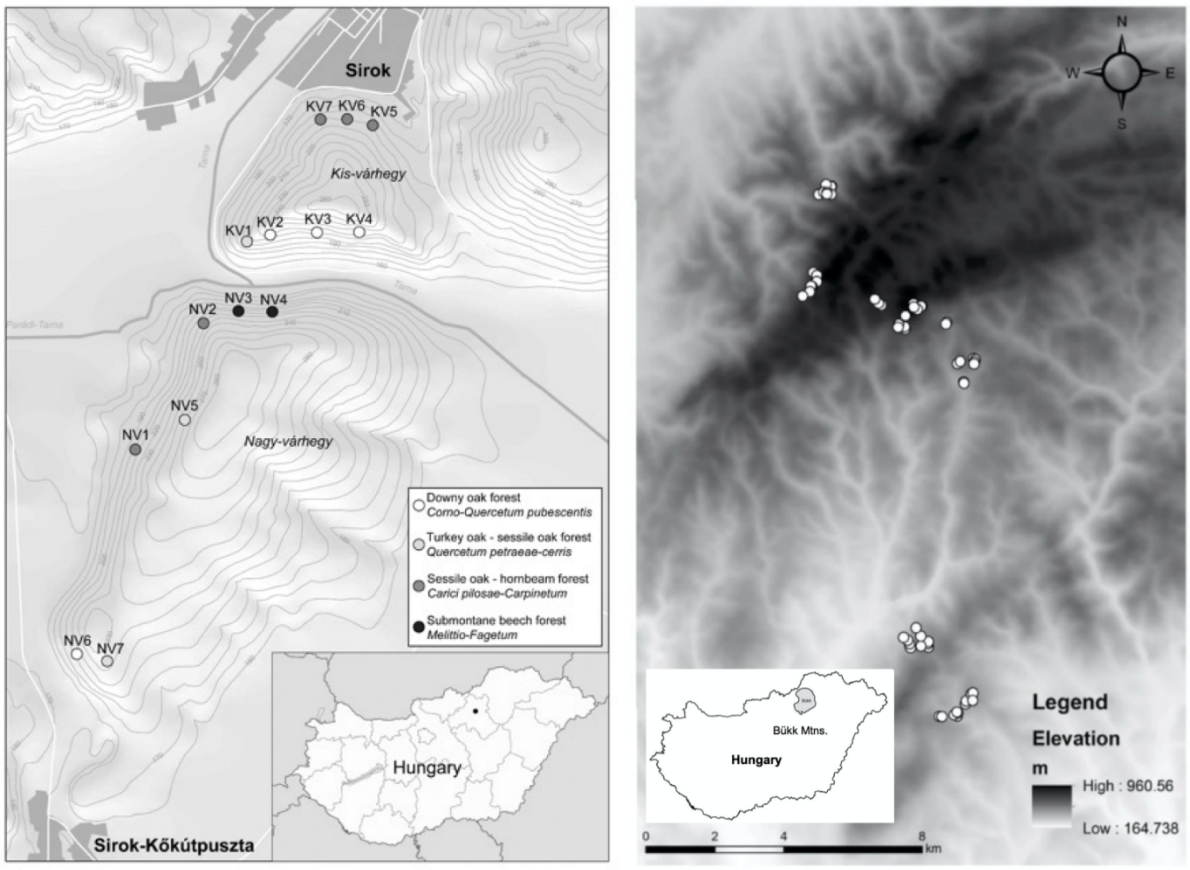


Figure 5.3. Sampling sites for the two studies of Pannonian forest types discussed in this chapter.

The fourteen sampling sites were evenly distributed in two hills (Kis-várhegy and Nagy-várhegy) just south of the village of Sirok, Heves county, Hungary. The area was chosen because it features, in a small area (< 2 km^2), four of the above-mentioned Pannonian forest types of northern Hungary (Figure 5.3). Potentially confounding factors that often limit the interpretation of ecological studies in natural habitats were minimal: (1) the Kis-várhegy and Nagy-várhegy are uniformly composed of Jurassic calcareous limestone (Pelikán 2010), (2) the regional climate is uniform throughout the small study area, (3) all forest types are represented by mature (> 70y) secondary forests that have already achieved their characteristic canopy heights, (4) the elevation differences among the sampling sites are minor (< 60 m) and are not related to aspect or to any other environmental conditions, and (5) the spatial proximity and the continuous natural or semi-natural landscape are expected to facilitate unrestricted dispersal of fungal propagules among the sites by wind, water and wildlife. Therefore, any observed compositional differences among the samples are expected to be the result of niche-based and stochastic processes, with the former primarily referring to environmental filtering according to differences in abiotic factors (mesoclimatic and edaphic) and biological communities (i.e. vegetation, meso- and microfauna and other soil biota) driven by topography: predominantly northerly vs. southerly aspect and to a lesser extent by slope angle.

The focal area of the second study was in the western half of the Bükk Mountains, with elevation ranging from ca. 300 to 980 m a.s.l. We sampled soil at 62 sites representing mature stands of the above-mentioned 11 forest types, in their most natural state possible. We intended

to maximize the spatial representation of the sampled forest types, by focusing on areas where several forest types were present in relatively close proximity (Figure 5.3).

At each site (ca. 10 × 25 m), 20 samples of top soil (to a depth of ca. 10 cm) were taken from underneath the litter layer and at least 2 m from each other, with a cylindrical soil corer. Soil samples collected at a given site were pooled, mixed, and sieved (2 mm), resulting in a composite soil sample for each site. Ca. 20 g of each composite sample was kept frozen until DNA extraction, while the rest was used for soil chemical analyses to measure pH (water-based), and total carbon (C), nitrogen (N), phosphorus (P) and various micronutrient contents following Sparks et al. (1996).

Data generation

In the two studies featured here, genomic DNA was extracted from 0.5 g of dry soil per sample with the Macherey-Nagel NucleoSpin® Soil kit, following the manufacturer's protocol. We used 1 ul of DNA template with DNA concentration normalized for all samples per study for PCR amplification of the ITS2 region (ca. 250 bp) of the nuclear ribosomal DNA repeat with primers fITS7 (Ihrmark et al. 2012) and ITS4 (White et al. 1990), as described in Geml et al. (2014b). The equimolar pools of uniquely barcoded amplicons were sequenced either with Ion Torrent using an Ion 318™ Chip (Geml 2019) or with paired-end (2 × 250 bp) Illumina MiSeq (Geml et al. 2022b). We generally obtained between 30,000 and 60,000 DNA sequence reads per sample. Routine chemical analyses of soil samples were carried out by different commercial laboratories.

For the first study (Geml 2019), the initial clean-up of the raw data was carried out using Galaxy (https://main.g2.bx.psu.edu/root), in which the sequences were sorted according to samples and adapters (identification tags) were removed. The primers were removed and poor-quality ends were trimmed off based on 0.02 error probability limit in Geneious Pro 8 (BioMatters, New Zealand). Subsequently, sequences were filtered using USEARCH v.8.0 (Edgar 2010) based on the following settings: all sequences were truncated to 200 bp and sequences with expected error > 1 were discarded. For each sample, sequences were collapsed into unique sequence types, while preserving their counts. The quality-filtered sequences from all samples were grouped into operational taxonomic units (OTUs) at 97% sequence similarity and putative chimeric sequences were removed using USEARCH. I assigned sequences to taxonomic groups based on pairwise similarity searches against the curated UNITE+INSD fungal ITS sequence database (version released on October 10, 2017), containing identified fungal sequences with assignments to Species Hypothesis (SH) groups delimited based on dynamic sequence similarity thresholds (Kõljalg et al. 2013).

Only OTUs with > 90% similarity to a fungal SH with known ecological function were assigned to one of the following functional groups: animal pathogens, ECM fungi, lichens, litter decomposers, mycoparasites, plant pathogens, root-associated fungi (non-ECM orchid and ericoid mycorrhizal fungi and root endophytes), saprotrophs (generalists), and wood decomposers. Arbuscular mycorrhizal fungi were not included in the analyses, because only one representative OTU was found in the quality-filtered dataset. The initial functional assignments were made by FunGuild (Nguyen et al. 2015) and were manually checked afterwards. For genera that are known to comprise species from multiple functional guilds (e.g.,

Amanita, *Entoloma*, *Ramaria*, and many SH groups in the Sebacinales), I assigned ecological function for each OTU individually, based on available ecological information for the matching SH in the UNITE database. To further examine patterns of functional categories within ECM fungi, I classified ECM fungal OTUs into two aggregate extramatrical mycelial exploration type categories: contact/short-distance/medium-distance smooth with hydrophilic hyphae (C/SD/MDS) and medium-distance mat/medium-distance fringe/long-distance with hydrophobic hyphae (MDM/MDF/LD) following Agerer (2006), Tedersoo and Smith (2013), and the DEEMY database (http://deemy.de). In addition to the morphological differences, the above categories also indicate differences in nutrient acquisition strategies: ECM fungi with C/SD/MDS hyphae preferring labile N pools and ECM fungi with MDM/MDF/LD exploration types having greater ability to break down complex organic compounds (Hobbie and Agerer 2010).

For the second study (Geml et al. 2022b), raw DNA sequences were processed with the *dada2* package (Callahan et al. 2016), implemented in R v. 3.6.3 (R Development Core Team 2015), designed to resolve fine-scale DNA sequence variation with improved elimination of artifactual sequences. Because *dada2* does not involve clustering sequences into OTUs and is robust for removing spurious data, the output of unique amplicon sequence variants (ASVs) captures both intra- and interspecific genetic variation of fungi found in the samples. This allows for the exploration of strain-level differences in inter- and intraspecific interactions. Raw sequences were truncated to 240 bp for forward and 200 bp for reverse to maintain an average Phred score of >30, denoised, chimera filtered, merged and clustered into sequence variants. The maximum number of expected errors (maxEE) allowed in a read was 2. In order to minimize false presences, only ASVs with at least 10 sequences in a given sample were considered "present" in that sample. In addition, ASVs that occurred in only one sample were excluded from further analyses to avoid artifactual ASVs (Lindahl et al. 2013). After the above steps of quality filtering, there were 10 258 fungal ASVs from 539 139 ± 97 403 (mean ± st. dev.) assembled fungal sequences per sample. The fungal community matrix was normalized (rarefied) by random subsampling to the smallest library size (277 881 reads) on a per-sample basis. Taxonomic assignments of fungal ASVs were made based on the UNITE reference database of representative sequences all fungal species hypotheses (SHs) based on a dynamic delimitation (Kõljalg et al. 2013), using USEARCH v. 11 (Edgar 2010). Selection of ECM fungal ASVs were made based on genus-level identification, with > 90% sequence similarity, using the FungalTraits reference database (Põlme et al. 2020). ECM fungal ASVs were assigned to phylogenetic lineages of ECM fungi *sensu* Tedersoo and Smith (2013) based on the assignation of the matching SHs in UNITE. All sequences of ECM fungal ASVs analyzed in this paper have been submitted to GenBank (OP042390-OP043852).

For each sampling site, we obtained geographic coordinates and elevation data using a hand-held GPS device. We estimated insolation for each sampling site using the ArcGIS v. 10.4.1 Area Solar Radiation tool. This tool uses latitude of the site for calculations of solar declination and solar position, with correction of the radiation arriving at the surface based on a digital elevation model (DEM) to prepare a radiation raster with units of watt hours per square meter (WH/m2).

Because slope aspect and slope angle are known to influence mesoclimate, soil moisture, relative humidity, and soil chemical processes (McCune and Keon 2002, Dobos

2010, Gilliam et al. 2014, Méndez-Toribio et al. 2016), we accounted for the effect of slope aspect and slope angle, obtained from the digital elevation model and cross-checked with field measurements, as follows. When aspect is treated as a continuous variable from 0° to 360°, the two extreme values of this interval refer to the same slope aspect (north-facing). Therefore, we expressed aspect as northerly aspect following Calef et al. (2005) and Geml (2019), to better reflect the well-known environmental differences between north- and south-facing slopes, with values ranging from south = -90° to north = 90°. In addition, because high slope angle exacerbates the effect of slope aspect, we used the product of slope aspect and slope angle as a combined topographic variable, in addition to elevation.

We also calculated the Huglin heat sum index (or Huglin index) for all sampling sites, based on the input data obtained from the FORESEE v. 4.0 database, which is an open-access meteorological database that covers the 1951-2100 period and contains observed and projected daily maximum/minimum temperature and precipitation fields for Central Europe at 0.1° × 0.1° spatial resolution (http://nimbus.elte.hu/FORESEE/). The Huglin index, which was originally developed to characterize the mesoclimatic conditions of vineyards, is calculated as a product of the coefficient *K*, which depends on the latitude, and the sum of the arithmetic mean of daily mean- and daily maximum temperatures relative to the baseline temperature of 10 °C from April 1 through September 30 (Huglin 1986).

Statistical analyses

Unless otherwise noted, all statistical analyses were carried out in R. We statistically compared ASV richness and relative abundance of ECM fungal genera among the samples with ANOVA and Tukey's HSD test. ASV richness values were graphically presented as boxplots using the *ggplot2* R package (Wickham 2016). Correlations among the ASV richness values of the five most diverse ECM fungal lineages and abiotic environmental variables were tested using quadratic regressions, which were visualized with *ggplot2*. Compositional differences among samples were visualized using non-metric multidimensional scaling (NMDS) in the *vegan* R package (Oksanen et al. 2015) with Bray-Curtis distance measure on the Hellinger-transformed matrix. We performed PerMANOVA (adonis) in *vegan* to estimate the amount of variation explained by the isolation source, health state and cultivar. In addition, we performed indicator species analysis (Dufrêne and Legendre 1997) with the *multipatt* function in the *indicspecies* package (De Cáceres et al. 2012) to identify characteristic and differential taxa for forest types. Finally, to better understand the influence of abiotic factors on the habitat preference of indicators and to illustrate species-level ecological differences within genera, we explored relationships between read abundance of indicator species and selected environmental variables. Specifically, we used linear regressions to correlate the rarefied read counts of indicator species in three ECM lineages with the highest number of indicators (/cortinarius, /inocybe, and /russula-lactarius) with five selected environmental variables that capture most of the edaphic and mesoclimatic differences among the sampling sites (pH, soil moisture, elevation, northerly aspect, and the Huglin index).

5.3. Results and discussion

Aspect-driven structuring of fungal communities at landscape scale

The study of Geml (2019) was the first in-depth characterization of fungal communities in Pannonian forests based on soil DNA sequencing. Furthermore, I showed that fungal community composition at the selected Pannonian forest sites is strongly structured according to slope aspect. Total fungal richness was similar in all forest types, with mean per-plot OTU richness of 1228 ± 90. However, there were substantial differences among the taxonomic groups with respect to richness in the four forest types. In general, basidiomycetes tended to show higher proportional richness in the mesic and relatively cool forest types. This was particularly true for Agaricomycetes, where the differences between predominantly southern and northern slopes were significant. Conversely, ascomycetes in general showed higher proportional richness in the warmer and drier forest types, with corresponding significant differences observed in Dothideomycetes, Eurotiomycetes, and Sordariomycetes, while proportional richness was comparable across forest types in Leotiomycetes and Pezizomycetes. Finally, representatives of the phyla Mortierellomycota and Mucoromycota, both formerly classified in Zygomycota, had significantly higher proportional richness on north-facing slopes (Figure 5.4).

Although total fungal richness generally was not statistically different between north- and south-facing slopes, a strong compositional difference driven by slope aspect was evident in all fungal functional groups. Four out of the nine functional groups exhibited significant differences among the four forest types in terms of proportional richness. Namely, lichens showed greatest proportional richness in the zonal turkey oak - sessile oak forest and lowest in the mesic sessile oak - hornbeam forest. Plant pathogens and generalist saprotrophs had higher proportional richness in the oak-dominated forests of the south-facing slopes, while wood decomposers showed an opposite trend with lowest proportional richness in the xerothermic downy oak forest and highest in the submontane beech forest (Figure 5.4). Richness of ECM fungi did not differ among the forest types, there were some differences at the phylum level and in terms of mycelial exploration types. Namely, proportional richness of ECM basidiomycetes was significantly higher in the mesic oak - hornbeam forests than in the zonal and xerotherm oak forests. This pattern was driven by an increase in the proportional richness of ECM basidiomycetes with C/SD/MDS exploration types (e.g., *Inocybe*, *Laccaria*, *Lactarius*, *Russula*, *Sebacina*), while proportional richness of ECM ascomycetes (all C/SD/MDS) and ECM basidiomycetes with MDM/MDF/LD exploration types did not differ significantly among the forest types.

Fungal community composition differed significantly between north- and south-facing slopes, as suggested by the multivariate analyses (Figure 5.5). Community composition of all fungi in the sampling sites is structured according to slope aspect, which represents the first axis. This is also confirmed by the strong positive relationship ($r^2 = 0.547$, $p < 0.001$) between pairwise differences in northerly aspect and community turnover. In addition, there are numerous fungal taxa that predominantly occur on either south-facing or north-facing slopes, as suggested by the NMDS plots as well as the indicator species analysis (Geml 2019). This likely is due to environmental filtering according to contrasting mesoclimatic and edaphic

conditions as well as differences in vegetation. Similarly, fungi with different life strategies seem to be favored by different environmental conditions, as indicated by the functional differences between slopes of northerly or southerly aspect. Even in functional groups with no significant differences in richness, strong compositional differences are apparent between slopes of northerly and southerly aspects (Figure 5.5).

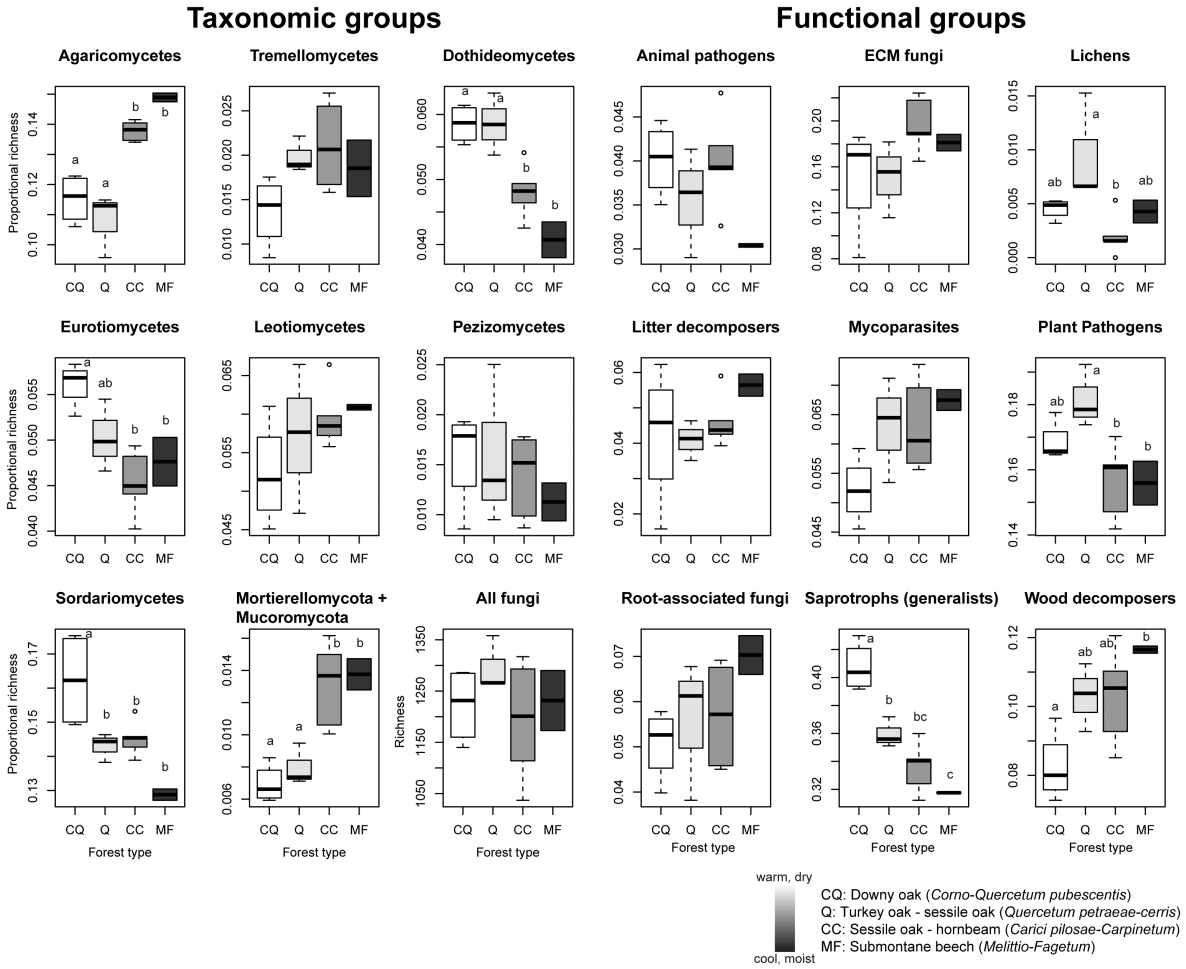


Figure 5.4. Comparison of total fungal richness and proportional richness of taxonomic and functional groups across the four sampled forest types. Means were compared using ANOVA and Tukey's HSD tests, with letters denote significant differences (Geml 2019).

The results summarized here confirm the following expectation based on the competitive dynamics model, i.e. opportunistic, drought-tolerant generalist saprotrophic fungi were favored by environmental conditions present on south-facing slopes (e.g., *Acremonium*, Aspergillaceae, Chaetomiaceae, Didymosphaeriaceae, Helotiaceae, Lasiosphaeriaceae, Microascaceae, Onygenaceae, Sporormiaceae, Stachyobotryaceae, *Tetracladium*, Trichocomaceae, Trichomeriaceae, and Trichosporonaceae), while most forest specialist litter and wood decomposers (e.g., Chaetosphaeriaceae, Crepidotaceae, Helotiaceae, *Trechispora*, and Xylariaceae), and to a lesser extent mycoparasites and non-ECM root-associated fungi, were found on north-facing slopes, presumably as a result of their competitive advantage in mesic conditions.

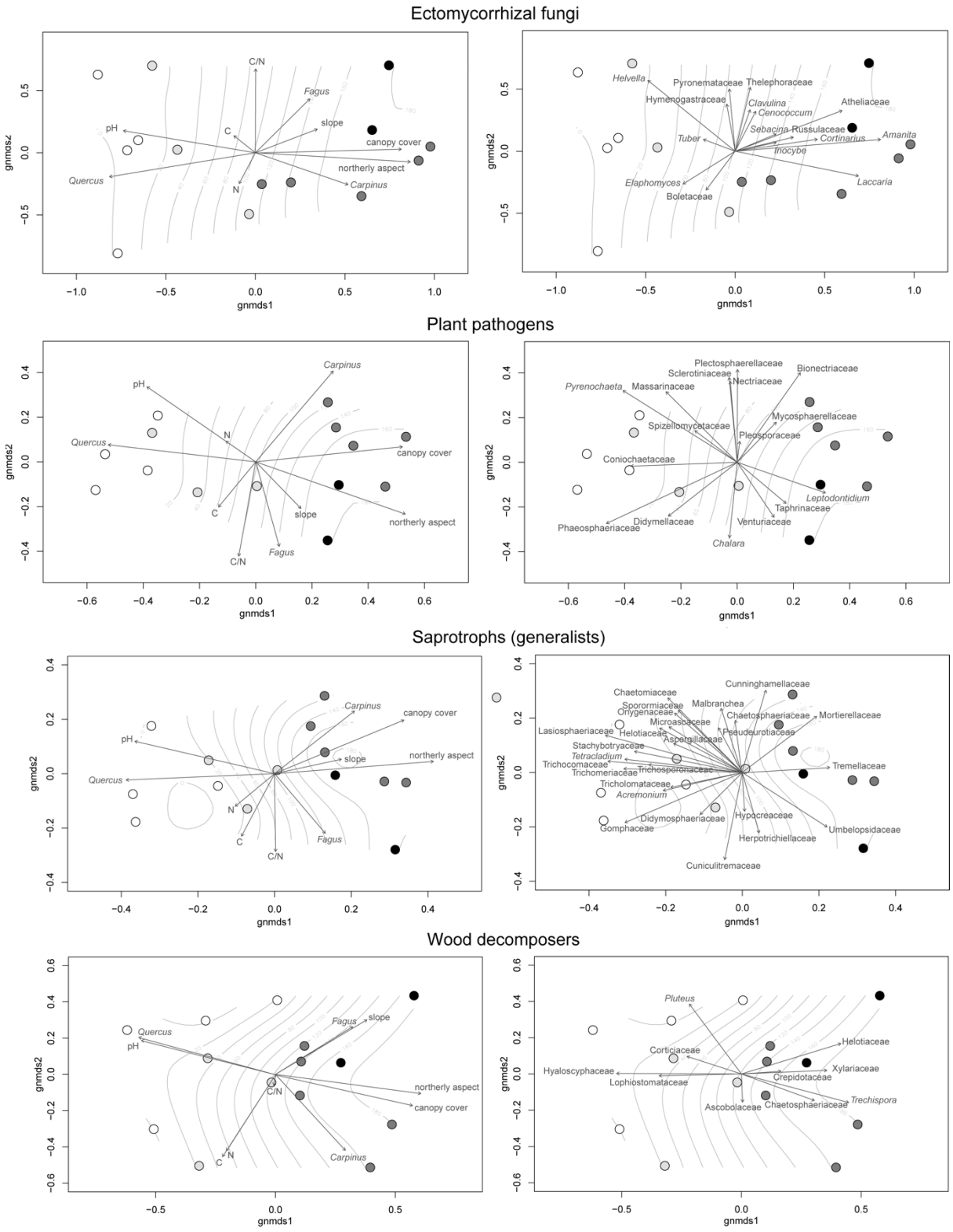


Figure 5.5. Non-metric multidimensional scaling (NMDS) ordination plots of the four most diverse functional groups of fungi in the sampled forest types based on Hellinger-transformed data, with northerly aspect displayed as isolines. Vectors of environmental variables and OTU richness of fungal families correlated with ordination axes are displayed. Where a certain family was represented by only one genus, the genus name is shown. Final stress values: ECM fungi (0.1046), plant pathogens (0.0679), saprotrophs (0.0947), and wood decomposers (0.1471) (Geml 2019).

The cooler microclimate may be more advantageous for root-associated fungi, because this group had been shown to be more diverse at higher elevations in altitudinal gradient studies (Geml et al. 2014b). On the other hand, although richness of wood decay fungi and mycoparasites have been shown to decline with decreasing temperature in elevation gradients (Geml et al. 2014b), considering the given moisture limitation in this study area, their higher richness in north-facing slopes may be more strongly driven by the greater availability of moisture. Lichens and plant pathogens were more species rich in the oak-dominated forests. Regarding lichens, this may be a consequence of the more open canopy of the oak forests that allows for more light to penetrate and apparently fosters the growth of the generally shade-intolerant and drought-tolerant lichens. On the other hand, plant pathogens and generalist saprotrophs may benefit more from the warmer mesoclimate characteristic of the south-facing slopes, as richness values of these groups generally correlate positively with temperature in altitudinal as well as in global studies (Geml et al. 2014b, Tedersoo et al. 2014, Geml et al. 2022a). In addition, based on the above-mentioned theory on competitive dynamics, drought-tolerant generalist saprotrophic fungi may be outcompeted on the north-facing slopes by mesophilic specialists.

Conversely, I did not find statistical support for either proportional richness or proportional read abundance of ECM ascomycetes being statistically different among the forest types. Only the lower proportional richness of ECM basidiomycetes in the south-facing slopes agreed with formerly reported higher prevalence of ECM ascomycetes and relative scarcity of ECM basidiomycetes in drought-stressed habitats, but even this was driven by a decrease in taxa with C/SD/MDS mycelial exploration types, contrary to the expectation of ECM fungi with short extraradical mycelia being more adaptable to drought stress (Castaño et al. 2018). However, it is worth mentioning that only ascomycete ECM genera showed clear preference for south-facing slopes (*Elaphomyces*, *Helvella*, and *Tuber*), while almost all ECM genera that preferred mesic forests of northerly aspect were basidiomycetes: *Amanita*, *Clavulina*, *Cortinarius*, *Inocybe*, *Laccaria*, *Sebacina* as well as those in Atheliaceae and Russulaceae, which lends some weak support to the difference in habitat preferences between ECM ascomycetes and basidiomycetes. It is plausible that the observed increase in C/SD/MDS ECM basidiomycetes in the mesic forests may be related to differences in rooting density. Sites with high rooting density, such as mature forests, generally are dominated by short- and medium-distance exploration types as opposed to early-successional forests with lower rooting density, where the proportion of long-distance exploration types often are higher (Peay et al. 2011). While all study sites in this project were mature forests and were dominated by C/SD/MDS mycelial exploration types, it is possible that the higher richness of C/SD/MDS ECM fungi on the north-facing slopes may be caused by higher rooting density in the mesic forests, when compared to the more xerothermic oak forests. Leuschner et al. (2004) found that beech forests in Germany had a higher number of root tips per square meter in sites with higher precipitation, suggesting indeed a positive relationship between soil moisture and rooting density. Somewhat surprisingly though, I did not find a statistical difference between proportional abundance among the south- and north-facing slopes despite the prevailing mesic conditions on the latter, which presumably are more conducive to mycelial growth and rooting density. There appear to be substantial functional and ecological variations at various taxonomic scales that can result in contrasting patterns within the above categories (e.g., between C/SD/MDS ascomycetes and

basidiomycetes) that could drive the observed patterns. Certainly, more studies on the environmental and functional components of the ecological niches of these fungi are needed.

The effect of slope aspect on fungal community composition and richness is mediated through abiotic and biotic factors that are driven either directly or indirectly by the differences in net solar radiation received in north- and south-facing slopes (McCune and Keon 2002). For example, aspect strongly influences local air and surface temperature, soil moisture, relative humidity, and soil chemical processes (Gilliam et al. 2014). Consequently, the habitats found on north- and south-facing slopes have distinct meso- and microclimatic as well as edaphic conditions. These differences are particularly marked regarding available moisture and pH, as had been observed in the study region previously (Dobos 2010), which, in turn, influence the composition of biotic communities and their interactions.

The availability of soil moisture is one of the most important environmental conditions that determines richness as well as community composition in fungi (Crowther et al. 2014, Tedersoo et al. 2014). At landscape scale, as in the study area, annual precipitation is considered uniform across the sampling sites due to their proximity. Therefore, topography likely is the most important factor that influences moisture availability through contrasting levels of evapotranspiration between north- and south-facing slopes, as has been observed in several biomes (Fekedulegn et al. 2003, Méndez-Toribio et al. 2016).

Soil pH also plays an important role in shaping fungal communities (Porter et al. 1987, Coughlan et al. 2000, Lauber et al. 2008, Rousk et al. 2010, Geml et al. 2014ab, Tedersoo et al. 2014, Glassman et al. 2017) and is often influenced by slope aspect (Gilliam et al. 2014, Chu et al. 2016). Because many fungal species have a relatively wide pH optimum (e.g. Wheeler et al. 1991, Nevarez et al. 2009), it is likely that the observed correlation of pH with community composition is mainly indirect, e.g., via altering nutrient availability and competitive interactions between soil fungi and bacteria (Rousk et al. 2008), and other soil biota. In the study sites, there was a strong negative correlation of soil pH with northerly aspect, and it is difficult to disentangle the ‘pure’ effect of pH from that of aspect. Nevertheless, for some fungal groups that are known to be influenced by soil pH, the data presented here agree with previous results. For example, several species of true truffles (*Tuber* spp.) are known to prefer high soil pH (García-Montero et al. 2006) as observed in the study sites (Figure 5.5). Furthermore, root endophytic fungi had been shown to prefer low soil pH (Postma et al. 2006) and the strong preference of non-ECM root-associated fungi for the northerly sites with lower pH in this study confirms the above trend (Figure 5.3).

The only other edaphic factors with strong correlation with fungal community structure was C/N ratio, which was not related to aspect. Instead, changes in C/N ratio appeared to be related to different forest types on the north-facing slopes, i.e. oak - hornbeam and submontane beech forests. Because C/N is considered a direct measure of resource quality (Nielsen et al. 2010), it is possible that the higher C/N values in the beech forests are driven by differences in litter quality between beech and hornbeam and oak. Measurements from more beech and oak - hornbeam stands are needed to test this hypothesis.

Although the two dominant tree genera (*Carpinus* and *Quercus*) occur in most of the sites, their relative abundance is strongly influenced by aspect. Furthermore, as indicated by the strong positive relationship between northerly aspect and canopy cover, the forest structure is notably different between south- and north-facing slopes even in communities composed of

the same tree genera, which further increases the mesoclimatic differences between the south- and north-facing slopes. Therefore, and because most plant-associated fungi are not strictly specific to a tree genus or family, I argue that to a great extent the observed fungal community patterns are caused by a complex array of aspect-driven environmental variables and not by the tree composition alone.

The results of the partial mantel tests as well as the permutational multivariate analysis of variance suggest that northerly aspect by itself explained greatest proportion of variation in community composition in all fungi and in most functional groups, while the effect of the tree community, although still strong, is secondary, followed by soil chemical characteristics. Mantel tests showed that neither spatial proximity nor slope angle had any significant correlation with fungal community composition or with aspect, relative abundance of tree genera, and edaphic factors. On the other hand, aspect was strongly correlated with the relative abundance of tree genera ($r = 0.526$, $p < 0.001$) and weakly with the measured edaphic factors ($r = 0.151$, $p = 0.046$), while there was moderate correlation between tree genera and edaphic factors ($r = 0.266$, $p = 0.035$). Fungal community composition was strongly correlated with aspect ($r = 0.743$, $p < 0.001$), relative abundance of tree genera ($r = 0.558$, $p < 0.001$), and edaphic factors ($r = 0.535$, $p < 0.001$). Partial mantel tests indicated that aspect had a strongly significant effect on community structure ($r = 0.637$, $p < 0.001$) when the abundance of tree genera was accounted for (control matrix), while the effect of tree genera was substantially weaker, though still significant ($r = 0.295$, $p = 0.018$) when aspect was controlled. Conversely, the correlations of aspect ($r = 0.793$, $p < 0.001$) and edaphic factors ($r = 0.639$, $p < 0.001$) with fungal community composition were both strong when edaphic factors or aspect were controlled for, respectively.

It is likely that environmental variables not yet measured contribute substantially to the environmental differences currently accounted for only under slope aspect. For example, I did not measure soil and air temperature, relative humidity, and soil moisture at the sites, partly because it is already well-known that these factors tend to correlate strongly with aspect on mesoclimate scale and partly because obtaining a realistic characterization of these variables would have required measurements taken throughout the growing season at the sampling sites, which was beyond the scope and logistic possibilities of this case study. Future studies should include site-specific microclimate data as well as a more extensive list of edaphic variables to obtain more insights into the variation of environmental factors at small spatial scales as well as their influence on fungal community composition and turnover.

In summary, a large proportion (33.27% to 51.64%) of variation in community composition in all fungal groups was explained by forest types, which were described formerly based on detailed coenological studies of woody plants, forbs, graminoids as well as non-vascular plants and are used as a framework for vegetation and phytogeographic studies (Vojtkó 2002, Borhidi 2003, Vojtkó et al. 2010, Bölöni et al. 2011). These coenological habitat types seem to capture well the consistent and largely predictable environmental differences and their delimitation and mapping are useful to better understand the distribution and community dynamics of fungi at landscape scales.

Habitat preference of ECM fungi in Pannonian forest types

Our study (Geml et al. 2022b), which was the first to characterize ECM fungal communities across a wide range of Pannonian forest types that span mesoclimatic and edaphic gradients, clearly showed that 1) the composition of ECM fungi differ among coenological forest types; 2) the diversity and distribution of ECM fungi on the landscape are driven primarily by edaphic factors, such as soil pH, Ca and C content and soil moisture, as well as by temperature; 3) there are important ecological differences among ECM fungi at fine taxonomic scales with regard to habitat preference, as suggested by the indicator species and the pronounced differences among genera as well as congeneric species with respect to their relationships with abiotic variables. These key findings highlight various components within the conceptual framework of community assembly, the non-stochastic component of which likely is driven, at least in part, by species-level differences in competitive abilities under certain environmental conditions and which manifests itself in environmental filtering and in habitat partitioning detectable as patterns of community composition.

It is reassuring to see that the forest types detailed above, formerly described based on detailed coenological studies of woody plants, forbs, graminoids as well as non-vascular plants (Vojtkó 2002, Borhidi 2003, Vojtkó et al. 2010, Bölöni et al. 2011), seem to capture well the consistent and largely predictable mesoclimatic and edaphic differences driven by topography and geology. It is noteworthy, that although ECM fungi are associated with the dominant trees that form the above forest types and are widely distributed throughout the landscape, the coenological associations are mostly differentiated based on understory non-ECM plants that seem to reflect better the edaphic and mesoclimatic conditions prevailing at the sites. Based on their above-mentioned connection with the ECM fungal community, the delimitation and mapping of Pannonian forest types provide useful tools to better understand the distribution of ECM fungi at landscape scales in this biogeographic region.

ECM fungi were represented by 3,759,052 DNA sequences that were grouped into 1463 ASVs belonging to 58 genera and 39 phylogenetic lineages, mostly belonging to Basidiomycota. Of these, the twenty most ASV-rich lineages were /inocybe (239 ASVs), /sebacina (232), /tomentella-thelephora (201), /cortinarius (194), /russula-lactarius (129), /paxillus-gyrodon (47), /clavulina (39), /tuber-helvella (37), /hebeloma-alnicola (33), /cenococcum (29), /hysterangium (28), /genea-humaria (23), /boletus (20), /elaphomyces (19), /pseudotomentella (18), /piloderma (17), /marcelleina-peziza (16), /sphaerosporella-wilcoxina (14), /hygrophorus (14), /hygrophorus (11), /amanita (9). There were substantial differences among the phylogenetic lineages with respect to patterns of ASV richness among the forest types. For example, /cortinarius was most diverse in the mesic sessile oak - hornbeam forests (*Carici pilosae-Carpinetum*) and least diverse in the limestone oak forests (*Seslerio-Quercetum*), while the /inocybe lineage was represented by the highest number of ASVs in the submontane beech forests (*Melittio-Fagetum*) and had the lowest number of ASVs in the acidophilous oak forests (*Luzulo-Quercetum*) (Figure 5.6). Somewhat similar trend was observed on the /paxillus-gyrodon lineage, where oak - hornbeam and submontane beech forests had significantly more ASVs than the acidophilous oak and the turkey oak - sessile oak (*Quercetum petraeae-cerris*) forests, with rest of the forest types showing intermediate ASV richness. Conversely, the /russula-lactarius lineage the most ASV-rich in the relatively warm

turkey oak - sessile oak forests and had the fewest ASVs in the cool submontane beech, montane beech (*Aconito-Fagetum*), limestone beech (*Seslerio-Fagetum*), and whitebeam-linden (*Tilio-Sorbetum*) forests. The /sebacina lineage was most diverse in beech-dominated forests, while the /tomentella-thelephora lineage was comparably diverse in all forest types, although showed the highest richness in the thermophilous downy oak (*Corno-Quercetum pubescentis*) forests (Figure 5.6).

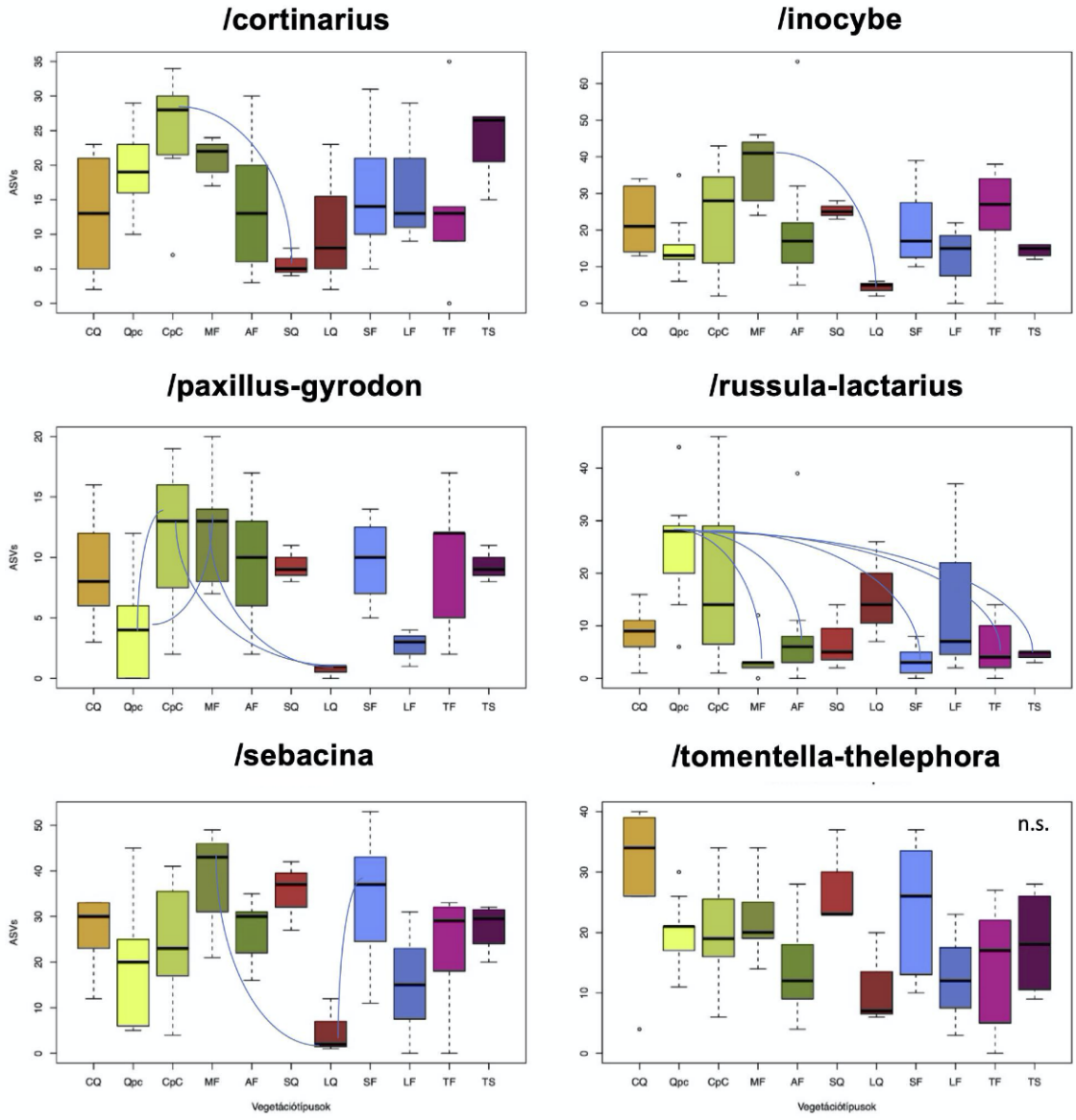


Figure 5.6. Comparison of ASV richness of the dominant ECM fungal lineages among the sampled forest types. Means were compared using ANOVA and Tukey's HSD tests, with arches denoting significant differences (Geml et al. 2022b). Abbreviations and information related to forest types are given in Table 5.1.

Regression analyses revealed different trends among ECM fungal genera with respect to relationships between ASV richness and various environmental variables. For example, richness of /cortinarius and /russula-lactarius was highest in mid-elevation, around 600 m a.s.l., while richness values of /tomentella-thelephora showed a strong monotonic decrease with increasing elevation (Figure 5.7).

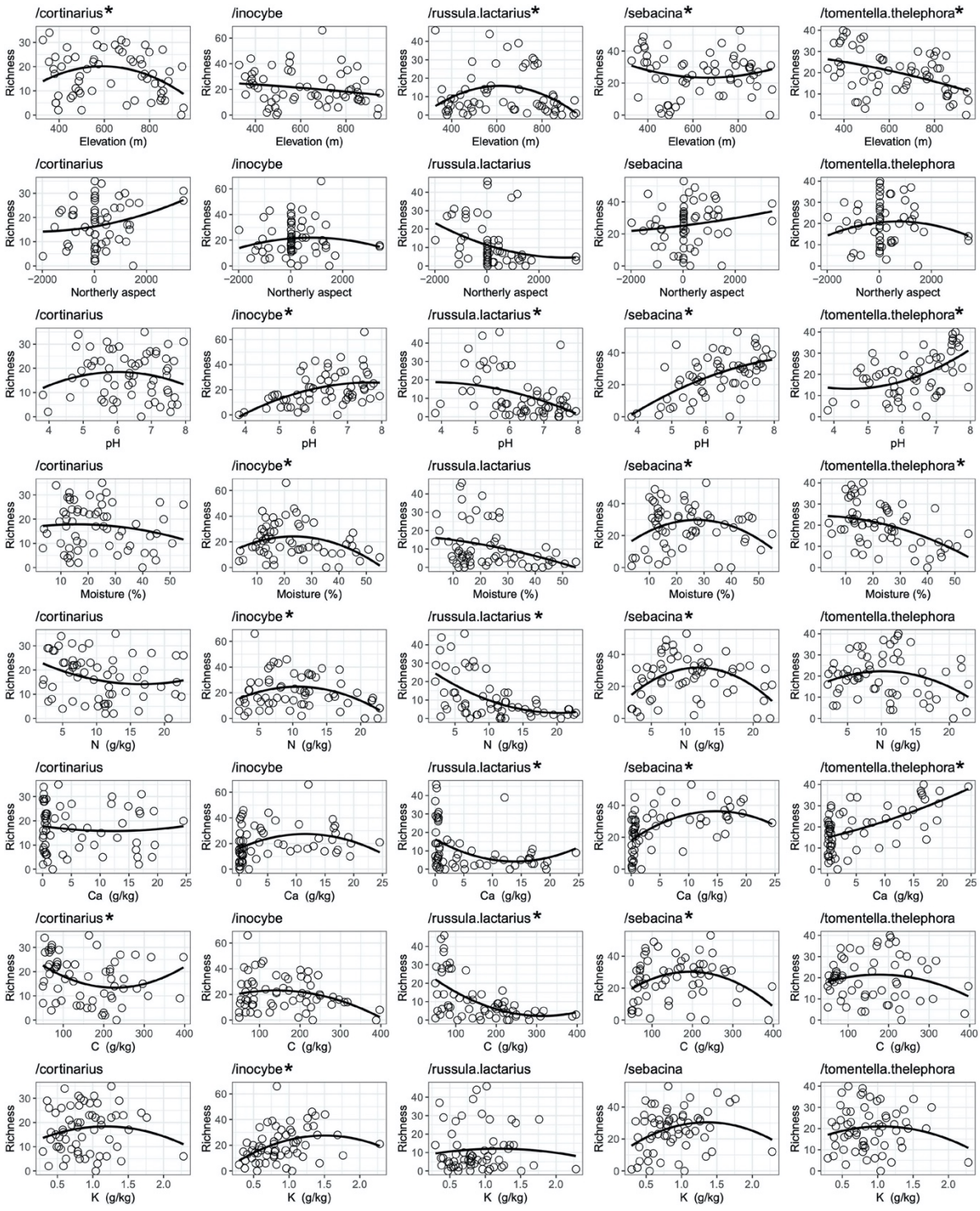


Figure 5.7. Correlations between ASV richness of the dominant ECM fungal lineages and selected topographic and edaphic variables at the sampled sites. Asterisks (*) indicate significant correlations (Geml et al. 2022b).

Northerly aspect did not show a significantly strong correlation with richness in the dominant fungal lineages, although we observed a weak positive relationship in /cortinarius and /sebacina and a weak negative relationship in the case of /russula-lactarius with northerly aspect. Soil pH showed strong positive correlation with richness in /inocybe, /sebacina, and /tomentella-thelephora, while negative correlation was observed with /russula-lactarius. The

/inocybe and /sebacina lineages had the highest richness values at medium soil moisture levels, while /tomentella-thelephora correlated negatively with soil moisture. We observed negative correlation between richness in /russula-lactarius and soil N and C content, with /inocybe and /sebacina showing richness peaks at intermediate values. With respect to K content, only /inocybe showed a significant relationship, which was positive (Figure 5.7). Although not among the dominant lineages overall, the two most ASV-richness ascomycete lineages both correlated negatively with soil moisture: /cenococcum (r^2 = 0.275, p < 0.0001) and /tuber-helvella (r^2 = 0.1374, p < 0.0089) and with elevation: /cenococcum (r^2 = 0.241, p = 0.0003) and /tuber-helvella (r^2 = 0.0741, p = 0.0481).

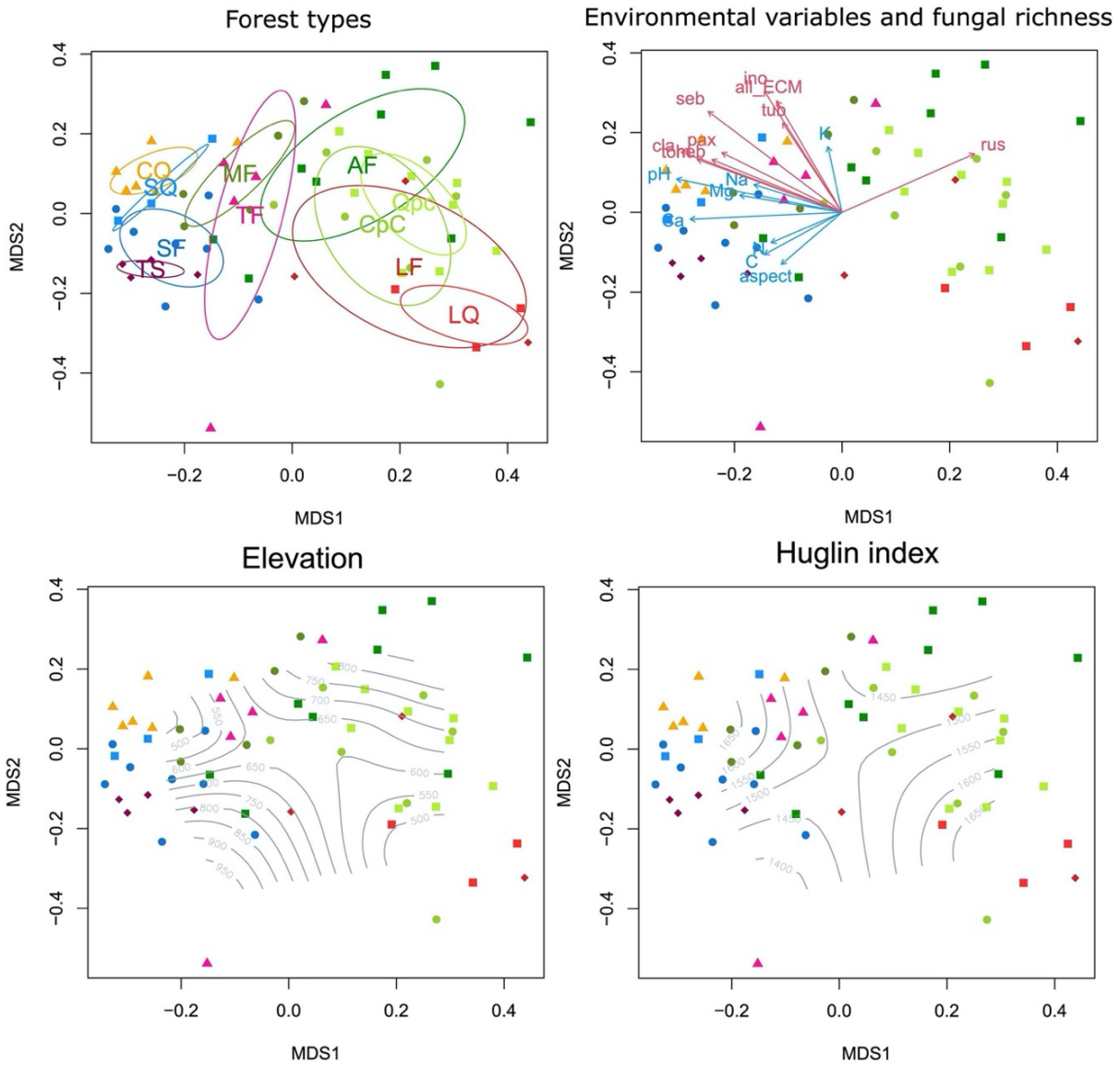


Figure 5.8. Non-metric multidimensional scaling (NMDS) ordination plot (final stress: 0.15734) of the total ECM fungal community in the sampled forest types based on Hellinger-transformed data. Ellipses indicating standard deviation of compositional differences of forest types, vectors of environmental variables and richness values of ECM fungal lineages showing significant correlations with ordination axes, and isolines of elevation and Huglin index are displayed in four identical ordination plots (Geml et al. 2022b). Abbreviations and information related to forest types are given in Table 5.1.

Community composition of ECM fungal communities was strongly structured among Pannonian forests, mostly driven by soil pH and other edaphic factors (Figure 5.8). Soil pH (r_{NMDS1} = -0.9602, p < 0.0001), C content (r_{NMDS1} = -0.8181, p < 0.0001) and concentrations of cations, such as Ca (r_{NMDS1} = -0.9989, p < 0.0001), Mg (r_{NMDS1} = -0.9709, p < 0.0001), and Na (r_{NMDS1} = -0.9155, p < 0.0001) correlated strongly with the first axis. PERMANOVA analyses confirmed that ECM fungal community composition was strongly structured by coenological forest type, explaining 28.06% of compositional differences among all samples (Table 6.2). With respect to edaphic variables, pH, soil moisture and Ca, C, K, and P content contributed significantly to the combined model after accounting for correlations among variables. Of these, pH explained more than 9% and Ca explained 3.42% of the compositional variance, with the rest explaining less than 3%. Of the mesoclimatic and topographic variables, the Huglin index and northerly slope aspect remained significant, explaining 2.14% of variance (Table 5.2).

Table 5.2. Proportions (%) of compositional variance explained by categorical variable forest type and by continuous environmental variables in individual models based PERMANOVA. The effect of forest type on community composition was strongly significant in all fungal groups. After accounting for correlations among continuous variables, those providing significant contribution to the combined model are in bold (Geml et al. 2022b).

Variables	All ECM fungi	/cortinarius	/inocybe	/russula-lactarius	/sebacina	/tomentella-thelephora
Categorical variable						
Forest type	28.059	27.803	24.721	28.275	25.488	29.102
Continuous variables						
pH	**9.004**	**8.352**	**6.754**	**6.980**	**5.963**	**10.440**
C	**4.674**	**4.422**	**4.060**	**5.932**	**4.279**	**3.933**
N	4.083	4.218	3.450	5.341	3.315	3.353
CN	1.919	2.282	1.348	1.051	1.745	2.512
Na	4.071	4.605	3.358	**4.783**	2.491	3.788
K	**2.950**	3.065	**4.319**	**2.931**	**2.623**	**3.115**
Ca	**8.380**	**7.773**	**6.329**	**8.202**	**7.528**	**9.356**
Mg	4.865	4.441	4.016	6.188	3.484	5.620
P	**2.486**	2.441	2.167	2.266	2.943	2.722
Huglin index	**3.875**	2.600	2.445	2.844	**3.175**	**2.769**
Soil moisture	**3.655**	**3.385**	**2.114**	**4.578**	**2.503**	**3.199**
Elevation	3.444	2.797	2.637	3.317	3.899	3.555
Northerly aspect	**3.438**	3.639	3.019	**4.349**	2.768	**2.617**

The role of soil pH in shaping fungal communities has been widely documented at various spatial scales (Coughlan et al. 2000, Lauber et al. 2008, Rousk et al. 2010, Geml et al. 2014ab, Tedersoo et al. 2014, Kutszegi et al. 2015, Glassman et al. 2017, Rosinger et al. 2018, Geml 2019, Větrovský et al. 2019). Beside the geological parent material, soil pH is often influenced by mesoclimatic factors, such as temperature and soil moisture, with soils exposed to lower temperatures and higher moisture generally having lower pH than warmer and dried soils on the same landscape (Geml et al. 2014b, Gilliam et al. 2014, Chu et al. 2016). Such

mesoclimatic differences affecting soil characteristics could be due to differences elevation or to slope aspect, both of which influence surface temperature, soil moisture, relative humidity, and soil chemical processes (McCune and Keon 2002, Fekedulegn et al. 2003, Dobos 2010, Gilliam et al. 2014, Méndez-Toribio et al. 2016). Elevation is also known to influence fungal community composition (Coince et al. 2014, Geml et al. 2014b, Javis et al. 2015, Geml et al. 2017, Wicaksono et al. 2017, Geml et al. 2022a), although in this study, the effect of elevation was not significant in the combined model, likely because of the tight relationship with temperature (Huglin index), which had somewhat higher correlation with community composition when environmental variables were analyzed separately.

The influential roles of soil moisture and Ca in shaping fungal communities, other than their influence on pH, observed in our study are in agreement with what has been found in the global soil fungal community study of Tedersoo et al. (2014). Calcium plays crucial roles in numerous physiological processes related to growth and stress responses (McLaughlin and Wimmer 1999) and shapes plant and animal communities (Beier et al. 2012). Because of its low mobility, the availability of Ca often poses limitations on forest structure and function, particularly in dry and acidic soils. The roles of Ca, that are particularly relevant to ECM fungi, include effects on the structure and function of plant cell membranes that influence nutrient uptake by roots and fluxes through leaf membranes, the transport of carbohydrates from leaves to other plant parts, such as roots that directly interact with mycorrhizal fungi, litter decompositon rates, and the formation of humus and soil aggregates (McLaughlin and Wimmer 1999).

Similarly, C and N contents are among the most important edaphic variables globally that influence richness and community composition in fungi (Crowther et al. 2014, Tedersoo et al. 2014). Although both C and N content correlated significantly with richness values in three out of five ECM fungal lineages, the strong contribution of C content to explain community composition in all dominant lineages and the lack of significance of N content in the combined model seems unexpected. Because N content correlated significantly with fungal community composition in all lineages when analyzed separately, it is likely that its lack of unique contribution to the combined model is because of a strong correlation between N and C contents ($r^2 = 0.8398$, $p < 0.0001$).

When the dominant ECM fungal lineages were analyzed separately, forest types always had a significant correlation with community structure, explaining between 24.72% and 29.1% of the variance. After accounting for correlations among environmental variables, soil pH, Ca and C content, and soil moisture contributed to the combined model, explaining significant proportions of the community composition in all tested lineages and K content in all except /cortinarius. Northerly aspect remained significant to explain part of the compositional variance in /russula-lactarius, /tomentella-thelephora, and in the total ECM fungal community, while the contributions of the Huglin index and soil P content were only significant in the combined model in total ECM community (Table 6.2).

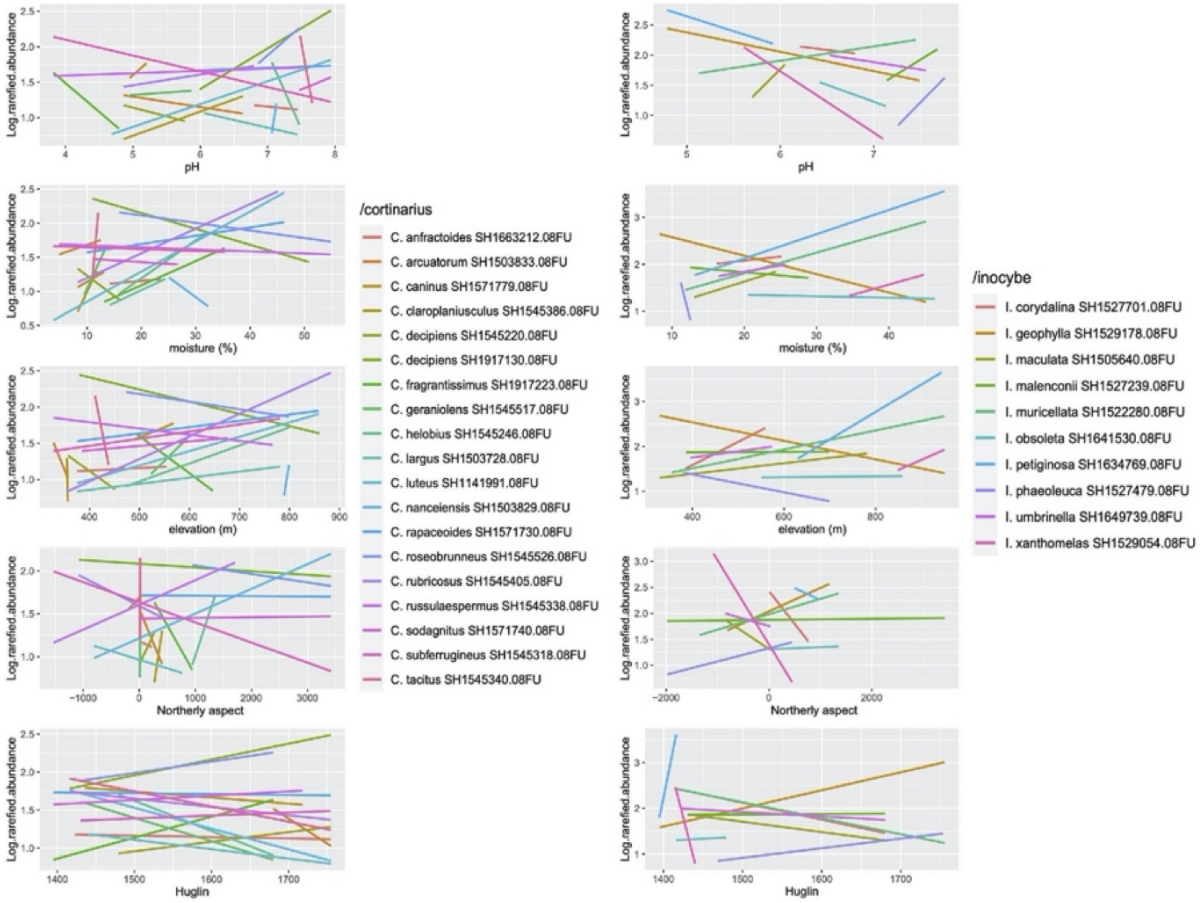


Figure 5.9. Correlations between selected environmental variables and log-transformed rarefied read abundance of indicator species of various forest types in two dominant ECM fungal lineages. The slopes and the positioning of the regression lines along the x axis suggest species-level ecological differences among congeneric species (Geml et al. 2022b).

One hundred thirty-seven ECM fungal ASVs were significant ($p < 0.05$) indicators of a certain coenological forest type. Of these, thermophilous downy oak forests and oak - hornbeam forests had the highest number of indicators (18 ASVs each), followed by submontane beech and whitebeam - linden forests (16 each), turkey oak - sessile oak and limestone oak forests (15 each), and acidophilous oak forests (11), the rest having less than 10 indicators (Geml et al. 2022b). In most ECM fungal genera, ASVs assigned to different SHs tended to be indicators for distinct forest types, particularly when the sequence similarities were high (above 99%). As expected from the indicator species analysis, we found strong species-level differences within all the selected phylogenetic lineages with respect to their correlations with the tested environmental variables. These differences were partly directional (positive or negative correlation) and partly were differences in range breadth and overlap with respect to the given variable (Figure 5.9). For example, some indicator species occurred along a wide range of pH, moisture or elevation, while others seemed more restricted. In the latter group, we found indicators that seemed restricted to acidic vs. non-acidic or alkaline pH, dry vs. mesic soil or low vs. high elevation. Interestingly, some indicator species had relatively wide occupied range for some variables and a narrow range for others (e.g., *Inocybe obsoleta*, *Russula globispora*) (Figure 5.9).

Contribution to the knowledge on Pannonian forest fungi

Beside the ecological information obtained, these two studies also provide the first overview of taxonomic diversity and identity of soil-inhabiting fungi in the dominant Pannonian forest types. The full list of fungi detected in the corresponding samples, with taxonomic classification (available in the supporting material of both Geml 2019 and Geml et al. 2022b) aims to facilitate future mycological and fungal ecological studies in the region.

Our studies show a remarkably high fungal diversity in both sampled regions in northern Hungary. In a small area (< 2 km^2) of secondary deciduous forests in the eastern edge of the Mátra mountains, Geml (2019) found representatives of 707 fungal genera, of which 467 belonged to Ascomycota, 225 to Basidiomycota, 6 to Chytridiomycota, and 7 represented early-diverging lineages formerly classified in Zygomycota. Approximately half of all fungal sequences were assigned to functional groups, particularly in taxa with macroscopic fruiting bodies for which extensive reference data are available from Europe (e.g., agarics, boletes, coral fungi, polypores, and several true and false truffles). With respect to the identified microfungi, the results presented here may be the first data on their diversity and possible habitat preference in the Pannonian biogeographic region, serving as potential reference data for future studies as well. Nonetheless, the true generic diversity likely is even higher because most fungi in the sampled sites, as well as globally, are microfungi and many of them could only be assigned to families, orders or classes due to the lack of sufficiently identified reference sequence data. Consequently, these represent species with unknown identity, several of which may still be undescribed.

Even in ECM fungi, that represent one of the most studied fungal functional group, there likely are more species that occur in these forests, some of them likely is still unddescribed. Geml et al. (2022b) found 1463 ASVs representing 58 ECM fungal genera, which indicates high diversity, although the true diversity of ECM fungi in the region certainly is considerably higher, because many species known to occur in the sampling region based on sporocarp studies was not found in the soil samples. This is not surprising given the well-known spatial patchiness of fungal genets in soil and the random nature of soil sampling, which is particularly true for diverse lineages that are well represented in sporocarp-based studies, e.g., /amanita and /russula-lactarius, but are relatively underrepresented in soil DNA due to their low mycelial biomass in soil compared to other ECM genera (Geml et al. 2012b).

On the other hand, the data also showed a high diversity of ECM basidiomycetes with inconspicuous fruiting bodies, such *Sebacina* and *Tomentella*, that represent two of the dominant fungal lineages and that generally are underrepresented in sporocarp surveys worldwide (Gardes and Bruns 1996, Kõljalg et al. 2000, Geml et al. 2012). Furthermore, we detected numerous hypogeous ECM fungi, such as *Elaphomyces muricatus* and *E. papillatus*, *Gautieria graveolens*, *Genea arenaria*, *G. dentata*, and *Genea verrucosa*, *Hydnotrya* sp., *Hymenogaster australis*, *H. citrinus*, *H. griseus*, *H. huthii*, *H. luteus,* and *H. rehsteineri*, *Hysterangium calcareum*, *Hy. nephriticum*, *Hy. pompholyx*, and *Hy. stoloniferum*, *Melanogaster ambiguus*, *M. broomeanus*, *M. spurius*, and *M. variegatus*, *Scleroderma areolatum*, and *Wakefieldia macrospora*, as well as several species of truffles, such as *T. aestivum*, *T. borchii*, *T. brumale*, *T. excavatum*, *T. maculatum*, *T. puberulum*, *T. rapaeodorum*, *T. rufum*, and possibly *T. fulgens*. Most of these are known to occur in Hungary, except for

Gautieria graveolens, as this genus is only represented by an unidentified species in the list of hypogeous fungi for the Carpathian-Pannonian region compiled by Bratek et al. (2013). Representatives of these hypogeous fungi were found in all forest types, indicating that they probably are relatively common in Pannonian forests. Although our data provides unprecedented insight into these inconspicuous ECM fungal groups, many more samples will be needed to capture their true diversity in the region.

In addition, soil DNA studies, such as this, can provide valuable spatial data for mapping the distribution of rare, protected ECM fungi and provide valuable information on their habitat preference. For example, we found the protected *Strobilomyces strobilaceus* in soil from a sessile oak - hornbeam forest and from an acidophilous oak forest, which agrees in terms of habitat preference with sporocarp records of this species from mesic acidic forests in Hungary (Siller et al. 2006). Other examples of fungi considered rare in Hungary based on sporocarp records include *Coltricia cinnamomea*, *Cortinarius alcalinophilus*, *C. bulliardii*, *Pachyphlodes melanoxantha*, and *Russula maculata*.

The spatial data presented in this paper complement sporocarp-based assessments and highlights the potential of DNA-based characterization of fungal communities in biological monitoring and conservation of fungi. In addition, the ecological data on the abiotic factors influencing the diversity and distribution of various ECM fungi on the landscape provide a baseline data for climate change studies as well as inform us about possible responses of ECM fungal communities to climate change. This is particularly relevant for the sustainable management of our natural resources, as ECM fungi are vital symbionts of the dominant trees in Pannonian forests and contribute to tree health by providing water and nutrients and mitigating abiotic stresses. The habitat specificity and rapid reaction of soil fungi to changes in environmental factors provides us with the possibility of detecting trends in forest dynamics early and take action accordingly to maintain diverse and resilient forest ecosystems with diverse ecosystem functions.

6. Conclusions and future directions

In this dissertation, I discussed factors that shape the diversity and distribution of fungi at various spatial scales. I started with fungal phylogeographic studies to illustrate processes that influence the present distribution of fungi at different latitudes. Understanding these processes and their consequences are important because they directly determine the regional species pool, from which local communities assemble through niche-driven and stochastic processes. Dispersal capabilities, distribution of symbionts and interactions with other microorganisms are among the most important factors that limit the extent to which a species can occupy its fundamental niche, i.e. where environmental conditions are suitable.

Where dispersal is effective, the realized niche of a species can make up a high percentage of its fundamental niche. Indeed, tundra vegetation throughout the Arctic has very similar plant and fungal communities, where small-scale differences driven by meso- or microtopographic and edaphic factors often are more pronounced than any intercontinental differences (Walker et al. 2005, József Geml, pers. obs.).

Based on my phylogeographic research in the 2000s, I led publications that featured results that were novel at that time. For example, we were the first to show that circumpolar phylogeographic patterns arctic fungi differ from those of boreal fungi, because of their different capabilities to disperse over log distances. Overall, the emerging picture of accummulating body of fungal phylogeographic research is that the distribution patterns of fungi are similar to those observed in plants, i.e. they tend to mirror biogeographic regions and most are limited by the same dispersal barriers, e.g. oceans, large deserts and high mountain ranges. The similarities between plant and fungal biogeography is apparent even in the Arctic, where intercontinental dispersal has been frequent enough, in both plants and fungi, to prevent genetic differentiation among continents and to allow for relatively rapid colonization of newly deglaciated land during interglacials (Alsos et al. 2007, Geml et al. 2012ab). The special case of the Arctic can partly be explained by the relative proximity of the continental landmasses, the strong winds, open landscapes, and the presence of sea ice for much of the year that is expected to facilitate the dispersal of spores and seeds as opposed to open water, and that arctic species have likely been selected for effective dispersal during the repeated cycles in glacial and interglacial periods in the last 2 million years. Some arctic plants, e.g., *Empetrum nigrum* (Popp et al. 2011), and fungi, e.g., *Flavocetraria nivalis* and *Lichenomphalia umbellifera* (Geml et al. 2010a, Geml et al. 2012a) are so effective at long-distance dispersal that they became established in the Southern Hemisphere, likely via migratory birds, resulting in their bipolar distribution. In general, the capacity to migrate is of particular importance, because climate warming is causing a northward shift in the distribution of many arctic and boreal species, and the dispersal capabilities of individual species will greatly influence the composition of future communities, particularly in newly colonized areas (Alsos et al. 2007).

On global scales, however, successful long-distance dispersal events and establishment are considered relatively rare for fungi in nature (Brown and Hovmøller 2002) and a number of molecular phylogenetic studies have demonstrated inter-continental genetic breaks in fungal morphospecies. As we proceed towards the Equator, intercontinental differences increase in the species pool for plants and fungi alike. Overall, the accumulating data in our and other

papers suggest that most phylogenetic lineages within of boreal-temperate fungal species complexes are allopatric, inhabiting different biogeographic regions or continents. For example, in boreal and temperate forests, we often see species pairs corresponding to continents, sometimes with additional geographical endemism observed in various biogeographic regions within continents (e.g., Shen et al. 2002, Geml et al. 2006, Taylor et al. 2006, Geml et al. 2008b, Geml et al. 2009, Geml et al. 2010a, Geml 2011). Because in most studied fungi such allopatric phylogenetic clades inhabit similar environments in different continents, this implies a phylogenetic structure that has arisen from the lack of gene flow. Thus, these fungi likely occupy only a fraction of their fundamental niche due to dispersal limitation. Exceptions to this general trend predominantly come from fungi associated with humans, which are therefore more likely to be dispersed via shipment of goods: e.g., plant pathogens of agricultural crops (Couch et al. 2005), indoor fungi (Kauserud et al. 2006), and fungi that are almost exclusively clonal and produce very high quantities of airborne mitospores (Rydholm et al. 2006). The occasional, mostly anthropogenic release from dispersal limitation also explains the successful establishment of several fungi following their introduction to suitable habitats on continents where they naturally did not occur. Several such fungi have become invasive in their newly colonized areas, e.g., *Amanita muscaria* in the temperate regions of the Southern Hemisphere and *Amanita phalloides* in the western United States (Wolfe et al. 2010, Dunk et al. 2012, Vargas et al. 2019).

Geographic endemism reaches its peak in the Tropics resulting in the most pronounced inter- and intracontinental biogeographic differences in plant, fungal, and animal communities (Merckx et al. 2015, Geml et al. 2022a), of which fungi are still the least known. While many plants and animals show high degree of endemism in the Tropics, often with distribution restricted to a single mountain or valley (Ackerman et al. 2007, Kessler and Kluge 2008, Merckx et al. 2015), such detailed information currently is unavailable for fungi in general and those in the Tropics in particular. Although spatial information on the distribution of fungal species is accummulating globally with the increasing number of DNA-based environmental studies, most of these still are focused on temperate regions, where research funding is concentrated, and, despite recent progress particularly in South America (Roy et al. 2017), mycological and fungal ecological studies in tropical regions are still laggig behind and likely harbor most undescribed and endemic species.

On the processes that drive fungal community composition at various spatial scales

On the global scale, soil fungal communities, as well as other biological assemblages, are shaped by many environmental factors, among which temperature, precipitation and soil pH tend to be the most important for the diversity and distribution of fungi (Tedersoo et al. 2014, Větrovský et al. 2019). Our studies, including but not restricted to those summarized in this dissertation, as well as the accumulating body of knowledge generated by our peers, show that practically the same climatic and edaphic factors, particularly temperature, soil pH, and soil moisture, appear to be the main drivers shaping the diversity and distribution of soil fungi at regional and landcape scales as well. For example, my ecological analyses of DNA sequences of yeast fungi from globally collected soil samples published in Boekhout et al. (2021) showed that even free-living yeast fungal communities, represented by 1242 species in

197 genera in our study, show significant compositional differences among biomes, driven mainly by the above-mentioned abiotic factors.

The same environmental variables also influence the distribution of plants at various spatial scales, mirrored in biome classification and in coenologically described vegetation types, which correspond to habitats for the purpose of our studies. Disentangling causal relationships among soil parameters, vegetation and fungal community composition in these natural ecosystems is beyond the scope of this dissertation and would require experimental approaches with controlled variables. The establishment of fungi along landscape-scale environmental gradients likely is driven by their physiological limits, life strategies (competitive, stress tolerant or ruderal), and functional attributes. Because most fungi can disperse effectively at landscape scales, the richness and composition of the established species pool at any location is primarily the result of environmental filters, such as edaphic and (meso)climatic conditions (Fierer et al. 2012, Geml et al. 2014ab, Tedersoo et al. 2014, Cox et al. 2016, Goldmann et al. 2016, Geml et al. 2017, Geml 2019, Geml et al. 2022ab).

Even though the functional properties of individual fungal species are poorly understood (Anderson and Cairney 2007), the high species richness of fungi in many ecosystems suggests a high level of functional heterogeneity even at local scale (Allen et al. 2003). The high physical and chemical complexity of soils provides a high number of micro-niches at various spatial scales, which likely explain the enormous fungal diversity in even a gram of soil. In addition, interactions among soil and macro-, meso-, and microclimatic factors, driven in part by topography, and, in some cases, the biogeographic distribution of symbionts together influence vegetation, microbial processes (e.g., decomposition), and the availability of water and nutrients that drive the spatial turnover of fungal communities at various spatial scales. The resulting environment (or often microenvironment) is spatially and temporally dynamic and the given states of variables are more favorable to certain taxa with a given set of functionalities than others, thereby altering species interaction dynamics, which results in a subset of the local species pool. The observed correlations of the richness and composition with edaphic factors suggest that some effects on the fungal community could be direct, e.g., physiologically constraining, while most effects may be indirect, e.g., via nutrient availability and nutrient acquisition capabilities. Despite the relatively high proportions of compositional variance explained by the tested environmental variables, the proportion of residual variance not explained by the above variables still exceeded 60%, indicating that both niche (environmental filtering) and neutral (stochastic) processes influence ECM fungal communities at landscape level.

A large part of the complex influences of the environment on fungi is via niche-based deterministic processes, where species occupy niches as a result of environmental filtering and competitive interactions. Although the exact mechanisms are yet to be elucidated, it is likely that the chemical differences among the sampling sites influence the competitive dynamics of fungi and, thus, they represent environmental filters regarding establishment and persistence in the community (Lennon et al. 2012). Although the role of competition among fungi in community composition likely is important, it is difficult to study directly. In studies focusing on natural habitats in a rather descriptive manner, as in this dissertation, competitive dynamics are difficult to parse from strictly physiological preferences and limits of the respective fungi, because even within the physiological boundaries of certain species, environmental factors

undoubtedly influence competitive abilities and, thus, interaction dynamics. As a result, competitively inferior fungi likely are forced to survive in unfavorable (e.g., dry and/or nutrient-poor) habitats that they can tolerate, but their stronger competitors cannot. Functional groups that compete for nutrients and water, such as ECM vs. soil saprotrophic fungi, often show negative correlations in richness and/or abundance in most of our studies detailed above. The opposite trends of ECM and saprotrophic fungi observed are particularly noteworthy, because they constitute the two most species-rich and abundant functional groups in most terrestrial ecosystems (with lowland neotropical forests being a notable exception). Plants and their ECM fungal symbionts are known to outcompete saprotrophic fungi and other microbial decomposers by decreasing the availability of N in the soil (Leake 2002). Saprotrophs generally are most diverse and abundant in warm and wet conditions, as shown by our elevation gradient studies in the Neotropics, where ECM fungi are much less diverse, less abundant, and mostly are restricted to montane forests due to the distribution of their hosts. Conversely, in the Paleotropics and particularly in northern temperature and arctic regions, where ECM fungi reach the peak of their diversity and abundance because of the abundance of hosts, saprotrophic fungi often appear to be outcompeted from more favorable habitats at landscape level and are more diverse in habitats with greater environmental stress, such as those with pronounced fluctuations in temperature and available water. This hypothesis is supported by the observed increase in saprotroph richness and abundance along both latitudinal and mesotopographic gradients in the Arctic (Timling et al. 2014, Geml et al. 2016, Grau et al. 2017, Geml et al. 2021) and in xerotherm temperate forests (Geml 2019). The decrease in decomposers, due to competitive exclusion by mycorrhizal fungi, is expected to slow soil C respiration and increase soil C storage (Orwin et al. 2011, Averill and Hawkes 2016). Moreover, ECM fungi store large amounts of C in their hyphae (Clemmensen et al. 2013), which may also contribute to the high accumulation of C in habitats where ECM fungi are prevalent. The higher levels of soil organic C observed in habitats dominated by ECM fungi, such as tropical montane forests (Geml et al. 2014b, Geml et al. 2017, Geml et al. 2022a), mesic temperate forests (Geml 2019, Geml et al. 2022b), and shrub-dominated arctic tundra communities (Timling et al. 2014, Grau et al. 2017, Geml et al. 2021), support the above line of reasoning.

Our studies also highlight the taxonomic and functional differences among fungi assigned to the same broad functional category. Because of the paucity of functional knowledge of fungal species, the current state-of-the-art methods rely on genus-level identification to assign fungi to functional categories, as in the studies summarized in this dissertation. It is obvious that this situation is far from ideal and that there must be important differences both in habitat specificity and in functionality among fungi grouped in the same broad functional guild. Some of these differences are highlighted in our papers above, e.g., the contrasting habitat preference among several genera across different functional categories. In addition, we often find that even within the same genus, pronounced differences exist among species with respect to habitat, as shown by the indicator species analyses, likely driven by niche-based processes and competition. In addition, there often is a partitioning of congeneric species in different soil horizons, i.e. some species only occurring in organic and others only in mineral horizons, as has been shown for ECM fungi in Alaska (Taylor et al. 2010).

An ever-present feature of fungal community studies is the large amount of unexplained variation in richness and community composition even at small spatial scales (Geml et al. 2014ab, Peay et al. 2016, Geml et al. 2016, Geml 2019). Although in general the most significant compositional differences are observed among different habitats at landscape scale, there always is substantial compositional differences among replicate samples taken in the same habitat in short distances from each other. The environmental variables measured in our studies generally explain less than half of the variation in fungal community composition, leaving a relatively large unexplained component of community assembly. Other factors not examined in our studies, such as density-dependent processes (e.g., intra- and interspecific competitions and pathogen-host interactions) as well potentially important environmental variables not yet measured, may also contribute to the unexplained component of beta diversity.

In addition to these niche-based, deterministic processes discussed above, there is a stochastic (neutral) component of fungal community assembly. As often observed in diverse biological communities, few species are common and most species are locally rare, which is a well-known species abundance distribution pattern in ecology regarding highly diverse communities (McGill et al. 2007). Because a truly exhaustive soil sampling is practically impossible to achieve in the field, some rare fungal species are inevitably missed at any given plot due to random sampling. This inability to obtain an exhaustive list for all rare species present at the sampling plot is a methodological limitation. In addition, locally rare species likely are not actually established in all sampled plots, because of random processes in community assembly, such as order of arrival, i.e. the priority effect. Within a given species pool of a particular habitat, stochastic dispersal determines the order in which newly available (micro)habitats are colonized and resources are utilized by different species, which, in turn, drives to a large extent the composition of the community (Peay et al. 2016).

Disturbance events of various nature and scale are expected to play a role in this process by altering environmental conditions, creating patches of newly available habitats and thus creating opportunities for new colonists to get established. Disturbance can be a relatively rare event (e.g., deforestation) or can be chronic (e.g., climate change) and vary in severity. Disturbance events of intermediate frequency or intensity, where the biological potential of the habitat is not severely altered, often result in fungal communities in these regenerating communities that differ from pre-disturbance communities in composition, but not necessarily in richness. In addition to the altered environmental conditions, the stochastic component of fungal community assembly is greater in early stages of secondary succession for the above-mentioned reasons. In other words, sites categorized into the same disturbed habitat type, e.g., early successional secondary forest, regularly exhibit higher site-to-site variation in community composition than old-growth secondary and primary forests. For example, in our study on the successional dynamics of fungi in tropical rainforests (Adamo et al. 2021), we found that fungal diversity and compositional turnover were greater among replicate plots in early- and mid-succesional regenarating secondary forests than in undisturbed primary forests. In addition, fungal diversity was highest in mid-successional secondary tropical forests. This highlights the role of intermediate disturbance in habitat diversity and in interspecific interactions. Low to moderate levels of disturbance slightly decreases the dominance of competitive strategists adapted to the limiting resources in old-growth forests and aids the local establishment of ruderal strategists that normally dominate in early successional stages. In theory, mid-

successional forests are expected to have representatives of both early- and late-successional species and, therefore, higher richness. While fungal diversity measures supported this theory, tree communities in our study were more diverse in primary forests (Adamo et al. 2021). In addition, and even for fungi, primary forests had by far the highest number of indicator species, i.e. old-growth forest specialists, highlighting the vital role of undisturbed forests in preserving biodiversity. Admittedly, all above conclusions are based on the observed landscape-scale distribution patterns in the field and experimental studies directly testing the effect of competitive interactions on the relative fitness of individual fungal species under different environmental conditions are needed for more conclusive evidence.

Current limitations and new directions of research

Conceptually, most of fungal ecological research activities have focused on rather simple questions, the sorts of which had already been answered for plants a hundred years ago: how many species are in an area and what species are these? Because fungi are predominantly microscopic organisms with mostly ephemeral sexual reproductive structures and with vegetative parts that have very few informative morphological traits, fungal ecologists and taxonomists had to wait for the arrival molecular tools to obtain a classification that reflects evolutionary relationships and to be able to identify fungi reliably from various types of samples. In addition to the above methodological time lag of fungal research, compared to botany and vegetation science, the taxonomic diversity of fungi likely is about a magnitude greater than that of plants, and, according to various estimates, probably less then 10% of all existing fungal species have been decribed. Even for those fungi that have scientific names, we know very little about their distribution, ecological characteristics, and functional traits.

In this dissertation, I summarized my work on the large-scale and small-scale distribution and ecology of fungi: i.e. phylogeography and landscape-level habitat preference to provide novel answers to questions related to how species composition of fungal communities are shaped by the environment and by dispersal. The fact that a high proportion of fungi are still undescribed poses an obvious limitation on the DNA-based identification of fungi. Despite the fast growth of identified fungal sequences in reference databases, currently only a little more than half of all fungal sequence types can be identified to genus in any given European or North American soil sample, these regions being the most intensively studies by far, while the proportion of fungi that can be identified is substantially smaller in other continents. In addition, fungal taxonomy is lagging behind in formally naming and classifying species detected only by environmental sequencing studies. The semi-automated system of the UNITE reference database (Abarenkov et al. 2010, Kõljalg et al. 2013, Abarenkov et al. 2024) offers a workable solution with the use of the phylogeny-based and periodically updated Species Hypotheses that can be cross-referenced among studies. The limitation of this system, despite being by far the most useful reference database in the last decades, is that these entities are based on a single locus, while ideally sequences from multiple unlinked loci are necessary for phylogenetic species delimitation (Taylor et al. 2000). To my knowledge, parallel sequencing of multiple unlinked loci of the same individual from an environmental sample containing hundreds of fungal species is not possible with current methods in way that the

sequences can realiably traced back to the individual. Although recent developments in long-read sequencing do permit the sequencing of DNA regions several thousands base pairs long that can span several genes, these are linked loci and are, therefore, unsuitable for phylogenetic species delimitation. Further technological advancements are needed before we can use phylogenetic species as biological units in eDNA work.

Acquiring knowledge on the functional traits of fungi remains elusive. For eDNA-based fungal community ecological studies, the state-of-the-art methods to assign function to species are based on taxonomic identification to at least genus level and can only be used at broad functional categories, such as ectomycorrhizal or plant pathogen etc. Admittedly, this method is crude and offers only general information, where finer, but potentially important, ecological differences among species are ignored. While in plants a long series of studies focusing on morphology-based functional traits of individual species have been used to infer ecological characteristics and survival strategies, such method seems unfeasible in fungi not only because of the high number of species, but because most fungi cannot be maintained in culture given our current knowledge or because they are obligate symbiotrophs. Metagenomics and metatranscriptomics offer promising alternatives for studying the functions of microorganisms, although with some remaining limitations. Metagenomics is used to characterize the set of genes present in the entire biological community in the sample including all living organisms. Because it is based on DNA, metagenomics offers an overview of potential functionality based on the set of genes present in the community, which theoretically is stable if species composition is unaltered. It is important to note that potential functionality is based on the presence and copy number of genes and does not take into account wich genes and organisms are active. In order to obtain information on expression levels of genes belonging to the members of the community, one must use RNA: mRNA for functional genes and rRNA for ribosomal genes. By using rRNA, one can characterize the metabolically active fraction of the community, while mRNA will give information on the functional genes that are actively expressed and the type of biochemical pathways they may be associated with. Because RNA is labile in nature and mostly degrade within minutes, the transcriptome profile of a sample reflects the functional genes that are expressed at the moment of sampling. Therefore, this approach can be very useful to identify genes that are expressed differently under various environmental conditions. Naturally, the functional annotation and taxonomic identification of the sequenced genes are based on reference databases and are, thus, limited to genes and organisms that are known and to their close relatives. Because genomic databases contain sequence data from a relatively small number of fungal species, combining DNA metabarcoding and metatranscriptomics may offer the best approach to studying fungal communities and their metabolically active functional genes. For example, in a recent paper of ours, we characterized the expressed functional genes of fungi in noble rot grape berries that are the raw material for the *aszú* wines and were able to identify genes and associated metabolic pathways that likely play roles in interspecific, mostly antagonistic interactions among fungal species present in grape berries (Otto et al. 2023). Such metatranscriptomic methods are promising for characterizing metabolic activities and functions in soil fungal communities, although with extra steps to deplete prokaryotic genes that generally dominate the soil transcriptome (Žifčáková et al 2016).

As a closing remark, soil microbial communities are extremely diverse and it is increasingly recognized that soil biodiversity and functionality have key roles in determining the structure and ecological responses of terrestrial ecosystems (Bardgett and van der Putten 2014). Soil fungi are known to affect plant diversity and productivity and are crucial for ecosystem functioning and resilience towards disturbance (van der Heijden et al. 2008). Because most fungi have high habitat specificity and tend to respond quickly to changes in environmental conditions as discussed in this dissertation, fungi have a promising potential as indicators of habitat quality in biological monitoring programs. More specifically, assessments of richness and composition of fungal communities in a variety of habitats can inform decision-makers with respect to land use strategies that foster the sustainable preservation of diverse and resilient ecosystems with a wide range of ecosystem functions.

7. Authored scientific output and metrics

Publications in scientific journals: 103 in the last 10 years: 79
Independent citations: 5411
Hirsch index: 37
Cumulative impact factor: 630.26 in the last 10 years: 489.23

First- or last-authored publications in scientific journals: 46
Independent citations: 1321
Cumulative impact factor: 166.93

7.1. Publications featured in this dissertation

Scientific publications: 27
Independent citations: 1326
Cumulative impact factor: 181.26

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