

Plant-fungal interactions in alpine ecosystems

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Declaration of originality

I hereby declare that this thesis is my own work. Where others have contributed or where information comes from other sources, this has been clearly acknowledged and referenced in the text.

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Abstract

The fundamental understanding of diversity, composition and functions of biological communities and their ecological drivers has long been recognized as essential for the study of climate change and its implications for ecosystems. Despite significant advances on our understanding of the dynamics of animal and plant communities and how they respond to environmental variability, little is still known about belowground dynamics, particularly those involving ectomycorrhizal (EM) fungi that play pivotal roles in soil nutrient cycling and plant nutrition. This mutualistic symbiosis is the dominant plant-fungus association in alpine ecosystems, which are among the most threatened by experiencing rapid change as a consequence of climatic shifts and human-related activities. Therefore, to better understand the resilience of these ecosystems to climate variability, it is of paramount importance to study the EM fungal communities that help sustain these habitats. In this thesis I aim to generate baseline diversity data and investigate the biotic and abiotic drivers of alpine EM fungal communities across the European Alps. To do this I assessed the EM fungal communities in the soil and roots of *i*) 47 populations of *Dryas octopetala*, *Bistorta vivipara* and *Salix herbacea* across altitudinal and environmental gradients in 5 countries of the Alps and *ii*) from 87 willows across a hybrid zone between *Salix purpurea* and *Salix helvetica* in the Rhône glacier valley. The results reveal that alpine and sub-alpine habitats harbour a high diversity of EM fungi mostly dominated by lineages with non- or inconspicuous reproductive structures such as *Tomentella-Thelephora*, *Sebacina* and *Cenococcum*. Moreover, alpine EM fungal communities are mostly generalists and functionally redundant, influenced by fine-scale habitat changes in edaphic properties, like soil pH and total nitrogen, rather than elevation or biotic variables such as host phylogeny (at family or genus level). This thesis provides important contributions to our understanding of the diversity and ecology of belowground alpine EM fungal communities in the European Alps and how they may respond to future environmental change. It is expected that the outcomes of this study aid the development of management and mitigation plans to tackle the decline of unique alpine habitats in the face of a changing climate.

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Chapter 1

General Introduction

1.1 The ectomycorrhizal symbiosis

Mycorrhizas are major components of terrestrial ecosystems that play important roles in soil nutrient cycling and plant nutrition (Smith & Read, 2008; Tedersoo *et al.* 2019). These mutualistic relationships have evolved independently multiple times across several plant and fungal lineages (Bidartondo *et al.*, 2011; Strullu-Derrien *et al.*, 2018). Estimates suggest that there are *ca* 50,000 fungal species that form mycorrhizal associations with *ca* 250,000 plant species (van der Heijden *et al.*, 2015; Brundrett & Tedersoo, 2018) comprising four major types based on their structure and function; ectomycorrhizas, arbuscular mycorrhizas, orchid mycorrhizas and ericoid mycorrhizas (Smith & Read, 2008). Even rootless non-vascular plants (e.g. liverworts and hornworts) form mycorrhizal-like symbioses (Rimington *et al.*, 2019). Mycorrhizal fungi facilitate plant nutrient uptake; up to 80% of mycorrhizal plant nitrogen (N) and 100% of phosphorous (P) can be obtained from mycorrhizal fungi in exchange for 20% of plant carbon (C) (Simard *et al.*, 2002; Smith & Read, 2008). With highly specialized traits, such as fine hyphae that can access soil pores too small for roots or root hairs, long mycelial cords (rhizomorphs) that can transport water and nutrients over long distances in soil, or even the capacity for mining nutrients from organic substrates, mycorrhizal fungi can cover most plant soil nutrient and water uptake needs. Unlike decomposers, mycorrhizal fungi lost the ability to obtain carbon from dead organic matter, and typically lack cellulose-degrading exoenzymes (Kohler *et al.*, 2015), therefore they source C from photosynthates provided

directly by a living host plant (Smith & Read, 2008). Thus, they can both drive soil C sequestration and suppress decomposer activity via the Gadgil effect (Averill *et al.*, 2014; Fernandez & Kennedy, 2016). The prevalence of this symbiotic relationship along evolutionary history and its conspicuous distribution across most terrestrial ecosystems are clear indicators of the pivotal roles of mycorrhizas that ensure essential ecosystem processes and functions (van der Heijden *et al.*, 2015; Tedersoo & Bahram, 2019).

The present work focuses on the study of ectomycorrhizal (EM) associations and the biotic and abiotic factors that influence their diversity and distribution. In ectomycorrhizas, the fungi envelope the surface of plant fine roots to form a mantle or sheath and grow in the epidermal and/or cortical intercellular spaces of roots forming the Hartig net (Smith & Read, 2008; Moore *et al.*, 2011). Estimates suggest that *ca* 20,000 species of EM fungi, mostly from the Basidiomycota and Ascomycota phyla, establish associations with *ca* 2.2% of global plant species (Brundrett, 2017; Brundrett & Tedersoo, 2018). Predominantly, but not exclusively, EM fungi associate with large woody perennial plants from the *Betulaceae*, *Dipterocarpaceae*, *Fagaceae*, *Nothofagaceae* and *Pinaceae* families (Brundrett & Tedersoo, 2018). Therefore, the biogeographic patterns of EM fungi are defined by the ecological constraints that shape the distribution of their tree hosts (Tedersoo *et al.*, 2012). Ectomycorrhizal symbioses are mostly dominant in temperate and boreal forests, Mediterranean biomes, and with some plant hosts in tropical ecosystems (Read, 1991; Tedersoo *et al.*, 2010a; Soudzilovskaia *et al.*, 2017). Nevertheless, because EM fungi facilitate plant nutrition, fitness and establishment, these mutualistic relationships are also dominant belowground in more extreme environments, such as alpine ecosystems.

1.2 Ectomycorrhizal communities in the European Alps

Alpine ecosystems are defined by their relative position along a bioclimatic gradient in mountain environments (Körner, 2003; Nagy & Grabherr, 2009).

Across the Holarctic mountains, these ecosystems are located between the *treeline ecotone* - a transition zone from the upper limit of tree growth (forest) and alpine tundra - and the *nival zone* that is sparsely vegetated and covered by snow throughout most of the year. Alpine ecosystems represent *ca* 3% of the terrestrial surface, where *ca* 4% of the Earth's flora can be found (Körner, 1995). Moreover, these ecosystems encompass a range of unique habitats with different ecological conditions, such as wind exposure, snow cover and duration, soil availability, soil depth, nutrients and moisture content (Nagy & Grabherr, 2009). Across the European Alps, the vegetation in the alpine zone is mostly made up of dwarf shrubs and a variety of graminoid-dominated communities that are commonly called alpine grasslands. Floristically, these communities are mostly composed of dwarf shrub (e.g. *Salix reticulata*, *S. retusa*, *S. herbacea*, *Dryas octopetala* and others) heaths, sedges (e.g. *Carex curvula*, *C. ferruginea*, *C. firma*, *C. sempervirens* and *C. tristis*), rushes (e.g. *Juncus jacquinii*), and grasses (e.g. *Festuca halleri* or *F. varia* group) (Ozenda & Borel, 2003). In the Alps, most of the alpine EM plants are woody perennials that form extensive mats such as *Salix spp.* and *Dryas octopetala*. However, a few herbaceous plants (e.g. *Bistorta vivipara* and *Kobresia myosuroides*) can also form ectomycorrhizas (Read & Wandter, 1981; Gardes & Dahlberg, 1996). The survival of these plant communities in such harsh environmental conditions, dominated by cold temperatures and nutrient depleted soils, is highly dependent on their mutualistic relationships. Nevertheless, despite their importance, belowground symbioses in these alpine habitats remain poorly investigated.

The swiss geologist Jules Favre (1882–1959) was one of the first mycologists who explored the alpine macrofungal communities in the Alps. His work on the fungi occurring in the alpine zone of the Swiss National Park (Favre, 1955) described about 90 EM fungal species of which 40 species of the genus *Inocybe* and 26 *Cortinarius* species were among the most abundant EM fungi forming ectomycorrhizas. In the French Alps, Kühner & Lamoure (1986) described 116

EM fungal species from alpine zones across Vanoise National Park. In a comparative study of the macrofungal communities associated with acidic and alkaline alpine snowbeds, Senn-Irlet (1988) identified 36 EM fungal species mostly belonging to the genera *Cortinarius*, *Inocybe* and *Russula*. More recently, Jamoni (2008) described 194 species and varieties of macrofungi (24 Ascomycota and 165 Basidiomycota) across the western Alps combining taxonomic descriptions with ecological information including associated plant communities. Collectively, these studies report a remarkable diversity of fungi in these harsh environments. However, these mycological surveys followed a classical approach by collecting only fruiting bodies, and typically only those that are macroscopic and grow aboveground (epigeous). This, coupled with seasonality and phenological variability, may have led to underestimates of the diversity since EM communities are often dominated by fungi that form belowground, inconspicuous, or no fruitbodies (Gardes & Bruns, 1996; van der Linde *et al.*, 2018).

The incorporation of molecular identification techniques using DNA markers, coupled with visual investigation of ectomycorrhizas belowground, opened the horizon for more in depth analysis of EM fungal communities (Schmit & Lodge, 2005). Using morphotyping techniques and sequencing the internal transcribed spacer (ITS) of the ribosomal DNA (rDNA), Mühlmann & Peintner (2008) performed the first intensive study of the EM communities of the dwarf willow *S. herbacea* at an alpine primary successional site in the Tyrolean Alps of Austria. The authors distinguished 21 EM morphotypes and identified 19 fungal species with *Cenococcum geophilum*, *Sebacina* spp., *Tomentella* spp. and *Cortinarius* spp. among the dominants. In the same glacier valley, Mühlmann *et al.* (2008) found a similar EM fungal community composition of 18 EM taxa associated with the roots of the alpine bistort, *B. vivipara* (syn. *Polygonum viviparum* L.), one of the first EM plants colonising primary successional sites. These results highlight that the presence and importance of EM species with inconspicuous

fruiting (e.g. *Cenococcum*, *Tomentella* and *Sebacina*) had been under-estimated in these habitats, as fruitbodies of these genera had rarely or never been reported from alpine sites.

With the advent of high-throughput sequencing (HTS) coupled with new bioinformatic methods to classify EM fungi into operational taxonomical units (OTUs - a proxy for species in ecology), the detectability of inconspicuous root-associated fungi has drastically increased (Buée *et al.*, 2009; Hawksworth & Lücking, 2017). Generating millions of DNA sequences, these new HTS techniques allow for the assessment of the entire soil microbiome or mycobiome (Talbot *et al.*, 2014; Tedersoo *et al.*, 2014; Nilsson *et al.*, 2019a). In an alpine primary successional gradient of the Blåisen glacier in central Norway, Blaaid *et al.* (2012) investigated changes in the root-associated fungal communities of *B. vivipara* using 454 pyrosequencing. The authors detected 470 EM fungal OTUs, predominantly *Agaricales*, *Thelephorales* and *Sebacinales*. Similarly, in a nearby location, Yao *et al.* (2013) described 589 and 584 EM fungal OTUs associated with *B. vivipara* in alpine ridges and snowbeds, respectively, where the order *Helotiales* was one of the most abundant. However, across the European Alps, despite the recent increase in the number of studies using HTS to characterise soil microbial communities (Pellissier *et al.*, 2014; Rime *et al.*, 2015, 2016; Frey *et al.*, 2016; Luláková *et al.*, 2019), only very few studies attempted to analyse EM fungal communities specifically (Brunner *et al.*, 2017; Adamczyk *et al.*, 2019). At higher taxonomic levels (e.g. class and phylum), Pellissier *et al.* (2014), Rime *et al.* (2015) and Frey *et al.* (2016) reported high diversity of *Agaricomycetes*, a fungal class comprising many, but not only, EM lineages across the Swiss Alps. Moreover, when characterizing the soil microbial communities of the alpine zone in the Global Observation Research Initiative in Alpine environments (GLORIA) mountain summits in Switzerland, Adamczyk *et al.* (2019) reported that EM fungi were among the most dominant functional guilds. These results highlight the pressing need to bridge methods and better characterize EM fungal

communities across the European Alps (Brunner *et al.*, 2017). Assembling high-resolution datasets and coupling them with relevant ecological information can also be critical to study the dynamics of these communities.

1.3 Ecological drivers of ectomycorrhizal communities

Global biogeographical patterns of species distributions may not necessarily reflect the primary drivers of communities at smaller scales (Willis & Whittaker, 2002). On a global scale, the abiotic factors that most influence EM fungal richness are soil pH, mean annual temperature and mean annual precipitation (Tedersoo *et al.*, 2012, 2014). However, at local, regional or continental scales, edaphic properties such as nutrient availability (e.g. P and N), play a fundamental role determining EM fungal communities (Cox *et al.*, 2010a; Suz *et al.*, 2014; van der Linde *et al.*, 2018; Lilleskov *et al.*, 2019). These abiotic drivers of EM fungal communities have been extensively investigated across temperate and boreal forests (e.g. Suz *et al.*, 2014; van der Linde *et al.*, 2018), arctic environments (e.g. Timling *et al.*, 2012) and tropical forests (e.g. Peay *et al.*, 2010; McGuire *et al.*, 2012). However, we still largely ignore the drivers of alpine EM community richness, composition and function.

Some biotic interactions such as host phylogeny and richness (Ishida *et al.*, 2007; Tedersoo *et al.*, 2013; van der Linde *et al.*, 2018; Sudová *et al.*, 2020) and competition with other EM fungi (Pickles *et al.*, 2010; Moeller & Peay, 2016) are likely to influence EM community composition. Ishida *et al.* (2007) found a significant positive relationship between host phylogenetic relatedness and EM fungal community for *Pinaceae*, *Fabaceae* and *Betulaceae* hosts in two Japanese forests with similar environmental conditions and different co-occurring hosts. Co-occurring and congeneric host species might also harbour distinctive EM communities (Morris *et al.*, 2008, 2009; Kohout *et al.*, 2011). At an intraspecific level, van der Heijden & Kuyper (2001) suggested that many dominant EM fungi display some degree of host preference and such preferences may be dependent

on host genetic variation. In the case of alpine and arctic ecosystems, it appears that some EM fungal communities have low levels of host specificity, with communities mostly dominated by generalist fungi (Ryberg *et al.*, 2009; Botnen *et al.*, 2014). However, our understanding of the complex interaction network between alpine plant hosts and their associated EM communities is still limited. Thus, to disentangle the roles that EM fungi play on the mediation of primary production, C storage and nutrient cycling in alpine ecosystems, we need a better understanding of the biotic and abiotic factors that drive these communities, especially for threatened habitats under future climate change.

Alpine ecosystems are highly heterogeneous, offering a diverse array of habitats with singular ecological conditions and where wind exposure, snow cover and duration, soil availability, soil depth, nutrients and moisture, and disturbance regimes vary. In the Alps, the vertical zonation of these habitats is characterized by temperature decreases of about 0.55–0.62 °C per 100 m gains in elevation, while precipitation and duration of snow cover increase with altitude (Barry, 2008; Larcher, 2012). Moreover, under cloudless conditions, the UV-B irradiance can vary about 15–25% and total irradiance about 10–15% for gains of 1,000 m in elevation (Blumthaler *et al.*, 1992; Blumthaler, 2012). Therefore, mountains provide unique opportunities to test various ecological theories given these sharp gradients of abiotic factors (Nagy & Grabherr, 2009; Geml, 2017). For this reason, altitudinal gradients in cold biomes have been used to assess the impacts of climate change on above and belowground organisms including plants and soil microbes (Donhauser & Frey, 2018). Ectomycorrhizal fungal community richness tends to decline towards higher elevations following the decline in host species richness (Bahram *et al.*, 2012; Geml, 2017; Geml *et al.*, 2017). However, alternative hypotheses have been suggested relatively to the distribution of EM fungi across altitudinal gradients. For instance, Miyamoto *et al.* (2014) showed that EM fungi richness peak at mid elevations in Mount Fuji (Japan) in accordance with the Mid-Domain Effect (MDE) model. This model predicts

random placement of species ranges within a bounded geographical domain leading to increased range overlap toward the centre of that particular domain, producing a peak in species richness in that area (Colwell & Lees, 2000). The same pattern was observed in Mount Kinabalu, Borneo by Geml *et al.* (2017), however, the authors suggested that this mid-elevation peak in EM fungal richness was primarily driven by environmental characteristics of habitats and not by the MDE.

Not only richness, but also EM fungal community composition has been shown to vary with elevation (Kernaghan & Harper, 2001; Bahram *et al.*, 2012; Collins *et al.*, 2018). However, studies aiming to assess how altitudinal gradients affect EM communities richness, structure and composition are still scarce and scattered across different terrestrial ecosystems (Geml, 2017). In particular, across the European Alps, only Adamczyk *et al.* (2019) attempted to characterize EM fungal communities along altitudinal gradients as part of a much broader study about the soil microbiome of GLORIA mountain summits in the Swiss Alps. Therefore, to predict future responses of belowground plant-fungal interactions to ongoing climatic changes in these characteristic habitats, it is crucial to study how local EM community richness, composition and function are shaped by environmental conditions along elevation gradients across regional scales.

1.4 Alpine ectomycorrhizal communities: What is their future?

Biological communities in mountains are experiencing a rapid turnover, with drastic implications for the biodiversity in these ecosystems as a consequence of direct and indirect anthropogenic activities (Lenoir *et al.*, 2008; Pauli *et al.*, 2012). Some of the most direct impacts are related to changes in land use practices, infrastructural development, unsustainable tourism or overexploitation of natural resources that lead to habitat fragmentation (EEA, 2002). However, due to the complex topography and to the high level of specialization of the

biological communities of each bioclimatic zone, alpine ecosystems are particularly vulnerable to change due to variability in atmospheric pollution and climate change (Theurillat & Guisan, 2001). In fact, high altitude ecosystems such as alpine ecosystems, are expected to experience greater warming and more variable precipitation regimes than temperate regions (Zimmermann *et al.*, 2013; IPCC, 2014). In this thesis, I focus on the effects of climate change (e.g. variation in air temperature and precipitation) and changes in atmospheric deposition (N deposition) in the alpine zone of the European Alps. Future climatic scenarios, coupled with nutrient additions from exogenous sources in soil, may have direct implications for soil nutrient cycling and plant growing seasons, inducing different feedback responses from plants and fungi and affecting the ecosystem services they provide.

At regional scales, climate has been shown to influence macrofungal distributions (Wollan *et al.*, 2008), phenology (Gange *et al.*, 2007; Kauserud *et al.*, 2008, 2010) and differentially affect EM species respiration rates (Malcolm *et al.*, 2008). Across the Alps, many fungal species (including EM) have been fruiting at increasingly higher elevations in the last decades due to breakdown of their climatic constraints (Diez *et al.*, 2020). In the low arctic tundra of Alaska, long-term air temperature increase has been shown to have contrasting effects among different EM fungal genera and different habitats (Geml *et al.*, 2015; Morgado *et al.*, 2015). Atmospheric N deposition also induces shifts in structure and function of EM fungal communities (Lilleskov *et al.*, 2019). From local to regional scales, aboveground sporocarp surveys consistently indicate the decline of particular EM fungal genera (e.g. *Cortinarius*, *Tricholoma*) due to an increase of air pollutants (Arnolds, 1991; Peter *et al.*, 2001). Similarly, observations of belowground EM fungal communities in temperate and boreal forests have shown differentiated and lineage-specific responses to long-term N inputs with e.g. *Thelephora* and *Laccaria* responding positively while *Cortinarius* and *Piloderma* consistently show negative responses (Lilleskov *et al.*, 2002; Cox *et al.*, 2010b;

Suz *et al.*, 2014; van der Linde *et al.*, 2018). Together, these results reveal that we still understand poorly how future climate change and nutrient cycling disturbances may influence the distribution, richness and composition of belowground EM fungal communities, especially in alpine ecosystems. Thus, given the ongoing decline of these habitats, it is extremely important to assess the current biogeographical patterns and environmental drivers of these pivotal plant-fungus associations, their ecological roles and the ecosystems services they provide.

1.5 Project overview

Rationale, research questions and hypotheses

Alpine plant and fungal communities are models for understanding pioneer communities, the primary components of resilient ecosystems. Climate change is one of the biggest threats to organismal and functional diversity, yet little is known about its potential impacts on fungus-plant interactions. In alpine habitats, EM fungi are an essential functional guild as they are the main mutualists of the dominant woody perennial vegetation and play a fundamental role in C and nutrient cycling. Yet, despite their importance, alpine mycorrhizal fungi are poorly known and the majority remain undocumented and undescribed; baseline diversity data on these fungal communities and their environmental drivers is needed in the face of future climate changes.

In this study I investigated the drivers of EM fungal communities in the European Alps across five different countries along altitudinal gradients covering a wide range of environmental conditions. To assess the biotic and abiotic drivers of the diversity and distribution of these fungi, I sampled the EM fungal communities associated with *Dryas octopetala* L. (Rosaceae), *Bistorta vivipara* (L.) Delarbre (Polygonaceae) and *Salix herbacea* L. (Salicaceae) and hypothesised that:

- i) EM fungal community richness decreases at increasing elevation.
- ii) EM community composition changes along altitudinal and environmental gradients.
- iii) EM plant-fungal interaction networks become more specialized at higher elevations.
- iv) host plant population structure influences EM communities.

To investigate how future changes in temperature and precipitation and soil nutrient availability will influence alpine ectomycorrhizal communities across the European alps, I assessed the responses to predicted changes in these variables and the environmental thresholds of change of EM fungal communities associated with the three EM host plants and hypothesised that:

- v) future expected warmer and drier summers will lead to higher EM community richness in alpine habitats.
- vi) the specialized EM fungal communities of snowbed habitats will be replaced by communities with wider ecological niches from lower elevations.

Finally, to further investigate the role of host genetics on EM fungal community composition and structure, I selected two subalpine and alpine willow species, *Salix helvetica* Vill. and *S. purpurea* L., and their F1 hybrids (*S. helvetica* x *purpurea*) and hypothesised that:

- vii) hybrids and parental willows, able to colonize different habitats, associate with different EM fungi.
- viii) within the same valley, host genotype explains most of the variability in EM community variability.

Thesis structure

Chapter 1 - Explains the study system, the rationale and research questions behind this research project.

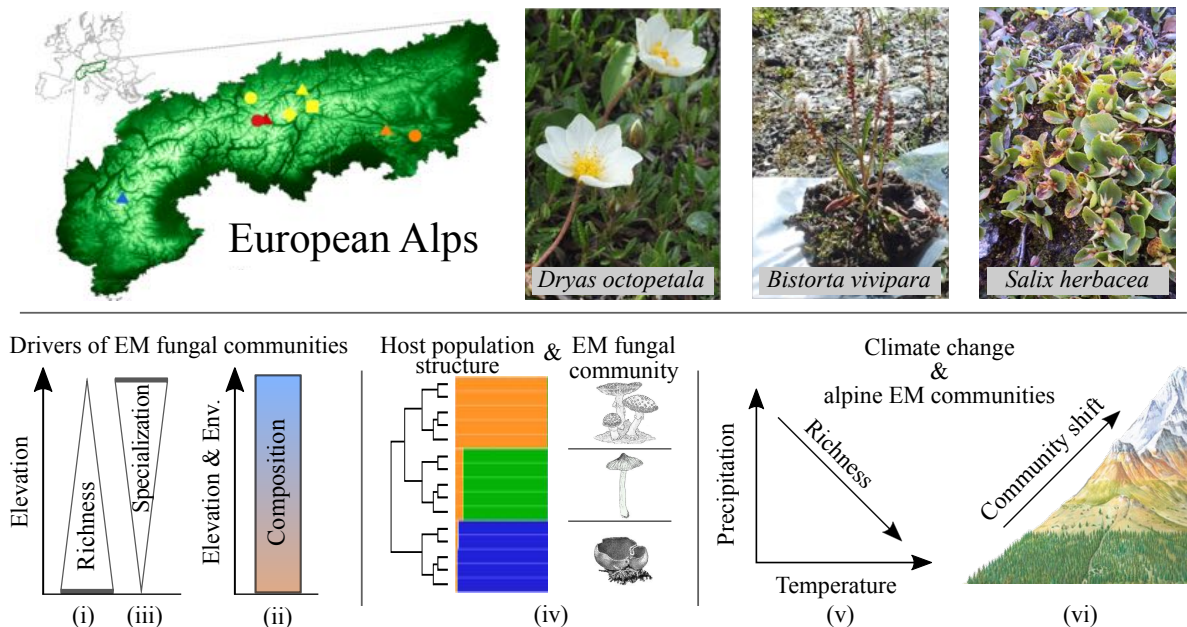
Chapter 2 – Explores the biotic and abiotic drivers of EM fungal communities associated with *Dryas octopetala*, *Bistorta vivipara* and *Salix herbacea* across the European Alps. (Hypotheses i - iv)

Chapter 3 – Examines alpine indicator EM fungal species and their environmental thresholds (Hypotheses v and vi)

Chapter 4 – Investigates the role of plant host genotype as determinant of EM fungal community structure and composition in hybrid zones. (Hypotheses vii and viii)

Chapter 5 – Summarises the main findings and discusses future perspectives.

Chapters 2 & 3



Chapter 4

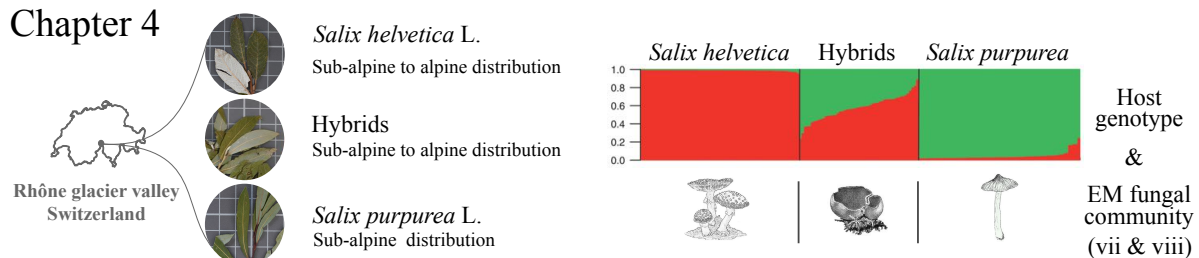


Figure 1.1 Thesis schematic overview and hypotheses tested (i to viii) in chapters 2 and 3 (top) and chapter 4 (bottom).

Scientific outcomes

Publications

- 1) **Arraiano-Castilho R**, Bidartondo MI, Niskanen T, Zimmermann S, Frey B, Brunner I, Senn-Irlet B, Hörandl E, Gramlich S & Suz LM. (accepted Feb. 2020) Plant-fungal interactions in hybrid zones: ectomycorrhizal communities of willows (*Salix* L.) in an alpine glacier forefield. *Fungal Ecology*
- 2) **Arraiano-Castilho R**, Bidartondo MI, Niskanen T, Clarkson JJ, Brunner I, Zimmermann S, Senn-Irlet B, Frey B, Peintner U, Mrak T & Suz LM. (*in prep.*) Habitat specialization controls ectomycorrhizal fungi above the treeline in the European Alps.
- 3) **Arraiano-Castilho R**, Bidartondo MI, Niskanen T, Brunner I, Zimmermann S, Senn-Irlet B, Frey B, Peintner U, Mrak T & Suz LM. (*in prep.*) Snowbed mycorrhizal fungi decline across the European Alps.

Oral presentations

- 1) **Arraiano-Castilho R**. 2019. Plant-Fungal interactions in alpine ecosystems. Autumn Open Meeting, British Mycological Society, Kew, United Kingdom
- 2) **Arraiano-Castilho R**, Bidartondo MI, Niskanen T, Clarkson JJ, Brunner I, Zimmermann S, Senn-Irlet B, Frey B, Peintner U, Mrak T & Suz LM. 2019. Above the tree line: Drivers of ectomycorrhizal fungal communities in the European Alps - 10th International Conference on Mycorrhizae, Mérida, Mexico.
- 3) **Arraiano-Castilho R**, Bidartondo MI, Niskanen T, Zimmermann S, Frey B, Brunner I, Senn-Irlet B, Clarkson JJ, Hörandl E, Gramlich S, Peintner U, Mrak

T & Suz LM. 2018 Plant-Fungal Interactions in Alpine Ecosystems. North European Forest Mycologists Meeting, Oulanka, Finland.

Poster presentations

- 1) **Arraiano-Castilho R**, Bidartondo MI, Niskanen T, Clarkson JJ, Brunner I, Zimmermann S, Senn-Irlet B, Frey B, Peintner U, Gramlich S, Mrak T & Suz LM. 2018. Plant-Fungal interactions in alpine ecosystems. State of the World's Fungi Symposium, Kew, United Kingdom.

Chapter 2

Habitat specialization controls ectomycorrhizal fungi above the treeline in the European Alps.

2.1 Abstract

Mountains harbour wide gradients of environmental variables and are hotspots of diversity for many organisms including plants and fungi. Alpine habitats are some of the most vulnerable ecosystems under environmental change, however, little is known about the drivers of plant-fungal interactions in these ecosystems and the consequences of changes in these interactions for the resilience of alpine habitats to climate change. In this chapter, I investigate the main biotic and abiotic drivers of ectomycorrhizal (EM) fungal communities along elevation and environmental gradients in the alpine zone across five countries in the European Alps. Ectomycorrhizas of *Dryas octopetala*, *Bistorta vivipara* and *Salix herbacea*, and their associated soil fungal communities were collected across 28 sampling locations from the treeline to the nival zone. I hypothesize that: 1) EM fungal community richness decreases at increasing elevations; 2) EM community composition changes along elevation and environmental gradients, 3) EM plant-fungal interaction networks become more specialized at higher elevations, and 4) host plant population structure influences EM communities. The results show that: i) EM fungal community composition, but not richness, changes significantly along elevation gradients, ii) EM fungal networks in the alpine zone and within these, EM fungi associated with *S. herbacea*, are more specialized than in the treeline ecotone, iii) plant host population structure does not have a significant influence at least on *D. octopetala* EM fungi, and iv) most variability

found in EM fungal communities is explained by fine-scale changes in edaphic properties, like soil pH and total nitrogen. In alpine habitats, the higher levels of specialization and narrower ecological niche of *S. herbacea* EM fungal communities makes them particularly vulnerable to environmental change.

Keywords

Alpine; Elevation gradients; Environmental drivers; Ectomycorrhizal communities; Soil fungal community; *Dryas octopetala*; *Bistorta vivipara*; *Salix herbacea*, plant-fungal networks.

2.2 Introduction

Anthropogenic activities since the industrial revolution have led to shifts in soil properties due to atmospheric deposition (e.g. pH and nutrient availability), climatic conditions, and mean annual temperature and precipitation (Tilman & Lehman, 2001). Habitat loss due to environmental change is one of the main threats to biodiversity, affecting both plant and fungal distributions. This is of particular relevance in mountain ecosystems where climate change is already driving mountain species upslope (Steinbauer *et al.*, 2018), favouring more resilient and well adapted communities to the new environmental conditions over more specialized ones, such as those from alpine habitats (Gottfried *et al.*, 2012). Across global and continental scales, environment and host are the main drivers of ectomycorrhizal (EM) fungal communities (Tedersoo *et al.*, 2012, 2014; van der Linde *et al.*, 2018), but in order to better understand the impact of environmental change in alpine ecosystems and the resilience of their plant-fungal networks, it is essential to know how the main biotic and abiotic drivers of EM fungal communities operate across their sharp altitudinal and environmental gradients.

Altitudinal gradients strongly affect the diversity of plants and animals (Körner, 2003; Gobbi *et al.*, 2006), yet little is known about their effects on the

distribution of soil organisms, including fungi (Geml, 2017; Donhauser & Frey, 2018). Kernaghan & Harper (2001) found that richness and diversity of fruitbodies of EM fungi decreased with elevation from the sub-alpine forest to the alpine zone at two sites in the Canadian Rockies. In the Hyrcanian forests of northern Iran, Bahram *et al.* (2012) found that EM fungal richness declined monotonically with increasing elevation. This declining trend in richness and diversity of EM fungi with increasing elevation has been reported from mountains around the globe, from Mt. Fuji in Japan (Miyamoto *et al.*, 2014) to the Peruvian Andes (Nottingham *et al.*, 2018) and the White Mountains of California (Collins *et al.*, 2018). However, these studies were carried out across multiple habitats and including different plant hosts that covaried with elevation resulting in confounding effects. In contrast, when studying the EM communities of one host, no significant differences were found in the EM fungal richness associated with *Fagus sylvatica* L. (Coince *et al.*, 2014) or *Pinus sylvestris* L. (Jarvis *et al.*, 2015) along elevation gradients. Large-scale studies across multiple hosts are needed to understand how elevation and underlying environmental covariates drive EM fungal communities in mountain ecosystems and how these communities are shaped across different mountain zones.

Ectomycorrhizal fungal communities are well known to respond to a wide array of biotic and abiotic factors (e.g. Waldrop *et al.*, 2006; Tedersoo *et al.*, 2012, 2014; Suz *et al.*, 2017; van der Linde *et al.*, 2018). However, across the European Alps, only a few studies have attempted to assess the environmental drivers of these communities and how they influence their richness, composition and function. At local scales, it has been shown that alpine EM fungal communities in the Alps are very diverse (Mühlmann *et al.*, 2008; Mühlmann & Peintner, 2008; Pellissier *et al.*, 2014; Brunner *et al.*, 2017) similarly to other alpine areas (Ryberg *et al.*, 2009; Gao & Yang, 2010; Bjorbækmo *et al.*, 2010; Mundra *et al.*, 2016; Botnen *et al.*, 2019) and usually dominated by generalist fungi showing no host preference (Ryberg *et al.*, 2009; Botnen *et al.*, 2014; Brunner *et al.*, 2017).

In the western Swiss Alps, fungal richness (including mycorrhizal fungi) has been shown to improve the predictive power of plant species distribution models in alpine habitats, and that fungal community richness is positively correlated with the distribution of plants occurring at higher elevations (Pellissier *et al.*, 2013). Moreover, Adamczyk *et al.* (2019) demonstrated that fungal alpha and beta diversities were influenced by a complex grid of environmental variables (e.g. soil pH in combination with vegetation cover) across the Swiss GLORIA mountain summits. However, it is expected that future climatic scenarios will have differentiated impacts across the European Alps (Zimmermann *et al.*, 2013), and thus triggering different feedbacks on soil microbial communities across different valleys. Therefore, baseline diversity data on these fungal communities and their environmental drivers at regional scales is needed in the face of ongoing climate change.

Alpine ecosystems encompass a wide range of habitats with heterogeneous geomorphology and different ecological conditions (Nagy & Grabherr, 2009). Alpine plants respond to these variable and harsh conditions with high levels of morphological and physiological specialization (Körner, 2003). In the Alps, some of the most characteristic habitats above the treeline are formed by grasslands and dwarf-shrub heath formations typically dominated by EM mountain avens (*Dryas octopetala* L., Rosaceae) and dwarf willows (*Salix* spp., including *Salix herbacea* L., Salicaceae). In contrast, the alpine bistort (*Bistorta vivipara* (L.) Delarbre, Polygonaceae) is a widespread arctic-alpine EM plant (Wang & Qiu, 2006) that occurs across the whole range of the European Alps from the montane to the nival zone (Delarze *et al.*, 2015). Alpine ecosystems are expected to be heavily impacted by climate change; therefore, in this chapter, I explored the main biotic and abiotic drivers of EM fungal communities in the alpine zone along elevation gradients across the European Alps. From the treeline ecotone to the nival zone, I analysed the EM fungal communities associated with three important EM alpine plants, and I hypothesized that: 1) EM fungal richness decreases and composition

changes at increasing elevation and harsher environmental conditions (decreasing temperatures and increasing precipitation and snow cover periods); 2) these plant-fungal interaction networks are more specialized at higher elevations, and 3) host plant population genetic structure determines EM communities.

2.3 Materials and methods

Root, soil and plant tissue sampling

Sampling was carried out in the European Alps across five countries during the summers of 2016 and 2017. Forty-seven sites (10 x 30 m, sub-divided into four 5 x 15 m quadrants) *ca.* 1,500 to 2,600 m a.s.l. were sampled from the treeline to the nival zone, covering environmental and climatic gradients along the range of *D. octopetala*, *B. vivipara*, and *S. herbacea* (Table 2.1). *Dryas octopetala* is a sub-alpine to alpine plant that occurs mostly in calcareous open habitats forming extensive mats. Poor in species richness, these habitats are characterized by the common presence of *Carex firma* and dwarf willows such as *Salix reticulata*, *S. retusa* and *S. serpyllifolia* (Davies *et al.*, 2004). *Salix herbacea*, however, occurs mostly in highly acidic soils (pH < 5) along snow-bed communities covered by snow for up to ten months. In these habitats there is a sparse presence of lawns formed by pioneer and acidophilic plant species (Delarze *et al.*, 2015). *Bistorta vivipara* is less restricted by soil conditions and co-occurs with both *D. octopetala* and *S. herbacea*. When possible, sampling sites were selected at least at two different elevations, from the treeline up to the lower limit of the nival zone in each valley. Geological and lithological soil properties at the sampling locations are diverse. French sites are a mixture of limestone, marl and gypsum. In Switzerland, dolomite dominates at sites with *ca.* pH 7 while migmatites and siliceous moraines predominate at the other sites. In Austria, sampling sites were characterised by carbonate sedimentary rocks (site INNSBR, see Table 2.1), limestone (site GARFUL), gneiss (site VIZZE) or rocks rich in quartz and

Table 2.1 The twenty-eight sampling locations included in this study and their main topographic and environmental characteristics

Location	Country	Longitude	Latitude	Host species	Elevation (m)	Habitat	Corine Land Cover	Ann. mean temp. (°C)	Ann. precip. (mm/year)	Soil pH
LAUTAR_01	France	45.063547	6.402991	<i>S. herbacea</i> , <i>B. vivipara</i>	2,592	Alpine	333_Sparsely vegetated areas	-0.61	1,003	4.79
LAUTAR_02	France	45.062923	6.404146	<i>S. herbacea</i>	2,579	Alpine	333_Sparsely vegetated areas	-0.61	1,003	6.42
LAUTAR_03	France	45.053431	6.404901	<i>D. octopetala</i> , <i>B. vivipara</i>	2,429	Alpine	333_Sparsely vegetated areas	0.86	912	6.77
LAUTAR_04	France	45.037795	6.400640	<i>D. octopetala</i> , <i>B. vivipara</i>	2,114	Alpine	322_Moors and heathland	2.51	822	6.72
LAUTAR_05	France	45.052905	6.388098	<i>S. herbacea</i> , <i>B. vivipara</i>	2,359	Alpine	333_Sparsely vegetated areas	0.34	984	4.58
ZERNEZ_01	Switzerland	46.628144	10.287766	<i>D. octopetala</i>	2,450	Alpine	332_Bare rocks	-0.48	906	7.40
ZERNEZ_02	Switzerland	46.632964	10.284639	<i>D. octopetala</i> , <i>B. vivipara</i>	2,288	Treeline	321_Natural grasslands	-0.25	895	6.24
ZERNEZ_03	Switzerland	46.682419	10.238911	<i>D. octopetala</i> , <i>B. vivipara</i>	2,396	Alpine	333_Sparsely vegetated areas	0.20	836	7.29
ZERNEZ_04	Switzerland	46.737765	9.963139	<i>S. herbacea</i>	2,449	Alpine	333_Sparsely vegetated areas	-1.06	939	3.81
ZERNEZ_05	Switzerland	46.743415	9.980309	<i>S. herbacea</i>	2,188	Alpine	321_Natural grasslands	0.16	817	3.67
ZERNEZ_06	Switzerland	46.641510	10.237138	<i>D. octopetala</i>	2,380	Alpine	333_Sparsely vegetated areas	-0.24	884	7.29
SCHARL_01	Switzerland	46.678148	10.374443	<i>D. octopetala</i>	2,300	Alpine	321_Natural grasslands	0.05	813	7.34
SCHARL_02	Switzerland	46.671996	10.361511	<i>B. vivipara</i>	2,346	Alpine	321_Natural grasslands	0.86	651	4.21
SCHARL_03	Switzerland	46.682399	10.364270	<i>D. octopetala</i> , <i>B. vivipara</i>	2,127	Treeline	231_Pastures	0.75	692	7.09
SCHARL_04	Switzerland	46.692224	10.347199	<i>D. octopetala</i> , <i>B. vivipara</i>	2,329	Alpine	321_Natural grasslands	0.21	722	5.45
SCHARL_05	Switzerland	46.682380	10.365192	<i>D. octopetala</i> , <i>B. vivipara</i>	2,137	Treeline	321_Natural grasslands	0.75	692	7.03
GARFUL_01	Austria	47.174157	9.920619	<i>D. octopetala</i> , <i>B. vivipara</i>	1,830	Alpine	321_Natural grasslands	1.88	1,971	7.08
GARFUL_02	Austria	47.180725	9.921334	<i>D. octopetala</i> , <i>B. vivipara</i>	1,478	Treeline	321_Natural grasslands	3.58	1,863	6.71
OBERGU_01	Austria	46.828354	11.043108	<i>S. herbacea</i> , <i>B. vivipara</i>	2,398	Alpine	333_Sparsely vegetated areas	-1.34	863	7.55
OBERGU_02	Austria	46.840277	11.032048	<i>S. herbacea</i> , <i>B. vivipara</i>	2,296	Alpine	333_Sparsely vegetated areas	-0.88	884	6.67
OBERGU_03	Austria	46.845662	11.020627	<i>B. vivipara</i>	2,266	Alpine	411_Inland marshes	-0.15	815	4.36
INNSBR_01	Austria	47.313880	11.396169	<i>D. octopetala</i> , <i>B. vivipara</i>	2,201	Alpine	333_Sparsely vegetated areas	0.61	1,283	5.9
INNSBR_02	Austria	47.317318	11.391506	<i>D. octopetala</i> , <i>B. vivipara</i>	2,021	Treeline	333_Sparsely vegetated areas	1.63	1,386	6.38
VIZZE_01	Italy	46.992634	11.667176	<i>S. herbacea</i>	2,388	Alpine	333_Sparsely vegetated areas	0.02	921	3.86
VIZZE_02	Italy	46.993388	11.674160	<i>S. herbacea</i> , <i>B. vivipara</i>	2,492	Alpine	332_Bare rocks	-0.56	963	4.04
VRASIC_01	Slovenia	46.427458	13.750879	<i>D. octopetala</i> , <i>B. vivipara</i>	1,727	Treeline	333_Sparsely vegetated areas	3.44	2,279	7.32
VRASIC_02	Slovenia	46.437767	13.738510	<i>D. octopetala</i> , <i>B. vivipara</i>	1,987	Alpine	332_Bare rocks	1.46	2,473	7.29
KRVAVE_01	Slovenia	46.309117	14.542299	<i>D. octopetala</i> , <i>B. vivipara</i>	1,946	Treeline	333_Sparsely vegetated areas	2.63	1,814	6.31

feldspar like amphibolite and phyllite (site OBERGU). In Slovenia, limestone and limestone-dolomite characterised the sites KRAVEC and VRSIC, respectively. At each site, twenty individuals per target host plant (5 per quadrant) were selected maximising the distance among them and then soil blocks of approx. 10 cm³ were collected underneath plants including both roots and above ground plant structures. Samples were stored at 4°C for up to 10 days until processed. Leaf samples from all plants were collected and preserved in silica gel for host genetic analyses. Extra soil samples (*ca.* 250 mg) were collected under each plant and pooled by quadrant for chemical and DNA fungal community analysis (Illumina amplicon sequencing of the ITS2 region). Soils for chemical analysis were dried at 40–60°C and stored at room temperature while soils for DNA community analysis were sieved through a 2 mm mesh under sterile conditions and freeze-dried.

Environmental data

Annual mean temperature and annual precipitation from each site and sampling year were retrieved from the CHELSA database at 30 arc-sec resolution (Karger *et al.*, 2017). All soil chemistry analyses were performed at the Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf (WSL). Soil pH was measured potentiometrically in 0.01M CaCl₂. Total carbon (C_{total}) and total nitrogen (N_{total}) content were measured in ground samples by dry combustion using a C/N analyser NC 2500 (CE Instruments, Milan, Italy). Exchangeable cation soil content (Calcium [Ca²⁺]_{soil}, Potassium [K⁺]_{soil} and Magnesium [Mg²⁺]_{soil}) was measured in soil extracts (1M NH₄Cl, 1:10 soil:solution ratio, 1h extraction time) by inductive plasma atomic emission spectrometry with an Optima 3000 (Perkin-Elmer, ON, Canada). Cation exchange capacity (CEC) was calculated as the sum of the measured acid and base cations (mmol/kg). Additionally, percentage of total plant cover, the co-occurrence of other EM plant

hosts and their position in the elevation gradient (treeline vs alpine) were recorded at each sampling site.

Mycorrhizal assessment

All roots of each plant were rinsed with water and carefully disentangled from the soil and roots of other plants. Twelve roots traced from the aboveground structures were selected from each plant and one ectomycorrhiza from each root was collected for further analyses under a dissecting microscope. All individual ectomycorrhizas were characterized according to colour and soil exploration type characteristics (Agerer, 2001, 2006). Genomic DNA was extracted from individual ectomycorrhizas using Extract-N-Amp (Sigma-Aldrich, Darmstadt, Germany) and the ITS region of the rDNA was amplified using the fungal-specific primers ITS1F (Gardes & Bruns, 1993) and ITS4 (White *et al.*, 1990). Amplicons were purified using ExoSAP-IT (USB, Cleveland, OH, USA) and sequenced bidirectionally using BigDye v. 3.1 (Applied Biosystems, Foster City, CA, USA) in an ABI 3730 (Applied Biosystems).

Sequences were first analyzed with KB basecaller v1.1.1 (Applied Biosystems) and bases called with minimum quality value (QV) of 20 (i.e. 99% of base call accuracy). Forward and reverse sequences from each ectomycorrhiza were assembled using *phrap* v1.090518 (de la Bastide & McCombie, 2007). When the assembly of both sequences was not possible due to poor quality of one of the sequences or to uncertainty determining their overlapping region, the longest and highest quality sequence (with higher QV) was used for further analyses. To avoid misleading results in the DNA sequence identification process and to facilitate direct comparison with the fungal community in the soil, adjacent conserved regions (18S, 5.8S and 28S) were removed using ITSx v1.0.11 (Bengtsson-Palme *et al.*, 2013) and the ITS2 region was selected for further analyses. Sequences were clustered in OTUs at a 97% similarity threshold using the UPARSE pipeline implemented in USEARCH v9.2 (Edgar, 2013), while simultaneously excluding chimeric sequences. The taxonomic affiliation of each

OTU was inferred by blasting each OTU centroid sequence to the UNITE fungal ITS sequence database v7.2 as a reference for assignment of a species hypothesis (Nilsson *et al.*, 2011; Kõljalg *et al.*, 2013). The ecological functions of each OTU (i.e. trophic level and type of mycorrhizal association) were assigned according to UNITE (Kõljalg *et al.*, 2013) and only EM fungi were used in downstream analyses. Representative sequences of the centroid of each EM OTU were deposited in NCBI under accession numbers MT095121 to MT095543.

Soil DNA analysis

Genomic DNA was extracted from 25 mg of each freeze-dried soil sample pool per quadrant using the DNeasy PowerSoil Kit (Qiagen, Valencia, CA) and quantified using the Qubit 2.0 fluorometric system (Life Technologies, Paisley, UK). The four DNA extractions per site were pooled for further analysis. The PCR amplifications of the ITS2 region of the nuclear rDNA were performed using the primer set fITS7 (Ihrmark *et al.*, 2012) and ITS4, run in triplicates and pooled for library preparation. The PCRs, library preparation and paired-end sequencing on the Illumina MiSeq v3 platform (Illumina Inc., San Diego, CA, USA) were conducted by Génome Québec Innovation Center at McGill University (Montréal, Canada).

Quality filtering and clustering into OTUs were performed using a customized pipeline based on UPARSE implemented in USEARCH (Edgar, 2013) with additional modifications. Paired-end reads were merged using the USEARCH fastq_mergepairs algorithm (Edgar & Flyvbjerg, 2015) allowing staggered alignment constructs in order to accommodate potentially short ITS2 amplicons. The PCR primers were detected and trimmed using Cutadapt (Martin, 2011) allowing for one mismatch. Reads not matching the primers or with lengths below 150 bp were discarded. Trimmed reads were quality-filtered using the USEARCH fastq_filter function with a maximum expected error threshold of one. Sequences were de-replicated to retrieve information on abundance

distribution, and singleton reads were removed prior to clustering in order to avoid artificial OTU inflation. Sequences were clustered into OTUs at 97% sequence identity using the USEARCH cluster_otu function that includes an ‘on-the-fly’ chimera detection algorithm. The OTU centroid sequences were subjected to an additional round of chimera filtering by running UCHIME (Edgar, 2016a) against the uchime version of the UNITE database. The remaining centroid sequences were tested for the presence of ribosomal signatures using ITSx (Bengtsson-Palme *et al.*, 2013). Finally, all quality-filtered reads were mapped against the final set of centroid sequences using the usearch global algorithm with the most comprehensive search criteria (maxrejects 0, maxaccepts 0, and top hit only). The taxonomic affiliation of each OTU was inferred by blasting each OTU centroid sequence to the UNITE fungal ITS sequence database v7.2. Representative sequences of the centroid of each EM OTU were deposited in NCBI with accession numbers MT095544 to MT096017.

Plant host genotype assessment

Plant genomic DNA from five plants per site and per species (85 *D. octopetala*, 105 *B. vivipara* and 45 *S. herbacea*) was isolated using the DNeasy Plant Mini Kit (Qiagen, Valencia, CA) from approx. 20 mg of dried leaf tissue. Ten nuclear microsatellite loci (SSR) for *D. octopetala* (Vik *et al.*, 2010), ten for *B. vivipara* (Vik *et al.*, 2012) and seven for *S. herbacea* (Stamati *et al.*, 2003) were amplified according to the methods in the original publications. Primers were fluorescently labelled with FAM or JOE (Eurofins Scientific), and analysed using an ABI 3730 (Applied Biosystems, Foster City, CA, USA). The molecular sizes of the DNA fragments in base pairs (bp) were visually scored against the GeneScan-500 ROX size standard (Applied Biosystems) using Geneious® 8.1.9.

Population sub-division for each host across the Alps was inferred using distance-based methods as implemented in the *polysat* R package (PCoA – Bruvo’s Distance) (Clark & Jasieniuk, 2011) and using a model-based approach

as implemented in STRUCTURE v.2.3.4 (Pritchard *et al.*, 2000). Because *B. vivipara* and *S. herbacea* revealed ploidy levels higher than two, *loci* scores were coded as dominant and exported to the STRUCTURE input format as implemented in *polysat*. The STRUCTURE parameters included the use of the admixture ancestry model, independent allele frequencies among populations and RECESSIVEALLELES flag set to one for the two polyploid hosts. The STRUCTURE runs were set to 100,000 iterations with burn-in length of 10,000 to investigate the best *K* (number of clusters) from 1 to 15. The best value of *K* was evaluated through Evanos's method and plotted as implemented in *pophelper* R package. Genetic dissimilarities among sub-populations were assessed by calculating pairwise F_{st} values among clusters with clear separation observed in STRUCTURE. Standard analysis of molecular variance (AMOVA) was conducted in GenoDive v.2.0 (Meirmans & Van Tienderen, 2004) to analyse the genetic variation within and among populations.

Statistical analyses

All statistical analyses were carried out using R version 3.5.1 (R Development Core Team 2009). Normal distribution of the residuals and homogeneity of variances of each variable were assessed by analysing *qqnorm* plots and significant deviations of Shapiro and Levene test routines implemented in R. Data with non-normal distribution of the residuals were square root or log transformed. The DNA sequence read numbers from both roots and soil community samples were standardized using the Hellinger method as implemented in the *decostand* function of the *vegan* package (Oksanen *et al.*, 2019).

i) Alpha and beta diversity of alpine EM fungi

The observed number of OTUs per site and the abundance-based estimator (ACE, Chao & Lee, 1992) were calculated using the *estimateR* function of the *vegan* package. Differences in observed and estimated values among hosts were

assessed by one-way ANOVA and Tukey's HSD *post hoc* tests. The percentage of OTUs recovered per host was calculated as the proportion of the number of observed OTUs and the estimated number of OTUs (ACE). *Bistorta vivipara* co-occurred with the other two hosts in most of the sites, therefore, two values of OTU richness were assessed, one when co-occurring with *D. octopetala* and another when co-occurring with *S. herbacea*. To assess the proportion of shared OTUs between the root and soil samples, a local blast was performed using the *blastn* algorithm with the soil OTUs centroids as references and the root OTUs centroids as queries. The OTUs with blast hits superior or equal to 97% and with congruent taxonomy (i.e. equal UNITE Species Hypothesis number) were considered equivalent. Non-metric multidimensional scaling (NMDS) ordination was used to visualize dissimilarities in EM communities in the root dataset across different plant hosts using Bray-Curtis dissimilarity distances. Permutational multivariate analysis of variance (PERMANOVA) was used to assess differences among plant hosts using the *adonis* function from the *vegan* package.

ii) EM communities across elevation

To test the effect of elevation on EM fungal communities I used a two-step approach: i) I tested for differences in OTU richness across the elevation gradient using a linear regression model with estimated OTU richness per sampling site as a function of the absolute value of elevation; ii) I grouped the sites in two habitat zones (alpine and treeline) according to their position in the mountain and compared the OTU richness between the two groups using *t*-test statistics as implemented in the *stats* package. Differences in community composition were assessed by PERMANOVA, fitting the pairwise Bray-Curtis distance matrix as a function of the absolute value of elevation in our first approach, and with and without constraining permutations to habitat in the second approach.

Differences in EM functional diversity across hosts and between treeline and alpine zones were tested by one-way ANOVA comparing the average number of

OTUs and the number of ectomycorrhizas within each soil exploration type observed (contact, short distance or medium fringe distance) per zone and across hosts. Functional trait variation (presence-absence of hyphae and rhizomorphs) between treeline and alpine zones was assessed by *t*-test statistics and by one-way ANOVA across hosts. When variances were heterogeneous, a one-way test for equal means (Welch ANOVA) was used as implemented in the *stats* package. Tukey and Games-Howell *post hoc* tests were used after simple ANOVA and Welch ANOVA, respectively, to examine pairwise differences when significant differences were observed.

Specialization of the different EM OTUs to host and mountain zone along the elevation gradients was tested using an ecological network approach. Two network indices were calculated: i) the network-wide specialization index $H2'$, that characterizes the degree of specialization in the entire network, and ii) the degree of specialization of elements within the network d' (Blüthgen *et al.*, 2006). I used the methods in the *bipartite* package (Dormann *et al.*, 2008) and three variants of OTU abundance matrices: a) OTU vs plant host across all alpine sites, b) OTU vs plant host across all treeline sites, both used for $H2'$, and c) overall abundance of OTUs vs hosts across all sites, used for d' . To test for the significance of the network indices calculated, 1,000 matrices were generated from a null model constraining row and column sums as implemented in *vegan::nullmodel* and computed *p*-values and standard scores (z-scores) over the deviations of the observed values with those predicted by the null models.

iii) Environmental drivers of EM communities

To elucidate the drivers of EM fungal communities across the Alps I applied the hierarchical Bayesian framework described by Ovaskainen *et al.* (2017). This framework implemented in *Hmsc* package v3.0, allows to assess how much variation in fungal OTU abundances is due to environmental filtering, biotic interactions and random processes. To do this, OTUs present in five or more

sampling sites and with counts of ten or more ectomycorrhizas were selected. The main environmental drivers of EM communities were selected by fitting all environmental variables collected for this study in the NMDS ordination described previously, using the *envfit* function from the *vegan* package after 999 permutations. Only the variables showing significant correlation values (p -value ≤ 0.05) with community dissimilarities were selected for downstream analyses. Collinearity among selected variables was assessed with the *chart.correlation* function from the *PerformanceAnalytics* package (Peterson & Carl, 2018) and pairwise variable combinations that showed a Pearson correlation coefficient ≥ 0.7 were inspected, discarding one of the pairs from posterior analyses. Seven different model variants were assembled grouping the environmental variables in biotic (host species + habitat + total plant cover), climatic (annual mean temperature + annual precipitation), and edaphic (soil pH + N_{total} + $[Mg]_{\text{soil}}$) components, and all interactions among them. All models were fitted with the abundance of dominant OTUs as response variable, the exploration type for each OTU as a categorical variable with three levels (contact, short distance and medium-distance fringe) and a maximum likelihood phylogenetic tree obtained from the ITS2 alignment of each OTU centroid using muscle alignment algorithm as implemented in MUSCLE v3.8.31 (Edgar, 2004) and analysed under the GTRGAMMA model over 1,000 multiple bootstrap analysis in RAxML v8.2.4 (Stamatakis, 2006). Sampling site was included as random effect, because sampling was assumed to be spatially structured and hence incorporated with the help of spatial latent factors (Ovaskainen *et al.*, 2016). All model variants were set with a lognormal Poisson distribution for OTU abundances including zeros and non-zeros using the default priors and the posterior distribution sampled from four Markov chain Monte Carlo (MCMC) chains. Each chain was run for 105,000 iterations, out of which the first 5,000 were removed as transient and the remaining ones were thinned by 100 to yield 1,000 posterior samples per chain, thus resulting in a total of 4,000 posterior samples retrieved per model. The

MCMC convergence was assessed by observing the distributions of the effective number of posterior samples for the estimated parameters and by Gelman and Rubin's convergence diagnostic (Gelman & Rubin, 1992). Model fit was evaluated by calculating the predictive and explanatory power of each model variant. The predictive power was assessed by two-fold cross-validation with half of the data for test and the other half for training the model, while the explanatory power of the models was evaluated by the area under the receiver operating characteristic curve (AUC) statistic and by the coefficient of discrimination Tjur R^2 (Tjur, 2009). The best model (i.e. with highest explanatory power) was used to explore the parameter estimates, partition the variance of the explained variability and to assess how fungal OTU traits (i.e. presence-absence of hyphae and rhizomorphs) and EM lineage correlate with their ecological niches.

iv) Host population structure and EM communities

To test if EM fungal communities were shaped by host population structure, I used a subset the root dataset based on the best number of clusters (K) defined by STRUCTURE from each host plant. Sampling sites from which all individuals shared similar admixture proportions were assigned to a genotype. One-way ANOVA was used to infer significant differences on estimated OTU richness across genotypes and differences in community composition were assessed by PERMANOVA fitting a Bray-Curtis dissimilarity matrix as a function of host genotype.

2.4 Results

Alpha and beta diversity of alpine EM fungi

A total of 10,945 ectomycorrhizas were sampled from the roots of 950 individual plants (340 *D. octopetala*, 430 *B. vivipara* and 180 *S. herbacea*) across 47 sampling sites (17 *D. octopetala*, 21 *B. vivipara* and 9 *S. herbacea*). From these,

9,393 DNA sequences were retrieved, of which 8,945 were high quality and belonged to EM lineages (*sensu* Tedersoo *et al.*, 2010 and Tedersoo & Smith, 2013). After clustering and filtering, 423 OTUs were identified across 33 phylogenetic lineages. Approximately 68% of the fungi forming ectomycorrhizas belonged to Basidiomycota and 32% to Ascomycota, with the dominant lineages being *Tomentella-Thelephora*, *Cenococcum* and *Sebacina* (Fig. 2.1A). The lineages with highest richness were *Tomentella-Thelephora* (134 OTUs), *Inocybe* (66 OTUs), *Sebacina* (64 OTUs), *Cortinarius* (36 OTUs) and *Hebeloma* (21 OTUs).

A total of 3,792,112 raw DNA reads were generated from soil samples, from which 1,448,522 high quality ones were retrieved. In total, 3,695 fungal OTUs were identified, of which 778 (average per soil sample 54.9 ± 29.4) belonged to 32 EM fungal lineages after removing OTUs from non-EM lineages, 30 centroid sequences with ribosomal origin not sufficiently supported, and 20 EM OTUs known to be specialists on conifers s.l. (Tedersoo *et al.*, 2009; Nilsson *et al.*, 2019b) and that were not detected forming ectomycorrhizas in this study. The dominant EM lineages in soil were *Inocybe*, *Tomentella-Thelephora* and *Cortinarius* (Fig. 2.1A). The highest OTU richness in soil was in *Inocybe* (205 OTUs), *Tomentella-Thelephora* (178 OTUs), *Sebacina* (80 OTUs), *Cortinarius* (74 OTUs) and *Tuber-Helvella* (25 OTUs).

The number EM OTUs found in both roots and soil was 302, whilst 121 were found only in roots and 476 only in soil (Appendix A: Table S2.1). Across all sites, 272 EM OTUs were observed in roots of *D. octopetala*, 341 in *B. vivipara*, and 134 in *S. herbacea*. Per site, the observed number of OTUs in the roots was on average 73% of the estimated EM diversity in *D. octopetala* and 81% in *B. vivipara* and *S. herbacea*. In the soil, 554 EM OTUs were found under *D. octopetala*, 548 under *B. vivipara*, and 208 under *S. herbacea* individuals. On average, the observed number of OTUs in the soil was 93% of the estimated EM diversity under *D. octopetala*, 95% under *B. vivipara* and 96% under *S. herbacea*.

Across hosts, the results revealed significantly lower estimated OTU richness in *S. herbacea* in both roots and soil ($F_{\text{Roots}} = 16.933$, $p\text{-value} < 0.001$; $F_{\text{Soil}} = 5.115$, $p\text{-value} = 0.010$) (Fig. 2.1B). When comparing the mean estimated OTU richness per site in *B. vivipara* when it co-occurs either with *D. octopetala* or *S. herbacea*, significant differences were observed in the estimated OTU richness between sites containing *D. octopetala* + *B. vivipara* and *S. herbacea* + *B. vivipara* ($F = 5.764$, $p\text{-value} = 0.002$) (Fig. 2.1C).

Ordination (NMDS, Fig. 2.2) and PERMANOVA results ($F = 2.505$, $R^2 = 0.102$, $p\text{-value} = 0.001$) in the root dataset revealed significant differences among hosts particularly between *D. octopetala* and *S. herbacea*, while EM communities of *B. vivipara* were more similar to those of the other two hosts.

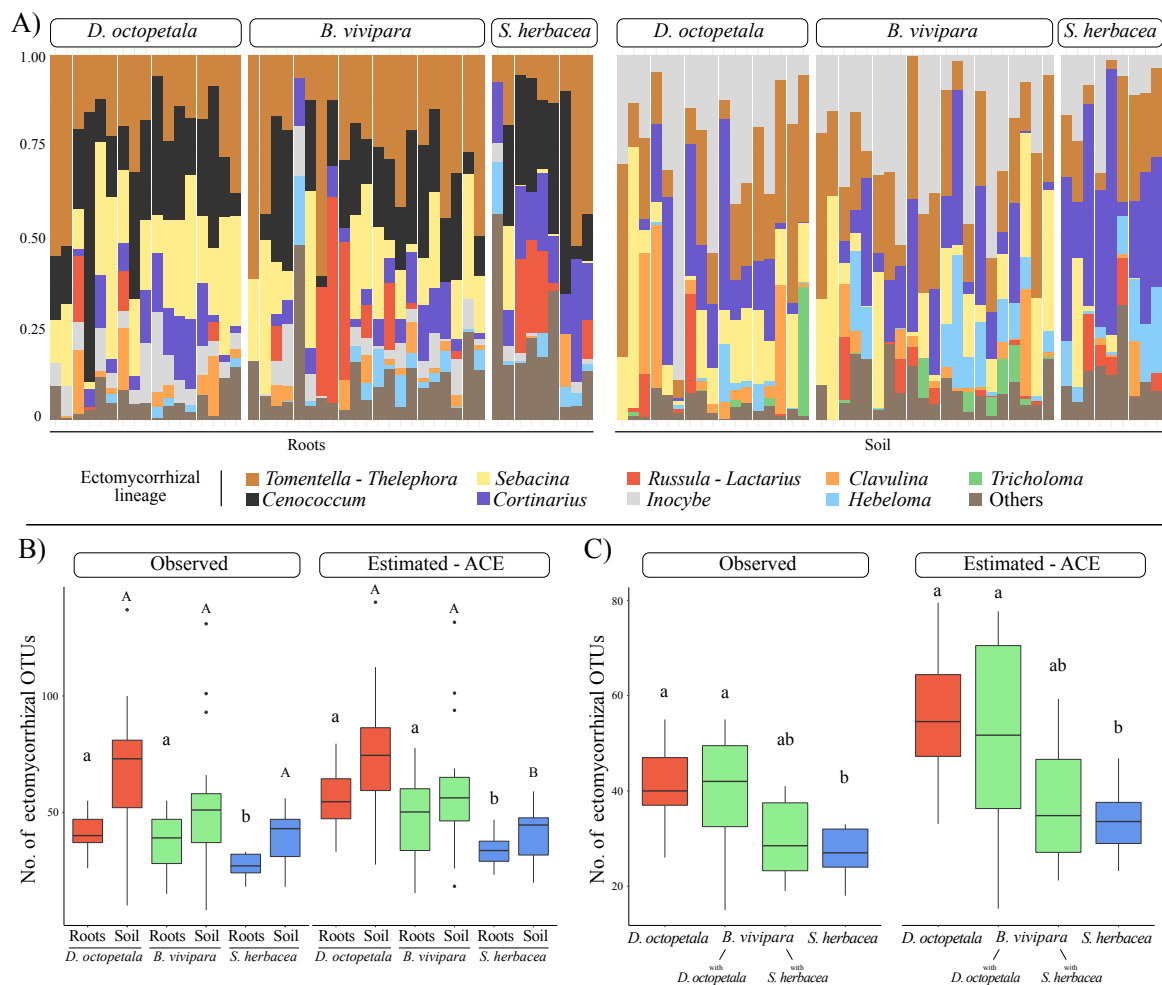


Figure 2.1 A) Relative abundance of each EM fungal lineage per site across plant hosts as ectomycorrhizas in the roots (left) and in the soil (right). B) Mean observed and estimated (ACE) number of EM fungal OTUs in roots (ectomycorrhizas) and soil across hosts. C) Mean observed and estimated (ACE) number of EM fungal OTUs in roots across hosts, separating *Bistorta vivipara* when co-occurring either with *Dryas octopetala* or with *Salix herbacea*.

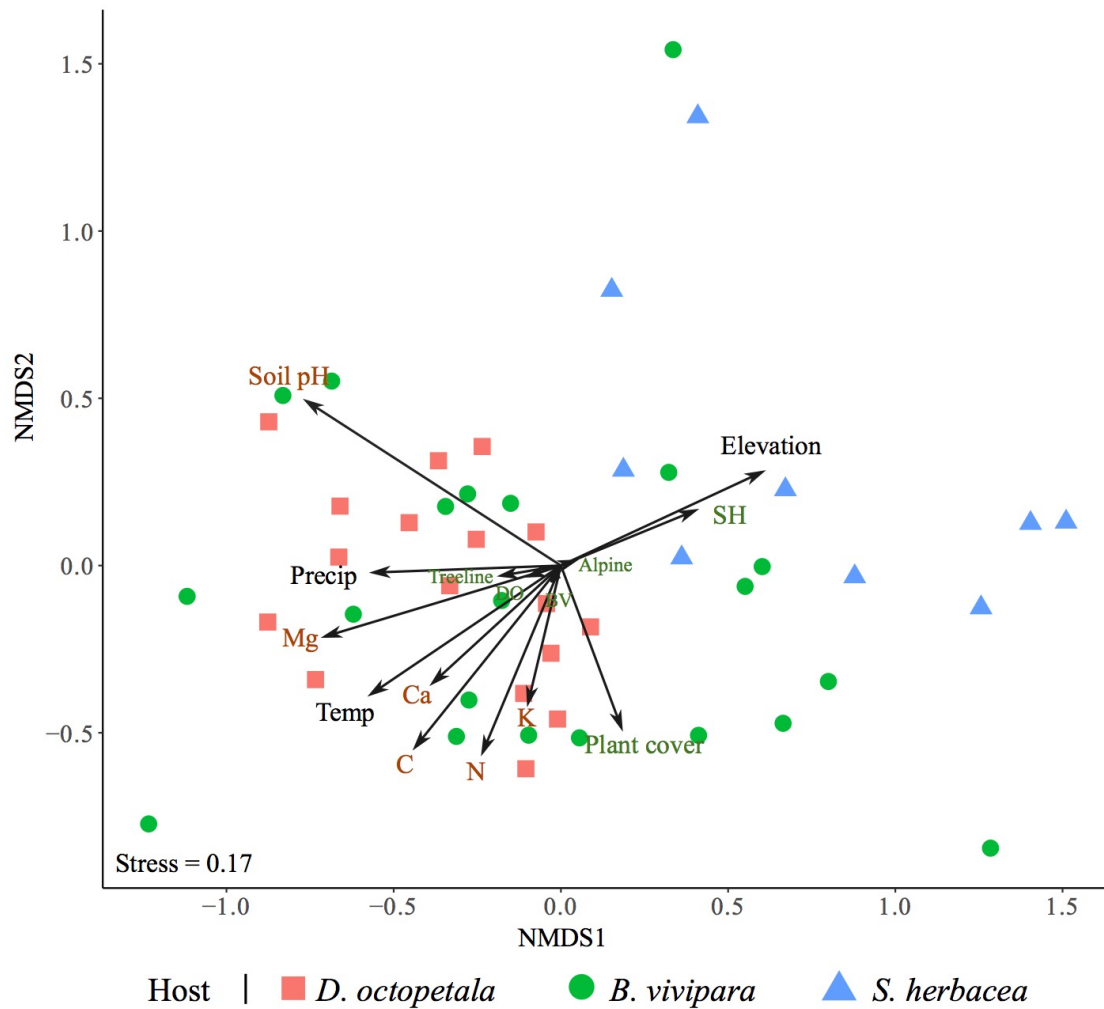


Figure 2.2 Non-metric multidimensional scaling (NMDS) ordination of the Bray-Curtis dissimilarity matrix of EM fungal communities associated with the roots (ectomycorrhizas) of *Dryas octopetala* (red), *Bistorta vivipara* (green) and *Salix herbacea* (blue). Arrows show the direction and strength of correlation of the environmental variables with significant contribution (p -value ≤ 0.05) to community dissimilarities. Environmental variable labels represent edaphic properties (brown), host and habitat (green) and elevation and climate (black).

EM communities along elevation gradients

No significant differences in fungal OTU richness along the elevation gradient were observed when using the absolute value of elevation or when comparing sites in the treeline versus alpine zones. However, significant differences in community composition were observed between alpine and treeline zones using constrained ($R^2 = 0.079$, p -value = 0.001) and unconstrained permutations ($R^2 = 0.043$, p -value = 0.004). These differences in community composition were not

constrained by phylogenetic signal (EM lineage), but by taxonomical composition (Appendix A: Fig. S2.1).

On average, across sites, the observed mycorrhizal soil exploration type with higher number of EM taxa (OTUs) was the short distance type (treeline: 29 ± 7 ; alpine: 22 ± 8), followed by contact (treeline: 7 ± 3 ; alpine: 8 ± 5) and medium-distance fringe (treeline: 3 ± 2 ; alpine: 6 ± 3) exploration types (Fig. 2.3A). The number of taxa with short-distance soil exploration types was higher in the treeline while more taxa showing medium-distance fringe types were found in the alpine zone (p -value ≤ 0.05 ; Fig. 2.3B). Across the three hosts, the most abundant soil exploration type was also short-distance (Fig. 2.3C), with significantly lower numbers of OTUs and average number of colonised root tips in *S. herbacea* than in the other hosts (Fig. 2.3D). On average, the number of ectomycorrhizas per site with medium fringe distance soil exploration type was higher in *S. herbacea* (Appendix A: Fig. S2.2D).

The overall network specialization index ($H2'$) revealed that both treeline and alpine networks were more specialized than expected at random (treeline: p -value = 0.007, z -score = 3.277; alpine: p -value < 0.001, z -score = 6.706) with the alpine network showing higher values of specialization ($H2'_{\text{treeline}} = 0.305$, $H2'_{\text{alpine}} = 0.454$). Across hosts, the highest level of specialization was observed in *S. herbacea* ($d'_{\text{obs}} = 0.571$, p -value < 0.001, z -score = 9.158) followed by *D. octopetala* ($d'_{\text{obs}} = 0.409$, p -value = 0.001, z -score = 4.833), and then *B. vivipara* ($d'_{\text{obs}} = 0.261$, p -value = 0.960, z -score = -1.566).

Environmental drivers of EM communities

Across sites, twelve environmental variables contributed significantly to the dissimilarity of EM fungal communities in roots: elevation, annual mean temperature, annual precipitation, soil total C, soil total N, soil pH, $[\text{Ca}^{2+}]_{\text{soil}}$,

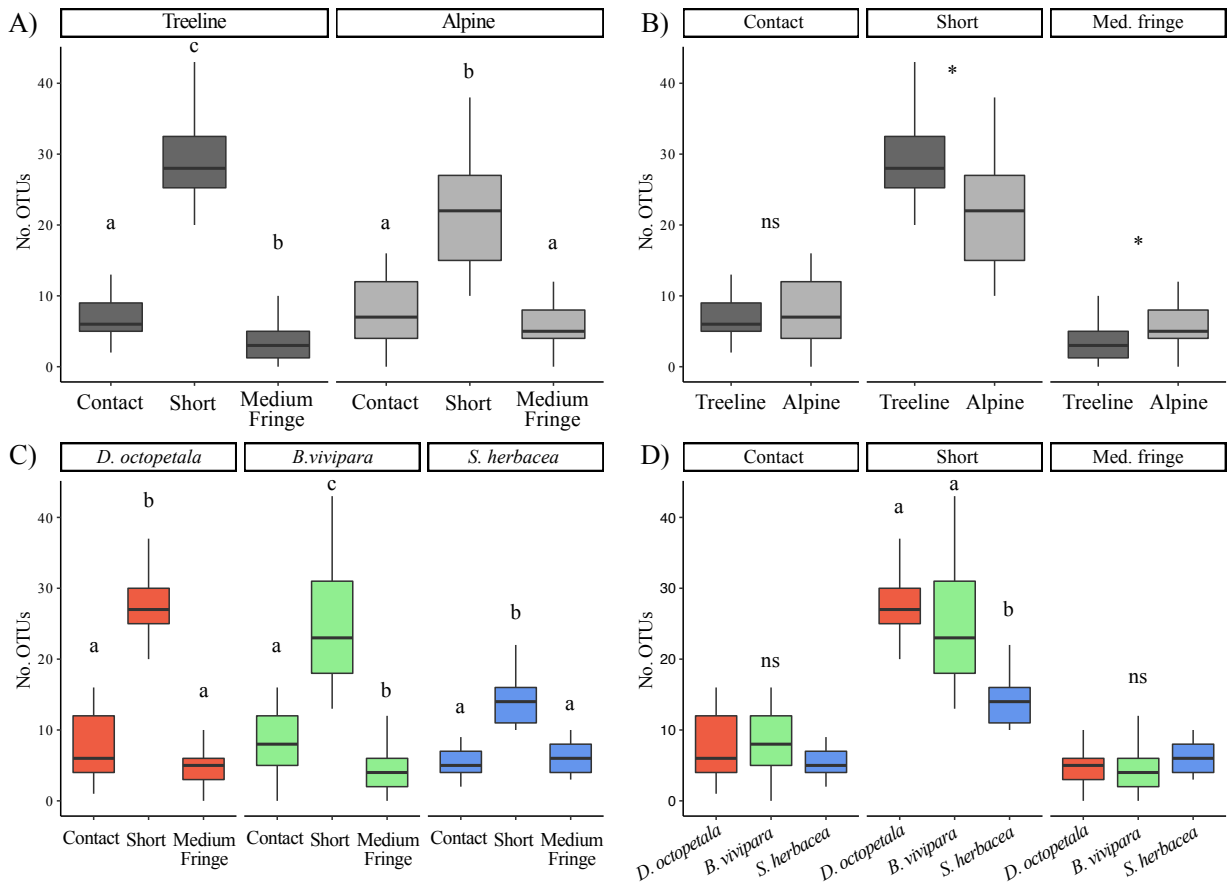


Figure 2.3 Comparison of the number of EM fungal OTUs showing different soil exploration types: A) within the treeline and alpine zones, B) in alpine versus treeline zones, C) within hosts, and D) among hosts. Significant differences (p -value ≤ 0.05) are represented by different letters and asterisks.

$[K^+]_{\text{soil}}$, $[Mg^{2+}]_{\text{soil}}$, percentage of plant cover, plant host species and habitat (treeline vs alpine) (Fig. 2.2 & Appendix A: Table S2.2). Elevation, soil total C, $[Ca^{2+}]_{\text{soil}}$ and $[K^+]_{\text{soil}}$ were discarded from further analyses due to high collinearity with other environmental variables (Pearson correlation $r \geq 0.7$). The model incorporating all the biotic, edaphic and climatic variables had the highest explanatory power in EM community data (*ca.* 23%, Table 2.2). The explained variance partitioning of the best model fit showed that across OTUs the mean contribution of the biotic factors was 54%, followed by edaphic variables (30.7%), climatic variables (11.2%), and least by site (random effect) (4.1%) (Fig. 2.4). Soil exploration type explained 12% of the variation in communities found in the different environmental niches, but no influence of EM lineage was

Table 2.2 Hierarchical models structure ranked by increasing explanatory power. All models were fitted with the abundance matrix of EM fungal OTUs (Y) as a function of each covariate combinations.

Model description	Covariates	Tjur R^2	AUC
Y ~ Biotic	Host + Habitat + %Plant cover	0.1249014	0.8308060
Y ~ Climatic	Mean annual temperature + Annual precipitation	0.1344104	0.7905452
Y ~ Biotic & Climatic	Host + Habitat + %Plant cover + Mean annual temperature + Annual precipitation	0.1565941	0.8326551
Y ~ Edaphic	Soil pH + N _{total} + Mg _{Soil}	0.1722163	0.8351184
Y ~ Climatic & Edaphic	Mean annual temperature + Annual precipitation + Soil pH + N _{total} + Mg _{Soil}	0.1900532	0.8396078
Y ~ Biotic & Edaphic	Host + Habitat + %Plant cover + Soil pH + N _{total} + Mg _{Soil}	0.2002692	0.8563508
Y ~ Biotic & Climatic & Edaphic	Host + Habitat + %Plant cover + Mean annual temperature + Annual precipitation + Soil pH + N _{total} + Mg _{Soil}	0.2293536	0.8798085

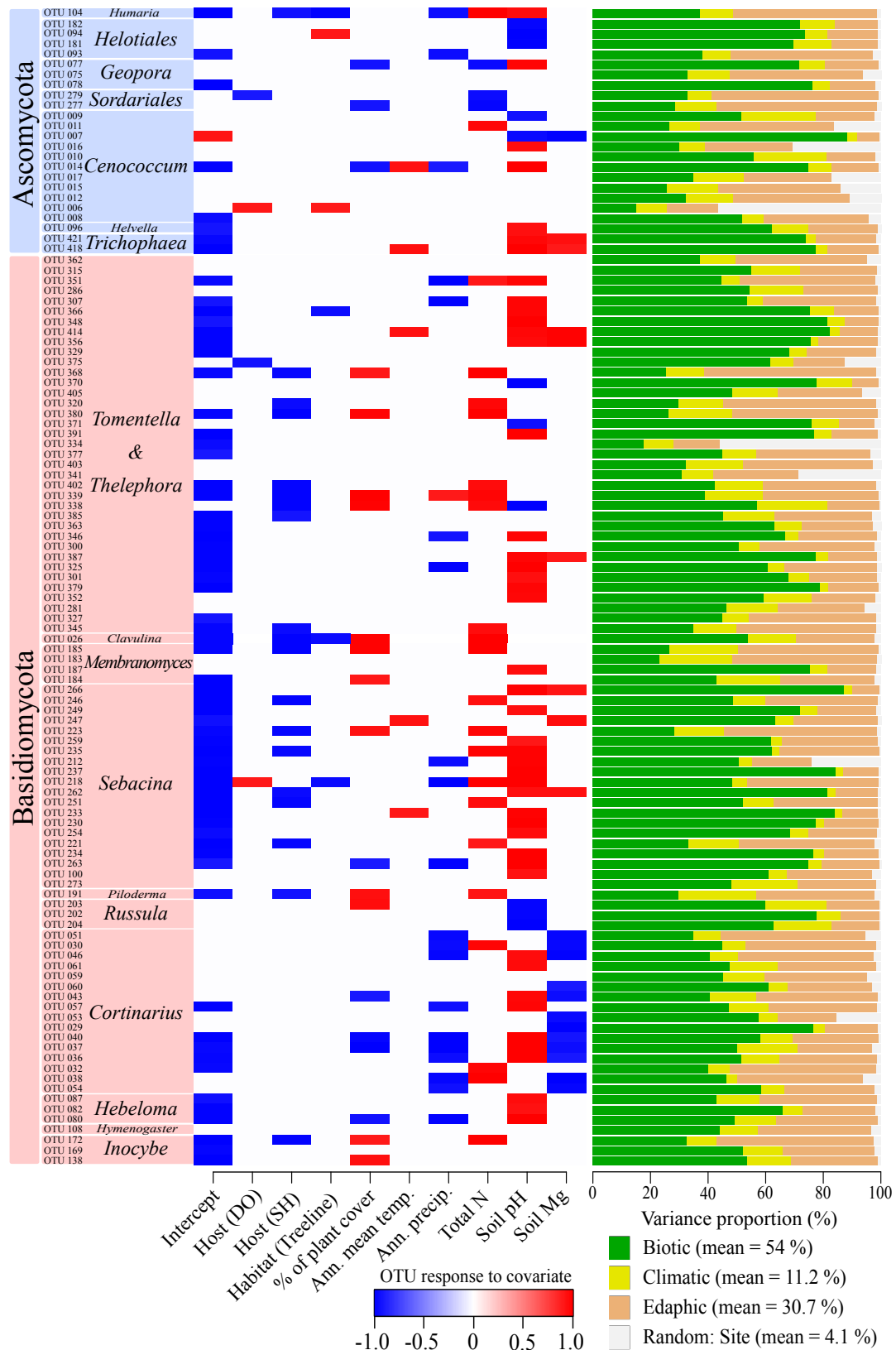


Figure 2.4 Posterior support values for the ectomycorrhizal fungal OTU environmental responses. Only highly values (≥ 0.95) are shown. Horizontal bar plots represent variance partitioning in the abundance of each individual OTU with covariates contributions grouped by biotic (host species + habitat + total plant cover), climatic (annual mean temperature + annual precipitation), edaphic (soil pH + N_{total} + $[Mg]_{soil}$) and random effects (site).

observed based on the posterior mean of the correlation parameter ($\rho = 0.52$, with a 95% CI of 0.23 to 0.72). Many OTUs showed significant responses to the environmental covariates (posterior support level > 0.95). Most fungal OTUs responded positively to increasing soil pH and total soil N and negatively to increasing annual precipitation. A generalised negative response of *Cortinarius* OTUs to increasing soil Mg^{2+} was also observed.

Host population structure and EM communities

The effect of host genotype on EM communities was only estimated in *D. octopetala* and *B. vivipara*. Scoring genetic markers in *S. herbacea* was difficult and no population structure was found. The STRUCTURE analysis revealed that the optimum number of clusters in *D. octopetala* was four and in *B. vivipara* six (Appendix A: Fig. S2.3), but only the four most distinct ones from the latter were selected for further analyses due to unclear population subdivision. Pairwise F_{st} values were calculated among clusters (Appendix A: Table S2.3) and ranged from 0.018 (cluster 3 vs cluster 4) to 0.063 (cluster 1 vs cluster 2) in *D. octopetala* and 0.017 (cluster 3 vs cluster 4) to 0.084 (cluster 1 vs cluster 2) in *B. vivipara*. Analysis of molecular variance revealed no significant differentiation among clusters in *D. octopetala* or *B. vivipara* (Appendix A: Table S2.4). Analysis of variance in the mean estimated EM OTU richness per site and PERMANOVA analyses showed that there were no significant differences among genotype clusters of *D. octopetala* or *B. vivipara* in community richness and composition.

2.5 Discussion

To the best of my knowledge, this is the most extensive sampling of ectomycorrhizas across the European Alps testing how fungal communities above the treeline and up to the nival zone are shaped along altitudinal and environmental gradients. Over four hundred EM fungi were detected in the alpine

zone living across an extensive variety of ecological niches and influenced by complex interactions among biotic and abiotic factors. The results of this study revealed differences in community composition between the treeline and the alpine zone. In addition, I observed that alpine zone EM communities establish more specialized networks. This can have significant implications for mountain biodiversity and the ecosystem functions that plants and fungi provide, because alpine ecosystems are expected to experience relatively rapid rates of environmental change compared to lower elevations (Winkler *et al.*, 2019), thus placing highly specialized communities at risk.

Ectomycorrhizal diversity

In mountains generally, from the treeline ecotone to the nival zone, soils are nutrient deficient and inorganic nitrogen and phosphorus are scarce (Kielland, 1994); these areas are characterised by a high exposure to wind, high solar radiation, low temperatures and they are covered by snow for the most of the year (Nagy & Grabherr, 2009). Despite their small size, *D. octopetala*, *B. vivipara* and *S. herbacea* associate with 423 EM taxa across the Alps. Previous studies of EM on these plants at smaller scales also found a high number of fungal species in the Alps (Mühlmann *et al.*, 2008; Mühlmann & Peintner, 2008; Pellissier *et al.*, 2014; Brunner *et al.*, 2017) and across other alpine areas (Ryberg *et al.*, 2009; Gao & Yang, 2010; Bjorbækmo *et al.*, 2010; Mundra *et al.*, 2016; Botnen *et al.*, 2019). Here, the dominant EM fungal genera were *Tomentella* and *Thelephora*, *Cenococcum* and *Sebacina*, as in other belowground studies of alpine meadows (Read & Wandter, 1981; Ryberg *et al.*, 2011; Gao & Yang, 2016), alpine glacier valleys (Mühlmann *et al.*, 2008; Mühlmann & Peintner, 2008) and alpine cliff edges (Ryberg *et al.*, 2009). Dominants like *Cenococcum* spp., *Tomentella* spp. and *Sebacina* spp., that form sclerotia or crusts, do not correspond with dominant fruitbody-formers aboveground, which are predominantly mushroom-forming

Cortinarius, *Inocybe*, *Hebeloma* and *Russula* species (Favre, 1955; Senn-Irlet, 1988; Graf, 1994; Jamoni, 2008). In this study, many hypogeous fungi usually overlooked in fruitbody inventories such as *Genabaea*, *Hydnobolites*, *Hymenogaster*, *Melanogaster*, *Elaphomyces* and *Gauteria* were also detected.

The results showed that these three plants recruit approximately 39% of the available EM fungi detected in soil. This relatively small percentage can be partly due to the presence of other EM hosts harbouring additional fungi and/or partly to analysing communities based on soil DNA which does not discriminate active, dormant or dead organisms, or intra- versus extra-cellular sources (Carini *et al.*, 2016; Wutkowska *et al.*, 2019). For instance, *Cenococcum geophilum* OTUs were not detected in soil DNA, whereas these were dominant as ectomycorrhizas. Kauserud *et al.* (2012) reported methodological bias during library preparation in the detection of *C. geophilum* when comparing 454 pyrosequencing with cloning followed by Sanger sequencing of root communities in *B. vivipara*, with relatively low overlap in fungal OTUs observed between the two methods, even among the most abundant taxa. Both HTS and Sanger do not seem to result in significant differences at high taxonomic levels, like order (Amend *et al.*, 2010), and both techniques yield roughly similar phylogenetic community structure (Tedersoo *et al.*, 2010b). However, in this study and at species level, some dominant OTUs in roots were not detected in soil, calling for caution when analysing and extrapolating results from soil mycobiome analysis. The results of the present study were also congruent with Pellissier *et al.* (2014), Rime *et al.* (2015) and Frey *et al.* (2016) where *C. geophilum* was not detected in soil DNA. Thus, a possible explanation for the obtained results may be the temporal dynamics of mycelial growth or limited extraradical growth and/or reproduction of one of the dominant EM fungi in alpine ecosystems.

The influence of host on EM community structure and composition has been observed in previous studies (Ishida *et al.*, 2007; Gao *et al.*, 2013; Tedersoo *et*

al., 2013; van der Linde *et al.*, 2018), but the extent of this influence remains poorly understood, mainly due to the difficulty in disentangling confounding interactions among plant hosts, microbial communities and edaphic and environmental variables (Aponte *et al.*, 2010; Peay *et al.*, 2015). In this study, I found that *S. herbacea* associates with the most specialized set of EM fungi, followed by *Dryas octopetala*, while *B. vivipara* had the least specialised communities. *Salix herbacea* occurs in a narrower ecological niche than the other two species studied, in very particular edaphic conditions, soils poor in nutrients, mostly acidic and with snow cover up to ten months per year, which might also explain the less species rich EM communities adapted to these harsh conditions. *Bistorta vivipara*, on the other hand, grows in a wider environmental range and can co-occur with the other two species. To disentangle host effect from other confounding environmental factors like soil pH, I analysed the EM communities associated with *B. vivipara* when it co-occurred either with *S. herbacea* or with *D. octopetala*. I found that *B. vivipara* harboured very similar communities to the corresponding co-occurring host, but contrasting communities at different habitat conditions, therefore, disentangling host from habitat effects. Similar confounding effects were observed by Fujimura & Egger (2012); they detected highly specialized EM communities associated with *Salix arctica*, and both host identity and environment explained similar proportions of EM community variability. Botnen *et al.* (2014) detected a lack of host fungal specificity in EM communities of *B. vivipara*, *D. octopetala* and *S. polaris* suggesting that: i) associating with fungi with as many different physiological attributes as possible may be favourable for the host plant to access a broader range of nutrient pools, and ii) association with more generalist fungi may allow plants to more rapidly and easily colonize new habitats. On the other hand, fungal host specialization could provide greater physiological compatibility with the targeted plant host, resulting in greater competitive ability on that host or greater access to the host's

resources (Bruns *et al.*, 2002). Nevertheless, lack of host specificity may facilitate dispersal across the complex mosaic of alpine habitats with highly heterogeneous edaphic properties and a limited number of putative EM plant hosts. Moreover, the lack of EM specialist fungi in these harsh environments may also be related to the short growing season of their hosts and the steep changes in temperature conditions. The small window of opportunity provided by the snow-free season in alpine ecosystems may result in a disadvantage for specialized fungi in case their hosts do not achieve their metabolic optimum conditions, resulting in less carbon availability for the fungi. Thus, the results of this study indicate that in the Alps, these three plants and EM fungi tend to be generalists in their interactions, but their distribution range is limited by the ecological niche they occupy and by the complex and heterogeneous environmental characteristics, inherent to alpine habitats.

EM communities along elevation gradients

Disentangling the effects of elevation in mountains is difficult due to underlying co-varying factors, such as temperature, precipitation and soil nutrient content. Across host plants, EM community composition in the alpine zone shifted along the elevation gradient up to the nival zone, but no significant differences were detected in richness. Strong negative effects of elevation on EM fungal richness and changes in community composition have been observed in several mountain ecosystems worldwide at local scales. Bahram *et al.* (2012) found that EM fungal richness declined monotonically along an increasing elevation gradient in the old-growth Hyrcanian forests of Iran, explained by a lower resource availability (e.g. soil nutrient and water content) at higher elevations reducing the competitive ability of rare species and having a negative effect on EM richness. Similarly, EM richness decreased at increasing elevations in the Peruvian Andes (Nottingham *et al.*, 2018) with increasing dissimilarities in community

composition at further distances between elevations. Those studies, however, were not restricted to the alpine zone, so significant differences in richness were found due to wider elevation gradients. Kernaghan & Harper (2001) observed changes in EM fungal community composition and richness with elevation in the Canadian Rockies by sampling ectomycorrhizas and fruitbodies across a sub-alpine montane forest of *Picea* and *Abies* spp., a treeline ecotone with scattered willows and ericaceous shrubs, and an alpine zone dominated by *Dryas* spp. Changes were only significant between the sub-alpine forest and the alpine zone, not between treeline ecotone and alpine zone. Similarly, Collins *et al.* (2018) found that overall soil fungal richness and diversity declined with elevation, but differences were more pronounced between sub-alpine and alpine sites and were not significant within alpine sites. Adamczyk *et al.* (2019) however, analysed fungal communities from low alpine to the nival zone (2,400 – 3,200 m) in the same valleys in Switzerland sampled in this study and did not detect correlation between fungal richness and elevation, while pH was the strongest predictor of fungal beta diversity. In the present study, a declining trend in EM richness with elevation was observed, but it was not significant (Appendix A: Table S2.5). On a global scale, EM fungal community richness is primarily influenced by the relative proportion and richness of host plants, soil pH, mean annual temperature and precipitation (Tedersoo *et al.*, 2012, 2014). In mountains, climatic variables (Nottingham *et al.*, 2018) and plant host distributions (Pellissier *et al.*, 2014; Geml *et al.*, 2017) explain most of the variation in EM fungal community richness. The complex collinearity among climatic, edaphic and topographic predictors in mountain ecosystems makes it difficult to address the isolated effect of elevation across regional scales. In this study, I addressed this issue by sampling along multiple elevation gradients across a wide environmental gradient. Elevation on its own was not a good predictor of EM fungal richness in the alpine zone, this is probably due to the variation across sites in elevation for

the treeline and the alpine zones, that at regional scales and in the case of the treeline, is usually associated with thermal conditions (Holtmeier & Broll, 2017). Instead, an indirect effect of elevation was detected through climate and soil conditions.

Some EM lineages like *Hebeloma* or *Inocybe* spp., are dominant in arctic ecosystems at northern latitudes and show differential tolerance to temperature (Tibbett *et al.*, 1998; Geml *et al.*, 2012; Timling *et al.*, 2012; Blaaliid *et al.*, 2014). In this extensive study, I found that only *Cortinarius* OTUs were influenced by environmental factors. Many OTUs of *Cortinarius* were found more frequently associated with the host plants in alpine sites than in sites closer to the treeline. This habitat specialization to snowbed communities by *Cortinarius* OTUs was also observed by Yao *et al.* (2013) in a study comparing the EM fungal community turnover from alpine ridges to snowbeds in Norway. Similarly, Koizumi & Nara (2020) showed a temperature dependency of *Cortinarius* at the treeline, with more frequent records at lower mean summer temperatures.

Variation in EM functional traits (i.e. presence of hyphae and rhizomorphs, which define soil exploration types) in alpine EM fungal communities were more related to alpine ecosystem properties (e.g. edaphic properties and short snow-free periods) than to elevation or host specificity. Moreover, despite the high EM taxonomic diversity in the Alps, there is a high degree of functional redundancy with many different fungi showing similar traits. In addition, the results of this study revealed that EM communities were dominated by short distance soil explorers. In forest ecosystems, short soil explorers seem to be preferentially associated with higher nutrient availability in soils (Lilleskov *et al.*, 2011; Jarvis *et al.*, 2013), with colder climates where hosts have lower photosynthetic capacity (Fernandez *et al.*, 2017), or with colder and drier environments (Castaño *et al.*, 2018; Botnen *et al.*, 2019; Defrenne *et al.*, 2019). In alpine ecosystems plant resources are limited by short growing seasons restricted to snow-free periods,

large temperature shifts and ultraviolet radiation affecting photosynthetic reactions, and by strong wind exposure in steep slopes that can affect soil water retention (Nagy & Grabherr, 2009; Donhauser & Frey, 2018). Moreover, poorly developed soils with high gravel content lead to a highly heterogeneous soil matrix. Alpine plants are adapted to these harsh conditions, at least partly through reliance on fungi with limited soil exploration abilities (short distance and contact explorers; Fig. 2.3A). A high C demand from medium and long explorers (Lilleskov *et al.*, 2011) could be a disadvantage in harsh environments and potentially these are only cost effective at even lower nutrient conditions. This was shown by the higher abundance of EM taxa (OTUs) associated with *S. herbacea* with medium fringe exploration types in alpine sites (Appendix A: Fig. S2.2D). This is probably driven by the preferential association of *Cortinarius* spp. with *S. herbacea* and the particular ecological niche where they occur. In those nutrient-depleted acidic soils, medium-fringe explorers' ability to mine organic sources of nitrogen appears critical.

Environmental drivers of EM fungal communities

Hierarchical modelling revealed that the occurrences of EM fungi across the European Alps are shaped by a complex grid of biotic and abiotic drivers. The results showed that, within the explained variability of the best model, alpine EM communities are mostly influenced by host species (29.4%), soil Mg^{2+} (18%), mountain zone (treeline vs alpine, 14.4%) and soil pH (10.9%). However, the large explained variability assigned to host species could have been influenced by the underlying ecological niche preferences (e.g. soil pH) of *D. octopetala* and *S. herbacea*. At a continental scale in European forests, EM fungal communities respond to host and environment (van der Linde *et al.*, 2018) with soil nutrient availability among the most important drivers of EM community richness and composition (Cox *et al.*, 2010b; Suz *et al.*, 2014). In alpine and arctic ecosystems,

changes in *B. vivipara* root-associated fungal community composition have been shown to be correlated with changes in soil pH, C, N and P content (Blaalid *et al.*, 2012; Yao *et al.*, 2013). The higher pH characteristic of calcareous and dolomite soils, usually linked to more species rich plant communities, and the high content of Mg (as $\text{CaMg}(\text{CO}_3)_2$) in the latter, might partly explain the emergence of both variables as drivers of communities in these habitats. In contrast to other studies where climatic variables were found to be drivers of EM fungal communities at global (Tedersoo *et al.*, 2012, 2014) and regional scales (Bahram *et al.*, 2012; Botnen *et al.*, 2019), the results of this study revealed that precipitation and temperature were the weakest predictors of EM community composition across the Alps. This can probably be explained by the lower variability in mean annual precipitation and temperature at regional scales in mountains, where host identity, distance from the treeline and soil chemistry become more important, explaining *ca.* 23% of the EM community variability.

It was also observed that environmental filtering leads to variable occurrence of EM fungi across the Alps, but only the occurrence of *Cortinarius* spp, seemed to show phylogenetic signal. The highest number of *Cortinarius* OTUs were observed at higher elevations where the N content in soil was lower. Fungi with different soil exploration types respond differently to N concentrations in soil (Lilleskov *et al.*, 2011; Suz *et al.*, 2014), with evidence that specialized organic N miners with proteolytic abilities, such as *Cortinarius* spp., are negatively influenced by the presence of high levels of inorganic forms of nitrogen in the soil, particularly from anthropogenic atmospheric N deposition (Cox *et al.*, 2010b; Lilleskov *et al.*, 2011; Suz *et al.*, 2014; van der Linde *et al.*, 2018). Moreover, this study revealed that in the alpine zone, only 12% of OTUs niche preference was explained by the soil exploration type of the ectomycorrhizas. Therefore, isolating environmental filtering from other non-random processes that could affect EM fungal community structure and composition remains

difficult. Nevertheless, the responses of individual fungal taxa to environmental factors help to better understand EM fungal community resilience to environmental change across the Alps. Despite the weak effect of climate on these communities, habitat loss due to climate change (e.g. via upward expansion of sub-alpine forests) can have crucial consequences in the most specialised EM communities (Pauli *et al.*, 2012; Wipf *et al.*, 2013). Experiments are now necessary to assess resilience of alpine ecosystems to future climate change scenarios. Extending analysis to other alpine habitats (e.g. grasslands), hosts and sampling seasons will help to better understand the space-time variability of communities in the alpine zone. It is also necessary to extend the study of EM communities from the sub-alpine to the nival zone to assess how richness, composition and functional traits vary along mountain environmental gradients.

Host population structure and EM communities

The genetic structure of natural plant populations is the result of life history traits and ecological factors affecting reproduction and dispersal, as well as population genetic processes such as bottlenecks and genetic drift. The frequency of sexual reproduction in plants has been shown to decrease with increasing latitude and elevation (Peck *et al.*, 1998). Plants tend to invest more in vegetative clonal growth because it enables individuals to persist and grow in an extreme environment where sexual reproduction often is unsuccessful (Nagy & Grabherr, 2009). On the other hand, if survivorship is based too heavily on clonal growth, intra-specific genetic diversity could eventually be reduced (Wookey *et al.*, 1995). Both *D. octopetala* and *S. herbacea* reproduce sexually by airborne seeds and grow forming extensive carpets covering the ground, while *B. vivipara* is apomictic, reproducing asexually. It was expected that these differences in lifestyles and the complex geomorphology and high habitat variability in the Alps

could have an effect on the population structure of these plants and therefore influence their EM communities.

The lack of allele polymorphism in the SSR markers used for *S. herbacea* and the high ploidy levels in *B. vivipara* made it difficult to assign individual genotypes to each of the populations. The SSR markers used in *D. octopetala* provided enough resolution to distinguish between ramets and therefore provide useful information at a regional scale. However, despite the strong effect of host species identity on community variability, no influence of *D. octopetala* genotype was found on fungi, potentially due to confounding effects of environmental variability. Future studies involving well-known phenotypically-expressed plant traits (e.g. drought tolerance) and controlling for environmental variability could help to better understand host genotype effects on EM communities.

2.6 Conclusions

This extensive study characterized the biotic and abiotic drivers of EM fungal communities along elevation gradients in the European Alps. Despite the harsh environmental conditions, alpine EM fungal communities are highly diverse, and richness does not decrease with elevation, but fungal composition varies from the treeline to the alpine zone. Given the complex mosaic of habitats with diverse climatic and edaphic conditions in these ecosystems, mountain habitat zonation (alpine vs treeline), soil pH and total nitrogen in the soil explain most of the variation in EM fungal communities of above-treeline plants across the Alps. Moreover, this study highlights the uniqueness and vulnerability of the EM communities in snow-patch and snowbed communities of dwarf willows characteristic of alpine habitats.

Chapter 3

Snowbed ectomycorrhizal fungi decline across the European Alps.

3.1 Abstract

The European Alps are experiencing more than twice the increase in air temperature compared to the rest of the world. As a consequence, many unique habitats from the alpine and nival zones are suffering drastic changes in their biological communities. However, our knowledge about the impacts of future climatic scenarios belowground is scarce. Here I investigate how changes in soil nutrient content and future predicted climatic shifts in temperature and precipitation may influence alpine ectomycorrhizal (EM) communities associated to *Dryas octopetala*, *Bistorta vivipara* and *Salix herbacea* across the European Alps. This study revealed i) significant changes in EM fungal community composition between alpine habitats and the treeline ecotone under predicted scenarios; ii) that EM fungal communities characteristic of alpine habitats will be mostly negatively affected by increase in precipitation of the warmest quarter; and iii) indicator species from alpine acidic habitats will be the most negatively affected by future environmental climatic scenarios, while indicator fungi from the treeline ecotone will increase in relative abundance. These results suggest that under future climatic scenarios the EM fungal communities from the acidic alpine snowbeds are expected to be replaced by lowland species with wider ecological niches. The decline of snowbed EM fungal communities and the ecosystem functions they support will have strong impacts on alpine habitats.

Keywords

Climate change, Temperature, Precipitation, Ectomycorrhizal fungi, Environmental thresholds, Alpine ecosystems, Snowbeds, *Dryas octopetala*, *Salix herbacea*, *Bistorta vivipara*.

3.2 Introduction

Habitat loss due to climate change is one of the main challenges to global biodiversity conservation. Shifts in climatic conditions at regional and global scales influence plant species phenology and distribution ranges leading to either new habitat colonisation or to species extinction. These shifts become of particular relevance in mountain ecosystems where habitat zonation and species distributions are highly defined along the altitudinal gradient by their climatic optimum (Lenoir *et al.*, 2008; Pauli *et al.*, 2012) so that thermal conditions define the treeline (Holtmeier & Broll, 2017). Recent increases in atmospheric temperatures and changes in hydrological periods have been contributing to the upwards expansion of lowland habitats towards the highlands (Chen *et al.*, 2011). For example, the upwards expansion of the treeline ecotone and subsequently the montane and sub-alpine habitats due to breakdown of their climatic constraints have been already observed all around the palearctic region (Garamvölgyi & Hufnagel, 2013). Across the European Alps, it is well established that due to the contraction of the alpine and nival zones, their highly specialized plant communities will tend to be replaced by others more resilient and adapted to new environmental conditions (Pauli *et al.*, 2007; Engler *et al.*, 2011; Matteodo *et al.*, 2016). However, little is still known about the impacts in their associated belowground communities, in particular ectomycorrhizal (EM) fungi, the main nutritional mutualists of woody perennial plants above the treeline that play pivotal roles in plant establishment and colonisation of new habitats in these harsh environments.

The global trend of rising atmospheric temperature is expected to continue in association with drastic shifts in precipitation regimes (IPCC, 2007). In the Alps, warming has been shown to be more than twice as high than in the northern hemisphere overall, with shifts already registered up to +1.7 °C in some regions (Rebetez & Reinhard, 2008; Zimmermann *et al.*, 2013). In addition, higher temperatures combined with smaller snowfalls during the spring season are expected to result in earlier melting of the snowpack (IPCC, 2014). Future climate projections predict a general warming trend in the range of 1.8 to 4.0 °C in the annual mean temperature in the Alps in 2051-2080, with least warming in the winter half, and highest warming in the summer months. Moreover, precipitation regimes are also expected to change with some regions in the Central Alps receiving less than 30% of the current summer rainfall amounts (Zimmermann *et al.*, 2013). As a consequence, numerous plant biochemical processes, such as growth rate, carbon allocation, nutrient cycling and competitive interactions, may be affected leading to changes in plant community structure and composition, in particular at high-altitudes (Nagy & Grabherr, 2009). Recent studies showed an increase in species and an upward range extension of some plants from lower elevations (Stöckli *et al.*, 2011). In the Swiss Alps, Matteodo *et al.* (2016) showed that the arrival of exogenous species to alpine belt habitats has been contributing to the homogenization of the composition of native communities. Moreover, snowbeds showed pronounced vegetation changes due to climatic shifts towards drier conditions with shorter snow cover periods. Thus, snowbed plant communities, adapted to up to ten-month periods of snow cover, are among the most vulnerable alpine habitats to climate change and their persistence in the near future is seriously threatened.

Climate change impacts on plant and animal communities have been well documented (Parmesan & Yohe, 2003; Root *et al.*, 2003) and for fungi at least the direct effect of climate change on aboveground fungal reproduction or

indirect effects on their habitats have become apparent (Büntgen *et al.*, 2012; Fisher *et al.*, 2012; Boddy *et al.*, 2014; Andrew *et al.*, 2018). However, little is still known about climate change impact in fungi belowground. Changes in fungal fruitbody phenology, including EM fungi, have been reported to follow the extension of plant growing seasons (Kausrud *et al.*, 2008). However, these effects are highly variable among species and are partly explained by individual life-history characteristics (Diez *et al.*, 2013).

In a study across 68 North American sites of Pinaceae forests, Steidinger *et al.* (2020) predicted that rising mean annual temperature along the boreal-temperate forest ecotone may result in loss of EM fungal species and decline in relative abundance of certain groups of fungi with different abilities to explore the soil and scavenge nutrients (Agerer, 2001, 2006). Across the Alps, many fungal species have been fruiting at increasingly higher elevations during the last fifty years, with species growing at higher elevations changing their altitudinal fruiting patterns significantly more than lowland species (Diez *et al.*, 2020). Changes in soil nutrient contents driven by atmospheric pollution can also influence the distributions of soil microorganisms (Singh *et al.*, 2010). From local to continental scales, EM fungal communities respond strongly to long-term nitrogen (N) deposition with the loss of key taxa and functional groups, especially medium-distance soil explorers with hydrophobic walls, proteolytic capacity, and peroxidases for acquiring N from soil organic matter (Cox *et al.*, 2010b; Suz *et al.*, 2014; van der Linde *et al.*, 2018; Lilleskov *et al.*, 2019). However, there had been no regional scale studies in mountain ecosystems covering wide environmental gradients to produce better estimates of the resilience of these fungal communities and how changes at regional scales may impact habitats at higher risk of extinction.

Building on the generated dataset and results from **Chapter 2**, here I aim to assess how changes in soil nutrient content and future climatic shifts in

temperature and precipitation will influence alpine EM fungal communities across the European Alps. To do this I investigated the environmental responses and thresholds of EM fungal communities associated with *Dryas octopetala*, *Bistorta vivipara* and *Salix herbacea* across 45 sites classified in three highly differentiated habitats, the alkaline treeline ecotone, alkaline *Dryas* mats, and siliceous snowbed habitats. I hypothesised that in these alpine habitats i) future predicted warmer and drier summers will enhance community richness and ii) more specialized EM fungal communities associated with alpine snowbed habitats will be replaced by EM fungal communities with wider ecological niches.

3.3 Materials and Methods

Ectomycorrhizal community data

Based on results emerging from exploratory analyses in **Chapter 2**, here I re-focus and expand investigation using EM fungal community data from *Dryas octopetala*, *Bistorta vivipara* and *Salix herbacea* ectomycorrhizas from a subset of 45 sampling sites grouped in three main habitat types: 1) the alkaline treeline ecotone, dominated by alpine grasslands with scattered shrubs of *Arctostaphylos uva-ursi*, patches of *D. octopetala* and pioneering seedlings of *Pinus cembra*, *P. montana* or *P. mugo*, 2) alpine mats in alkaline soils (hereafter “alpine alkaline”) mainly dominated by *D. octopetala*, *Carex firma* and dwarf willows such as *S. reticulata*, *S. retusa* and *S. serpyllifolia*, and 3) siliceous snowbed plant communities (hereafter “alpine acidic”) dominated by *S. herbacea* and other creeping willows. The community matrix retrieved was composed of abundance data for 414 EM fungal OTUs across 14 sites in the treeline ecotone, 20 in alpine alkaline and 11 in alpine acidic.

Environmental data collection

To assess how warmer and drier summers will influence alpine EM fungal communities, I selected six bioclimatic variables from the CHELSA database at 30 arc-sec resolution (approx. 1km²) (Karger *et al.*, 2017). These were Mean Annual Temperature (MAT), Mean Temperature of the Driest Quarter (MTDQ), Mean Temperature of the Warmest Quarter (MTWQ), Annual Precipitation (AP), Precipitation of the Driest Quarter (PDQ) and Precipitation of the Warmest Quarter (PWQ). Moreover, to assess how alpine EM fungal communities will respond to increasing levels of soil nutrient contents, I also retrieved soil total nitrogen (N_{soil}) from **Chapter 2** and the total atmospheric nitrogen deposition in kg N ha⁻¹ yr⁻¹ (N_{depo}). The N_{depo} estimates were derived from the EMEP/MSC-W unified atmospheric dispersion model (Simpson *et al.*, 2012) using the type II model results referring to the year 2016 (Fagerli *et al.*, 2019). The available N_{depo} 50x50 km grid was downsampled to 1x1km pixel size using the bilinear method implemented in the *resample* function of the *raster* package v2.9-23 for R. The total amount of N_{depo} per site was calculated by adding the oxidized and reduced forms of dry and wet N deposition.

Statistical analyses

All statistical analyses were carried out using R version 3.5.1 (R Development Core Team 2009). Normal distribution of the residuals and homogeneity of variances in all model approaches were assessed by analysing *qqnorm* plots and significant deviations of Shapiro and Levene test routines implemented in R. Data with non-normal distribution of the residuals were square root or log transformed. The relative abundance of the community matrix was standardized using the Hellinger method as implemented in the *decostand* function of the *vegan* package (Oksanen *et al.*, 2019).

The observed number of EM fungal OTUs per habitat and the abundance-based richness estimators ACE and Chao1 (Chao & Lee, 1992) were calculated using the *estimateR* function of the *vegan* package. Significant differences within the observed and estimated values among habitats were assessed by one-way ANOVA and Tukey's HSD *post hoc* tests. Permutational multivariate analysis of variance (PERMANOVA) was used to assess EM fungal community composition differences among habitats using the Bray-Curtis dissimilarity matrix over 999 permutations as implemented in the *adonis* function of the *vegan* package.

To analyse the level of specialization of each EM fungal OTU to habitat type I calculated the indicator value (IndVal) using the *multipatt* function over 999 permutations as implemented in the *indicspecies* package (De Cáceres & Legendre, 2009) and the Paired Differences Index (PDI) as implemented in the *bipartite* package (Dormann *et al.*, 2008).

To assess the relationship between EM fungal community richness at each habitat type and the environmental predictors selected for this study, I used linear regressions to model ACE per sampling site as a function of each environmental predictor, their cumulative effect and their interactions. The environmental variables selected for this study were tested for collinearity with the *chart.correlation* function from *PerformanceAnalytics* (Peterson & Carl, 2018). Pairwise variable combinations that showed a Pearson correlation coefficient ≥ 0.7 were inspected and one of the pairs removed from posterior analyses.

Finally, to determine the resilience of the EM fungal communities and the individual taxon responses to the environmental gradients across the European Alps to future environmental change, I used the threshold indicator species analyses as implemented in *TITAN2* (Baker & King, 2010). The sums of the indicator species scores of all OTUs were used to detect lower and upper EM community thresholds for each environmental variable.

3.4 Results

Richness and composition of EM communities

A total of 414 EM fungal OTUs were detected across the three habitat types (238 in the treeline, 284 in alpine alkaline and 134 in alpine acidic). The dominant EM lineages across the three habitats were *Tomentella-Thelephora*, *Cenococcum*, *Sebacina* and *Russula-Lactarius*. *Tomentella-Thelephora*, *Inocybe* and *Sebacina* were the EM lineages with highest number of taxa (OTUs) in the treeline and alpine alkaline, however in alpine acidic *Tomentella-Thelephora*, *Cortinarius* and *Cenococcum* were the lineages with highest number of OTUs (Fig. 3.1).

On average, the number of observed and estimated (ACE) EM fungal OTUs per site was 28 ± 8.026 and 35 ± 12.200 in the alpine acidic habitats, 38 ± 11.271 and 51 ± 19.116 in the alpine alkaline and 39 ± 8.389 and 51 ± 13.594 for the treeline. A significantly lower number of observed and estimated (ACE) EM OTUs was found in alpine acidic sites compared to the other two habitats ($F_{\text{obs}} = 5.047$, $p\text{-value} = 0.011$; $F_{\text{ACE}} = 4.009$, $p\text{-value} = 0.026$) (Fig. 3.2). The PERMANOVA revealed significant differences in EM fungal community composition among the three habitat types ($F = 3.818$, $R^2 = 0.154$, $p\text{-value} = 0.001$).

Ectomycorrhizal richness response to environmental predictors

After accounting for collinearity among the environmental predictors only the mean temperature and total precipitation of the warmest quarter (MTWQ and PWQ respectively) were kept. When exploring the effect of the selected climatic variables in the estimated number of EM taxa (ACE) in each habitat, I only observed a significant decrease in ACE with the increase of PWQ in the two alpine habitats (alpine alkaline: $p\text{-value} = 0.012$; alpine acidic: $p\text{-value} = 0.026$) but not in the alkaline ecotone (Fig. 3.3A). When exploring the cumulative effects of MTWQ and PWQ, the overall regression models were only significant in the

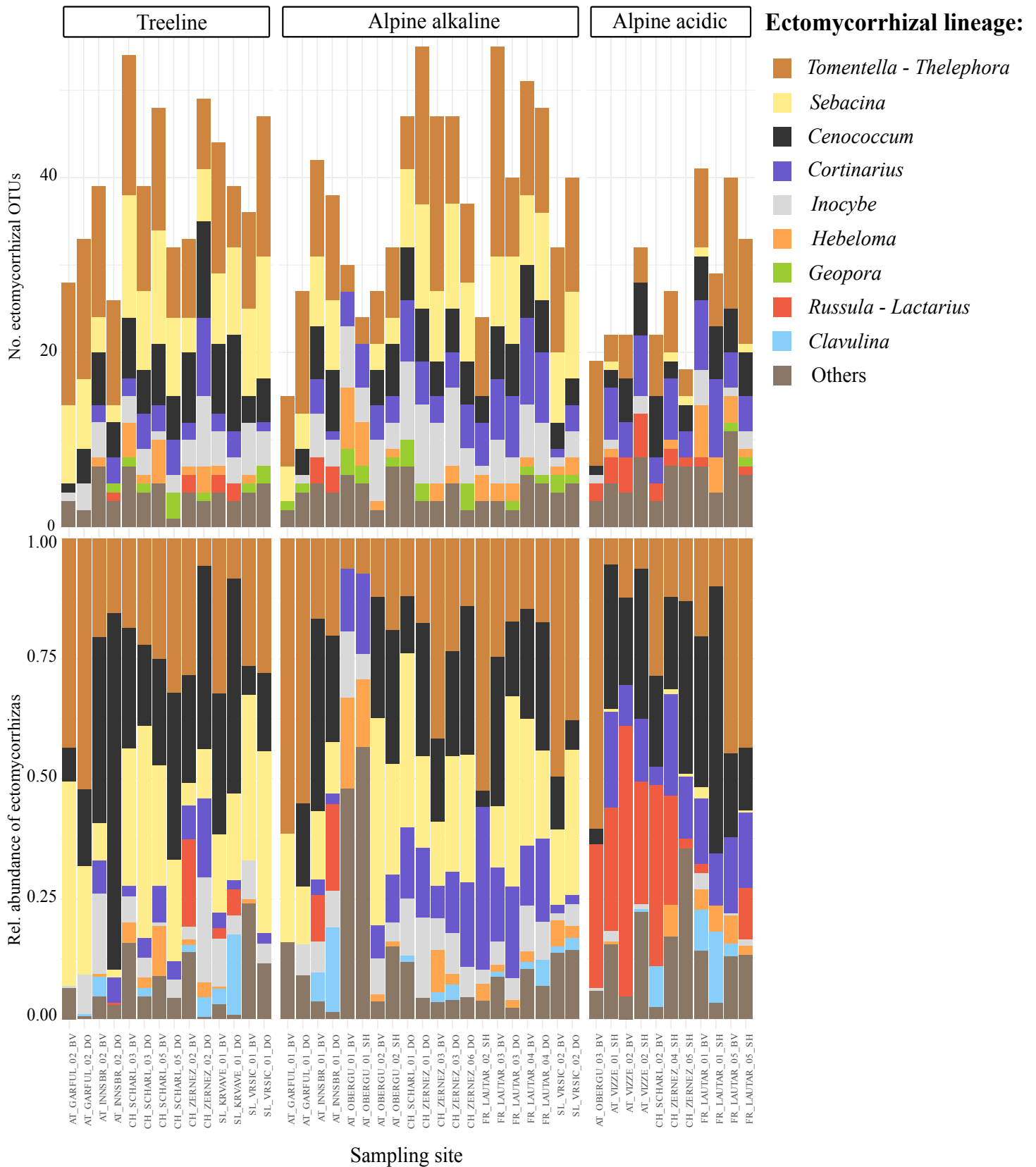


Figure 3.1 Richness and composition of EM fungal communities per habitat. A) Number of EM fungal OTUs per lineage; B) Relative abundance of ectomycorrhizas per lineage

alpine alkaline habitat. However, when exploring the significant terms of the model, only the effect of the PWQ was significant (p -value = 0.013). When modelling the effect of the interaction between MTWQ and PWQ, I observed significant effects in both alpine alkaline and acidic habitats. However, in the alpine alkaline habitat model, the interaction term between the climatic variables was not significant, so only the interaction of climatic variables in the model of alpine acidic was taken into account. I observed that in alpine acidic habitats, the higher estimated EM OTU richness was associated with sites with higher MTWQ and lower PWQ (Fig. 3.3B). The best-fit models (i.e. lowest AIC) were all from the alpine acidic habitats (Table 3.1).

No significant effects were observed when exploring the response of ACE to nitrogen-related variables in each habitat (results not shown).

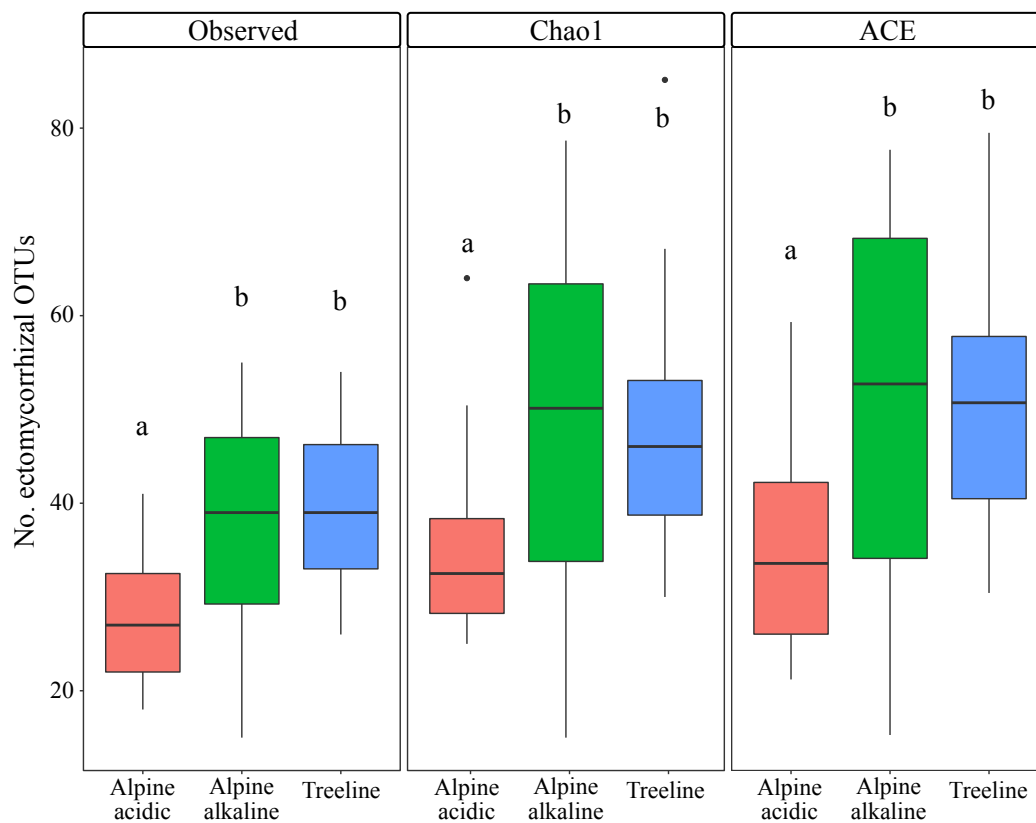


Figure 3.2 Mean number of observed and estimated (Chao1 and ACE) number of EM fungal OTUs per site across all habitats. Different lower-case letters above the boxplots represent significant differences of the means (p -value ≤ 0.05).

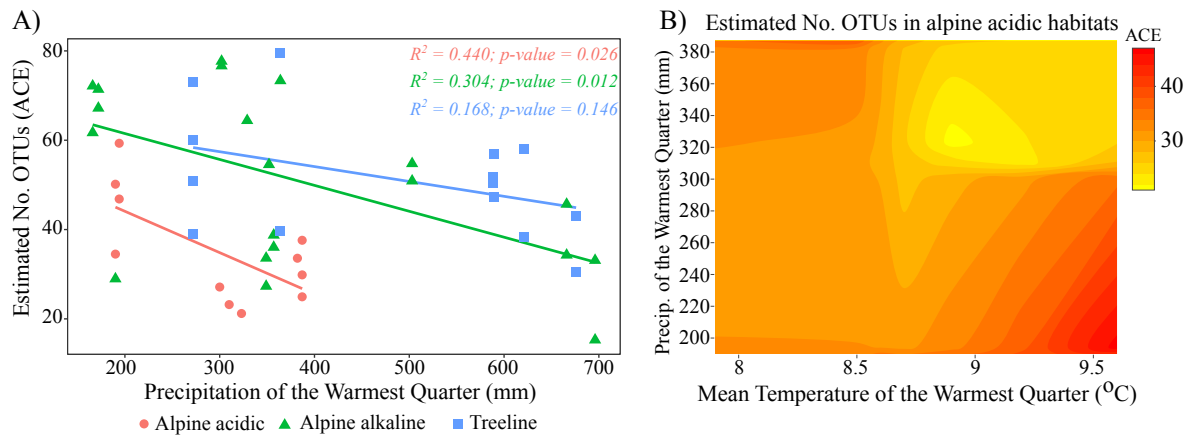


Figure 3.3 Estimated number of EM fungal OTUs (ACE) in response to summer related climatic variables. A) ACE per habitat in response to precipitation of the warmest quarter; B) ACE in alpine acidic sites in response to mean temperature and precipitation of the warmest quarter

Table 3.1 Linear regression models structure per habitat type. All models were fitted with the estimated number of EM fungal OTUs per site (ACE) as a function of each covariate combinations (MTWQ - Mean temperature of the warmest quarter; PWQ - Precipitation of the warmest quarter). Numbers in bold represent significant interactions ($p\text{-value} \leq 0.05$).

Model	$p\text{-value}$	R^2	AIC	df
Alpine acidic ACE ~ MTWQ	0.206	0.171	89.136	9
Alpine acidic ACE ~ PWQ	0.026	0.440	84.818	9
Alpine acidic ACE ~ MTWQ + PWQ	0.098	0.440	86.815	8
Alpine acidic ACE ~ MTWQ $\times$ PWQ	0.019	0.738	80.471	7
Alpine alkaline ACE ~ MTWQ	0.387	0.042	178.898	18
Alpine alkaline ACE ~ PWQ	0.012	0.304	172.508	18
Alpine alkaline ACE ~ MTWQ + PWQ	0.013	0.330	171.516	17
Alpine alkaline ACE ~ MTWQ $\times$ PWQ	0.038	0.289	173.489	16
Treeline ecotone ACE ~ MTWQ	0.097	0.213	114.413	12
Treeline ecotone ACE ~ PWQ	0.146	0.168	115.188	12

Indicator and threshold analyses

The indicator species analysis revealed 15 indicator EM taxa of the treeline habitat, five of alpine alkaline and 26 of alpine acidic (Appendix B: Table S3.1). The PDI index observed in all the indicators (Fig. 3.4) ranged from 0.5 in *Laccaria trichodermophora* (OTU176) to 1.0 in *Cortinarius decipiens*

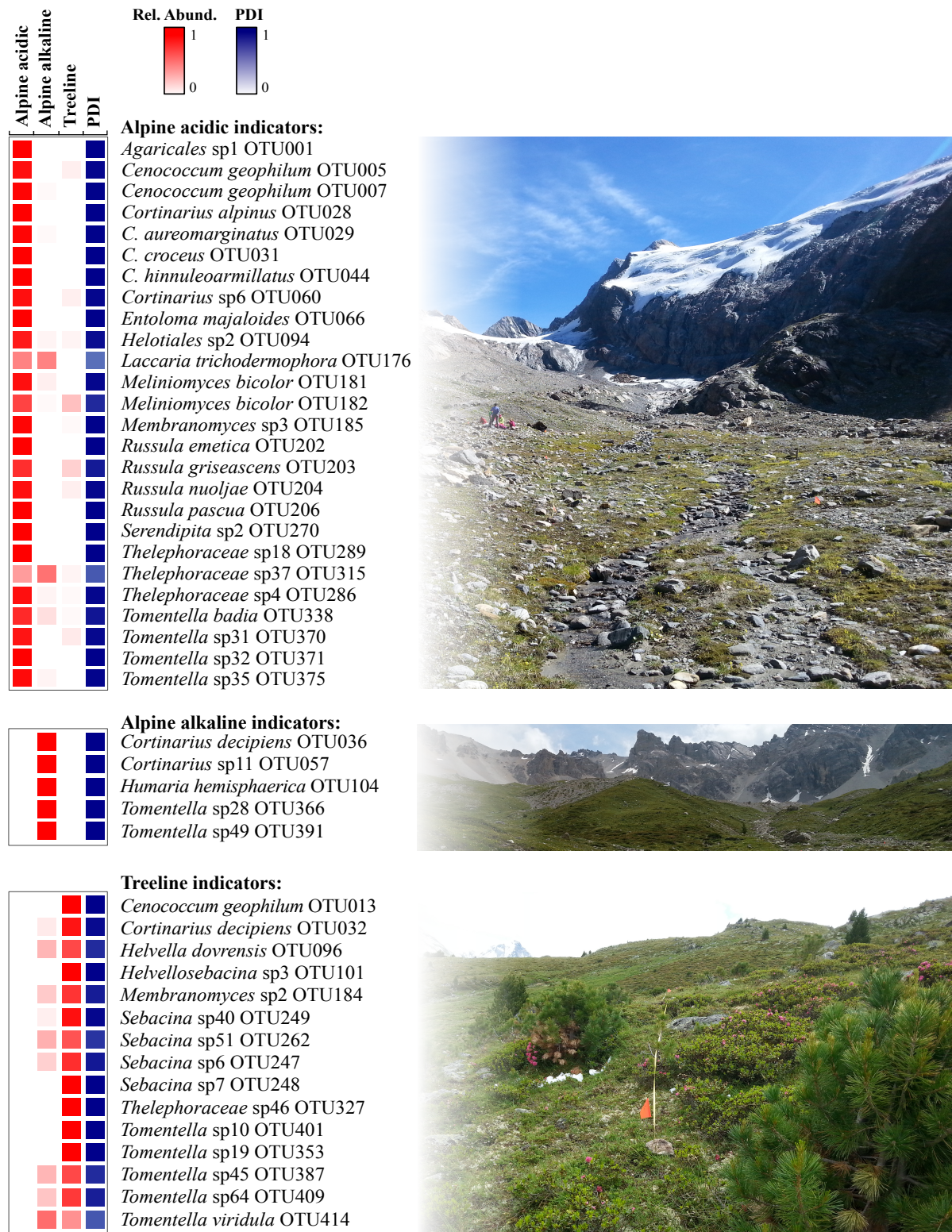


Figure 3.4 Indicator ectomycorrhizal fungal OTUs per habitat. Alpine acidic indicators (top), alpine alkaline indicators (centre) and treeline indicators (bottom). Heatmap colours represent the Paired Differences Index (blue) and the relative abundance of each EM fungal OTU per habitat (red).

(OTU036). The TITAN analysis revealed a set of 27 indicator species that were negatively (z-) or positively (z+) influenced by the environmental variables tested. The community-level thresholds among negative and positive taxa were assessed by summing all the z- and z+ scores for each environmental predictor. For MTWQ, the results of the sum(z-) peak at 9.0°C and a sum(z+) peak at 10.8°C. For PWQ, a sum(z-) peak at 286 mm yr⁻¹ and a sum(z-) at 605 mm yr⁻¹ were observed. When analysing the community responses to atmospheric N (N_{depo}) and soil N (N_{soil}), the sum(z-) peaked at 1.72 kg N ha⁻¹ and 0.167 % N respectively and the sum(z+) peaked at 8.94 kg N ha⁻¹ and 0.933 % N respectively (Table 3.2). At taxon level (individual OTUs), indicators of alpine acidic habitats tended to respond negatively at increasing gradients of the selected environmental variables, while indicators of treeline habitats respond positively (Fig. 3.5).

Table 3.2 Community-level change points in response to each environmental covariate.

Env. variable	Change point (z-)	Change point (z+)
Mean temp. warmest quarter (°C)	9.00	10.80
Precip. warmest quarter (mm)	286.00	605.00
Nitrogen deposition (kg ha ⁻¹)	1.72	8.94
Nitrogen in the soil (%)	0.16	0.93

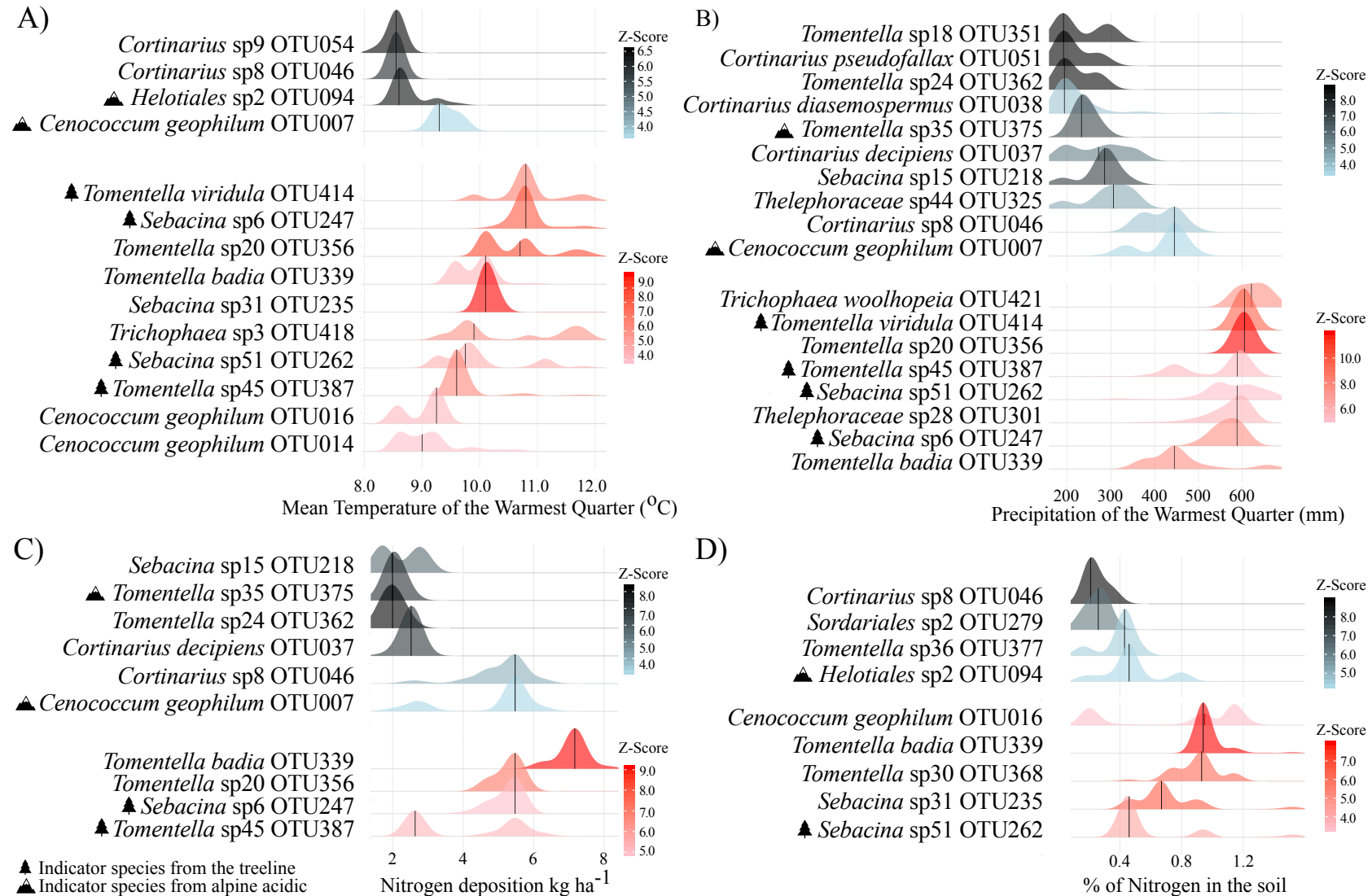


Figure 3.5 Individual fungal OTU responses to the environmental gradients assessed in the threshold indicator analysis (TITAN). Taxa declining with increasing environmental covariates (z-) are represented in grey while taxa increasing in relative abundance with increasing environmental covariates (z+) are represented in red. Individual taxon responses to A) Mean temperature of the warmest quarter; B) Precipitation of the warmest quarter; C) Total nitrogen deposition during the year 2016; D) Percentage of nitrogen in the soil.

3.5 Discussion

In this study I explored the expected impacts of climate change on EM fungi in unique alpine habitats of the European Alps. I found that snowbed habitats are at particular risk due to a predicted decline followed by replacement of their specialized EM fungi. Ectomycorrhizal fungal communities from the treeline ecotone, however, due to their wider ecological niches, will be positively influenced by future climatic conditions, expanding upwards in the mountains. This, together with glacier retreats, will facilitate the colonization of alpine snowbed habitats by new EM plant and associated fungal communities bringing additional ecological pressures on local EM fungal communities leading to potential species extinctions.

I observed a significantly lower number of EM fungal OTUs in alpine acidic habitats compared to alkaline alpine and treeline ones. This corroborates the trend found in **Chapter 2** where lower species EM fungal richness was associated with *S. herbacea* and *B. vivipara* in alpine snowbed habitats. From the treeline ecotone to the nival zone in mountain ecosystems, soils are nutrient deficient and inorganic N and phosphorus (P) are scarce (Kielland, 1994). These habitats are characterised by high exposure to wind, high solar radiation, low temperatures, long snow cover periods (Nagy & Grabherr, 2009) and poor EM plant host richness (Davies *et al.*, 2004). Thus, the combination of harsh environmental conditions with very particular edaphic properties and lower availability of plant hosts at snowbed habitats, are likely the main drivers of EM fungal richness in these habitats.

Variables related to atmospheric temperature analysed in this study showed little or no significant evidence of links with EM fungal richness within each habitat. These results also concur with **Chapter 2** where climate variables were the least important variables explaining the variability in EM fungal communities of the alpine zone across the European Alps. However, here I observed significant effects of precipitation (PWQ) in the estimated EM fungal richness in both alpine

acidic and alkaline habitats. The effects of precipitation-related variables on EM fungal communities may vary regionally, since in the Alps, expected trends in precipitation will vary, increasing or decreasing depending on region and season (Auer *et al.*, 2007; Zimmermann *et al.*, 2013). The results of this study show that alpine fungal communities' composition, particularly those in snowbed habitats, are expected to change with indicator species of these habitats decreasing in relative abundance under future climatic conditions. Aboveground, it is known that mushroom phenology has been affected by global climate change (Kausrud *et al.*, 2008). Moreover, across the European Alps many fungal species (including EM fungi) are fruiting at significantly higher elevations driven by climatic and habitat shifts (Diez *et al.*, 2020). These findings, coupled with my results based on direct observations of belowground and root-associated EM fungi, indicate that the effect of future climatic conditions on alpine EM fungal communities may first be reflected in a shift of species phenology patterns eventually culminating in community turnover, with more adapted EM communities from the lowlands becoming dominant across the alpine landscape at higher elevations.

When exploring interactions among climatic predictors, I observed that in alpine acidic habitats, higher EM OTU richness was associated with sites with higher MTWQ and lower PWQ. This combined effect of higher temperature and lower precipitation during spring and summer, results in shorter snow cover periods, promoting earlier meltdowns and longer growing seasons for alpine plants. These particular conditions have also led to an increase in plant species richness at higher elevations during the last century (Stöckli *et al.*, 2011) with newly arrived species originating from subalpine and lower alpine habitats (Engler *et al.*, 2011; Pauli *et al.*, 2012). Higher numbers of EM fungal species have been linked to high plant host richness in the Alps (Pellissier *et al.*, 2013) and drastic changes in plant community composition due to replacement by species more adapted to drier conditions and shorter snow cover periods are predicted in snowbed habitats (Matteodo *et al.*, 2016). Under future climate

changes, in particular for the southern Alps where summers are predicted to be drier and warmer, an increase in EM fungal community richness of snowbed habitats is thus expected, but drastic changes in plant community composition might also lead to compositional changes in available EM fungi and extinction of fungal species adapted to the current environmental conditions in these habitats.

When determining the ecological thresholds of EM fungal communities across the Alps, I observed that the more negatively affected fungal OTUs were alpine indicators, while those that responded positively were treeline indicators. By affecting the structure and function of soil microbial communities, climate change may lead to changes in nutrient and C cycles, implying changes in soil nutritional status and productivity, plant survival and biotic interactions (Donhauser & Frey, 2018). Ectomycorrhizal fungal community composition has been shown to respond to soil N content (Cox *et al.*, 2010b; Lilleskov *et al.*, 2011; Suz *et al.*, 2014; van der Linde *et al.*, 2018). In alpine ecosystems, fluctuations in soil N content can be driven by cycles of boom and decline of soil microbial communities linked to snow-covered and snow-free periods (Lipson *et al.*, 1999). During winter most soil N is immobilized by microbial community biomass. After snowmelt in spring, immobilized N is released to the soil primarily in organic forms as amino acids due to decline in soil microbial biomass. In the West Elk Mountains of Colorado, USA, EM fungal communities are positively influenced by pulses of N after snowmelt periods (Sorensen *et al.*, 2020). The results of the present study indicate that treeline EM communities are the most likely to thrive under increases of soil inorganic N content in the Alps. In the particular case of snowbed indicators, e.g. *Cortinarius* spp., some of which are specialized organic soil N miners with proteolytic abilities (Lilleskov *et al.*, 2011), I observed a negative effect of increasing soil inorganic N. Moreover, the input of nutrients from exogenous sources in recently deglaciated alpine soils, can facilitate the establishment of pioneer microbial communities (Rime *et al.*, 2016). Thus, the increase of inorganic forms of N from exogenous sources (e.g.

through atmospheric deposition) coupled with the negative impacts of temperature and precipitation regimes, can lead to the decline of alpine EM fungi and in particular their specialized snowbed communities. However, whether human activities regarding land use and land cover (e.g. managing alpine grazing meadows) influence alpine EM fungal communities remains unknown. Nonetheless, the results of this study highlight the dramatic consequences of climate change for one the most unique alpine habitats through decline in specialized snowbed mycorrhizal communities.

Chapter 4

Plant-fungal interactions in hybrid zones: ectomycorrhizal communities of willows (*Salix* L.) in an alpine glacier forefield.

4.1 Abstract

Ectomycorrhizal (EM) fungi are essential for the establishment of woody perennial plants in the European Alps. From continental to local scales, environmental conditions and plant host characteristics can predict EM community structure and composition. However, it is unclear whether EM communities of congeneric host species and their hybrids are differentially structured at local scales. This study aims to i) characterize EM communities of *Salix helvetica*, *S. purpurea* and their hybrids and ii) elucidate the abiotic and biotic factors affecting EM communities in hybrid zones. The EM fungal communities associated with these willows in the glacier valley were analysed by combining molecular identification of fungi from individual ectomycorrhizas and from soil. The results of this study revealed diverse EM fungi forming non-modular and unnested networks, but without significant differences in the overall EM fungal community richness or composition among parental species and hybrids. Nevertheless, individual fungi differed regarding host preference. These results demonstrate that in a sub-alpine hybrid zone with heterogeneous geomorphology, host genotype is not a strong predictor of overall EM fungal community, but it influences the occurrence of particular fungi.

Keywords

Ectomycorrhizal; fungi, host specificity; sub-alpine, hybrids; *Salix helvetica*; *Salix purpurea*; network analysis; Sanger sequencing; high throughput sequencing

4.2 Introduction

In **Chapter 2** of this thesis I assessed the main biotic and abiotic factors that shape EM fungal communities across the European Alps. Among the biotic factors tested were plant host phylogeny (at family level) and intraspecific population subdivision. However, plant host genotype and competition with other fungi can play important roles in structuring EM communities (Dickie, 2007; Ishida *et al.*, 2007). In general, plant host influences EM fungal community structure (Dickie, 2007; Tedersoo *et al.*, 2012; van der Linde *et al.*, 2018) and more closely related hosts share more similar EM communities (Ishida *et al.*, 2007; van der Linde *et al.*, 2018), but in some cases, congeneric hosts may show significant differences in EM community composition by providing distinct ecological niches for EM fungi (Morris *et al.*, 2008). However, the influence of plant host genotype on EM fungal communities is still poorly understood, specially across host hybridization zones and harsh environments, such as alpine glacier forefields.

In alpine ecosystems, where many dominant plants like willows are ectomycorrhizal, environmental change may have strong effects on EM plant hosts and their associated fungal communities (Donhauser & Frey, 2018). At a regional scale, the richness of alpine EM fungal communities has been shown to be positively correlated with plant species richness, suggesting that EM fungal richness is an important driver of ecosystem functioning (Pellissier *et al.*, 2013, 2014). Several studies have addressed this question at host family level (Ishida *et al.*, 2007; Tedersoo *et al.*, 2008; Smith *et al.*, 2009), but our understanding of the interaction network between closely related plant hosts (i.e. at genus or intraspecific level) and their associated EM communities is still limited. Host

identity in willows, when different willow species co-occur in similar environmental conditions, can have little influence on soil fungal community composition (Erlandson *et al.*, 2016, 2018). Arctic and alpine willows have also been shown to have low host specificity compared to other co-occurring EM plants (Ryberg *et al.*, 2009, 2011; Botnen *et al.*, 2014). Consequently, the variability of EM fungal communities across the distribution of these shrub willows has been linked predominantly to abiotic factors.

In addition to host species richness and identity, plant-host genetic variability may also affect EM fungal communities, although studies show varied results. For instance, EM fungal community composition in differently drought-tolerant genotypes of *Pinus edulis* was strongly influenced by host plant genetics (Gehring *et al.*, 2017), while host genotype in *Populus* clones had little effect in determining the structure and composition of their fungal symbionts (Karliński *et al.*, 2013). These contradictory and context-dependent results highlight our restricted understanding of how plant host genetic structure interacts with the environment to shape EM fungal communities.

Ectomycorrhizal fungal communities may be influenced by host hybridisation, but this has been rarely tested, even though increasing plant genetic variation and its associated phenotypes may influence species interactions and ecosystem processes (Crutsinger *et al.*, 2006; Bailey *et al.*, 2009). Host genotypic variation can result in different phenotypes that putatively favour specific associated organisms, while in return these organisms feedback differently on the plant host (Whitham *et al.*, 2012). The combination of different host genotypes in hybrids has the potential to generate much greater genetic variation than that found in the parents (Whitham *et al.*, 1999), and genetically based variation in the phenotype of hybrids (e.g. leaf surface, root structure or density) can influence belowground communities. In a study of cottonwoods and their hybrids, controlling for environmental effects, host genotype played a minor role in mycorrhizal colonization compared to environmental factors (Gehring *et al.*

2006). Nevertheless, natural hybridisation and introgression create a genetic continuum between the two parental species that is ideal for examining changes in EM community structure and composition. Thus, studying EM fungal communities associated with congeneric hosts and their hybrids in alpine systems could provide further insights into host specificity across plant hybrid zones and a deeper understanding of the role of EM fungi in the resilience of these habitats to environmental change.

Network analysis at the population and genotype levels enables identification of key interactions in plant-fungal mutualistic relationships in an ecological framework. Species may show varying levels of preference and/or specialization, resulting in certain network structures in which some species are more or less frequently connected than expected from random interactions. Nestedness and modularity indices are commonly used to characterize plant-fungal networks (Toju *et al.*, 2013, 2014, 2015, 2016; Bahram *et al.*, 2014). Nestedness measures the tendency of specialist nodes in one level of the network (plants or fungi) to interact with generalist nodes in the other level to infer the generalist-specialist balance in the community. Modularity allows inferring the existence of groups of species that form more closely interacting communities within the entire network and whether interactions within these groups are more common than among groups (Guimerà & Amaral, 2005; Almeida-Neto & Ulrich, 2011). Thus, network analysis can generate new insights into the structure of complex fungal-host communities complementing and expanding our knowledge about descriptive measures of alpha and beta diversity (Barberán *et al.*, 2012). Extensively applied to the study of community structure in plant-fungal interactions (Caruso *et al.*, 2012; Toju *et al.*, 2013; Bennett *et al.*, 2013; Bahram *et al.*, 2014; Pölme *et al.*, 2018), network analyses could provide information on fungal niche preference and its role on plant establishment in harsh and heterogenous alpine habitats.

The assessment of EM fungal community diversity and dynamics has been transformed by high-throughput sequencing (HTS) techniques targeting the ITS1

or ITS2 regions. Despite generating millions of DNA sequence reads across numerous samples, the use of these data has limitations, such as the inability to discern between dead, dormant or active sources of DNA template, which combined with the PCR-based nature of these techniques, can lead to potentially biased observations (Lindahl *et al.*, 2013; Nguyen *et al.*, 2015; Hawksworth & Lücking, 2017; Wutkowska *et al.*, 2019). Moreover, the use of HTS on bulk soil samples does not provide direct evidence of plant-fungus associations. Therefore, comparing direct sequencing of ectomycorrhizas with HTS of soil samples potentially offers robust and in-depth complementary views of EM diversity and allows to infer host specialization regarding the available EM inoculum in soil.

Alpine willows (*Salix* spp.) offer an excellent opportunity to compare the EM communities in congeneric species and their intermediate individuals in hybrid zones given their genetic and ecological differentiation. This study focuses on *Salix helvetica* Vill., a shrub that occurs naturally in the sub-alpine to alpine zone, and *S. purpurea* L., a widespread lowland species, able to colonize higher elevations due to global warming and sub-sequent glacier retreat (Gramlich *et al.*, 2016, 2018). Using plant microsatellite markers, Gramlich *et al.* (2016) analysed the composition of two hybrid populations of *S. purpurea* and *S. helvetica* in the Swiss Alps and found evidence for a recent origin of the hybrids. The fine-scale environmental variation common in alpine ecosystems offered many unoccupied niches for hybrid establishment. The hybrids seemed to have a broad ecological amplitude and were able to grow under more extreme conditions, regarding soil pH, moisture and nutrient supply, than either parental species, enabling the coexistence of both parental species and the hybrids in a patchy habitat. Therefore, this chapter aims to i) characterize the EM communities that associate with *S. helvetica*, *S. purpurea* and their hybrids in one of the valleys included in Gramlich *et al.* (2016) and ii) elucidate the main abiotic and biotic factors that affect the structure and composition of EM communities in a hybrid zone. Furthermore, given their ability to colonize different niches in a very restricted

geographical area, it is hypothesized that (1) hybrids and parental willows associate with different EM fungi, and (2) within the same valley, host genotype explains most EM community variability.

4.3 Materials and Methods

Sampling

The sampling location was in the Rhône glacier valley in southern Switzerland (46°34'03.0''N, 08°22'12.3''E). Soil geological properties at the valley are mainly dominated by granite and granodiorite parent materials (Oberhänsli *et al.*, 1988), formed from unconsolidated glacier and colluvial deposits building eutric dystric regosols (FAO-UNESCO, 2007). The sampling area was *ca* 0.14 km² with a maximum distance between sampling sites of one km (Fig. 4.1) ranging between 1,775 and 1,800 m a.s.l.. The EM plant community included other *Salix* spp., *Alnus viridis* (Chaix) DC., *Larix decidua* Mill., *Picea abies* (L.) H. Karst. and *Betula* spp.

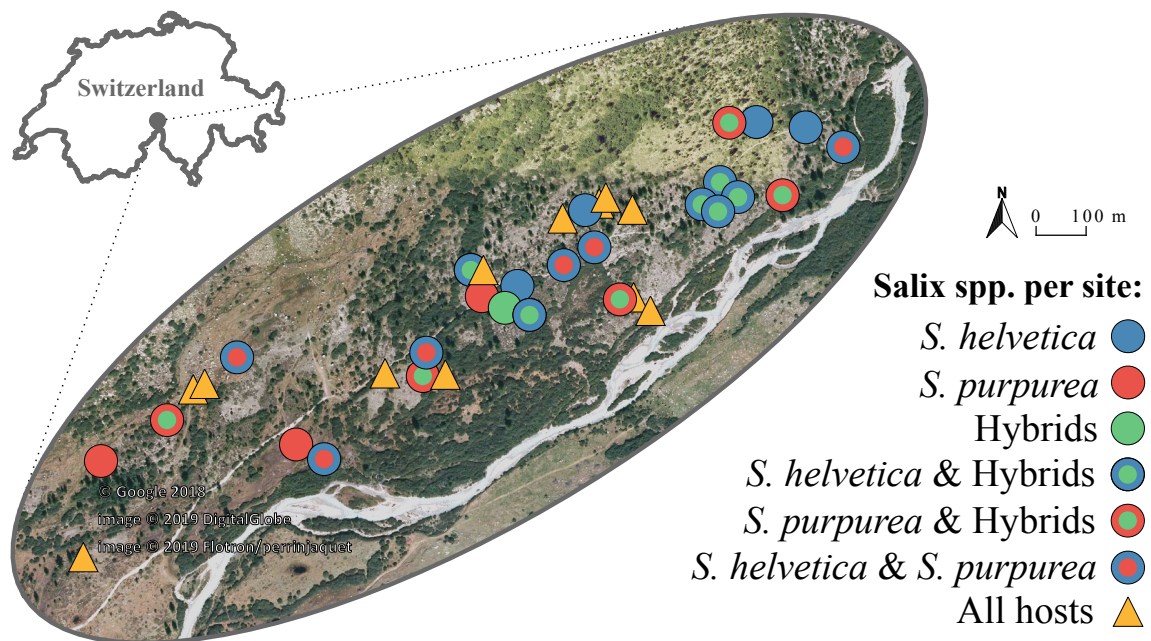


Figure 4.1 Sampling sites included in this study, based on Gramlich *et al.* (2016)

Previously genotyped individuals of *Salix helvetica*, *S. purpurea*, and their first-generation hybrids (*S. helvetica* $\times$ *purpurea*) were selected based on Gramlich *et al.* (2016). In total, roots of 97 individual adult plants (*S. helvetica*: 31, *S. purpurea*: 33, hybrids: 33) distributed across 38 sites were sampled. The hybrid populations were a maximum of 20-30 years old (Gramlich *et al.*, 2016), with plants about 50-200 cm high, and distributed over the valley in a mosaic-like pattern. *Salix purpurea* grows at the more alkaline, nutrient-rich and warm sites, while *S. helvetica* occupies more acidic, nutrient-poor and colder sites. Their hybrids occur at the most extreme, acidic and nutrient-poor sites (Gramlich *et al.*, 2016). Sites were defined as locations where individual(s) from the same or different host co-occurred within a distance of 8 m.

At least 16 roots from each individual plant were tracked from the stem, where the rocky ground permitted, carefully excavated, and stored in plastic bags at 4°C for up to seven days until further processing. Approximately 100 cm³ of soil was collected with a spade under each individual sampled plant for chemistry and bulk soil EM community analyses. Soil samples for DNA community analysis were stored at 4°C for up to 7 days, then stored at -80°C, and freeze-dried before processing.

Environmental data

Soil samples were collected down to 10 cm beneath each plant for soil chemistry analyses. Samples were dried at 40–60°C and sieved with a 2 mm mesh. Soil pH was measured potentiometrically in 0.01M CaCl₂. Total carbon (C_{total}) and total nitrogen (N_{total}) contents were measured in ground samples by dry combustion using a C/N analyser NC 2500 (CE Instruments, Italy). All soil chemistry analyses were conducted at the Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf (WSL). Geographic coordinates and ectomycorrhizal plant community composition were recorded within a radius of 10 m from each sampled individual plant.

Mycorrhizal root assessment

Root samples were rinsed in water and 16 EM tips from 16 different roots traced from the stem were selected from each individual plant when possible. The presence of hyphae and/or rhizomorphs was recorded (Agerer, 2001, 2006) before DNA extraction. Genomic DNA was extracted from individual ectomycorrhizas using Extract-N-Amp (Sigma-Aldrich, Darmstadt, Germany) and the ITS region of the rDNA was amplified using the fungal-specific primers ITS1F (Gardes & Bruns, 1993) and ITS4 (White *et al.*, 1990). Amplicons were purified using ExoSAP-IT (USB, Cleveland, OH, USA) and sequenced bidirectionally using BigDye v. 3.1 (Applied Biosystems, Foster City, CA, USA) in an ABI 3730 (Applied Biosystems).

Sequences were first analysed with KB basecaller v1.1.1 (Applied Biosystems) and bases called with minimum quality value (QV) of 20 (i.e. 99% of base call accuracy). Forward and reverse sequences from each ectomycorrhiza were assembled using *phrap* v1.090518 (de la Bastide & McCombie, 2007). When the assembly of both sequences was not possible due to the poor quality of one of the sequences or to uncertainty determining their overlapping region, a high quality base-pair ($QV \geq 20$) per sequence length ratio was applied and the longest sequence (>200 bp) with ratio scores $\geq 85\%$ was selected for further analyses. To avoid misleading results in the DNA sequence identification process and to facilitate direct comparison with the fungal community in the soil, adjacent conserved regions (18S, 5.8S and 28S) were removed using ITSx v1.0.11 (Bengtsson-Palme *et al.*, 2013) and the ITS2 region was selected for further analyses. Sequences were clustered in OTUs at a 97% similarity threshold using the UPARSE algorithm implemented in USEARCH v9.2 (Edgar, 2013), while simultaneously excluding chimeric sequences. The taxonomic affiliation of each OTU was inferred by blasting each OTU centroid sequence to the UNITE fungal ITS sequence database v7.2 as a reference for assignment of a species hypothesis (Nilsson *et al.*, 2011; Kõljalg *et al.*, 2013). For centroids with less than 97% blast

id we used the SINTAX algorithm (Edgar, 2016b) with a 0.8 cut-off to predict OTU taxonomy. The ecological functions of each OTU (i.e. trophic level and type of mycorrhizal association) were assigned according to UNITE (Kõljalg *et al.*, 2013) and only EM fungi were used in downstream analyses. Representative sequences of each EM OTU were deposited in NCBI under accession numbers MK838121-MK838189.

Soil DNA analysis

The soil fungal communities were analysed from soil samples collected adjacent to the roots. Samples were sieved (2 mm mesh) and genomic DNA was extracted from 25 mg of 97 freeze-dried soil samples using the DNeasy PowerSoil Kit (Qiagen, Valencia, CA) and quantified using the Qubit 2.0 fluorometric system (Life Technologies, Paisley, UK). Amplifications of the ITS2 region using the primer set fITS7 (Ihrmark *et al.*, 2012) and ITS4 (White *et al.*, 1990) were run in triplicates and pooled for library preparation. The PCR, library preparation and paired-end sequencing on the Illumina MiSeq v3 platform (Illumina Inc., San Diego, CA, USA) were conducted by Génome Québec Innovation Center at McGill University (Montréal, Canada).

Quality filtering and clustering into OTUs was performed using a customized pipeline based on UPARSE implemented in USEARCH (Edgar, 2013), but with some additional modifications as follows. Paired-end reads were merged using the USEARCH fastq mergepairs algorithm (Edgar & Flyvbjerg, 2015) allowing staggered alignment constructs in order to accommodate potentially short ITS2 amplicons. The PCR primers were detected and trimmed using Cutadapt (Martin, 2011) allowing for one mismatch. Reads not matching the primers or with lengths below 150 bp were discarded. Trimmed reads were quality-filtered using the USEARCH fastq filter function with a maximum expected error threshold of one. Sequences were de-replicated to retrieve information on abundance distribution, and singleton reads were removed prior to clustering in order to avoid artificial

OTU inflation. Sequences were clustered into OTUs at 97% sequence identity using the USEARCH cluster_otu function that includes an ‘on-the-fly’ chimera detection algorithm. The OTU centroid sequences were subjected to an additional round of chimera filtering by running UCHIME against the uchime version of the UNITE database. The remaining centroid sequences were tested for the presence of ribosomal signatures using ITSx (Bengtsson-Palme *et al.*, 2013) and 33 (out of 2708) centroid sequences with the ribosomal origin not sufficiently supported were discarded. Finally, all quality-filtered reads were mapped against the final set of centroid sequences using the usearch global algorithm with the most comprehensive search criteria (maxrejects 0, maxaccepts 0 and top hit only). The taxonomic affiliation of each OTU was inferred by blasting each OTU centroid sequence to the UNITE fungal ITS sequence database v7.2. For centroids with less than 97% blast id we used the SINTAX algorithm (Edgar, 2016b) with a 0.8 cutoff to predict OTU taxonomy. Representative sequences of each EM OTU were deposited in NCBI with accession numbers MK838190-MK838412 as well as raw HTS reads deposited in the Sequence Read Archive under the accession number PRJNA575244.

Alpha and beta diversity of EM fungi

Analyses were carried out using R version 3.5.1 (R Development Core Team 2009). Sequence and read numbers from both root and soil community matrices were normalized using the cumulative sum scaling (CSS) method as implemented in the *metagenomeSeq* package (<http://www.cbcb.umd.edu/software/metagenomeSeq>). Observed OTU diversity and the abundance-based estimators Chao1 and ACE were calculated using the *estimateR* function of the *vegan* package (Oksanen *et al.*, 2019). Differences between observed and estimated values among hosts were assessed by one-way ANOVA and Tukey’s HSD *post hoc* tests. The percentage of OTU diversity recovered was calculated taking the proportion of OTUs observed from the number of estimated (ACE) OTUs per

host. Normal distribution of the residuals and homogeneity of variance were evaluated by analysing *qqnorm* plots and significant deviations of Shapiro and Levene test routines implemented in R. Data with non-normal distribution were square root or log transformed when necessary.

The proportion of shared OTUs between root and soil datasets, was assessed performing a local blast using the *blastn* algorithm with the soil OTUs centroids as reference and the root OTUs centroids as queries. The OTUs with blast hits superior or equal to 97% and with congruent taxonomy (i.e. equal Species Hypothesis number) were considered equivalent.

The local contribution for beta diversity (LCBD) was calculated to measure the degree of uniqueness of each sample to the variation in community composition following the method described by Legendre & De Cáceres (2013) and implemented in the *microbiomeseq* package, grouping OTUs by their corresponding EM lineage according to UNITE. Non-metric multidimensional scaling (NMDS) ordination was used to visualize dissimilarities in EM communities across different plant hosts and in both root and soil datasets using Bray-Curtis dissimilarity distances. Permutation analysis of variance (PERMANOVA) was used to assess differences between groups (3 hosts x 2 datasets, roots or soil) using the *adonis* function and significant differences among pairwise homogeneity of group dispersions (variances) were calculated using *betadisper*.

Plant-fungal network analysis

The interaction network between EM fungi and their host plants, was explored by computing three ecological network indices (Modularity, Nestedness and C-score) using the *bipartite* package for R (Dormann *et al.*, 2008). Modularity and nestedness were calculated for both binary and weighted matrices. Modularity was computed using the QuaBiMo algorithm (Dormann & Strauss, 2014) to identify aggregated sets of interacting OTUs (i.e. modules). To further investigate

the architecture of the bipartite network, the nestedness indices “NODF” and “weighted NODF” (Almeida-Neto & Ulrich, 2011) were calculated for the binary and weighted matrices, respectively. In bipartite networks, nested communities (i.e. with values towards 1) are characterized by specialist nodes in one level of the network (e.g. EM fungi) that connect to generalist nodes of the other level of the network (e.g. plant hosts) but never with other specialists and *vice versa* (Bascompte *et al.*, 2003). To analyse co-occurrence patterns among all EM fungal OTUs, the average number of checkerboard units (C-score) (Stone & Roberts, 1990) was computed for each unique fungal OTU pair in both soil and root datasets. The higher the C-score, the less co-occurrence, on average, among all of the fungal OTU pairs. A relatively large C-score indicates a more segregated matrix (i.e. with a checkerboard pattern where the distribution of particular fungal OTUs is influenced by the presence of other fungal OTUs), and a relatively small C-score indicates a more aggregated matrix (i.e. where this influence among particular OTUs is not found).

To assess the significance of all network indices calculated, 1,000 matrices from a conservative “fixed-fixed” null model constraining row and column marginal sums were generated as implemented in *vegan::nullmodel* and *p*-values and standard scores (z-scores) computed over the deviations of the observed values with those predicted by the null models. The C-score was calculated using only the binary matrix. Bipartite networks from both root and soil datasets were visualized using the *igraph* package.

Hierarchical modelling of EM communities

The dependence of each fungal OTU on environmental conditions, was assessed through a hierarchical joint species distribution model approach (Ovaskainen *et al.*, 2017). This framework allows the assessment of how much variation in each OTU occurrence is due to environmental filtering, biotic interactions and random processes. Furthermore, to allow this statistical framework to calculate

community-level synthesis of how species respond to the environment, it is assumed that the overall OTU responses to environment adhere to a multivariate normal distribution.

The distribution of EM fungal OTUs was modelled using soil pH, total soil nitrogen (N_{total}) and total soil carbon (C_{total}), and to account for biotic interactions we used Chao1 estimates of soil total fungal community ($S_{\text{fungi.total}}$) and soil EM community ($S_{\text{fungi.EM}}$). Sampling site and plant host identity were used as random effects. The *bestNormalize::bestNormalize* function (Peterson, 2017) was used to determine and apply the ordered quantile normalizing transformation to N_{total} and C_{total} , and the square root to $S_{\text{fungi.EM}}$ covariates. Two independent models were run for each of the datasets (roots and soil) using the binary (presence/absence) or the relative abundance matrix. Model priors were set to default and family distribution to probit for the binary models and lognormal Poisson distribution for the abundance variants. Parameter estimation was achieved by Markov Chain Monte Carlo (MCMC) posterior sampling for 100,000 iterations, 10,000 burning and 10 thinning. Parameter convergence was checked by trace visualization. The level of statistical support for whether the probability of an OTU abundance increased or decreased with the increasing value of a given environmental covariate, was assessed by defining the 95% credible interval by computing the 0.025 and 0.975 quantiles of each parameter. The explanatory power of the models was calculated using the coefficient of discrimination Tjur R^2 (Tjur, 2009) for each individual fungal OTU and its average at community level.

The assessment of how much of the variability in fungal OTU occurrence was due to biotic, abiotic or random processes, was performed by partitioning the variance of the explained portion of the model with higher explanatory power by grouping covariates as abiotic (soil pH + N_{total} + C_{total}), biotic ($S_{\text{fungi.total}}$ + $S_{\text{fungi.EM}}$) and for each covariate independently using the *variPart* function of the *HMSC* package.

4.4 Results

Soil chemistry

Values of soil pH ranged from 3.58 to 5.59, with significantly lower values observed under *S. helvetica* than *S. purpurea* (p -value = 0.019; Fig. 4.2A). Total soil nitrogen across all sampling sites ranged from 0.028% to 2.4% and soils under *S. purpurea* showed significantly higher values than those under hybrids (p -value = 0.012; Fig. 4.2B). Total soil carbon values ranged from 0.46% to 42.5% with soils collected under *S. purpurea* showing significantly higher values than hybrids (p -value = 0.047; Fig. 4.2C).

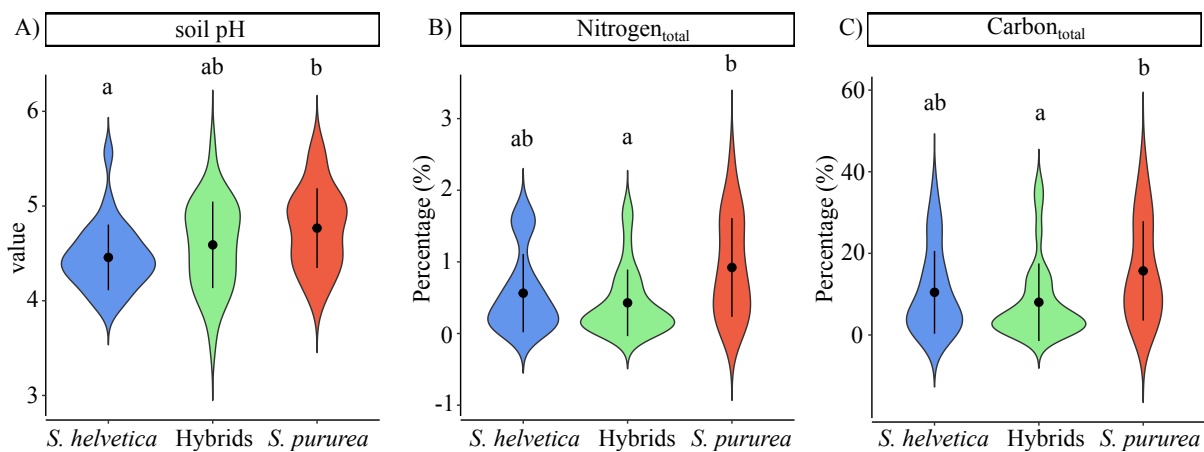


Figure 4.2 Soil chemistry parameters measured under *Salix helvetica* (n=27), *S. purpurea* (n=27) and their hybrids (n=28) across the sampling area. Each violin plot represents the mean (dot), standard deviation (bars) and the probability density of the data. Different letters indicate significant differences after ANOVA at p -value < 0.05.

Alpha and beta diversity of EM fungi

A total of 1,233 ectomycorrhizas were sampled from the roots of 82 out of 97 individual plants (*S. helvetica*: 27, *S. purpurea*: 27, hybrids: 28) distributed across 37 of the sampling sites. In total, 1,076 DNA sequences were retrieved, from which 1,044 high quality sequences belonging to EM lineages were kept (*sensu* Tedersoo *et al.*, 2010; Tedersoo & Smith, 2013). After clustering and filtering, 69 OTUs (average per individual 3.42 ± 1.52) were identified across 14

phylogenetic lineages. Approximately 90% of the EM fungi in roots belonged to Basidiomycota and 10% to Ascomycota. The EM lineages with higher OTU richness were *Tomentella-Thelephora* (28 OTUs), *Cortinarius* (16 OTUs), *Inocybe* (5 OTUs) and *Hebeloma* (5 OTUs).

From soil samples, a total of 9,036,820 raw DNA reads were generated, from which 3,099,112 high quality ones were retrieved. In total, 2,078 fungal OTUs were identified from which 223 (average per soil sample 9.30 ± 6.32) were kept and assigned to 32 EM fungal lineages after removing OTUs from non-EM lineages and 22 EM OTUs known to be specialists of conifers s.l. or *Alnus* spp. (Tedersoo *et al.*, 2009; Nilsson *et al.*, 2019b) and that were not detected in the roots. The EM lineages with higher OTU richness found in the soil were *Cortinarius* (51 OTUs), *Tomentella-Thelephora* (47 OTUs), *Inocybe* (22 OTUs), *Sebacina* (15 OTUs), *Russula-Lactarius* (13 OTUs) and *Laccaria* (12 OTUs).

Fifty-five EM OTUs were detected in both roots and soil, whilst 14 were found only in roots and 168 only in soil (Appendix C: Table S4.1). Across all sites, 40 EM OTUs were observed in roots of *S. purpurea*, 44 in roots of hybrids, and 48 in *S. helvetica* roots. In the soil, 142 EM OTUs were found under *S. purpurea*, 143 under hybrids, and 141 under *S. helvetica*. No significant differences were observed when comparing observed and estimated (ACE) OTU richness among hosts. The dominant EM fungal lineages forming ectomycorrhizas were *Tomentella-Thelephora*, *Cenococcum* and *Cortinarius*, whilst in the soil the most abundant reads belonged to *Tomentella-Thelephora*, *Cortinarius* and *Russula-Lactarius* (Fig. 4.3).

Ordination results showed no significant dissimilarities among hosts in the EM communities found in roots or in soil (Fig. 4.4). However, differences in community composition were observed when comparing root with soil datasets within hosts (Fig. 4.3). These results were corroborated by adonis ($F = 3.337$, $R^2 = 0.097$, p -value = 0.001) and by pairwise betadisper analysis (Appendix C: Table S4.2).

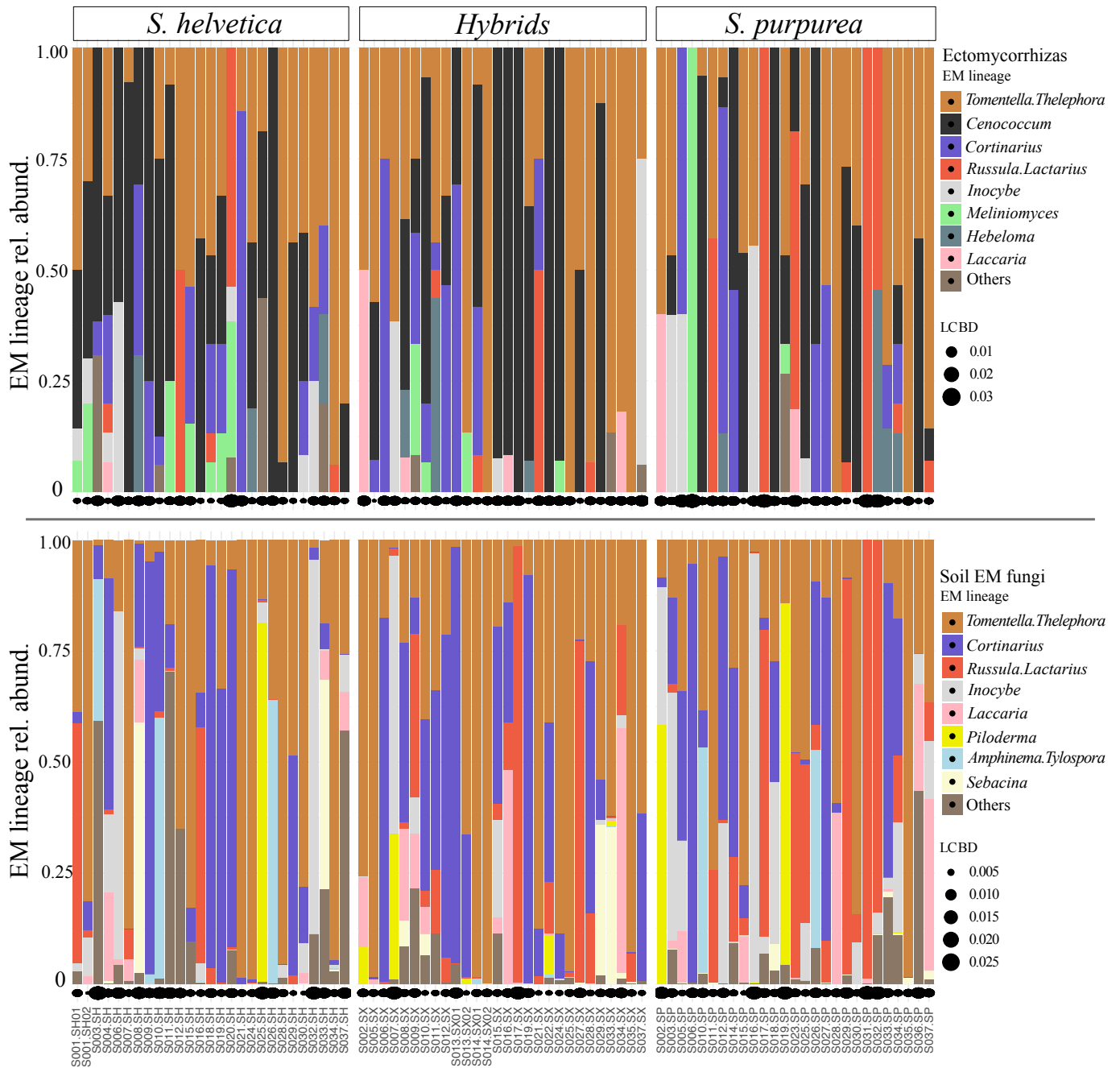


Figure 4.3 Relative abundance and local contribution for beta diversity (LCBD) of the most abundant EM lineages found as ectomycorrhizas (top) and in the soil (bottom) in each individual willow.

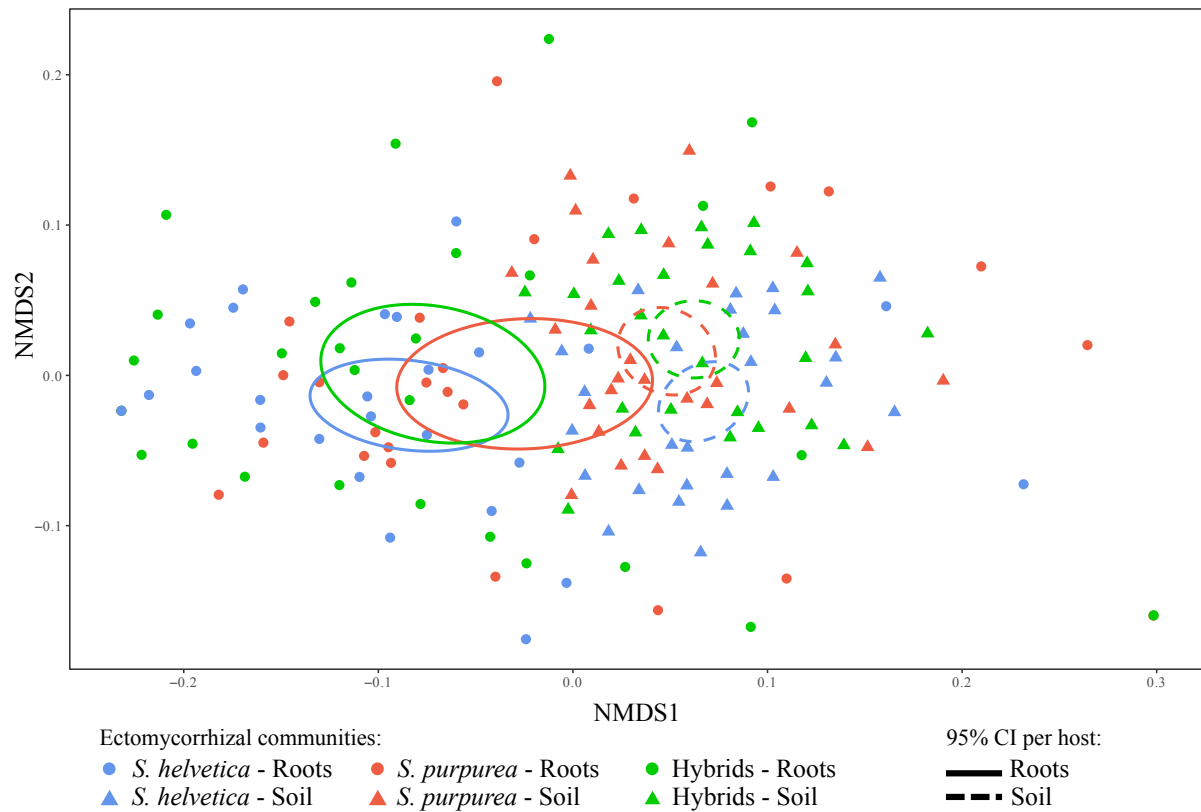


Figure 4.4 Nonmetric multidimensional scaling (NMDS) of community dissimilarities using Bray–Curtis distances. Circular points represent EM communities associated with roots (ectomycorrhizas) and triangular shape points represents EM communities in soil under each individual plant. Circumferences represent the 95% confidence interval of samples for each plant host. Stress of the ordination was 0.19.

Plant-fungal network analysis

Three network compartments (i.e. modules) were identified using the QuaBiMo algorithm both in the soil EM fungi (Fig. 4.5A, soil) and in the roots (Fig. 4.5B, ectomycorrhizas) using presence-absence and abundance association matrices respectively (Fig. 4.5). Modularity likelihood (Q) observed values in the network between willows and EM fungi in roots did not show significant differences from the null models ($Q_{\text{root.bin}} = 0.396$, $p\text{-value} = 0.112$; $Q_{\text{root.weighted}} = 0.242$, $p\text{-value} = 0.073$). In the association network between willows and EM fungi from soil samples, significant differences from the null models were observed when using

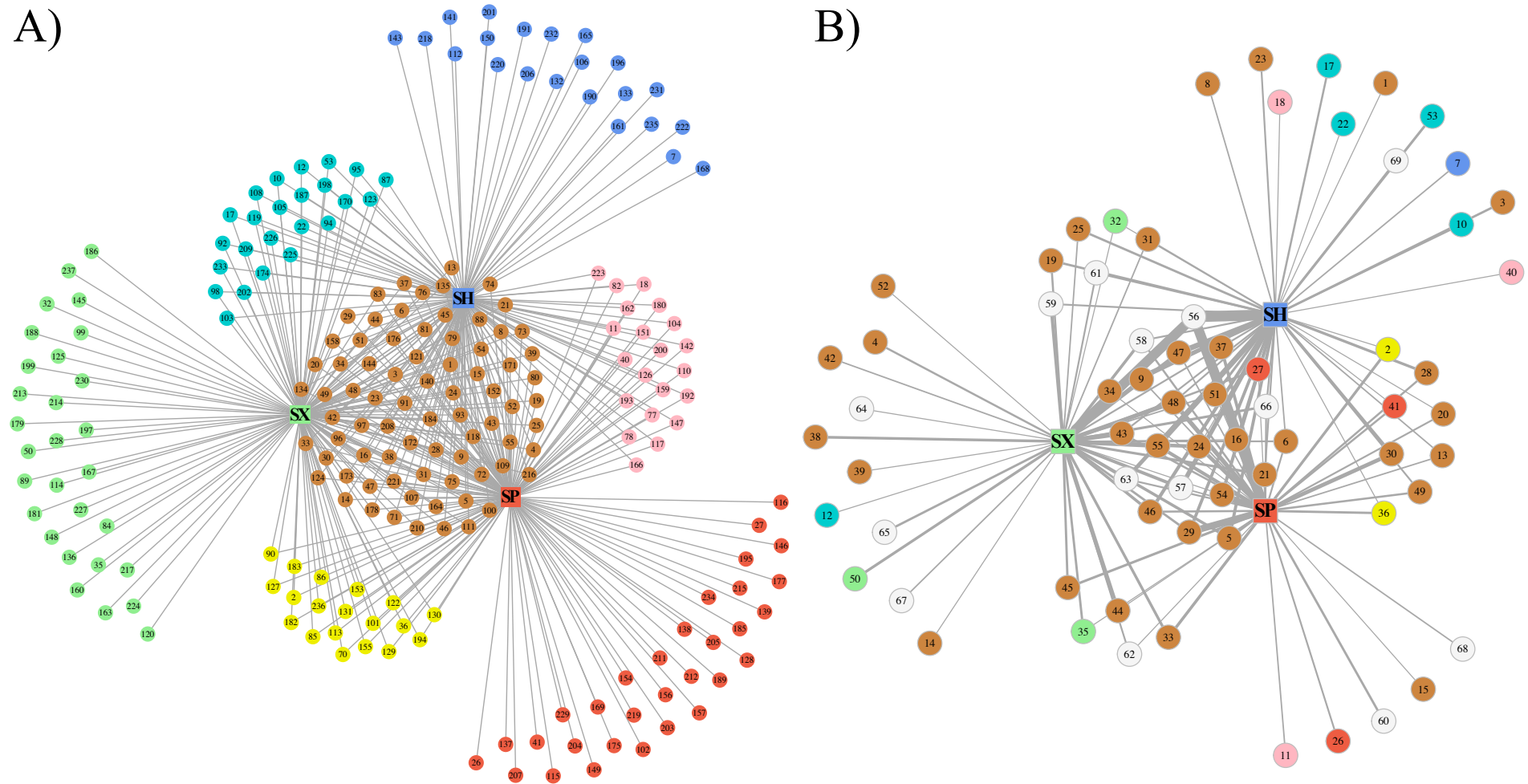


Figure 4.5 Visualisation of EM networks in a) presence-absence of soil EM fungi vs willows and b) abundance of ectomycorrhizas vs willows, based on the Fruchterman Reingold algorithm. Host plants and fungal OTUs are represented by squares and circles, respectively. Host plant abbreviations are: SH – *Salix helvetica* (blue square), SX – Hybrids (green square) and SP – *S. purpurea* (red square). Network edge thickness on plot b represent the strength of the association (i.e. the number of times that particular association was observed). Coloured vertices on b) represent the shared OTUs between soil EM fungi and ectomycorrhizas and derive from their relative position in plot a). White vertices represent OTUs only present as ectomycorrhizas.

the weighted matrix ($Q_{\text{soil.bin}} = 0.388$, $p\text{-value} = 0.129$; $Q_{\text{soil.weighted}} = 0.329$, $p\text{-value} < 0.001$, $z\text{-score} = 6.167$) (Appendix C: Table S4.3).

The network nestedness (NODF) values observed in the soil and roots datasets were similar but only the roots vs willows network showed significant differences from the null models ($\text{NODF}_{\text{roots}} = 59.2$, $p\text{-value} = 0.032$, $z\text{-score} = -0.061$; $\text{NODF}_{\text{soil}} = 58.5$, $p\text{-value} = 0.420$). Using the weighted matrices, the observed nestedness (WNODF) values were lower and only the soil observed value in the soil fungi vs willows was significantly lower than expected by the null models ($\text{WNODF}_{\text{roots}} = 37.7$, $p\text{-value} = 0.315$; $\text{WNODF}_{\text{soil}} = 39.2$, $p\text{-value} < 0.001$, $z\text{-score} = -2.994$).

The C-score analysis revealed significant deviations from expected by the null models in the co-occurrence patterns of the EM fungi found in the soil dataset, but not in the EM fungi found in the roots ($\text{C-score}_{\text{roots}} = 0.502$, $p\text{-value} = 0.404$; $\text{C-score}_{\text{soil}} = 0.511$, $p\text{-value} = 0.003$, $z\text{-score} = 2.127$).

Hierarchical modelling of EM communities

No significant improvements were observed in the hierarchical models of EM fungal OTU occurrences using the same environmental predictors for roots and soil datasets. The explanatory power (R^2) of the models using the soil EM community data was on average 0.06 (95% CI: 0.05 - 0.07) and 0.07 (95% CI: 0.04 - 0.10) for the presence-absence and abundance data matrices, respectively. In the case of the root EM community data, R^2 was on average 0.06 (95% CI: 0.05 - 0.07) and 0.05 (95% CI: 0 - 0.09) for the presence-absence and abundance data matrices, respectively. Due to lack of reliability of the models based on the abundance data, only the results of the presence-absence models were considered.

The partitioning of the overall explained variance in the presence-absence models revealed that sampling site and plant host species (random effects) explained the majority of the variation in both datasets (Fig. 4.6). In the root dataset, on average, 51% of the explained variation in the data was accounted for

by plant host (41%) and site (10%), whilst the abiotic variables accounted for 35% ($C_{\text{total}} = 14\%$, $N_{\text{total}} = 13\%$, and soil pH = 8%) and the biotic variables 14% ($S_{\text{fungi.total}} = 6\%$ and $S_{\text{fungi.EM}} = 8\%$). In the bulk soil dataset, approx. 46% of the explained variation in the data was accounted for by plant host = 32% and site = 14%. The proportion of the explained variance accounted, on average, by fixed effects in this dataset was 36% by abiotic variables ($C_{\text{total}} = 15\%$, $N_{\text{total}} = 15\%$ and soil pH = 6%) and 18% by biotic variables ($S_{\text{fungi.total}} = 13\%$ and $S_{\text{fungi.EM}} = 5\%$).

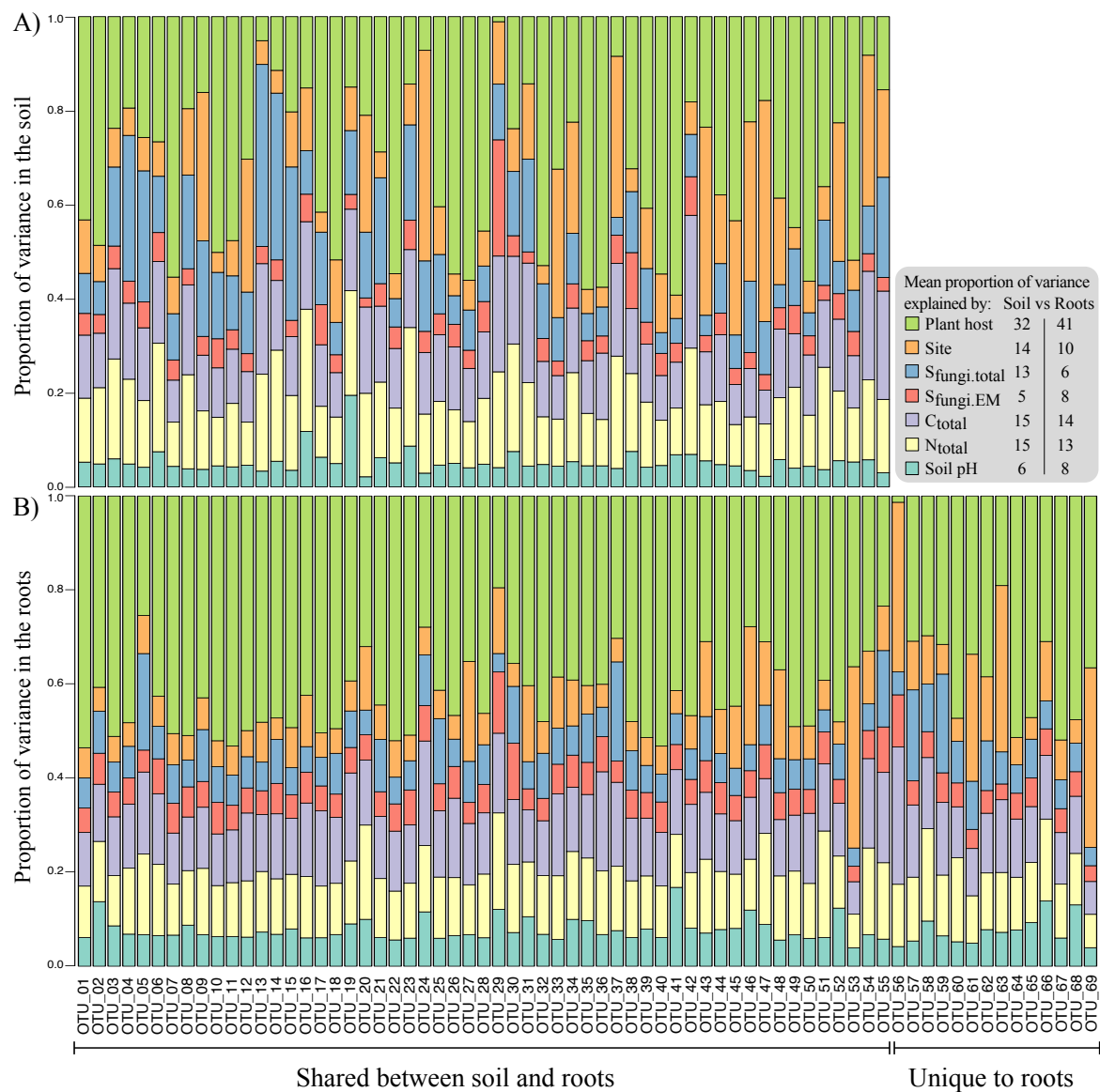


Figure 4.6 Variance partitioning in EM fungal communities in A) soil and B) roots (ectomycorrhizas). Variance partitioning was calculated using the presence-absence of fungal OTUs in response to site, plant host, soil pH, total C, total N, estimated total fungal community in the soil and estimated soil EM community. Only shared OTUs between soil and root datasets are illustrated in A).

4.5 Discussion

The aim of this study was to explore whether host intra-specific genetics and hybridization could influence EM fungal communities. However, the results show that host identity did not significantly influence the richness or composition of the EM fungal communities associated with *S. helvetica*, *S. purpurea* and their hybrids in the Rhône glacier valley, despite their previously observed different habitat/niche preferences (Gramlich *et al.*, 2016). Lack of host specificity among willows has been previously reported beyond the Alps (Ryberg *et al.*, 2009; Botnen *et al.*, 2014; Erlandson *et al.*, 2016, 2018). Ryberg *et al.* (2011) found similar EM communities associated with *Salix polaris* and *S. herbacea* in a Swedish alpine tundra. In a study comparing *Salix viminalis* growing in arable soils versus adjacent natural or naturalized stands in Sweden, Hryniewicz *et al.* (2012) detected site and host identity effects on EM root colonisation, but no effects on EM fungal abundance and diversity. However in other ecosystems and plant host species, host genetics has been found directly or indirectly influence EM communities, for instance, long-term studies of *Pinus edulis* populations showed an effect of host plant genetics on EM community composition (Gehring *et al.*, 2014, 2017) and individual spruce trees (*Picea abies*) were found to be partly responsible for the high diversity and patchy distribution of EM communities in boreal forests (Korkama *et al.*, 2006; Velmala *et al.*, 2013). A lack of host specificity in arctic and alpine ecosystems might be a mechanism that favours plant hosts to more rapidly and easily colonize newly available habitats, favoured by the establishment of symbiotic relationships with fungi with different physiological attributes (Botnen *et al.*, 2014). Nevertheless, the overall role that EM fungi may play on the colonization and establishment of hosts in these habitats cannot be disregarded.

The high soil heterogeneity characteristic of alpine ecosystems might also influence EM fungi and mask differential host effects on EM composition and structure. In this study, the observed variation in soil pH, C and N content,

revealed the presence of many microhabitats with distinct edaphic characteristics. The same soil heterogeneity was also highlighted by Gramlich *et al.* (2016) reporting that despite its recent emergence, the hybrid population occupies ecologically distinct sites in the studied forefield with respect to the parent species, scattered over the whole area of the alluvial plains in a mosaic-like spatial pattern. The results of my study show, however, that the dominant EM fungi colonising roots were shared among parents and hybrids; these fungi may be better adapted to the extreme environmental characteristics in sub-alpine habitats than host-specialists, thus explaining the lack of plant-fungal specificity or preference observed across willows. Nara & Hogetsu (2004) compared the growth rate of *Salix reinii* seedlings growing next to already established willow shrubs and observed that EM fungi associated with the latter were essential in facilitating seedling establishment of later-successional plant species. When comparing EM fungal community composition in roots (ectomycorrhizas) versus fungi in soil, Goldmann *et al.* (2016) observed that plant host neighbour effects were stabilizers of fungal community composition. They showed less distance decay in root-associated fungal communities compared to the soil fungal communities in a beech-dominated forest, suggesting that host trees could buffer the effects of changes in microclimatic and environmental conditions that could directly influence fungal community composition in soil. In the current study, other EM hosts, including other willow species, present in the valley may have prevented EM community differentiation among hosts by being a permanent source of diverse generalist inoculum.

Fungal community richness and composition

On average, 89% of the estimated EM richness (ACE) was recovered in willow roots (87% in *S. helvetica*, 90% in hybrids and 91% in *S. purpurea*). Despite the harsh environmental conditions in sub-alpine habitats, these willows harbour a considerable number of EM fungal species within a relatively small geographical

area. As suggested by previous studies, the large number of EM fungal species found in alpine and sub-alpine habitats might be linked to the high richness of EM plant hosts in these habitats (Krpata *et al.*, 2007; Pellissier *et al.*, 2014), moreover, hybrid zones are considered centers of biodiversity for many organisms (Whitham *et al.*, 1994).

As expected, due to the presence of other EM hosts in the valley and probably to the methodological bias from using rDNA in bulk soil samples that does not discriminate active, dormant or dead organisms, or intra- versus extra-cellular DNA template sources (Carini *et al.*, 2016; Wutkowska *et al.*, 2019), the EM OTU richness found in the soil was significantly higher than in ectomycorrhizas (142 OTUs under *S. purpurea*, 143 under hybrids and 141 under *S. helvetica* compared to 40, 44 and 48 in their roots, respectively). Nevertheless, the EM community richness and composition observed did not differ significantly across hosts, following the same pattern observed in roots. Collecting data from both ectomycorrhizas and from soil allowed testing for fungal specificity or preference of the three hosts from the potential fungal inoculum available. The results of this study indicate that a small proportion of the full potential inoculum (approx. 25%) was actually recruited by the plants. Similar rates of recruitment (27%) were also inferred by Goldmann *et al.* (2016) in a temperate beech forest. In contrast, approximately 80% of the OTUs observed as ectomycorrhizas were detected in the soil.

Soil has been suggested as a good proxy for estimating fungal richness at regional scales (Landeweert *et al.*, 2005); however, the inability to detect in soil some dominant fungi associated with roots (e.g. *Cenococcum geophilum*, ca. 32%) reveals the bias and risk of using only bulk soil data as a source of fungal community information. *Cenococcum geophilum* is an anamorphic complex of species that associates with a vast range of host plants globally, forming abundant black sclerotia in soil (Obase *et al.*, 2017) and increasing host plant drought tolerance (Pigott, 1982; Jany *et al.*, 2003). Studying bulk soil communities

without accounting for autecology, potential methodological biases, target limitations of genetic markers, and bioinformatic challenges, can lead to biased views of EM communities, artificial results and misleading conclusions (Lindahl *et al.*, 2013). In my study, three OTUs of *C. geophilum* were among the most abundant and conspicuous fungi observed in roots (Fig. 4.3), as in other studies sampling ectomycorrhizas in alpine glacier valleys (Krpata *et al.*, 2007; Mühlmann *et al.*, 2008; Mühlmann & Peintner, 2008). However, the obtained results are also congruent with Pellissier *et al.* (2014), Rime *et al.* (2015) and Frey *et al.* (2016) where *C. geophilum* was not detected in soil. This might be due to primer bias, inability of DNA extraction methods to break thickly melanized cell walls, removing larger sclerotia through sample sieving before DNA extraction, and/or ephemeral or sporadic hyphal growth in soil from a stable population of ectomycorrhizas. In this study, the putative sources of bias that could have contributed to the non-detectability of *C. geophilum* in the soil dataset, were assessed by i) manual verification of the binding region of the fITS7 primer in all *C. geophilum* OTUs found in roots and the respective UNITE reference sequences, ii) blasting all centroid sequences from the soil dataset against the UNITE+INSD v8.0 database (no blast hits observed), and iii) ensuring the detectability of *C. geophilum* in other studies using the same DNA extraction kit and similar analyses in soil (Kirker *et al.*, 2017), roots (Evans *et al.*, 2015), mesh bags (Ning *et al.*, 2019) and cultures (Peter *et al.*, 2016). Thus, my findings appear to reflect limited extraradical growth by a dominant EM fungus.

Plant-fungal network structure

Network modularity, which can be directly attributable to partner selectivity, measures how aggregated some sets of interacting species can be in a community (Dormann & Strauss, 2014) while nestedness measures the degree of interaction of specialists in one guild with generalists in the other guild (Bascompte *et al.*, 2003). In the Rhône Glacier valley, plant-fungal networks of willow hosts vs EM

fungi are non-modular and unnested. The networks of soil fungi vs willows and root fungi vs willows revealed low likelihood values of modularity and no significant deviations from the null models, except when using the weighted matrix of soil fungi vs willows (Appendix C: Table S4.3). The lack of modularity in plant-EM fungi networks has been previously suggested and inferred to be context-dependent, varying with species identity and potentially with the phylogeny of both partners (Bahram *et al.*, 2014; Pöhlme *et al.*, 2018). Moreover, modularity indexes are known to be sensitive to network size, as networks with many species and links allow for more possible combinations of species-in-modules, leading to higher values of modularity (Allesina & Pascual, 2009). Similarly to our study, Pöhlme *et al.* (2018) also found weak modularity values in EM fungal networks due to a low number of hosts.

Significantly higher modularity than expected by the null models was observed when using the weighted version (i.e. abundance data) of the soil fungi vs willows matrix instead of the binary one (i.e. presence-absence). These results may represent an artefact due to difficulties in the process of generating null models for abundance matrices. The null models were generated by constraining matrix row and column sums, but due to the high discrepancies in read numbers (even though CSS-normalized) and to the small number of hosts (i.e. reduced matrix size), the randomization scheme was very constrained, thus increasing the probability of type I errors (Lavender *et al.*, 2016).

In accordance with other studies (Bahram *et al.*, 2014; Toju *et al.*, 2014; Pöhlme *et al.*, 2018), the results of this study revealed that the network of plant hosts vs EM fungi are unnested. The highest values of nestedness in this study were observed in the binary matrices, however significant deviations from the null models were only detected in the binary matrix from the roots and the weighted matrix from the soil. Despite these differences, none of the indexes were indicative of nestedness in the studied networks (i.e. values towards 1 indicate nestedness). Similarly to modularity, measuring nestedness in plant-EM fungal

networks is challenging due to specific matrix properties (e.g. matrix size) (Bascompte *et al.*, 2003; Pöhlme *et al.*, 2018).

In a competitively structured community, the observed C-score is significantly higher than that generated by null models. Lack of significance suggests that species co-occur randomly, and significant lower C-score than expected from null models indicates species aggregation (Gotelli & Entsminger, 2001). Here, the C-score analyses did not show significantly higher values than the null models in the ectomycorrhizas suggesting that overall, the EM community is not competitively structured. However, since the C-score only measures the average number of checkerboard units (Stone & Roberts, 1990), it cannot be ruled out that unseen co-occurrence patterns among particular pairs of EM OTUs could occur in willow roots. Nevertheless, results revealed that C-scores were significantly higher than the null models for the EM fungi detected in soil, suggesting in this case a non-random distribution of species meaning that these communities could be competitively structured. Moreover, other hidden processes, such as differentiation on fungal OTU niche preference or other historical or evolutionary processes also may have led to less coexistence than expected. Non-random distributions of EM communities were previously described by Koide *et al.* (2004) who found that some EM fungal species occurrences were negatively correlated, suggesting that these negative interactions among species at small scales could affect community structure. Using the same C-score analysis, Pickles *et al.* (2012) found that EM communities in roots of Scots pine in a forest plantation in Scotland were strongly structured by competitive interactions, or ecological processes generating a similar spatial pattern, rather than neutral processes. The C-score analysis only revealed significantly higher values than expected in the soil dataset; however, describing the dynamics of soil fungal communities based on environmental DNA may be biased as it does not discriminate between metabolically active

cells, dead biomass, or dormant structures such as spores, potentially masking any competition pattern by generating false positive fungal co-occurrences.

Biotic and abiotic drivers of EM communities

The joint species distribution modelling revealed that the occurrences of EM fungi in the Rhône glacier valley were shaped by a complex grid of biotic and abiotic drivers. Despite the number of environmental variables measured, the majority of the variability in EM fungal community composition remained unexplained. The high soil heterogeneity, the effects of the abiotic factors across fine-scale microhabitats characteristic of alpine ecosystems and the dominance of generalist fungi might partly explain this. In microbial communities, habitat generalists respond mostly to spatial variables rather than to local environmental variability (Pandit *et al.*, 2009; Luo *et al.*, 2019). Thus, given the relatively small scale of the present study and the dominance of EM fungi that are habitat generalists, the small amount of explained variability may still be indicative of the role of these biotic and abiotic factors in the EM fungal community in this glacier valley.

The results of this study indicate a weak effect of host on EM fungal communities associated with willows across the valley. However, when exploring the factors influencing the explained variability of the overall EM fungal community distribution models ($R^2 = 0.06$), host identity emerged as the best predictor of EM community composition. On average, plant host explained the larger fraction of variance on the occurrence of each EM OTU in both soil and roots. Nonetheless, the effect of host identity on EM community structure might be masked by the different characteristics of the ecological niches in which these plants occur (Fig. 4.2). In contrast, when using relative abundance in the models instead of presence/absence (Appendix C: Fig. S4.1), site emerged as a better predictor of OTU relative abundance than host, indicating high spatial variation of EM communities. Using relative abundance data from HTS read

counts, Collins *et al.* (2018) observed that fungal diversity and relative abundance had high spatial variation, overwhelming the predictive power of other abiotic factors. Moreover, Feinstein & Blackwood (2012) found high spatial variation in forest floor fungal communities and little explanatory power of plant traits or plant species identity. Even though using relative abundance data from communities is becoming more frequent than using presence-absence data, without reliable abundance data from HTS technologies, understanding the drivers of fungal community composition and function will remain limited (Friedman & Alm, 2012; Taylor *et al.*, 2016).

Variation partitioning revealed that host and site effects were the main predictors of the explained variation in the overall EM fungal community composition. However, the presence-absence of some OTUs in particular was mainly explained by soil chemistry and soil fungal community. Individual OTU responses to environmental factors help to better understand EM fungal community resilience to environmental change, in particular, across the European Alps where complex geomorphology and an array of microclimates contribute to a wide variety of habitats and high levels of biodiversity. For instance, the occurrences of *Russula emetica* (OTU_029) and *Tomentella* sp. 11 (OTU_053) ectomycorrhizas were predominantly but differently explained by soil chemistry and soil fungal community (Fig. 4.6B), revealing that the relative importance of environmental and stochastic effects varies sharply among taxa.

4.6 Conclusions

Overall, the results of this study indicate that alpine willow EM communities are highly diverse and dominated by generalist fungi. These communities are non-modular, unnested and they are not competitively structured. The strengths and weaknesses of two EM fungi detection approaches were identified; caution is needed when analysing and extrapolating results from soil DNA that can miss dominant fungi in the roots. Hybrids and parental species did not associate with

significantly different EM communities despite their ability to colonise different ecological niches. When accounting for the effects of environmental variables, a differential effect of host on EM composition was found. However, this host effect seems to be masked by the high soil heterogeneity in the valley. Further studies increasing sampling effort to additional valleys along a wider gradient of environmental variables, and including manipulative experiments, are now needed to disentangle the biotic and abiotic factors shaping EM fungal communities in alpine zones.

Chapter 5

Final considerations and future perspectives

5.1 Final considerations

Mountains are storehouses of biodiversity, however, they are among the terrestrial ecosystems experiencing the most rapid changes due to global climate change and anthropogenic activities. The European Alps, which are one of the most intensively populated and exploited mountain regions in the world, encapsulate a wide range of unique habitats with specialized plant and animal communities adapted to these particular ecological conditions (Spehn *et al.*, 2010). Nevertheless, with the advent of new metacommunity sampling strategies coupled with new sequencing technologies, the emergent field of environmental metagenomics allow us to have a better overview of the so far cryptic or unknown diversity of belowground microbial communities present in these harsh environments. Combining two sampling strategies (direct Sanger sequencing of ectomycorrhizas and HTS for soil metacommunity assessment), my research on 950 samples across 47 sites in 5 countries, revealed 423 EM fungal OTUs associated with the roots of the *D. octopetala*, *B. vivipara* and *S. herbacea*, and 778 EM fungal OTUs present in the soil underneath them. Moreover, in a single stretch of Rhône glacier valley, I reported 69 EM fungal OTUs in association with *S. helvetica*, *S. purpurea* and their hybrids and 223 EM fungal OTUs in soil. The baseline diversity data generated in this thesis, result from the most intensive survey covering the entire European Alps targeting EM fungal communities so far. These results complement surveys conducted at local scales (e.g. Senn-Irlet, 1988; Graf & Brunner, 1996; Mühlmann *et al.*, 2008; Mühlmann & Peintner,

2008; Brunner *et al.*, 2017), and enhance our knowledge on the distribution, richness and composition of alpine EM fungal communities across the European Alps, in particular for alpine heaths and snowbed habitats. Moreover, **Chapters 2 and 4** also show that different methodologies yield different results. For instance, the use of new HTS techniques generate in depth community data and reveal inconspicuous fungi but given its inability to distinguish metabolically active from dead or dormant structures, and to detect some of the most abundant fungal OTUs directly observed in the roots (e.g. *C. geophilum*), the results from these technologies need to be interpreted with caution.

Alpine ecosystems are highly heterogeneous with very particular ecological conditions such as high wind exposure, snow cover over long periods and low soil availability, soil depth, nutrients and moisture. Given the complexity and collinearity among these environmental factors, it is challenging to disentangle the effects of individual variables in alpine biological communities. I found that alpine EM fungal communities have similar environmental drivers than the plant communities they associate with. Edaphic properties (e.g. soil pH and soil nutrient availability) were the main drivers of EM fungal communities across the Alps. By analysing the EM fungal communities associated with three plant hosts from different families in **Chapter 2** and three different hosts from the same genus in **Chapter 4**, I conclude that alpine EM fungal communities are mostly composed by generalist fungi, with low host specificity across plant families and within genera. Moreover, at this regional scale, while elevation (as a continuous variable) does not directly influence EM fungal communities, I found significant differences in EM fungal community composition between the treeline ecotone and the alpine sites due to their different ecological conditions. These results revealed that the complex grid of biotic and abiotic factors that shapes these communities in these highly heterogeneous habitats poses challenges to studies at regional scale since small scale habitat variability can have a drastic influence. For instance, EM fungal community composition is expected to change

significantly at local scales in recently deglaciated areas, or along primary successional sites in glacier valleys. In **Chapter 2**, these changes in community composition were particularly relevant across the Rotmoos glacier forefield (OBERGU, Austria), where the sampling sites closer to the glacier (only recently ice-free) were dominated by fungi of the phylum Ascomycota (e.g. *Sordariales* and *Geopora* spp.) whereas sites deglaciated longer were mostly dominated by Basidiomycota (e.g. *Tomentella-Thelephora* and *Russula* spp.). Therefore, despite the importance of large-scale studies to better understand the response of EM fungal communities in future climate change scenarios, it is important to continue monitoring EM fungal communities at local scales to elucidate the resilience of these communities to local environmental variability in these highly heterogeneous habitats.

Strikingly, climatic variables were among the variables that contributed less to the EM fungal variability across the Alps. In part this is due to the limited variability in temperature and precipitation in the alpine zone across the European Alps, at least at the sampling sites. However, in **Chapter 3**, when analysing each habitat type individually, I verified that small changes in temperature and precipitation may lead to drastic changes in EM fungal community composition. These results revealed that climatic shifts leading to earlier snow melting and extension of the growing season, will favour EM taxa with wider ecological niches (mostly from the treeline ecotone) that will increase in abundance and colonize or even replace the EM fungal communities in habitats characterized by more restricted ecological conditions. In particular, these changes may be stronger in the snowbed habitats, where plant and fungal communities have less resilience to future environmental variability, being replaced by lowland communities. Alpine snowbed plant communities are one of the most threatened by climate change (Matteodo *et al.*, 2016). Given the critical roles of EM fungi in nutrient cycling and plant establishment and nutrition in snowbed habitats, a

decline in these highly specialized EM fungal communities due to climate change may have dramatic consequences for one the most unique alpine habitats

5.2 Future perspectives

This study provided baseline diversity, structure and function data of alpine EM fungal communities across the European Alps. However, ca. 60% of the EM fungal OTUs were identified only to genus level, while ca. 27% and 12% of the OTUs were identified at the species and family levels, respectively. This shows that there is an urgent need to better curate public DNA sequence databases in order to improve taxonomical resolution for dark taxa. For the most conspicuous fungal groups, such as *Cortinarius* and *Inocybe*, this could be achieved by the incorporation of sequences from existing type specimens (fruitbodies). However, this would be more challenging for the less conspicuously fruiting lineages such as *Tomentella-Thelephora* or *Sebacina*. The use of DNA sequence clustering methods for OTUs defined by the pre-established 97% or 99% sequence similarity cut-offs has boosted the field of microbial community ecology (Hugerth & Andersson, 2017). However, the use of these OTU-based approaches suffers from several drawbacks, for instance, over- or underestimating fungal diversity depending on species-specific population histories (Ryberg, 2015). Moreover, over the last decades, the development of new bioinformatic tools combined with sequencing cost reduction, contributed to the emergence of a panoply of pipelines for OTU assignment with different sensitivities that may yield different results making it difficult to compare among studies. Therefore, it is important to establish unified frameworks, bridging historical datasets with new DNA-based species delimitation methods using molecular phylogenetic approaches, to obtain higher resolution in the taxonomical diversity of EM fungi across the European Alps and to better understand the role of these fungal communities in these harsh environments.

Biogeography studies the distribution patterns of biodiversity across space and time. In this thesis, I attempted to address the main distribution patterns of alpine EM fungal communities across the European Alps. However, focusing the study to two of the multiple habitats in the Alps and to one sampling season might limit our understanding of the distribution and seasonality of these EM fungal communities. At local scales, alpine EM fungal communities have been shown to vary significantly between consecutive years and to have high spatial heterogeneity (Mühlmann & Peintner, 2008). Therefore, to better understand the biogeographical patterns of these dynamic communities and how they may respond to future climate change scenarios, it is necessary to replicate this study across other alpine habitats and across seasons. Botnen *et al.* (2019) examined communities of root-associated fungi (including EM fungi) in *B. vivipara* at large biogeographical scales in the North Atlantic region and including the European Alps, highlighting a robust biogeographical structuring of the fungal communities and a high proportion of fungal OTUs unique to the European Alps. However, the authors only sampled two locations in the Austrian Alps. Therefore, a better estimation of the uniqueness of EM fungal communities across the European Alps is yet to be revealed at larger sampling scales. The baseline diversity data generated here will support comparative studies aiming to evaluate large scale biogeographical patterns of alpine EM communities and their extinction risk under future climatic scenarios.

Finally, in this thesis, a strong emphasis was placed on the study of host phylogeny (at family and intrageneric level) and demographic effects (population structure) on their associated EM fungal communities. In **Chapter 2**, I reported that plant host identity and within host species genetic variation have no significant effects on EM fungal communities. Moreover, this was confirmed in **Chapter 4**, when comparing the EM communities associated with two willow species and their hybrids. Due to methodological bias linked to the microsatellite DNA markers used, it was particularly challenging to assess the effect of host

population structure on EM fungal communities. However, there is growing evidence that plant host genetic background may be correlated with root-associated fungal communities (Gehring *et al.*, 2014, 2017; Lamit *et al.*, 2016). Despite the resulted lack of significant evidence of the influence of host genotype on EM fungal communities, one may expect that plant host population dynamics follow the strong habitat heterogeneity, and so do symbiotic fungal communities. For instance, to better assess the influence of host genotype on EM fungal communities, future studies should address this question in controlled laboratory conditions (e.g. common garden experiments) with a more targeted selection of phenotypically expressed genotypes, such as drought or solar radiation tolerance or by using genomic approaches to assess host genetic diversity (e.g. RAD-sequencing).

Appendix A

Table S2.1 Ectomycorrhizal OTUs in the roots and in soil found in this study (Chapter 2 and Chapter 3).

OTU				
number	Compartment	Top Blast hit to UNITE database v7.2	Blast hit	Taxonomy
OTU_001	Roots	Agaricales_sp UDB027430 SH218856.07FU reps	91.87	<i>Agaricales</i> sp1
OTU_003	Roots	Amphinema_sp KJ195349 SH489963.07FU reps_singleton	98.86	<i>Amphinema</i> sp1
OTU_004	Roots	Cenococcum_geophilum JQ347036 SH199614.07FU reps	93.15	<i>Cenococcum</i> sp1
OTU_005	Roots	Cenococcum_geophilum JQ347036 SH199614.07FU reps	97.24	<i>Cenococcum geophilum</i>
OTU_006	Roots	Cenococcum_geophilum JQ347036 SH199614.07FU reps	97.26	<i>Cenococcum geophilum</i>
OTU_007	Roots	Cenococcum_geophilum JQ347036 SH199614.07FU reps	97.95	<i>Cenococcum geophilum</i>
OTU_008	Roots	Cenococcum_geophilum KC967375 SH199615.07FU reps	100.00	<i>Cenococcum geophilum</i>
OTU_009	Roots	Cenococcum_geophilum KP348245 SH214459.07FU reps	95.17	<i>Cenococcum</i> sp2
OTU_010	Roots	Cenococcum_geophilum KP348245 SH214459.07FU reps	97.20	<i>Cenococcum geophilum</i>
OTU_011	Roots	Cenococcum_geophilum KX510009 SH199612.07FU reps	96.43	<i>Cenococcum</i> sp3
OTU_012	Roots	Cenococcum_geophilum KX510009 SH199612.07FU reps	97.14	<i>Cenococcum geophilum</i>
OTU_013	Roots	Cenococcum_geophilum KX510009 SH199612.07FU reps	97.16	<i>Cenococcum geophilum</i>
OTU_014	Roots	Cenococcum_geophilum KX510009 SH199612.07FU reps	98.56	<i>Cenococcum geophilum</i>
OTU_015	Roots	Cenococcum_geophilum KX510009 SH199612.07FU reps	98.57	<i>Cenococcum geophilum</i>
OTU_016	Roots	Cenococcum_geophilum KX510009 SH199612.07FU reps	99.28	<i>Cenococcum geophilum</i>
OTU_017	Roots	Cenococcum_geophilum UDB004845 SH199621.07FU reps	96.53	<i>Cenococcum</i> sp4
OTU_019	Roots	Ceratobasidiaceae_sp UDB008789 SH196460.07FU reps	97.41	<i>Ceratobasidiaceae</i> sp1
OTU_027	Roots	Cortinarius_alpinus DQ295079 SH265621.07FU refs	97.18	<i>Cortinarius alpinus</i>
OTU_032	Roots	Cortinarius_decipiens FN428988 SH188469.07FU refs	99.45	<i>Cortinarius decipiens</i>
OTU_033	Roots	Cortinarius_decipiens FN428992 SH248762.07FU refs	91.71	<i>Cortinarius</i> sp1
OTU_034	Roots	Cortinarius_decipiens FN428992 SH248762.07FU refs	92.82	<i>Cortinarius</i> sp2
OTU_035	Roots	Cortinarius_decipiens FN428992 SH248762.07FU refs	97.19	<i>Cortinarius decipiens</i>
OTU_036	Roots	Cortinarius_decipiens FN428992 SH248762.07FU refs	97.79	<i>Cortinarius decipiens</i>
OTU_045	Roots	Cortinarius_laetissimus UDB005684 SH188480.07FU reps	94.76	<i>Cortinarius</i> sp3
OTU_048	Roots	Cortinarius_parvannulatus KY640615 SH188588.07FU reps	100.00	<i>Cortinarius parvannulatus</i>
OTU_049	Roots	Cortinarius_parvannulatus UDB016062 SH188475.07FU refs	98.36	<i>Cortinarius parvannulatus</i>
OTU_050	Roots	Cortinarius_pseudobovinus UDB001463 SH094642.07FU refs_singleton	100.00	<i>Cortinarius pseudobovinus</i>
OTU_056	Roots	Cortinarius_sp GU817134 SH188579.07FU reps	97.52	<i>Cortinarius</i> sp4
OTU_058	Roots	Cortinarius_subturibulosus FN428984 SH188545.07FU reps	97.33	<i>Cortinarius subturibulosus</i>
OTU_059	Roots	Cortinarius_vernus GQ159826 SH188560.07FU reps	94.76	<i>Cortinarius</i> sp5
OTU_060	Roots	Cortinarius_vernus UDB000742 SH188477.07FU refs	94.24	<i>Cortinarius</i> sp6
OTU_065	Roots	Entoloma_borgenii LN850521 SH181017.07FU reps	99.58	<i>Entoloma borgenii</i>
OTU_066	Roots	Entoloma_majaloides LN850478 SH181009.07FU refs	99.80	<i>Entoloma majaloides</i>
OTU_067	Roots	Entoloma_paludicola LN850517 SH181030.07FU refs	98.34	<i>Entoloma paludicola</i>
OTU_068	Roots	Genabea_fragilis AJ893243 SH195287.07FU reps	99.42	<i>Genabea fragilis</i>
OTU_071	Roots	Geopora_sp FM206420 SH213653.07FU refs	97.56	<i>Geopora</i> sp1
OTU_072	Roots	Geopora_sp GQ281480 SH031661.07FU reps_singleton	95.24	<i>Geopora</i> sp2
OTU_074	Roots	Geopora_sp JF927142 SH216639.07FU reps	98.28	<i>Geopora</i> sp3
OTU_075	Roots	Geopora_sp JQ890264 SH213682.07FU reps	100.00	<i>Geopora</i> sp4
OTU_076	Roots	Geopora_sp JX630441 SH213679.07FU reps	98.15	<i>Geopora</i> sp5

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OTU_077	Roots	Geopora_sp JX630509 SH213680.07FU reps	99.39	<i>Geopora</i> sp6
OTU_079	Roots	Hebeloma_aanenii KM390537 SH490461.07FU reps_singleton	98.18	<i>Hebeloma aanenii</i>
OTU_081	Roots	Hebeloma_cavipes UDB003187 SH215994.07FU refs	99.52	<i>Hebeloma cavipes</i>
OTU_083	Roots	Hebeloma_mesophaeum EF451057 SH218845.07FU refs	98.50	<i>Hebeloma mesophaeum</i>
OTU_085	Roots	Hebeloma_parvicystidium JQ751184 SH218905.07FU reps	92.17	<i>Hebeloma</i> sp1
OTU_086	Roots	Hebeloma_sp JX436893 SH218894.07FU reps	97.16	<i>Hebeloma</i> sp2
OTU_090	Roots	Hebelomataceae_sp AY310842 SH030768.07FU reps_singleton	91.13	<i>Hebeloma</i> sp3
OTU_093	Roots	Helotiales_sp HQ445486 SH198123.07FU reps	98.61	<i>Helotiales</i> sp1
OTU_094	Roots	Helotiales_sp UDB026008 SH181080.07FU reps	97.20	<i>Helotiales</i> sp2
OTU_098	Roots	Helvella_sp UDB019802 SH214366.07FU reps	93.62	<i>Helvella</i> sp1
OTU_105	Roots	Hydnobolites_cerebriformis EU784271 SH207912.07FU refs	100.00	<i>Hydnobolites cerebriformis</i>
OTU_108	Roots	Hymenogaster_sp UDB025649 SH523874.07FU reps	100.00	<i>Hymenogaster</i> sp1
OTU_110	Roots	Hymenogaster_sp UDB027885 SH204371.07FU reps	100.00	<i>Hymenogaster</i> sp2
OTU_111	Roots	Inocybaceae_sp EU326157 SH209545.07FU reps	100.00	<i>Inocybaceae</i> sp1
OTU_137	Roots	Inocybe_nemorosa HQ445027 SH179835.07FU reps	97.98	<i>Inocybe nemorosa</i>
OTU_143	Roots	Inocybe_sp AB848513 SH489906.07FU reps_singleton	97.44	<i>Inocybe</i> sp1
OTU_144	Roots	Inocybe_sp DQ054573 SH179845.07FU reps	100.00	<i>Inocybe</i> sp2
OTU_153	Roots	Inocybe_sp HQ215787 SH197270.07FU reps	100.00	<i>Inocybe</i> sp3
OTU_165	Roots	Inocybe_sp KF297126 SH001183.07FU reps_singleton	98.13	<i>Inocybe</i> sp4
OTU_168	Roots	Inocybe_sp UDB031699 SH629359.07FU reps_singleton	96.24	<i>Inocybe</i> sp5
OTU_180	Roots	Meliniomyces_bicolor AJ430147 SH426644.07FU refs	93.15	<i>Inocybe</i> sp6
OTU_181	Roots	Meliniomyces_bicolor AJ430147 SH426644.07FU refs	97.02	<i>Meliniomyces bicolor</i>
OTU_182	Roots	Meliniomyces_bicolor AJ430147 SH426644.07FU refs	98.59	<i>Meliniomyces bicolor</i>
OTU_189	Roots	Pezizaceae_sp UDB008929 SH193724.07FU reps	98.93	<i>Pezizaceae</i> sp1
OTU_195	Roots	Pustularia_sp UDB025063 SH521506.07FU reps	99.36	<i>Pustularia</i> sp1
OTU_197	Roots	Pyronemataceae_sp KC791022 SH026155.07FU reps_singleton	92.64	<i>Pyronemataceae</i> sp1
OTU_200	Roots	Russula_emetica UDB000300 SH218421.07FU refs	94.64	<i>Russula</i> sp1
OTU_201	Roots	Russula_emetica UDB000300 SH218421.07FU refs	95.82	<i>Russula</i> sp2
OTU_207	Roots	Russula_sanguinea UDB000899 SH218425.07FU refs	95.60	<i>Russula</i> sp3
OTU_215	Roots	Sebacina_sp AB506901 SH027711.07FU reps_singleton	97.99	<i>Sebacina</i> sp1
OTU_229	Roots	Sebacina_sp FR852358 SH214752.07FU reps	99.00	<i>Sebacina</i> sp2
OTU_243	Roots	Sebacina_sp HQ667823 SH214658.07FU refs	100.00	<i>Sebacina</i> sp3
OTU_244	Roots	Sebacina_sp HQ667838 SH214600.07FU refs	99.02	<i>Sebacina</i> sp4
OTU_245	Roots	Sebacina_sp HQ667898 SH263673.07FU refs	95.61	<i>Sebacina</i> sp5
OTU_247	Roots	Sebacina_sp HQ667898 SH263673.07FU refs	97.55	<i>Sebacina</i> sp6
OTU_248	Roots	Sebacina_sp HQ667898 SH263673.07FU refs	97.60	<i>Sebacina</i> sp7
OTU_250	Roots	Sebacina_sp JQ666715 SH214695.07FU reps	96.86	<i>Sebacina</i> sp8
OTU_253	Roots	Sebacina_sp JX630438 SH214709.07FU refs	98.02	<i>Sebacina</i> sp9
OTU_264	Roots	Sebacina_sp UDB016385 SH197124.07FU refs	97.56	<i>Sebacina</i> sp10
OTU_268	Roots	Sebacina_sp UDB017187 SH197134.07FU refs	98.53	<i>Sebacina</i> sp11
OTU_274	Roots	Inocybe_sp AM882733 SH180069.07FU refs	97.87	<i>Inocybe</i> sp6
OTU_275	Roots	Melanogaster_broomeanus UDB027758 SH182656.07FU reps	97.02	<i>Melanogaster broomeanus</i>
OTU_276	Roots	Hebeloma_mesophaeum EF451057 SH218845.07FU refs	98.50	<i>Hebeloma mesophaeum</i>
OTU_277	Roots	Sordariaceae_sp EU195342 SH205113.07FU reps	100.00	<i>Sordariaceae</i> sp1
OTU_278	Roots	Sordariales_sp KC965599 SH205115.07FU reps	100.00	<i>Sordariales</i> sp1
OTU_279	Roots	Sordariales_sp KF617590 SH212904.07FU reps	100.00	<i>Sordariales</i> sp2
OTU_283	Roots	Thelephoraceae_sp EF218838 SH250543.07FU refs	96.36	<i>Thelephoraceae</i> sp1

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OTU_284	Roots	Thelephoraceae_sp EF218838 SH250543.07FU refs	96.38	<i>Thelephoraceae</i> sp2
OTU_285	Roots	Thelephoraceae_sp EF218838 SH250543.07FU refs	96.83	<i>Thelephoraceae</i> sp3
OTU_286	Roots	Thelephoraceae_sp EF218838 SH250543.07FU refs	99.55	<i>Thelephoraceae</i> sp4
OTU_288	Roots	Thelephoraceae_sp FJ013066 SH184510.07FU reps	100.00	<i>Thelephoraceae</i> sp5
OTU_297	Roots	Thelephoraceae_sp JF927100 SH184556.07FU reps	94.09	<i>Thelephoraceae</i> sp6
OTU_298	Roots	Thelephoraceae_sp JF927100 SH184556.07FU reps	99.54	<i>Thelephoraceae</i> sp7
OTU_304	Roots	Thelephoraceae_sp JX630819 SH002709.07FU reps_singleton	98.10	<i>Thelephoraceae</i> sp8
OTU_307	Roots	Thelephoraceae_sp KC966202 SH010106.07FU reps_singleton	96.38	<i>Thelephoraceae</i> sp9
OTU_308	Roots	Thelephoraceae_sp KC966202 SH010106.07FU reps_singleton	98.19	<i>Thelephoraceae</i> sp10
OTU_312	Roots	Thelephoraceae_sp KF514699 SH007331.07FU reps_singleton	97.73	<i>Thelephoraceae</i> sp11
OTU_313	Roots	Thelephoraceae_sp KF514724 SH189486.07FU reps	98.00	<i>Thelephoraceae</i> sp12
OTU_317	Roots	Thelephoraceae_sp KX444331 SH629578.07FU reps_singleton	97.12	<i>Thelephoraceae</i> sp13
OTU_318	Roots	Thelephoraceae_sp KX510038 SH630565.07FU reps_singleton	98.58	<i>Thelephoraceae</i> sp14
OTU_322	Roots	Thelephoraceae_sp UDB012540 SH189468.07FU reps	97.92	<i>Thelephoraceae</i> sp15
OTU_331	Roots	Thelephora_sp KM403039 SH184713.07FU reps	97.74	<i>Thelephora</i> sp1
OTU_338	Roots	Tomentella_badia HM545736 SH177782.07FU reps	98.64	<i>Tomentella badia</i>
OTU_344	Roots	Tomentella_badia JX630675 SH177988.07FU reps	98.64	<i>Tomentella badia</i>
OTU_346	Roots	Tomentella_fuscocinerea UDB005497 SH184521.07FU reps	97.25	<i>Tomentella fuscocinerea</i>
OTU_347	Roots	Tomentella_galzinii UDB000263 SH177815.07FU refs	97.24	<i>Tomentella galzinii</i>
OTU_354	Roots	Tomentella_sp AB848641 SH177825.07FU reps	97.26	<i>Tomentella</i> sp1
OTU_355	Roots	Tomentella_sp AY635171 SH177818.07FU reps	100.00	<i>Tomentella</i> sp2
OTU_358	Roots	Tomentella_sp DQ150115 SH177817.07FU reps	95.89	<i>Tomentella</i> sp3
OTU_361	Roots	Tomentella_sp EF218830 SH177996.07FU reps	98.64	<i>Tomentella</i> sp4
OTU_369	Roots	Tomentella_sp HQ215806 SH177870.07FU reps	97.78	<i>Tomentella</i> sp5
OTU_372	Roots	Tomentella_sp HQ445188 SH189361.07FU reps	98.18	<i>Tomentella</i> sp6
OTU_376	Roots	Tomentella_sp JF304367 SH177788.07FU reps	93.24	<i>Tomentella</i> sp7
OTU_384	Roots	Tomentella_sp KC965735 SH177990.07FU reps	98.17	<i>Tomentella</i> sp8
OTU_392	Roots	Tomentella_sp KU176247 SH177848.07FU reps	100.00	<i>Tomentella</i> sp9
OTU_401	Roots	Tomentella_sp UDB018381 SH002663.07FU reps_singleton	96.76	<i>Tomentella</i> sp10
OTU_408	Roots	Tomentella_stuposa JN652983 SH177816.07FU reps	93.64	<i>Tomentella</i> sp11
OTU_411	Roots	Tomentella_subclavigera UDB005176 SH189362.07FU reps	100.00	<i>Tomentella subclavigera</i>
OTU_413	Roots	Tomentella_viridula HF675501 SH177795.07FU reps	97.72	<i>Tomentella viridula</i>
OTU_420	Roots	Trichophaea_sp KX510020 SH631324.07FU reps_singleton	100.00	<i>Trichophaea</i> sp1
OTU_002	Roots & Soil	Amphinema_byssoides UDB008257 SH197943.07FU refs	100.00	<i>Amphinema byssoides</i>
OTU_018	Roots & Soil	Ceratobasidiaceae_sp FN298243 SH196458.07FU reps	100.00	<i>Ceratobasidiaceae</i> sp2
OTU_020	Roots & Soil	Clavulinaceae_sp HQ444977 SH179200.07FU reps	95.61	<i>Clavulinaceae</i> sp1
OTU_021	Roots & Soil	Clavulinaceae_sp KX444218 SH631645.07FU reps_singleton	90.23	<i>Clavulinaceae</i> sp2
OTU_022	Roots & Soil	Clavulinaceae_sp LC035140 SH524046.07FU reps	99.58	<i>Clavulinaceae</i> sp3
OTU_023	Roots & Soil	Clavulina_cinerea UDB027736 SH220218.07FU reps	98.72	<i>Clavulina cinerea</i>
OTU_024	Roots & Soil	Clavulina_rugosa EU862224 SH191180.07FU reps	99.59	<i>Clavulina rugosa</i>
OTU_025	Roots & Soil	Clavulina_sp FJ237119 SH031651.07FU reps_singleton	99.57	<i>Clavulina</i> sp1
OTU_026	Roots & Soil	Clavulina_sp HF675427 SH630396.07FU reps_singleton	100.00	<i>Clavulina</i> sp2
OTU_028	Roots & Soil	Cortinarius_alpinus DQ295081 SH183209.07FU refs	99.02	<i>Cortinarius alpinus</i>
OTU_029	Roots & Soil	Cortinarius_aureomarginatus UDB017178 SH188575.07FU reps	100.00	<i>Cortinarius aureomarginatus</i>
OTU_030	Roots & Soil	Cortinarius_casimiri FN429013 SH188471.07FU refs	98.91	<i>Cortinarius casimiri</i>
OTU_031	Roots & Soil	Cortinarius_croceus UDB021419 SH135194.07FU refs	99.50	<i>Cortinarius croceus</i>
OTU_037	Roots & Soil	Cortinarius_decipiens FN428992 SH248762.07FU refs	98.89	<i>Cortinarius decipiens</i>

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OTU_038	Roots & Soil	Cortinarius_diasemospermus UDB001230 SH188470.07FU refs	99.45	<i>Cortinarius diasemospermus</i>
OTU_039	Roots & Soil	Cortinarius_ferrugineovelatus KP137508 SH188536.07FU refs	100.00	<i>Cortinarius ferrugineovelatus</i>
OTU_040	Roots & Soil	Cortinarius_fulvescens AB588957 SH188481.07FU refs	99.47	<i>Cortinarius fulvescens</i>
OTU_041	Roots & Soil	Cortinarius_fulvescens GQ159913 SH188585.07FU refs	100.00	<i>Cortinarius fulvescens</i>
OTU_042	Roots & Soil	Cortinarius_fuscumbrinus KP137495 SH533329.07FU refs	93.53	<i>Cortinarius</i> sp7
OTU_043	Roots & Soil	Cortinarius_helobius AY286192 SH188485.07FU refs	98.98	<i>Cortinarius helobius</i>
OTU_044	Roots & Soil	Cortinarius_hinnuleoarmillatus UDB001458 SH188504.07FU refs	98.40	<i>Cortinarius hinnuleoarmillatus</i>
OTU_046	Roots & Soil	Cortinarius_laetissimus UDB005684 SH188480.07FU refs	96.34	<i>Cortinarius</i> sp8
OTU_047	Roots & Soil	Cortinarius_leucopus FR851994 SH188577.07FU refs	100.00	<i>Cortinarius leucopus</i>
OTU_051	Roots & Soil	Cortinarius_pseudofallax KF048130 SH248776.07FU refs	98.92	<i>Cortinarius pseudofallax</i>
OTU_052	Roots & Soil	Cortinarius_puellaris KT591582 SH188632.07FU refs	97.41	<i>Cortinarius puellaris</i>
OTU_053	Roots & Soil	Cortinarius_saniosus DQ102671 SH188476.07FU refs	100.00	<i>Cortinarius saniosus</i>
OTU_054	Roots & Soil	Cortinarius_sp EF655689 SH188595.07FU refs	99.45	<i>Cortinarius</i> sp9
OTU_055	Roots & Soil	Cortinarius_sp FJ378756 SH188569.07FU refs	98.37	<i>Cortinarius</i> sp10
OTU_057	Roots & Soil	Cortinarius_sp JF304325 SH188576.07FU refs	98.34	<i>Cortinarius</i> sp11
OTU_061	Roots & Soil	Cortinarius_vernus UDB000742 SH188477.07FU refs	94.82	<i>Cortinarius</i> sp12
OTU_062	Roots & Soil	Cortinarius_xanthocephalus UDB011265 SH222378.07FU refs	98.51	<i>Cortinarius xanthocephalus</i>
OTU_063	Roots & Soil	Elaphomyces_asperulus UDB027542 SH215736.07FU refs	100.00	<i>Elaphomyces asperulus</i>
OTU_064	Roots & Soil	Elaphomyces_papillatus UDB005089 SH190237.07FU refs	100.00	<i>Elaphomyces papillatus</i>
OTU_069	Roots & Soil	Genabea_fragilis UDB008869 SH195286.07FU refs	98.96	<i>Genabea fragilis</i>
OTU_070	Roots & Soil	Geopora_nicaeensis JF908022 SH213659.07FU refs	100.00	<i>Geopora nicaeensis</i>
OTU_073	Roots & Soil	Geopora_sp HM044527 SH213803.07FU refs	100.00	<i>Geopora</i> sp7
OTU_078	Roots & Soil	Geopora_sp UDB027272 SH213802.07FU refs	100.00	<i>Geopora</i> sp8
OTU_080	Roots & Soil	Hebeloma_cavipes JN943855 SH432010.07FU refs	100.00	<i>Hebeloma cavipes</i>
OTU_082	Roots & Soil	Hebeloma_cylindrosporum UDB003235 SH218851.07FU refs	96.76	<i>Hebeloma</i> sp3
OTU_084	Roots & Soil	Hebeloma_nigellum KX765786 SH628864.07FU refs_singleton	95.37	<i>Hebeloma</i> sp4
OTU_087	Roots & Soil	Hebeloma_sp JX436893 SH218894.07FU refs	98.57	<i>Hebeloma</i> sp5
OTU_088	Roots & Soil	Hebelomataceae_sp AM711491 SH030754.07FU refs_singleton	96.73	<i>Hebelomataceae</i> sp2
OTU_089	Roots & Soil	Hebelomataceae_sp AM711491 SH030754.07FU refs_singleton	99.06	<i>Hebelomataceae</i> sp3
OTU_091	Roots & Soil	Hebelomataceae_sp AY310842 SH030768.07FU refs_singleton	92.68	<i>Hebelomataceae</i> sp4
OTU_092	Roots & Soil	Hebeloma_theobrominum JX275966 SH127574.07FU refs	100.00	<i>Hebeloma theobrominum</i>
OTU_095	Roots & Soil	Helvella_capucina JX462564 SH489023.07FU refs_singleton	98.99	<i>Helvella capucina</i>
OTU_096	Roots & Soil	Helvella_dovrensis AF046223 SH175206.07FU refs	98.90	<i>Helvella dovrensis</i>
OTU_097	Roots & Soil	Helvella_lacunosa UDB019758 SH210614.07FU refs	100.00	<i>Helvella lacunosa</i>
OTU_099	Roots & Soil	Helvellosebacina_concrescens JQ665516 SH216685.07FU refs	88.54	<i>Helvellosebacina</i> sp1
OTU_100	Roots & Soil	Helvellosebacina_sp EF655694 SH214501.07FU refs	100.00	<i>Helvellosebacina</i> sp2
OTU_101	Roots & Soil	Helvellosebacina_sp GQ985425 SH214511.07FU refs	100.00	<i>Helvellosebacina</i> sp3
OTU_102	Roots & Soil	Helvellosebacina_sp UDB007962 SH291217.07FU refs	100.00	<i>Helvellosebacina</i> sp4
OTU_103	Roots & Soil	Helvellosebacina_sp UDB013734 SH214504.07FU refs	97.34	<i>Helvellosebacina</i> sp5
OTU_104	Roots & Soil	Humaria_hemisphaerica UDB015480 SH179622.07FU refs	99.04	<i>Humaria hemisphaerica</i>
OTU_106	Roots & Soil	Hymenogaster_bulliardii GU479231 SH218869.07FU refs	97.67	<i>Hymenogaster bulliardii</i>
OTU_107	Roots & Soil	Hymenogaster_megasporus UDB027410 SH218874.07FU refs	97.70	<i>Hymenogaster megasporus</i>
OTU_109	Roots & Soil	Hymenogaster_sp UDB025672 SH496928.07FU refs_singleton	99.52	<i>Hymenogaster</i> sp3
OTU_112	Roots & Soil	Inocybaceae_sp EU326161 SH205612.07FU refs	96.99	<i>Inocybaceae</i> sp2
OTU_113	Roots & Soil	Inocybaceae_sp FJ554164 SH209553.07FU refs	96.93	<i>Inocybaceae</i> sp3
OTU_114	Roots & Soil	Inocybaceae_sp JQ393073 SH209556.07FU refs	95.94	<i>Inocybaceae</i> sp4
OTU_115	Roots & Soil	Inocybaceae_sp JX436907 SH209550.07FU refs	99.49	<i>Inocybaceae</i> sp5

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OTU_116	Roots & Soil	Inocybe_aeruginascens GU949590 SH179015.07FU reps	90.54	<i>Inocybe</i> sp7
OTU_117	Roots & Soil	Inocybe_agordina JF908104 SH028420.07FU reps_singleton	100.00	<i>Inocybe agordina</i>
OTU_118	Roots & Soil	Inocybe_amethystina JF908123 SH219984.07FU reps	93.40	<i>Inocybe</i> sp8
OTU_119	Roots & Soil	Inocybe_appendiculata UDB015559 SH220485.07FU refs	99.02	<i>Inocybe appendiculata</i>
OTU_120	Roots & Soil	Inocybe_armeniaca UDB017935 SH176303.07FU reps	98.89	<i>Inocybe armeniaca</i>
OTU_121	Roots & Soil	Inocybe_bulbosissima FJ904158 SH183292.07FU refs	98.86	<i>Inocybe bulbosissima</i>
OTU_122	Roots & Soil	Inocybe_cincinnata AM882849 SH176517.07FU refs	99.02	<i>Inocybe cincinnata</i>
OTU_123	Roots & Soil	Inocybe_egenula UDB026847 SH197275.07FU reps	98.88	<i>Inocybe egenula</i>
OTU_124	Roots & Soil	Inocybe_fuscescentipes KJ399947 SH191989.07FU refs	99.06	<i>Inocybe fuscescentipes</i>
OTU_125	Roots & Soil	Inocybe_fuscidula JX630596 SH219203.07FU reps	96.62	<i>Inocybe</i> sp9
OTU_126	Roots & Soil	Inocybe_giacomi AM882742 SH194465.07FU refs	100.00	<i>Inocybe giacomii</i>
OTU_127	Roots & Soil	Inocybe_glabrescens UDB008812 SH208018.07FU reps	99.43	<i>Inocybe glabrescens</i>
OTU_128	Roots & Soil	Inocybe_guttulifer FJ237107 SH221723.07FU reps	100.00	<i>Inocybe guttulifer</i>
OTU_129	Roots & Soil	Inocybe_impexa AM882821 SH201234.07FU refs	96.15	<i>Inocybe</i> sp10
OTU_130	Roots & Soil	Inocybe_inodora UDB015287 SH188067.07FU reps	98.49	<i>Inocybe inodora</i>
OTU_131	Roots & Soil	Inocybe_lacera HQ604178 SH177120.07FU reps	96.04	<i>Inocybe</i> sp11
OTU_132	Roots & Soil	Inocybe_leptocystis JF908158 SH174203.07FU reps	100.00	<i>Inocybe leptocystis</i>
OTU_133	Roots & Soil	Inocybe_leucoloma GU980615 SH209539.07FU refs	96.88	<i>Inocybe</i> sp12
OTU_134	Roots & Soil	Inocybe_leucoloma GU980626 SH283251.07FU refs	97.25	<i>Inocybe leucoloma</i>
OTU_135	Roots & Soil	Inocybe_lindrothii KJ399915 SH132137.07FU refs	96.02	<i>Inocybe</i> sp13
OTU_136	Roots & Soil	Inocybe_mixtilis AM882840 SH214071.07FU reps	98.88	<i>Inocybe mixtilis</i>
OTU_138	Roots & Soil	Inocybe_nemorosa HQ445027 SH179835.07FU reps	99.49	<i>Inocybe nemorosa</i>
OTU_139	Roots & Soil	Inocybe_nitidiuscula HQ604458 SH219201.07FU reps	93.22	<i>Inocybe</i> sp14
OTU_140	Roots & Soil	Inocybe_obscurabadia AM882802 SH000066.07FU reps_singleton	96.77	<i>Inocybe</i> sp15
OTU_141	Roots & Soil	Inocybe_praetervisa KM226889 SH200844.07FU reps	99.49	<i>Inocybe praetervisa</i>
OTU_142	Roots & Soil	Inocybe_pruinosa UDB017663 SH188065.07FU reps	98.50	<i>Inocybe pruinosa</i>
OTU_145	Roots & Soil	Inocybe_sp EF619708 SH000065.07FU reps_singleton	97.66	<i>Inocybe</i> sp16
OTU_146	Roots & Soil	Inocybe_sp EF635762 SH192342.07FU reps	100.00	<i>Inocybe</i> sp17
OTU_147	Roots & Soil	Inocybe_sp EU711216 SH179839.07FU reps	97.41	<i>Inocybe</i> sp18
OTU_148	Roots & Soil	Inocybe_sp FJ378763 SH196061.07FU reps	99.47	<i>Inocybe</i> sp19
OTU_149	Roots & Soil	Inocybe_sp FJ904156 SH016085.07FU reps_singleton	100.00	<i>Inocybe</i> sp20
OTU_150	Roots & Soil	Inocybe_sp FN550906 SH022231.07FU reps_singleton	96.92	<i>Inocybe</i> sp21
OTU_151	Roots & Soil	Inocybe_sp FR852259 SH208381.07FU reps	91.04	<i>Inocybe</i> sp22
OTU_152	Roots & Soil	Inocybe_sp HG796975 SH003775.07FU reps_singleton	89.12	<i>Inocybe</i> sp23
OTU_154	Roots & Soil	Inocybe_sp HQ445236 SH179834.07FU reps	98.98	<i>Inocybe</i> sp24
OTU_155	Roots & Soil	Inocybe_sp JF304408 SH216845.07FU reps	99.14	<i>Inocybe</i> sp25
OTU_156	Roots & Soil	Inocybe_sp JX436914 SH222184.07FU reps	96.54	<i>Inocybe</i> sp26
OTU_157	Roots & Soil	Inocybe_sp JX630511 SH190795.07FU reps	95.20	<i>Inocybe</i> sp27
OTU_158	Roots & Soil	Inocybe_sp JX630539 SH222179.07FU reps	95.43	<i>Inocybe</i> sp28
OTU_159	Roots & Soil	Inocybe_sp JX630700 SH190793.07FU reps	97.62	<i>Inocybe</i> sp29
OTU_160	Roots & Soil	Inocybe_sp JX630896 SH220486.07FU reps	98.15	<i>Inocybe</i> sp30
OTU_161	Roots & Soil	Inocybe_sp KC111001 SH187317.07FU reps	98.92	<i>Inocybe</i> sp31
OTU_162	Roots & Soil	Inocybe_sp KC965198 SH008584.07FU reps_singleton	97.84	<i>Inocybe</i> sp32
OTU_163	Roots & Soil	Inocybe_sp KC965253 SH031789.07FU reps_singleton	88.07	<i>Inocybe</i> sp33
OTU_164	Roots & Soil	Inocybe_sp KF000684 SH179203.07FU reps	100.00	<i>Inocybe</i> sp34
OTU_166	Roots & Soil	Inocybe_sp KT630096 SH528624.07FU reps	92.86	<i>Inocybe</i> sp35
OTU_167	Roots & Soil	Inocybe_sp UDB026523 SH178673.07FU reps	98.06	<i>Inocybe</i> sp36

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OTU_169	Roots & Soil	Inocybe_sp UDB031699 SH629359.07FU reps_singleton	97.31	<i>Inocybe</i> sp37
OTU_170	Roots & Soil	Inocybe_squarrosoannulata GU980609 SH283269.07FU refs	99.50	<i>Inocybe squarrosoannulata</i>
OTU_171	Roots & Soil	Inocybe_squarrosoannulata HM209795 SH024001.07FU reps_singleton	99.56	<i>Inocybe squarrosoannulata</i>
OTU_172	Roots & Soil	Inocybe_subpaleacea KJ538548 SH219804.07FU refs	99.12	<i>Inocybe subpaleacea</i>
OTU_173	Roots & Soil	Inocybe_substraminipes FN550935 SH209538.07FU refs	97.38	<i>Inocybe substraminipes</i>
OTU_174	Roots & Soil	Inocybe_vulpinella UDB001758 SH221153.07FU refs	98.99	<i>Inocybe vulpinella</i>
OTU_175	Roots & Soil	Laccaria_sp GU969247 SH179272.07FU reps	99.51	<i>Laccaria</i> sp1
OTU_176	Roots & Soil	Laccaria_trichodermophora JX625288 SH220959.07FU reps	98.01	<i>Laccaria trichodermophora</i>
OTU_177	Roots & Soil	Laccaria_trichodermophora JX625288 SH220959.07FU reps	98.51	<i>Laccaria trichodermophora</i>
OTU_178	Roots & Soil	Lactarius_hysginoides KR090931 SH176421.07FU reps	98.81	<i>Lactarius hysginoides</i>
OTU_179	Roots & Soil	Mallocybe_sp JX630891 SH024006.07FU reps_singleton	100.00	<i>Mallocybe</i> sp1
OTU_183	Roots & Soil	Membranomyces_sp EF417799 SH184889.07FU reps	91.78	<i>Membranomyces</i> sp1
OTU_184	Roots & Soil	Membranomyces_sp HQ445149 SH222265.07FU reps	99.58	<i>Membranomyces</i> sp2
OTU_185	Roots & Soil	Membranomyces_sp KC686885 SH184886.07FU reps	91.55	<i>Membranomyces</i> sp3
OTU_186	Roots & Soil	Membranomyces_sp KC966200 SH033050.07FU reps_singleton	94.07	<i>Membranomyces</i> sp4
OTU_187	Roots & Soil	Membranomyces_sp KM247672 SH222271.07FU reps	93.64	<i>Membranomyces</i> sp5
OTU_188	Roots & Soil	Parascutellinia_carneosanguinea UDB025618 SH198305.07FU reps	99.51	<i>Parascutellinia carneosanguinea</i>
OTU_190	Roots & Soil	Peziza_sp GU817102 SH193720.07FU reps	100.00	<i>Peziza</i> sp1
OTU_191	Roots & Soil	Piloderma_lanatum UDB001743 SH196709.07FU reps	99.49	<i>Piloderma lanatum</i>
OTU_192	Roots & Soil	Pseudotomentella_sp LC035238 SH524049.07FU reps	97.60	<i>Pseudotomentella</i> sp1
OTU_193	Roots & Soil	Pseudotomentella_sp UDB008861 SH218586.07FU reps	100.00	<i>Pseudotomentella</i> sp2
OTU_194	Roots & Soil	Pulvinula_sp KF618004 SH020451.07FU reps_singleton	97.66	<i>Pulvinula</i> sp1
OTU_196	Roots & Soil	Pyronemataceae_sp JX630941 SH198961.07FU reps	100.00	<i>Pyronemataceae</i> sp2
OTU_198	Roots & Soil	Russula_chloroides HQ445395 SH220517.07FU reps	100.00	<i>Russula chloroides</i>
OTU_199	Roots & Soil	Russula_dryadicola UDB016122 SH187177.07FU reps	98.93	<i>Russula dryadicola</i>
OTU_202	Roots & Soil	Russula_emetica UDB000300 SH218421.07FU refs	97.71	<i>Russula emetica</i>
OTU_203	Roots & Soil	Russula_griseascens UDB016038 SH218422.07FU refs	98.78	<i>Russula griseascens</i>
OTU_204	Roots & Soil	Russula_nuoljiae KU205270 SH176552.07FU reps	98.20	<i>Russula nuoljiae</i>
OTU_205	Roots & Soil	Russula_olivobrunnea UDB011113 SH187355.07FU refs	97.33	<i>Russula olivobrunnea</i>
OTU_206	Roots & Soil	Russula_pascua JX436947 SH176550.07FU reps	100.00	<i>Russula pascua</i>
OTU_208	Roots & Soil	Russula_sanguinea UDB000899 SH218425.07FU refs	96.40	<i>Russula</i> sp4
OTU_209	Roots & Soil	Russula_sp GU998715 SH176559.07FU reps	98.89	<i>Russula</i> sp5
OTU_210	Roots & Soil	Sebacinaceae_sp JQ347205 SH021818.07FU reps_singleton	96.00	<i>Sebacinaceae</i> sp1
OTU_211	Roots & Soil	Sebacina_incrustans EF644113 SH214605.07FU refs	100.00	<i>Sebacina incrustans</i>
OTU_212	Roots & Soil	Sebacina_incrustans EF655701 SH214612.07FU refs	100.00	<i>Sebacina incrustans</i>
OTU_213	Roots & Soil	Sebacina_incrustans JQ665550 SH214617.07FU reps	100.00	<i>Sebacina incrustans</i>
OTU_214	Roots & Soil	Sebacina_sp AB506901 SH027711.07FU reps_singleton	96.47	<i>Sebacina</i> sp12
OTU_216	Roots & Soil	Sebacina_sp AB701397 SH197126.07FU refs	99.51	<i>Sebacina</i> sp13
OTU_217	Roots & Soil	Sebacina_sp AF440663 SH214627.07FU refs	100.00	<i>Sebacina</i> sp14
OTU_218	Roots & Soil	Sebacina_sp AY192164 SH214604.07FU refs	100.00	<i>Sebacina</i> sp15
OTU_219	Roots & Soil	Sebacina_sp EF218815 SH214607.07FU refs	97.00	<i>Sebacina</i> sp16
OTU_220	Roots & Soil	Sebacina_sp EF417823 SH214697.07FU refs	98.46	<i>Sebacina</i> sp17
OTU_221	Roots & Soil	Sebacina_sp EU444538 SH125974.07FU refs	99.00	<i>Sebacina</i> sp18
OTU_222	Roots & Soil	Sebacina_sp EU517032 SH027718.07FU reps_singleton	99.49	<i>Sebacina</i> sp19
OTU_223	Roots & Soil	Sebacina_sp EU645629 SH197133.07FU refs	100.00	<i>Sebacina</i> sp20
OTU_224	Roots & Soil	Sebacina_sp EU668266 SH125980.07FU refs	98.52	<i>Sebacina</i> sp21
OTU_225	Roots & Soil	Sebacina_sp EU910925 SH197127.07FU refs	98.48	<i>Sebacina</i> sp22

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OTU_226	Roots & Soil	Sebacina_sp FJ827240 SH214645.07FU refs	97.48	<i>Sebacina</i> sp23
OTU_227	Roots & Soil	Sebacina_sp FR852342 SH214689.07FU refs	98.48	<i>Sebacina</i> sp24
OTU_228	Roots & Soil	Sebacina_sp FR852357 SH104960.07FU refs	99.51	<i>Sebacina</i> sp25
OTU_230	Roots & Soil	Sebacina_sp GQ219876 SH027696.07FU reps_singleton	100.00	<i>Sebacina</i> sp26
OTU_231	Roots & Soil	Sebacina_sp GU256183 SH214641.07FU refs	99.50	<i>Sebacina</i> sp27
OTU_232	Roots & Soil	Sebacina_sp GU817065 SH214632.07FU refs	98.97	<i>Sebacina</i> sp28
OTU_233	Roots & Soil	Sebacina_sp GU817087 SH125951.07FU refs	99.50	<i>Sebacina</i> sp29
OTU_234	Roots & Soil	Sebacina_sp HM230656 SH197122.07FU refs	97.54	<i>Sebacina</i> sp30
OTU_235	Roots & Soil	Sebacina_sp HQ154281 SH380589.07FU refs	99.51	<i>Sebacina</i> sp31
OTU_236	Roots & Soil	Sebacina_sp HQ154311 SH214679.07FU refs	98.03	<i>Sebacina</i> sp32
OTU_237	Roots & Soil	Sebacina_sp HQ154330 SH214703.07FU refs	100.00	<i>Sebacina</i> sp33
OTU_238	Roots & Soil	Sebacina_sp HQ154375 SH214708.07FU refs	99.49	<i>Sebacina</i> sp34
OTU_239	Roots & Soil	Sebacina_sp HQ154376 SH197146.07FU refs	100.00	<i>Sebacina</i> sp35
OTU_240	Roots & Soil	Sebacina_sp HQ330995 SH214676.07FU refs	98.99	<i>Sebacina</i> sp36
OTU_241	Roots & Soil	Sebacina_sp HQ445284 SH214631.07FU refs	98.50	<i>Sebacina</i> sp37
OTU_242	Roots & Soil	Sebacina_sp HQ445474 SH214673.07FU reps	99.49	<i>Sebacina</i> sp38
OTU_246	Roots & Soil	Sebacina_sp HQ667898 SH263673.07FU refs	97.04	<i>Sebacina</i> sp39
OTU_249	Roots & Soil	Sebacina_sp HQ667898 SH263673.07FU refs	98.05	<i>Sebacina</i> sp40
OTU_251	Roots & Soil	Sebacina_sp JQ666715 SH214695.07FU reps	98.00	<i>Sebacina</i> sp41
OTU_252	Roots & Soil	Sebacina_sp JQ666717 SH214620.07FU refs	99.00	<i>Sebacina</i> sp42
OTU_254	Roots & Soil	Sebacina_sp KF000675 SH487549.07FU reps_singleton	99.49	<i>Sebacina</i> sp43
OTU_255	Roots & Soil	Sebacina_sp KF618000 SH214636.07FU reps	100.00	<i>Sebacina</i> sp44
OTU_256	Roots & Soil	Sebacina_sp KF871204 SH214713.07FU reps	100.00	<i>Sebacina</i> sp45
OTU_257	Roots & Soil	Sebacina_sp LC013793 SH214749.07FU reps	99.03	<i>Sebacina</i> sp46
OTU_258	Roots & Soil	Sebacina_sp UDB005300 SH214668.07FU refs	99.01	<i>Sebacina</i> sp47
OTU_259	Roots & Soil	Sebacina_sp UDB005437 SH197137.07FU refs	98.54	<i>Sebacina</i> sp48
OTU_260	Roots & Soil	Sebacina_sp UDB005787 SH214648.07FU refs	97.07	<i>Sebacina</i> sp49
OTU_261	Roots & Soil	Sebacina_sp UDB008802 SH214615.07FU refs	100.00	<i>Sebacina</i> sp50
OTU_262	Roots & Soil	Sebacina_sp UDB009836 SH125997.07FU refs	98.99	<i>Sebacina</i> sp51
OTU_263	Roots & Soil	Sebacina_sp UDB013733 SH214665.07FU refs	100.00	<i>Sebacina</i> sp52
OTU_265	Roots & Soil	Sebacina_sp UDB016419 SH214601.07FU refs	99.50	<i>Sebacina</i> sp53
OTU_266	Roots & Soil	Sebacina_sp UDB016431 SH197125.07FU refs	98.50	<i>Sebacina</i> sp54
OTU_267	Roots & Soil	Sebacina_sp UDB017183 SH214705.07FU refs	99.50	<i>Sebacina</i> sp55
OTU_269	Roots & Soil	Serendipita_sp AB669668 SH179996.07FU reps	99.03	<i>Serendipita</i> sp1
OTU_270	Roots & Soil	Serendipita_sp HQ211712 SH180002.07FU reps	98.02	<i>Serendipita</i> sp2
OTU_271	Roots & Soil	Serendipita_sp JN704824 SH201952.07FU refs	100.00	<i>Serendipita</i> sp3
OTU_272	Roots & Soil	Serendipita_sp UDB002608 SH180003.07FU refs	100.00	<i>Serendipita</i> sp4
OTU_273	Roots & Soil	Serendipita_sp UDB008509 SH179999.07FU refs	99.02	<i>Serendipita</i> sp5
OTU_280	Roots & Soil	Tarzetia_sp EU326167 SH469397.07FU reps_singleton	100.00	<i>Tarzetia</i> sp1
OTU_281	Roots & Soil	Thelephora_caryophyllea UDB000212 SH189359.07FU reps	99.08	<i>Thelephora caryophyllea</i>
OTU_282	Roots & Soil	Thelephoraceae_sp AB506097 SH189355.07FU reps	98.16	<i>Thelephoraceae</i> sp16
OTU_287	Roots & Soil	Thelephoraceae_sp EF619803 SH189559.07FU reps	96.83	<i>Thelephoraceae</i> sp17
OTU_289	Roots & Soil	Thelephoraceae_sp FJ013066 SH184510.07FU reps	96.33	<i>Thelephoraceae</i> sp18
OTU_290	Roots & Soil	Thelephoraceae_sp FJ553986 SH217475.07FU reps	100.00	<i>Thelephoraceae</i> sp19
OTU_291	Roots & Soil	Thelephoraceae_sp FJ553986 SH217475.07FU reps	96.80	<i>Thelephoraceae</i> sp20
OTU_292	Roots & Soil	Thelephoraceae_sp FJ897222 SH189481.07FU reps	98.73	<i>Thelephoraceae</i> sp21
OTU_293	Roots & Soil	Thelephoraceae_sp GU224049 SH184538.07FU reps	99.06	<i>Thelephoraceae</i> sp22

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OTU_294	Roots & Soil	Thelephoraceae_sp HG426040 SH189391.07FU reps	96.33	<i>Thelephoraceae</i> sp23
OTU_295	Roots & Soil	Thelephoraceae_sp JF304368 SH177972.07FU reps	98.62	<i>Thelephoraceae</i> sp24
OTU_296	Roots & Soil	Thelephoraceae_sp JF927096 SH189470.07FU reps	98.63	<i>Thelephoraceae</i> sp25
OTU_299	Roots & Soil	Thelephoraceae_sp JQ890243 SH002716.07FU reps_singleton	97.73	<i>Thelephoraceae</i> sp26
OTU_300	Roots & Soil	Thelephoraceae_sp JX316331 SH184529.07FU reps	96.33	<i>Thelephoraceae</i> sp27
OTU_301	Roots & Soil	Thelephoraceae_sp JX474856 SH006978.07FU reps_singleton	99.05	<i>Thelephoraceae</i> sp28
OTU_302	Roots & Soil	Thelephoraceae_sp JX630600 SH205653.07FU reps	99.55	<i>Thelephoraceae</i> sp29
OTU_303	Roots & Soil	Thelephoraceae_sp JX630620 SH189570.07FU reps	90.78	<i>Thelephoraceae</i> sp30
OTU_305	Roots & Soil	Thelephoraceae_sp KC965385 SH184646.07FU reps	97.70	<i>Thelephoraceae</i> sp31
OTU_306	Roots & Soil	Thelephoraceae_sp KC965825 SH006971.07FU reps_singleton	94.63	<i>Thelephoraceae</i> sp32
OTU_309	Roots & Soil	Thelephoraceae_sp KC966202 SH010106.07FU reps_singleton	98.66	<i>Thelephoraceae</i> sp33
OTU_310	Roots & Soil	Thelephoraceae_sp KF000681 SH527424.07FU reps	96.33	<i>Thelephoraceae</i> sp34
OTU_311	Roots & Soil	Thelephoraceae_sp KF000681 SH527424.07FU reps	99.54	<i>Thelephoraceae</i> sp35
OTU_314	Roots & Soil	Thelephoraceae_sp KF617390 SH010130.07FU reps_singleton	97.26	<i>Thelephoraceae</i> sp36
OTU_315	Roots & Soil	Thelephoraceae_sp KF779449 SH002694.07FU reps_singleton	99.54	<i>Thelephoraceae</i> sp37
OTU_316	Roots & Soil	Thelephoraceae_sp KM247741 SH494063.07FU reps_singleton	93.12	<i>Thelephoraceae</i> sp38
OTU_319	Roots & Soil	Thelephoraceae_sp LC013849 SH494717.07FU reps_singleton	94.12	<i>Thelephoraceae</i> sp39
OTU_320	Roots & Soil	Thelephoraceae_sp UDB005328 SH189412.07FU reps	95.46	<i>Thelephoraceae</i> sp40
OTU_321	Roots & Soil	Thelephoraceae_sp UDB008009 SH189413.07FU reps	98.62	<i>Thelephoraceae</i> sp41
OTU_323	Roots & Soil	Thelephoraceae_sp UDB013735 SH184546.07FU reps	99.54	<i>Thelephoraceae</i> sp42
OTU_324	Roots & Soil	Thelephoraceae_sp UDB014448 SH002625.07FU reps_singleton	95.50	<i>Thelephoraceae</i> sp43
OTU_325	Roots & Soil	Thelephoraceae_sp UDB014531 SH006931.07FU reps_singleton	97.24	<i>Thelephoraceae</i> sp44
OTU_326	Roots & Soil	Thelephoraceae_sp UDB017139 SH184639.07FU reps	100.00	<i>Thelephoraceae</i> sp45
OTU_327	Roots & Soil	Thelephoraceae_sp UDB017515 SH010055.07FU reps_singleton	95.85	<i>Thelephoraceae</i> sp46
OTU_328	Roots & Soil	Thelephoraceae_sp UDB026049 SH189549.07FU reps	95.31	<i>Thelephoraceae</i> sp47
OTU_329	Roots & Soil	Thelephoraceae_sp UDB026586 SH525613.07FU reps	99.54	<i>Thelephoraceae</i> sp48
OTU_330	Roots & Soil	Thelephora_sp FJ196986 SH184613.07FU reps	96.82	<i>Thelephora</i> sp2
OTU_332	Roots & Soil	Thelephora_sp LC035327 SH184603.07FU reps	98.18	<i>Thelephora</i> sp3
OTU_333	Roots & Soil	Thelephora_sp UDB015188 SH184554.07FU refs	99.55	<i>Thelephora</i> sp4
OTU_334	Roots & Soil	Tomentella_alpina EF655702 SH177861.07FU refs	100.00	<i>Tomentella alpina</i>
OTU_335	Roots & Soil	Tomentella_asperula UDB018469 SH191762.07FU reps	99.06	<i>Tomentella asperula</i>
OTU_336	Roots & Soil	Tomentella_badia HM164617 SH177806.07FU reps	97.75	<i>Tomentella badia</i>
OTU_337	Roots & Soil	Tomentella_badia HM545736 SH177782.07FU reps	96.41	<i>Tomentella</i> sp12
OTU_339	Roots & Soil	Tomentella_badia HQ445447 SH177841.07FU reps	99.12	<i>Tomentella badia</i>
OTU_340	Roots & Soil	Tomentella_badia JQ711987 SH177828.07FU reps	95.50	<i>Tomentella</i> sp13
OTU_341	Roots & Soil	Tomentella_badia JQ711987 SH177828.07FU reps	95.93	<i>Tomentella</i> sp14
OTU_342	Roots & Soil	Tomentella_badia JQ711987 SH177828.07FU reps	96.00	<i>Tomentella</i> sp15
OTU_343	Roots & Soil	Tomentella_badia JQ711987 SH177828.07FU reps	98.18	<i>Tomentella badia</i>
OTU_345	Roots & Soil	Tomentella_ellisii UDB005085 SH189369.07FU reps	99.08	<i>Tomentella ellisii</i>
OTU_348	Roots & Soil	Tomentella_galzinii UDB000263 SH177815.07FU refs	99.05	<i>Tomentella galzinii</i>
OTU_349	Roots & Soil	Tomentella_lapida JF748069 SH177864.07FU reps	93.24	<i>Tomentella</i> sp16
OTU_350	Roots & Soil	Tomentella_lapida UDB001659 SH355813.07FU refs	95.93	<i>Tomentella</i> sp17
OTU_351	Roots & Soil	Tomentella_lapida UDB001659 SH355813.07FU refs	96.38	<i>Tomentella</i> sp18
OTU_352	Roots & Soil	Tomentella_lilacinogrisea UDB014116 SH178628.07FU reps	99.54	<i>Tomentella lilacinogrisea</i>
OTU_353	Roots & Soil	Tomentella_lilacinogrisea UDB017118 SH189577.07FU reps	91.82	<i>Tomentella</i> sp19
OTU_356	Roots & Soil	Tomentella_sp AY874379 SH177873.07FU reps	99.51	<i>Tomentella</i> sp20
OTU_357	Roots & Soil	Tomentella_sp DQ150115 SH177817.07FU reps	94.55	<i>Tomentella</i> sp21

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OTU_359	Roots & Soil	Tomentella_sp DQ150116 SH177835.07FU reps	100.00	<i>Tomentella</i> sp22
OTU_360	Roots & Soil	Tomentella_sp EF218826 SH184516.07FU reps	97.71	<i>Tomentella</i> sp23
OTU_362	Roots & Soil	Tomentella_sp EU292520 SH177833.07FU reps	99.54	<i>Tomentella</i> sp24
OTU_363	Roots & Soil	Tomentella_sp GU220615 SH189360.07FU reps	99.04	<i>Tomentella</i> sp25
OTU_364	Roots & Soil	Tomentella_sp HF565111 SH177847.07FU reps	96.36	<i>Tomentella</i> sp26
OTU_365	Roots & Soil	Tomentella_sp HF565111 SH177847.07FU reps	97.70	<i>Tomentella</i> sp27
OTU_366	Roots & Soil	Tomentella_sp HF565111 SH177847.07FU reps	98.17	<i>Tomentella</i> sp28
OTU_367	Roots & Soil	Tomentella_sp HQ215806 SH177870.07FU reps	94.98	<i>Tomentella</i> sp29
OTU_368	Roots & Soil	Tomentella_sp HQ215806 SH177870.07FU reps	97.72	<i>Tomentella</i> sp30
OTU_370	Roots & Soil	Tomentella_sp HQ215806 SH177870.07FU reps	98.64	<i>Tomentella</i> sp31
OTU_371	Roots & Soil	Tomentella_sp HQ215823 SH189465.07FU reps	100.00	<i>Tomentella</i> sp32
OTU_373	Roots & Soil	Tomentella_sp HQ445218 SH177857.07FU reps	94.98	<i>Tomentella</i> sp33
OTU_374	Roots & Soil	Tomentella_sp HQ445218 SH177857.07FU reps	95.91	<i>Tomentella</i> sp34
OTU_375	Roots & Soil	Tomentella_sp JF304358 SH217476.07FU reps	99.54	<i>Tomentella</i> sp35
OTU_377	Roots & Soil	Tomentella_sp JF304367 SH177788.07FU reps	99.54	<i>Tomentella</i> sp36
OTU_378	Roots & Soil	Tomentella_sp JF304372 SH177843.07FU reps	98.65	<i>Tomentella</i> sp37
OTU_379	Roots & Soil	Tomentella_sp JN197795 SH177796.07FU reps	96.35	<i>Tomentella</i> sp38
OTU_380	Roots & Soil	Tomentella_sp JX030255 SH002720.07FU reps_singleton	96.33	<i>Tomentella</i> sp39
OTU_381	Roots & Soil	Tomentella_sp JX030255 SH002720.07FU reps_singleton	96.79	<i>Tomentella</i> sp40
OTU_382	Roots & Soil	Tomentella_sp JX316236 SH177821.07FU reps	96.36	<i>Tomentella</i> sp41
OTU_383	Roots & Soil	Tomentella_sp JX630358 SH177862.07FU reps	95.28	<i>Tomentella</i> sp42
OTU_385	Roots & Soil	Tomentella_sp KC965820 SH177801.07FU reps	99.55	<i>Tomentella</i> sp43
OTU_386	Roots & Soil	Tomentella_sp KC965844 SH177926.07FU reps	97.64	<i>Tomentella</i> sp44
OTU_387	Roots & Soil	Tomentella_sp KF000560 SH177808.07FU reps	99.54	<i>Tomentella</i> sp45
OTU_388	Roots & Soil	Tomentella_sp KF000592 SH177974.07FU reps	99.54	<i>Tomentella</i> sp46
OTU_389	Roots & Soil	Tomentella_sp KP403048 SH177919.07FU reps	97.25	<i>Tomentella</i> sp47
OTU_390	Roots & Soil	Tomentella_sp KT275603 SH496388.07FU reps_singleton	94.98	<i>Tomentella</i> sp48
OTU_391	Roots & Soil	Tomentella_sp KT353049 SH643220.07FU reps	98.17	<i>Tomentella</i> sp49
OTU_393	Roots & Soil	Tomentella_sp KX497175 SH177879.07FU reps	99.09	<i>Tomentella</i> sp50
OTU_394	Roots & Soil	Tomentella_sp UDB002905 SH177851.07FU reps	98.17	<i>Tomentella</i> sp51
OTU_395	Roots & Soil	Tomentella_sp UDB008530 SH177854.07FU reps	100.00	<i>Tomentella</i> sp52
OTU_396	Roots & Soil	Tomentella_sp UDB008971 SH178629.07FU reps	99.08	<i>Tomentella</i> sp53
OTU_397	Roots & Soil	Tomentella_sp UDB011105 SH010149.07FU reps_singleton	87.10	<i>Tomentella</i> sp54
OTU_398	Roots & Soil	Tomentella_sp UDB014545 SH217408.07FU reps	99.55	<i>Tomentella</i> sp55
OTU_399	Roots & Soil	Tomentella_sp UDB016199 SH178635.07FU reps	96.79	<i>Tomentella</i> sp56
OTU_400	Roots & Soil	Tomentella_sp UDB017390 SH184544.07FU reps	96.80	<i>Tomentella</i> sp57
OTU_402	Roots & Soil	Tomentella_sp UDB018515 SH177813.07FU refs	98.64	<i>Tomentella</i> sp58
OTU_403	Roots & Soil	Tomentella_sp UDB025800 SH185320.07FU reps	100.00	<i>Tomentella</i> sp59
OTU_404	Roots & Soil	Tomentella_sp UDB025953 SH205667.07FU reps	97.16	<i>Tomentella</i> sp60
OTU_405	Roots & Soil	Tomentella_sp UDB027247 SH177827.07FU reps	97.71	<i>Tomentella</i> sp61
OTU_406	Roots & Soil	Tomentella_sp UDB031755 SH184738.07FU reps	99.08	<i>Tomentella</i> sp62
OTU_407	Roots & Soil	Tomentella_stuposa JN652983 SH177816.07FU reps	93.12	<i>Tomentella</i> sp63
OTU_409	Roots & Soil	Tomentella_stuposa JN652983 SH177816.07FU reps	96.33	<i>Tomentella</i> sp64
OTU_410	Roots & Soil	Tomentella_stuposa UDB016174 SH177785.07FU refs	97.24	<i>Tomentella</i> stuposa
OTU_412	Roots & Soil	Tomentella_terrestris UDB003315 SH189365.07FU refs	97.62	<i>Tomentella</i> terrestris
OTU_414	Roots & Soil	Tomentella_viridula HF675501 SH177795.07FU reps	99.54	<i>Tomentella</i> viridula
OTU_415	Roots & Soil	Tricholoma_argyraceum UDB011574 SH219342.07FU refs	100.00	<i>Tricholoma</i> argyraceum

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OTU_416	Roots & Soil	Tricholoma_sulphureum LT000065 SH190404.07FU reps	100.00	<i>Tricholoma sulphureum</i>
OTU_417	Roots & Soil	Trichophaea_sp KC986257 SH487546.07FU reps_singleton	99.55	<i>Trichophaea</i> sp2
OTU_418	Roots & Soil	Trichophaea_sp KF000553 SH523315.07FU reps	100.00	<i>Trichophaea</i> sp3
OTU_419	Roots & Soil	Trichophaea_sp KF000606 SH521561.07FU reps	88.83	<i>Trichophaea</i> sp4
OTU_421	Roots & Soil	Trichophaea_woolhopeia UDB026377 SH215398.07FU reps	99.57	<i>Trichophaea woolhopeia</i>
OTU_422	Roots & Soil	Tuber_wenchuanense JX267044 SH210422.07FU refs	98.45	<i>Tuber wenchuanense</i>
OTU_424	Soil	Agaricales_sp AY351628 SH218849.07FU reps	100.00	<i>Agaricales</i> sp2
OTU_425	Soil	Agaricales_sp GU479323 SH218866.07FU reps	91.90	<i>Agaricales</i> sp3
OTU_426	Soil	Agaricales_sp KX438330 SH218889.07FU reps	90.88	<i>Agaricales</i> sp4
OTU_427	Soil	Albatrellus_ovinus UDB018057 SH199699.07FU reps	100.00	<i>Albatrellus ovinus</i>
OTU_428	Soil	Amanita_cylindrispora AY325839 SH212888.07FU reps	86.57	<i>Amanita</i> sp1
OTU_429	Soil	Amanita_cylindrispora AY325839 SH212888.07FU reps	88.06	<i>Amanita</i> sp2
OTU_430	Soil	Amanita_olivaceogrisea UDB015459 SH101622.07FU refs	95.75	<i>Amanita</i> sp3
OTU_431	Soil	Amanita_ponderosa KJ950801 SH191204.07FU reps	94.23	<i>Amanita</i> sp4
OTU_432	Soil	Amanita_sp AY436477 SH002858.07FU reps_singleton	95.39	<i>Amanita</i> sp5
OTU_433	Soil	Amanita_sp KP071065 SH494361.07FU reps_singleton	100.00	<i>Amanita</i> sp6
OTU_434	Soil	Amphinema_sp AB636467 SH206583.07FU reps	98.79	<i>Amphinema</i> sp2
OTU_435	Soil	Amphinema_sp KJ195349 SH489963.07FU reps_singleton	95.67	<i>Amphinema</i> sp3
OTU_436	Soil	Amphinema_sp KJ938038 SH206756.07FU reps	96.81	<i>Amphinema</i> sp4
OTU_437	Soil	Amphinema_sp KM588762 SH492790.07FU reps_singleton	93.07	<i>Amphinema</i> sp5
OTU_438	Soil	Amphinema_sp UDB000841 SH197766.07FU reps	83.01	<i>Amphinema</i> sp6
OTU_439	Soil	Auricularia_sp HM488497 SH470965.07FU reps_singleton	84.98	<i>Auricularia</i> sp1
OTU_440	Soil	Balsamia_platyspora UDB013693 SH209666.07FU reps	100.00	<i>Balsamia platyspora</i>
OTU_441	Soil	Balsamia_sp JX474857 SH209665.07FU reps	82.69	<i>Balsamia</i> sp1
OTU_442	Soil	Balsamia_sp JX630958 SH478098.07FU reps_singleton	99.57	<i>Balsamia</i> sp2
OTU_443	Soil	Balsamia_sp UDB013602 SH177121.07FU reps	97.87	<i>Balsamia</i> sp3
OTU_444	Soil	Boletus_luridus UDB000648 SH176266.07FU refs	99.64	<i>Boletus luridus</i>
OTU_445	Soil	Ceratobasidiaceae_sp DQ273373 SH014667.07FU reps_singleton	91.23	<i>Ceratobasidiaceae</i> sp3
OTU_446	Soil	Clavulina_cinerea UDB027028 SH220241.07FU reps	98.15	<i>Clavulina cinerea</i>
OTU_447	Soil	Clavulina_coralloides HQ215767 SH191174.07FU reps	99.62	<i>Clavulina coralloides</i>
OTU_448	Soil	Clavulina_sp FJ237119 SH031651.07FU reps_singleton	94.44	<i>Clavulina</i> sp3
OTU_449	Soil	Clavulina_sp GQ240920 SH220228.07FU reps	93.10	<i>Clavulina</i> sp4
OTU_450	Soil	Clavulina_sp JX630952 SH191181.07FU reps	99.32	<i>Clavulina</i> sp5
OTU_451	Soil	Clavulina_sp UDB007478 SH220220.07FU reps	99.66	<i>Clavulina</i> sp6
OTU_452	Soil	Clavulinaceae_sp FJ553192 SH202674.07FU reps	97.26	<i>Clavulinaceae</i> sp4
OTU_453	Soil	Clavulinaceae_sp HQ444977 SH179200.07FU reps	99.29	<i>Clavulinaceae</i> sp5
OTU_454	Soil	Clavulinaceae_sp KF618036 SH003388.07FU reps_singleton	97.98	<i>Clavulinaceae</i> sp6
OTU_455	Soil	Cortinarius_agathosmus UDB002228 SH188566.07FU reps	99.17	<i>Cortinarius agathosmus</i>
OTU_456	Soil	Cortinarius_alboviolaceus UDB002442 SH196666.07FU reps	98.83	<i>Cortinarius alboviolaceus</i>
OTU_457	Soil	Cortinarius_ammiratii UDB021475 SH304023.07FU refs	94.43	<i>Cortinarius</i> sp13
OTU_458	Soil	Cortinarius_ammiratii UDB021475 SH304023.07FU refs	95.73	<i>Cortinarius</i> sp14
OTU_459	Soil	Cortinarius_ammiratii UDB021475 SH304023.07FU refs	96.79	<i>Cortinarius</i> sp15
OTU_460	Soil	Cortinarius_armeniacus EU057122 SH202923.07FU reps	100.00	<i>Cortinarius armeniacus</i>
OTU_461	Soil	Cortinarius_aureomarginatus UDB017178 SH188575.07FU reps	97.57	<i>Cortinarius aureomarginatus</i>
OTU_462	Soil	Cortinarius_biformis UDB008566 SH188479.07FU reps	98.83	<i>Cortinarius biformis</i>
OTU_463	Soil	Cortinarius_centrifusus KP165577 SH188517.07FU refs	98.05	<i>Cortinarius centrifusus</i>
OTU_464	Soil	Cortinarius_claroplaniusculus KP013184 SH188671.07FU refs	100.00	<i>Cortinarius claroplaniusculus</i>

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OTU_465	Soil	Cortinarius_decipiens FN428992 SH248762.07FU refs	96.23	<i>Cortinarius sp16</i>
OTU_466	Soil	Cortinarius_delibutus UDB002159 SH222348.07FU refs	98.45	<i>Cortinarius delibutus</i>
OTU_467	Soil	Cortinarius_depressus FJ553539 SH188478.07FU refs	98.41	<i>Cortinarius depressus</i>
OTU_468	Soil	Cortinarius_diasemospermus UDB000066 SH188559.07FU refs	96.72	<i>Cortinarius sp17</i>
OTU_469	Soil	Cortinarius_diasemospermus UDB000066 SH188559.07FU refs	93.88	<i>Cortinarius sp18</i>
OTU_470	Soil	Cortinarius_diasemospermus UDB000066 SH188559.07FU refs	95.89	<i>Cortinarius sp19</i>
OTU_471	Soil	Cortinarius_diasemospermus UDB000066 SH188559.07FU refs	95.87	<i>Cortinarius sp20</i>
OTU_472	Soil	Cortinarius_diasemospermus UDB001230 SH188470.07FU refs	95.92	<i>Cortinarius sp21</i>
OTU_473	Soil	Cortinarius_fulvescens JQ393043 SH222593.07FU refs	98.49	<i>Cortinarius fulvescens</i>
OTU_474	Soil	Cortinarius_glaucopus DQ097885 SH640218.07FU refs	98.03	<i>Cortinarius glaucopus</i>
OTU_475	Soil	Cortinarius_hinnuleus UDB001042 SH188586.07FU refs	100.00	<i>Cortinarius hinnuleus</i>
OTU_476	Soil	Cortinarius_juxtadibaphus KF732329 SH221480.07FU refs	100.00	<i>Cortinarius juxtadibaphus</i>
OTU_477	Soil	Cortinarius_maculatocaesпитosus KF732346 SH222477.07FU refs	98.84	<i>Cortinarius maculatocaesпитosus</i>
OTU_478	Soil	Cortinarius_pastoralis KX302258 SH222459.07FU refs	97.42	<i>Cortinarius pastoralis</i>
OTU_479	Soil	Cortinarius_roseobasilis KU041740 SH644281.07FU refs	97.83	<i>Cortinarius roseobasilis</i>
OTU_480	Soil	Cortinarius_roseobasilis KU041740 SH644281.07FU refs	95.34	<i>Cortinarius sp22</i>
OTU_481	Soil	Cortinarius_saniosus DQ102671 SH188476.07FU refs	95.26	<i>Cortinarius sp23</i>
OTU_482	Soil	Cortinarius_saniosus DQ102671 SH188476.07FU refs	96.05	<i>Cortinarius sp24</i>
OTU_483	Soil	Cortinarius_saturninus AM713179 SH188493.07FU refs	97.99	<i>Cortinarius saturninus</i>
OTU_484	Soil	Cortinarius_scandens GQ159849 SH188527.07FU refs	100.00	<i>Cortinarius scandens</i>
OTU_485	Soil	Cortinarius_scaurocaninus KF732641 SH222476.07FU refs	98.83	<i>Cortinarius scaurocaninus</i>
OTU_486	Soil	Cortinarius_sp DQ481671 SH222649.07FU refs	95.77	<i>Cortinarius sp25</i>
OTU_487	Soil	Cortinarius_sp EF655689 SH188595.07FU refs	93.72	<i>Cortinarius sp26</i>
OTU_488	Soil	Cortinarius_sp EF655689 SH188595.07FU refs	96.20	<i>Cortinarius sp27</i>
OTU_489	Soil	Cortinarius_sp FJ378749 SH188650.07FU refs	96.68	<i>Cortinarius sp28</i>
OTU_490	Soil	Cortinarius_sp FJ378756 SH188569.07FU refs	96.28	<i>Cortinarius sp29</i>
OTU_491	Soil	Cortinarius_sp JX630733 SH222629.07FU refs	98.80	<i>Cortinarius sp30</i>
OTU_492	Soil	Cortinarius_sp JX630733 SH222629.07FU refs	98.79	<i>Cortinarius sp31</i>
OTU_493	Soil	Cortinarius_sp JX630733 SH222629.07FU refs	96.40	<i>Cortinarius sp32</i>
OTU_494	Soil	Cortinarius_sp KP191867 SH222916.07FU refs	93.15	<i>Cortinarius sp33</i>
OTU_495	Soil	Cortinarius_sp KP191867 SH222916.07FU refs	91.95	<i>Cortinarius sp34</i>
OTU_496	Soil	Cortinarius_sp KP191910 SH529440.07FU refs	85.82	<i>Cortinarius sp35</i>
OTU_497	Soil	Cortinarius_sp KY462606 SH631557.07FU refs_singleton	77.71	<i>Cortinarius sp36</i>
OTU_498	Soil	Cortinarius_sp KY462703 SH641241.07FU refs	80.00	<i>Cortinarius sp37</i>
OTU_499	Soil	Cortinarius_sp UDB024930 SH525493.07FU refs	95.80	<i>Cortinarius sp38</i>
OTU_500	Soil	Cortinarius_uraceisporus KP165543 SH525380.07FU refs	97.33	<i>Cortinarius uraceisporus</i>
OTU_501	Soil	Cortinarius_uraceisporus KP165543 SH525380.07FU refs	94.36	<i>Cortinarius sp39</i>
OTU_502	Soil	Cortinarius_uraceisporus KP165543 SH525380.07FU refs	95.47	<i>Cortinarius sp40</i>
OTU_503	Soil	Cortinarius_vernus FN429004 SH094391.07FU refs	95.20	<i>Cortinarius sp41</i>
OTU_504	Soil	Cortinarius_vernus GQ159826 SH188560.07FU refs	93.28	<i>Cortinarius sp42</i>
OTU_505	Soil	Cortinarius_vernus UDB000742 SH188477.07FU refs	92.77	<i>Cortinarius sp43</i>
OTU_506	Soil	Craterellus_sp KM576328 SH523816.07FU refs	96.41	<i>Craterellus sp1</i>
OTU_507	Soil	Densospora_sp UDB028692 SH490876.07FU refs_singleton	89.86	<i>Densospora sp1</i>
OTU_508	Soil	Densospora_sp UDB028692 SH490876.07FU refs_singleton	89.86	<i>Densospora sp2</i>
OTU_509	Soil	Endogone_lactiflua AY997045 SH026695.07FU refs_singleton	87.06	<i>Endogone sp1</i>
OTU_510	Soil	Endogone_lactiflua AY997045 SH026695.07FU refs_singleton	84.84	<i>Endogone sp2</i>
OTU_511	Soil	Endogone_lactiflua AY997045 SH026695.07FU refs_singleton	83.92	<i>Endogone sp3</i>

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OTU_512	Soil	Endogone_lactiflua AY997045 SH026695.07FU refs_singleton	86.28	<i>Endogone sp4</i>
OTU_513	Soil	Endogone_lactiflua AY997045 SH026695.07FU refs_singleton	85.71	<i>Endogone sp5</i>
OTU_514	Soil	Endogone_lactiflua AY997045 SH026695.07FU refs_singleton	82.62	<i>Endogone sp6</i>
OTU_515	Soil	Endogone_sp KC152094 SH213348.07FU reps	85.07	<i>Endogone sp7</i>
OTU_516	Soil	Endogone_sp KC152094 SH213348.07FU reps	92.11	<i>Endogone sp8</i>
OTU_517	Soil	Endogone_sp KC152094 SH213348.07FU reps	87.50	<i>Endogone sp9</i>
OTU_518	Soil	Endogone_sp KC152094 SH213348.07FU reps	89.89	<i>Endogone sp10</i>
OTU_519	Soil	Endogone_sp UDB027735 SH490881.07FU reps_singleton	83.99	<i>Endogone sp11</i>
OTU_520	Soil	Endogone_sp UDB027735 SH490881.07FU reps_singleton	84.66	<i>Endogone sp12</i>
OTU_521	Soil	Endogone_sp UDB027735 SH490881.07FU reps_singleton	81.63	<i>Endogone sp13</i>
OTU_522	Soil	Gautieria_caudata AF377057 SH008280.07FU reps_singleton	85.24	<i>Gautieria sp1</i>
OTU_523	Soil	Genea_balsleyi DQ218302 SH215740.07FU refs	95.83	<i>Genea sp1</i>
OTU_524	Soil	Geopora_sp JF927142 SH216639.07FU reps	100.00	<i>Geopora sp9</i>
OTU_525	Soil	Hebeloma_nigellum KX765786 SH628864.07FU reps_singleton	98.16	<i>Hebeloma nigellum</i>
OTU_526	Soil	Hebeloma_vesterholtii UDB003255 SH215996.07FU refs	93.81	<i>Hebeloma sp6</i>
OTU_527	Soil	Helvella_corium AF046226 SH183707.07FU reps	96.04	<i>Helvella sp2</i>
OTU_528	Soil	Helvella_corium AF046226 SH183707.07FU reps	88.93	<i>Helvella sp3</i>
OTU_529	Soil	Helvella_corium AF046226 SH183707.07FU reps	88.49	<i>Helvella sp4</i>
OTU_530	Soil	Helvella_corium AF046226 SH183707.07FU reps	88.13	<i>Helvella sp5</i>
OTU_531	Soil	Helvella_orienticrispa KR493443 SH181258.07FU reps	98.05	<i>Helvella orienticrispa</i>
OTU_532	Soil	Helvella_pseudoreflexa JX462593 SH522342.07FU refs	93.18	<i>Helvella sp6</i>
OTU_533	Soil	Helvella_pseudoreflexa JX462593 SH522342.07FU refs	85.29	<i>Helvella sp7</i>
OTU_534	Soil	Helvella_pseudoreflexa JX462593 SH522342.07FU refs	98.87	<i>Helvella pseudoreflexa</i>
OTU_535	Soil	Helvella_sp AJ879678 SH006539.07FU reps_singleton	92.89	<i>Helvella sp8</i>
OTU_536	Soil	Helvella_sp AJ879678 SH006539.07FU reps_singleton	92.31	<i>Helvella sp9</i>
OTU_537	Soil	Helvella_sp FJ803929 SH471567.07FU reps_singleton	98.48	<i>Helvella sp10</i>
OTU_538	Soil	Helvella_sp UDB013605 SH190723.07FU reps	89.02	<i>Helvella sp11</i>
OTU_539	Soil	Helvella_sp UDB013605 SH190723.07FU reps	88.97	<i>Helvella sp12</i>
OTU_540	Soil	Helvella_sp UDB013605 SH190723.07FU reps	94.25	<i>Helvella sp13</i>
OTU_541	Soil	Helvella_sp UDB013605 SH190723.07FU reps	88.93	<i>Helvella sp14</i>
OTU_542	Soil	Helvella_sp UDB013605 SH190723.07FU reps	85.23	<i>Helvella sp15</i>
OTU_543	Soil	Helvella_subglabra KU739802 SH630667.07FU reps_singleton	95.55	<i>Helvella sp16</i>
OTU_544	Soil	Helvellosebacina_sp JX630670 SH199721.07FU refs	97.33	<i>Helvellosebacina sp6</i>
OTU_545	Soil	Helvellosebacina_sp JX630670 SH199721.07FU refs	95.80	<i>Helvellosebacina sp7</i>
OTU_546	Soil	Helvellosebacina_sp UDB007962 SH291217.07FU refs	98.04	<i>Helvellosebacina sp8</i>
OTU_547	Soil	Helvellosebacina_sp UDB007962 SH291217.07FU refs	98.04	<i>Helvellosebacina sp9</i>
OTU_548	Soil	Helvellosebacina_sp UDB007962 SH291217.07FU refs	96.08	<i>Helvellosebacina sp10</i>
OTU_549	Soil	Helvellosebacina_sp UDB007962 SH291217.07FU refs	98.04	<i>Helvellosebacina sp11</i>
OTU_550	Soil	Helvellosebacina_sp UDB013734 SH214504.07FU refs	95.80	<i>Helvellosebacina sp12</i>
OTU_551	Soil	Humaria_hemisphaerica UDB015480 SH179622.07FU refs	96.20	<i>Humaria sp1</i>
OTU_552	Soil	Hygrophorus_gliocyclus UDB000581 SH192798.07FU reps	100.00	<i>Hygrophorus gliocyclus</i>
OTU_553	Soil	Hymenogaster_australis GU479266 SH218876.07FU reps	100.00	<i>Hymenogaster australis</i>
OTU_554	Soil	Hymenogaster_citrinus GU479360 SH218900.07FU reps	97.41	<i>Hymenogaster citrinus</i>
OTU_555	Soil	Hymenogaster_huthii UDB025671 SH218882.07FU reps	95.56	<i>Hymenogaster sp4</i>
OTU_556	Soil	Hymenogaster_rehsteineri GU479365 SH030759.07FU reps_singleton	96.01	<i>Hymenogaster sp5</i>
OTU_557	Soil	Hymenogaster_sp FJ454914 SH030755.07FU reps_singleton	92.25	<i>Hymenogaster sp6</i>
OTU_558	Soil	Hysterangium_sp UDB025455 SH491671.07FU reps_singleton	90.94	<i>Hysterangium sp1</i>

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OTU_559	Soil	Inocybaceae_sp EF417796 SH464385.07FU reps_singleton	86.67	<i>Inocybaceae sp1</i>
OTU_560	Soil	Inocybaceae_sp EU554937 SH201233.07FU reps	98.49	<i>Inocybaceae sp7</i>
OTU_561	Soil	Inocybaceae_sp JF304331 SH209541.07FU reps	96.61	<i>Inocybaceae sp1</i>
OTU_562	Soil	Inocybaceae_sp JF304331 SH209541.07FU reps	95.97	<i>Inocybaceae sp1</i>
OTU_563	Soil	Inocybaceae_sp KF617717 SH201237.07FU reps	98.49	<i>Inocybaceae sp10</i>
OTU_564	Soil	Inocybe_acuta HQ604258 SH013427.07FU reps_singleton	99.11	<i>Inocybe acuta</i>
OTU_565	Soil	Inocybe_amethystina JF908123 SH219984.07FU reps	95.43	<i>Inocybe sp38</i>
OTU_566	Soil	Inocybe_appendiculata UDB015559 SH220485.07FU refs	92.50	<i>Inocybe sp39</i>
OTU_567	Soil	Inocybe_arenicola FJ904134 SH222044.07FU refs	97.53	<i>Inocybe arenicola</i>
OTU_568	Soil	Inocybe_arthrocytis FN550941 SH210565.07FU reps	99.25	<i>Inocybe arthrocytis</i>
OTU_569	Soil	Inocybe_assimilata DQ822815 SH214854.07FU reps	98.25	<i>Inocybe assimilata</i>
OTU_570	Soil	Inocybe_aurea UDB000612 SH174368.07FU refs	100.00	<i>Inocybe aurea</i>
OTU_571	Soil	Inocybe_brunneotomentosa UDB008062 SH220489.07FU reps	88.09	<i>Inocybe sp40</i>
OTU_572	Soil	Inocybe_bulbosissima FJ904158 SH183292.07FU refs	97.48	<i>Inocybe bulbosissima</i>
OTU_573	Soil	Inocybe_bulbosissima FJ904158 SH183292.07FU refs	98.72	<i>Inocybe bulbosissima</i>
OTU_574	Soil	Inocybe_calamistrata JQ801386 SH188902.07FU reps	98.31	<i>Inocybe calamistrata</i>
OTU_575	Soil	Inocybe_calamistrata UDB011882 SH188895.07FU refs	98.79	<i>Inocybe calamistrata</i>
OTU_576	Soil	Inocybe_cervicolor UDB000605 SH187098.07FU refs	99.61	<i>Inocybe cervicolor</i>
OTU_577	Soil	Inocybe_chalcodoxantha HQ201341 SH026991.07FU refs_singleton	84.75	<i>Inocybe sp41</i>
OTU_578	Soil	Inocybe_dulcamara GU980629 SH119832.07FU refs_singleton	95.15	<i>Inocybe sp42</i>
OTU_579	Soil	Inocybe_exilis KC965374 SH179837.07FU reps	99.61	<i>Inocybe exilis</i>
OTU_580	Soil	Inocybe_favrei FN550886 SH188062.07FU refs	100.00	<i>Inocybe favrei</i>
OTU_581	Soil	Inocybe_flavella AM882782 SH222039.07FU refs	97.53	<i>Inocybe flavella</i>
OTU_582	Soil	Inocybe_flocculosa UDB000627 SH178660.07FU refs	89.38	<i>Inocybe sp43</i>
OTU_583	Soil	Inocybe_flocculosa UDB015335 SH187316.07FU refs	98.82	<i>Inocybe flocculosa</i>
OTU_584	Soil	Inocybe_flocculosa UDB015335 SH187316.07FU refs	95.33	<i>Inocybe sp44</i>
OTU_585	Soil	Inocybe_flocculosa UDB015335 SH187316.07FU refs	96.44	<i>Inocybe sp45</i>
OTU_586	Soil	Inocybe_fuscescentipes KJ399947 SH191989.07FU refs	88.79	<i>Inocybe sp46</i>
OTU_587	Soil	Inocybe_fuscidula AM882883 SH190501.07FU refs	85.12	<i>Inocybe sp47</i>
OTU_588	Soil	Inocybe_fuscomarginata FN550940 SH210567.07FU reps	100.00	<i>Inocybe fuscomarginata</i>
OTU_589	Soil	Inocybe_geranioidora FN550945 SH028696.07FU reps_singleton	96.23	<i>Inocybe sp48</i>
OTU_590	Soil	Inocybe_griseolilacina HQ650732 SH010866.07FU reps_singleton	89.19	<i>Inocybe sp49</i>
OTU_591	Soil	Inocybe_guttulifer FJ237107 SH221723.07FU reps	97.23	<i>Inocybe guttulifer</i>
OTU_592	Soil	Inocybe_guttulifer FJ237107 SH221723.07FU reps	96.44	<i>Inocybe sp50</i>
OTU_593	Soil	Inocybe_guttulifer FJ237107 SH221723.07FU reps	97.63	<i>Inocybe guttulifer</i>
OTU_594	Soil	Inocybe_inodora HQ604520 SH023580.07FU reps_singleton	98.46	<i>Inocybe inodora</i>
OTU_595	Soil	Inocybe_lacera AM882815 SH201232.07FU refs	99.62	<i>Inocybe lacera</i>
OTU_596	Soil	Inocybe_lacera HQ215795 SH219806.07FU reps	98.31	<i>Inocybe lacera</i>
OTU_597	Soil	Inocybe_lanatopurpurea KJ432290 SH174199.07FU refs	95.39	<i>Inocybe sp51</i>
OTU_598	Soil	Inocybe_leucoblema GU980630 SH209544.07FU refs	99.63	<i>Inocybe leucoblema</i>
OTU_599	Soil	Inocybe_maculipes UDB027281 SH202671.07FU reps	99.62	<i>Inocybe maculipes</i>
OTU_600	Soil	Inocybe_melanopus UDB017925 SH221652.07FU refs	94.07	<i>Inocybe sp52</i>
OTU_601	Soil	Inocybe_melanopus UDB017925 SH221652.07FU refs	93.96	<i>Inocybe sp53</i>
OTU_602	Soil	Inocybe_moelleri FN550913 SH003922.07FU reps_singleton	100.00	<i>Inocybe moelleri</i>
OTU_603	Soil	Inocybe_monticola KJ538547 SH219793.07FU refs	98.25	<i>Inocybe monticola</i>
OTU_604	Soil	Inocybe_monticola KJ538547 SH219793.07FU refs	84.46	<i>Inocybe sp54</i>
OTU_605	Soil	Inocybe_monticola KJ538547 SH219793.07FU refs	84.46	<i>Inocybe sp55</i>

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OTU_606	Soil	Inocybe_nematoloma AM882713 SH197271.07FU reps	97.06	<i>Inocybe nematoloma</i>
OTU_607	Soil	Inocybe_nemorosa HQ445027 SH179835.07FU reps	96.21	<i>Inocybe sp56</i>
OTU_608	Soil	Inocybe_nitidiuscula HQ604458 SH219201.07FU reps	95.53	<i>Inocybe sp57</i>
OTU_609	Soil	Inocybe_obscurobadia JF908203 SH201991.07FU reps	100.00	<i>Inocybe obscurobadia</i>
OTU_610	Soil	Inocybe_ochroalba AM882880 SH220483.07FU refs	98.73	<i>Inocybe ochroalba</i>
OTU_611	Soil	Inocybe_phaeocystidiosa JF304399 SH200843.07FU reps	96.39	<i>Inocybe sp58</i>
OTU_612	Soil	Inocybe_pseudohiulca KT897911 SH524192.07FU reps	98.81	<i>Inocybe pseudohiulca</i>
OTU_613	Soil	Inocybe_pseudohiulca KT897911 SH524192.07FU reps	96.03	<i>Inocybe sp59</i>
OTU_614	Soil	Inocybe_pseudohiulca KT897911 SH524192.07FU reps	94.84	<i>Inocybe sp60</i>
OTU_615	Soil	Inocybe_queletii AM882968 SH217346.07FU reps	94.44	<i>Inocybe sp61</i>
OTU_616	Soil	Inocybe_queletii AM882968 SH217346.07FU reps	90.69	<i>Inocybe sp62</i>
OTU_617	Soil	Inocybe_queletii AM882968 SH217346.07FU reps	93.20	<i>Inocybe sp63</i>
OTU_618	Soil	Inocybe_rimosa FJ904147 SH221720.07FU reps	99.58	<i>Inocybe rimosa</i>
OTU_619	Soil	Inocybe_rufoalba FN550883 SH211892.07FU refs	100.00	<i>Inocybe rufoalba</i>
OTU_620	Soil	Inocybe_rufoalba HQ604804 SH197268.07FU refs	99.58	<i>Inocybe rufoalba</i>
OTU_621	Soil	Inocybe_sindonia HQ604384 SH180353.07FU reps	96.86	<i>Inocybe sp64</i>
OTU_622	Soil	Inocybe_sororia HQ604604 SH221719.07FU reps	100.00	<i>Inocybe sororia</i>
OTU_623	Soil	Inocybe_sp AB848503 SH489908.07FU reps_singleton	89.67	<i>Inocybe sp65</i>
OTU_624	Soil	Inocybe_sp AM882914 SH003773.07FU reps_singleton	99.21	<i>Inocybe sp66</i>
OTU_625	Soil	Inocybe_sp AM882914 SH003773.07FU reps_singleton	95.60	<i>Inocybe sp67</i>
OTU_626	Soil	Inocybe_sp DQ054545 SH197320.07FU reps	97.89	<i>Inocybe sp68</i>
OTU_627	Soil	Inocybe_sp EF619707 SH004106.07FU reps_singleton	93.77	<i>Inocybe sp69</i>
OTU_628	Soil	Inocybe_sp EU375712 SH003391.07FU reps_singleton	93.37	<i>Inocybe sp70</i>
OTU_629	Soil	Inocybe_sp FJ378770 SH485987.07FU reps_singleton	96.89	<i>Inocybe sp71</i>
OTU_630	Soil	Inocybe_sp FJ827203 SH188898.07FU reps	93.25	<i>Inocybe sp72</i>
OTU_631	Soil	Inocybe_sp FJ904135 SH032890.07FU reps_singleton	100.00	<i>Inocybe sp73</i>
OTU_632	Soil	Inocybe_sp FJ904156 SH016085.07FU reps_singleton	94.78	<i>Inocybe sp74</i>
OTU_633	Soil	Inocybe_sp FN550890 SH021753.07FU reps_singleton	100.00	<i>Inocybe sp75</i>
OTU_634	Soil	Inocybe_sp FN550929 SH190794.07FU reps	100.00	<i>Inocybe sp76</i>
OTU_635	Soil	Inocybe_sp FR852237 SH220487.07FU reps	100.00	<i>Inocybe sp77</i>
OTU_636	Soil	Inocybe_sp GQ893000 SH032427.07FU reps_singleton	95.65	<i>Inocybe sp78</i>
OTU_637	Soil	Inocybe_sp GQ893001 SH032425.07FU reps_singleton	96.15	<i>Inocybe sp79</i>
OTU_638	Soil	Inocybe_sp GQ893001 SH032425.07FU reps_singleton	96.15	<i>Inocybe sp80</i>
OTU_639	Soil	Inocybe_sp GQ893001 SH032425.07FU reps_singleton	96.15	<i>Inocybe sp81</i>
OTU_640	Soil	Inocybe_sp HE687067 SH191112.07FU reps	99.62	<i>Inocybe sp82</i>
OTU_641	Soil	Inocybe_sp HG796975 SH003775.07FU reps_singleton	96.03	<i>Inocybe sp83</i>
OTU_642	Soil	Inocybe_sp HG796989 SH009789.07FU reps_singleton	90.73	<i>Inocybe sp84</i>
OTU_643	Soil	Inocybe_sp HQ215780 SH008434.07FU reps_singleton	99.62	<i>Inocybe sp85</i>
OTU_644	Soil	Inocybe_sp HQ215782 SH222049.07FU reps	99.63	<i>Inocybe sp86</i>
OTU_645	Soil	Inocybe_sp HQ215787 SH197270.07FU reps	97.14	<i>Inocybe sp87</i>
OTU_646	Soil	Inocybe_sp HQ215787 SH197270.07FU reps	95.07	<i>Inocybe sp88</i>
OTU_647	Soil	Inocybe_sp HQ215787 SH197270.07FU reps	95.51	<i>Inocybe sp89</i>
OTU_648	Soil	Inocybe_sp HQ271363 SH016876.07FU reps_singleton	87.67	<i>Inocybe sp90</i>
OTU_649	Soil	Inocybe_sp HQ445445 SH015238.07FU reps_singleton	95.85	<i>Inocybe sp91</i>
OTU_650	Soil	Inocybe_sp HQ445536 SH211894.07FU reps	100.00	<i>Inocybe sp92</i>
OTU_651	Soil	Inocybe_sp JF304339 SH187318.07FU reps	96.41	<i>Inocybe sp93</i>
OTU_652	Soil	Inocybe_sp JQ347101 SH197269.07FU reps	94.92	<i>Inocybe sp94</i>

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OTU_653	Soil	Inocybe_sp JQ347105 SH202672.07FU reps	91.12	<i>Inocybe sp95</i>
OTU_654	Soil	Inocybe_sp JQ347123 SH003756.07FU reps_singleton	96.00	<i>Inocybe sp96</i>
OTU_655	Soil	Inocybe_sp JX630443 SH220484.07FU reps	84.44	<i>Inocybe sp97</i>
OTU_656	Soil	Inocybe_sp JX630508 SH198506.07FU reps	96.54	<i>Inocybe sp98</i>
OTU_657	Soil	Inocybe_sp JX630508 SH198506.07FU reps	98.08	<i>Inocybe sp99</i>
OTU_658	Soil	Inocybe_sp JX630508 SH198506.07FU reps	97.55	<i>Inocybe sp100</i>
OTU_659	Soil	Inocybe_sp JX630511 SH190795.07FU reps	91.90	<i>Inocybe sp101</i>
OTU_660	Soil	Inocybe_sp JX630511 SH190795.07FU reps	97.89	<i>Inocybe sp102</i>
OTU_661	Soil	Inocybe_sp JX630539 SH222179.07FU reps	99.60	<i>Inocybe sp103</i>
OTU_662	Soil	Inocybe_sp JX630623 SH031444.07FU reps_singleton	99.61	<i>Inocybe sp104</i>
OTU_663	Soil	Inocybe_sp JX630664 SH219955.07FU reps	99.61	<i>Inocybe sp105</i>
OTU_664	Soil	Inocybe_sp JX630700 SH190793.07FU reps	98.81	<i>Inocybe sp106</i>
OTU_665	Soil	Inocybe_sp JX630700 SH190793.07FU reps	96.09	<i>Inocybe sp107</i>
OTU_666	Soil	Inocybe_sp JX630700 SH190793.07FU reps	88.65	<i>Inocybe sp108</i>
OTU_667	Soil	Inocybe_sp JX630700 SH190793.07FU reps	88.69	<i>Inocybe sp109</i>
OTU_668	Soil	Inocybe_sp JX630885 SH174369.07FU reps	98.88	<i>Inocybe sp110</i>
OTU_669	Soil	Inocybe_sp JX990096 SH192343.07FU reps	92.28	<i>Inocybe sp111</i>
OTU_670	Soil	Inocybe_sp KC791069 SH017041.07FU reps_singleton	88.56	<i>Inocybe sp112</i>
OTU_671	Soil	Inocybe_sp KC791072 SH003770.07FU reps_singleton	96.55	<i>Inocybe sp113</i>
OTU_672	Soil	Inocybe_sp KC791072 SH003770.07FU reps_singleton	93.99	<i>Inocybe sp114</i>
OTU_673	Soil	Inocybe_sp KC791072 SH003770.07FU reps_singleton	95.08	<i>Inocybe sp115</i>
OTU_674	Soil	Inocybe_sp KC965252 SH008580.07FU reps_singleton	98.86	<i>Inocybe sp116</i>
OTU_675	Soil	Inocybe_sp KC965253 SH031789.07FU reps_singleton	94.65	<i>Inocybe sp117</i>
OTU_676	Soil	Inocybe_sp KC965966 SH222178.07FU reps	99.60	<i>Inocybe sp118</i>
OTU_677	Soil	Inocybe_sp KC966041 SH187319.07FU reps	98.81	<i>Inocybe sp119</i>
OTU_678	Soil	Inocybe_sp KF297126 SH001183.07FU reps_singleton	96.67	<i>Inocybe sp120</i>
OTU_679	Soil	Inocybe_sp KJ729879 SH221728.07FU reps	97.75	<i>Inocybe sp121</i>
OTU_680	Soil	Inocybe_sp KJ729879 SH221728.07FU reps	97.42	<i>Inocybe sp122</i>
OTU_681	Soil	Inocybe_sp KP171132 SH489869.07FU reps_singleton	94.52	<i>Inocybe sp123</i>
OTU_682	Soil	Inocybe_sp KT630096 SH528624.07FU reps	91.80	<i>Inocybe sp124</i>
OTU_683	Soil	Inocybe_sp KT630096 SH528624.07FU reps	92.43	<i>Inocybe sp125</i>
OTU_684	Soil	Inocybe_sp KT800123 SH492740.07FU reps_singleton	92.11	<i>Inocybe sp126</i>
OTU_685	Soil	Inocybe_sp KT800219 SH488150.07FU reps_singleton	98.40	<i>Inocybe sp127</i>
OTU_686	Soil	Inocybe_sp KX499163 SH630417.07FU reps_singleton	96.57	<i>Inocybe sp128</i>
OTU_687	Soil	Inocybe_sp KX510016 SH631325.07FU reps_singleton	97.52	<i>Inocybe sp129</i>
OTU_688	Soil	Inocybe_sp LC013883 SH495742.07FU reps_singleton	82.66	<i>Inocybe sp130</i>
OTU_689	Soil	Inocybe_sp LC035187 SH527205.07FU reps	96.15	<i>Inocybe sp131</i>
OTU_690	Soil	Inocybe_sp LC035197 SH525698.07FU reps	98.86	<i>Inocybe sp132</i>
OTU_691	Soil	Inocybe_sp LC035197 SH525698.07FU reps	91.35	<i>Inocybe sp133</i>
OTU_692	Soil	Inocybe_sp UDB004930 SH190505.07FU reps	100.00	<i>Inocybe sp134</i>
OTU_693	Soil	Inocybe_sp UDB008816 SH018358.07FU reps_singleton	90.70	<i>Inocybe sp135</i>
OTU_694	Soil	Inocybe_sp UDB008816 SH018358.07FU reps_singleton	88.59	<i>Inocybe sp136</i>
OTU_695	Soil	Inocybe_sp UDB025277 SH495853.07FU reps_singleton	95.65	<i>Inocybe sp137</i>
OTU_696	Soil	Inocybe_sp UDB026019 SH222061.07FU reps	99.23	<i>Inocybe sp138</i>
OTU_697	Soil	Inocybe_sp UDB026703 SH219962.07FU reps	97.28	<i>Inocybe sp139</i>
OTU_698	Soil	Inocybe_sp UDB026703 SH219962.07FU reps	96.90	<i>Inocybe sp140</i>
OTU_699	Soil	Inocybe_sp UDB026703 SH219962.07FU reps	98.44	<i>Inocybe sp141</i>

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OTU_700	Soil	Inocybe_splendens JF908156 SH219798.07FU reps	99.13	<i>Inocybe splendens</i>
OTU_701	Soil	Inocybe_squarrosoannulata GU980609 SH283269.07FU refs	91.32	<i>Inocybe sp142</i>
OTU_702	Soil	Inocybe_squarrosoannulata GU980609 SH283269.07FU refs	97.85	<i>Inocybe squarrosoannulata</i>
OTU_703	Soil	Inocybe_tigrina JF908254 SH178662.07FU reps	88.68	<i>Inocybe sp143</i>
OTU_704	Soil	Inocybe_tjallingiorum KJ399956 SH219792.07FU refs	97.11	<i>Inocybe tjallingiorum</i>
OTU_705	Soil	Inocybe_xanthomelas FN550895 SH179934.07FU refs	100.00	<i>Inocybe xanthomelas</i>
OTU_706	Soil	Laccaria_alba JX504175 SH220987.07FU reps	89.09	<i>Laccaria sp2</i>
OTU_707	Soil	Laccaria_alba JX504175 SH220987.07FU reps	85.97	<i>Laccaria sp3</i>
OTU_708	Soil	Laccaria_alba JX504175 SH220987.07FU reps	85.91	<i>Laccaria sp4</i>
OTU_709	Soil	Laccaria_amethystina JX504092 SH220970.07FU reps	88.01	<i>Laccaria sp5</i>
OTU_710	Soil	Laccaria_angustilamella UDB025307 SH220974.07FU reps	87.12	<i>Laccaria sp6</i>
OTU_711	Soil	Laccaria_laccata UDB025819 SH199898.07FU reps	100.00	<i>Laccaria laccata</i>
OTU_712	Soil	Laccaria_pseudomontana DQ149871 SH220986.07FU reps	97.11	<i>Laccaria pseudomontana</i>
OTU_713	Soil	Laccaria_sp KU685685 SH496750.07FU reps_singleton	83.21	<i>Laccaria sp7</i>
OTU_714	Soil	Laccaria_sp KU685725 SH630357.07FU reps_singleton	85.15	<i>Laccaria sp8</i>
OTU_715	Soil	Lactarius_evosmus UDB000860 SH176418.07FU refs	100.00	<i>Lactarius evosmus</i>
OTU_716	Soil	Lactarius_scrobiculatus AF140262 SH176436.07FU reps	100.00	<i>Lactarius scrobiculatus</i>
OTU_717	Soil	Lactarius_sp AF249286 SH220113.07FU refs	99.37	<i>Lactarius sp1</i>
OTU_718	Soil	Melanogaster_broomeanus UDB027758 SH182656.07FU reps	98.97	<i>Melanogaster broomeanus</i>
OTU_719	Soil	Melanogaster_broomeanus UDB027758 SH182656.07FU reps	97.25	<i>Melanogaster broomeanus</i>
OTU_720	Soil	Membranomyces_sp HQ444973 SH222266.07FU reps	98.98	<i>Membranomyces sp6</i>
OTU_721	Soil	Membranomyces_sp KC686885 SH184886.07FU reps	89.80	<i>Membranomyces sp7</i>
OTU_722	Soil	Membranomyces_sp KC686885 SH184886.07FU reps	98.33	<i>Membranomyces sp8</i>
OTU_723	Soil	Membranomyces_sp KC966200 SH033050.07FU reps_singleton	97.94	<i>Membranomyces sp9</i>
OTU_724	Soil	Naucoria_bohemica UDB001775 SH188455.07FU reps	100.00	<i>Naucoria bohemica</i>
OTU_725	Soil	Paxillus_involutus EU078734 SH210480.07FU refs	100.00	<i>Paxillus involutus</i>
OTU_726	Soil	Paxillus_obscuriporus JN673717 SH210481.07FU reps	95.90	<i>Paxillus sp1</i>
OTU_727	Soil	Peziza_badia JF908544 SH193723.07FU refs	98.83	<i>Peziza badia</i>
OTU_728	Soil	Peziza_sp GU817102 SH193720.07FU reps	97.07	<i>Peziza sp2</i>
OTU_729	Soil	Peziza_sp JX989909 SH188836.07FU reps	99.59	<i>Peziza sp3</i>
OTU_730	Soil	Pezizaceae_sp UDB004620 SH221476.07FU reps	96.36	<i>Pezizaceae sp2</i>
OTU_731	Soil	Piloderma_bicolor KP814367 SH203894.07FU reps	100.00	<i>Piloderma bicolor</i>
OTU_732	Soil	Piloderma_sp EU292523 SH196706.07FU reps	88.14	<i>Piloderma sp1</i>
OTU_733	Soil	Pseudotomentella_sp EU597060 SH030574.07FU reps_singleton	86.92	<i>Pseudotomentella sp3</i>
OTU_734	Soil	Pseudotomentella_sp FR852215 SH218578.07FU refs	99.38	<i>Pseudotomentella sp4</i>
OTU_735	Soil	Pseudotomentella_sp FR852216 SH029964.07FU reps_singleton	96.85	<i>Pseudotomentella sp5</i>
OTU_736	Soil	Pseudotomentella_sp UDB008861 SH218586.07FU reps	95.47	<i>Pseudotomentella sp6</i>
OTU_737	Soil	Pulvinula_convexella KM580041 SH489886.07FU reps_singleton	81.15	<i>Pulvinula sp2</i>
OTU_738	Soil	Pulvinula_convexella UDB008883 SH204542.07FU reps	78.06	<i>Pulvinula sp3</i>
OTU_739	Soil	Pulvinula_convexella UDB008883 SH204542.07FU reps	97.40	<i>Pulvinula convexella</i>
OTU_740	Soil	Pulvinula_convexella UDB008883 SH204542.07FU reps	99.13	<i>Pulvinula convexella</i>
OTU_741	Soil	Pulvinula_sp JQ917851 SH020452.07FU reps_singleton	85.46	<i>Pulvinula sp4</i>
OTU_742	Soil	Pulvinula_sp KF617886 SH020450.07FU reps_singleton	88.00	<i>Pulvinula sp5</i>
OTU_743	Soil	Pulvinula_sp KF617886 SH020450.07FU reps_singleton	86.88	<i>Pulvinula sp6</i>
OTU_744	Soil	Pulvinula_sp KF618004 SH020451.07FU reps_singleton	92.95	<i>Pulvinula sp7</i>
OTU_745	Soil	Pulvinula_sp UDB025652 SH210654.07FU reps	99.56	<i>Pulvinula sp8</i>
OTU_746	Soil	Pulvinula_sp UDB032992 SH210657.07FU reps	85.93	<i>Pulvinula sp9</i>

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OTU_747	Soil	Pustularia_sp KC965384 SH222143.07FU reps	98.21	<i>Pustularia sp2</i>
OTU_748	Soil	Pustularia_sp KC965384 SH222143.07FU reps	98.21	<i>Pustularia sp3</i>
OTU_749	Soil	Pyronemataceae_sp JN197783 SH183394.07FU reps	94.35	<i>Pyronemataceae sp3</i>
OTU_750	Soil	Pyronemataceae_sp KX444229 SH631644.07FU reps_singleton	94.44	<i>Pyronemataceae sp4</i>
OTU_751	Soil	Ramaria_sp UDB013266 SH032196.07FU reps_singleton	91.05	<i>Ramaria sp1</i>
OTU_752	Soil	Russula_graveolens KM576511 SH176560.07FU reps	92.63	<i>Russula sp6</i>
OTU_753	Soil	Russula_puiggarii KT354747 SH641473.07FU reps	88.12	<i>Russula sp7</i>
OTU_754	Soil	Russula_purpureofusca UDB027293 SH190565.07FU reps	98.49	<i>Russula purpureofusca</i>
OTU_755	Soil	Russula_suecica GU997761 SH210577.07FU reps	96.22	<i>Russula sp8</i>
OTU_756	Soil	Sarcodon_sp EU293827 SH005917.07FU reps_singleton	89.61	<i>Sarcodon sp1</i>
OTU_757	Soil	Sebacina_cystidiata KF000452 SH214599.07FU refs	97.65	<i>Sebacina cystidiata</i>
OTU_758	Soil	Sebacina_epigaea UDB026785 SH197161.07FU reps	87.73	<i>Sebacina sp56</i>
OTU_759	Soil	Sebacina_flagelliformis KF000464 SH214608.07FU refs	99.62	<i>Sebacina flagelliformis</i>
OTU_760	Soil	Sebacina_incrustans AF490395 SH214609.07FU refs	96.06	<i>Sebacina sp57</i>
OTU_761	Soil	Sebacina_sp AY534208 SH221402.07FU reps	93.73	<i>Sebacina sp58</i>
OTU_762	Soil	Sebacina_sp EF417823 SH214697.07FU refs	95.60	<i>Sebacina sp59</i>
OTU_763	Soil	Sebacina_sp EU444538 SH125974.07FU refs	96.21	<i>Sebacina sp60</i>
OTU_764	Soil	Sebacina_sp GU452516 SH103784.07FU refs_singleton	97.00	<i>Sebacina sp61</i>
OTU_765	Soil	Sebacina_sp HG796953 SH214686.07FU refs	99.61	<i>Sebacina sp62</i>
OTU_766	Soil	Sebacina_sp HM146868 SH199504.07FU refs	96.89	<i>Sebacina sp63</i>
OTU_767	Soil	Sebacina_sp HM230656 SH197122.07FU refs	98.45	<i>Sebacina sp64</i>
OTU_768	Soil	Sebacina_sp HQ331006 SH104993.07FU refs	98.08	<i>Sebacina sp65</i>
OTU_769	Soil	Sebacina_sp HQ445284 SH214631.07FU refs	96.53	<i>Sebacina sp66</i>
OTU_770	Soil	Sebacina_sp HQ667886 SH214603.07FU refs	99.62	<i>Sebacina sp67</i>
OTU_771	Soil	Sebacina_sp JF519013 SH214629.07FU refs	99.61	<i>Sebacina sp68</i>
OTU_772	Soil	Sebacina_sp KF000675 SH487549.07FU reps_singleton	95.85	<i>Sebacina sp69</i>
OTU_773	Soil	Sebacina_sp KF618000 SH214636.07FU reps	97.22	<i>Sebacina sp70</i>
OTU_774	Soil	Sebacina_sp KT461340 SH027667.07FU reps_singleton	90.79	<i>Sebacina sp71</i>
OTU_775	Soil	Sebacina_sp UDB025284 SH491682.07FU reps_singleton	87.81	<i>Sebacina sp72</i>
OTU_776	Soil	Sebacina_sp UDB033250 SH197145.07FU reps	98.47	<i>Sebacina sp73</i>
OTU_777	Soil	Serendipita_sp EU668270 SH201962.07FU reps	97.30	<i>Serendipita sp6</i>
OTU_778	Soil	Serendipita_sp FJ197211 SH201979.07FU reps	88.29	<i>Serendipita sp7</i>
OTU_779	Soil	Serendipita_sp GU452533 SH201954.07FU reps	85.44	<i>Serendipita sp8</i>
OTU_780	Soil	Serendipita_sp JN704824 SH201952.07FU refs	89.19	<i>Serendipita sp9</i>
OTU_781	Soil	Serendipita_sp JN704824 SH201952.07FU refs	88.39	<i>Serendipita sp10</i>
OTU_782	Soil	Serendipita_sp JN704824 SH201952.07FU refs	87.36	<i>Serendipita sp11</i>
OTU_783	Soil	Serendipita_sp JN704824 SH201952.07FU refs	96.92	<i>Serendipita sp12</i>
OTU_784	Soil	Serendipita_sp UDB008509 SH179999.07FU refs	87.28	<i>Serendipita sp13</i>
OTU_785	Soil	Sistotrema_muscicola UDB002254 SH187707.07FU refs	85.62	<i>Sistotrema sp1</i>
OTU_786	Soil	Sistotrema_sp EU668935 SH192853.07FU refs	79.64	<i>Sistotrema sp2</i>
OTU_787	Soil	Sistotrema_sp FN610946 SH192855.07FU reps	81.46	<i>Sistotrema sp3</i>
OTU_788	Soil	Sistotrema_sp HM021160 SH192851.07FU reps	87.06	<i>Sistotrema sp4</i>
OTU_789	Soil	Sistotrema_sp JX198540 SH014874.07FU reps_singleton	94.66	<i>Sistotrema sp5</i>
OTU_790	Soil	Sistotrema_sp JX198540 SH014874.07FU reps_singleton	91.73	<i>Sistotrema sp6</i>
OTU_791	Soil	Sistotrema_sp JX198540 SH014874.07FU reps_singleton	99.23	<i>Sistotrema sp7</i>
OTU_792	Soil	Sistotrema_sp KC965792 SH014875.07FU reps_singleton	87.88	<i>Sistotrema sp8</i>
OTU_793	Soil	Sistotrema_sp UDB024826 SH496886.07FU reps_singleton	89.29	<i>Sistotrema sp9</i>

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OTU_794	Soil	Sistotrema_sp UDB031568 SH478952.07FU reps_singleton	81.23	<i>Sistotrema sp10</i>
OTU_795	Soil	Sistotrema_sp UDB031568 SH478952.07FU reps_singleton	82.96	<i>Sistotrema sp11</i>
OTU_796	Soil	Sordariales_sp UDB004088 SH213994.07FU reps	83.95	<i>Sordariales sp3</i>
OTU_797	Soil	Tarzetia_sp KC966151 SH017567.07FU reps_singleton	96.88	<i>Tarzetia sp2</i>
OTU_798	Soil	Tarzetia_sp KC966365 SH021109.07FU reps_singleton	99.58	<i>Tarzetia sp3</i>
OTU_799	Soil	Tarzetia_sp KC966365 SH021109.07FU reps_singleton	84.87	<i>Tarzetia sp4</i>
OTU_800	Soil	Tarzetia_sp UDB008838 SH210863.07FU reps	97.84	<i>Tarzetia sp5</i>
OTU_801	Soil	Tarzetia_sp UDB008838 SH210863.07FU reps	93.94	<i>Tarzetia sp6</i>
OTU_802	Soil	Thelephora_sp FJ378808 SH006940.07FU reps_singleton	97.84	<i>Thelephora sp5</i>
OTU_803	Soil	Thelephora_sp KR019824 SH189513.07FU reps	91.50	<i>Thelephora sp6</i>
OTU_804	Soil	Thelephora_sp UDB015188 SH184554.07FU reps	95.70	<i>Thelephora sp7</i>
OTU_805	Soil	Thelephoraceae_sp AB218121 SH189578.07FU reps	96.40	<i>Thelephoraceae sp49</i>
OTU_806	Soil	Thelephoraceae_sp AB250947 SH184606.07FU reps	93.94	<i>Thelephoraceae sp50</i>
OTU_807	Soil	Thelephoraceae_sp AB700457 SH185252.07FU reps	91.61	<i>Thelephoraceae sp51</i>
OTU_808	Soil	Thelephoraceae_sp AB769916 SH189503.07FU reps	99.64	<i>Thelephoraceae sp52</i>
OTU_809	Soil	Thelephoraceae_sp AJ972894 SH002714.07FU reps_singleton	94.18	<i>Thelephoraceae sp53</i>
OTU_810	Soil	Thelephoraceae_sp AY702810 SH010119.07FU reps_singleton	97.04	<i>Thelephoraceae sp54</i>
OTU_811	Soil	Thelephoraceae_sp DQ273409 SH010138.07FU reps_singleton	97.80	<i>Thelephoraceae sp55</i>
OTU_812	Soil	Thelephoraceae_sp DQ273412 SH189542.07FU reps	97.52	<i>Thelephoraceae sp56</i>
OTU_813	Soil	Thelephoraceae_sp DQ822831 SH189524.07FU reps	97.10	<i>Thelephoraceae sp57</i>
OTU_814	Soil	Thelephoraceae_sp DQ974788 SH189523.07FU reps	94.60	<i>Thelephoraceae sp58</i>
OTU_815	Soil	Thelephoraceae_sp FN391333 SH189568.07FU reps	94.49	<i>Thelephoraceae sp59</i>
OTU_816	Soil	Thelephoraceae_sp FN397143 SH006965.07FU reps_singleton	99.27	<i>Thelephoraceae sp60</i>
OTU_817	Soil	Thelephoraceae_sp GU220681 SH184593.07FU reps	95.49	<i>Thelephoraceae sp61</i>
OTU_818	Soil	Thelephoraceae_sp HG937638 SH189414.07FU reps	91.03	<i>Thelephoraceae sp62</i>
OTU_819	Soil	Thelephoraceae_sp HM105536 SH184404.07FU reps	96.74	<i>Thelephoraceae sp63</i>
OTU_820	Soil	Thelephoraceae_sp HQ289866 SH010042.07FU reps_singleton	96.07	<i>Thelephoraceae sp64</i>
OTU_821	Soil	Thelephoraceae_sp HQ445483 SH189531.07FU reps	99.65	<i>Thelephoraceae sp65</i>
OTU_822	Soil	Thelephoraceae_sp JQ890243 SH002716.07FU reps_singleton	97.46	<i>Thelephoraceae sp66</i>
OTU_823	Soil	Thelephoraceae_sp JQ991882 SH002994.07FU reps_singleton	86.51	<i>Thelephoraceae sp67</i>
OTU_824	Soil	Thelephoraceae_sp JQ991892 SH189499.07FU reps	96.18	<i>Thelephoraceae sp68</i>
OTU_825	Soil	Thelephoraceae_sp JX630837 SH184560.07FU reps	96.40	<i>Thelephoraceae sp69</i>
OTU_826	Soil	Thelephoraceae_sp KC965658 SH177995.07FU reps	100.00	<i>Thelephoraceae sp70</i>
OTU_827	Soil	Thelephoraceae_sp KC965818 SH010133.07FU reps_singleton	98.54	<i>Thelephoraceae sp71</i>
OTU_828	Soil	Thelephoraceae_sp KC965825 SH006971.07FU reps_singleton	94.96	<i>Thelephoraceae sp72</i>
OTU_829	Soil	Thelephoraceae_sp KF779449 SH002694.07FU reps_singleton	96.36	<i>Thelephoraceae sp73</i>
OTU_830	Soil	Thelephoraceae_sp KM247741 SH494063.07FU reps_singleton	95.22	<i>Thelephoraceae sp74</i>
OTU_831	Soil	Thelephoraceae_sp LC013808 SH495744.07FU reps_singleton	95.05	<i>Thelephoraceae sp75</i>
OTU_832	Soil	Thelephoraceae_sp LC013846 SH205652.07FU reps	96.36	<i>Thelephoraceae sp76</i>
OTU_833	Soil	Thelephoraceae_sp LC035300 SH529647.07FU reps	95.92	<i>Thelephoraceae sp77</i>
OTU_834	Soil	Thelephoraceae_sp UDB004775 SH178496.07FU reps	88.89	<i>Thelephoraceae sp78</i>
OTU_835	Soil	Thelephoraceae_sp UDB005761 SH177947.07FU reps	96.43	<i>Thelephoraceae sp79</i>
OTU_836	Soil	Thelephoraceae_sp UDB008818 SH010066.07FU reps_singleton	95.64	<i>Thelephoraceae sp80</i>
OTU_837	Soil	Thelephoraceae_sp UDB017515 SH010055.07FU reps_singleton	95.99	<i>Thelephoraceae sp81</i>
OTU_838	Soil	Thelephoraceae_sp UDB026840 SH185313.07FU reps	94.88	<i>Thelephoraceae sp82</i>
OTU_839	Soil	Tomentella_badia KM464682 SH178005.07FU reps	96.42	<i>Tomentella sp65</i>
OTU_840	Soil	Tomentella_bryophila UDB000253 SH177881.07FU reps	94.56	<i>Tomentella sp66</i>

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OTU_841	Soil	Tomentella_bryophila UDB000253 SH177881.07FU reps	95.25	<i>Tomentella sp67</i>
OTU_842	Soil	Tomentella_bryophila UDB000253 SH177881.07FU reps	92.91	<i>Tomentella sp68</i>
OTU_843	Soil	Tomentella_bryophila UDB000253 SH177881.07FU reps	94.58	<i>Tomentella sp69</i>
OTU_844	Soil	Tomentella_cinereoumbrina FM999507 SH177811.07FU reps	97.50	<i>Tomentella cinereoumbrina</i>
OTU_845	Soil	Tomentella_lateritia UDB016439 SH185279.07FU refs	97.82	<i>Tomentella lateritia</i>
OTU_846	Soil	Tomentella_hilacinogrisea UDB017118 SH189577.07FU reps	96.39	<i>Tomentella sp70</i>
OTU_847	Soil	Tomentella_pilosa UDB003324 SH177790.07FU refs	99.64	<i>Tomentella pilosa</i>
OTU_848	Soil	Tomentella_punicea UDB020341 SH184524.07FU reps	99.66	<i>Tomentella punicea</i>
OTU_849	Soil	Tomentella_sp AB211278 SH184543.07FU reps	99.28	<i>Tomentella sp71</i>
OTU_850	Soil	Tomentella_sp AB211278 SH184543.07FU reps	96.76	<i>Tomentella sp72</i>
OTU_851	Soil	Tomentella_sp EU498743 SH177839.07FU reps	94.91	<i>Tomentella sp73</i>
OTU_852	Soil	Tomentella_sp EU498743 SH177839.07FU reps	99.64	<i>Tomentella sp74</i>
OTU_853	Soil	Tomentella_sp EU554744 SH177849.07FU reps	98.18	<i>Tomentella sp75</i>
OTU_854	Soil	Tomentella_sp EU726311 SH177911.07FU reps	96.76	<i>Tomentella sp76</i>
OTU_855	Soil	Tomentella_sp HE687131 SH177965.07FU reps	98.91	<i>Tomentella sp77</i>
OTU_856	Soil	Tomentella_sp HF565106 SH177899.07FU reps	96.54	<i>Tomentella sp78</i>
OTU_857	Soil	Tomentella_sp HQ215815 SH184533.07FU reps	97.14	<i>Tomentella sp79</i>
OTU_858	Soil	Tomentella_sp HQ215823 SH189465.07FU reps	96.40	<i>Tomentella sp80</i>
OTU_859	Soil	Tomentella_sp JF506816 SH178015.07FU reps	98.20	<i>Tomentella sp81</i>
OTU_860	Soil	Tomentella_sp JN197795 SH177796.07FU reps	99.28	<i>Tomentella sp82</i>
OTU_861	Soil	Tomentella_sp JX630358 SH177862.07FU reps	96.73	<i>Tomentella sp83</i>
OTU_862	Soil	Tomentella_sp KC965735 SH177990.07FU reps	97.46	<i>Tomentella sp84</i>
OTU_863	Soil	Tomentella_sp KP123608 SH184514.07FU reps	97.10	<i>Tomentella sp85</i>
OTU_864	Soil	Tomentella_sp KP889648 SH189473.07FU reps	94.93	<i>Tomentella sp86</i>
OTU_865	Soil	Tomentella_sp KP889648 SH189473.07FU reps	96.01	<i>Tomentella sp87</i>
OTU_866	Soil	Tomentella_sp UDB008549 SH177837.07FU reps	96.31	<i>Tomentella sp88</i>
OTU_867	Soil	Tomentella_sp UDB008549 SH177837.07FU reps	94.97	<i>Tomentella sp89</i>
OTU_868	Soil	Tomentella_sp UDB008549 SH177837.07FU reps	94.97	<i>Tomentella sp90</i>
OTU_869	Soil	Tomentella_sp UDB008549 SH177837.07FU reps	96.33	<i>Tomentella sp91</i>
OTU_870	Soil	Tomentella_sp UDB008549 SH177837.07FU reps	95.32	<i>Tomentella sp92</i>
OTU_871	Soil	Tomentella_sp UDB008549 SH177837.07FU reps	96.28	<i>Tomentella sp93</i>
OTU_872	Soil	Tomentella_sp UDB020311 SH189506.07FU reps	100.00	<i>Tomentella sp94</i>
OTU_873	Soil	Tomentella_sp UDB025932 SH177872.07FU reps	99.64	<i>Tomentella sp95</i>
OTU_874	Soil	Tomentella_sp UDB026913 SH525626.07FU reps	95.62	<i>Tomentella sp96</i>
OTU_875	Soil	Tomentella_stuposa JN652983 SH177816.07FU reps	96.88	<i>Tomentella sp97</i>
OTU_876	Soil	Tomentella_stuposa JN652983 SH177816.07FU reps	96.19	<i>Tomentella sp98</i>
OTU_877	Soil	Tomentella_stuposa UDB016174 SH177785.07FU refs	96.70	<i>Tomentella sp99</i>
OTU_878	Soil	Tomentella_subclavigera UDB003320 SH177838.07FU refs	99.66	<i>Tomentella subclavigera</i>
OTU_879	Soil	Tomentellopsis_sp KF617459 SH215671.07FU refs	98.66	<i>Tomentellopsis sp1</i>
OTU_880	Soil	Tomentellopsis_sp UDB017158 SH184853.07FU refs	100.00	<i>Tomentellopsis sp2</i>
OTU_881	Soil	Tremellodendropsidales_sp KJ188556 SH494395.07FU reps_singleton	86.26	<i>Tremellodendropsidales sp1</i>
OTU_882	Soil	Tremellodendropsidales_sp KJ188556 SH494395.07FU reps_singleton	86.26	<i>Tremellodendropsidales sp2</i>
OTU_883	Soil	Tremellodendropsidales_sp KP889587 SH488451.07FU reps_singleton	97.11	<i>Tremellodendropsidales sp3</i>
OTU_884	Soil	Tremellodendropsidales_sp UDB008445 SH178751.07FU refs	90.21	<i>Tremellodendropsidales sp4</i>
OTU_885	Soil	Tricholoma_imbricatum UDB011626 SH219357.07FU refs	99.62	<i>Tricholoma imbricatum</i>
OTU_886	Soil	Tricholoma_moseri UDB007430 SH219378.07FU reps	97.83	<i>Tricholoma moseri</i>
OTU_887	Soil	Tricholoma_sp KU058497 SH630693.07FU reps_singleton	89.64	<i>Tricholoma sp1</i>

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OTU_888	Soil	Tricholoma_sp KU058497 SH630693.07FU reps_singleton	96.91	<i>Tricholoma sp2</i>
OTU_889	Soil	Tricholoma_sp KU058497 SH630693.07FU reps_singleton	89.88	<i>Tricholoma sp3</i>
OTU_890	Soil	Tricholoma_sp KU058497 SH630693.07FU reps_singleton	87.07	<i>Tricholoma sp4</i>
OTU_891	Soil	Tricholoma_sp KU058497 SH630693.07FU reps_singleton	97.67	<i>Tricholoma sp5</i>
OTU_892	Soil	Tricholoma_sp KU058497 SH630693.07FU reps_singleton	90.28	<i>Tricholoma sp6</i>
OTU_893	Soil	Tricholoma_sp KU058497 SH630693.07FU reps_singleton	94.64	<i>Tricholoma sp7</i>
OTU_894	Soil	Trichophaea_sp KC966273 SH026035.07FU reps_singleton	97.78	<i>Trichophaea sp5</i>
OTU_895	Soil	Trichophaea_sp KF000606 SH521561.07FU reps	100.00	<i>Trichophaea sp6</i>
OTU_896	Soil	Trichophaea_sp KM247635 SH489883.07FU reps_singleton	86.96	<i>Trichophaea sp7</i>
OTU_897	Soil	Trichophaea_sp UDB008859 SH215400.07FU reps	91.11	<i>Trichophaea sp8</i>
OTU_898	Soil	Trichophaea_woolhopeia GU811248 SH196143.07FU reps	88.57	<i>Trichophaea sp9</i>

Table S2.2: Envfit results for the environmental variables used in NMDS ordination.

VECTORS:	NMDS1	NMDS2	R^2	p-value	
Latitude	-0.4164	-0.90918	0.0575	0.267	
Longitude	-0.96377	-0.26672	0.0411	0.4012	
Elevation (m)	0.9069	0.42134	0.4383	0.0001	***
Annual mean temperature °C	-0.82804	-0.56067	0.4687	0.0001	***
Annual precipitation (mm/year)	-0.9993	-0.03728	0.3136	0.0008	***
Soil total N (%)	-0.38634	-0.92236	0.3652	0.0001	***
Soil total C (%)	-0.62561	-0.78013	0.483	0.0001	***
Soil pH (CaCl2)	-0.83995	0.54267	0.8183	0.0001	***
Soil Ca (mmolc/kg)	-0.7373	-0.67556	0.2694	0.0009	***
Soil K (mmolc/kg)	-0.23215	-0.97268	0.1774	0.0155	*
Soil Mg (mmolc/kg)	-0.95761	-0.28806	0.5414	0.0001	***
No. EM plants in site	-0.27984	0.96005	0.1035	0.0884	.
Total plant cover (%)	0.34939	-0.93698	0.2662	0.0026	**
Signif. codes: 0‘***’,0.001‘**’,0.01‘*’,0.05‘.’					
Permutation: free					
Number of permutations 9999					

FACTORS:	NMDS1	NMDS2
Host species <i>B. vivipara</i>	-0.0522	-0.0871
Host species <i>D. octopetala</i>	-0.3373	-0.0571
Host species <i>S. herbacea</i>	0.7589	0.3111
CorineLandCover231_Pastures	-0.3056	0.0769
CorineLandCover321_Natural_grasslands	-0.1864	-0.2442
CorineLandCover322_Moors_and_heathland	-0.1101	-0.1091
CorineLandCover332_Bare_rocks	-0.0785	0.1743
CorineLandCover333_Sparsely_vegetated_areas	0.0984	0.1339
CorineLandCover411_Inland_marshes	1.2846	-0.8449
Habitat Alpine	0.1405	0.0468
Habitat Treeline	-0.3311	-0.1103

Goodness of fit:	R^2	p-value	
Host species	0.2785	0.0002	***
CorineLandCover	0.1579	0.1576	
Habitat	0.0819	0.0253	*
Signif. codes: 0‘***’,0.001‘**’,0.01‘*’,0.05‘.’			
Permutation: free			
Number of permutations 9999			

Table S2.3 Population differentiation (F_{st}) values among clusters identified in STRUCTURE analysis for A) *Dryas octopetala*, B) *Bistorta vivipara*

A)				
	DO_Cluster_1	DO_Cluster_2	DO_Cluster_3	DO_Cluster_4
DO_Cluster_1	-	-	-	-
DO_Cluster_2	0.063	-	-	-
DO_Cluster_3	0.028	0.024	-	-
DO_Cluster_4	0.051	0.052	0.018	-
B)				
	BV_Cluster_1	BV_Cluster_2	BV_Cluster_3	BV_Cluster_4
BV_Cluster_1	-	-	-	-
BV_Cluster_2	0.084	-	-	-
BV_Cluster_3	0.026	0.043	-	-
BV_Cluster_4	0.033	0.060	0.017	-

Table S2.4: AMOVA results among clusters identified in STRUCTURE analysis for A) *Dryas octopetala* and B) *Bistorta vivipara*.

A)								
Source of variation	Nested in	%var	F-stat	F-value	Std.Dev.	c.i.2.5%	c.i.97.5%	p-value
Within individual	--	1.040	R_it	-0.040	0.044	-0.156	0.007	-
Among individual	Population	-0.034	R_is	-0.034	0.051	-0.162	0.020	0.715
Among cluster	--	-0.006	R_st	-0.006	0.010	-0.016	0.016	0.713
B)								
Source of variation	Nested in	%var	F-stat	F-value	Std.Dev.	c.i.2.5%	c.i.97.5%	p-value
Within individual	--	1.044	R_it	-0.044	0.047	-0.113	0.004	-
Among individual	Population	-0.084	R_is	-0.088	0.020	-0.130	-0.059	0.999
Among cluster	--	0.041	R_st	0.041	0.028	0.002	0.068	0.003

Table S2.5: Summary table of the effect of elevation in ectomycorrhizal fungal communities.

Reference	Context	Elevation range (m.a.s.l.)	Mountain habitat zonation sampled	Effect of elevation in EM communities
Present study	EM community richness and structure along elevation gradients in the European Alps	1,478 - 2,592	From treeline ecotone to alpine	No significant differences in species richness along elevation gradients
Kernaghan & Harper (2001)	Community structure of EM fungi across an alpine/subalpine ecotone	2,000 - 2,500	Sub-alpine to alpine	Ectomycorrhizal diversity decreased with increasing elevation, although the decrease from the ecotone to the alpine zone was not significant
Bahram <i>et al.</i> (2012)	Regional and local patterns of EM fungal diversity and community structure along an altitudinal gradient in the Hyrcanian forests of northern Iran	100 - 2,700	Sub-montane and montane deciduous forests to subalpine shrubland	Species richness declined monotonically with increasing altitude
Nottingham <i>et al.</i> (2018)	Microbes follow Humboldt: temperature drives plant and soil microbial diversity patterns from the Amazon to the Andes	194 - 3,644	Tropical forest to high elevation grassland	Species richness declined as elevation increased
Collins <i>et al.</i> (2018)	Shrub range expansion alters diversity and distribution of soil fungal communities across an alpine elevation gradient	3,200, 3,500 and 3,800	From subalpine to alpine	Fungal diversity declines with increasing elevation

Figure S2.1: Ectomycorrhizal fungi community composition across habitats; panel A) across lineage, panel B) across taxa with higher contribution to community dissimilarities.



Figure S2.2: Comparison of the number of ectomycorrhizas showing different soil exploration types: A) within the treeline and alpine zones, B) in alpine versus treeline zones, C) within hosts, and D) among hosts. Significant differences are represented by letters and asterisks (* p -value ≤ 0.05 ; ** p -value ≤ 0.01)

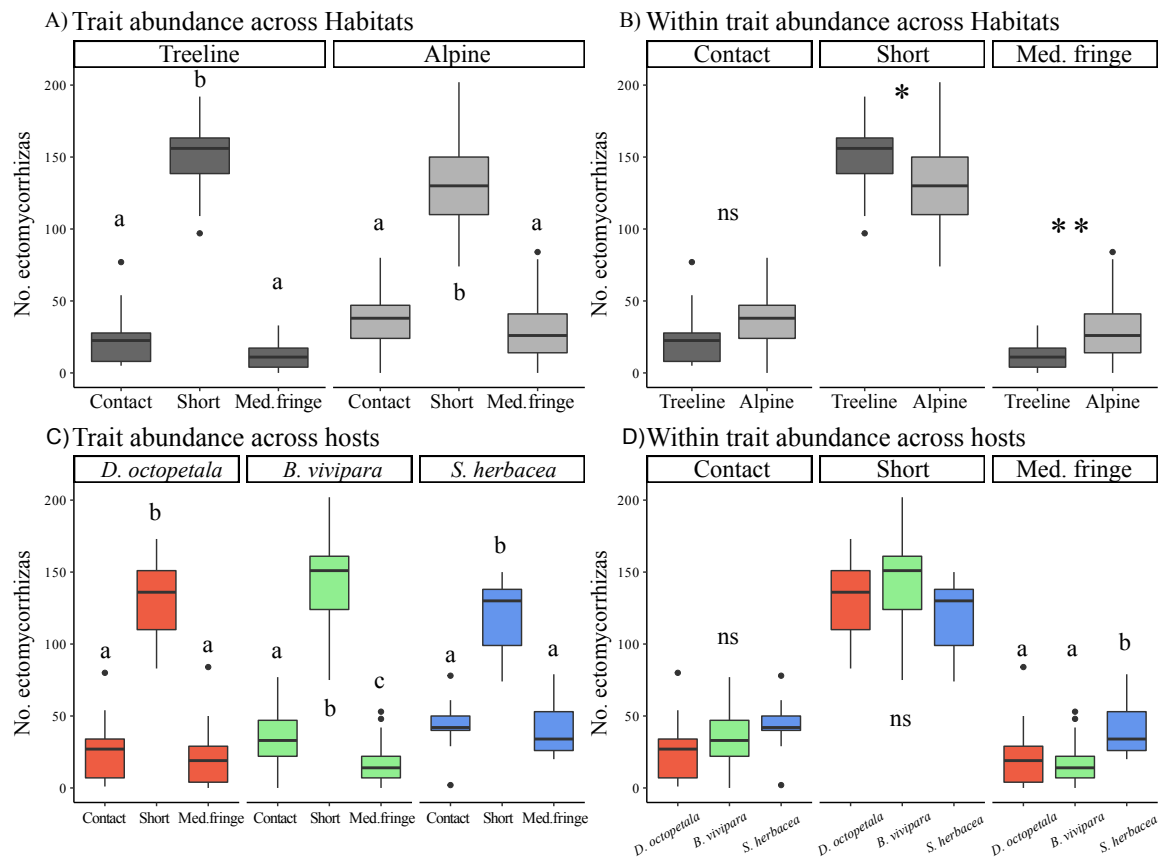
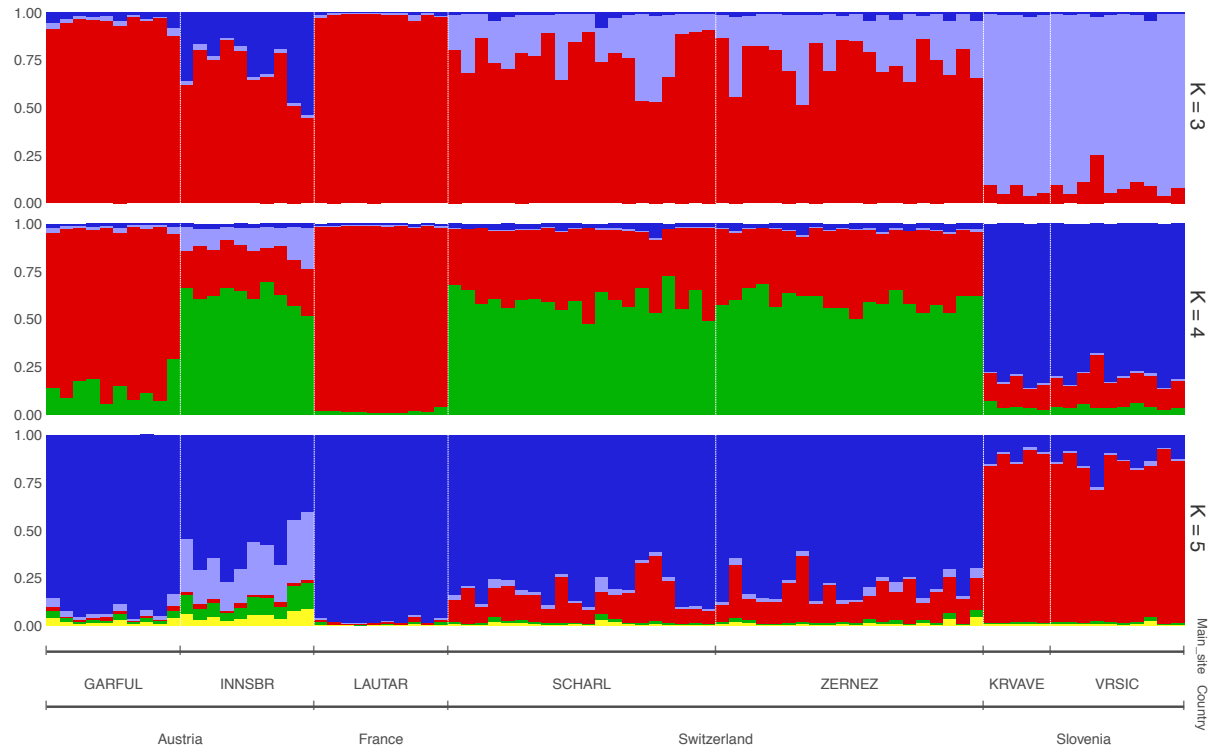
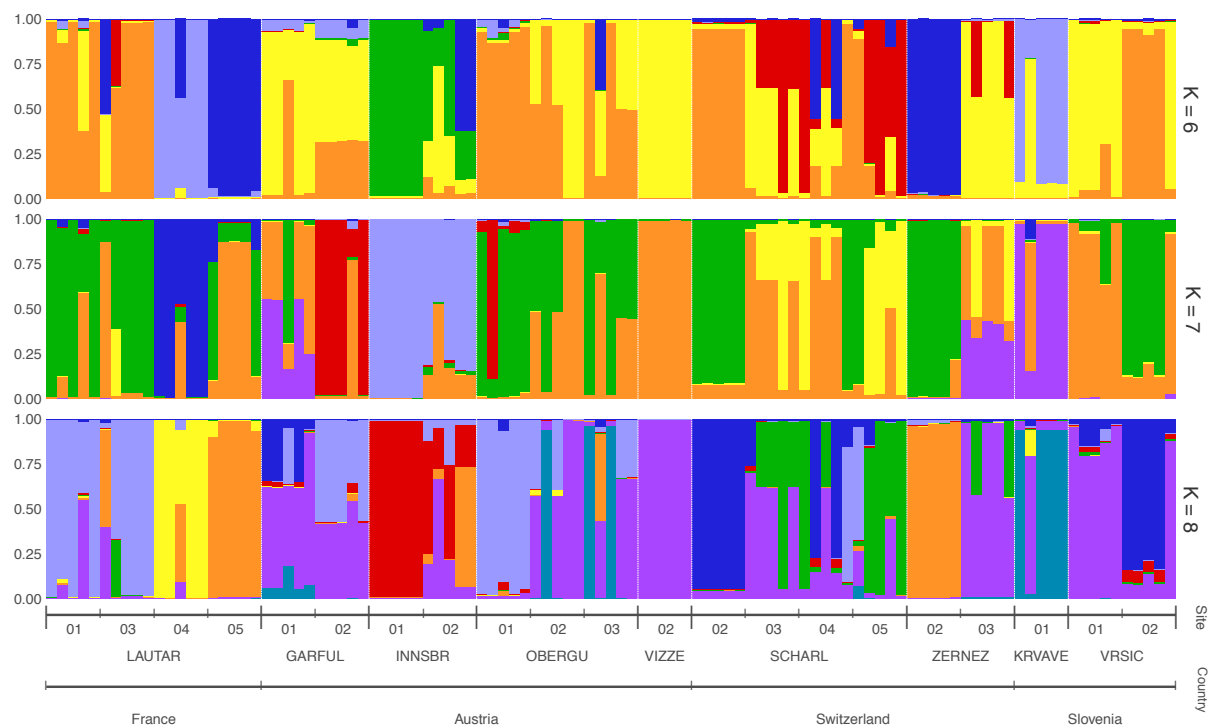


Figure S2.3: STRUCTURE plots with population sub-division in A) *D. octopetala* and B) *B. vivipara*. The best number of K in *D. octopetala* was four (Cluster 1: GARFUL + LAUTAR, Cluster 2: INNSBR, Cluster 3: SCHARL + ZERNEZ, Cluster 4: KRVAVE + VRSIC). The best number of K in *B. vivipara* was six, but only four were selected for further analysis (Cluster 1: LAUTAR_05 + ZERNEZ_02, Cluster 2: INNSBR_01, Cluster 3: GARFUL_01 + VIZZE_02 + VRSIC_01 + ZERNEZ_03, Cluster 4: OBERGU_01 + SCHARL_02).

A)



B)



Appendix B

Table S3.1: Indicator species analysis results.

Multilevel pattern analysis

Association function: IndVal.g

Significance level (alpha): 0.05

List of species associated to each group:

Group Alpine acidic #sps. 26

	A	B	stat	p-value
<i>Cenococcum geophilum</i> OTU_007	0.9297	1	0.964	0.001***
<i>Helotiales</i> sp2 OTU_094	0.8963	0.8182	0.856	0.001***
<i>Tomentella</i> sp31 OTU_370	0.8822	0.7273	0.801	0.002**
<i>Tomentella</i> sp32 OTU_371	1	0.5455	0.739	0.001***
<i>Meliniomyces bicolor</i> OTU_182	0.7124	0.7273	0.72	0.002**
<i>Russula emetica</i> OTU_202	1	0.4545	0.674	0.001***
<i>Cortinarius hinnuleoarmillatus</i> OTU_044	1	0.4545	0.674	0.001***
<i>Cortinarius aureomarginatus</i> OTU_029	0.9574	0.4545	0.66	0.003**
<i>Meliniomyces bicolor</i> OTU_181	0.9329	0.4545	0.651	0.003**
<i>Thelephoraceae</i> sp4 OTU_286	0.8721	0.4545	0.63	0.008**
<i>Tomentella badia</i> OTU_338	0.8235	0.4545	0.612	0.005**
<i>Agaricales</i> sp1 OTU_001	1	0.3636	0.603	0.004**
<i>Membranomyces</i> sp3 OTU_185	0.9375	0.3636	0.584	0.008**
<i>Tomentella</i> sp35 OTU_375	0.9086	0.3636	0.575	0.008**
<i>Cortinarius</i> sp6 OTU_060	0.8958	0.3636	0.571	0.008**
<i>Russula nuoljae</i> OTU_204	0.8906	0.3636	0.569	0.009**
<i>Russula griseascens</i> OTU_203	0.8214	0.3636	0.547	0.009**
<i>Russula pascua</i> OTU_206	1	0.2727	0.522	0.019*
<i>Thelephoraceae</i> sp18 OTU_289	1	0.2727	0.522	0.014*
<i>Serendipita</i> sp2 OTU_270	1	0.2727	0.522	0.015*
<i>Cortinarius croceus</i> OTU_031	1	0.2727	0.522	0.011*
<i>Entoloma majaloides</i> OTU_066	1	0.2727	0.522	0.010**
<i>Cortinarius alpinus</i> OTU_028	1	0.2727	0.522	0.019*
<i>Thelephoraceae</i> sp37 OTU_315	0.6734	0.3636	0.495	0.040*
<i>Cenococcum geophilum</i> OTU_005	0.8842	0.2727	0.491	0.025*

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Laccaria trichodermophora OTU_176 0.7701 0.2727 0.458 0.047*

Group Alpine alkaline #sps. 5

	A	B	stat	p-value
<i>Tomentella</i> sp49 OTU_391	1	0.3	0.548	0.014*
<i>Tomentella</i> sp28 OTU_366	1	0.3	0.548	0.028*
<i>Humaria hemisphaerica</i> OTU_104	1	0.25	0.5	0.037*
<i>Cortinarius</i> sp11 OTU_057	1	0.25	0.5	0.024*
<i>Cortinarius decipiens</i> OTU_036	1	0.25	0.5	0.026*

Group Treeline #sps. 15

	A	B	stat	p-value
<i>Tomentella</i> sp45 OTU_387	0.7508	0.6429	0.695	0.002**
<i>Sebacina</i> sp51 OTU_262	0.6957	0.5	0.59	0.032*
<i>Tomentella viridula</i> OTU_414	0.6876	0.4286	0.543	0.035*
<i>Sebacina</i> sp6 OTU_247	0.807	0.3571	0.537	0.021*
<i>Cenococcum geophilum</i> OTU_013	1	0.2857	0.535	0.010**
<i>Tomentella</i> sp19 OTU_353	1	0.2857	0.535	0.008**
<i>Tomentella</i> sp10 OTU_401	1	0.2857	0.535	0.008**
<i>Helvella dovrensis</i> OTU_096	0.745	0.3571	0.516	0.034*
<i>Sebacina</i> sp40 OTU_249	0.8741	0.2857	0.5	0.043*
<i>Cortinarius decipiens</i> OTU_032	0.8577	0.2857	0.495	0.027*
<i>Tomentella</i> sp64 OTU_409	0.8465	0.2857	0.492	0.040*
<i>Membranomyces</i> sp2 OTU_184	0.8291	0.2857	0.487	0.034*
<i>Thelephoraceae</i> sp46 OTU_327	1	0.2143	0.463	0.037*
<i>Helvellosebacina</i> sp3 OTU_101	1	0.2143	0.463	0.040*
<i>Sebacina</i> sp7 OTU_248	1	0.2143	0.463	0.044*

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Appendix C

Table S4.1: Ectomycorrhizal OTUs observed in the roots and in the soil (Chapter 4).

OTU number	Compartment	Top blast hit to UNITE database v7.2	%id	Taxonomy
OTU_001	Roots & Soil	Amphinema_sp UDB000841 SH197766.07FU reps	100	<i>Amphinema sp1</i>
OTU_002	Roots & Soil	Cortinarius_pastoralis KX302258 SH222459.07FU reps	97.42	<i>Cortinarius pastoralis</i>
OTU_003	Roots & Soil	Cortinarius_alboviolaceus UDB002442 SH196666.07FU reps	99.5	<i>Cortinarius alboviolaceus</i>
OTU_004	Roots & Soil	Cortinarius_casimiri FN429013 SH188471.07FU refs	97.3	<i>Cortinarius casimiri</i>
OTU_005	Roots & Soil	Cortinarius_casimiri FN429013 SH188471.07FU refs	99.46	<i>Cortinarius casimiri</i>
OTU_006	Roots & Soil	Cortinarius_decipiens FN428988 SH188469.07FU refs	100	<i>Cortinarius decipiens</i>
OTU_007	Roots & Soil	Cortinarius_decipiens KM576374 SH188589.07FU reps	100	<i>Cortinarius decipiens</i>
OTU_008	Roots & Soil	Cortinarius_depressus FJ553539 SH188478.07FU reps	98.41	<i>Cortinarius depressus</i>
OTU_009	Roots & Soil	Cortinarius_diasemospermus UDB001230 SH188470.07FU refs	99.58	<i>Cortinarius diasemospermus</i>
OTU_010	Roots & Soil	Cortinarius_hinnuleus FJ039708 SH188520.07FU reps	100	<i>Cortinarius hinnuleus</i>
OTU_011	Roots & Soil	Cortinarius_parvannulatus UDB016062 SH188475.07FU refs	98.76	<i>Cortinarius parvannulatus</i>
OTU_012	Roots & Soil	Cortinarius_praestigiosus KM576354 SH188620.07FU reps	100	<i>Cortinarius praestigiosus</i>
OTU_013	Roots & Soil	Cortinarius_saniosus DQ102671 SH188476.07FU refs	100	<i>Cortinarius saniosus</i>
OTU_014	Roots & Soil	Cortinarius_scandens GQ159849 SH188527.07FU reps	100	<i>Cortinarius scandens</i>
OTU_015	Roots & Soil	Cortinarius_sp EF655689 SH188595.07FU reps	98.31	<i>Cortinarius sp1</i>
OTU_016	Roots & Soil	Cortinarius_vernus UDB000742 SH188477.07FU refs	96.36	<i>Cortinarius sp2</i>
OTU_017	Roots & Soil	Elaphomyces_decipiens EU846311 SH190241.07FU reps	100	<i>Elaphomyces decipiens</i>
OTU_018	Roots & Soil	Hebeloma_asperulatum HQ179675 SH293510.07FU refs	99.25	<i>Hebeloma asperulatum</i>
OTU_019	Roots & Soil	Hebeloma_erebium KT218429 SH215998.07FU reps	97.05	<i>Hebeloma erebium</i>
OTU_020	Roots & Soil	Hebeloma_nigellum KX765786 SH628864.07FU reps_singleton	100	<i>Hebeloma nigellum</i>
OTU_021	Roots & Soil	Hebeloma_radicoides LC009704 SH529344.07FU reps	96.71	<i>Hebeloma sp1</i>
OTU_022	Roots & Soil	Inocybaceae_sp EU554937 SH201233.07FU reps	98.11	<i>Inocybaceae sp1</i>
OTU_023	Roots & Soil	Inocybe_lacera AM882815 SH201232.07FU refs	100	<i>Inocybe lacera</i>
OTU_024	Roots & Soil	Inocybe_lacera HQ215795 SH219806.07FU reps	98.31	<i>Inocybe lacera</i>
OTU_025	Roots & Soil	Inocybe_rufoalba HQ604804 SH197268.07FU refs	99.58	<i>Inocybe rufoalba</i>
OTU_026	Roots & Soil	Laccaria_laccata UDB025819 SH199898.07FU reps	100	<i>Laccaria laccata</i>
OTU_027	Roots & Soil	Laccaria_trichodermophora JX625288 SH220959.07FU reps	98.86	<i>Laccaria trichodermophora</i>
OTU_028	Roots & Soil	Piloderma_bicolor KP814367 SH203894.07FU reps	100	<i>Piloderma bicolor</i>
OTU_029	Roots & Soil	Russula_emetica UDB000300 SH218421.07FU refs	98.11	<i>Russula emetica</i>
OTU_030	Roots & Soil	Russula_pascua JX436947 SH176550.07FU reps	100	<i>Russula pascua</i>
OTU_031	Roots & Soil	Sebacina_sp EF417823 SH214697.07FU refs	98.4	<i>Sebacina sp1</i>
OTU_032	Roots & Soil	Sistotrema_muscicola UDB002254 SH187707.07FU refs	100	<i>Sistotrema muscicola</i>
OTU_033	Roots & Soil	Thelephora_caryophyllea UDB000212 SH189359.07FU reps	99.54	<i>Thelephora caryophyllea</i>
OTU_034	Roots & Soil	Thelephoraceae_sp AB506097 SH189355.07FU reps	99.64	<i>Thelephoraceae sp1</i>
OTU_035	Roots & Soil	Thelephoraceae_sp AB669641 SH029724.07FU reps_singleton	100	<i>Thelephoraceae sp2</i>
OTU_036	Roots & Soil	Thelephoraceae_sp EF218838 SH250543.07FU refs	97.47	<i>Thelephoraceae sp3</i>
OTU_037	Roots & Soil	Thelephoraceae_sp EF218838 SH250543.07FU refs	98.55	<i>Thelephoraceae sp4</i>
OTU_038	Roots & Soil	Tomentella_sp JF304358 SH217476.07FU reps	99.28	<i>Tomentella sp1</i>

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OTU_039	Roots & Soil	Thelephoraceae_sp JX630837 SH184560.07FU reps	99.28	<i>Thelephoraceae sp5</i>
OTU_040	Roots & Soil	Thelephora_atra UDB016470 SH189377.07FU refs	98.91	<i>Thelephora atra</i>
OTU_041	Roots & Soil	Thelephoraceae_sp UDB031729 SH002646.07FU reps_singleton	97.27	<i>Thelephoraceae sp6</i>
OTU_042	Roots & Soil	Thelephora_sp FJ378792 SH189708.07FU reps	100	<i>Thelephora sp1</i>
OTU_043	Roots & Soil	Tomentella_badia JQ711987 SH177828.07FU reps	95.48	<i>Tomentella sp2</i>
OTU_044	Roots & Soil	Tomentella_badia JQ711987 SH177828.07FU reps	95.93	<i>Tomentella sp3</i>
OTU_045	Roots & Soil	Thelephoraceae_sp DQ273412 SH189542.07FU reps	97.52	<i>Thelephoraceae sp7</i>
OTU_046	Roots & Soil	Tomentella_sp EU554744 SH177849.07FU reps	98.91	<i>Tomentella sp4</i>
OTU_047	Roots & Soil	Tomentella_sp HQ215806 SH177870.07FU reps	100	<i>Tomentella sp5</i>
OTU_048	Roots & Soil	Tomentella_sp HQ215823 SH189465.07FU reps	100	<i>Tomentella sp6</i>
OTU_049	Roots & Soil	Tomentella_sp HQ445368 SH184523.07FU reps	99.29	<i>Tomentella sp7</i>
OTU_050	Roots & Soil	Tomentella_sp UDB008530 SH177854.07FU reps	100	<i>Tomentella sp8</i>
OTU_051	Roots & Soil	Tomentella_sp UDB008971 SH178629.07FU reps	99.64	<i>Tomentella sp9</i>
OTU_052	Roots & Soil	Tomentella_sp UDB012515 SH189357.07FU reps	100	<i>Tomentella sp10</i>
OTU_053	Roots & Soil	Tomentella_sp UDB025800 SH185320.07FU reps	99.09	<i>Tomentella sp11</i>
OTU_054	Roots & Soil	Tomentella_sp UDB027247 SH177827.07FU reps	98.17	<i>Tomentella sp12</i>
OTU_055	Roots & Soil	Tomentella_sp UDB031755 SH184738.07FU reps	99.08	<i>Tomentella sp13</i>
OTU_056	Roots	Cenococcum_geophilum JQ347036 SH199614.07FU reps	97.26	<i>Cenococcum geophilum</i>
OTU_057	Roots	Cenococcum_geophilum KP348245 SH214459.07FU reps	97.2	<i>Cenococcum geophilum</i>
OTU_058	Roots	Cenococcum_geophilum KX510009 SH199612.07FU reps	98.56	<i>Cenococcum geophilum</i>
OTU_059	Roots	Cortinarius_diasemospermus UDB000066 SH188559.07FU reps	95.7	<i>Cortinarius sp3</i>
OTU_060	Roots	Hebelomataceae_sp AY310842 SH030768.07FU reps_singleton	92.68	<i>Hebeloma sp2</i>
OTU_061	Roots	Inocybe_rufolba HQ604804 SH197268.07FU refs	98.38	<i>Inocybe rufolba</i>
OTU_062	Roots	Laccaria_trichodermophora JX625288 SH220959.07FU reps	97.56	<i>Laccaria trichodermophora</i>
OTU_063	Roots	Meliniomyces_bicolor AJ430147 SH426644.07FU refs	92.96	<i>Meliniomyces sp1</i>
OTU_064	Roots	Peziza_sp GU817102 SH193720.07FU reps	97.02	<i>Peziza sp1</i>
OTU_065	Roots	Thelephoraceae_sp EF218838 SH250543.07FU refs	96.36	<i>Thelephoraceae sp8</i>
OTU_066	Roots	Thelephoraceae_sp EF218838 SH250543.07FU refs	96.38	<i>Thelephoraceae sp9</i>
OTU_067	Roots	Thelephoraceae_sp FJ013066 SH184510.07FU reps	97.22	<i>Thelephoraceae sp10</i>
OTU_068	Roots	Thelephoraceae_sp UDB031729 SH002646.07FU reps_singleton	95.91	<i>Thelephoraceae sp11</i>
OTU_069	Roots	Tomentella_sp KP403048 SH177919.07FU reps	100	<i>Tomentella sp14</i>
OTU_070	Soil	Russula_chloroides AY061663 SH220557.07FU reps	99.36	<i>Russula chloroides</i>
OTU_071	Soil	Laccaria_amethystina JX504092 SH220970.07FU reps	96.85	<i>Laccaria sp1</i>
OTU_072	Soil	Cortinarius_diasemospermus UDB000066 SH188559.07FU reps	95.89	<i>Cortinarius sp4</i>
OTU_073	Soil	Inocybe_giacomi AM882742 SH194465.07FU refs	99.56	<i>Inocybe giacomii</i>
OTU_074	Soil	Thelephoraceae_sp UDB012442 SH189384.07FU reps	98.91	<i>Thelephoraceae sp12</i>
OTU_075	Soil	Cortinarius_comptulus AB848441 SH188473.07FU reps	99.17	<i>Cortinarius comptulus</i>
OTU_076	Soil	Thelephoraceae_sp FJ013066 SH184510.07FU reps	98.18	<i>Thelephoraceae sp13</i>
OTU_077	Soil	Amphinema_byssoides JN943904 SH197944.07FU reps	100	<i>Amphinema byssoides</i>
OTU_078	Soil	Cortinarius_murinascens KP165570 SH188592.07FU refs	100	<i>Cortinarius murinascens</i>
OTU_079	Soil	Serendipita_sp HQ211712 SH180002.07FU reps	98.07	<i>Serendipita sp1</i>
OTU_080	Soil	Tomentella_badia JQ711987 SH177828.07FU reps	97.86	<i>Tomentella badia</i>
OTU_081	Soil	Amphinema_byssoides UDB008257 SH197943.07FU refs	100	<i>Amphinema byssoides</i>
OTU_082	Soil	Pulvinula_sp UDB032992 SH210657.07FU reps	99.56	<i>Pulvinula sp1</i>

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OTU_083	Soil	Tremellodendropsidales_sp KJ188556 SH494395.07FU reps_singleton	93.82	<i>Tremellodendropsidales sp1</i>
OTU_084	Soil	Cortinarius_ammiratii UDB021475 SH304023.07FU refs	97.14	<i>Cortinarius ammiratii</i>
OTU_085	Soil	Piloderma_sp UDB026694 SH527567.07FU reps	99.15	<i>Piloderma sp1</i>
OTU_086	Soil	Cortinarius_alpinus DQ295079 SH265621.07FU refs	99.63	<i>Cortinarius alpinus</i>
OTU_087	Soil	Tomentella_cinereoumbrina FM999507 SH177811.07FU reps	97.5	<i>Tomentella cinereoumbrina</i>
OTU_088	Soil	Thelephoraceae_sp EU516692 SH189579.07FU reps	100	<i>Thelephoraceae sp14</i>
OTU_089	Soil	Cortinarius_betuletorum UDB002406 SH188503.07FU reps	100	<i>Cortinarius betuletorum</i>
OTU_090	Soil	Tomentella_terrestris FJ236853 SH189378.07FU reps	99.64	<i>Tomentella terrestris</i>
OTU_091	Soil	Tricholoma_squarulosum LT000179 SH219367.07FU reps	91.88	<i>Tricholoma sp1</i>
OTU_092	Soil	Clavulina_sp FJ237119 SH031651.07FU reps_singleton	99.38	<i>Clavulina sp1</i>
OTU_093	Soil	Lactarius_semisanguifluus UDB000320 SH220111.07FU refs	97.58	<i>Lactarius semisanguifluus</i>
OTU_094	Soil	Tomentella_stuposa AF272922 SH178263.07FU reps	100	<i>Tomentella stuposa</i>
OTU_095	Soil	Inocybe_impexa AM882821 SH201234.07FU refs	96.96	<i>Inocybe sp1</i>
OTU_096	Soil	Cortinarius_xanthocephalus UDB011265 SH222378.07FU refs	98.44	<i>Cortinarius xanthocephalus</i>
OTU_097	Soil	Thelephoraceae_sp KF779449 SH002694.07FU reps_singleton	99.64	<i>Thelephoraceae sp15</i>
OTU_098	Soil	Laccaria_laccata JF273528 SH220963.07FU reps	98.47	<i>Laccaria laccata</i>
OTU_099	Soil	Cortinarius_illibatus UDB001089 SH222443.07FU refs	100	<i>Cortinarius illibatus</i>
OTU_100	Soil	Peziza_sp GU817102 SH193720.07FU reps	98.75	<i>Peziza sp2</i>
OTU_101	Soil	Cortinarius_sp UDB012740 SH009446.07FU reps_singleton	99.6	<i>Cortinarius sp5</i>
OTU_102	Soil	Cortinarius_balteatus KF732262 SH130438.07FU refs_singleton	98.5	<i>Cortinarius balteatus</i>
OTU_103	Soil	Cortinarius_roseobasilis KU041740 SH644281.07FU reps	96.42	<i>Cortinarius sp6</i>
OTU_104	Soil	Sistotrema_sp EU668935 SH192853.07FU refs	80.09	<i>Agaricomycetes sp1</i>
OTU_105	Soil	Cortinarius_ammiratii UDB021475 SH304023.07FU refs	97.52	<i>Cortinarius ammiratii</i>
OTU_106	Soil	Tomentella_sp HQ204729 SH177887.07FU reps	96.22	<i>Tomentella sp15</i>
OTU_107	Soil	Cortinarius_acutovelatus UDB001000 SH222362.07FU refs	99.62	<i>Cortinarius acutovelatus</i>
OTU_108	Soil	Thelephoraceae_sp JQ991854 SH184597.07FU reps	94.18	<i>Thelephoraceae sp16</i>
OTU_109	Soil	Thelephoraceae_sp FJ897222 SH189481.07FU reps	98.64	<i>Thelephoraceae sp17</i>
OTU_110	Soil	Lactarius_torminosus UDB000375 SH220114.07FU refs	99.05	<i>Lactarius torminosus</i>
OTU_111	Soil	Sebacina_sp AB096870 SH214672.07FU refs	98.82	<i>Sebacina sp2</i>
OTU_112	Soil	Geopora_nicaeensis JF908022 SH213659.07FU reps	99.55	<i>Geopora nicaeensis</i>
OTU_113	Soil	Piloderma_sp UDB014832 SH493561.07FU reps_singleton	90.2	<i>Piloderma sp2</i>
OTU_114	Soil	Cortinarius_sp UDB026205 SH188693.07FU reps	99.18	<i>Cortinarius sp7</i>
OTU_115	Soil	Peziza_badia JF908544 SH193723.07FU refs	98.83	<i>Peziza badia</i>
OTU_116	Soil	Inocybe_calamistrata JQ801386 SH188902.07FU reps	98.73	<i>Inocybe calamistrata</i>
OTU_117	Soil	Tomentella_sp HF565112 SH189466.07FU reps	95.44	<i>Tomentella sp16</i>
OTU_118	Soil	Russula_puiggarii KT354747 SH641473.07FU reps	88.12	<i>Russulaceae sp1</i>
OTU_119	Soil	Cortinarius_diasemospermus UDB000066 SH188559.07FU reps	99.59	<i>Cortinarius diasemospermus</i>
OTU_120	Soil	Cortinarius_alboamarensis KR011137 SH522340.07FU reps	96.36	<i>Cortinarius sp8</i>
OTU_121	Soil	Laccaria_alba JX504175 SH220987.07FU reps	85.97	<i>Laccaria sp2</i>
OTU_122	Soil	Serendipita_sp GU452533 SH201954.07FU reps	84.75	<i>Serendipita sp2</i>
OTU_123	Soil	Inocybe_rufoalba FN550883 SH211892.07FU refs	100	<i>Inocybe rufoalba</i>
OTU_124	Soil	Sistotrema_sp KC965792 SH014875.07FU reps_singleton	88.21	<i>Sistoderma sp1</i>
OTU_125	Soil	Auricularia_sp HM488497 SH470965.07FU reps_singleton	97.98	<i>Auricularia sp1</i>
OTU_126	Soil	Cortinarius_pastoralis KX302258 SH222459.07FU reps	93.38	<i>Cortinarius sp9</i>

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OTU_127	Soil	Inocybe_sp GQ893001 SH032425.07FU reps_singleton	96.15	<i>Inocybe sp2</i>
OTU_128	Soil	Peziza_sp JX414199 SH193740.07FU reps	97.02	<i>Peziza sp3</i>
OTU_129	Soil	Russula_sapinea UDB015996 SH187353.07FU refs	99.67	<i>Russula sapinea</i>
OTU_130	Soil	Helvellosebacina_sp UDB007962 SH291217.07FU refs	98.04	<i>Helvellosebacina sp1</i>
OTU_131	Soil	Pezizaceae_sp UDB008929 SH193724.07FU reps	98.76	<i>Pezizaceae sp1</i>
OTU_132	Soil	Inocybe_teraturgus AM882789 SH190703.07FU refs	95.87	<i>Inocybe sp3</i>
OTU_133	Soil	Inocybe_xanthomelas FN550895 SH179934.07FU refs	100	<i>Inocybe xanthomelas</i>
OTU_134	Soil	Pseudotomentella_sp LC035238 SH524049.07FU reps	98.75	<i>Pseudotomentella sp1</i>
OTU_135	Soil	Serendipita_sp UDB008509 SH179999.07FU refs	98.55	<i>Serendipita sp3</i>
OTU_136	Soil	Inocybe_sp HQ445445 SH015238.07FU reps_singleton	95.06	<i>Inocybe sp4</i>
OTU_137	Soil	Sistotrema_sp JX198540 SH014874.07FU reps_singleton	94.66	<i>Sistoderma sp1</i>
OTU_138	Soil	Ramaria_bataillei AF441082 SH485553.07FU reps_singleton	98.46	<i>Ramaria bataillei</i>
OTU_139	Soil	Cortinarius_uraceisporus KP165543 SH525380.07FU refs	94.01	<i>Cortinarius sp10</i>
OTU_140	Soil	Tremellodendropsidales_sp KP889587 SH488451.07FU reps_singleton	97.11	<i>Tremellodendropsidales sp2</i>
OTU_141	Soil	Tomentella_badia HM164617 SH177806.07FU reps	99.64	<i>Tomentella badia</i>
OTU_142	Soil	Cortinarius_ferrugineovelatus KP137508 SH188536.07FU refs	100	<i>Cortinarius ferrugineovelatus</i>
OTU_143	Soil	Tomentella_terrestris UDB003315 SH189365.07FU refs	98.55	<i>Tomentella terrestris</i>
OTU_144	Soil	Russula_graveolens KM576511 SH176560.07FU reps	92.63	<i>Russula sp2</i>
OTU_145	Soil	Amphinema_sp UDB000841 SH197766.07FU reps	83.01	<i>Amphinema sp2</i>
OTU_146	Soil	Cortinarius_niveotraganus KM273103 SH188538.07FU refs	100	<i>Cortinarius niveotraganus</i>
OTU_147	Soil	Laccaria_alba JX504175 SH220987.07FU reps	88.42	<i>Laccaria sp3</i>
OTU_148	Soil	Thelephoraceae_sp HG426040 SH189391.07FU reps	97.9	<i>Thelephoraceae sp18</i>
OTU_149	Soil	Helvellosebacina_sp UDB007962 SH291217.07FU refs	96.08	<i>Helvellosebacina sp2</i>
OTU_150	Soil	Clavulinaceae_sp HQ444977 SH179200.07FU reps	99.65	<i>Clavulinaceae sp1</i>
OTU_151	Soil	Leccinum_scabrum AF454583 SH209697.07FU refs	99.46	<i>Leccinum scabrum</i>
OTU_152	Soil	Helvellosebacina_sp UDB007962 SH291217.07FU refs	98.04	<i>Helvellosebacina sp3</i>
OTU_153	Soil	Laccaria_sp KU685748 SH631814.07FU reps_singleton	85.37	<i>Laccaria sp4</i>
OTU_154	Soil	Tomentella_alpina EF655702 SH177861.07FU refs	99.64	<i>Tomentella alpina</i>
OTU_155	Soil	Sistotrema_sp AB839395 SH014877.07FU reps_singleton	97.7	<i>Sistotrema sp4</i>
OTU_156	Soil	Lactarius_rufus EF493296 SH182377.07FU refs	100	<i>Lactarius rufus</i>
OTU_157	Soil	Tomentella_cinereascens UDB003309 SH205650.07FU refs	99.64	<i>Tomentella cinereascens</i>
OTU_158	Soil	Thelephoraceae_sp FJ013066 SH184510.07FU reps	98.53	<i>Thelephoraceae sp19</i>
OTU_159	Soil	Leccinum_scabrum UDB001608 SH209698.07FU reps	99.7	<i>Leccinum scabrum</i>
OTU_160	Soil	Cortinarius_anomalus UDB026965 SH196665.07FU reps	99.22	<i>Cortinarius anomalus</i>
OTU_161	Soil	Cortinarius_alboamarescens KR011137 SH522340.07FU reps	99.64	<i>Cortinarius alboamarescens</i>
OTU_162	Soil	Sordariales_sp UDB004088 SH213994.07FU reps	83.95	<i>Sordariomycetes sp1</i>
OTU_163	Soil	Laccaria_alba JX504175 SH220987.07FU reps	96.45	<i>Laccaria sp5</i>
OTU_164	Soil	Tomentella_sp KP889648 SH189473.07FU reps	96.74	<i>Tomentella sp17</i>
OTU_165	Soil	Tomentellopsis_sp UDB017158 SH184853.07FU refs	100	<i>Tomentellopsis sp1</i>
OTU_166	Soil	Helvellosebacina_sp UDB007962 SH291217.07FU refs	98.04	<i>Helvellosebacina sp4</i>
OTU_167	Soil	Russula_vinosa UDB000350 SH176549.07FU refs	100	<i>Russula vinosa</i>
OTU_168	Soil	Cortinarius_glaucopus DQ097885 SH640218.07FU reps	100	<i>Cortinarius glaucopus</i>
OTU_169	Soil	Cortinarius_caninus KX302240 SH196670.07FU reps	96.24	<i>Cortinarius sp11</i>
OTU_170	Soil	Inocybe_auricomella FN550900 SH219810.07FU reps	99.64	<i>Inocybe auricomella</i>

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OTU_171	Soil	Cortinarius_rubricosus HE687038 SH188580.07FU reps	95.87	<i>Cortinarius sp12</i>
OTU_172	Soil	Balsamia_sp UDB013602 SH177121.07FU reps	97.87	<i>Balsamia sp1</i>
OTU_173	Soil	Laccaria_sp GU969247 SH179272.07FU reps	100	<i>Laccaria sp6</i>
OTU_174	Soil	Sebacina_sp UDB025284 SH491682.07FU reps_singleton	87.81	<i>Sebacina sp3</i>
OTU_175	Soil	Piloderma_sp KC791145 SH015692.07FU reps_singleton	86.9	<i>Piloderma sp3</i>
OTU_176	Soil	Sebacina_sp EF417823 SH214697.07FU refs	95.6	<i>Sebacina sp4</i>
OTU_177	Soil	Terfezia_leptoderma AF396864 SH012921.07FU reps_singleton	79.91	<i>Pezizaceae sp2</i>
OTU_178	Soil	Balsamia_sp UDB013602 SH177121.07FU reps	97.87	<i>Balsamia sp2</i>
OTU_179	Soil	Laccaria_alba JX504175 SH220987.07FU reps	83.51	<i>Laccaria sp7</i>
OTU_180	Soil	Inocybe_impexa AM882821 SH201234.07FU refs	99.25	<i>Inocybe impexa</i>
OTU_181	Soil	Laccaria_alba JX504175 SH220987.07FU reps	85.07	<i>Laccaria sp8</i>
OTU_182	Soil	Endogone_sp KC152094 SH213348.07FU reps	93.81	<i>Endogone sp1</i>
OTU_183	Soil	Densospora_sp UDB028692 SH490876.07FU reps_singleton	89.86	<i>Densospora sp1</i>
OTU_184	Soil	Endogone_sp KC152094 SH213348.07FU reps	94.14	<i>Endogone sp2</i>
OTU_185	Soil	Helvellosebacina_sp UDB007962 SH291217.07FU refs	98.04	<i>Helvellosebacina sp5</i>
OTU_186	Soil	Lactarius_austrotorminosus EF141532 SH176439.07FU refs	86.49	<i>Russulaceae sp1</i>
OTU_187	Soil	Hymenogaster_huthii UDB025671 SH218882.07FU reps	100	<i>Hymenogaster huthii</i>
OTU_188	Soil	Tricholoma_imbricatum UDB011626 SH219357.07FU refs	100	<i>Tricholoma imbricatum</i>
OTU_189	Soil	Inocybe_sp JX630700 SH190793.07FU reps	98.81	<i>Inocybe sp5</i>
OTU_190	Soil	Russula_sp KF245490 SH032039.07FU reps_singleton	96.82	<i>Russula sp3</i>
OTU_191	Soil	Cortinarius_callochrous UDB001836 SH222361.07FU refs	100	<i>Cortinarius callochrous</i>
OTU_192	Soil	Inocybe_sp KC965253 SH031789.07FU reps_singleton	90.91	<i>Inocybe sp6</i>
OTU_193	Soil	Strobilomyces_strobilaceus JQ318970 SH211708.07FU reps	95.46	<i>Strobilomyces sp1</i>
OTU_194	Soil	Pustularia_sp KC965384 SH222143.07FU reps	98.08	<i>Pustularia sp1</i>
OTU_195	Soil	Piloderma_sp FJ236851 SH197934.07FU reps	83.53	<i>Piloderma sp4</i>
OTU_196	Soil	Pustularia_sp FJ013060 SH222141.07FU reps	98.08	<i>Pustularia sp2</i>
OTU_197	Soil	Cortinarius_roseobasilis KU041740 SH644281.07FU reps	93.91	<i>Cortinarius sp13</i>
OTU_198	Soil	Pustularia_sp KC965384 SH222143.07FU reps	98	<i>Pustularia sp3</i>
OTU_199	Soil	Geopora_clausa JF908766 SH213668.07FU reps	99.57	<i>Geopora clausa</i>
OTU_200	Soil	Sebacina_incrustans EF655701 SH214612.07FU refs	100	<i>Sebacina incrustans</i>
OTU_201	Soil	Amanita_sp JQ347156 SH208391.07FU reps	89.02	<i>Amanita sp1</i>
OTU_202	Soil	Amanita_sp KP071065 SH494361.07FU reps_singleton	100	<i>Amanita sp2</i>
OTU_203	Soil	Cortinarius_saniosus DQ102671 SH188476.07FU refs	96.88	<i>Cortinarius sp14</i>
OTU_204	Soil	Inocybe_sp KP171136 SH524897.07FU reps	85.19	<i>Inocybe sp7</i>
OTU_205	Soil	Sebacina_sp UDB016431 SH197125.07FU refs	100	<i>Sebacina sp5</i>
OTU_206	Soil	Terfezia_claveryi GU474801 SH104786.07FU refs_singleton	98.11	<i>Terfezia claveryi</i>
OTU_207	Soil	Cortinarius_pastoralis KX302258 SH222459.07FU reps	99.63	<i>Cortinarius pastoralis</i>
OTU_208	Soil	Thelephoraceae_sp EF218838 SH250543.07FU refs	98.2	<i>Thelephoraceae sp20</i>
OTU_209	Soil	Cortinarius_albocyaneus UDB026032 SH222483.07FU reps	99.22	<i>Cortinarius albocyaneus</i>
OTU_210	Soil	Tomentella_sp JQ347208 SH177820.07FU reps	97.81	<i>Tomentella sp18</i>
OTU_211	Soil	Inocybe_flocculosa UDB015335 SH187316.07FU refs	97.23	<i>Inocybe flocculosa</i>
OTU_212	Soil	Otidea_sp UDB008809 SH016746.07FU reps_singleton	100	<i>Otidea sp1</i>
OTU_213	Soil	Laccaria_amethystina JX504092 SH220970.07FU reps	96.15	<i>Laccaria sp9</i>
OTU_214	Soil	Astraeus_telleriae UDB026525 SH190455.07FU reps	99.35	<i>Astraeus telleriae</i>
OTU_215	Soil	Russula_emetica UDB000300 SH218421.07FU refs	94.65	<i>Russula sp4</i>

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OTU_216	Soil	Inocybe_bulbosissima FJ904158 SH183292.07FU refs	98.71	<i>Inocybe bulbosissima</i>
OTU_217	Soil	Cortinarius_argenteolilacinus UDB031686 SH216564.07FU reps	95.87	<i>Cortinarius sp15</i>
OTU_218	Soil	Inocybe_adaequata AM882706 SH216136.07FU refs	99.57	<i>Inocybe adaequata</i>
OTU_219	Soil	Inocybe_sp JX630511 SH190795.07FU reps	96.83	<i>Inocybe sp8</i>
OTU_220	Soil	Endogone_sp KC152094 SH213348.07FU reps	90.88	<i>Endogone sp3</i>
OTU_221	Soil	Helvellosebacina_sp UDB007962 SH291217.07FU refs	91.05	<i>Helvellosebacina sp6</i>
OTU_222	Soil	Helvellosebacina_sp UDB007962 SH291217.07FU refs	98.04	<i>Helvellosebacina sp7</i>
OTU_223	Soil	Sebacina_sp GQ219876 SH027696.07FU reps_singleton	99.22	<i>Sebacina sp6</i>
OTU_224	Soil	Tomentella_badia HM164617 SH177806.07FU reps	97.12	<i>Tomentella badia</i>
OTU_225	Soil	Clavulina_sp FJ237119 SH031651.07FU reps_singleton	95.08	<i>Clavulina sp2</i>
OTU_226	Soil	Cortinarius_pluvius UDB001058 SH222390.07FU reps	98.47	<i>Cortinarius pluvius</i>
OTU_227	Soil	Helvellosebacina_sp UDB007962 SH291217.07FU refs	98.04	<i>Helvellosebacina sp8</i>
OTU_228	Soil	Pustularia_sp FJ013060 SH222141.07FU reps	98.08	<i>Pustularia sp4</i>
OTU_229	Soil	Cortinarius_sp EF655689 SH188595.07FU reps	94.09	<i>Cortinarius sp16</i>
OTU_230	Soil	Cortinarius_roseobasilis KU041740 SH644281.07FU reps	93.53	<i>Cortinarius sp17</i>
OTU_231	Soil	Inocybe_amethystina JF908123 SH219984.07FU reps	92.67	<i>Inocybe sp9</i>
OTU_232	Soil	Cortinarius_bivelus UDB019630 SH188497.07FU reps	100	<i>Cortinarius bivelus</i>
OTU_233	Soil	Cortinarius_pastoralis KX302258 SH222459.07FU reps	96.68	<i>Cortinarius sp18</i>
OTU_234	Soil	Tomentella_galzinii UDB000263 SH177815.07FU refs	98.64	<i>Tomentella galzinii</i>
OTU_235	Soil	Tomentella_sp JN197795 SH177796.07FU reps	99.28	<i>Tomentella sp19</i>
OTU_236	Soil	Amanita_sp KP071065 SH494361.07FU reps_singleton	100	<i>Amanita sp3</i>
OTU_237	Soil	Pezizaceae_sp UDB004620 SH221476.07FU reps	85	<i>Pezizaceae sp2</i>

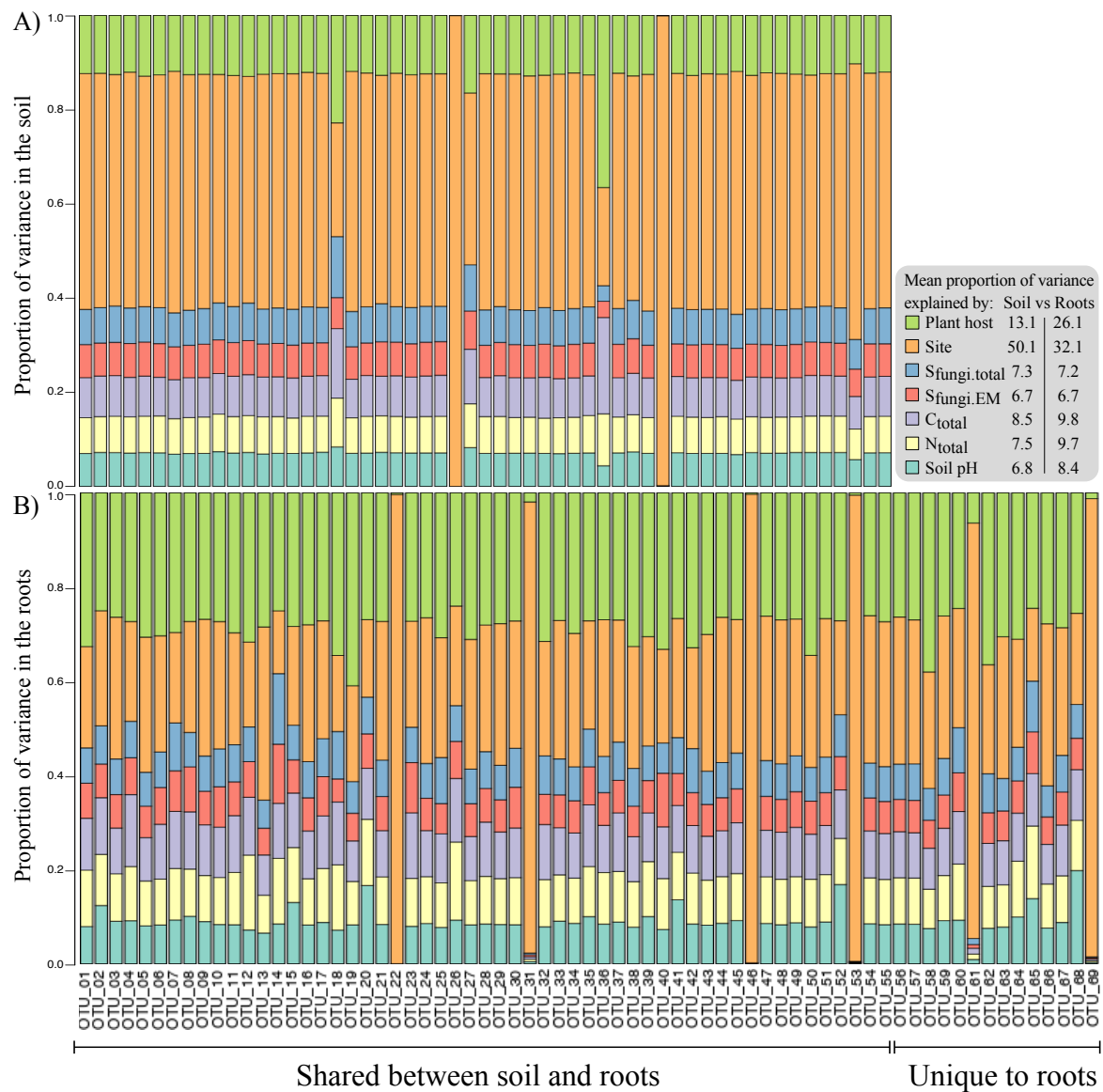
Table S4.2: Adonis and betadisper results. Significant values are represented as: * p -value ≤ 0.05 , ** p -value ≤ 0.01 , *** p -value ≤ 0.001 . SH – *S. helvetica*, SP – *S. purpurea* and SX - Hybrids

Test	groups	R^2	p -value
adonis	All	0.0966	0.0010***
	SH.roots - SH.soil	-	0.0002**
	SH.roots - SP.roots	-	0.2256
	SH.roots - SP.soil	-	0.0007***
	SH.roots - SX.roots	-	0.2092
	SH.roots - SX.soil	-	0.0003***
	SH.soil - SP.roots	-	0.0053**
	SH.soil - SP.soil	-	0.3904
betadisper	SH.soil - SX.roots	-	0.0093**
	SH.soil - SX.soil	-	0.5057
	SP.roots - SP.soil	-	0.0178*
	SP.roots - SX.roots	-	0.9602
	SP.roots - SX.soil	-	0.0088**
	SP.soil - SX.roots	-	0.0266*
	SP.soil - SX.soil	-	0.7355
	SX.roots - SX.soil	-	0.0145*

Table S4.3: The results of selected indices of network analysis. Significant deviations of the null models are represented in bold.

		Modularity					Nestedness					C-score				
		Obs	p-value	z-score	NM L95 %CI	NM U95 %CI	Obs	p-value	z-score	NM L95 %CI	NM U95 %CI	Obs	p-value	z-score	NM L95 %CI	NM U95 %CI
roots	weighted	0.242	0.073	1.59015	0.21035	0.21274	37.7	0.315	0.49094	36.50326	36.76220	-	-	-	-	-
	binary	0.396	0.112	1.15107	0.39444	0.39463	59.2	0.032	-0.06051	59.17620	59.21876	0.502	0.404	0.03288	0.50126	0.50264
soil	weighted	0.329	<0.001	6.16708	0.16794	0.17115	39.2	<0.001	-2.99491	43.19428	43.36399	-	-	-	-	-
	binary	0.388	0.129	1.16788	0.38745	0.38746	58.5	0.420	0.11060	58.44173	58.45367	0.511	0.003	2.12684	0.49910	0.49979

Fig. S4.1: Variance partitioning in the EM fungi in A) soil and B) roots (ectomycorrhizas). Variance partitioning was calculated using the relative abundance of the EM OTUs in response to, site, plant host, soil pH, total C, total N, and estimated total fungal and EM communities in soil. Only shared OTUs between soil and root datasets are illustrated in A).



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