



## Distinct environmental variables drive the community composition of mycorrhizal and saprotrophic fungi at the alpine treeline ecotone



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### ABSTRACT

Soil inhabiting fungi have an important role in ecosystems around the treeline representing both plant symbionts and organic matter decomposers. To identify the drivers of their diversity and community structure, amplicon sequencing of soil fungal DNA was conducted on six elevation transects across the transition from spruce forests to dwarf pine stands in the Krkonoše Mts. (Czech Republic, Central Europe). Between 104 and 269 operational taxonomic units (OTUs) per plot were detected, however, no relation between OTU richness and elevation was found. Importantly, the dominant (representing more than 5% of all sequences per plot) OTUs assigned to ectomycorrhizal taxa decreased with elevation. Whereas the community composition of mycorrhizal fungi followed the elevation gradient and most of the total variability was explained by tree height, communities of saprotrophs were shaped mainly by vegetation, soil cover and soil properties, and differed among the transects.

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### 1. Introduction

The alpine treeline is an essential boundary in mountain relief, being the edge of the habitat at which trees are capable of growing. It is defined as a line connecting the highest patches of forest composed of trees of at least 3 m height (Körner, 2012). A transition zone from mountain forests into shrubland or grassland habitats, delimited by the forest line (=timberline) and the tree species limit (the highest elevation at which scattered and stunted individuals of forest-forming tree species are found) is called the alpine treeline ecotone (Holtmeier and Broll, 2005). Climate and topography are considered to be the main factors influencing the conditions along the elevation gradient at the treeline (Wieser and Tausz, 2007).

These factors largely determine the soil properties and vegetation, which interact and can mitigate the effect of climate and topography, at least at the microsite level. The soil - vegetation interactions are strongly mediated by fungi, because almost all plants at the treeline are mycorrhizal. Mycorrhizal fungi provide trees with nutrients and water in exchange for carbon and so influence their survival at the limits of their ecophysiological abilities. Saprotrophic fungi decompose litter thus making nutrients available for other system components. Despite these important roles, there is surprisingly little information about fungal communities at the treeline and the main factors driving their structure.

Several studies of ectomycorrhizal (ECM) root tips (morphotyping, morphotyping and Sanger sequencing) reported a decrease of ECM species richness towards the tree line (Kernaghan and Harper, 2001; Bahram et al., 2012 – two of three transects; Miyamoto et al., 2014), however these studies were influenced by the presence of more ECM host trees with different ECM fungal symbionts of different host range. A study of the ECM community of

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one host tree (*Pinus sylvestris*) by 454 pyrosequencing (Jarvis et al., 2015) revealed no change in species richness, but a distinct shift in ECM fungal community composition related to soil moisture and a temperature gradient. Moser (1982) found that there are ECM and saprotrophic fungi whose fruit bodies never occur above the forest line and attributed it to the different transpiration rates of the fruit bodies of different species.

Because alpine treelines are temperature sensitive - associated with a seasonal mean ground temperature of 6.7 °C (Körner and Paulsen, 2004), they are expected to respond to climate warming by advancing beyond their current position (Harsch et al., 2009). However many other factors could influence these processes, e.g. rising CO<sub>2</sub> concentration, increased nitrogen deposition, more frequent extreme weather events (Grace et al., 2002; Lindner et al., 2010), limiting nutrient availability (Hungate et al., 2003), seed dispersal capacities of the different tree species and their competitive abilities against understory vegetation (Dullinger et al., 2003), insect and disease outbreaks (Ayres and Lombardero, 2000; Volney and Fleming, 2000), etc.

Changes in the associations of plants and mycorrhizal fungi could also have a considerable influence, which is crucial at the treeline (Wieser and Tausz, 2007). Migration of hosts and symbionts, modification of interactions between plant and fungal species and changes in the contribution of both partners to the carbon cycle could lead to distinct shifts in ECM communities (Courty et al., 2010; Pickles et al., 2012). Similarly, decomposition rates of soil organic matter are likely to be affected due to global change (Kammer et al., 2009) leading to distinct shifts in the communities of saprotrophic taxa (van der Wal et al., 2013). This could be more pronounced in cold areas such as those around the treeline, where a low decomposition rate is caused by the temperature sensitivity of enzyme activities (Baldrian et al., 2013a), and affected by nitrogen limitation in the case of cold adapted decomposers (Wallenstein et al., 2009).

The aim of this study was to describe the diversity and composition of soil fungal communities across an alpine treeline ecotone and to identify the main environmental factors that drive fungal community assembly. In addition, we aimed to reveal the key fungal players in ecosystems along the gradient and to obtain reference data for monitoring future changes in treeline ecosystems.

Based on the plant holobiont concept (Lüttge, 2012), we supposed that fungal community structure will be largely determined by the composition of dominant plant species. We hypothesized that the mycorrhizal community is mainly affected by tree species composition and that its diversity is highest at plots with a co-occurrence of *Picea abies* and *Pinus mugo*. In contrast, saprotroph diversity was hypothesized to be more affected by microsite diversity (i.e. vegetation and soil cover heterogeneity). Alternatively, the elevation effect may lead to decreased fungal diversity towards the top of the gradient due to unfavourable climate conditions together with decreasing C supply from trees, in the case of mycorrhizal fungi, and lower plant necromass production in the case of saprotrophs.

## 2. Material and methods

### 2.1. Site descriptions

The Krkonoše Mts. (Giant Mts.) are located in the north of the Czech Republic and the south-west of Poland (Fig. 1). The biogeographic conditions are characterized by frequent weather changes and long, cold and damp winters with abundant and long snow cover. Annual average temperature in the studied altitudes varies from 2.6 to 3.5 °C, and precipitation ranges from 1300 to

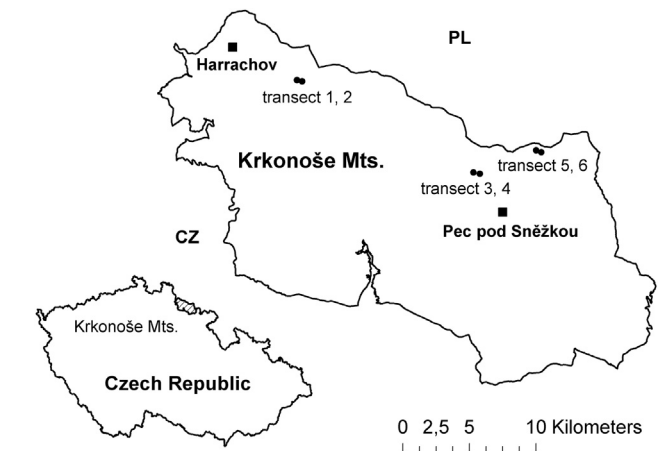


Fig. 1. Map of the study area with location of the six studied transects.

1414 mm (Kolář et al., 2015). Based on SO<sub>2</sub> emission inventories, sulphur throughfall deposition reached 62 kg S ha<sup>-1</sup> yr<sup>-1</sup> in the period 1980–1985 (Kopáček and Veselý, 2005) and decreased to 11.5 kg S ha<sup>-1</sup> yr<sup>-1</sup> in the period 2007–2011 (Kolář et al., 2015). The treeline ecotone has a simple vegetation structure and is therefore suitable as a model area. The mountain forests are formed by Norway spruce (*P. abies*) only, becoming less dense with altitude and gradually replaced by dwarf pine shrubs (*P. mugo*). Other tree species, such as *Sorbus aucuparia*, *Salix* spp., and *Betula pendula*, occur only rarely. The occurrence of spruce trees is limited by the force of wind and ice injury; this so-called summit phenomenon in the Krkonoše Mts. is stronger than in the Alps or Tatra Mts (Tremil and Banaš, 2000) and may be affected by avalanches. Dwarf pine, on the other hand, is not able to invade into closed forest stands because of its shade-intolerance.

Six altitudinal transects of circle plots (500 m<sup>2</sup>) were established at three localities (two per locality, being 100–150 m apart) to cover the vegetation gradient across the treeline ecotone. The main criteria for establishing plot location were: the absence of trees other than *P. abies* and *P. mugo*; absence of large *Sphagnum* patches (due to its association with specialized fungi and indication of a more humid water regime); cover of *P. abies* and *P. mugo*; and biometric characteristics of the *P. abies* trees (cover, height, crown placing). Four transects were composed of 5 plots in different altitudinal positions on the gradient: P0 – dwarf pine (*P. mugo*) shrub zone; P1 – dwarf pine shrubs with scattered spruce (*P. abies*) trees; P2 – spruce trees with scattered dwarf pine; P3 – spruce forest under the forest line; P4 mountain spruce forest (Table 1). Two transects were composed of four plots only (plots in position P0 in the dwarf pine shrub zone were missing due to vegetation structure). The altitudinal range of the plots was 1190–1404 m a.s.l., the transects ranged in length from 370 to 770 m, while the altitudinal differences between plots in a transect ranged from 111 to 190 m. In each plot, average height of the spruce trees and average crown placing were measured by laser technique, average diameter at breast height (DBH) and number of live and dead trees were assessed. The percent covers of all herb-layer species and the total percent covers of the moss layer 'E0', herb layer 'E1', shrub layer 'E2', and tree layer 'E3' (separately the total cover of live and dead canopy) were visually estimated, as well as other structures like wood (including lying dead wood and stumps), coarse woody debris (CWD) and litter. Species with covers below 1% were given the uniform value of 0.5% and 0.02% if the occurrence of plants was limited to one or very few individuals (Table S1).

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