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Functional diversity of soil microbial communities under Scots pine, Norway spruce, silver birch and mixed boreal forests

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ABSTRACT

Functional structure and diversity of forest soil microbial communities may depend on plant diversity. The objective of our study was to compare community level physiological profiles (CLPPs) of microbial communities from uppermost soil horizons under Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), silver birch (*Betula pendula*) and mixed pine–birch–spruce stands representing boreal forests differing in the identity of the dominant tree species and diversity of overstory and understory plant species in the system. The samples of O and A soil horizons were measured for pH, organic carbon, and total nitrogen. Microbial analyses included determination of microbial biomass (C_{mic}) and measurement of CLPPs with the MicroResp™ system. The studied forest types differed significantly in plant species diversity with birch and mixed forests being the most and the pine forest the least diverse. Functional microbial diversity only slightly differed between the studied forest types and was not related to plant diversity. Despite similar functional diversity of soil microbial communities there were significant differences in CLPPs in the O horizons under the pine, spruce and birch forests indicating that plant cover affects the rate at which particular organic compounds are degraded. Differences in physiological profiles between the birch, pine and spruce forest soils were mainly due to variable decomposition of readily decomposable organic compounds represented mainly by carboxylic acids.

Introduction

Forests play a major role in the global carbon cycle, especially in the sequestration of atmospheric CO_2 as they are a large and persistent global C sink (Lal, 2005; Pan et al., 2011). Among three principal forest biomes boreal forests constitute the largest stock of C, harbouring 49% of C stored in forest ecosystems (Dixon et al., 1994). Northern forest ecosystems contain about 559 Pg of C, wherein soils contain more than 80% (471 Pg) of this amount (Dixon et al. 1994).

Soil microorganisms are principal drivers of soil organic matter turnover. They are involved in numerous key soil processes including degradation, mineralization and humification of organic compounds in soils (Stevenson, 1982; Bauhus and Khanna, 1999). The soil organic matter mineralization rate may depend on composition of microbial communities and their ability to metabolize different organic compounds (Garcia-Pausas and Paterson, 2011).

The structure and diversity of soil microbial communities are thought to be affected by composition and diversity of plant cover (Ladygina and Hedlund, 2010). High plant diversity may enhance net primary productivity, leading to increased soil-carbon input owing to faster turnover of plant biomass and larger root exudation and may therefore positively affect carbon limited microbial communities in the soil (Bartelt-Ryser et al., 2005). Indeed, Zak et al. (2003) reported that increasing the number of plant species resulted in larger productivity of grasslands and positively affected soil microbial biomass, activity and composition. High plant diversity may support a greater diversity of decomposers due to high diversity of litter and root exudates (Kowalchuk et al., 2002; Bartelt-Ryser et al., 2005; De Deyn and Van der Putten 2005). However, the exact relationships between plant communities and soil microorganisms remain unclear (Porazinska et al., 2003) and a positive relationship between plant and microbial diversity has not always been observed (Wardle et al., 1999; Kielak et al., 2008).

Of particular importance for functioning of soil ecosystems is functional diversity of soil microbial communities (Zak et al., 1994). The functional diversity of soil microbial communities represents the sum of the ecological processes carried out by the organisms of

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a community (Insam et al., 1989) and results from genetic diversity of that community, environmental effects on gene expression and ecological interactions among taxa (Pignataro et al., 2012). The microbial functional diversity can be assessed by measuring metabolic activity of soil microbial communities although one should bear in mind that the currently available analytical methods measure potential rather than real activities (Nannipieri et al., 2003). Particularly useful for the assessment of functional microbial diversity is the MicroResp™ method developed by Campbell et al. (2003). The MicroResp™ is a community level physiological profile (CLPP) technique based on the addition of several C substrates directly to soil and measuring the microbial response as CO_2 evolution. In recent years the method has been applied to compare physiological profiles of natural and rehabilitated mine soils (Banning et al., 2012), tropical and arable soils (Brackin et al., 2013) as well as different geomorphological units in a semistable sand-dune ecosystem (Yu and Steinberger, 2012). The MicroResp™ method was used also to assess the effects of different factors (drought, fertilizers, changes in plant cover) on catabolic abilities of soil microbial communities (Bérard et al., 2011; Marshall et al., 2011; Sradnick et al., 2013).

The objective of our study was to compare community level physiological profiles (CLPPs) of microbial communities from uppermost soil horizons under boreal forests differing in plant diversity. We have chosen Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), silver birch (*Betula pendula*) and mixed pine–birch–spruce forests to represent vegetation types naturally differing in plant species diversity in order to assess the influence of plant cover on the physiological profiles and functional diversity of soil microbial communities and to test the relationship between the plant diversity and functional diversity of soil microbial communities.

Materials and methods

Research area

The study was carried out in Oulanka National Park, Finland located 800 km north of Helsinki, close to the Arctic Circle (latitude 66°26′ N, longitude 29°27′ E, elevation 135–500 m a.s.l.). The climate in the study area is continental, the mean annual precipitation averages 554 mm and the mean annual temperature is −0.8 °C. Snow cover lies from the end of October to the end of April. Soils of the area developed from moraine material mainly of sand texture and contain occasionally high amounts of lime originating from bedrock material detached by continental glacier movement (Langer, 2007). The study area belongs to the coniferous forest belt (Helle, 1981) and represents natural forest types unaffected by forest management measures. Dominant tree species are *P. abies* and *P. sylvestris*, but *Betula pubescens* and *B. pendula* are also common in the Park.

Soil sampling

Samples of the O and A soil horizons were taken in August 2013 from 20 sites representing four forest types: pine forest dominated by Scots pine (*P. sylvestris*), spruce forest dominated by Norway spruce (*P. abies*), birch forest dominated by birch species (*B. pendula* and *B. pubescens*) and mixed forest with all above tree species occurring there. Each forest type was represented by five independent sites (area 2500 m^2 each, 50 m × 50 m). The distance between the closest sites representing the same forest type was ca. 2 km. The exact location of stands and textural data are presented in Table S1.

The samples of O and A horizons consisted of five subsamples (area 25 cm × 25 cm) taken using a spade in the corners and in the middle part of each sampling site and bulked to produce a single sample representing the site. Directly after collection the samples were sieved (10 mm mesh for the O horizon and 2 mm for the A horizon) to remove the green parts of plants, stones and roots, packed into plastic boxes and transported field moist to the laboratory.

Upon arrival to the laboratory the samples were divided into two parts. One part was air-dried and used for physical and chemical analyses, and the other one was stored field-moist at 4 °C and used for microbial and biochemical analyses.

Vegetation diversity

The individual species were identified on site. Botanical relevés according to Braun-Blanquet were documented for 100 m^2 (10 m × 10 m) on each sampling site. Data on cover of plants in relevés were transformed from the Braun-Blanquet scale into a 0–9 ordinal scale (Van der Maarel, 1979). Detailed botanical data are presented in supplementary Table S2.

Soil physical and chemical analyses

The pH of the samples was measured in H_2O and in 1 M KCl solution (soil:liquid ratio 1:10, w:v) with a digital pH-metre (CP-401, ELMETRON). The soil texture of the mineral soils was determined hydrometrically. Maximum water holding capacity (WHC) was determined gravimetrically according to Schlichting and Blume (1966). Contents of organic C (C_{org}) and total N (N_t) were determined by dry combustion with a CN analyzer (Vario Macro Cube, Elementar Analysensysteme GmbH). Dissolved organic carbon (DOC) was measured after soil extraction in deionised water (1:10, w:v) and analyzed with ion chromatography (Shimadzu TOC-VCPN). All chemical analyses were done in duplicates, averaged and expressed on a dry weight basis soil. All chemical and physical soil analyses (except the measurement of DOC) were done in the laboratories of the Institute of Environmental Sciences, Jagiellonian University, Kraków. The DOC measurement was done in the Laboratory of Forest Environment Chemistry, Forest Research Institute, Sękocin Stary, Poland.

Near-infrared (NIR) analysis

The NIR spectra of the samples were recorded at 2-nm intervals between 700 and 2500 nm using a Foss NIRSystems spectrometer (Silver Spring, USA). Before the spectral measurements, the samples were dried (60 °C) and ground to pass a 0.06-mm mesh. Each sample was scanned once, thoroughly mixed and scanned a second time. The final spectrum was the mean of both scans. Absorbance values (log(1/reflectance)) were used for data transformation and statistical analysis. The NIR measurements were done in the Laboratory of Soil Physics and Chemistry at the Department of Management and Protection of Environment, AGH University of Science and Technology, Kraków, Poland.

Microbial biomass

To measure microbial biomass (C_{mic}), samples (5 g d.w. for the O horizon and 50 g d.w. for the A horizon), were adjusted to 50% of their maximum WHC, amended with 10 mg glucose $(g\ soil)^{-1}$ and incubated at 22 °C in gas-tight jars for 4 h. The jars contained small beakers with 5 ml of 0.2 M NaOH to trap the evolved CO_2. After the jars were opened, 2 ml of 1 M $BaCl_2$ was added to the NaOH and the excess of sodium hydroxide was titrated with 0.1 M HCl in the presence of phenolphthalein as indicator. The C_{mic} was calculated from the substrate-induced respiration rate