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ORIGINAL PAPER

Functional diversity of soil microbial communities in boreal and temperate Scots pine forests

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Abstract Scots pine (*Pinus sylvestris* L.) is one of the most widespread conifer species in Europe, able to tolerate a wide variety of climatic conditions. The aim of the study was to compare the activity, functional diversity and community-level physiological profiles (CLPPs) of soil microorganisms in Scots pine forests of the boreal and temperate climatic zones. The soil samples were taken from the O and A soil horizons in northern Finland (boreal pine forest, BP) and Poland (dry and mesic temperate pine forest, TDP and TMP, respectively) and measured for water-holding capacity, pH, organic C, dissolved organic C (DOC) and the total contents of N, P, Ca, Mg, K, Na and Mn. The microbial activity (multiple substrate-induced respiration rate) and functional diversification (community-level physiological profiles, CLPPs) were assessed using the MicroResp™ system with 22 different C substrates. The BP soils were finer textured and contained more Ca, K, Mg, Mn and Na but less N and P than the soils under the temperate forests. The pH values did not differ between the studied forests. The studied pine forests did not differ in the measured microbial properties in the O horizon. However, in the A horizon, the microorganisms from the BP soil were less active and less functionally diverse than those from the temperate forest soils. The CLPPs of the BP soils differed from those of the temperate forest soils, wherein the largest difference was from the use of carboxylic acids and amino acids. The microorganisms from the BP soils used carboxylic acids more efficiently but were much less efficient in decomposing amino acids than those from the temperate forest soils. These differences were related to the contents of DOC, N and P which are influenced by climate and bedrock properties. Our results indicate that soil microbial properties in the O horizon depend mainly on the vegetation, whereas in deeper layers, they depend to a larger extent on bedrock properties and climatic conditions.

Keywords CLPP · MicroResp™ · Functional microbial diversity · Podzols · *Pinus sylvestris* L.

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Introduction

Soil microorganisms are essential drivers of nutrient turnover in terrestrial ecosystems, being involved in numerous key soil processes including organic matter degradation, mineralisation and humification (Bauhus and Khanna 1999; Wardle et al. 2004). The functional diversity of soil microbial communities is regulated by physico-chemical soil properties, climate, as well as the composition of plant cover (Grayston et al. 2004; Ladygina and Hedlund 2010; Sherman and Steinberger 2012). In forest ecosystems, the dominating tree species influence the metabolic abilities of soil microbial communities by the production of litter of a specific chemical quality (Kiikkilä et al. 2006), root exudation (Attiwill and Adams 1993) and through affecting the

chemical and physical soil properties (Bauhus et al. 1998; Menyailo et al. 2002).

The Scots pine (*Pinus sylvestris*) has been described as supporting the development of distinct microbial communities (Priha et al. 2001; Hackl et al. 2005; Zechmeister-Boltenstern et al. 2011; Kuramae et al. 2012). Hackl et al. (2005) and Zechmeister-Boltenstern et al. (2011) found higher abundance of fungal phospholipid fatty acids (PLFAs) in soils under pine forests than under forests with other dominant tree species (beech, oak, spruce, fir) and suggested that this was because fungi are more efficient than bacteria in the degradation of recalcitrant pine litter. Högberg and Högberg (2002) reported that ectomycorrhizal fungi constituted nearly one-third of microbial biomass in Scots pine forest soils in northern Sweden. The large share of ectomycorrhizal fungi in soil microbial communities under pine forests may lead to the development of microbial communities with specific functional abilities (Heinonsalo et al. 2001; Finlay 2008). Ectomycorrhizal fungi are known to exude low molecular mass organic acids (Ahonen-Jonnarth et al. 2000; van Breemen et al. 2000) and in this way may influence soil microbial communities and their metabolic preferences (Heinonsalo et al. 2001; Banning et al. 2012).

The Scots pine is one of the most widespread conifer species on Earth (Matías and Jump 2012). In Europe, pine stands cover 24 % of forested area (Leski et al. 2010), spreading from Fennoscandia in the boreal climate zone to central and southern Europe in the temperate climate zone (Boratyński 1991; Kelly and Conolly 2000). In consequence, the microbial properties of pine forest soils may be variable. It is known that the interactions between the plant communities and soil microbial communities in forest ecosystems are often driven by abiotic factors such as the physico-chemical properties of soil parent materials (Thoms et al. 2010; Gartzia-Bengoetxea et al. 2016). Climatic conditions (temperature and precipitation regimes) may also affect soil microbial communities (Evans and Wallenstein 2014) by selection of specific microbial groups better adapted to local climatic conditions.

The functional diversity and structure of soil microbial communities are of particular importance for the functioning of soils (Zak et al. 1994) since the soil organic matter transformation rate depends on the ability of microbial communities to metabolise different organic compounds (Garcia-Pausas and Paterson 2011). Therefore, information on the metabolic abilities of microbial communities under Scots pine forests of boreal and temperate zones is essential for understanding how these forest ecosystems function.

In this study, we applied the MicroResp™ method (Campbell et al. 2003) to compare the functional structure and functional diversity of soil microbial communities under Scots pine forests growing in the boreal and temperate climate zones.

Materials and methods

Study sites

The study sites were located in the boreal climate zone in Finland, the Scandinavian Peninsula and in the temperate climate zone in Poland, an East-Central European country (Fig. 1). The sampling plots were chosen to be representative of the prevailing climatic conditions (boreal and temperate) and dominating tree species (Scots pine) and comprised only natural forest stands developed without, or with only minimal, forest management.

The boreal pine forest stands (BP) ($N = 5$) included *Vaccinium* type (VT) with understory dominated by *Vaccinium vitis-idaea* and *Empetrum nigrum* representative of sub-dry forest types (Tonteri et al. 1990). They were located in the region of Oulanka National Park, close to the Arctic Circle, with a mean annual precipitation of 550 mm

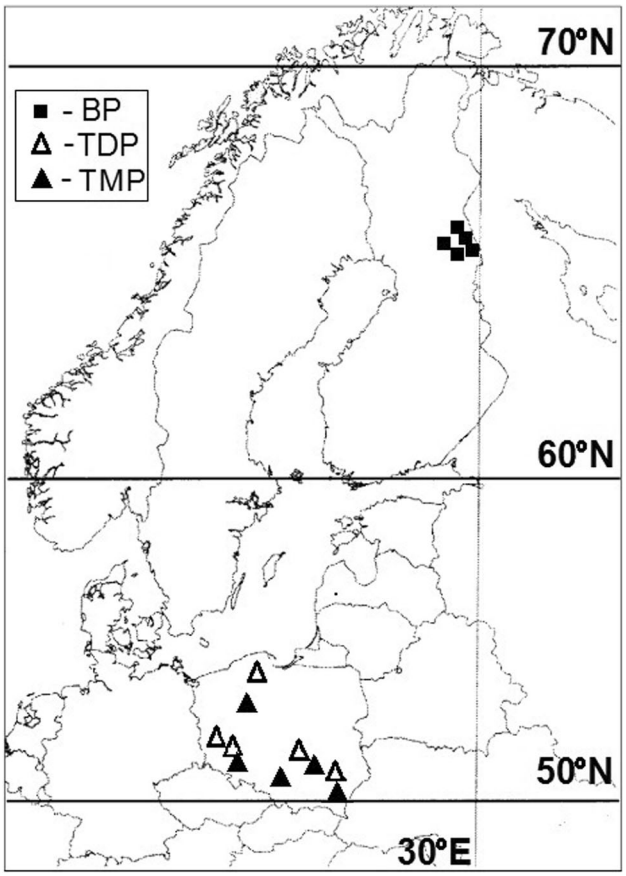

Fig. 1 Distribution of sampling sites for the boreal (BP), dry temperate (TDP) and mesic temperate pine (TMP) forest soils

and a mean annual temperature of −0.8 °C. The sampling area extended over ca. 560 km^2, and the distance between the nearest sites representing BP forests was ca. 7 km. At all sampling sites in the boreal forests, the soils were classified as podzols (FAO classification) developed from sandy materials. The depths of the O and A horizons in the BP forest soils averaged 7.5 and 4.5 cm, respectively.

The temperate pine forest stands were located in different sites in Poland (Fig. 1), with the mean annual temperature ranging from 6.5 to 8.5 °C and an average annual precipitation of ca. 550–750 mm. The temperate pine forests included dry pine forest type (TDP) ($N = 5$)–associations of *Cladonio-Pinetum* and *Vaccinio-Pinetum*, with typical poor forest floor with *Cladonia* lichens, and mesic pine forest type (TMP) (N = 5)–associations of *Peucedano-Pinetum* and *Leucobryo-Pinetum* (Matuszkiewicz 2006). Within both temperate pine forest types, five independent sites were sampled. The distance between the nearest sites representing the same forest type was ca. 50 km (Fig. 1). At all sampling sites in the temperate forests, the soils were classified as podzols (FAO classification) developed from sandy materials. In the TDP forest soils, the depth of the O horizon averaged 4.0 cm and of the A horizon 10.5 cm. In the TMP forest soils, the mean depth of the O horizon was 5.7 cm and of the A horizon 13.0 cm. There were 15 research sites altogether.

Soil sampling

The soil samples were collected during two sampling campaigns. The temperate pine forest soils were sampled in the first half of June 2013, and the boreal pine forest soils in the second half of July 2013. The duration of both sampling campaigns was one week. In Poland, the samples were packed in plastic boxes with air-permeable cover, placed in a portable cooling chamber and transported directly by car to our laboratory. In Finland, the soil samples were stored temporarily in the cooling chamber at the Oulanka Research Station.

One sample was collected using a steel core sampler on each site in the centre of a 100-m^2 plot used for botanical assessment, and four samples were collected from four corners around and bulked to obtain one mixed soil sample per plot, separately for the O and A soil horizons on each research site. These resulted in 15 soil samples of the O horizon and, correspondingly, 15 soil samples of the A horizon (totally $N = 30$).

Directly after collection, the samples were sieved (the O horizon through a 10-mm sieve and the A horizon through a 2-mm sieve) to remove the green parts of the plants, stones and roots, packed into plastic boxes with air-permeable covers and transported field-moist to the laboratory, preventing heating by the use of cool bags during the day and storing in a fridge during the night (at a temperature ca. 4 °C). Upon arrival at the laboratory, the samples were divided into two parts. One part was air-dried and used for physico-chemical analyses; the other part was stored at field-moist conditions at 4 °C for microbial analyses. The microbiological analyses begun around one month after collection of the sample set, so the storage time was the same for all samples. We treated all our samples in the same way in order not to introduce additional factors that could lead to different results in the studied soil groups.

Soil physical and chemical analyses

The soil dry weight (DW) was determined after drying the soil samples at 105 °C for 24 h. Water-holding capacity (WHC) was measured gravimetrically (Schlichting and Blume 1966). The soil pH was measured potentiometrically in water and in 1 M KCl solution (1:10 w/v). The C and N contents were analysed using a CHNS analyser (Vario EL III, Elementar Analysensysteme GmbH). The total element (Ca, K, Mg, Mn, Na, and P) concentrations in each soil sample were determined after wet digestion of 0.5 g of DW in 10 ml of suprapure-concentrated HNO_3 and $HClO_4$ (7:1 v/v) (Sigma-Aldrich). The concentrations of the metals in the digests were measured using atomic absorption spectrometry (AAS) with a flame or graphite furnace nebuliser (PerkinElmer), and the P concentration was measured on a flow injection analyser (FIA compact, MLE). The accuracy of the mineralisation process was assessed using blank samples and samples of standard certified material (CRM025-050, Sandy Loam 8, RT Corp.). The concentration of dissolved organic carbon (DOC) was measured in water extracts obtained from 3 g of soil dry mass equivalent shaken for 1 h at 10:1 water-to-soil ratio at 200 rpm (TOC-V_{CPN}, Shimadzu). The texture of mineral soil fraction (A horizon) was assessed hydrometrically (Casagrande 1934). Each analysis was performed in three replicates; the data were averaged and expressed based on the dry weight of the soil.

MicroResp™ measurements

The physiological abilities of pine forest soil microbial communities were determined using the MicroResp™ method (Campbell et al. 2003). The soils were adjusted to 40 % of their maximum WHC and loaded into 1.2 ml deep-well microtitre plates (1.2 ml, Nunc, Thermo Electron LED, Langenselbold, Germany). The soil mass per well was ca. 0.35 g DW for the A horizon samples and ca. 0.08 g DW for the O horizon. Subsequently, the samples were stored for 5 days at 22 °C before applying aqueous solutions of the different C sources and sealing the wells with a CO_2 trap.

The physiological profiles were determined by applying distilled water, 9 neutral sugars (D-glucose, D-fructose, D-galactose, D-maltose, D-xylose, D-arabinose, D-mannose, D-ribose and D-cellobiose), 5 amino acids (γ-aminobutyric acid, L-alanine, L-arginine, L-lysine and L-proline), 2 amines (D-glucosamine and N-acetyl-glucosamine), and 4 carboxylic acids (D-malic acid, L-ascorbic acid, α-ketoglutaric acid and oxalic acid), one aromatic carboxylic acid (protocatechuic acid) and one polymer (α-cyclodextrin). The C compounds were chosen to represent plant root exudates and microbial products (McIntosh et al. 2013; Sradnick et al. 2013) with a large potential to discriminate different soil microbial communities (Banning et al. 2012). The substrates were added at a concentration of 8 mg g^{-1} DW soil (Sradnick et al. 2013). Because of the low solubility at higher concentrations, only 0.8 mg g^{-1} DW soil of protocatechuic acid (3-4-dihydroxybenzoic acid) was applied. Each substrate was placed in 8 wells, giving 8 replicates for a sample. Application of the aqueous solutions increased soil moisture to ca. 60 % of their maximum WHC.

The colorimetric detector plates were prepared as described by Campbell et al. (2003) and contained 12.5 μg g^{-1} cresol red, 150 mM KCl and 2.5 mM $NaHCO_3$ set in 1 % Noble agar (150 μl per well). The samples were incubated for 4 h at 25 °C. Absorbance of the detector plates was determined using a microplate reader at 572 nm (μQuant, Biotek, Winooski, Vermont, USA) immediately before sealing (T0) and after 4-h incubation (T1). A calibration curve of absorbance change (T1–T0) versus headspace C–CO_2 concentration (0.20 μg ml^{-1}–10.50 μg ml^{-1}) was determined using gas mixtures with known C–CO_2 concentrations and fitted to an exponential decay model ($r^2 = 0.97$). The use of particular C substrates by soil microbes was calculated by subtracting the basal respiration rates (water blanks) from the substrate-induced respiration values (μg C–CO_2 g^{-1} h^{-1}) for particular substrates. The multiple substrate-induced respiration (MSIR) rate expressed in μg C–CO_2 g^{-1} h^{-1} was used as a measure of total microbial activity in the tested soils. In order to compare metabolic preferences of the soil microbial communities, the CLPPs were based on the relative use of substrates. The relative use of a substrate was calculated by dividing the SIR value for a particular substrate by the total (summed) substrate response (MSIR) of each sample.

The microbial functional diversity index, derived from the Shannon–Wiener biodiversity index H'_{mic}, which is based on the structure of substrate use:

$$H'_{mic} = -\sum_{i=1}^{s} p_s \log_{10} p_s$$

was derived from the number of substrates s and the utilisation of an individual substrate p_s (Derry et al. 1999). Community-level physiological profiles (CLPPs) were expressed as the substrate-induced respiration rate values (μg C–CO_2 g^{-1} h^{-1}) after subtracting the basal respiration values (water blanks), standardised to the sum of 1 within each soil sample.

Statistical analyses

Differences in the chemical, physical and microbial properties between the three forest types and two soil organic horizons were compared with one-way ANOVA with Tukey's test ($p < 0.05$), separately for the O and A horizons. Prior to the analysis, the data were checked for distribution normality and transformed if needed.

One-way analysis of similarities (ANOSIM) was used to test for significant differences in the CLPPs under the studied pine forest stands, separately for the O and A soil horizons (Clarke and Green 1988). ANOSIM is a non-parametric permutation procedure that compares between-group and within-group dissimilarities. This procedure calculates R statistic, wherein $R = 0$ indicates a completely random grouping and $R = 1$ only if all replicates within the groups are more similar to each other than any replicates across the groups. Global R-value was used to express overall dissimilarity between the stands. The significant global R-values indicated that the R-value differed significantly from 0, suggesting that the compared sites were significantly dissimilar. Dissimilarities between the stands based on Bray–Curtis distances were tested in pairwise comparisons, and their significance was assessed according to the sequential Bonferroni correction. Similarity percentage (SIMPER) procedure was applied in order to identify which plant species or C substrates made the largest contribution to the average dissimilarity between the samples (Clarke 1993).

Canonical correspondence analysis (CCA) was used to link the microbial CLPPs to soil properties and to compare CLPPs under different forest types, separately for the O and A soil horizons (ter Braak 1987). In this analysis, we used the DOC content as a variable representing a readily available energy source for microbes; concentrations of P and N, as well as C-to-N and C-to-P ratios, as variables representing the availability of essential nutrients; pH in KCl as a variable representing soil acidity; and WHC as a variable approximating the ability of the soil to retain water.

The ANOVA analysis was performed using Statgraphics Centurion XVI (StatPoint Technologies Inc., Warrenton VA, USA) and the multivariate analyses with PAST

software (Natural History Museum, University of Oslo, Norway).

Results

Soil physical and chemical properties

The mineral soils under the BP forests had the lowest share of sand fraction (81.0 %) and the highest share of silt fraction (14.8 %). The clay content was higher in the boreal soils (4.2 %) than in the temperate forest soils (1.6–2.6 %), but the difference was not statistically significant ($p = 0.11$). The highest sand content and the lowest silt content were under the TDP (93.3 and 5.2 %, respectively), whereas the TMP soils exhibited intermediate values (Table 1).

The soil A horizons of the BP forests were characterised by lower N and P contents than the temperate forests (however, the difference was statistically significant only between BP and TMP) (Table 2). In the O horizon, the N content was lower in the BP forests (7.5 mg g^{-1} DW) than in the temperate forests (8.9–9.9 mg g^{-1} DW) but the difference was not statistically significant ($p = 0.0694$). The P content was similar in all the studied forests. In both studied horizons, the BP soils contained more Ca, K, Mg, Mn and Na than the soils under the temperate forests (Table 2). There were no significant differences in soil pH between the studied forest soils. All the soils were acidic (pH in water ranged from 3.6 to 4.4; pH in KCl ranged from 2.7 to 3.8), wherein lower pH values were measured in the O horizon than in the A horizon (Table 2). The DOC contents in the O horizon did not differ between the studied forest types, but in the A horizon, the DOC content was significantly lower in the BP soils than in the temperate forest soils (Table 2).

Microbial activity, functional diversity and community-level physiological profiles

The MSIR and the H'_{mic} values in the O horizon were similar for all the studied forests (Fig. 2). However, in the A horizon, BP forests were characterised by the lowest MSIR and H'_{mic} values and differed significantly ($p = 0.0129$) from the TMP forests, where these values were the highest. The values for TDP forest fell between these two forests (Fig. 2).

For the O soil horizon, the calculated CCA axes on CLPP pattern were not significant, indicating that the considered soil properties did not affect the physiological abilities of the soil microbial communities (data not shown). The ANOSIM confirmed the similarity of CLPPs under all the studied pine forests in the O soil horizon (Table 3).

For the A horizon, the first two CCA axes explained, respectively, 64.0 % ($p = 0.0020$) and 21.3 % ($p = 0.0339$) of the variance in CLPPs and the environmental data (Fig. 3). The first CCA axis was strongly negatively related to DOC content (−0.92), and the concentrations of N (−0.75) and P (−0.70), whereas the second axis was strongly negatively related to pH (−0.52), C-to-P (−0.46) and C-to-N (−0.45) ratio.

The BP soils were clearly separated from the temperate pine forests along the first CCA axis (Fig. 3). The two temperate pine forests were also divided along the first axis; however, the separation was less distinct (Fig. 3). The analysis of the CCA triplot indicated a strong positive relationship between the DOC and N content in the soil and the use of L-arginine, L-lysine and L-proline. A negative effect of high DOC and N was observed for the use of D-malic acid, oxalic acid, α-ketoglutaric acid and L-ascorbic acid. The use of D-glucose was positively, and the use of D-glucosamine hydrochloride negatively, related to soil pH (Fig. 3).

The ANOSIM analysis indicated the differences in CLPPs between the BP soil microorganisms and both temperate pine forests in the A soil horizon to be statistically significant (Table 3). The SIMPER analysis revealed that the largest contribution to the average dissimilarity was from the utilisation of four carboxylic acids (D-malic, oxalic, L-ascorbic and α-ketoglutaric acid) and two amino acids (L-Arginine and L-Lysine) (Table 4). Boreal pine forest soil microorganisms used relatively more carboxylic acids but were less efficient in using other C substrates, in particular amino acids. Comparison of the C substrate use expressed in μg $C–CO_2$ g^{-1} h^{-1} (Table 4) indicated that only the carboxylic acids were decomposed at the similar rate in boreal and temperate soils. Decomposition of all the other C substrates was distinctly lower in the boreal forest soils.

Table 1 Mean values ($n = 5$) for texture of the studied boreal (BP), dry temperate (TDP) and mesic temperate pine (TMP) forest soils (standard deviations in parentheses)

Forest	Sand (2.0–0.05 mm) (%)	Silt (0.05–0.002 mm) (%)	Clay (<0.002 mm) (%)
BP	81.0 **a** (6.4)	14.8 **b** (7.5)	4.2 (1.1)
TDP	93.3 **b** (1.9)	5.2 **a** (2.2)	1.6 (2.3)
TMP	87.5 **ab** (3.5)	9.8 **ab** (4.0)	2.6 (1.8)

Significant differences (one-way ANOVA with Tukey's HSD test, $p = 0.05$) between the studied forests are indicated by different letters

Table 2 Mean values ($n = 5$) of soil physical and chemical properties in the soil O and A horizons of boreal (BP), dry temperate (TDP) and mesic temperate pine (TMP) forests (standard deviation in parentheses)

Forest %	WHC	pH_{H2O}	pH_{KCl}	DOC mg g^{-1}	C	N	P	C/N	C/P	Ca mg kg^{-1}	K	Mg	Mn	Na
O horizon														
BP	516 (123)	3.6 (0.1)	2.7 (0.1)	1.16 (0.36)	345.1 (42.6)	7.5 (1.4)	0.58 (0.10)	46.7 **b** (5.9)	603 (58)	2330 **b** (503)	790 **b** (190)	881 **b** (471)	179 **b** (91)	129 **b** (32)
TDP	420 (70)	3.8 (0.3)	2.9 (0.2)	0.77 (0.08)	322.1 (48.2)	8.9 (1.5)	0.51 (0.07)	36.6 **ab** (4.3)	640 (110)	577 **a** (366)	548 **a** (61)	304 **a** (97)	77 **a** (32)	54 **a** (19)
TMP	398 (91)	4.2 (0.7)	3.4 (0.7)	0.97 (0.29)	302.2 (61.2)	9.9 (1.5)	0.53 (0.10)	30.5 **a** (3.4)	577 (78)	1783 **a** (1644)	691 **a** (121)	381 **a** (116)	196 **b** (98)	46 **a** (14)
A horizon														
BP	54.5 (9.4)	4.3 (0.2)	3.5 (0.2)	0.09 **a** (0.02)	12.5 (10.6)	0.5 **a** (0.1)	0.05 **a** (0.02)	23.5 **b** (15.5)	216 (96)	1359 **b** (558)	586 **b** (213)	1230 **b** (900)	81 **b** (43)	186 **b** (72)
TDP	45.1 (8.0)	4.3 (0.2)	3.7 (0.2)	0.53 **b** (0.04)	19.1 (6.2)	0.9 **ab** (0.2)	0.07 **ab** (0.03)	21.7 **ab** (2.5)	318 (123)	202 **a** (146)	244 **a** (88)	141 **a** (109)	24 **a** (14)	16 **a** (4)
TMP	62.5 (12.8)	4.4 (0.8)	3.8 (0.9)	0.58 **b** (0.11)	36.4 (12.8)	1.6 **b** (0.7)	0.11 **b** (0.04)	22.7 **a** (3.0)	357 (126)	649 **a** (894)	334 **a** (109)	158 **a** (75)	47 **b** (32)	22 **a** (5)

Significant differences (one-way ANOVA with Tukey's HSD test, $p = 0.05$) between the studied forests within particular soil horizons are indicated by different letters

Discussion

Physical and chemical soil characteristics

The boreal pine forests grew on finer textured soils classified as loamy sands, whereas the temperate pine forests grew on sands. In particular, the dry pine forest soils in the temperate zone were characterised by a low content of fine particles (silt and clay). The studied boreal soils contained a higher level of nutrients (Ca, K, Mg, Mn and Na) than the temperate forest soils, resulting apparently from the bedrock properties. The soils of Oulanka developed from glaciofluvial deposits that contain volcanic rocks and carbonates (Koutaniemi 1979) and therefore have appreciable amounts of major and trace elements (Koutaniemi et al. 1988). In Poland, the natural pine forests occur mainly on poor postglacial soils, since on more fertile sites, the Scots pine has been outcompeted by broadleaved species.

All the studied soils were acidic, wherein lower pH values were measured in the O horizon than in the underlying mineral soil. Coniferous tree species are known to produce slow decomposing litter, rich in acid compounds, and to bring about soil acidification (Hansson et al. 2011; Mueller et al. 2012). Low soil pH may reduce microbial activity, leading to large accumulation of organic matter in the O horizon typical for mor-type humus (Klaminder et al. 2008; Mueller et al. 2012) and is one of the most important factors leading to development of podzol soils (Koutaniemi et al. 1988). In line with our results, Degórski (2007) reported low pH values in A and deeper soil horizons under pine forests in northern and central Europe, and concluded that soil pH was not related to geographic location. The N contents were slightly lower in the boreal forest soils than in the temperate forest soils. This was probably due to lower N_2 fixation and atmospheric deposition in the boreal zone compared to the temperate zone (Cleveland et al. 1999; Korhonen et al. 2013).

The DOC content in the O horizon was similar in all the studied forests. However, in the A horizon of boreal forest soils, the DOC content was lower than in the temperate forest soils. It is well known that organic matter accumulated in the O horizon is a major source of DOC, and that the DOC content decreases the soil profile downwards (Kalbitz et al. 2000). The concentration of DOC in soils depends largely on the quality of accumulated organic matter, which in turn is determined by the dominant vegetation (Kalbitz et al. 2000). Our study included only pine forests, and this explains the similar contents of DOC in the O horizons of the studied soils. In deeper soil horizons, the concentrations of DOC decrease mainly due to adsorption to mineral surfaces (Jardine et al. 1989; Kalbitz

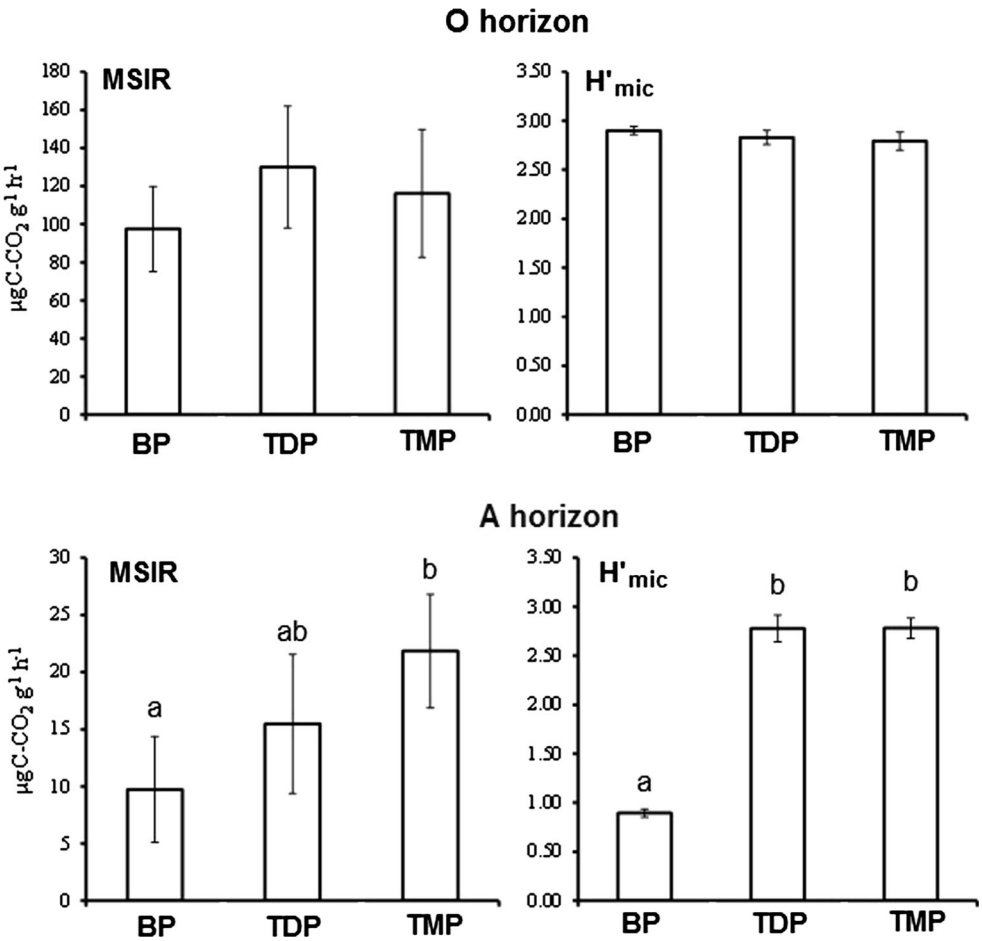

Fig. 2 Mean values ($n = 5$) of multiple substrate-induced respiration (MSIR) and Shannon–Wiener indices based on MicroResp™ data (H'_{mic}) in the O and A horizons of the boreal (BP), dry temperate (TDP) and mesic temperate pine (TMP) forest soils. *Whiskers* indicate standard deviations

Table 3 ANOSIM for CLPPs for the O and A soil horizons

O horizon		
Global $R = 0.0062$ ($p = 0.4335$)		
Forest	TDP	TMP
BP	0.024 (0.3881)	0.148 (0.1405)
TDP		−0.176 (0.9218)
A horizon		
Global $R = 0.4653$ ($p = 0.0004$)		
Forest	TDP	TMP
BP	**0.700 (0.008)**	**0.796 (0.0071)**
TDP		−0.014 (0.4563)

Presented are the R-values and their significance (p values according to sequential Bonferroni correction) in parentheses. For each soil horizon, global R and its significance level are also given. The significantly different pairs are in bold

et al. 2000). Since clay minerals are important adsorbents for DOC in soils (Jardine et al. 1989; Kalbitz et al. 2000), we presume that lower DOC content in the studied boreal forest soils was due to their higher clay content. Lower DOC in the boreal soils might have resulted from climatic conditions. Kalbitz et al. (2000) reported that higher temperatures, freeze–thaw cycles and wet–dry cycles increase DOC content in soil.

Microbial properties of the studied soils

The measured microbial properties in the soil O horizons did not differ between the studied forests. In all the forests, the microbial activity (MSIR) and functional diversity (H'_{mic}) in the O soil horizons were at nearly the same level and the CLPPs were similar. The vegetation influences soil microorganisms by affecting the chemical and physical properties of the soil. Among these properties, soil pH and the content of readily available C have been described as a major control on the taxonomic and functional structure of soil microbial communities (Rousk et al. 2010; Kuramae et al. 2012; Tripahti et al. 2012; Chodak et al. 2013). In our study, the O soil horizons were characterised by similar pH and DOC content. In consequence, there was no factor to bring about development of functionally different soil microbial communities. The differences in other chemical

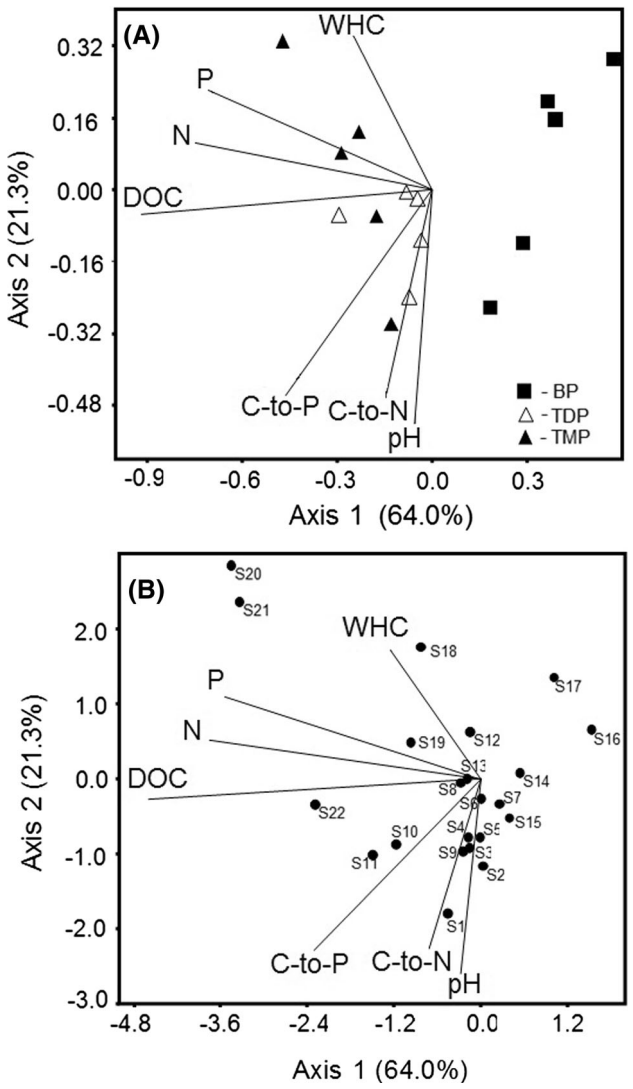

Fig. 3 Canonical correspondence analysis (CCA) ordination plot (**a**) of the functional microbial community structure in the A soil horizons of the boreal (BP), dry temperate (TDP) and mesic temperate pine (TMP) forest soils, and the plot of the use of different C substrates in relation to chemical properties of the A horizon (**b**). Soil properties include: soil pH in KCl (pH), contents of organic dissolved organic C (DOC), total N and P, the C-to-N and C-to-P ratios and the maximum water-holding capacity (WHC). The C substrates are: S1: D-glucose, S2: D-fructose, S3: D-galactose, S4: D-maltose, S5: D-xylose, S6: D-arabinose, S7: D-mannose, S8: D-ribose, S9: D-cellobiose, S10: α-cyclodextrin, S11: γ-aminobutyric acid, S12: 3-4-dihydroxybenzoic acid, S13: N-acetyl D-glucosamine, S14: α-ketoglutaric acid, S15: L-ascorbic acid, S16: D-malic acid, S17: Oxalic acid, S18: D-glucosamine hydrochloride, S19: L-alanine, S20: L-arginine, S21: L-lysine and S22: L-proline

soil properties (e.g. C-to-N ratio, the contents of Ca, Mg and K) between the studied forest soils apparently did not lead to the development of functionally different microbial communities.

For the A horizon, the measured microbial properties differed between the forest stands, with the boreal forest soil showing the lowest values of MSIR and H'_{mic} and distinctly different CLPPs than the temperate forests. The SIR is a method of biomass determination (Anderson and Domsch 1978); therefore, the MSIR may be regarded as a proxy of soil microbial biomass (Creamer et al. 2016). Lower MSIR values, indicative of lower microbial biomass in boreal pine forest soils, may be explained by lower contents of C, DOC, N and P in these soils. The microbial biomass in soils depends strongly on the energy source (C, DOC) and the content of essential nutrients such as N and P (Gallardo and Schlesinger 1994; Alden et al. 2001; Allen and Schlesinger 2004; Demoling et al. 2007). It is considered that up to a certain threshold, an increase in microbial biomass also induces an increase in functional diversity (Lynch et al. 2004). Accordingly, larger microbial communities in the temperate forest soils were characterised by higher functional diversity than those from the boreal forest soils.

The analysis of CLPPs indicated that microbial communities in the soil A horizons of boreal forests used carboxylic acids effectively but were less efficient in respiring other C substrates, in particular amino acids. In the temperate forest soils, the use of added C substrates was more uniform. Although the carboxylic acids were degraded very rapidly in the temperate forest soils, the metabolisation of amines and sugars was only slightly less efficient. Furthermore, the soil microbial communities in the temperate forests decomposed amino acids more effectively than those in the boreal forest soils. The results of CCA analysis underlined the importance of readily available C and nutrient contents for the functional structure of the soil microbial communities, as the CLPPs to the largest extent depended on the contents of DOC, N and P. The DOC represents a mobile and readily available fraction of soil organic matter (Zsolnay 1996), although the proportion of the labile part of DOC is highly variable (Zsolnay and Steindl 1991).

The metabolic abilities of soil microbial communities are likely to reflect the composition and bioavailability of soil organic matter (Orwin et al. 2006; Banning et al. 2012). Thus, high use of carboxylic acids suggests that although these compounds correspond to a minor fraction of the DOC (Van Hees et al. 2002), they constitute an important energy source for soil microbes. Carboxylic acids are involved in several soil processes and are intensively exuded by plant roots in low pH soils and under P deficiency (Jones 1999), such as in our study. Significantly higher relative use of carboxylic acids in the soil A horizons of boreal forests suggests that in these soils, carboxylic acids may constitute a larger fraction of readily available C. This may result from higher exudation of carboxylic acids by plant roots and ectomycorrhizal fungi in the boreal forest soils. These soils contained less P than

Table 4 Results of SIMPER analysis for CLPPs in the soil A horizons under boreal (BP), dry temperate (TDP) and mesic temperate pine (TMP) forests

Substrate	Dissimilarity measure		Relative use of substrate (%)			SIR (μg C-CO_2 g^{-1} h^{-1})		
	Average dissimilarity	Contribution (%)	BP	TDP	TMP	BP	TDP	TMP
D-Malic acid	3.6	16.2	17.8	8.3	7.5	1.55 (0.61)	1.21 (0.27)	1.64 (0.47)
Oxalic acid	2.4	11.1	13.0	7.6	7.4	1.16 (0.65)	1.12 (0.35)	1.61 (0.42)
L-Ascorbic acid	1.2	5.6	9.4	8.3	6.9	0.97 (0.55)	1.22 (0.32)	1.49 (0.37)
α-Ketoglutaric acid	1.2	5.3	8.1	5.7	5.5	0.88 (0.55)	0.89 (0.36)	1.18 (0.28)
L-Arginine	1.1	5.1	0.0	1.4	3.2	0.00 (0.00)	0.26 (0.33)	0.65 (0.26)
L-Lysine	1.1	5.0	0.0	1.3	3.2	0.00 (0.00)	0.24 (0.27)	0.66 (0.25)
D-Glucose	1.1	4.8	3.8	5.2	5.2	0.39 (0.35)	0.82 (0.39)	1.21 (0.61)
L-Alanine	1.0	4.5	2.5	4.8	4.5	0.26 (0.20)	0.71 (0.19)	0.96 (0.28)
L-Proline	0.9	4.2	0.0	2.9	2.6	0.01 (0.02)	0.44 (0.18)	0.55 (0.09)
D-Glucosamine hydrochloride	0.9	4.1	3.5	3.9	5.2	0.34 (0.19)	0.60 (0.22)	1.05 (0.43)
D-Fructose	0.9	4.0	5.0	5.3	4.6	0.49 (0.33)	0.82 (0.39)	1.03 (0.40)
γ-Aminobutyric acid	0.9	3.9	0.6	2.9	2.9	0.07 (0.05)	0.45 (0.18)	0.64 (0.22)
D-Cellobiose	0.8	3.5	3.5	4.4	4.6	0.34 (0.16)	0.70 (0.35)	1.02 (0.45)
α-Cyclodextrin	0.7	3.2	1.0	2.8	3.0	0.11 (0.06)	0.44 (0.18)	0.66 (0.22)
N-acetyl D-glucosamine	0.7	3.0	4.1	5.3	4.1	0.42 (0.24)	0.85 (0.43)	0.87 (0.16)
Protocatechuic acid	0.7	3.0	4.2	4.4	4.3	0.45 (0.32)	0.68 (0.28)	0.90 (0.10)
D-Maltose	0.6	2.6	4.0	4.2	4.9	0.41 (0.24)	0.64 (0.24)	1.10 (0.44)
D-Mannose	0.5	2.4	5.0	4.7	4.6	0.48 (0.21)	0.74 (0.33)	1.03 (0.38)
D-Galactose	0.5	2.3	3.7	4.1	4.2	0.38 (0.25)	0.63 (0.28)	0.94 (0.37)
D-Xylose	0.5	2.2	4.1	4.6	4.3	0.40 (0.19)	0.73 (0.37)	0.98 (0.39)
D-Arabinose	0.5	2.1	3.8	4.2	3.9	0.36 (0.15)	0.70 (0.43)	0.90 (0.42)
D-Ribose	0.4	1.9	2.8	3.7	3.4	0.27 (0.11)	0.59 (0.29)	0.78 (0.32)

The term 'Contribution' represents the contribution of a substrate to the average dissimilarity in CLPP between the forests. 'Contribution %' is the percentage share of a substrate to the average dissimilarity. For SIMPER analysis, the use of substrates on MicroResp™ plates is expressed as relative %. Substrate-induced respiration (SIR) values corrected for basal respiration for particular substrates are also given (mean value and standard deviation in parentheses, $n = 5$)

the temperate forest soils, and it is known that low availability of soil P may stimulates the release of carboxylic acids both by plants and ectomycorrhizal fungi. Malic acid is one of the primary organic components released by plant roots at P deficiency (Jones and Darah 1994; Jones 1998), whereas for ectomycorrhizal fungi, the release of the oxalic acid has been suggested as an important mechanism of P solubilisation (Ahonen-Jonnarth et al. 2000). These two acids were preferably metabolised by the boreal forest soil microbial communities.

The lower decomposition of amino acids in the boreal forest soils apparently resulted from their lower N content. Both carboxylic and amino acids represent rapidly decomposable organic compounds (Jones 1998, 1999; van Hees et al. 2002). However, amino acids are mostly used for microbial biomass build-up, whereas carboxylic acids are mostly used for respiration (Jones 1999). We presume that in N-poor boreal forest soils, a larger proportion of amino acids was assimilated for microbial biomass build-up and only a smaller proportion for respiration. In the temperate forest soils characterised by higher N content and narrower C-to-N ratios, a larger part of the added amino acids was used for respiration and a smaller part was assimilated for biomass production.

The MicroResp™ method has been developed to enable physiological profiling of whole soil microbial communities without the need for their extraction and culture (Campbell et al. 2003). However, one should bear in mind that the MicroResp™ method is a short-term assay and its results may refer not to the whole soil microbial community, represented by many different groups of soil microorganisms occurring in varying proportions, i.e. plant-associated mycorrhizal fungi, litter-decomposing fungi (asco- and basidiomycetes), wood-decomposing fungi, 'free-living' bacteria, root- and hyphal-associated bacteria and different kinds of pathogens etc., but to microorganisms capable of a rapid response to added C substrates. Despite this flaw of the MicroResp™ test, the

application of this method did provide relevant information on the metabolic preferences of soil microbial communities in boreal and temperate Scots pine forest soils.

Conclusions

In the O horizons, the activity and the functional diversity and structure of microbial communities were similar in all the studied pine forests suggesting that, in this horizon, the dominating tree species (pine) is the most important control on microbial properties. However, in the A horizon of boreal forest soils, the microbial communities were less active, less functionally diverse and exhibited different functional profiles than those under the temperate forests. The functional differences were related to the contents of DOC, N and P which are affected by climate, geographic location and bedrock properties. Our results suggest that soil microbial properties in the deeper soil layers depend to a larger extent on climatic conditions and bedrock properties.

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