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Regional environmental conditions shape microbial community structure stronger than local forest management intensity

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ABSTRACT

Microorganisms in forest soils provide essential ecosystem services, such as decomposition of organic matter and nutrient mineralization. However, microbial community structure and function can be affected by environmental conditions, such as regional climate and soil properties and, moreover, by human activity through forest management. We examined the biomass and composition of microbial assemblages in 150 forest stands in the organic layer (Oi, Oe, Oa) and upper mineral soil (0–10 cm) in three regions across Germany (Schwäbische Alb, Hainich-Dün, Schorfheide-Chorin) by phospholipid fatty acid (PLFA) analysis. Different explanatory environmental variables (total C, N, S, P, organic C, inorganic C, pH, water content) were identified. The intensity of land use was characterized with the Forest Management Intensity Index (ForMI).

The total amount of PLFAs, as measure for microbial biomass, was different among the three regions both in the organic layer and mineral soil. In the organic layer, total PLFAs decreased from Schwäbische Alb over Hainich-Dün to Schorfheide-Chorin, with the latter comprising a fourfold and twofold lower amount in fungal and bacterial PLFAs, respectively. In contrast, in the mineral soil the forests in the Hainich-Dün showed the highest microbial biomass. Discriminant function analysis of PLFA pattern indicated that Gram-positive bacteria and fungi accounted mainly for the regional differences in the organic layer, whereas in the mineral soil additionally Gram-negative and actinobacteria were important. Redundancy analysis showed that PLFA profiles were predominantly affected by sampling site and environmental variables, with the water content in the organic layer and the soil texture in the mineral soil explaining most of the variability in microbial communities between the three regions. Additionally, forest stands were classified into four management groups (conifer; deciduous with low, medium, and high intensity) based on the ForMI. In the mineral soil, forest management accounted for a small proportion of the observed regional differences. Within regions, fungal biomass in the organic layer decreased with management intensity at the Schwäbische Alb and increased in the mineral soils of Hainich-Dün region. Microbial community structure discriminated coniferous and deciduous forests in all three regions, and moreover showed a separation based on forest management intensity in the Schorfheide-Chorin. In conclusion, microbial biomass and community composition in forest organic layer and mineral soil were more influenced by regional conditions, including environmental properties such as moisture, soil texture, C/N ratio and pH, than by forest management intensity. However, within given environments, microbial assemblages can be influenced by forest management, in particular through changes in the tree species composition.

1. Introduction

Microbial communities play a key role in soil ecosystems and are essential for a large number of ecosystem services, such as decomposition and mineralization processes, with important impact on plant diversity and productivity (van der Heijden et al., 2008; Comerford et al., 2013). In forest soils fungi are major drivers for the degradation of organic matter due to their ability to catalyze the turnover of complex organic resources such as cellulose, hemicellulose and lignin (Ruess and Ferris, 2004; Hättenschwiler, Tiunov and Scheu, 2005; Gessner et al., 2010). Bacteria generally utilize such polymeric compounds after the previous decomposition by fungi (Romani et al., 2006), however can facilitate fungal degraders by providing electrons or essential micronutrients (Frey-Klett et al., 2011).

The composition and activity of soil microbial communities are influenced by a variety of environmental properties. Their abundance is

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tightly coupled with the availability of nutrients, whereas community structure is predominantly affected by soil temperature, pH and moisture (e.g. Lauber et al., 2008; Rasche et al., 2011; Brockett et al., 2012). In forest soils, tree species type and diversity affect microbial community structure due to differences in litter quality and quantity (Couteaux et al., 1995; Jacob et al., 2009), root morphology and exudation as well as associated mycorrhiza symbionts (Hölscher et al., 2002; Lang et al., 2011; Cong et al., 2014). Aboveground silvicultural management therefore can distinctly alter environmental conditions for belowground microbial communities and in turn forest productivity and health.

In Central Europe, nearly all forest stands have been altered by human activities over the past centuries and are managed actively on more than 95% of the area at varying intensities today (Bengtsson et al., 2000; Forests Europe, 2015). The most widespread stand-forming tree species in temperate forests are Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) for conifer, and beech (*Fagus sylvatica*) and oak (*Quercus* spp.) for broadleaved stands (Forests Europe, 2015). Forest management influences the occurrence of these tree species and hence the availability and quality of microbial resources, which can result in altered microbial community structure and succession (Prescott and Grayston, 2013; Goldmann et al., 2015; Purahong et al., 2015). In managed forest, one core activity is the harvest of living trees, which affects maximum stand density (Pretzsch, 2009) and thereby the organic matter input to the soil decomposer system. Moreover, the regular removal of wood alters the quality and quantity of dead wood compared to unmanaged forests (Jonsson et al., 2005). Wood specific decay rates were shown to affect organismic (e.g. beetles, fungi) as well as functional (i.e. enzymes laccase and endonuclease) diversity that in turn impacts on microbial C sequestration and turnover (Floren et al., 2014; Hoppe et al., 2016; Kahl et al., 2017).

In the last decades, profiling of soil phospholipid fatty acids (PLFA) was established as powerful tool to provide both functional and structural information on microbial communities (Leckie, 2005; Ramsey et al., 2006; Willers et al., 2015). This method allows the separation of microbial groups, due to specific fatty acids present in the phospholipid layer of membranes (Joergensen and Wichern, 2008). Several PLFA biomarkers for Gram-positive and Gram-negative bacteria, actinobacteria, saprophytic and arbuscular mycorrhizal fungi have been defined (Zelles, 1999; Ruess and Chamberlain, 2010; Willers et al., 2015). Additionally, specific ratios of PLFAs groups are used as environmental indicators, e.g. the fungal to bacterial PLFA ratio as index for shifts in the major soil carbon channels (Bailey et al., 2002; Schütz et al., 2009). Moreover, the ratios of Gram-positive to Gram-negative bacteria or iso- to anteiso- fatty acids indicate changes in habitat factors (e.g. temperature) or microbial stress (Kaneda, 1991; Romani et al., 2011; Yang et al., 2014; Francisco et al., 2016).

In the present study, PLFA profiles were used to assess the effects of forest management and related soil properties on microbial biomass and community composition in forest soils from three German regions. Within each region 50 forest sites differing in management intensity were investigated. The latter is expressed by the Forest Management Intensity Index (ForMI, Kahl and Bauhus, 2014), which takes into account the proportions of harvested tree volume, non-native tree species and dead wood. The 150 forest sites were assigned to the management groups “low”, “medium” and “high” for deciduous stands, and “conifer” for coniferous stands, and the microbial community structure was investigated in both the organic layer and the upper mineral soil (0–10 cm). The aim of this study was to determine (1) the relationship between regional environmental properties and microbial biomass and community composition in forest systems, (2) the impact of forest management intensity on belowground microbial communities.

2. Materials and methods

2.1. Study sites

The study was conducted within the framework of the “Biodiversity Exploratories”, a large-scale and long-term project for biodiversity and ecosystem research (www.biodiversity-exploratories.de; Fischer et al., 2010). The study design comprises three different exploratory regions across Germany: (1) the Schorfheide-Chorin Biosphere Reserve in the lowlands of north-eastern Germany (53°0′N, 13°46′E; 3–140 m a.s.l.), (2) the National Park Hainich-Dün in the hilly lands of central Germany (51°9′N, 10°28′E; 285–550 m a.s.l.), and (3) the Biosphere Reserve Schwäbische Alb, a low mountain range in south-west Germany (48°26′N, 9°23′E; 460–860 m a.s.l.). The three regions differ considerably in environmental conditions. The Schorfheide-Chorin is a young glacial landscape with a mean annual temperature of 8.0–8.5 °C and a mean annual precipitation of 500–600 mm. The most frequent soil type is Cambisol. Hainich-Dün and Schwäbische Alb both feature calcareous bedrock; in the Schwäbische Alb additionally karst occurs. The soil types in the Hainich-Dün are Luvisols and Stagnosols, the mean annual temperature is 6.5–8.0 °C and the precipitation 600–800 mm. The main soil types in the Schwäbische Alb are Cambisols and Leptosols, and annuals means are 6–7 °C for temperature and 700–1000 mm for precipitation.

In each of the exploratory regions 50 forest experimental plots with different management intensities were established in 2006 (Fischer et al., 2010). The plots include even-aged stands, uneven-aged selection stands, and unmanaged forests, comprising forests types ranging from intensively managed coniferous monocultures over mixed forest stands to natural old-growth beech forests. Across exploratories the plots are dominated by one of the following tree species: European beech (*Fagus sylvatica*), sessile/pedunculate oak (*Quercus petreal/ Quercus robur*), Scots pine (*Pinus sylvestris*) or Norway spurce (*Picea abies*) (for details see Fischer et al., 2010).

2.2. Soil sampling

The soil sampling campaign took place at the 150 forest plots in early May 2014. At each plot 14 soil samples were collected along two transects of 40 m length from north to south and from west to east. The organic layer (Oi, Oe, Oa) was sampled with a metal frame (15 × 15 cm) and mixed to obtain a composite sample for each plot. Afterwards, soil samples of the upper soil layer were collected from 0–10 cm depth using a split tube sampler (5 cm diam.). Soil samples were mixed to prepare one composite sample per plot and sieved at a mesh size of 2 mm for each plot. Both, organic layer and mineral soil samples were stored in cooling boxes and frozen the same day after return to the field lab; thereafter the samples were transported and stored at 20 °C until analysis.

2.3. Phospholipid fatty acid analysis

Microbial biomass was determined by the amount of soil phospholipid fatty acids (PLFAs) using a modified Bligh and Dyer method according to Frostegård et al. (1993). Lipids from 2–4 g litter and soil (wet weight) were extracted by adding 18.4 ml (litter) Bligh/Dyer solvent (chloroform: methanol: citrate buffer ratio of 1:2:0.8, pH 4), vortexed and rocked for 2 h. Samples were centrifuged at 2500 rotation min^{-1} for 10 min, solvent transferred to new tubes and soil re-extracted with 2.5 ml Bligh/Dyer. Both extraction solvents were unified and 3.1 ml chloroform plus 1.10 ml citrate buffer was added, samples vortexed and centrifuged (see above) and allowed to separate. From the organic fraction (bottom phase) 3 ml of each sample was transferred to silica acid columns (HF BOND ELUT–SI, Varian Inc.). Lipids were fractionated into neutral lipids, glycolipids and phospholipids by elution with 5 ml chloroform, 20 ml acetone and 5 ml methanol, respectively. Fatty