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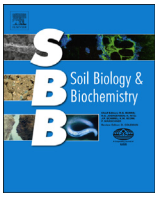

Do general spatial relationships for microbial biomass and soil enzyme activities exist in temperate grassland soils?

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ABSTRACT

In heterogeneous environments such as soil it is imperative to understand the spatial relationships between microbial communities, microbial functioning and microbial habitats in order to predict microbial services in managed grasslands. Grassland land-use intensity has been shown to affect the spatial distribution of soil microorganisms, but so far it is unknown whether this is transferable from one geographic region to another. This study evaluated the spatial distribution of soil microbial biomass and enzyme activities involved in C-, N- and P-cycling, together with physico-chemical soil properties in 18 grassland sites differing in their land-use intensity in two geographic regions: the Swabian Alb in south-west Germany and the Hainich National Park in the middle of Germany. Enzyme activities associated with the C- and N-cycles, namely β-glucosidase, xylosidase and chitinase, organic carbon (C_{org}), total nitrogen (N_t), extractable organic carbon, and mineral nitrogen (N_{min}) were higher in the Swabian Alb (Leptosols) than in the Hainich National Park (primarily Stagnosols). There was a negative relationship between bulk density and soil properties such as microbial biomass (C_{mic}, N_{mic}), urease, C_{org}, and N_t. The drivers (local abiotic soil properties, spatial separation) of the enzyme profiles (β-glucosidase, chitinase, xylosidase, phosphatase, and urease) were determined through a spatial analysis of the within site variation of enzyme profiles and abiotic properties, using the Procrustes rotation test. The test revealed that physical and chemical properties showed more spatial pattern than the enzyme profiles. β-glucosidase, chitinase, xylosidase, phosphatase, and urease activities were related to local abiotic soil properties, but showed little spatial correlation. Semivariogram modeling revealed that the ranges of spatial autocorrelation of all measured variables were site specific and not related to region or to land-use intensity. Nevertheless, land-use intensity changed the occurrence of spatial patterns measurable at the plot scale: increasing land-use intensity led to an increase in detectable spatial patterns for abiotic soil properties on Leptosols. The conclusion of this study is that microbial biomass and functions in grassland soils do not follow general spatial distribution patterns, but that the spatial distribution is site-specific and mainly related to the abiotic properties of the soils.

1. Introduction

The characterization of spatial relationships of soil microorganisms and their functions in terrestrial ecosystems is a prerequisite to our understanding of ecosystem function (Ettema and Wardle, 2002). Currently, ecological theories suggest that microbial biogeography is more influenced by local short-term habitat conditions than by dispersal barriers or historical events (Lindström and Langenheder, 2012). Therefore, ecological biogeography suggests that differences in microbial abundance and function are driven mainly by interactions among organisms as well as with their immediate physical and biotic environments. Generally, microbial abundance and function can be determined by local (within habitat) as well as regional factors that operate at scales larger than the habitat. Recent studies have addressed the distribution of soil microorganisms at continental (Fierer and Jackson, 2006), regional (Dequiedt et al., 2011; Griffiths et al., 2011), plot (Ritz et al., 2004; Berner et al., 2011; Keil et al., 2011; Regan et al., 2014), and micro scales (Ruamps et al., 2011). Some

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of the large scale studies identified a strong influence of soil pH on the biogeography of microbial communities (Fierer and Jackson, 2006; Griffiths et al., 2011). The study of Liu et al. (2015) revealed that the biogeographical distribution of fungal communities was driven mainly by the carbon content of black soils in northeast China. There is also evidence that regional, inter- and intra-site properties might differ in their influence on abundance, diversity and functioning of the soil microbial community (Aşkin and Kizilkaya, 2006; Šnajdr et al., 2008; Berner et al., 2011; Piotrowska et al., 2011).

Long-term nutrient management practices may also have long-lasting effects on the spatial distribution of soil microorganisms as well as on abiotic soil properties (Steenwerth et al., 2006; Lauber et al., 2008; Millard and Singh, 2010; Dao, 2014). Only a limited number of studies have focused on the interactions between site specific soil management and chemical as well as physical soil properties, despite the fact that understanding the spatial organization of microbial functions improves predictions of agro-ecosystem services (Berner et al., 2011; Keil et al., 2011). These studies include the history of land-use which affects the nutrient status of the soil and the composition of plants (Böhme et al., 2004; Smoliński et al., 2008; Piotrowska et al., 2011). Prober et al. (2015) and Aşkin and Kizilkaya (2006) found that above–below ground interactions in grassland soils subjected to different management practices may influence the composition and function of soil microorganisms.

To our knowledge no study has investigated the spatial variability of microbial biomass, soil enzyme activities and physico-chemical soil characteristics in grassland soils at four scales: different regions, various land-use intensities, between (inter-site) and within (intra-site) single grassland sites. More importantly, only a few studies on microbial biogeography have used variance partitioning or similar approaches to compare the relative importance of regional versus local factors (Lindström and Langenheder, 2012).

The aim of the present study was to determine whether general spatial relationships of microbial biomass and soil enzyme activities between regions and land-use intensities exist and how they may be affected by physico-chemical soil properties. We selected nine grassland sites in the region of the Hainich National Park, Germany, that differ in their land-use intensity, and analysed them for a number of soil chemical and microbiological properties. These results were compared with an equivalent data set from a second region, the Swabian Alb, published by Berner et al. (2011). The two selected regions differ in their climatic and topographic conditions as well as their soil types. We hypothesized that 1) higher land-use intensity would result in greater spatial homogeneity of both physico-chemical and biological soil properties, due to a more homogenous treatment of the site in terms of mowing and fertilizing. In addition we wanted to test whether 2) spatial dependence was more important for the distribution of soil enzyme activities than physico-chemical soil properties and whether 3) land-use intensity was the strongest driver of microbial biomass and soil enzyme activities, independent of region and site.

2. Materials and methods

2.1. Sampling sites

For the present study, nine grassland sites from the Hainich National Park region (HEG sites) were compared with nine sites from the Swabian Alb region (AEG sites) in an on-farm research approach. All the study sites belong to the German Biodiversity Exploratories (www.biodiversity-exploratories.de). At the time of sampling, the sites had been managed by farmers as continuous grasslands for more than 16 years under three different land-use intensity regimes, ranging from hardly managed, grazed pastures to frequently mowed and fertilized pastures and meadows (LUI classes as defined by Fischer et al. (2010)). In each region, samples were taken from three unfertilized pastures (low LUI class), three moderately fertilized and mowed pastures (intermediate LUI class) and three highly fertilized and mowed meadows (high LUI class) (Table 1). Although the overall management of the sites was grouped into three LUI classes, the grazing, mowing and fertilization intensities were specific to each site (Blüthgen et al., 2012). For a detailed description see Table S1. The Hainich National Park is located in the centre of Germany, at an altitude of between 285 and 450 m above sea level and the Swabian Alb is located in south-western Germany at an altitude of 660–808 m above sea level (Fischer et al., 2010). Although mean annual temperatures are comparable (6.5–8.0 °C in the Hainich National Park, 6.0–7.0 °C in the Swabian Alb), they differ in annual precipitation: 500 mm–800 mm in the Hainich National Park and 700–1000 mm in the Swabian Alb (Fischer et al., 2010). The regions are characterized by different geological formations and soil types: calcareous bedrock is found underneath Stagnosols in the Hainich National Park, while calcareous bedrock with karst phenomena lay underneath Leptosols in the Swabian Alb (Fischer et al., 2010).

2.2. Soil sampling

Soil sampling and analyses were similar in both regions. Sampling in the Hainich National Park took place in April 2008, one week after sampling in the Swabian Alb, at the start of the vegetation period, using a spatially explicit sampling regime: a raster of nine grid points, 2.5 m apart one from the other, was placed in the middle of a 10 × 10 m site. Starting from each grid point, samples were taken along a spatially randomized spiral with decreasing inter-sample distances: 1.5 m, 1 m, 0.5 m, 0.25 m, and 0.125 m as described by Keil et al. (2011). In total, 54 spatially referenced samples were taken per site, resulting in a total of 486 samples in each of the two regions. Soil samples were taken using core augers (internal diameter of 5.8 cm) from the top 10 cm depth and cooled immediately to 4 °C. Two intact cores were taken from each sampling location; the first was used to determine the bulk density and the second for chemical and biological analyses. The latter sample was sieved to 2 mm. Stones and plant material were removed as was the litter layer (top 1 cm). The samples were stored at −20 °C until use.

2.3. Analyses

Bulk density (BD) was determined after drying the soil core at 105 °C for three days. The soil water content (SWC) was determined gravimetrically by drying the samples until constant weight was reached (105 °C for 24 h). The SWC used for calculations in this paper was related to the water holding capacity (WHC), published by Birkhofer et al. (2012), of each site. Soil organic C (C_{org}) and total N (N_t) were measured with the MACRO CNS Elemental Analyzer (Elementar Analysensysteme GmbH, Hanau, Germany) according to ISO 10694:1995 (1996) and DIN ISO 13878 (1998), respectively. The soil pH was analysed with a pH-meter (ProfiLabph 597, WTW Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, Germany) in 0.01 M $CaCl_2$ (1:2.5 soil: $CaCl_2$). Mineral nitrogen (NH_4^+ and NO_3^-) was determined following DIN ISO 14256-2 (2006) using an AutoAnalyzer 3 (Bran & Luebbe, Norderstedt, Germany).

Microbial biomass carbon (C_{mic}) and nitrogen (N_{mic}) were measured using the chloroform-fumigation-extraction method (CFE) according to Vance et al. (1987). C and N were extracted from each fumigated and non-fumigated replicate (10 g) with 40 ml

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