



Effects of anthropogenic disturbances on soil microbial communities in oak forests persist for more than 100 years



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ABSTRACT

Land-use change and land-use intensification are considered amongst the most influential disturbances affecting forest diversity, community structure, and forest dynamics. Legacy effects of land-use changes in ecosystem functioning and services may last several hundred years. Although numerous studies have reported the short-term legacy effects of past management, analyses of long-term responses (>100 years) are still lacking. Here, we demonstrate shifts in soil microbial community structure and enzymatic activity levels resulting from a long-term past disturbance intensity gradient in oak forests (former arable farming – former heathland farming – ancient forest). Differences in microbial community composition among sites with contrasting historic land-use were related to differences in soil chemical properties and abundances of arbuscular mycorrhizal fungi, saprotrophic and ectomycorrhizal fungi, and actinobacteria. Both microbial biomass and enzymatic activity levels were distinctly lower in ancient forests compared to historically cultivated sites (i.e. agriculture or heathland farming). We found evidence that past land-use has long-lasting impacts on the recovery of soil community development, much longer than commonly assumed. This in turn highlights the importance of ecological continuity for ecosystem functioning and services. Conservation management, focussing on the stability and diversity of forest ecosystems, therefore needs to consider past land-use legacies for evaluating ecosystem functions (such as soil ecological processes) and for evaluating effective strategies to adapt to environmental changes.

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1. Introduction

Interactions between belowground and aboveground communities may strongly influence ecosystem functioning by regulating plant community dynamics and biogeochemical processes (Wardle et al., 2004a; Wurzburger and Hendrick, 2009; Mangan et al., 2010). Belowground, soil microbial communities decompose organic materials, mediate carbon and nitrogen cycling, and determine nutrient availability for plant growth (Sparling, 1997; Aubert et al., 2010). Aboveground plant communities significantly alter microbial community composition and functions through rooting patterns, rhizodeposition, water use, litter chemistry, canopy structure, and subsequent influences on soil properties and microclimate (Bauhus et al., 1998; Weintraub et al., 2007; Huang et al., 2008; Zhang et al., 2009; Aubert et al., 2010; Burton et al., 2010; Wu et al., 2012). An important caveat is that above–

belowground relationships are mediated by local edaphic factors, and thus such factors should be taken into consideration when assessing these relationships (Boyle et al., 2008; Wu et al., 2012).

Land-use changes can significantly alter the soil characteristics and aboveground species dynamics from which above- and belowground interactions develop (Lauber et al., 2008). Such land-use driven changes have been recognized as a main factor altering ecosystem functions, including carbon (C) and nitrogen (N) cycling or plant species diversity and productivity (Koerner et al., 1997; Brunet and von Oheimb, 1998; Guo and Gifford, 2002; Wakelin et al., 2009; Baeten et al., 2010; Cusack et al., 2013). Numerous studies have reported impacts of land-use changes on soil microbial communities (Fraterrigo et al., 2006; Lauber et al., 2008; Burton et al., 2010; Jangid et al., 2011), and microbial successional changes are increasingly used as an indicator of ecosystem recovery after anthropogenic disturbances (Harris, 2003; Banning et al., 2011). Land-use changes also influence microbial community structure and function and, consequently, nutrient cycling rates (e.g., Grayston and Rennenberg, 2006; Potthast et al., 2012; Ramirez et al., 2012).

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The persistence of these responses to land-use change is, however, still debated. Some chronosequence studies along successional gradients have shown that microbial communities tend to become more similar to those in native soils over time (Buckley and Schmidt, 2003; Jangid et al., 2010, 2011). However, there have been significant differences observed in microbial communities even after >50 years of conversion from agricultural cultivation to forests (Fraterrigo et al., 2005, 2006). To our knowledge, no study has investigated land-use legacies on microbial communities >100 years after afforestation. This is even though forest soils may continue to reflect their agricultural history for a far longer period, hypothetically through changes in soil chemical and structural properties (e.g. Verheyen et al., 1999; Compton and Boone, 2000; Jussy et al., 2002). Specifically, historical farming in temperate climates has resulted in higher soil phosphorous contents and lower soil carbon and nitrogen contents compared to sites with a long continuity of forest cover and soil development (Koerner et al., 1997; Dupouey et al., 2002; Fraterrigo et al., 2005; von Oheimb et al., 2008). Because microbial adaptation and recovery may play a significant role in ecosystem responses to human impacts (Mummy et al., 2002; Allison et al., 2010; Wallenstein and Hall, 2012), the long-term consequences of past land-use decisions on soil microbial communities are crucial for predicting changes in ecosystem functioning and services (Flinn and Vellend, 2005; Sun et al., 2011).

Here we examine the impact of land-use history on microbial community composition and functioning after more than 110 years of forest re-growth on former agricultural land. Very often, geographical past land-use patterns and environmental variation can be confounded (e.g. the fact that steeper slopes or poorer soils are more likely to be abandoned; Flinn and Vellend, 2005). To avoid this issue, we examined plots of sessile oak (*Quercus petraea*) dominated stands in the Lüneburg Heath region of Northwestern Germany that is characterized by homogeneous topography and soil conditions (Westphal, 2001). In addition, the land-use history in this region has been well documented over the last 240 years and detailed data on current site characteristics are available (Westphal, 2001; von Oheimb et al., 2008). Thus, we were able to select sites with very similar characteristics and tree species composition, but with different land-use histories. A previous study performed to determine past land-use effects on the edaphic properties of these forests (von Oheimb et al., 2008) showed that past agricultural practices resulted in long-term changes in essential soil characteristics, whereas differences between former heathlands and sites with a continuous forest history (ancient forest sites) were less pronounced.

Based on the previous research in these forests we hypothesized that different past land-uses would also have long-term impacts on microbial community composition and microbial extra-cellular enzyme activity. Specifically, we expected that long-term impacts on microbial communities would be strongest in former arable land compared to ancient forests, mirroring legacy effects of soil conditions related to past land-use intensity. Thus, our objective was to assess potential long-term effects of past land-use on (i) soil chemical properties, (ii) microbial biomass and community structure, and (iii) microbial extra-cellular enzyme activities. Furthermore we (iv) discuss the extent to which past land-use practices may have altered the recovery or trajectory of soil community development based on the results of our study. In order to measure microbial biomass and broad community structure simultaneously, we chose to use lipid analysis. Lipid analysis is a well-established method for quantitatively assessing microbial biomass and broad microbial groups including different fungal and bacterial communities (Vestal and White, 1989); it is also an effective measure of microbial responses to land-use and human impacts (for example:

Mummy et al., 2002; Fraterrigo et al., 2006; Williams, 2007; Kulmatiski and Beard, 2011; Gutknecht et al., 2012). Microorganisms produce extra-cellular enzymes in order to degrade complex organic substrates into monomers for nutrient acquisition (Keeler et al., 2009). Extra-cellular enzyme activities can, therefore, represent microbial nutrient limitation and decomposition potential in response to changes in soil quality or land-use change (Sinsabaugh et al., 2002; Rinkes et al., 2011).

2. Material and methods

2.1. Study area

This study was conducted in the Lüneburg Heath nature reserve (Lower Saxony, NW Germany; 53°15'N, 9°58'E, 70–150 m a.s.l.), which comprises an area of 24,000 ha. The study area is characterized by a humid suboceanic climate with a mean annual precipitation of 811 mm and a mean annual temperature of 8.4 °C (Müller-Westermeier, 1996). The geological substrate is composed of fluvioglacial sandy deposits and drift sands from the Saale Ice Age. As a result of the high substrate acidity, the soils are mainly Podzols (Rode, 1999). The potential natural vegetation is acidophytic mixed beech–oak forest.

The landscape has changed markedly due to various human management practices over the past 240 years. While heathland was the predominant land-use type in the 18th century (80%), a decline in historical farming activities, accompanied by afforestation measures during the last century, resulted in increased forest cover across the area (currently, app. 60%). At present the forests are dominated by coniferous species (68% *Pinus sylvestris*, 14% *Picea abies*, 5% *Larix decidua*, 2% *Pseudotsuga menziesii*), while deciduous trees account for 11% (5% *Quercus petraea*, *Quercus robur*; 3% *Fagus sylvatica*; 3% *Betula pendula*; Westphal, 2001).

2.2. Study design and stand characteristics

The study was based on a past land-use intensity gradient, using data from 18 mature sessile oak stands (Table 1). We restricted the analysis to oak forests for several reasons. Because significant differences have been observed in the (chemical) properties of the upper soil layers under different tree species planted on former cultivated land (e.g. Bauhus et al., 1998; Grayston and Prescott, 2005; Wu et al., 2012), it is important to exclude this confounding factor by keeping the tree species composition constant. The vast majority of the ancient forest sites are near-natural mixed broadleaved forests with a high proportion of oak and beech. However, afforestation of former agricultural land with broadleaved tree species always involved oak, never beech. In total, about 20% of the area of the Lüneburg Heath nature reserve that was converted from arable land and heathland to forest during the period 1878–1998 is now dominated by oak trees (Ernst and Hanstein, 2001). Furthermore, within the framework of “close-to-nature forestry”, most of the coniferous forests have been converted to mixed forests by planting oak trees over the last four decades.

Past land-use intensity was characterized on the basis of historical land-use systems: agriculture, heathland farming, and forestry. Information regarding past land-use was derived from historical maps of the “Kurhannoversche Landesaufnahme” from 1776 to 1786 and a forest management plan of 1887. The resulting gradient comprised (i) ‘FA’ oak stands established on former arable land, (ii) ‘FH’ oak stands established on former heathland and (iii) ‘AF’ oak stands on ancient forest sites. Agricultural practices in the 19th century included tillage and manure application. Fertilizer inputs were generally modest, with N-inputs mainly originating

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