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Effects of long-term drainage on microbial community composition vary between peatland types

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ABSTRACT

Peatlands represent an important reservoir of carbon, but their functioning can be threatened by water level drawdown caused by climate or land use change. Knowledge of how microbial communities respond to long-term drainage in different peatland types could help improve predictions of the effect of climate change on these ecosystems. We investigated the effect of long-term drainage on microbial community composition in bog, fen and spruce swamp forests (SSF) in the Šumava Mountains (Czech Republic), using high-throughput barcoded sequencing, in relation to peat biochemical properties. Long-term drainage had substantial effects, which depended strongly on peatland type, on peat biochemical properties and microbial community composition. The effect of drainage was most apparent on fen, followed by SSF, and lowest on bog. Long-term drainage led to lower pH, reduced peat decomposability and increased bulk density, which was reflected by reduced microbial activity. Bacterial diversity decreased and *Acidobacteria* became the dominant phylum on drained sites, reflecting a convergence in bacterial community composition across peatlands after long-term drainage. The archaeal communities changed very strongly and became similar across drained peatlands. Overall, the characteristic differences between distinct peatland types under natural conditions were diminished by long-term drainage. Bog represented a relatively resilient system while fen seemed to be very sensitive to environmental changes.

1. Introduction

Peatlands represent an important global reservoir of carbon (C) that has accumulated over millennia due to a net imbalance between primary production and microbial decomposition of organic matter. High water level and consequent anoxia, together with low litter quality and nutrient availability, suppress rapid aerobic decomposition and further much slower anaerobic decomposition. Peatlands and their C sink function may be threatened by predicted global climate change (Gorham, 1991). Historically, peatlands have been drained for agriculture or forestry; this may stimulate mineralisation and drastically change their function as C sinks (Martikainen et al., 1995; Paavilainen and Päivänen, 1995; Silvola et al., 1996). Microbial communities are the main drivers of organic matter decomposition, and there is still a lack of knowledge about how these complex communities respond to long-term drainage and how their responses vary between different peatland types.

In pristine peatlands, the composition and functioning of the microbial community have been shown to vary according to nutrient status of a site (Jaatinen et al., 2005; Yavitt et al., 2012; Urbanová and Bárta, 2014) and vegetation composition (Fisk et al., 2003; Thormann et al., 2004). Greater microbial diversity and activity was observed in nutrient-richer fens compared with nutrient-poor, acidic bogs (Kim et al., 2008; Lin et al., 2012; Urbanová and Bárta, 2014). *Acidobacteria* and *Proteobacteria* represent the dominant bacterial phyla in peatlands, and their relative abundances change in inverse proportion to each other when pH and substrate availability change (Smit et al., 2001; Hartman et al., 2008; Urbanová and Bárta, 2014). Methanogens represent the dominant group in the archaeal community, whose composition has also been shown to vary with environmental conditions (Juottonen et al., 2005; Lin et al., 2012). Moreover, microbial communities and associated decomposition processes change with depth, as redox conditions and C quality change (Sundh et al., 1997; Dedysh et al., 2006; Morales et al., 2006). These

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natural gradients in microbial community composition and functions can be disturbed by drainage and the resulting changes in peat physicochemical properties and vegetation structure.

It is to be expected that susceptibility and resilience of the microbial communities to drainage will differ among peatland types. It has been shown that long-term drainage alters the vegetation community most strongly on nutrient-richer sites (Minkkinen et al., 1999; Urbanová et al., 2011). Similarly, the changes in microbial community structure and activity after drainage were more apparent in fen than in bog, and the differences in fungal and actinobacterial communities between these peatland types were diminished after long-term drainage (Jaatinen et al., 2007; Peltoniemi et al., 2009). Increased aeration of peat can provide more favourable conditions for fungi and certain Gram-negative bacteria (Jaatinen et al., 2008). Long-term drainage has been shown to reduce activity and diversity of both methanogens and methanotrophs, and these changes were again more dramatic in fen than in bog (Jaatinen et al., 2005; Urbanová et al., 2011; Yrjälä et al., 2011). Methanogens are generally pushed deeper into the profile, though they may survive in anoxic micro-habitats after water level drawdown, where their CH_4 production is reduced and may limit methanotrophs through substrate depletion (Jaatinen et al., 2005; Yrjälä et al., 2011).

Most of the studies mentioned above were focused on specific groups of bacteria or *Archaea* rather than taking a comprehensive view of the changes in microbial community structure and function after drainage. Our knowledge about the below-ground microbial processes in peatlands remains fragmentary. We need to understand better the importance of different microbial guilds involved in carbon and nutrient cycling and specifically their response to environmental changes such as water level drawdown. Based on previous studies, the function and composition of the microbial community in some peatland types are expected to be more resilient to water level drawdown than in others. In order to predict the effect of climate change on peatland types and to aid in ecosystem restoration efforts, it will be useful to understand which peatlands are most sensitive to disturbance.

To elucidate the effect of long-term drainage in different peatland types, we studied three major types of peatlands: bog, fen and spruce swamp forest (SSF). We identified the effects of long-term drainage on bacterial and archaeal community composition in the different types, with a focus on changes in microbial community structure. We investigated the links between microbial community composition and different environmental variables influenced by long-term drainage. We expected an important shift in microbial community composition after long-term drainage, with changes being more apparent in fen and SSF than in bog. We hypothesised that differences between microbial communities of distinct peatland types would be diminished over a long-term drainage.

2. Material and methods

2.1. Study sites

Our study was conducted in the Šumava Mountains (Bohemian Forest), south-western Czech Republic (48°59′ N, 13°28′ E), in two ombrotrophic bogs, two minerotrophic, treeless poor fens and four spruce swamp forests. For all peatland types, study sites in both pristine and drained state were included: one pristine and one drained bog (BOGp, BOGd), two pristine and two drained spruce swamp forests (SSFp, SSFd) and one pristine and one drained fen (FENp, FENd). Peatlands were drained with ditches to increase productivity of forests and meadows in the 1960s; however, no tree planting or other type of management was carried out after drainage and the sites were left abandoned.

SSFp, SSFd and BOGp were situated on an upland plateau at altitudes from 1100 to 1260 m a.s.l. BOGd, FENp and FENd were located at an altitude of 900 m a.s.l. in a flat valley. This mountain region is characterised by a cold and humid climate with mean annual temperatures between 3.2 and 4 °C and mean annual rainfall between 1000 and 1200 mm, according to altitude (1961–1990, statistics by the Czech Hydro-Meteorological Institute).

The BOGp site included typical microtopographic variation with hummocks, hollows and lawns, each with its characteristic vegetation. Dominant plant species were *Andromeda polifolia*, *Vaccinium uliginosum*, *Eriophorum vaginatum*; *Carex limosa* and *Trichophorum caespitosum*. The moss layer consisted of *Sphagnum rubellum*, *S. capillifolium* and *S. magellanicum*. Such variation was lacking on the BOGd site, where sedges had disappeared and the dwarf shrubs *V. uliginosum* and *Vaccinium myrtillus* dominated as a consequence of long-term drainage. *Molinia caerulea* was predominant along the drainage ditches, while small trees of *Betula pubescens* and *Picea abies* were abundant. *Polytrichum strictum* and *Sphagnum russowii* comprised the field layer.

The FENp site represented typical treeless poor fen with dominant *Carex rostrata* and with a compact moss layer of *Sphagnum flexuosum*. However, on FENd vegetation had changed dramatically and was characterised by a mixture of different states of degradation, depending on the distance to a drainage ditch. *C. rostrata* grew only in wetter areas farther away from the ditches whereas drier parts were occupied by *Carex nigra*, *Carex brizoides*, *M. caerulea*, *Nardus stricta* and other graminoids. The moss layer was reduced to small patches with *Sphagnum girgensohnii*.

The SSFp sites were characterised by heterogeneous vegetation in the understorey. *E. vaginatum* was widespread and other sedges and grasses were common in wetter microhabitats, whereas drier microhabitats were occupied by *Vaccinium* dwarf shrubs. In the moss layer, *S. girgensohnii* and *Sphagnum magelanicum* were the most frequent species. The open tree canopy consisted of *P. abies* with heights of about 8–15 m. At the SSFd sites, however, an almost homogenous cover of *V. myrtillus* was present and the tree canopy was denser with a height about 20 m. The moss layer was fragmented and contained the dominant *Pleurozium schreberi* and other forest mosses.

The selected study sites did not represent true replication of all peatland types and treatments. The approach may be considered to involve pseudoreplication and does not allow strict tests of the general applicability of our results for a given peatland type. However, the study sites were selected in a small geographical region with uniform environmental conditions and the selected study sites represented well the peatland types in this region. The aim of our study was to link microbial community composition and biochemical properties that have been influenced by long-term drainage in three peatland types. Therefore, we chose to study fewer sites intensively rather than replicate sites. Our results conform with those from other studies (Andersen et al., 2006; Jaatinen et al., 2007; Peltoniemi et al., 2009; Basiliko et al., 2013) and therefore we assume that our approach is valid for evaluation of long-term drainage effect on peatland types with the same vegetation as the studied sites.

2.2. Soil sampling

The upper layer of peat (0–30 cm) was sampled using a corer. At each site, two 20 m long line transects were marked 20 m apart. One sample was taken at each sampling point at 0, 10 and 20 m along the transects on SSF and two samples taken at each sampling point at 0 and 20 m along the transects on BOG and FEN. At the drained sites, transects were perpendicular to the ditch. Totally, 6