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Ecological and environmental transition across the forested-to-open bog ecotone in a west Siberian peatland

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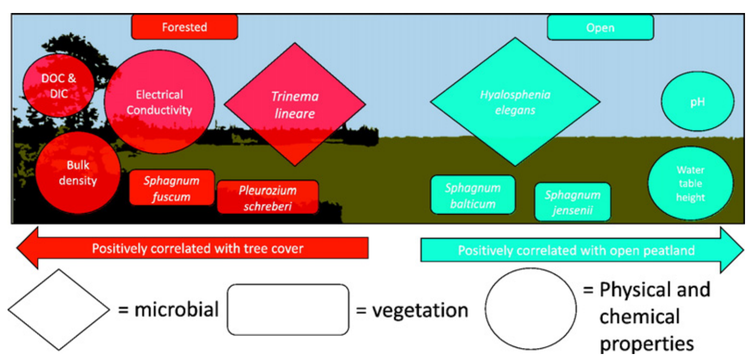
HIGHLIGHTS

- The implications of increasing tree cover in boreal peatlands are largely unknown.
- Forested and open peatlands support different microbial and vegetation communities.
- Tree cover has a strong influence on peat physical and chemical properties.
- Tree density in peatlands is likely to have a strong influence on peatland carbon.
- The ecotone between forested and open peatland has been dynamic through time.

GRAPHICAL ABSTRACT



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ABSTRACT

Climate change may cause increasing tree cover in boreal peatlands, and the impacts of this encroachment will be noted first at forested-to-open bog ecotones. We investigate key metrics of ecosystem function in five such ecotones at a peatland complex in Western Siberia. Stratigraphic analysis of three cores from one of these transects shows that the ecotone has been dynamic over time with evidence for recent expansion of forested peatland. We observed that the two alternative states for northern boreal peatlands (forested/open) clearly support distinct plant and microbial communities. These in turn drive and respond to a number of feedback mechanisms. This has led to steep ecological gradients across the ecotones. Tree cover was associated with lower water tables and pH, along with higher bulk density, aquatic carbon concentrations, and electrical conductivity. We propose that the conditions found in the forested peatland of Western Siberia make the carbon sink more vulnerable to warmer and drier conditions.

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1. Introduction

Although peatlands cover <3% of the earth's land surface they store the equivalent of half the carbon that is in the atmosphere as CO_2 (Dise, 2009). Peatlands develop due to an imbalance between primary production and decomposition, with anoxic, acidic and nutrient-poor conditions leading to the accumulation of carbon as peat (Clymo, 1978). The global peatland carbon pool is currently estimated at 612 GtC (Yu, 2011) and even relatively small changes in the size of this pool have the potential to affect climate. During the Holocene global peatlands have exerted a net cooling effect on global climate through the sequestration of atmospheric CO_2 and storage of carbon as peat (Frolking and Roulet, 2007). Future climate change is expected to alter peatland vegetation composition, ultimately impacting the long-term capacity of peatlands to sequester and store carbon (Heijmans et al., 2013; Limpens et al., 2014).

Northern peatlands exist in alternative quasi-stable states of unforested 'open' peatlands and forested peatlands (tree-covered), often referred to by their Russian name: *ryam* (Scheffer et al., 2012). By a conservative estimate 27.5% of global peatlands are forested (Zoltai et al., 1996), primarily in regions of continental climate (Crawford et al., 2003; Limpens et al., 2014). There is evidence that peatland tree cover has been dynamic with greater cover during warmer periods in the Holocene (Blyakharchuk and Sulerzhitsky, 1999; Gunnarson, 2008; MacDonald et al., 2008; Velichko, 1998), and pulses of tree colonisation coinciding with drier climatic conditions. Modelling studies predict that the current mosaic structure of peatland and boreal forest will alter in response to warming (Soja et al., 2007). Over the 20th century there has been a trend towards increasing tree recruitment and survival on previously open undrained peatland (Berg et al., 2009; Pellerin and Lavoie, 2003), including in Western Siberia (Blanchet et al., 2017). This is most prominent in high latitude regions which have experienced greater warming in the latter half of the 20th century, such as northern Eurasia (Gervais and Macdonald, 2000). It is likely that climatic change over this century will continue to alter the tree cover on peatlands with implications for biodiversity and carbon cycling (Bhatti et al., 2006; Limpens et al., 2014; Scheffer et al., 2012).

Forested and open peatlands differ in many ways. Both *Sphagnum* and peatland tree species can be viewed as ecosystem engineers and are capable of creating and maintaining fundamentally different environments over short spatial gradients (Agnew et al., 1993; Eppinga et al., 2007; Heijmans et al., 2013; Ohlson et al., 2001). Yet the degree to which the physical and chemical environment differs under field conditions is not well known. Likewise, the physical and chemical thresholds which determine tree cover on peatlands are poorly understood (Ohlson et al., 2001). Studies have found forested peatlands are strong sinks for carbon (Flanagan and Syed, 2011; Gažovič et al., 2013), but when comparing the carbon balance of forested peatland with nearby open peatland, Strilesky and Humphreys (2012) found the carbon sink to be reduced by 30% with the presence of trees. Ecosystem respiration increases with tree cover in peatlands (Golovatskaya and Dyukarev, 2008; Golovatskaya et al., 2011; Hartshorn et al., 2003). In addition, litterbag studies have suggested more rapid decomposition in the surface environment of forested peatlands compared to open peatlands, due to warmer and drier conditions (Koronatova, 2007). Whether higher respiration and decay rates translates to a difference in carbon accumulation rate is less clear. Golovatskaya and Dyukarev (2008) have suggested that the CO_2 sink was five times higher in open than forested peatland, but this result is compromised by the lack of consideration of fluxes from the trees (Artz et al., 2013).

The impacts of forest expansion on peat is likely to become apparent first at the ecotone between forested and open peatlands, with changes here presaging landscape level responses (Bhatti et al., 2006; Allen and Breshears, 1998; Hartshorn et al., 2003; Peteet, 2000). This ecotone forms a critical transition zone for peatland biota and biogeochemistry but the environmental and ecological transitions which occur across this zone have been, surprisingly, little studied either spatially or temporally. Here we focus on the forested-to-open bog ecotones at a peatland complex in Western Siberia. We first consider spatial differences in ecological and environmental parameters which occur along transects across these ecotones. We assess: i) biodiversity at two trophic levels, ii) key physical and chemical variables which may both influence and be influenced by biotic change, iii) porewater aquatic carbon as one key component of the peatland carbon cycle. We pair this spatial survey with a down-core assessment of change at one of these ecotones through the Holocene. In doing so we aim to characterise the structure of the ecotone, assess the differences between forested and open peatlands, assess how the ecotone has changed over time, and provide a baseline for future reassessments.

2. Methods

2.1. Study region and site

Western Siberia has the most extensive area of wetland in the world, 2.80 million km^2 (Peregon et al., 2009), and may contain as much as 40% of global peatlands (Walter, 1977). In the early Holocene, forests covered areas of the Western Siberian plain which are now dominated by peatland (Blyakharchuk and Sulerzhitsky, 1999; Peregon et al., 2009). At the Holocene Climatic Optimum forest cover was around 30% higher than it is today (Velichko, 1998) with much of this forest likely to have been on peat. Today, almost two thirds of the peatland in this region is forested (Naumov et al., 2007). Evidence of past dynamism in tree cover, combined with large spatial extent of peatlands, make this a particularly important location to consider forested-to-open-bog transitions.

Climate data suggests continental Siberia is warming at an anomalously fast rate compared to other regions (Cohen et al., 2014), and climate models predict this to continue (Miao et al., 2014). Western Siberia has experienced a pattern of increasing temperatures through the 20th century, as much as a 3 °C increase in mean summer air temperature (Kirpotin et al., 2009), with particularly strong increases in the last decades (Briffa et al., 1996; MacDonald et al., 2008). Additionally, there has been a trend of increasing summer precipitation and wet days since 1950 (Crawford et al., 2003), along with increasingly frequent drought events (Soja et al., 2007).

Our work was conducted in the boreal mid-taiga zone at Mukhrino peatland (60.883°N, 68.717°E), 22 km south west of Khanty-Mansiysk (Yugra Autonomous Okrug) in August 2014. Mukhrino is a ridge-hollow patterned bog, situated on the edge of a large mire complex which extends for hundreds of kilometres to the south and west. The mire has trees on the ridges and more continuous areas of forested bog ('low ryam'); open water is largely restricted to a few areas in the centre of wet lawns. The vegetation of low ryam areas consists primarily of an open canopy of *Pinus sibirica* and *Pinus sylvestris* (dominant) with carpets of *Sphagnum fuscum* and an understorey of shrubs including *Vaccinium uliginosum*, *Rhododendron tomentosum* and *Rubus chamaemorus*. In some areas 'high ryam' vegetation is also present with denser tree cover, and *Sphagnum* cover is rarer, usually replaced by *Pleurozium schreberi*. In open lawns *S. balticum* is the most abundant bryophyte with *S. majus*, *S. papillosum* and *S. jensenii* also frequent. Vascular plants of the open lawns include *Scheuzeria palustris* and *Andromeda polifolia*. The region has a continental subarctic climate with average monthly temperatures ranging from −20 °C in January to 17 °C in July with annual precipitation of 500 mm (Filippova and Bulyonkova, 2013).

2.2. Field sampling across ecotones

We positioned five transects orthogonal to forested-to-open-bog transitions around the northeast margin of Mukhrino peatland located on the west terrace of the Irtysh river (Fig. 1). Transect length was selected to be sufficient to span the complete transition and ranged from