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

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16 **ABSTRACT**

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

28 **KEYWORDS:** Mire; Ryam; Forest; Testate amoebae; Carbon; peat

29 1. Introduction

30 Although peatlands cover less than 3% of the earth's land surface they store the equivalent of half the
31 carbon that is in the atmosphere as CO₂ (Dise, 2009). Peatlands develop due to an imbalance between
32 primary production and decomposition, with anoxic, acidic and nutrient-poor conditions leading to the

1 accumulation of carbon as peat (Clymo, 1978). The global peatland carbon pool is currently estimated at
2 612 GtC (Yu, 2011) and even relatively small changes in the size of this pool have the potential to effect
3 climate. During the Holocene global peatlands have exerted a net cooling effect on global climate
4 through the sequestration of atmospheric CO₂ and storage of carbon as peat (Frolking and Roulet,
5 2007). Future climate change is expected to alter peatland vegetation composition, ultimately impacting
6 the long-term capacity of peatlands to sequester and store carbon (Heijmans et al., 2013; Limpens et al.,
7 2014).

8 Northern peatlands exist in alternative quasi-stable states of un-forested 'open' peatlands and forested
9 peatlands (tree-covered), often referred to by their Russian name: *ryam* (Scheffer et al., 2012). By a
10 conservative estimate 27.5% of global peatlands are forested (Zoltai and Martikainen, 1996), primarily in
11 regions of continental climate (Crawford et al., 2003; Limpens et al., 2014). There is evidence that tree
12 cover on peatlands has been dynamic with greater cover during warmer periods in the Holocene
13 (Blyakharchuk and Sulerzhitsky, 1999; Gunnarson, 2008; MacDonald et al., 2008; Velichko, 1998) with
14 pluses of tree colonisation coinciding with drier climatic conditions. Modelling studies predict that the
15 current mosaic structure of peatland and boreal forest will alter in response to warming (Soja et al.,
16 2007). Over the 20th century there has been a trend towards increasing tree recruitment and survival on
17 previously open undrained peatland (Berg et al., 2009; Linderholm and Leine, 2004; Pellerin and Lavoie,
18 2003), including in Western Siberia (Blanchet et al., 2017). This is most prominent in high latitude
19 regions which have experienced greater warming in the latter half of the 20th century, such as northern
20 Eurasia (Gervais and Macdonald, 2000). It is likely that climatic change over this century will continue to
21 alter the tree cover on peatlands with implications for biodiversity and carbon cycling (Bhatti et al.,
22 2006; Limpens et al., 2014; Scheffer et al., 2012).

23 Forested and open peatlands differ in many ways. Both *Sphagnum* and peatland tree species can be
24 viewed as ecosystem engineers and are capable of creating and maintaining fundamentally different
25 environments over short spatial gradients (Agnew et al., 1993; Eppinga et al., 2007; Heijmans et al.,
26 2013; Ohlson et al., 2001). Yet the degree to which the physical and chemical environment differs under
27 field conditions is not well known. Likewise, the physical and chemical thresholds which determine tree
28 cover on peatlands are poorly understood (Ohlson et al., 2001). Studies have found forested peatlands
29 to be strong sinks for carbon (Flanagan and Syed, 2011; Gažovič et al., 2013), but when comparing the
30 carbon balance of forested peatland against nearby open peatland Strilesky and Humphreys (2012)
31 found the carbon sink to be reduced by 30% with the presence of trees. Ecosystem respiration increases
32 with tree cover in peatlands (Golovatskaya and Dyukarev, 2008; Golovatskaya et al., 2011; Hartshorn et
33 al., 2003). In addition litterbag studies have suggested more rapid decomposition in the surface
34 environment of forested peatlands compared to open peatlands, due to warmer and drier conditions
35 (Koronatova, 2007). Whether higher respiration and decay rates translates to a difference in carbon
36 accumulation rate is less clear. Golovatskaya & Dyukarev (2008) have suggested that the CO₂ sink was
37 five times higher in open than forested peatland but this result is compromised by the lack of
38 consideration of fluxes from the trees (Artz et al., 2013).

39 The impacts of forest expansion on to peat is likely to become apparent first at the ecotone between
40 forested and open peatlands, with changes here presaging landscape level responses (Bhatti et al., 2006;

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

12 2. Methods

13 2.1 Study region and site

14 Western Siberia has the most extensive area of wetland in the world, 2.80 million km² (Peregon et al.,
15 2009) and may contain as much as 40% of global peatlands (Walter, 1977). In the early Holocene, forests
16 covered areas of the Western Siberian plain which are now dominated by peatland (Blyakharchuk and
17 Sulerzhitsky, 1999; Peregon et al., 2009). At the Holocene Climatic Optimum forest cover was around
18 30% higher than it is today (Velichko, 1998) with much of this forest likely to have been on peat. Today,
19 almost two thirds of the peatland in this region is forested (Naumov et al., 2007). Evidence of past
20 dynamism in tree cover, combined with large spatial extent of peatlands make this a particularly
21 important location to consider forested-to-open-bog transitions.

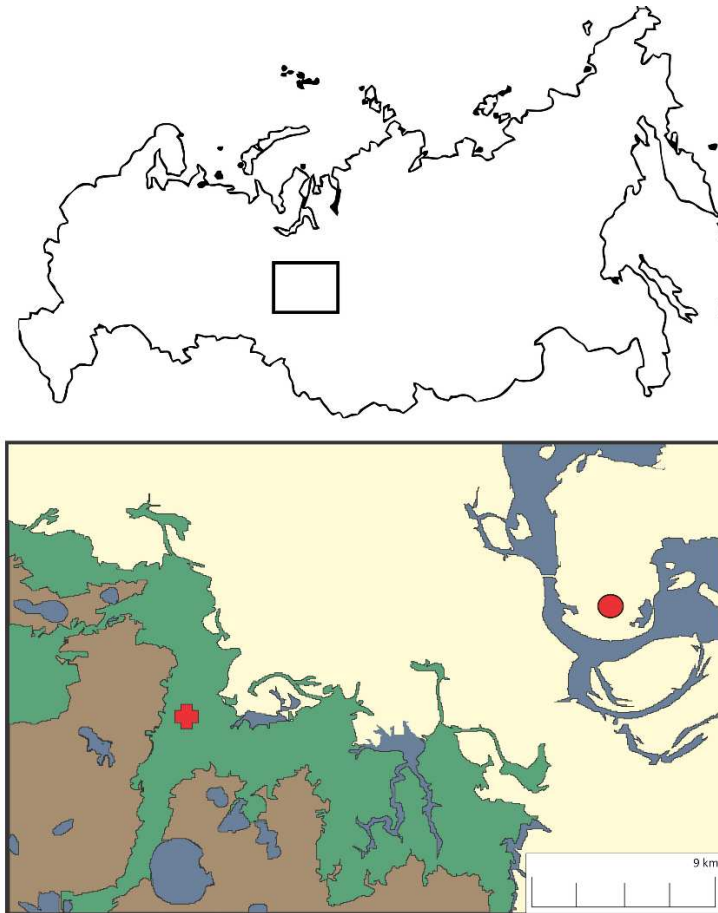
22 Climate data suggests continental Siberia is warming at an anomalously fast rate compared to other
23 regions (Cohen et al., 2014) and climate models predict this to continue (Miao et al., 2014). Western
24 Siberia has experienced a pattern of increasing temperatures through the 20th century, as much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

29 Our work was conducted in the boreal mid-taiga zone at Mukhrino peatland (60.883°N, 68.717°E), 22 km
30 south west of Khanty-Mansiysk (Yugra Autonomous Okrug) in August 2014. Mukhrino is a ridge-hollow
31 patterned bog, situated on the edge of a large mire complex which extends for hundreds of kilometres
32 to the south and west. The mire has trees on the ridges and more continuous areas of forested bog ('low
33 ryam'); open water is largely restricted to a few areas in the centre of wet lawns. The vegetation of low
34 ryam areas consists primarily of an open canopy of *Pinus sibirica* and *Pinus sylvestris* (dominant) with
35 carpets of *Sphagnum fuscum* and an understorey of shrubs including *Vaccinium uliginosum*,
36 *Rhododendron tomentosum* and *Rubus chamaemorus*. In some areas 'high ryam' vegetation is also
37 present with denser tree cover and *Sphagnum* cover rarer, replaced particularly by *Pleurozium schreberi*.
38 In open lawns *S. balticum* is the most abundant bryophyte with *S. majus*, *S. papillosum* and *S. jensenii*

1 also frequent. Vascular plants of the open lawns include *Scheuzeria palustris* and *Andromeda polifolia*.
2 The region has a continental subarctic climate with average monthly temperatures ranging from -20 ° C
3 in January to 17 ° C in July with annual precipitation of 500 mm (Filippova and Bulyonkova, 2013).

4 2.2 Field sampling across ecotones

5 We positioned five transects orthogonal to forested-to-open-bog transitions around the northeast
6 margin of Mukhrino peatland located on the west terrace of the Irtysh river (Figure 1). Transect length
7 was selected to be sufficient to span the complete transition and ranged from 30-70 m while the spacing
8 between transects was between 100 and 300 m. Our criteria for site selection were: 1) for transitions to
9 be from large areas of continuous forested bog to large areas of open bog (rather than just
10 ridges/hollows); 2) to span the range of transition types; 3) for areas to be accessible to allow for
11 repeated visits. All transects were in ombrotrophic areas of the peatland and included a combination of
12 open and closed canopy peat forest.



13
14 *Figure 1. Map showing location of Mukhrino field site (60.883°N, 68.717°E), marked as a red cross, within the Russian*
15 *federation. Circle indicates the city of Khanty-mansiysk.*

16 17 2.3 Physical and chemical data

1 We measured a large number of environmental variables at 5 m intervals along transects. Sampling was
2 conducted just outside the vegetation quadrat to avoid disturbance to vegetation but sampling spots
3 were selected to be equivalent in terms of topography and vegetation. To quantify surface bulk density
4 an open cylinder of known volume (130 ml) was cut into the peat until the base was level with the
5 surrounding surface, vegetation was then cut around and below the cylinder to remove a sample with as
6 little disturbance as possible. In the laboratory these samples were dried at 105°C and weighed
7 according to standard methods (Chambers et al., 2011)..

8 To quantify water table depth we dug a hole of at least 40 cm depth and after at least 24 hours
9 measured the height from the water surface to an average height of the surrounding vegetation. At the
10 same points we measured pH and electrical conductivity; conductivity readings were corrected for pH.
11 Water samples (30 ml) were collected, filtered at 0.7µm (Whatman Autotop GF/F) and analysed for
12 total carbon (TC) and inorganic carbon (IC) after purging the sample with phosphoric acid, by high
13 temperature catalytic combustion using a Shimadzu TOC-L. These data were used to calculate dissolved
14 organic carbon (DOC) and dissolved inorganic carbon (DIC) concentrations. Absorbance was measured at
15 465 and 665nm using a Camspec M350 UV/ Visible spectrophotometer and these data were used to
16 calculate the E4:E6 ratio which can indicate the relative contributions of humic and fulvic acids and the
17 degree of decomposition of the DOC (Chen et al., 1977). All field samples were collected in over a two
18 day period without precipitation.

19 *2.4 Vegetation*

20 We conducted vegetation surveys at two levels of resolution. At the finest spatial scale we conducted
21 point recording at 1 m intervals along the length of each transect. At each survey point a 1 m rule was
22 placed at right-angles to the transect line and all plant species touching this recorded as
23 presence/absence. At five metre intervals along the transects we conducted more intensive surveys by
24 placing a 1x1 m quadrat and recording the cover of all plant species on the Domin scale (Rodwell, 2006).

25 To quantify changes in tree species composition and size structure along transects we recorded the
26 number, basal stem diameter and species of all trees 5 m either side of the transect line with sections
27 separated every 5 m along the transect length (a total of 50 m² per section). From this data we
28 calculated total basal area for each tree species and both tree species combined.

29 *2.5 Testate amoebae*

30 Payne et al (2016) have previously reported the analysis of testate amoebae along four of these
31 transects, as well as several further transects in other sites. Here we re-visit these data to discuss them
32 in more detail and place them in context with the broader suite of data available for the Mukhrino site.
33 Samples (c.25 cm³) were extracted from the same locations as the plant samples. Samples were
34 prepared by soaking in water and the material was washed through a sieve (250µm) to remove plant
35 and coarse particulate matter; the fine-sieving process used in some studies was omitted to avoid the
36 loss of small taxa (Payne, 2009). The filtrate was allowed to stand overnight to concentrate the tests.
37 Amoeba tests were identified and counted at 200 x and 400 x magnification and search effort was
38 restricted to 100 individuals per sample (Mitchell and Gilbert, 2004; Payne and Mitchell, 2009)

1 Morphological identification was based on several guides (Charman et al., 2000; Mazei and Tsyganov,
2 2006; Ogden and Hedley, 1980) as well as some identification keys based on monographs to specific
3 genera or species groups (E.A.D Mitchell 2014, Personal communication). For some samples SEM
4 (Scanning Electron Microscope) pictures were taken to confirm the identification. This was achieved by
5 placing 0.2ml of the same solution used for optical microscopy onto aluminium stubs and air drying
6 samples in a desiccator for 3 days prior to SEM analysis.
7

8 *2.6 Stratigraphy*

9 At one transect (transect five) we studied the stratigraphic record of long-term vegetation change and
10 carbon accumulation across the forested-to-open-bog transition. We used a 5 cm-bore Russian corer to
11 extract three cores, positioned at point zero of the transect in the forested peat (ryam), at the ecotone
12 (20 m along the transect) and the open *Sphagnum* lawn (35 m along the transect). The cores were 3.4,
13 3.2 and 3.0 meters long. The cores were sub-divided into contiguous 10 cm sections and one sample
14 analysed for dry bulk density, loss on ignition and carbon content and a second sample for botanical
15 composition. Sub-samples of known volume were dried at 105°C, weighed and one sub-sample
16 incinerated at 550°C and re-weighed (Chambers et al., 2011). The second sub-sample was ground and C,
17 H and N contents determined using an elemental analyser (Eurovector EA 3000, Yugra state University).
18 The samples for botanical composition were disaggregated in water and inspected under low-power
19 microscopy at 20-40 -x resolution. Dominant species were identified and peat assigned to one of forty
20 stratigraphic units (see results). The abundance of fine, degraded unidentifiable organic matter (UOM)
21 was determined on a percentage scale using a grid graticule and used as an index of decomposition.

22 *2.7 Data analyses*

23 In presenting the data the mid-point of the ecotone (visually identified in the field based on vegetation
24 change) is given a value of 0, positive numbers represent points towards the open bog end of the
25 transect and negative numbers the forested end of the transect. To allow easy representation of change
26 along transects we summarised the testate amoeba and plant community data using first axis scores
27 from an NMDS ordination of all samples using Bray-Curtis dissimilarity (Bray and Curtis, 1957). To test
28 for correlations among variables we used Spearman Rank correlation coefficients. We tested for
29 differences in all variables either side of these ecotones using repeated measures analysis of variance
30 (RM-ANOVA) to account for the multiple-transect sampling structure. To test whether change in each
31 variable was maximised at the observed ecotone or whether there were consistent spatial off-sets, we
32 applied non-parametric change-point analysis (nCPA: (Qian et al., 2003)). This method identifies the
33 point along the transect which maximises reduction in deviance; these change-points can be considered
34 to represent environmental thresholds (Brenden et al., 2008). For most of the variables considered we
35 would expect to identify a change-point at the transition between forested and open bog and for
36 change-points in a variety of variables to occur at the same point. Statistical analyses were conducted in
37 R (R - Development Core Team, 2013) using the packages vegan (Oksanen et al., 2008), car (Fox and
38 Weisberg, 2010), and rpart (Therneau et al., 2014) and with thePAST software vers. 3.04 (Hammer et al.,

1 2001). To investigate the probable origin of organic carbon along transects we applied End Member
2 Mixing Analysis (EMMA) (Christophersen et al., 1990).

3 3. RESULTS

4 3.1 Physical and chemical data

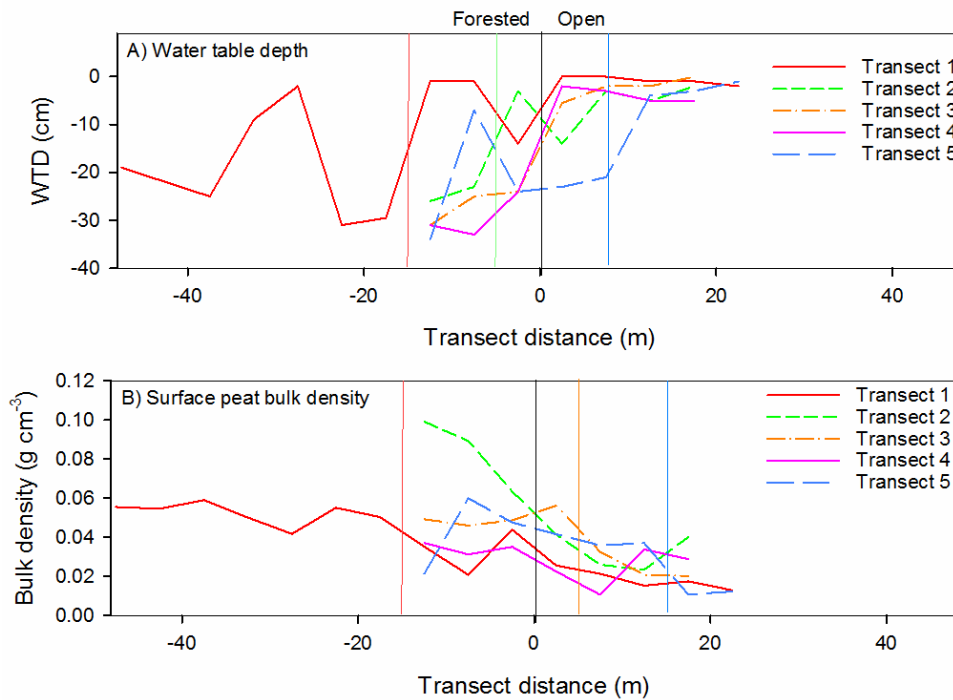
5 Both water table depth (WTD) and surface bulk density showed strong differences across the ecotones.
6 Water tables in the forested bog were considerably deeper (2.2 times the mean) and the surface peat
7 was considerably denser (1.9 times the mean) with both differences highly significant (Table 1; bulk
8 density $P=0.003$; WTD $P=0.013$). In both cases there was some scatter in change point locations due to
9 variability between and within transects (Figure 2). Particularly notable was the secondary peak in water
10 table due to the presence of a ridge prior to the transition to open bog in transect one. The high bulk
11 density of the forested end of transect two was also notable, most likely due to the high ryam
12 vegetation with low abundance of *Sphagnum*.

13

	F	P-value
WTD	6.8	0.013
Bulk density	9.7	0.003
pH	-	-
Conductivity	-	-
DOC	5.6	0.023
DIC	30.3	<0.001
E4:E6	-	-
Plants (NMDS)	6.4	0.015
Plants (H)	-	-
Plants (SR)	-	-
Tree Area	9.1	0.004
Testate amoebae (NMDS)*	5.0	0.033

14

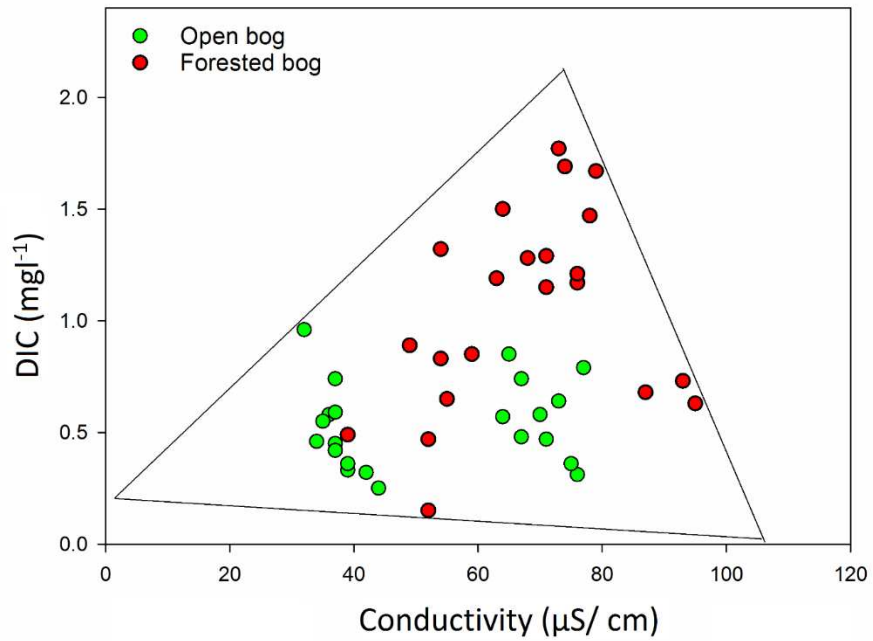
15 *Table 1. Tests of difference between samples from open and forested ends of transects (as judged in field) using repeated-*
16 *measures analysis of variance (RM-ANOVA) to account for sampling structure, showing F-score and P-value for significant*
17 *analyses ($P<0.05$) only. *Testate amoeba results are for four transects only so not directly comparable to other analyses.*



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Figure 2. Change in peat physical properties: A) water table depth and B) bulk density along Mukhrino transects. Black vertical line shows the field-assessed ecotone and nCPA change-points where not otherwise shown. Coloured vertical lines show nCPA change-points where these do not coincide with judged ecotone.

6 Aquatic carbon concentrations generally decreased from the forested ends to the open bog ends of the
7 transects (DOC: $P=0.023$, DIC: $P<0.001$). The difference was relatively minor for DOC with only slight
8 trends along transects 1 and 5. For DIC the relationship was stronger with very clear trends across nearly
9 all of the transects. nCPA change points lay at the observed ecotone with the exception of transect three
10 for DOC, but were more inconsistent for DIC. EMMA analysis (Figure 3) showed measurements can be
11 grouped into three end members. These are 1) measurement with Low conductivity ($\sim 20 \mu\text{S cm}^{-1}$), low
12 DIC ($\sim 0.2 \text{ mg l}^{-1}$) and E4/E6 ratio (~ 4) values (not shown) these are mostly composed of samples from
13 the open bog points. 2) those points with high conductivity ($\sim 110 \mu\text{S cm}^{-1}$), low DIC ($\sim 0.1 \text{ mg l}^{-1}$) and
14 E4/E6 (~ 4) values which are also associated with open peatland and 3) those points with intermediate
15 conductivity ($\sim 65 \mu\text{S cm}^{-1}$) value and high DIC ($\sim 2.3 \text{ mg l}^{-1}$) and E4/E6 (~ 20) values (not shown), which
16 here are clearly associated with forested peatlands.



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Figure 3. End member mixing analysis plots for water chemical variables across Mukhrino transects.

Electrical conductivity and pH were not significantly different across transects when tested using RM-ANOVA (Table 1) but were found to be significantly correlated with tree cover (Table 2), pH decreasing and conductivity increasing with greater tree cover. E4:E6 ratios were found to show no association with position along the transects or with tree cover.

	WTD	Bulk density	pH	Conductivity	DOC	DIC	E4:E6	Plants (NMDS)	Plants (H)	Plants (SR)	Tree area	Testate amoebae (NMDS)*
WTD	-	-0.60						0.79	-0.42	-0.38	-0.63	0.71
Bulk density	-0.60	-				0.45		-0.77	0.42	0.42	0.71	-0.71
pH			-	-0.58	-0.70	-0.50	-0.48	0.35		0.34	-0.47	0.37
Conductivity			-0.58	-	0.85	0.40	0.37	-0.38			0.40	
DOC			-0.70	0.85	-	0.66	0.46	-0.30			0.42	
DIC		0.45	-0.50	0.40	0.66	-		-0.34			0.52	-0.41
E4:E6			-0.48	0.37	0.46		-					
Plants (NMDS)	0.79	-0.77	0.35	-0.38	-0.30	-0.34		-	-0.35		-0.80	0.78
Plants (H)	-0.42	0.42						-0.35	-	0.72		
Plants (SR)	-0.38	0.42	0.34						0.72	-		
Tree Area	-0.63	0.71	-0.47	0.40	0.42	0.52		-0.80			-	-0.84
Testate amoebae (NMDS)*	0.71	-0.71	0.37			-0.41		0.78			-0.84	-

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*Table 2. Spearman rank correlation coefficients between variables considered in this study. Coefficients only shown where $P < 0.05$. Coefficients greater than 0.5 are highlighted in bold. *Testate amoeba data is only available for four transects; all correlations with testate amoebae data are only based on these transects and therefore not directly comparable with other results.*

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There were strong correlations between many of the variables considered along the transects (Table 2). Tree basal stem area was significantly correlated with all variables with the exception of plant diversity (species richness and H) and E4:E6 ratio. Plant community composition summarised by NMDS1 scores was similarly significantly correlated with all variables with the exception of plant species richness and E4:E6 ratio. Strong positive correlations were identified between tree stem area and plant community ($R_s=0.80$) and testate amoeba community ($R_s=0.84$) and between DOC concentration and electrical conductivity ($R_s=0.85$).

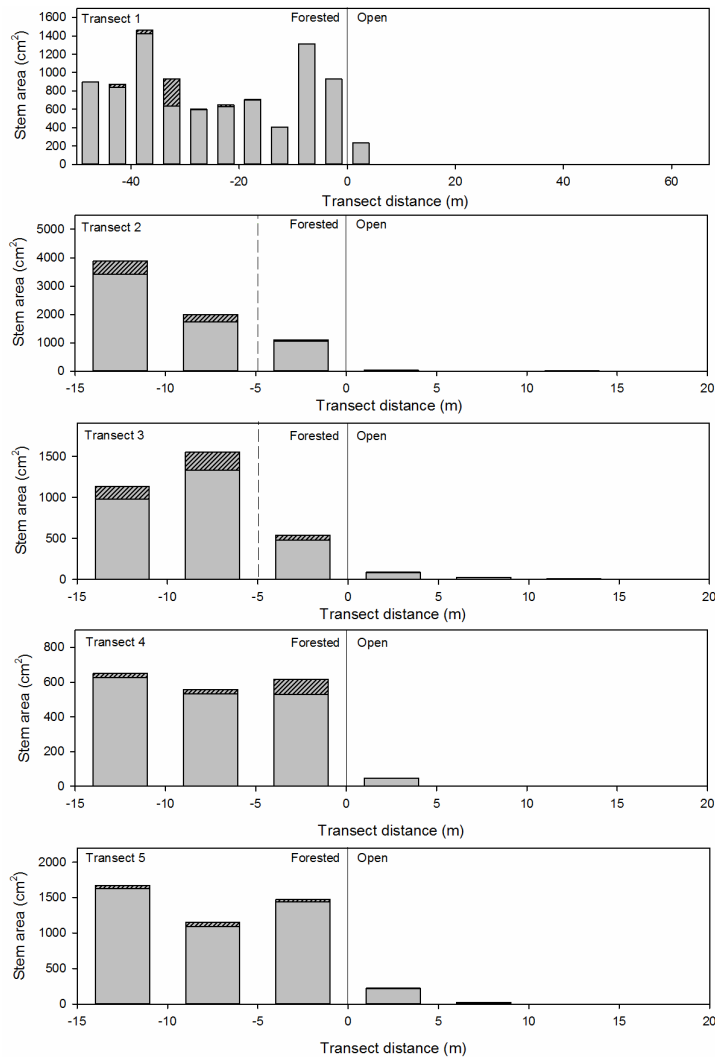
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3.2 Vegetation

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Tree cover, unsurprisingly, show abrupt change between forested and open bog. The tree basal stem area data (Figure 4) show that the forest is primarily dominated by *P. sylvestris* and both conifer species more-or-less abruptly disappeared at the ecotone with just a few small and scattered trees continuing subsequently amongst vegetation dominated by open bog species. The difference either side of the ecotone was highly significant ($P=0.004$, Table 1). There was little discernible difference in response between the two tree species with both declining at similar locations. The positions of the ecotones judged in the field generally aligned closely with those assessed by nCPA with only two exceptions where there was a drop in basal area prior to the ecotone.

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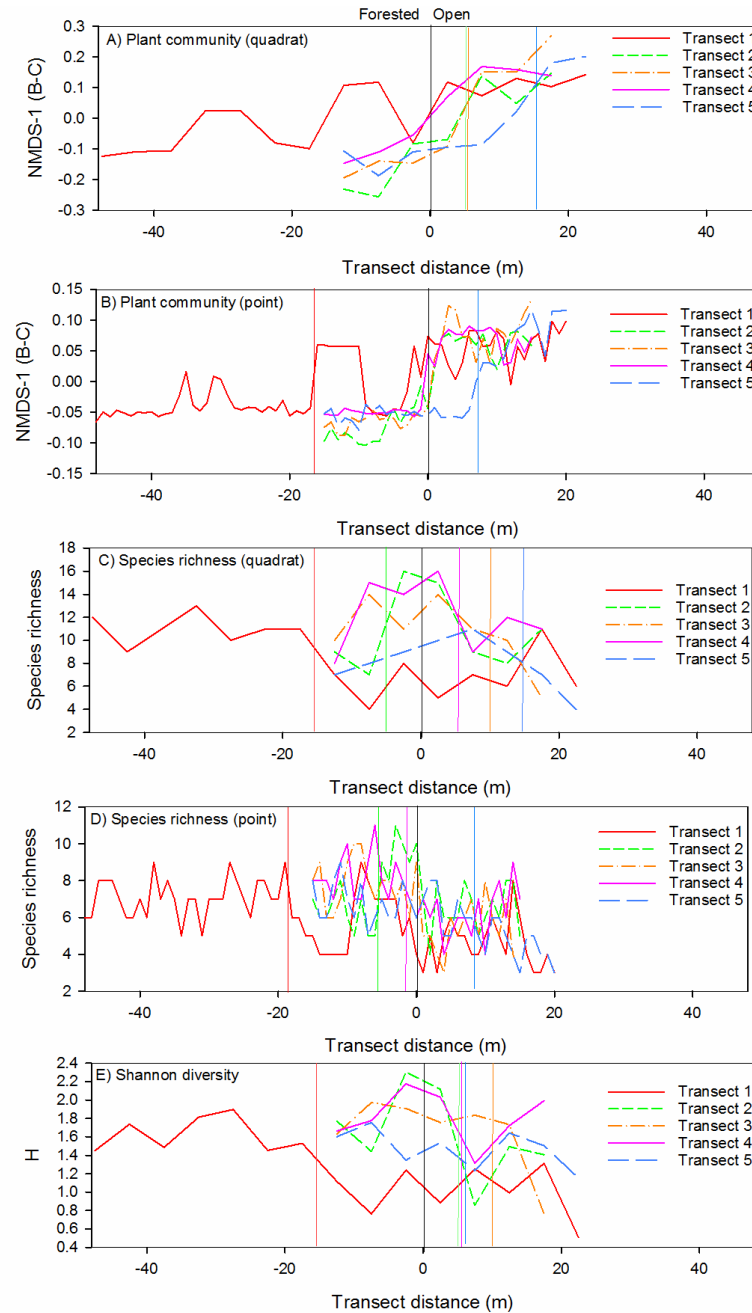
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2 *Figure 4. Change in total basal stem area along transects by species for P. sylvestris (open bars) and P. sibirica (hatched bars).*
 3 *Vertical solid lines show position of ecotone as judged in field. Vertical dashed lines show nCPA change-points; where not shown*
 4 *these align with the qualitatively-judged ecotone position.*

5

6 Plant community composition data (Figure 5) likewise showed strong trends along the transects. Typical
 7 species of the forested end of transects included *Sphagnum fuscum*, *Vaccinium uliginosum* and
 8 *Chamaedaphne calyculata*. Typical species of the open bog end of transects included *S. balticum*, *S.*
 9 *jensenii* and *Scheuzeria palustris* (Supplementary Figure 1A). Both the point measurements every 1 m
 10 and the quadrat measurements every 5 m showed abrupt changes at or adjacent to the field-assessed
 11 ecotone in most transects. Exceptions were primarily in transect one where the presence of a ridge with
 12 trees made the transition more complex, and transect five where the change was more gradual. The
 13 difference between community composition either side of the ecotone was significant ($P=0.04$, Table 1).
 14 There was a general trend towards lower plant species richness in the open bog, particularly apparent in
 15 the point measurements (Figure 5). Similar trends were apparent when considering Shannon diversity,
 16 which incorporates evenness as well as species numbers (Figure 5). However in both of these cases

- 1 differences across the ecotone were non-significant and nCPA change-points diverged considerably from
- 2 the observed ecotones with considerable scatter apparent (Figure 5).



3

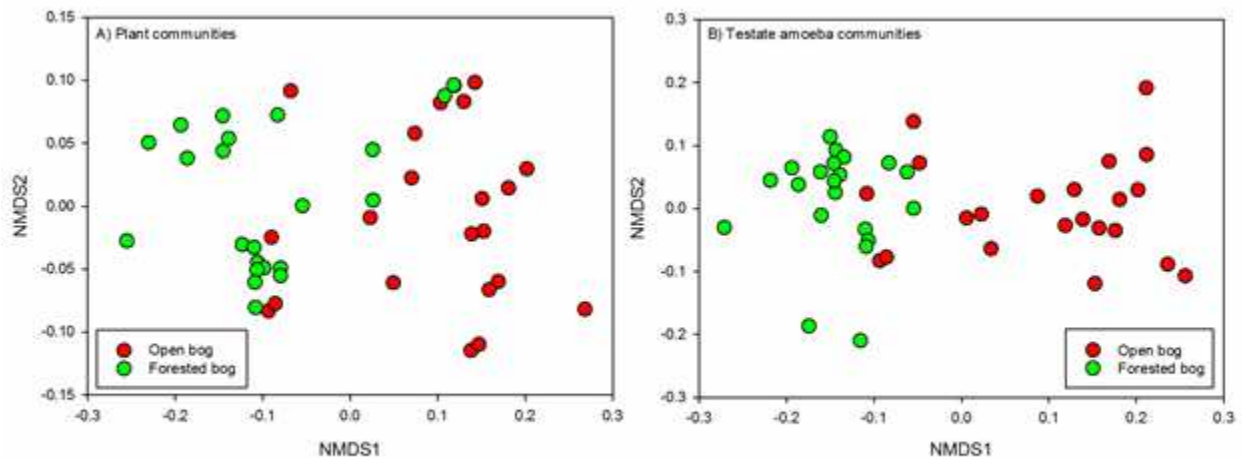
4 *Figure 5. Change in plant community along the transects from forested bog (left) to open bog (right): A) community composition*
 5 *summarised by NMDS axis one scores using Bray-Curtis dissimilarity for quadrats placed every 5 m subplot; B) community*
 6 *composition summarised by NMDS axis one scores using Bray-Curtis dissimilarity for point measurements every 1 m; C) species*
 7 *richness assessed by quadrat; D) Species at 1 m points along transects; E) Shannon Diversity (H) based on quadrat data (the lack*
 8 *of relative abundance data for the point measurements means H cannot be calculated). Black vertical line shows the field-*
 9 *assessed ecotone and nCPA change-points where not otherwise shown. Coloured vertical lines show nCPA change-points where*
 10 *these do not coincide with judged ecotone. Equivalent plots for testate amoeba data have been previously presented by Payne*
 11 *et al. (2016).*

1

2 3.3 Testate amoebae

3 Overall, the testate amoeba community was found to be relatively diverse with 60 taxa identified from
4 the twenty nine samples (Supplementary Figure 1b). The assemblage was primarily composed of taxa
5 frequently recorded in Eurasian peatlands. The most abundant taxa in descending order were: *Assulina*
6 *muscorum* (16% of all tests), *Trinema lineare* (10.4% of all tests). Photomicrographs of some of these
7 taxa are shown (Supplementary Figure 3). Trends along transects were highly apparent in the testate
8 amoeba data. At the forest end of the transects taxa such as *T. lineare*, *C. dubium*, *A. muscorum*, *Arcella*
9 *catinus* and *Trigonopyxis minuta* were more abundant. At the open bog end of transects taxa such as *H.*
10 *elegans*, *H. papilio*, *A. flavum* and *Diffugia globulosa* were more abundant. NMDS revealed a clear
11 distinction between forested and open bog testate amoebae communities (Figure 6). The difference
12 between community (summarised by NMDS first axis scores) was significant ($P=0.03$, Table 1) and nCPA
13 change points lay close to the observed ecotone (see Payne et al. 2016).

14



15 *Figure 6. NMDS ordination plots of A) plant communities (quadrat surveys) and B) testate amoebae. Plots highlight the*
16 *difference in assemblage either side of the field-assessed ecotone.*

17

18 3.4 Stratigraphy: Macrofossil composition

19 At the base of all three cores were clay sediments overlain by layers rich in wood macrofossils. In the
20 core from the forested end of the transect, the dominant macrofossil component through the majority
21 of the core was *Sphagnum fuscum* with a minor component of ericoid shrubs. From 90-130 cm there
22 was a shift to a community with a greater abundance of *Eriophorum* spp., and from 90-120 cm
23 *Sphagnum angustifolium*. Above this phase the dominance of *S. fuscum* was resumed with the only
24 really notable further change being the brief presence of *S. subsecundum* from 40-60 cm.

1 The core from the ecotone was considerably more variable. From the top of the basal clays sediments to
2 280 cm there was a progressive shift from woody peat to peat rich in macrofossil remains of *Carex*
3 followed in turn by an abrupt shift to peat dominated by *Eriophorum*. A brief phase with abundant
4 *Scheuchzeria* was followed by a more prolonged phase dominated by *S. fuscum*. Between 230 and 140
5 cm *Scheuchzeria* was the dominant macrofossil component but with considerable inter-sample
6 variability. From 140-70 cm the peat was composed of similar proportions of *Scheuchzeria*, *Sphagnum*
7 *balticum* and *S. jensenii* with *S. majus* also a frequent presence. *S. balticum* was dominant from 30-50
8 cm and *S. fuscum* for the uppermost 30 cm.

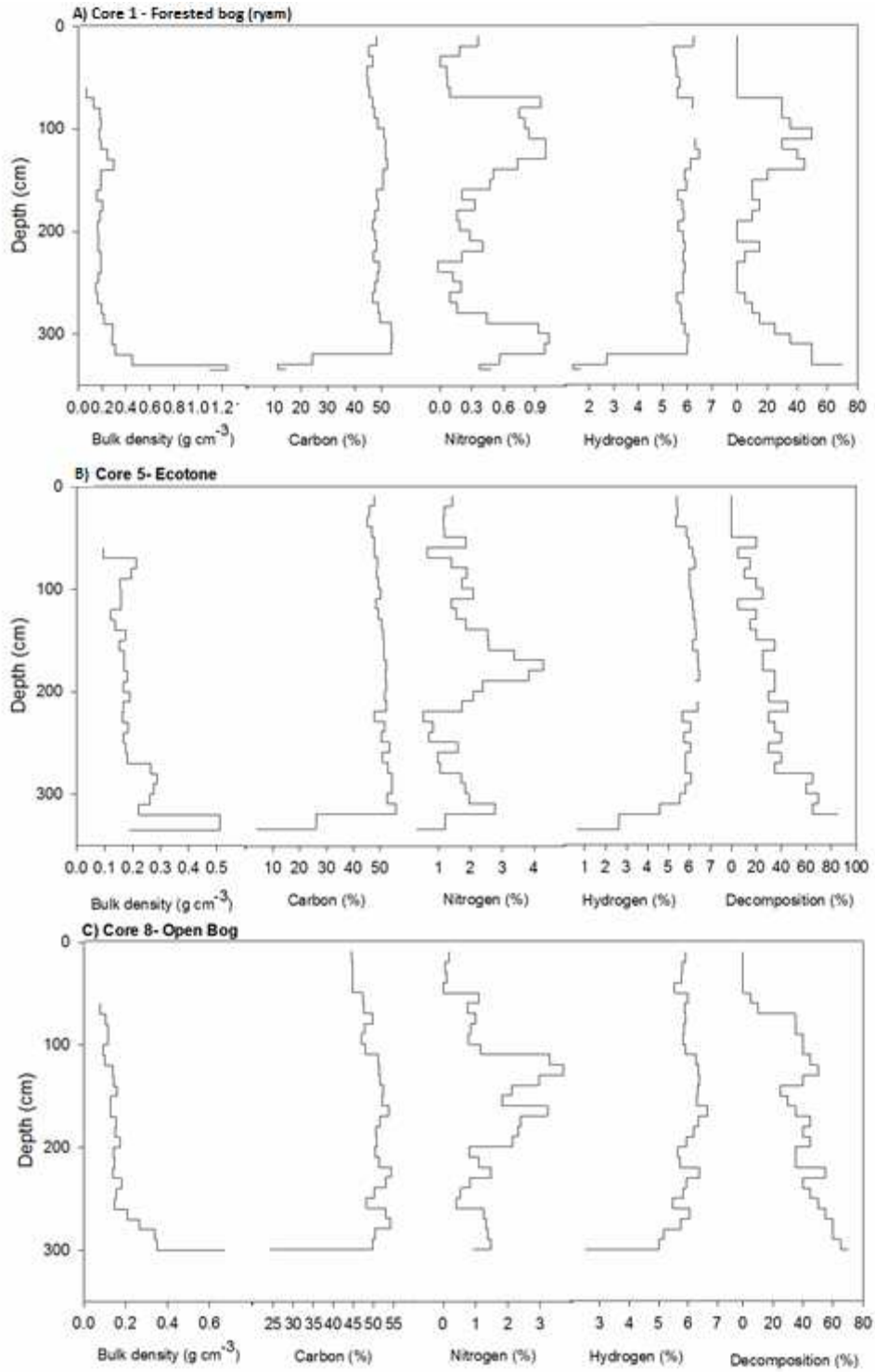
9 In the core from the open bog end of the transect the clay and woody peat at the base were overlain by
10 a stratigraphic unit with abundant *Eriophorum* (240-270 cm). From 220-240 cm *Sphagnum fuscum* was
11 the most abundant macrofossil component. Above this point until the relatively recent past
12 *Scheuchzeria* macrofossils were the most abundant group with *S. jensenii* sub-dominant. At 90-100 cm
13 there was a brief phase with much less *Scheuchzeria* and more *S. jensenii* and the presence of *S.*
14 *balticum*. From 60 cm there was a gradual decline in *Scheuchzeria* and increase in *S. balticum* which
15 constituted more than three quarters of identifiable macrofossils by the top of the core.

16 3.5 Stratigraphy: Peat properties

17 Across all three cores bulk density averaged 0.22 g cm^{-3} , carbon content 47.7%, nitrogen content 1.17%
18 and hydrogen content 5.61%. Bulk density increased down the cores but the trend was relatively gradual
19 until a sharp transition to higher bulk density wood peat and clay sediments at the base of all the cores.
20 Bulk density was higher in the forested core (0.271 g cm^{-3}) followed by the transitional ecotone core
21 (0.196 g cm^{-3}) then the open bog core (0.181 g cm^{-3}). Bulk density was not determined for the
22 uppermost 50 cm due to the difficulty in accurately sampling very undecomposed fresh peat. Carbon
23 content showed relatively little trend down the cores with the exception of the transition to low-carbon
24 clay rich sediment at the base of all three cores. Trends for hydrogen content were similar. Nitrogen
25 content showed the most-down core variability but percentages were low and therefore analytical error
26 more significant. In the forested core nitrogen content was greatest from 70-130 cm in the forested core
27 which overlaps with a phases of increased *Eriophorum* abundance in the macrofossil stratigraphy, this is
28 not apparent in the others cores. For the open and ecotone cores nitrogen content peaks at 260-320 cm
29 which is associated with a phase of *Scheuchzeria palustris* in the macrofossil stratigraphy. Compared to
30 the global averages calculated by our results suggest that carbon content of the peat in our study site is
31 relatively typical while bulk density is towards the higher end of the global range.

32 In all the cores there was a down-core trend of increasing peat decomposition reflected in the
33 abundance of degraded organic matter (Figure 7). In the forested core there was a phase of more
34 decomposed peat from 70-130 cm and a similar, but less pronounced, phase at similar depths was also
35 apparent in the open bog core. In the open bog and the ecotone core the increase in decomposition
36 with depth was relatively gradual, whereas in the forested core there was a sharp increase towards the
37 base of the core. Overall humification was lower in the forested core with 18.8% degraded material,
38 compared to the ecotone (29.7%) and the open bog (36.3%) For the lower 250 cm of the forested core
39 humification is lower than in the open bog and ecotone core however this pattern was reversed in the

- 1 more recent peat and could be related to the change from *Sphagnum fuscum* towards more easily
- 2 decomposable *Eriophorum* in the forested core.



3

4 *Figure 7. Stratigraphic change in the three cores from transect five showing bulk density, contents of C, N and H and peat*
 5 *decomposition determined microscopically.*

1

2 4. DISCUSSION

3 Our data suggest that if climate change leads to increasing tree cover in boreal peatlands peatland biota
4 and biogeochemistry will be substantially altered. Even across the short spatial distances we considered
5 here there were large differences in key variables controlling the structure and functioning of the
6 peatland ecosystem. Tree cover was, significantly and often strongly correlated with the biotic, physical
7 and chemical variables measured here with the only exception being plant diversity and E4:E6 ratios.

8 Differences in the plant communities of open and forested bog are marked, despite their close
9 proximity, with a high level of species turnover along individual transects. Ordination plots show near-
10 perfect separation of plant communities between forested and open bogs (Figure 6). The balance of
11 plant functional types differs between these communities with, in particular, a higher cover of dwarf
12 shrubs (and, of course, trees) in the forested bog. *Sphagnum* mosses are abundant in both communities,
13 with the exception of the denser high ryam of transect two. However, the *Sphagnum* species differ
14 between the open and forested communities and it is likely that productivity also differs due to shading
15 by the trees, for example the productivity of *Sphagnum fuscum* is dramatically reduced under closed
16 canopy conditions (Bauer et al., 2007) and is a poor competitor under closed canopy conditions (Vitt and
17 Slack, 1984). Shade tolerant bryophytes which may replace *S. fuscum* such as *S. teres* and *Pleurozium*
18 *schreberi* have comparatively low productivity, in the case of *S. teres* (Gunnarsson, 2005), or are
19 comparatively easy to degrade in the case of *P. schreberi* (Wardle et al., 2003) making them poor
20 peatformers. Shifts between species with different litter decomposability and productivity may have
21 implications for peatland carbon sequestration and storage capacity (Bauer, 2004). Indeed, *S. fuscum* is
22 known to be relatively resistant to decomposition (Johnson and Damman, 1991) and may produce more
23 recalcitrant litter than the dominant species of the open bog: *S. balticum* and *S. jensenii*. On the other
24 hand, with lower WTD in the forested bog (Figure 2), *S. fuscum* litter will likely be exposed to oxidative
25 decomposition for longer. The greater depth and bulk density of the *S. fuscum* dominated forested core
26 would suggest greater carbon accumulation in forested compared to open conditions. However open
27 canopy conditions may be most vulnerable to increases in tree cover due to the sensitivity of *S. fuscum*
28 to shading.

29 The testate amoeba data demonstrates that changes across the ecotone in below-ground microbiota
30 are of equivalent magnitude to those observed above-ground. Unlike the plant communities there are
31 many taxa with cosmopolitan distributions present in both the forested and open bog ends of the
32 transects but there is extensive replacement with assemblages from the forested bog closely resembling
33 those common in forests on mineral soils (Payne et al., 2016) The most abundant taxa found in the open
34 peatlands: *H. papilio*, *A. flavum* and *H. elegans* correspond well with those found in bogs elsewhere in
35 Siberia (Chernyshov, 2010; Rakhleeva, 2002). Of those taxa most common at the forested end of the
36 transect (*A. muscorum*, *T. lineare*, *C. dubium*, *A. arenaria* and *A. catinus*) only two, *A. arenaria* and *A.*
37 *catinus* are known to have a preference for peatlands (Chernyshov, 2010). The abundance of the other
38 species typifying the forested peatlands may reflect moisture availability (Mazei and Chernyshov, 2011)
39 and/or the availability of food sources. Our findings provide further evidence for the ecological

1 plasticity of *A. muscorum*, which has been found to dominate the forested end of our transects and has
2 been recorded as having a preference for dry habitats (Mazei and Chernyshov, 2011) but has also been
3 found to dominate the community in open bogs in other studies (Chernyshov, 2010; Kur'ina, 2011;
4 Kur'ina et al., 2010). As noted by Payne et al. (2016) there may be functional impacts of these changes
5 along the transects as the community from the open bog end has a higher proportion of mixotrophs and
6 taxa with typically larger apertures, suggesting larger prey sizes. Our additional environmental data
7 provide some indications as to the drivers behind these differences. The strongest correlates with
8 testate amoeba communities are tree cover, plant communities, water table depth and bulk density
9 (Table 2). The correlation with tree cover and plant communities is likely to partly reflect light availability
10 for mixotrophic amoebae but it is clear that mixotrophic taxa are not the only taxa which differ along
11 the transects. Other linkages may include bacterial prey affected by root exudates and the presence of
12 conifer-root associated mycorrhizal fungi. Mycorrhizas may be consumed by testate amoebae but
13 testate amoeba shells may also provide a food source for mycorrhizas (Vohník et al., 2011). The
14 influence of water table on testate amoebae is well-documented and both this and bulk density are
15 likely to influence the ability of amoebae to move and feed.

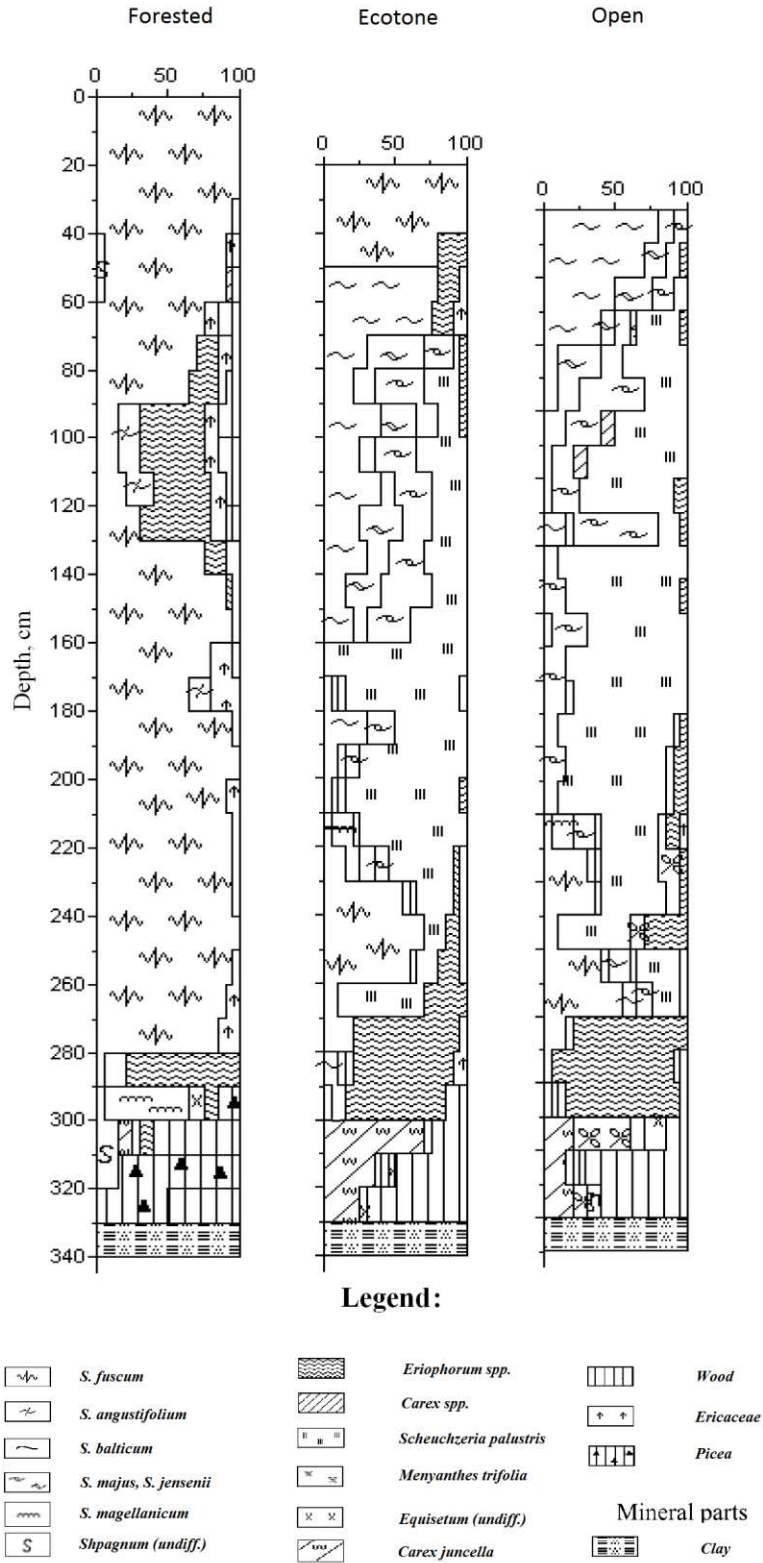
16 Dissolved organic carbon, and particularly dissolved inorganic carbon, are considerably higher at the
17 forested end of these transects and both are significantly correlated with tree basal area. The trend in
18 DOC is to be expected as forests tend to be more productive than open bogs and have a faster turnover
19 of carbon (Hommeltenberg et al., 2014; Meyer et al., 2013). However the deeper water table and higher
20 bulk density seen in the forested transects would also suggest greater decay occurs under forested
21 conditions. The E4/E6 ratio of peatland water can be used to analyse the degree of decomposition the
22 source material has undergone (Wilson et al., 2011), while there was no clear pattern across transects
23 when compared to literature values the E4/E6 ratios found here are consistently high, indicating the
24 source material across all sites is predominantly unhumified recently fixed carbon (Wilson et al., 2011).
25 After adjustment for pH, electrical conductivity of peatland water was higher at the forested ends of the
26 transect indicating there may be more water soluble nutrients in the forested peat.

27 The high E4/E6 ratio of porewater DOC would indicate that the lower concentration of DOC and DIC
28 values at the open end of the transects may be due to lower plant productivity. As our data are
29 concentrations rather than fluxes, it is difficult to draw firm conclusions on the effect of tree cover
30 change on DOC export. However, the increase in DOC concentration for forested peat demonstrates it is
31 possible that increasing tree cover could lead to increasing aquatic carbon export from boreal peatlands.
32 Whether this is the case or not will also depend also on the effect of trees on catchment discharge
33 which is complex (Waddington et al., 2015). Increased evaporative losses due to interception and
34 transpiration must be weighed against changes to surface evaporation driven by light penetration and
35 canopy resistance, with the resulting change in the water balance dependent on the vegetation
36 structure of the site along with climatic variables (Waddington et al., 2015). For example the net effect
37 of tree cover on total evaporation, including transpiration, in forested bogs may be greater in drought
38 years, but lower under normal conditions (Heijmans et al., 2013). A significant proportion (12-62%) of
39 DOC exported from a site will be released to the atmosphere as CO₂, by in-stream processes such as
40 photochemical reactions and heterotrophic respiration (Dawson et al., 2001; Worrall and Moody, 2014;

1 Worrall et al., 2006). Conversely even small changes in DOC export at the regional scale may cause large
2 alterations in fluvial and marine inputs of carbon, given the vast extent of peatland in Western Siberia
3 (2.8 million km² from Peregón et al (2009)).

4 The stratigraphic analysis of three cores clearly suggests that there has been dynamism in the position of
5 the ecotone through the Holocene and as such there is need for a longer-term perspective on the
6 vegetation of these sites. Wood macrofossils were rarely preserved above the base of all the cores.
7 However there were clear changes between assemblages which at the site today are typically associated
8 with tree cover (notably, abundance of *S. fuscum*) and those with taxa more typical of open peatlands.
9 For instance, although the core from the forested end of the transect was dominated by *S. fuscum* for
10 most of its history, the phase with *S. angustifolium* and *Eriophorum* is strongly suggestive of open
11 peatland. In the core from the open bog end of the transect *S. fuscum* was abundant during several
12 phases (particularly 220-240 cm) which may well have seen sufficiently dry conditions for trees to be
13 present. As expected, the core from the ecotone shows high-frequency variability in assemblage,
14 demonstrating the long-term dynamism of this zone. Macrofossil analysis from both the ecotone and
15 open bog demonstrate that the current vegetation (dominated by *S. fuscum* and *S. balticum*
16 respectively) has only been typical for a relatively short period of time with major changes from *S.*
17 *balticum* and *Scheuchzeria palustris* occurring 50 cm from the surface of the core (Figure 8). Changes in
18 vegetation may suggest a shift towards drier conditions in recent years and the appearance of *S. fuscum*
19 towards the surface of the ecotone core would indicate the recent expansion of the forested low ryam
20 peat. A similar change in recent macrofossil composition has been recorded at Mukhrino by
21 Lamentowicz et al. (2015) who found a shift from *S. balticum* and *E. vaginatum* towards *S. fuscum* at 40
22 cm, which was dated to AD 1950. Dendrochronology carried out on trees at Mukhrino reveal pulses of
23 growth and invasion onto open peat in the 16th and 18th centuries with a larger pulse in the 20th century
24 (Blanchet et al., 2017). The macrofossil analysis carried out here indicates only one expansion of tress in
25 the upper section of the core, which has since persisted and is likely to have been initiated over this
26 timescale.

27



1

2

Figure 8. Plant macrofossil stratigraphy of the three cores from Mukhrino Transect five.

3

1

2 Some of these vegetation changes recorded in the macrofossil analysis have resulted in changes in the
3 nature of the peat accumulated. There appears to have been increased sequestration of nitrogen in
4 some phases dominated by *Eriophorum* as opposed to *Sphagnum* (Bragazza et al., 2012). Without a
5 chronology for the cores it is impossible to say precisely when these changes in plant community may
6 have occurred and whether they were associated with changes in accumulation rates. Climatic forcing of
7 many of these changes seems probable. A shift to drier conditions during the little ice age has been
8 proposed (Blanchet et al., 2017; Lamentowicz et al., 2015) which is accompanied by abrupt changes in
9 macrofossil composition (Lamentowicz et al., 2015) and a pulse of tree expansion (Blanchet et al., 2017).

10 The dynamism clearly seen in tree cover for Western Siberia contrasts for instance with the apparent
11 stability seen in some lower latitude peatlands of Eastern Quebec (Pellerin and Lavoie, 2003). However
12 evidence for historical changes in tree cover has been found from peatlands across the world, spanning
13 many different types and climatic gradients (Gear and Huntley, 1991; Ogden et al., 1992; Ohlson et al.,
14 2001; Vitt et al., 1994). It has been proposed that expanding tree cover will have a contradictory impacts
15 on some environmental variables depending on the continentality of the climate (Heijmans et al., 2013).
16 To date there is insufficient data to determine regional differences. Given the large extent of the
17 peatland carbon sink, and the evidence for increasing tree cover, we argue there is a clear need for
18 improved understanding of the impact of tree cover on peatlands across a range of different peat types
19 and climatic gradients.

20

21 5. CONCLUSIONS

22 Our study demonstrates that the ecotone between forested and open peatlands is a dynamic zone,
23 which has been subject to abrupt vegetation shifts throughout history. Most recently this has been an
24 expansion of the forested bog onto previously open peatland. Contemporary data reveals forest and
25 open peatlands to be ecologically distinct with tree cover to be a strong predictor of both the plant and
26 testate amoeba community. Tree cover also appears to be highly predictive of a number of variables,
27 such as water table depth, pH, electrical conductivity, dissolved organic carbon concentration and bulk
28 density. The impact of expanding cover of *P. sylvestris* and *P. sibirica* on the carbon balance of previously
29 treeless peatland remains a question which needs to be answered. Predictions are difficult to make as
30 changes in litter quality and productivity must be weighed against alterations in the decomposer
31 community and variables such as water table depth and microclimatic conditions. Stratigraphic data
32 indicates the forested peatland has accumulated carbon faster than the open peatland, however this
33 has been highly dependent on one species *S. fuscum*, which is known to be sensitive to shading and is
34 missing from the most densely forested transects. The density of tree cover, not just presence or
35 absence of trees, was found to be important for the majority of chemical and ecological variables
36 measured. Considering the differences seen across biological, physical and chemical variables along
37 transects we anticipate that open and forested peatlands are likely to respond differently to
38 environmental drivers. Changing peatland tree cover is likely to be an important feedback between

1 peatlands and climate. The combination of lower water tables, higher nutrient conditions and increased
2 shading suggests tree cover increases the vulnerability of peatlands to warmer and drier conditions.

3

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13 EL and EZ conducted fieldwork. AC analysed testate amoebae, PG analysed water samples and EL and EZ
14 analysed core samples. RJP and JLR produced the first draft of the manuscript to which all authors
15 contributed comments and interpretation.

16

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