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Tree encroachment may lead to functionally-significant changes in peatland testate amoeba communities

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ABSTRACT

Climate change is likely to cause increased tree recruitment on open peatlands but we currently have little idea what consequences this vegetation change may have below-ground. Here we use transects across forested to open bog ecotones at three Russian peatland complexes to assess potential changes in the most abundant group of peatland protists – the testate amoebae. We show that the testate amoeba communities of forested and open bog are markedly different with a very abrupt boundary at, or near, the vegetation ecotone. Changes along our transects suggest that tree encroachment may reduce the trophic level of testate amoeba communities and reduce the contribution of mixotrophic testate amoebae to primary production. Our study strongly suggests that increased tree recruitment on open peatlands will have important consequences for both microbial biodiversity and microbially-mediated ecosystem processes.

KEYWORDS: Peatland; Forest; Tree; Protist; Climate; Carbon

Climate change is causing treelines to move pole-wards and to higher altitudes around the world (Harsch et al., 2009). Peatland ecosystems are a globally-significant carbon store (c.4-600 GtC (Yu,

2012; Loisel et al., 2014)) with two alternative stable states as unforested 'open' bogs and forested bogs (often known by their Russian name 'ryam')(Agnew et al., 1993). Modelling and experimental evidence show that climatic warming and water table drawdown can lead to a switch between these states with the establishment of trees on formerly-open peatland (Heijmans et al., 2013; Limpens et al., 2014; Holmgren et al., 2015). It is reasonable to expect that rising temperatures and increased drought frequency, combined with ongoing anthropogenic drainage, will lead to increasing areas of boreal peatland switching to tree domination. There is both palaeoecological evidence for greater forest cover in peatland-dominated boreal regions during warmer phases of the Holocene (MacDonald et al., 2008) and monitoring data suggesting recent increases in tree and shrub recruitment in many peatland regions (Esper and Schweingruber, 2004; Shiyatov et al., 2005; Berg et al., 2009). The incursion of trees into previously open bogs has the potential to create positive feedback loops through increased transpiration, interception and shade leading to drying of the bog surface (Waddington et al., 2015). The consequences for microbial communities of such a switch in vegetation are largely unknown but may have important consequences for carbon and nutrient cycling. Here we use a space-for-time substitution approach (Blois et al., 2013) to assess possible changes in communities of the key eukaryotic microbes of peatlands – the testate amoebae – with tree establishment.

We positioned ten transects of 30-45m length across the forested to open bog ecotone at three peatland complexes in western Siberia (Mukhrino 60.9°N, 68.7°E), the Karelia region of northwest Russia ('Black River' 66.5°N, 32.9°E) and the Penza region of European Russia (Morsovo 53.8°N, 42.3°E). Transects (3-4 per site) were labelled based on a qualitative judgement of the centre point of the vegetation ecotone (0m), with positive numbers representing the open bog and negative numbers the forested bog ends of the transect respectively. Samples were extracted every 5m by removing the upper 5cm of bryophytes and any litter (c. 25cm³), giving a total of 74 samples across all sites. Testate amoebae were extracted and enumerated under the microscope using standard methods (Booth et al., 2010). The mean count total was 211 tests and the minimum was 100 (Payne and Mitchell, 2009). To assess community change along the transects we summarised the datasets using first axis scores from an NMDS ordination on Bray-Curtis dissimilarity (Bray and Curtis, 1957). Results (Fig. 1) show large changes in most transects with a very abrupt shift between low and high axis scores. To identify points along the transects which maximised community difference we applied non-parametric change-point analysis (nCPA; (Qian et al., 2003)) (Fig. 1A). Identified change-points were all immediately adjacent to the centre-point of the vegetation ecotone as judged in the field, with two exceptions from the Morsovo site where the vegetation change is more gradual. Redundancy analysis (accounting for the transect structure) showed a highly significant difference between the amoeba communities either side of these points (Hellinger-transformed data; 17.8% variance, P=0.001). This difference remained highly significant even when accounting for water table depth (measured in Mukhrino only; 7.5% variance, P=0.002).

We used Indicator Value analysis (IndVal (Dufrière and Legendre, 1997)) to identify taxa typifying samples on either side of the change points. These groups have clear differences (Fig. 1A). Taxa typifying the open bog end of the transects are generally larger and mixotrophic (e.g. *Hyalosphenia papilio*; *Archerella flavum*) while taxa typifying the forested end are often smaller and bacterivorous (e.g. *Assulina muscorum*; *Corythion dubium*). We used Bray-Curtis dissimilarity to assess mean similarity to communities of mineral soil forests (111 analyses from across Siberia (Malysheva,

78 2011)) and open peatlands (68 analyses (Lamentowicz et al., 2015b)). These results showed some
79 variability but communities at the open bog end of the transects showed greater similarity to other
80 analyses from open peatland and differed strongly ($p < 0.01$; Figure 1) from communities at the
81 forested end, which were more similar to mineral soil forest.

82 To assess the possible functional significance of these changes we considered two key functional
83 traits of testate amoeba communities: the proportion of mixotrophic taxa and the community-
84 weighted mean aperture diameter, which is increasingly used as a metric of trophic position
85 (Fournier et al., 2012; Lamentowicz et al., 2013; Fournier et al., 2015; Lamentowicz et al., 2015a).
86 Aperture diameter data were taken from the literature and direct observations and assigned to five
87 size classes (1=0-10 μm ; 2=10-20 μm ; 3=20-30 μm ; 4=30-40 μm ; 5=>40 μm) using a mean of the
88 maximum and minimum dimensions where reported. Results show an abrupt increase in the
89 proportion of mixotrophs from forested to open bog (although mixotrophs were rare in Morsovo).
90 Testate amoebae from the open bog end of the transects generally had larger apertures, suggesting
91 larger prey and higher trophic position. Both these differences were highly significant ($P < 0.01$; Figure
92 1).

93 Differences in testate amoeba communities between forested and open bog are not particularly
94 surprising but we are not aware of any previous study which has directly demonstrated this. More
95 surprising is the scale of the difference and the abruptness of the change demonstrated by our data,
96 which has the non-linear characteristics of an ecological threshold (Groffman et al., 2006). An open
97 question is whether this response reflects alternative stable states within the testate amoeba
98 community *itself* or whether this is driven by similarly abrupt changes in plant communities and
99 environmental conditions. Changes along the transects may be partly driven by moisture availability,
100 paralleling evidence from many previous studies, but variance partitioning suggests that other
101 factors must also be involved. The most distinct change along the transects is a loss of mixotrophic
102 testate amoebae with tree cover, suggesting that reduced light penetration is an important factor
103 driving the change in community (*cf.* Marcisz et al., 2014). Recent research has suggested that
104 mixotrophic testate amoebae may make a non-trivial contribution to peatland primary production
105 (Jassey et al., 2015). Although microbially-fixed carbon is likely to be a relatively small input
106 compared to plant production, greater lability may make this pool disproportionately important in
107 driving change in the microbial food-web. Our data also show that testate amoebae in open
108 peatland tend to have larger apertures than those of forested peatland. This may reflect differences
109 in available food sources with larger food items such as microalgae and ciliates likely to be more
110 abundant in the open peatland. It is possible that tree encroachment might lead to greater grazing
111 pressure from testate amoebae on bacteria due to the loss of alternative food types, with
112 consequences for the biogeochemical processes those bacteria control.

113 Our study does not allow us to assess how quickly TA communities respond to tree establishment or
114 whether these changes are reversible, but opens the way to palaeoecological studies, which could
115 address this question. Our dataset also provides a baseline for reassessments of these sites in the
116 future.

117 On the basis of our results it seems probable that tree encroachment may lead to large changes in
118 testate amoeba community with important implications for ecosystem processes.

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130 Author contributions: RJP, JR and YuM conceived the study. RJP, AC, JR, RA, EM, ANT, YuM, ML and
131 EDL conducted fieldwork. AC, EM, KM and MZ analysed testate amoebae. RJP, YuM, ML, JGR and RA
132 obtained funding and/or supervised research students. RJP conducted the data analysis and wrote
133 the first draft of the paper. All authors commented on the draft and provided interpretation.

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210 FIGURE CAPTION

211 Figure 1. Testate amoeba community change along forested to open bog transects. A) nCPA change-
 212 points (vertical lines) and significant indicator species as identified by IndVal showing taxa IV>50 and
 213 P<0.05. B) Community change as summarised by first axis scores from an NMDS ordination using
 214 Bray-Curtis dissimilarity. C) Proportion of mixotrophic taxa. D) Community weighted mean (CWM)
 215 aperture diameter in five size classes (1=0-10µm; 2=10-20µm; 3=20-30µm; 4=30-40µm; 5=>40µm).
 216 E) Mean Bray-Curtis dissimilarity relative to testate amoebae communities of open bog
 217 (Lamentowicz et al. unpublished data). F) Mean Bray-Curtis dissimilarity relative to testate amoeba
 218 communities of conifer forests on mineral soil (Mazei et al. unpublished data). In all plots lines
 219 represent individual transects from Mukhrino (shades of red); Morsovo (shades of green) and Black
 220 River (shades of blue). In the bottom right of each plot are results of one way repeated measures
 221 analysis of variance (RM-ANOVA) contrasting data either side of the nCPA change-point.

