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Short communication

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 implications 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. Testate amoebae are the most abundant protists in peatlands (Gilbert et al., 1998) and play important roles in carbon and nutrient cycling (Wilkinson and Mitchell, 2010).

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. 25cm^3), giving a total of 74 samples across all sites. Testate amoebae were extracted, identified and enumerated under the microscope using standard methods (Booth et al., 2010)(Supplementary Table 1). The mean count total was 211 tests per sample and the minimum was 100, sufficient to adequately characterise the community (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. 1B) 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 when accounting for water table depth (measured in Mukhrino only; 7.5% variance, P=0.002) and more variance was explained by the difference across the change points than by tree stem density for the only site where this was recorded (Mukhrino only; 29.9% variance, P=0.001 versus 19.2% variance, P=0.001).

We used Indicator Value analysis (IndVal (Dufrêne 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 pairwise mean similarity to communities of mineral soil forests (111 analyses from across Siberia (Malysheva, 2011)) and open peatlands (68 analyses (Lamentowicz et al., 2015b)). These results showed some variability but communities at the open bog end of the transects showed greater similarity to other analyses from open peatland and differed strongly ($p<0.01$; Supplementary Fig. 1) from communities at the forested end, which were more similar to mineral soil forest.

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

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

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

On the basis of our results it seems probable that tree encroachment may lead to large changes in testate amoeba community with important implications for ecosystem processes such as microbial primary production and predation.

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

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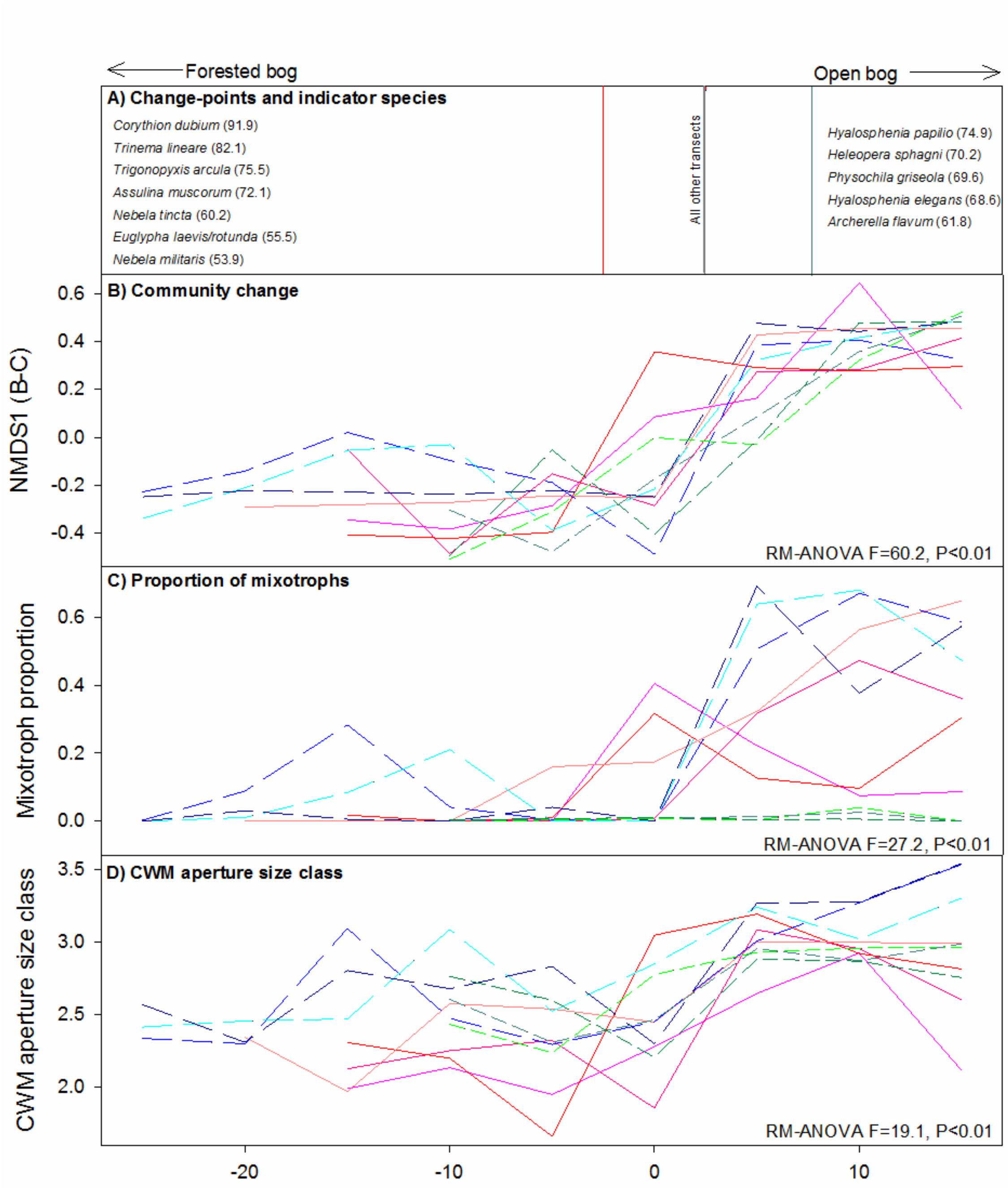
FIGURE CAPTION

Figure 1. Testate amoeba community change along forested to open bog transects. A) nCPA change-points (vertical lines) and significant indicator species as identified by IndVal showing taxa IV>50 and P<0.05. B) Community change as summarised by first axis scores from an NMDS ordination using Bray-Curtis dissimilarity. C) Proportion of mixotrophic taxa. D) Community weighted mean (CWM) aperture diameter in five size classes (1=0-10µm; 2=10-20µm; 3=20-30µm; 4=30-40µm; 5=>40µm). In all plots lines represent individual transects from Mukhrino (shades of red); Morsovo (shades of green) and Black River (shades of blue). In the bottom right of each plot are results of one way repeated measures analysis of variance (RM-ANOVA) contrasting data either side of the nCPA change-point.



Supplementary Table 1. Species abundance across the three study sites.

Supplementary Figure 1. A) Pairwise mean Bray-Curtis dissimilarity relative to testate amoebae communities of open bog (Lamentowicz et al. 2015b). B) Pairwise mean Bray-Curtis dissimilarity relative to testate amoeba communities of conifer forests on mineral soil (Malysheva, 2011). Details as for Figure 1.