



## Original Articles

## Ecology of peatland testate amoebae in the Alaskan continuous permafrost zone

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## ABSTRACT

Arctic peatlands represent a major global carbon store, but rapid warming poses a threat to their long-term stability. Testate amoebae are sensitive hydrological indicators that offer insight into Holocene environmental change in peatlands. However, in contrast to temperate peatlands, there have only been a few studies into the ecology of testate amoebae and their efficacy as environmental indicators in permafrost peatlands. We present the first study of testate amoeba ecology from peatlands in the continuous permafrost zone, based on samples from across the Alaskan North Slope. Multivariate statistical analyses show that pore water electrical conductivity (EC), a proxy for nutrient status along the ombrotrophic-minerotrophic gradient, is the dominant control on testate amoeba distribution. Water-table depth (WTD) is also a significant control on testate amoeba distribution, but is secondary to EC. We present two new testate amoeba-based transfer functions to reconstruct both EC ( $TF_{EC}$ ) and WTD ( $TF_{WTD}$ ), the first for peatlands in the continuous permafrost zone. The transfer functions are based on Weighted Averaging Partial Least Squares (WAPLS) regression and were assessed using leave-one-out (LOO) cross-validation. We find that both transfer functions have good predictive power.  $TF_{WTD}$  is the best performing model ( $R^2_{JACK} = 0.84$ ,  $RMSEP_{JACK} = 6.66$  cm), but  $TF_{EC}$  also performs well ( $R^2_{JACK} = 0.76$ ,  $RMSEP_{JACK} = 146 \mu S cm^{-1}$ ). Our findings are similar to those conducted in peatlands in discontinuous permafrost regions. The new transfer functions open the opportunity for reconstructing the Holocene dynamics of peatlands of the continuous permafrost zone in Alaska, which represent rapidly changing ecosystems.

## 1. Introduction

Climate warming over the last century has been most rapid at high-latitudes (Stocker et al., 2013). Permafrost temperatures in the Northern Hemisphere have increased by as much as 2 °C since 1850, with the continuous permafrost zone warming most rapidly (Vaughan et al., 2013). Peatlands in permafrost areas are especially vulnerable to rapid change and anthropogenic warming (Minayeva et al., 2016) and there is evidence that they are thawing at an accelerating rate (Payette et al., 2004). Arctic peatlands are a major global carbon store of ~277 PgC and occupy 18.9% of Northern circumpolar permafrost area (Tarnocai et al., 2009). Concern exists that as permafrost peatlands thaw, a large proportion of their carbon stock may become unstable and return to the atmosphere (Routh et al., 2014; Schuur et al., 2009). Alternatively, surface peat may insulate permafrost below and limit such degradation (Mann et al., 2010). Palaeoecological approaches have been used to identify recent hydrological changes in domed permafrost

peatlands, including conversion to inundated Arctic fen systems (Swindles et al., 2015a; Gałka et al., 2017). The associated changes in vegetation structure (Christensen et al., 2004) and hydrology (Quinton et al., 2011), combined with continued warming, are likely to promote elevated methane release from degrading permafrost peatlands, with feedbacks to the global climate system.

Permafrost peatlands are predominantly found in Eurasia and Canada, but remain relatively unstudied given their remoteness. In Alaska, peatlands cover at least 78,000 km<sup>2</sup> (Xu et al., 2018) and are found across the Pacific coast, Aleutian Arc and North Slope. Alaskan peatlands hold around 1% of carbon stored in Arctic peatlands (Tarnocai et al., 2009), but are rapidly warming owing to rising air temperatures. This has caused a 1–2 °C warming of surface permafrost in the Northern Brooks Foothills since 1977 (Osterkamp, 2007; Osterkamp, 2005; Osterkamp and Romanovsky, 1999). Warming and degradation of Alaskan permafrost peatlands may be broadly similar to changes observed in peatlands across the wider Arctic, yet reliable

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proxy methods to reconstruct past changes are incomplete for continuous permafrost regions. Indeed, no such contemporary proxy record to reconstruct palaeohydrology exists in any continuous permafrost peatlands globally, despite their vital role in the carbon cycle and the importance of hydrology in carbon accumulation (Charman et al., 2013; Holden, 2005; Belyea and Malmer, 2004).

Testate amoebae are single-celled protists that have been used extensively to reconstruct peatland palaeohydrology in many regions of the world (e.g. Wilmshurst et al., 2003; Payne and Mitchell, 2007; Lamentowicz et al., 2008; Swindles et al., 2014; Swindles et al., 2015a; Amesbury et al., 2016). Testate amoebae form hard shells (tests) that are often well preserved in Holocene peats (Mitchell et al., 2008a). Species-level associations with a limited range of environmental and hydrological conditions (Charman and Warner, 1992) mean that sub-fossil testate amoeba assemblages have been widely utilised in palaeoenvironmental reconstructions, particularly for water-table depth (WTD). Although testate amoebae have been used to reconstruct hydrological change in discontinuous permafrost peatlands across Europe (Zhang et al., 2017; Swindles et al., 2015b) and Canada (Lamarre et al., 2013), little is known about their ecology and effectiveness as ecological indicators in continuous permafrost. Previous studies have reported the presence of testate amoebae in both the contemporary and fossil record of continuous permafrost (e.g. Müller et al., 2009; Mitchell, 2004). However, the potential to use testate amoebae as part of a multi-proxy study in palaeohydrological reconstruction has not yet been fully developed in the continuous permafrost zone.

Our aim is to conduct the first detailed study of testate amoeba ecology in continuous permafrost peatlands. In this investigation, we:

- i. Examine the ecology of testate amoebae in continuous permafrost peatlands from the North Slope, Alaska;
- ii. Produce transfer functions that can be used to reconstruct the most important environmental driver(s) of testate amoeba distribution and;
- iii. Test the hypothesis that WTD is the primary control on the distribution of testate amoebae species in continuous permafrost peatland ecosystems.

## 2. Study sites

Our study comprises five sites across the Alaskan North Slope, within a 55 km radius of Toolik Field Station (Fig. 1; Table 1), and encompasses a range of ecological and hydrological conditions. The five sites span a large trophic gradient, from ombrotrophic bogs to minerotrophic fens, with electrical conductivity (EC) ranging from  $37 \mu\text{S cm}^{-1}$  to  $1176 \mu\text{S cm}^{-1}$ . The landscape is Arctic acidic tundra, with thermokarst lakes and palaeoglaciological features remnant of the last ice age (Gałka et al., 2018; Hinkel et al., 1987; Hamilton, 1986). Active layer (seasonally thawed permafrost) thickness of the continuous permafrost at Toolik is between 40 and 50 cm (Brown, 1998). Air temperature is a key control on seasonal permafrost thaw in the Alaskan North Slope, although topography can create local spatial variability between sites (Hinkel and Nelson, 2003).

Peatlands around Toolik Lake initiated between 8 and 10 kyr in the Brooks foothills (Reyes and Cooke, 2011; Jones and Yu, 2010) as a result of rapid warming (Mann et al., 2010; Morris et al., 2018). Palaeoecological studies have used macrofossil and pollen records to identify the vegetation succession in this region (Gałka et al., 2018). Gałka et al. (2018) also used outline testate amoeba data to infer palaeohydrological changes. However, no quantitative reconstruction of past conditions was possible because no suitable transfer function existed at the time.

## 3. Methods

We collected 100 surface moss samples, 20 each from five peatlands

across the Alaskan North Slope, reflecting a range of hydrological conditions. A well was augered at each sampling point and water level measured at regular intervals until it equalised to determine depth to water table. pH and EC of pore water from each well were measured using calibrated field meters. Approximately 5 g of each sample were weighed, dried at  $105^\circ\text{C}$  overnight, re-weighed to determine gravimetric moisture content (MC), and ignited in a muffle furnace at  $550^\circ\text{C}$  for at least 4 h to determine loss-on-ignition (LOI) (Chambers et al., 2011). We used the EC of pore water as a proxy for peatland nutrient status (see Lamentowicz et al., 2013).

We isolated testate amoebae following Booth et al. (2010). Approximately half of each moss sample was placed in boiling water for 15 min, shaken, passed through a  $300 \mu\text{m}$  sieve and back-sieved through a  $15 \mu\text{m}$  mesh before being stored in a  $4^\circ\text{C}$  cold store. Sub-samples were taken and used to prepare microscope slides which were subsequently examined under a high-power transmitted light microscope at 200 and 400 x magnification. We aimed to count 100 individuals per sample, in addition to *Euglypha* sp., *Trinema* sp. and *Tracheuglypha* sp., as these species do not preserve well in the subfossil peat record (Swindles and Roe, 2007; Mitchell et al., 2008b). Four samples had < 100 individuals ( $n = 97, 96, 88, 41$ ), but we retained samples with counts 50–100 as they have been deemed statistically reliable when diversity is low (Swindles et al., 2007). Individuals were catalogued to species level or ‘type’ (lowest division possible) using identification keys from Charman et al. (2000), Booth and Sullivan (2007) and online guides (Siemensma, 2018).

Statistical analysis was performed in R version 3.4.1. (R Core Team, 2014), using the *vegan* (Oksanen et al., 2017) and *analogue* (Simpson and Oksanen, 2016) packages. Taxa were selected to isolate those that appear in abundance ( $\geq 2\%$ ) in any one sample to reduce the influence of rare taxa (following Swindles et al., 2009). Detrended Correspondence Analysis (DCA) revealed that the data are characterised by long axis gradient length, therefore Canonical Correspondence Analysis (CCA) was subsequently performed on the 100 samples. Given the conflicting criticisms of CCA (see Greenacre, 2013), we also performed ordination with non-metric multidimensional scaling (NMDS) with the Bray-Curtis dissimilarity index and redundancy analysis (RDA) with Hellinger transformed taxon data.

Transfer functions were developed using C2 version 1.7.5 (Juggins, 2007). Weighted Averaging (WA), Weighted Averaging Partial Least Squares (WAPLS) and Maximum Likelihood (ML) transfer functions were developed and tested with the full data set to identify the best performing method.  $R^2$ , RMSEP, and Maximum bias values were used as metrics of performance. ML was dismissed due to relatively poor performance. WA and WAPLS were selected as the best performing models and cross-validated with the ‘leave-one-out’ method and sites with residual values  $\geq 20\%$  of the range (EC:  $n = 228$ ; WTD:  $n = 11$ ) removed. The  $\geq 20\%$  threshold is used as the standard cut-off in the development of testate amoeba based transfer functions (e.g. Charman et al., 2007; Payne and Mitchell, 2007; Swindles et al., 2015b; Amesbury et al., 2016). Tolerance and optima statistics for each taxa were calculated through WA. We applied our transfer functions to a short core from the Lakeshore peatland (Gałka et al., 2018). Transfer functions in peatlands from discontinuous permafrost peatlands (Swindles et al., 2015b) are not suitable as there are several non-analogue taxa. Common taxa that are found across Alaskan North Slope peatlands that are not well-represented in the Swindles et al. (2015b) transfer function include *Conicocassis pontigulasiformis*, *Diffflugia bryophila* and *Gibbocarina galeata*.

We also explored how the host vegetation at each site was influenced by contrasting environmental conditions in our peatlands. Additional sub-samples were suspended in deionised water and the host vegetation was identified with light microscopy at  $200\times$  magnification. Individuals were catalogued to species or ‘type’ level using identification guides from Flora of North America North of Mexico (2007, 2014), Hadenäs (2003) and Smith (2004). Nomenclature follows

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