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Ecology of peatland testate amoebae in the Alaskan continuous permafrost zone

Liam S. Taylor[a], Graeme T. Swindles[a,b], Paul J. Morris[a], Mariusz Gałka[c]

[a] School of Geography, University of Leeds, Leeds, UK.

[b] Ottawa-Carleton Geoscience Centre and Department of Earth Sciences, Carleton University, Ottawa, Ontario, Canada.

[c] Department of Biogeography and Paleoecology, Faculty of Geographical and Geological Sciences, Adam Mickiewicz University, Poznan, Poland.

Corresponding Author: Liam S. Taylor, gylst@leeds.ac.uk

Highlights:

- We examine testate amoebae distribution in continuous permafrost peatlands
- Electrical conductivity is the dominant control on testate amoebae distribution
- Water-table depth is a secondary control on testate amoebae distribution
- Two new transfer functions for reconstructing WTD and conductivity are presented

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 amoeba 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 ($R^2_{JACK} = 0.76$, $RMSEP_{JACK} = 146$ µS 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.

Key Words: Arctic, Ecology, Palaeohydrology, Ecohydrology, Transfer Function, Trophic Gradient.

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^2 (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℃ 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 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 subfossil 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 (Figure 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 μS cm^{-1} to 1176 μS 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).

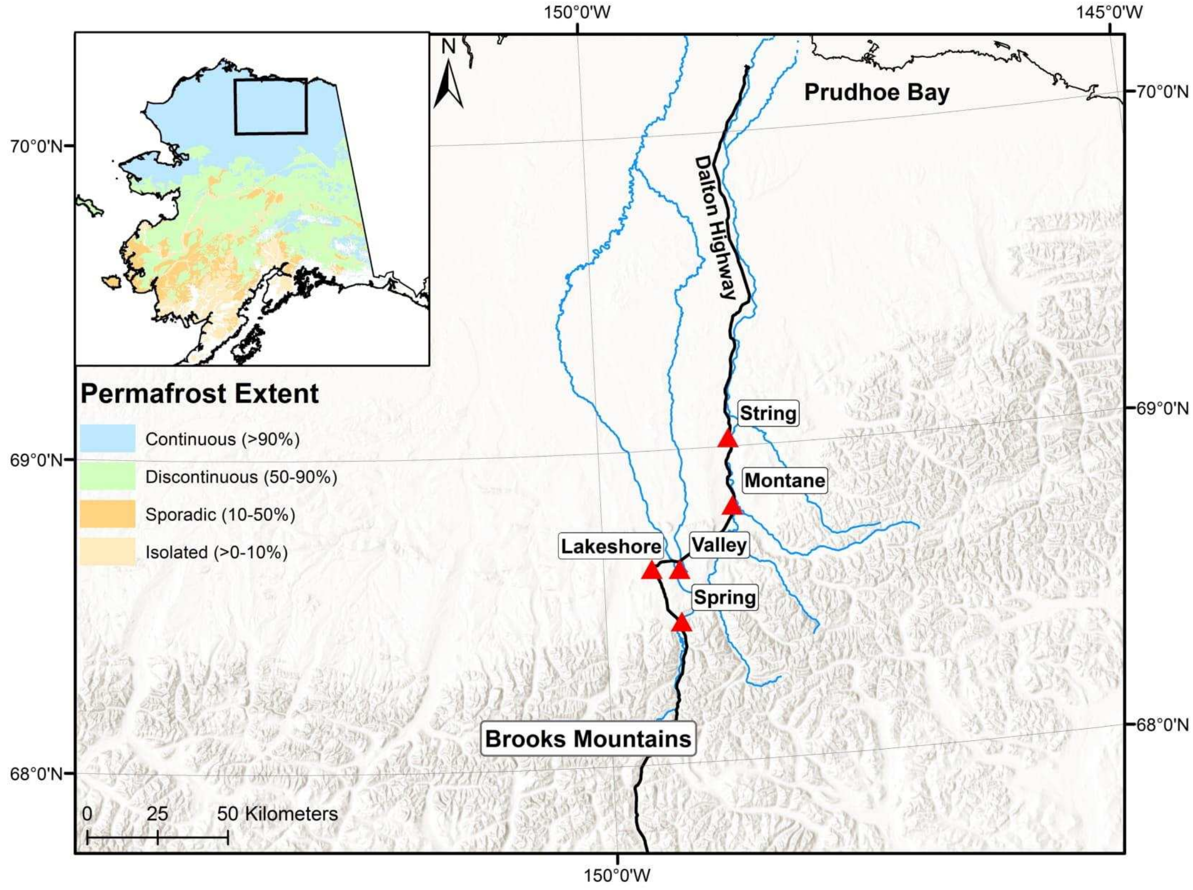

Figure 1 – Map outlining the five sites studied on the Northern Brooks foothills, Alaska. All sites are peatlands within the continuous permafrost zone (Jorgenson et al., 2008).

Site	Latitude (°N)	Longitude (°W)	Elevation (m)	WTD range (cm)	pH range	EC range (μS cm^{-1})	Most common plant species (% abundance)
Montane	68.81367	148.841	451	16 – 56	5.82 – 6.50	224 – 509	T. nitens (70%)
Spring	68.45228	149.346	804	0 - 25	6.96 – 7.95	257 – 505	T. nitens (45%)
Valley	68.61953	149.338	864	4 - 53	5.41 – 6.66	595 – 1176	S. terres/squarrosum (85%)
String	69.02852	148.839	405	0 - 54	6.40 – 6.95	881 – 1124	A. glaucophylla / S. scorpioides (35%)
Lakeshore	68.62472	149.580	753	0 - 30	5.17 – 6.84	37 – 156	S. cossoni (45%)

Table 1. Site overview and hydrological conditions. Full details of plant species are given in Appendix A.

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℃ overnight, re-weighed to determine gravimetric moisture content (MC), and ignited in a muffle furnace at 550℃ for at least 4 hours 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 minutes, shaken, passed through a 300 μm sieve and back-sieved through a 15 μm mesh before being stored in a 4℃ 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, 2007a; Mitchell et al., 2008b). Four samples had fewer than 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., 2007b). 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 (≥ 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 will 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 ≥ 20% of the range (EC: n = 228; WTD: n = 11) removed. The ≥ 20% threshold is used as the standard cut-off in the development of testate amoebae 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, Difflugia 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 × magnification. Individuals were catalogued to species or ‘type’ level using identification guides from Flora of North America North of Mexico (2007, 2014), Hedenäs (2003) and Smith (2004). Nomenclature follows Walker et al. (1994) for vascular plants and Flora of North America North of Mexico (2007, 2014) for bryophytes.

4. Results

4.1 Relationship between environmental variables and species distribution

We identified 94 testate amoebae taxa from 29 genera and a total count of 15,723 individuals. The most abundant species were Centropyxis aerophila, Euglypha degraded (individuals from the Euglypha genus that were not sufficiently well preserved for species-level identification), Cyclopyxis eurystoma, Phryganella acropodia, Trinema lineare and Centropyxis ecornis. NMDS shows that EC, LOI and WTD are the most important variables in controlling the distribution of testate amoebae species in these sites ($p < 0.001$) (Figure 2; Table 2). CCA supports this, also identifying EC as the dominant control on testate amoebae distribution (Figure 3; Table 2). Partial CCAs show that EC explains 25.0% of data variance ($p < 0.001$), WTD explains 16.5% ($p < 0.001$) and MC explains 13.3% ($p < 0.001$). RDA further supports the premise that the trophic gradient (for which EC is a proxy) is controlling species distribution. We also found a significant correlation between pH and EC ($r = 0.499$, $p < 0.1$), which is not unexpected as pH is also indicative of peatland trophic status (Gorham et al., 1987).

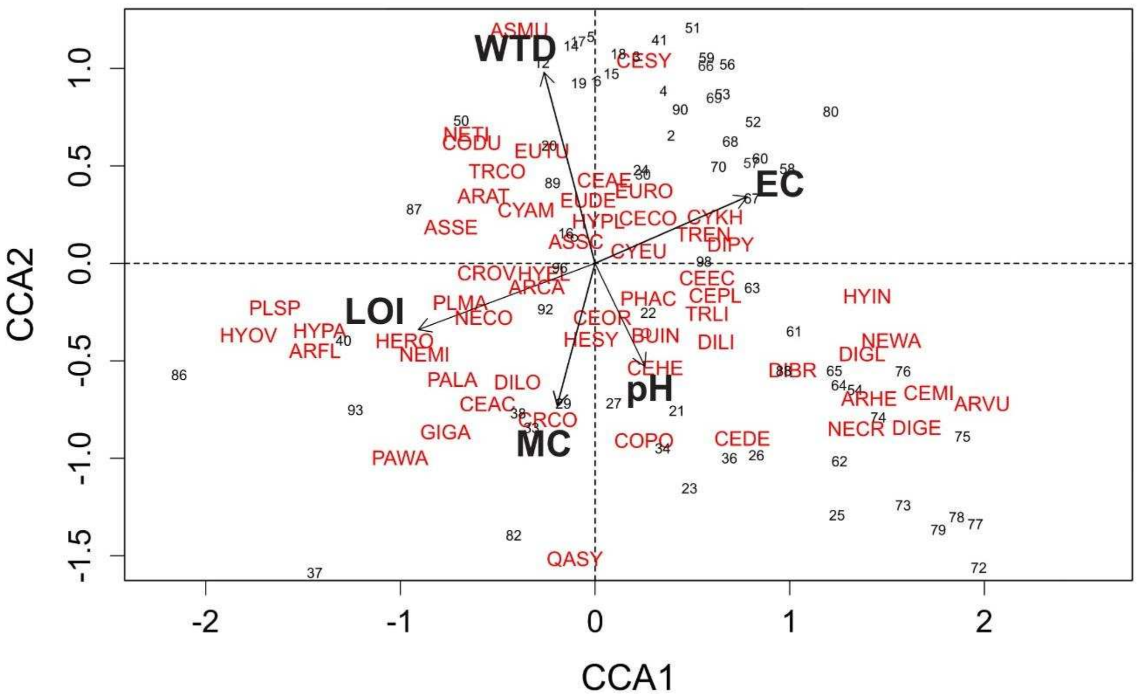

Figure 2 – CCA plot highlighting key controls on testate amoebae distribution. The environmental controls are EC (Electrical Conductivity), WTD (Water-Table Depth), LOI (Loss-on-ignition), MC (Moisture Content) and pH. Species codes are given in Table 4.

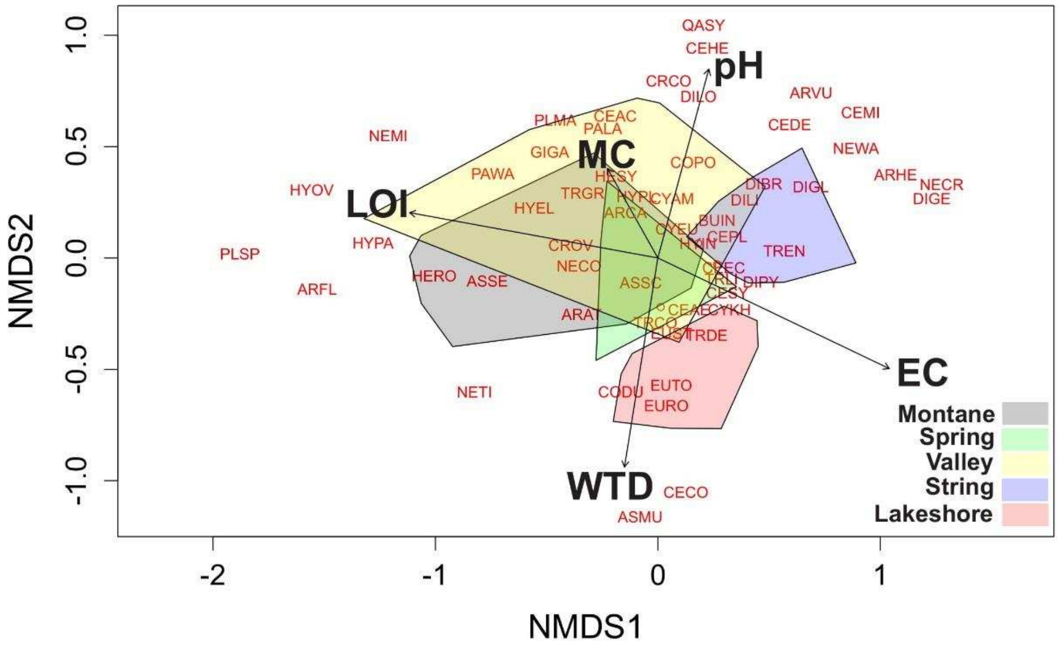

Figure 3) NMDS plot highlighting key controls on testate amoebae distribution. The environmental controls are EC (Electrical Conductivity), WTD (Water-Table Depth), LOI

(Loss-on-ignition), MC (Moisture Content) and pH. The species are broken down according to Table 4.

	NMDS				**pCCA**	
Variable	NMDS1	NDMS2	R^2	Significance	Variance explained	Significance
pH	0.261	0.966	0.289	$p < 0.001$	10.07%	$p = 0.005$
EC	0.902	-0.431	0.499	$p < 0.001$	24.98%	$p < 0.001$
WTD	-0.158	-0.988	0.339	$p < 0.001$	16.54%	$p < 0.001$
MC	-0.491	0.871	0.080	$p = 0.021$	13.26%	$p < 0.001$
LOI	-0.984	0.179	0.483	$p < 0.001$	8.93%	$p = 0.04$

Table 2. Ordination statistics of environmental variables.

The most abundant plant species at sampling sites included Warnstorfia cf. exannulata, Andromedia glaucophylla, Campylium stellatum, Cinclidium stygium, Scorpidium cossoni, Tomentypnum nitens, Sphagnum teres, and Andromedia glaucophylla (Appendix A). Forty plant taxa were identified from a total of 27 genera. Partial CCAs show that all variables are highly significant ($p < 0.001$). The most important variables are wetness indicators, as MC explains 5.23% of data variance and WTD explains 3.02%. There is a significant correlation (Pearson's $r = 0.197$, $p = 0.0497$, $n = 100$) between the species richness of testate amoebae and plants.

Mean EC at each sampling location is strongly correlated ($p < 0.001$) with LOI, and WTD with MC ($p < 0.001$), emphasising two strong hydrological gradients of trophic status and wetness in our sites. We identified a statistically significant difference in testate amoebae communities (ANOSIM $r = 0.428$, $p < 0.001$; PERMANOVA $r = 0.303$, $p < 0.001$) and plant communities (ANOSIM $r = 0.730$, $p < 0.001$; PERMANOVA $r = 0.757$, $p < 0.001$) among sites (Appendix B).

4.2 Transfer function development

Transfer functions were developed for WTD (TF_{WTD}) and EC (TF_{EC}), because both variables were highly significant in ordination. R^2_{JACK} and $RMSEP_{JACK}$ values were used to identify the best performing models. For TF_{WTD}, WAPLS component 2 performed better than WA.inv (Table 3) after removing large residuals (> 11 cm).

WA.inv did not perform well at either end of the WTD range, with high residuals at extreme wet and dry sites. We removed 31 samples to improve performance (R^2_{JACK} = 0.842, $RMSEP_{JACK}$ = 6.66 cm, Maximum bias = 14.30 cm, n = 69). One species (Arcella vulgaris), present in one sample at 2.44% abundance, was also removed due to its high residual value. Dry indicator species include Assulina muscorum, Nebela tincta, Corythion dubium and Euglypha spp. Key wet indicator species include Netzelia corona, Centropyxis declivistoma, Conicocassis pontigulasiformis and Difflugia bryophila (Figure 4). Optimum and tolerance statistics can be found in Figure 7.

TF_{EC} is also based on the second component of a WAPLS regression. ML appears to perform well prior to residual removal (Table 3). However, almost all of the large residuals that needed to be removed were in low-EC sites. Removal of the majority of low-EC sites would yield a transfer function with low skill in ombrotrophic conditions, biased towards minerotrophic sites. As a result, ML was not pursued further. WA and WAPLS represented the full gradient, with WAPLS outperforming WA. We removed 23 samples with large residuals (residuals > 228 μS cm^{-1}) from the transfer function to improve performance (after removal: R^2_{JACK} = 0.756, $RMSEP_{JACK}$ = 146 μS cm^{-1}, maximum bias = 189 μS cm^{-1}, n = 77). Minerotrophic habitat indicator species include Cyclopyxis kahli, Centropyxis ecornis, Phryganella acropodia and Difflugia globulosa. Key oligotrophic habitat indicator species include Archerella flavum, Hyalosphenia papilio, Gibbocarina galeata and Centropyxis aculeata (Figure 5).

	TF_{WTD}			TF_{EC}		
Model	R^2_{JACK}	$RMSEP_{JACK}$	Max Bias	R^2_{JACK}	$RMSEP_{JACK}$	Max Bias
Initial transfer function performance						
WAPLS	0.414	14.76	17.56	0.493	249.69	331.68
WA.inv	0.414	14.76	17.60	0.382	273.61	444.14
ML	0.471	16.20	19.38	0.452	269.63	478.26
After removing high residual sites (< 20%)						
WAPLS	0.842	6.66	14.30	0.756	146.04	188.82
WA.inv	0.734	9.36	14.18	0.680	151.52	606.32

Table 3 – Transfer function performance metrics. WAPLS statistics are all reported from the second component, as this was the best performing.

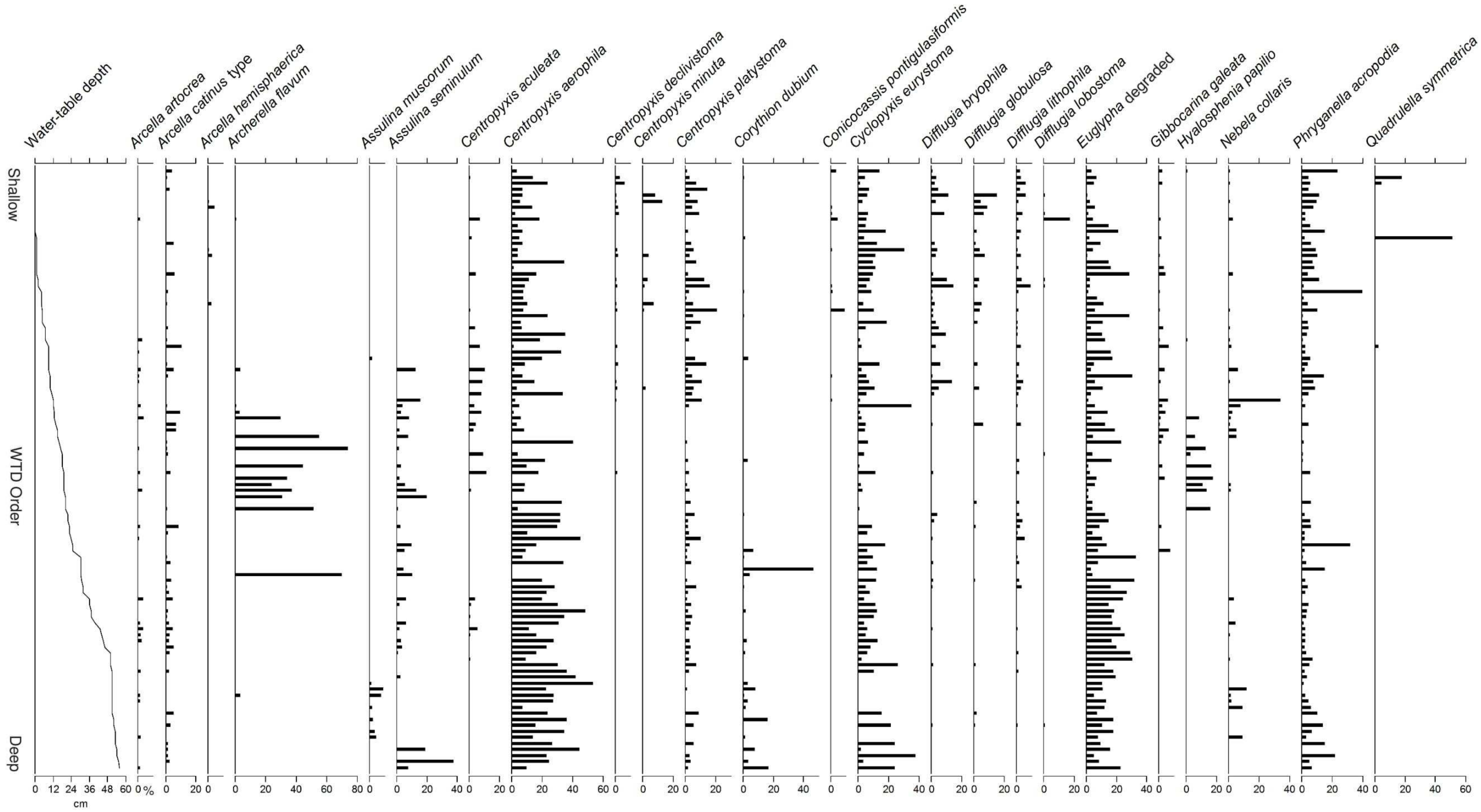

Figure 4) Percentage abundance of selected testate amoebae taxa that indicate a range of WTD conditions, ranked by observed WTD.

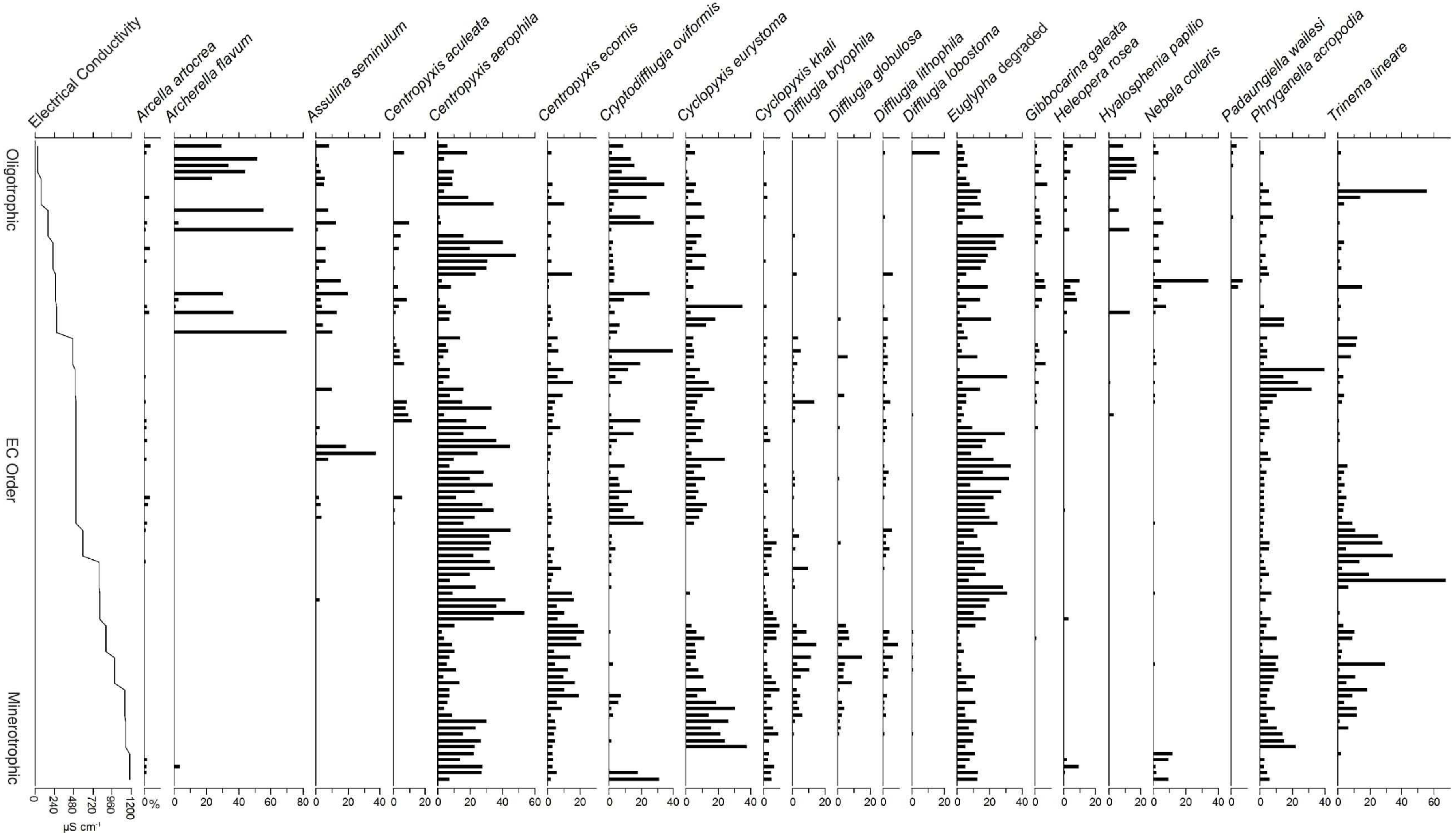

Figure 5) Percentage abundance of selected testate amoebae taxa that indicate a range of EC conditions, ranked by observed conductivity values.

4.3 Removing high conductivity sites

We removed the 35 samples with the greatest (top 50%) EC values (≥600 μS cm^{-1}) from the full dataset. This allows us to test whether the control of trophic status on the distribution of testate amoebae species was being affected by sites that are unusually nutrient rich. NMDS continued to show EC as the primary control on species distribution, while MC, LOI, and WTD also remained highly significant ($p < 0.001$). CCA showed WTD as the primary control, with MC, EC and organic matter content also highly significant ($p < 0.001$).

4.4 Transfer function performance

Both transfer functions perform well in terms of performance statistics (Table 3, Figure 6), so we applied them to a short core (from Gałka et al., 2018) from a peatland adjacent to Toolik Lake (Appendix C). Gałka et al. (2018) found that no existing transfer function was suitable for reconstructing WTD in their core, instead opting to use the percentage of wet indicators as a semi-quantitative index of wetness. Our WTD transfer function offers a significant improvement over this approach and shows that the peatland has remained moderately dry throughout the core. Wetness gradually increases from the bottom of the core and peaks at 12.5 cm depth. TF_{WTD} offers extra insight to the wetness indicators, by quantifying the dry periods either side of this peak. This shows that the peatland has gradually increased in wetness and transitioned recently to a state that is notably drier than any period in its past, reaching a WTD of 85.0 cm at the surface. In addition, TF_{EC} shows that this transition to dryness at the top of the core is accompanied by a shift towards minerotrophic conditions.

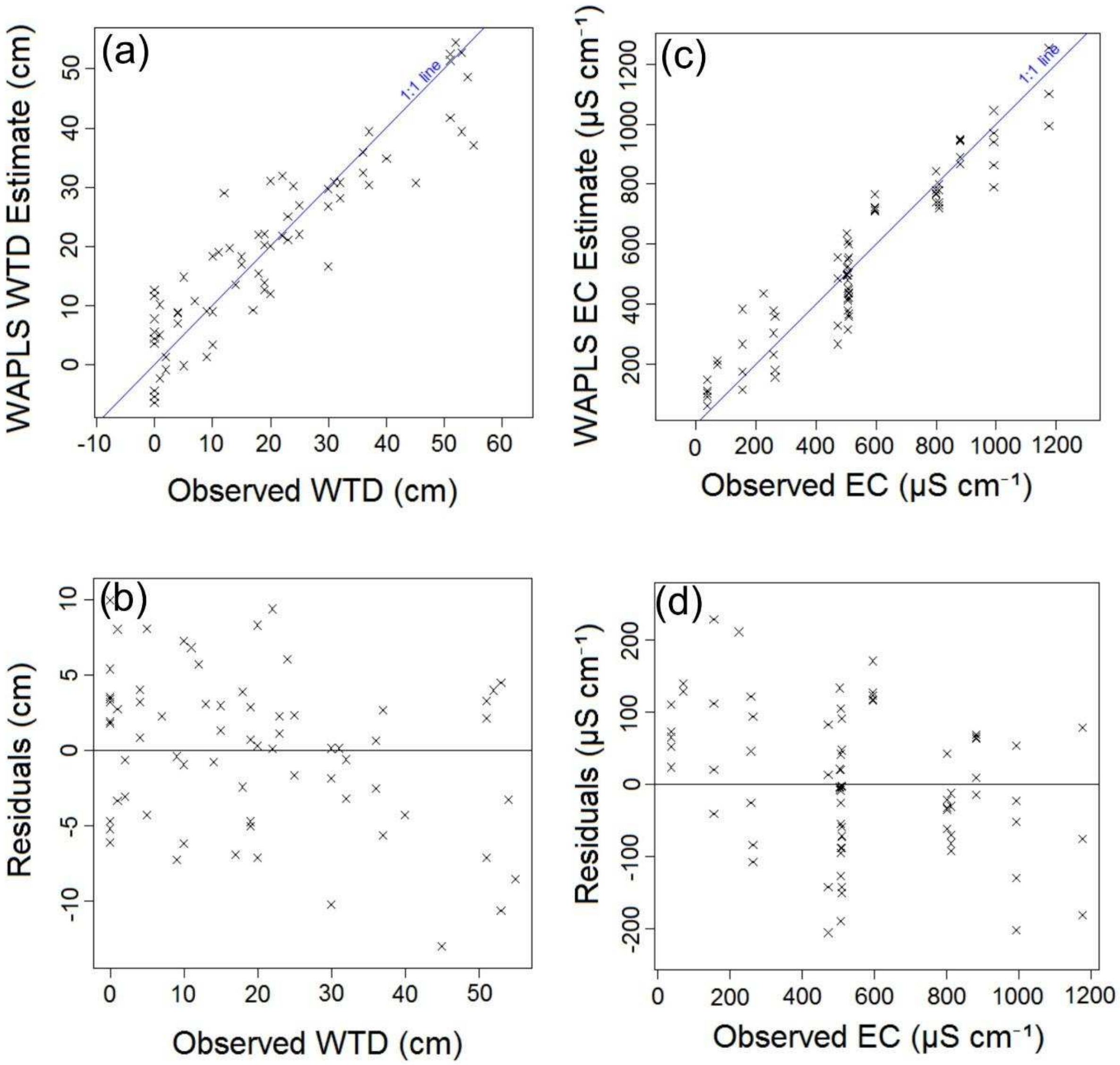

Figure 6) Transfer function performance. (a) TF_{WTD} estimates of each site against observations and (b) residuals of each site against observed WTD. (c) TF_{EC} estimates of each site against observations and (d) residuals of each site against observed conductivity.

Code	Taxa name	In n samples	Maximum abundance (%)
ARAT	Arcella artocrea	33	4.2
ARCA	Arcella catinus type	56	10.6
ARHE	Arcella hemisphaerica	5	4.5
ARFL	Archerella flavum	20	74.1
ASMU	Assulina muscorum	12	9.4
ASSC	Assulina scandinavica	40	10.9
ASSE	Assulina seminulum	35	37.7
BUIN	Bullinularia indica	37	6.4
CEAC	Centropyxis aculeata	30	11.8
CEAE	Centropyxis aerophila	96	53.8
CECO	Centropyxis constricta	3	7.1
CEDE	Centropyxis declivistoma	23	6.3

CEEC	Centropyxis ecornis	92	22.6
CEHE	Centropyxis hemisphaerica	13	3.3
CEMI	Centropyxis minuta	8	13.1
CEOR	Centropyxis orbicularis	48	6.7
CEPL	Centropyxis platystoma	75	20.8
CESY	Centropyxis sylvatica	11	2.9
CODU	Corythion dubium	39	47.0
CRCO	Cryptodifflugia compressa	24	55.7
CROV	Cryptodifflugia oviformis	77	40.0
COPO	Conicocassis pontigulasiformis	14	9.6
CYEU	Cyclopyxis eurystoma	81	37.7
CYKH	Cyclopyxis kahli	73	9.8
CYAM	Cyphoderia ampulla	10	2.5
DIBR	Difflugia bryophila	49	14.5
DIGE	Difflugia geosphaira	2	2.7
DIGL	Difflugia globulosa	3	15.5
DILI	Difflugia lithophila	58	9.7
DILO	Difflugia lobostoma	1	0.5
DIPY	Difflugia pyriformis	15	6.8
EUDE	Euglypha degraded	99	33.3
EURO	Euglypha rotunda	51	20.7
EUST	Euglypha strigosa	47	8.1
EUTU	Euglypha tuberculata	30	4.7
GIGA	Gibbocarina galeata	40	8.1
HERO	Heleopera rosea	30	10.3
HESY	Heleopera sylvatica	61	10.4
HYEL	Hyalosphenia elegans	21	4.4
HYIN	Hyalosphenia insecta	7	3.8
HYOV	Hyalosphenia ovalis	1	5.4
HYPA	Hyalosphenia papilio	17	18.1
HYPL	Hyalosphenia platystoma	27	4.7
NECO	Nebela collaris	48	34.1
NEMI	Nebela militaris	4	2.4
NETI	Nebela tincta	17	33.3
NECR	Netzelia corona	4	4.5
NEWA	Netzelia wailesi	8	5.2
PALA	Padaungiella lageniformis	20	4.0
PAWA	Padaungiella wailesi	16	7.1
PHAC	Phryganella acropodia	88	39.8
PLSP	Placocista spinosa	1	2.8
PLMA	Planocarina marginata	2	3.2
QASY	Quadrulella symmetrica	5	51.7
TRDE	Tracheleuglypha dentata	31	9.5
TRCO	Trinema complanatum	60	10.5
TREN	Trinema enchelys	2	53.5
TRGR	Trinema grandis	11	2.1
TRLI	Trinema lineare	73	67.1

Table 4. Overview of testate amoebae identified in abundances greater than 2% in any one sample.

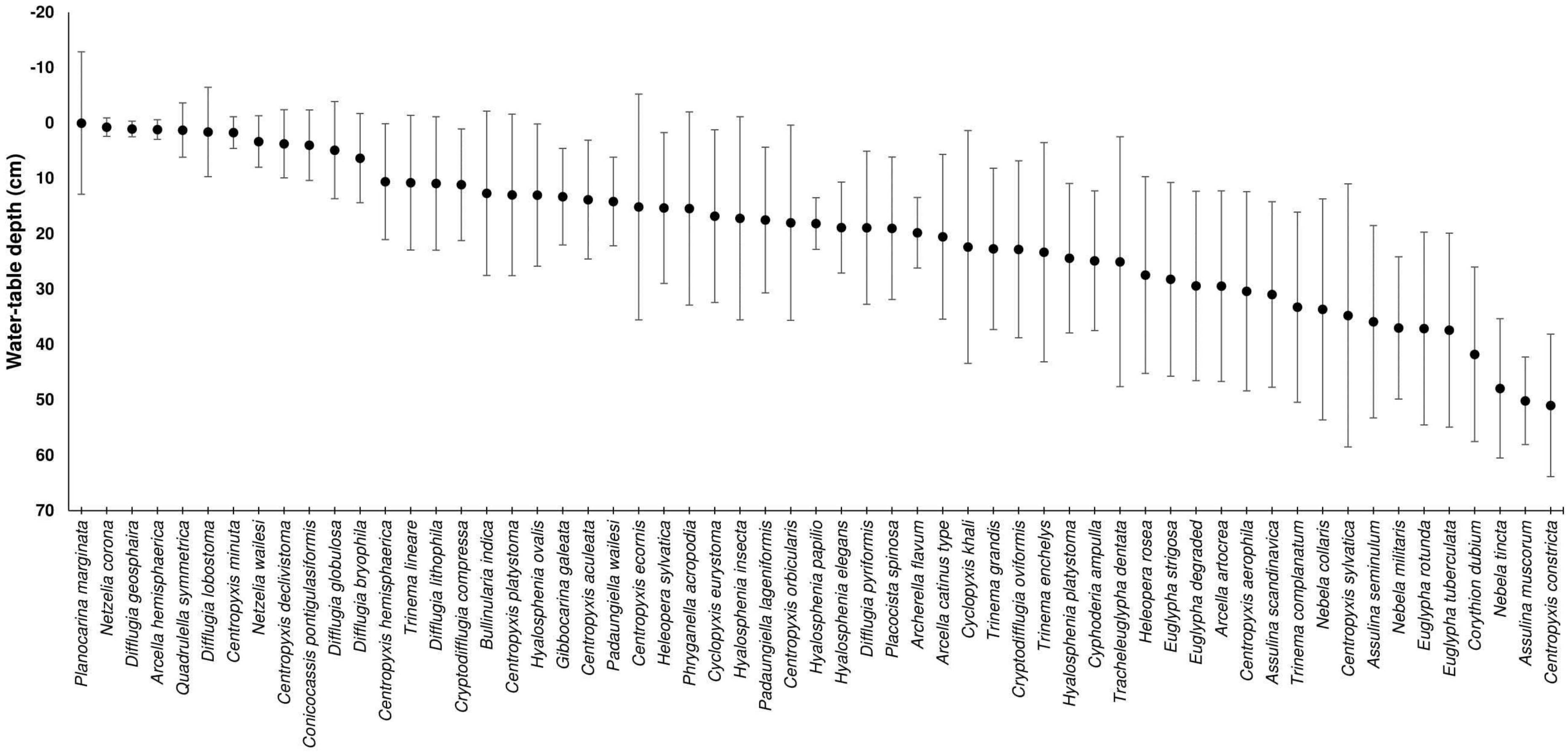

Figure 7 – WTD tolerance and optima statistics for testate amoebae calculated through Weighted Averaging.

5. Discussion

Our new transfer functions can be used for palaeoenvironmental reconstruction in permafrost peatlands to understand both long-term and recent changes in wetness and hydrochemistry. This is the first study examining testate amoebae as environmental indicators in continuous permafrost peatlands. This study supports existing research that suggests testate amoebae are a useful way to reconstruct palaeohydrology in permafrost peatlands (Swindles et al., 2015b; Lamarre et al., 2012, 2013; Bunbury et al., 2012; Gałka et al., 2017). Testate amoebae based reconstructions can form part of a multi-proxy toolkit to better understand the changing nature of peatlands in the continuous permafrost zone through the Holocene. The ecology of testate amoebae in continuous permafrost is similar to those found in discontinuous permafrost, although the key hydrological control on species distribution is different. EC plays a more important role in continuous permafrost, suggesting a strong ombrotrophic-minerotrophic gradient may dominate Alaskan North Slope peatlands. Our results also show that the peatlands in this region are a mixture of both ombrotrophic and minerotrophic systems, and contain variability between these categories within-site. Therefore, a transfer function encompassing the entire nutrient-status gradient is more appropriate than splitting the model into individual ombrotrophic and minerotrophic models.

5.1 Species diversity

Testate amoeba diversity is high (96 taxa identified from 15,723 classified individuals across 5 sites), which gives us confidence that they are robust hydrological indicators as they are found across the permafrost zone. Most testate amoebae studies are performed exclusively in either oligotrophic or eutrophic environments, rather than across a trophic gradient. Studies of testate amoebae and vegetation diversity across trophic gradients produce conflicting results. The study carried out by Lamentowicz et al. (2010) in temperate zone in sub-alpine peatlands of the Upper Engadine (Swiss Alps) identified a weak correlation in the fen-bog gradient between testate amoebae and moss diversity, while research by Opravilova and Hajek (2006), in a mountain peatland located in the Western Carpathians, found no correlation. We find that WTD is the only significant ($p < 0.001$) variable influencing the species richness of both surface plant species and testate amoebae. EC shows a very weak ($r = -0.177$, $p = 0.078$) correlation. MC is the most important influence on testate amoebae species diversity.

5.2 Nutrient level as the dominant factor

This study is one of the first where the ombrotrophic-minerotrophic gradient is the primary controlling factor on testate amoebae distribution, across a full range of peatlands from bogs to fens. This accurately represents our observations of peatlands in this region, as varying significantly in their trophic status. As a result, this has allowed us to produce a transfer function to reconstruct EC throughout the Holocene, which can allow future studies to better identify the timing of fen-bog transitions or the change of a peatlands' nutrient status. This can directly influence the net ecosystem productivity and subsequent carbon sequestration of Arctic peatlands (Bubier et al., 1999). This distribution of testate amoebae along the oligotrophic-eutrophic gradient has also been observed in aquatic ecosystems (e.g. Beyens et al., 1986; Qin et al., 2009; Ju et al., 2014). The observed trophic gradient does not affect surface vegetation though, as proxies for moisture (WTD, MC) controlled their distribution. As WTD is a statistically significant second-order control on species distribution from sites across a long trophic gradient, our transfer functions can be applied to reconstruct ecosystem change across the Holocene (such as a fen-bog transition), which contrasts findings from Payne (2011) from the Mediterranean.

The response of particular testate amoebae species to the trophic gradient closely matches an existing study from a peatland adjacent to Toolik Lake (Mitchell, 2004), where species diversity of testate amoebae was examined in response to increased nitrogen and phosphorus levels. We confirm results from Mitchell (2004) that Archerella flavum and Hyalosphenia papilio are indicators of nutrient-poor peatlands, while Centropyxis aerophila and Phryganella acropodia indicate minerotrophic conditions. However, unlike Mitchell (2004), we found that Assulina muscorum was indicative of minerotrophy in our dataset. We identified Centropyxis aerophila as a dominant species, which has also been observed in Arctic lakes (Beyens et al., 1986). However, Beyens et al. (1986) describe Centropyxis aerophila as a low-conductivity indicator, whereas we find this species across the trophic gradient and in greater abundance in higher EC sites.

5.3 Reconstructing water-table depth

We also present the first testate amoebae based transfer function to reconstruct WTD in continuous permafrost peatlands. This increases the global extent of testate amoebae as palaeohydrological indicators and opens opportunities to better understand how high-latitude ecosystems have responded to a changing climate throughout the Holocene. Individual taxa behave broadly as expected, comparing results to other studies in discontinuous permafrost (Amesbury et al., 2013; Swindles et al., 2015b; Zhang et al., 2017). Our largest anomaly was Archerella flavum, which we observe to be an intermediate indicator with an optimum WTD of around 19 cm. While the presence of A. flavum at this WTD has been observed in the compared studies, it is generally an indicator of much wetter conditions. Conversely, we do not observe A. flavum in abundance (≥ 2%) drier than 9 cm WTD. This could be because of the observed strong control of low nutrient status on this taxon.

5.4 Future applications

Testate amoebae can be used to investigate environmental change across Arctic peatlands, as they respond to changes in climate throughout the Holocene. This, in combination with other testate amoeba records from the Arctic (e.g. Müller et al., 2009), expands the potential for using testate amoebae as palaeoenvironmental indicators around the world. We applied both transfer functions to a short core from a peatland in the Alaskan Arctic. We found that the site has been moderately dry in the past, with gradually increasing wetness from the bottom of the core to a peak WTD of 9.4 cm at 12.5 cm depth, but has entered a state of rapid transition towards dryness from 12.5 cm depth to a WTD of 85.0 cm at the surface. There is now the opportunity to apply our transfer functions to a fossil record from the continuous permafrost zone to investigate WTD and ombrotrophic-minerotrophic transitions since peatlands first began to develop in this area.

6. Conclusion

1. We present the first testate amoeba based transfer functions for reconstruction of water-table depth and electrical conductivity in peatlands from the Alaskan continuous permafrost zone.
2. Testate amoebae are valuable environmental indicators in continuous permafrost peatlands.
3. Pore water electrical conductivity is the primary control on the distribution of testate amoeba species in these sites. Electrical conductivity is a proxy for the nutrient status of peatlands, suggesting that testate amoebae can be used as reliable indicators of trophic status in peatlands of the North Brooks foothills, Alaska.
4. The species richness of contemporary plants and testate amoebae taxa are significantly correlated to each other, and independently to water-table depth.
5. Our new transfer functions may be valuable components of multi-proxy investigations into the responses of Arctic permafrost peatlands to climate change over the Holocene and in recent centuries.

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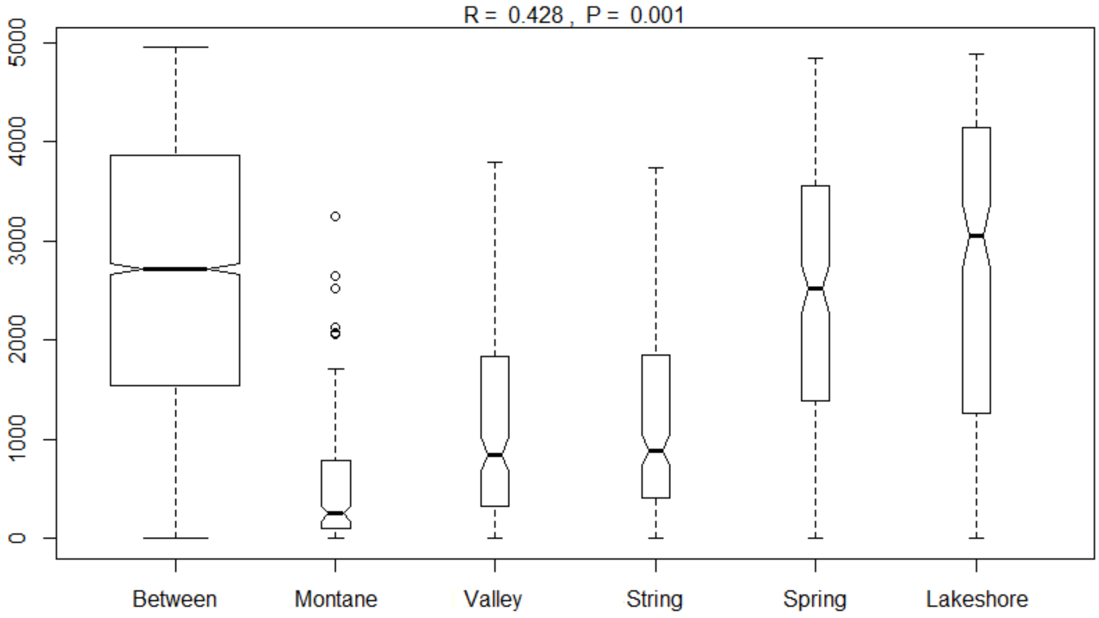
Appendix A - Details of plant species identified at each of the five sampling sites in the Alaskan North Slope.

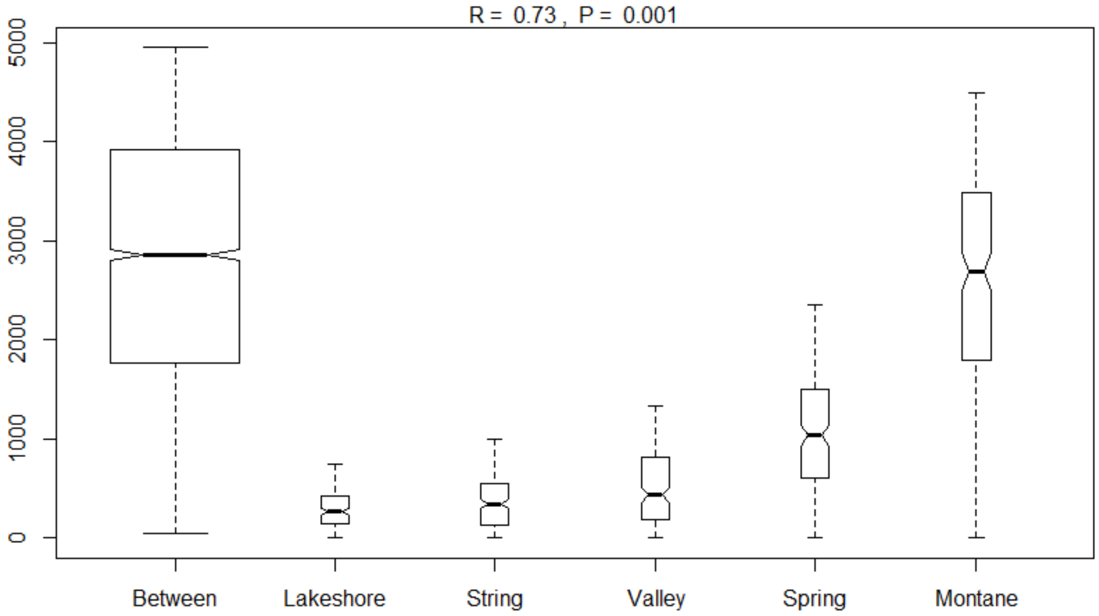
Taxa name	In n samples	Percentage of samples taxa is present in				
		Montane	Spring	Valley	String	Lakeshore
Andromeda glaucophylla	23	50	5	5	35	20
Aulacomnium palustre	6	0	15	10	5	0
Aulacomnium turgidum	7	5	5	0	0	25
Betula nana	7	20	0	5	0	10
Brachythecium mildeanum	1	0	5	0	0	0
Bryum sp.	14	15	20	0	30	5
Calliergon cordifolium	2	0	0	0	0	10
Calliergon richardsonii	2	0	0	0	0	10
Campylium cf. laxifolium	1	0	5	0	0	0
Campylium stellatum	22	40	20	0	30	20
Cinclidium stygium	17	20	40	0	15	10
Cirriphyllum piliferum/cirrosum	1	0	0	0	0	5
Dicranella sp.	8	5	10	0	15	10
Dryas integrifolia	6	5	25	0	0	0
Fissidens sp.	4	20	0	0	0	0
Hylocomnium splenders	6	10	5	0	0	15
Hypnum pratense	2	0	10	0	0	0
Loeskypnum badium	1	0	0	0	0	5
Meesia triquetra	13	0	20	0	30	15
Paludella squarrosa	5	0	5	0	0	20
Pohlia sp.	2	0	0	10	0	0
Polytrichum cf. juniperinum	2	0	10	0	0	0
Polytrichum commune	12	0	0	60	0	0
Polytrichum juniperinum	4	0	0	20	0	0
Pseudocalliergon sp.	3	15	0	0	0	0
Salix reticulata	2	10	0	0	0	0
Salix sp.	5	5	20	0	0	0
Sarmentypnum sarmentosum	1	0	0	0	5	0
Scorpidium cossoni	14	0	0	0	25	45
Scorpidium cossoni/revolvens	16	55	25	0	0	0
Scorpidium scorpioides	9	0	10	0	35	0
Sparganium sp.	1	0	0	5	0	0
Sphagnum capillifolium	4	0	0	0	0	20
Sphagnum contortum	1	0	0	0	0	5
Sphagnum teres	3	0	0	0	0	15

Sphagnum teres/squarrosum	17	0	0	85	0	0
Sphagnum wahrnstorfii	7	0	15	0	0	20
Straminergon stramineum	9	0	0	30	0	15
Tomentypnum nitens	33	70	45	0	20	30
Warnstorfia cf. exannulata	7	0	0	35	0	0

Appendix B – ANOSIM analysis of testate amoebae and plant distribution between our five sites.



ANOSIM analysis of testate amoebae distribution between sites.



ANOSIM analysis of contemporary plant species distribution between sites.

Appendix C – Example Reconstruction