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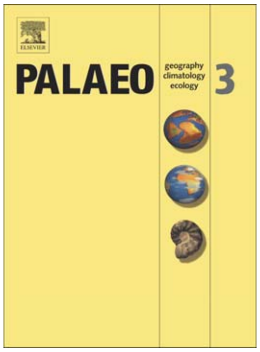

Evaluating the use of testate amoebae for palaeohydrological reconstruction in permafrost peatlands

Graeme T. Swindles, T. Edward Turner, Jonathan L. Carrivick, Clare Woulds, Lauren Parry, Joseph Holden, Matthew J. Amesbury, Thomas P. Roland, Dan J. Charman, Cassandra Raby, Donal Mullan, Jennifer M. Galloway, Ulla Kokfelt, Michelle Garneau

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Evaluating the use of testate amoebae for palaeohydrological reconstruction in permafrost peatlands

Manuscript for *Palaeogeography, Palaeoclimatology, Palaeoecology*

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Abstract

The melting of high-latitude permafrost peatlands is a major concern due to a potential positive feedback on global climate change. We examine the ecology of testate amoebae in permafrost peatlands, based on sites in Arctic Sweden (~200 km north of the Arctic Circle). Multivariate statistical analysis confirms that water-table depth and moisture content are the dominant controls on the distribution of testate amoebae, corroborating the results from studies in mid-latitude peatlands. We present a new testate amoeba-based water table transfer function and thoroughly test it for the effects of spatial autocorrelation, clustered sampling design and uneven sampling gradients. We find that the transfer function has good predictive power; the best-performing model is based on tolerance-downweighted weighted averaging with inverse deshrinking (performance statistics with leave-one-out cross validation: $R^2 = 0.87$, RMSEP = 5.25 cm). The new transfer function was applied to a short core from Stordalen mire, and reveals a major shift in peatland ecohydrology coincident with the onset of the Little Ice Age (c. AD 1400). We also applied the model to an independent contemporary dataset from Stordalen and find that it outperforms predictions based on other published transfer functions. The new transfer function will enable palaeohydrological reconstruction from permafrost peatlands in Northern Europe, thereby permitting greatly improved understanding of the long-term ecohydrological dynamics of these important carbon stores as well as their responses to recent climate change.

Introduction

Northern peatlands contain approximately 25-50% of the total carbon (C) stored in northern latitude soils (McGuire et al., 2009). Although it is established that peatlands have had a net cooling effect on climate through the Holocene (Frolking et al., 2006), it is not known how they will respond to climate warming in coming decades. There is considerable concern over melting permafrost peatlands as they may create thaw lakes and fens that are hotspots of methane (CH_4) emissions (Christensen, 2014), that could represent a potentially major positive climate change feedback (Hodkins et al., 2014). Thawing mires can also act as a source of pollutants to the environment (Klaminder et al., 2008) and impact regional hydrology by altering water storage and runoff (Quinton and Baltzer, 2013). As major changes in hydrology, vegetation and C-dynamics in permafrost peatlands are occurring across the sub-arctic (e.g. Kokfelt et al., 2009; Hodkins et al., 2014), it is now vital that proxy methods to examine past and present changes in these peatlands are developed and tested to better understand and predict future changes.

Testate amoebae are a group of single-celled organisms found in abundance on the surface of peatlands and form a shell that can be well-preserved in sedimentary records (Charman and Warner, 1992; Tolonen et al., 1992, 1994; Charman et al., 2000). Testate amoebae are a major component of soil microbial networks, constituting up to 30% of microbial biomass, and have distinct environmental preferences (Charman et al., 2000). Testate amoebae have been used for tracing hydrological changes in temperate peatlands in several regions of the world (Woodland et al., 1998; Booth, 2002; Lamentowicz et al., 2008; Swindles et al., 2009; Turner et al., 2013). Testate amoebae have also been increasingly used as proxies of past hydrological conditions within the boreal and subarctic peatlands of Canada (Loisel and Garneau, 2010; van Bellen et al., 2011; Bunbury et al., 2012; Lamarre et al., 2012; Lamarre et al., 2013). However, the potential of testate amoebae for peatland palaeohydrological reconstruction has not been evaluated in the Arctic.

In this paper we i) examine the ecology of testate amoebae in permafrost peatlands (palsa mires and arctic fens) in the Abisko region, Arctic Sweden (Figure 1); ii) test the hypothesis that the distribution of testate amoebae is primarily driven by hydrology in these peatlands; iii) develop a transfer function for reconstructing past hydrological change in these systems and iv) apply the transfer function to a peat profile.

Study region

The climate of Abisko is considerably milder and drier than other locations at similar latitudes (Tveito et al., 2000; Yang et al., 2012). Lying in the rain shadow of the Norwegian mountains, mean annual precipitation is just 332 mm (1981-2010), which is relatively low compared with neighbouring locations such as Narvik, Norway (<100 km) where annual precipitation reaches around 800mm (Callaghan et al., 2010). The seasonal precipitation variability is high, with lowest mean totals of 46 mm during the spring months and highest mean totals of 136 mm during summer (1981-2010). Temperatures are relatively mild for a location inside the Arctic Circle, with a long-term mean annual temperature of -0.6°C for 1913-2006 (Akerman and Johansson, 2008), and a recent thirty year average of 0.1°C from 1981-2010. For this time period, mean winter and summer temperatures have been -9.3°C and 10.1°C respectively. These relatively mild temperatures are largely a consequence of the relatively close proximity to the Atlantic Ocean (<100 km) and the moderating effect of the North Atlantic Drift.

Long-term climate records for Abisko Scientific Research Station from 1913 reveal an abrupt warming phase from the late 1930s to the early 1940s, and a more recent shift towards warming from the mid-1970s to present (Yang et al., 2012). Mean annual temperatures have increased by 2.5°C since 1913, with an accelerated increase of ~1.5°C since 1974 (Callaghan et al., 2010). Based on the most recent thirty-year averaging period (1984-2013), the mean annual temperature now regularly exceeds 0°C - an important threshold temperature above which permafrost is particularly vulnerable (Smith and Riseborough, 1983).

Lowland areas of Norrbotten are characterised by extensive peatlands. These include ombrotrophic bogs, arctic fen and palsa mires (Figure 2). Palsa mires are particularly common feature of the Abisko region. Palsa mires are frost-heaved peat mounds with a permanently frozen core and are characteristic of the circumpolar discontinuous permafrost zone (Lundqvist, 1969; Seppälä, 1972; Nelson et al., 1992; Seppälä, 1997; Gurney, 2001). There is much concern over the future of palsa mires in a warmer world as their frozen core needs to survive the heat of the summer season (Seppälä, 2006). As these peatlands are very sensitive to climate change there has been much discussion regarding the decreasing areal extent and degradation of palsas due to climate warming, and the effect this will have on C dynamics (Matthews et al., 1997; Zuidhoff and Kolstrup, 2000; Luoto and Seppala, 2002, 2003; Luoto et al., 2004a; Luoto et al., 2004b; Payette et al., 2004).

There has been a lot of peatland research in the Abisko region (e.g. Malmer and Wallén, 1996 ; Dorrepaal et al., 2009; Kokfelt et al., 2009) including some experimental studies of testate amoebae (Tsyganov et al., 2011; Tsyganov et al., 2012; Tsyganov et al., 2013a; Tsyganov et al., 2013b). The Stordalen mire complex is probably one of the most researched and instrumented peatlands in the world. Recent studies have shown there to be deepening of the active layer and accelerated decay of permafrost at Stordalen due to increased temperature and snow depth, which has caused enlargement of minerotrophic areas and decline of relatively dry ombrotrophic peatland (Christensen et al., 2004; Malmer et al., 2005; Johansson et al., 2006; Kokfelt et al., 2009).

Materials and methods

Samples were collected from nine peatlands comprising palsa mire, bog and arctic fens in the Abisko region, Norrland, Arctic Sweden (Figure 1, Table 1). At each site, 4 to 10 samples of a selected monospecific moss were collected along a hydrological transect from open pools to the tops of hummocks (Table 1). At each sampling location a hole was augured using a Russian corer. Water table was allowed to stabilise in each hole before water-table depth (WTD) was measured (all measurements were taken in late August – early September 2012, so that all sampling was carried out under similar seasonal conditions).

Dissolved oxygen of water (DO), electrical conductivity and pH were also recorded in the auger hole using calibrated field meters. Approximately one half of each moss sample was weighed, oven dried and re-weighed to determine moisture content. The samples were subsequently burnt in a muffle furnace at 450°C for 8 hours to determine loss-on-ignition values (Schulte and Hopkins, 1996). A 0.5 m long peat monolith, spanning the full length of the active layer was extracted from the Stordalen site in an area still containing permafrost. This was wrapped in plastic wrap and aluminium foil, and stored at 4˚C prior to analysis. Above-ground remains of plant macrofossils were extracted from the Stordalen profile and submitted to the DirectAMS laboratory for AMS radiocarbon dating. The dates were calibrated using IntCal13 (Reimer et al., 2013). Peat samples were extracted and submitted to Geotop-UQAM Radiochronology laboratory for ^{210}Pb analysis. Full information on the core chronology and palaeoecology will be published elsewhere.

Testate amoebae were extracted using a modified version of Booth et al. (2010). Moss (contemporary) and peat (palaeo) samples were placed in boiling water for 15 minutes and shaken. Extracts were passed through a 300 µm sieve, back-sieved at 15 μm and allowed to settle before sub-samples were used to make slides for microscopy. 100 to 200 amoebae were counted and identified to species level or 'type' in each sample using high-power transmitted light microscopy at 200 to 400x magnification. Identification was aided with reference to several sources (Leidy, 1879; Penard, 1902; Cash and Hopkinson, 1905; Cash and Hopkinson, 1909; Cash et al., 1915; Deflandre, 1936; Grospietsch, 1958; Corbet, 1973; Ogden and Hedley, 1980; Charman et al., 2000; Meisterfeld, 2001a; Meisterfeld, 2001b). The taxonomy used was a modified version of Charman et al. (2000), where some 'type' groupings are split to the species level (e.g. *Phryganella acropodia* and *Difflugia globulosa* were split out of *Cyclopyxis arcelloides* type when possible). This is an established, pragmatic taxonomic approach for analysis of Holocene peat samples (Charman et al., 2000).

Statistical analyses were carried out in R version 3.0.2 (R-Core-Team, 2014) using the packages vegan (Oksanen, 2012), rioja (Juggins, 2012) and palaeoSig (Telford, 2013). Non-metric Multidimensional Scaling (NMDS) was carried using the Bray-Curtis dissimilarity index and used to identify the important axes of variation in the data (e.g. Legendre et al., 1998). The stress was analysed in several runs to ensure a robust analysis was achieved. ENVFIT was used to fit and test the significance of environmental vectors. One-way Analysis of Similarity (ANOSIM) was undertaken on the testate amoebae data to determine the significance of site (Bray Curtis dissimilarities, 999 permutations). Partial Canonical Correspondence Analysis (pCCA) was used to explore the relationships between testate amoebae and environmental variables. A series of partial CCAs were applied to examine the variance explained by each environmental variable. Monte-Carlo permutation tests (999 permutations) were used to test statistical significance. All taxa were included in the multivariate analyses and no transformations were applied.

Three different transfer function models were developed and tested; weighted averaging (WA), tolerance-downweighted weighted averaging (WA-Tol) and maximum likelihood (ML) (Juggins, 2012). We found that there was no improvement of weighted averaging partial least squares (WAPLS) over WA, so did not pursue that model type further. For WA and WA-Tol, the 'best performing' (mostly root mean squared error of prediction (RMSEP) and R^2 but average and maximum bias also considered) version of each was chosen (i.e. inverse/classical deshrinking). The transfer functions were firstly developed on the full dataset, then samples with residual values >20% of the range of water-table measurements were removed to improve performance. The 20% cutoff is the precedent in testate amoebae-based transfer function literature (Woodland et al., 1998; Swindles et al., 2009; Turner et al., 2013; Amesbury et al., 2013; Lamarre et al., 2013). Thus, we apply it here so the models have been constructed in a comparable way. Leave-one-site out (LOSO) RMSEP was calculated using the 'lgo' (leave group out) command and ordering groups by site. Segment-wise RMSEP wise was calculated manually by ordering samples into evenly spaced (5 cm) segments based on WTD values. RMSEP values were then calculated for each segment using the outputted residual values from the relevant model (RMSEP = sq. root of the average of all squared residuals from any given segment). A spatial autocorrelation test was carried out using the 'rne' (random, neighbour, environment) function in the palaeoSig package. The transfer functions were applied to the short core from Stordalen. The 'randomTF' function in palaeoSig (Telford and Birks, 2011b) was used to test the significance of the transfer function reconstruction.

A powerful test of the transfer function model based on an independent contemporary dataset was also carried out. Twenty-nine moss samples were taken from the Stordalen mire and water-table depth (WTD) was measured. We used the transfer function to predict for these contemporary samples and examined the relationship using Spearman's rank correlation. Our results were compared to reconstructions based on other published models.

Results

A total of 55 testate amoeba taxa from 21 genera were identified in the modern samples from the Abisko peatlands (Table 2). The taxa occurring in most samples include *Assulina muscorum*, *Euglypha rotunda* type, *Archerella flavum*, *Nebela tincta*, *Hyalosphenia papilio* and *Corythion dubium* (Figure 3). NMDS illustrates the strong influence of WTD and moisture content on testate amoebae communities as these variables are strongly correlated with NMDS co-ordinate 1 (Figure 4). ENVFIT illustrates that WTD and moisture content are highly significant ($p < 0.002$). A series of partial CCAs shows that WTD explains 17.4% of the variance in the data ($p < 0.002$) and moisture content explains 19.2% ($p < 0.002$). The other environmental variables are less significant (Table 3). ANOSIM shows that there was no statistically significant effect of site.

The performance statistics for the transfer function models are shown in Table 4. The best performing transfer function model (Figure 5, Supplementary file 1) is based on WA.tol with inverse deshrinking ($R^2_{LOO} = 0.49$, $RMSEP_{LOO} = 11.56$). Several previous studies of peatland testate amoebae have shown WA.tol.inv to be the best performing model (Swindles et al., 2009; Amesbury et al., 2013; Turner et al., 2013). The removal of 30 samples with high residual values significantly improved the model performance ($R^2_{LOO} = 0.87$, $RMSEP_{LOO} = 5.25$, $RMSEP_{LOSO} = 7.49$). It was found that the effects of spatial autocorrelation (Telford and Birks, 2009), uneven sampling of an environmental gradient (Telford and Birks, 2011a) and clustered data sets (Payne et al., 2012) were not major problems for these data (Supplementary files 2 and 3, Table 4). However, it is likely that ML is struggling to cope with rare taxa (high LOSO-RMSEP and steep decline of 'neighbour' line on Supplementary file 3) and thus the WA-based models are more reliable in this case.

The most common subfossil testate amoebae present in the core from Stordalen mire include *Archerella flavum, Hyalosphenia papilio, Nebela tincta, Placocista spinosa* type and *Trigonopyxis arcula* type (Figure 6), and test preservation was generally good (cf. Swindles and Roe, 2007). The transfer function was applied to the subfossil data with no missing modern analogues. We checked the quality of analogues by comparing the percentage abundances in the contemporary and palaeo datasets. We also determined that the optima were well constrained through calculation of Hill's N2 values. The reconstruction suggests a major shift from deep to near surface water tables at 16 cm reflecting the shift of dominance from *Trigonopyxis arcula* type to *Archerella flavum*. This hydrological shift occurred at c. AD 1400 and reflects the onset of the European Little Ice Age (e.g.

Grove, 1988; Mann et al., 2009). The wet shift is also reflected in the reconstructions based on the temperate European and Subarctic Canadian transfer functions (Figure 6).

The randomTF function in the R package palaeoSig tests the amount of variance explained by the TF compared to randomly generated models – *p* values should be < 0.05 (i.e. explain more than 95%) to be considered significant (Telford and Birks, 2011b). The randomTF test suggests the reconstruction based on our chosen model (WA.tol.inv) is only statistically significant at $p = 0.08$. In contrast, the WA model is significant at $p = 0.03$ (Table 4, Supplementary files 4 and 5). However, we chose the WA.tol.inv over the WA.inv model due to better performance in terms of both LOO-RMSEP and SW-RMSEP (Table 4). The transfer function was also applied to the independent contemporary training set and a significant relationship was found between the observed and predicted WTD values ($R^2 = 0.87$, $p < 0.0001$). Less predictive power was achieved by the model from Subarctic Canada ($R^2 = 0.56$, $p < 0.0001$) and temperate Europe ($R^2 = 0.34$, $p < 0.001$) (Figure 7, Supplementary file 6). This highlights the good predictive power of our new transfer function.

Discussion

This study highlights that testate amoebae can be used to quantitatively reconstruct past water table changes in permafrost peatlands. Our statistical results corroborate the findings of several previous studies from temperate peat bogs that have shown that hydrological variables (WTD and moisture content) are the strongest controls on the distribution of testate amoebae in peatlands (e.g.Charman et al., 2007; Lamentowicz et al., 2008; Swindles et al., 2009; Turner and Swindles, 2012; Amesbury et al., 2013; Lamarre et al., 2013; Turner et al., 2013). The taxa observed in this study occupy similar positions along the water table gradient compared to many other published studies (Supplementary file 1). Consistently wet indicators include *Arcella discoides, Centropyxis* *aculeata* type*, Difflugia bacillifera, Difflugia globulosa and Nebela carinata*; dry indicators include *Arcella catinus* type and *Trigonopyxis arcula* type (Figure 3).

Although the European (ACCROTELM) transfer function works well for the major hydrological change in the peat profile it performs relatively poorly for the independent contemporary samples due to missing or poor quality analogues caused by taxa only being in a small number of samples (Figure 6, Supplementary file 6). Several taxa are relatively common in the Abisko peatlands that are not well-represented in the European transfer function (e.g. *Arcella hemisphaerica, Arcella gibossa* type, *Cryptodifflugia oviformis and Placocista spinosa*). Thus, we suggest that the European model is less applicable to high-latitude peatlands, highlighting the importance of our development of a high-latitude model.

The results of the randomTF test are difficult to reconcile as there is a major change from the dry indicator *Trigonopyxis arcula* type to the wet species *Archerella flavum* in the Stordalen peat profile (Figure 6). These are hydrological indicator species in peatlands as shown in our dataset (Figures 3 and 4), as well as numerous published studies (e.g. Woodland et al., 1998; Charman et al., 2007; Swindles et al., 2009; Amesbury et al., 2013; Lamarre et al., 2013; Turner et al., 2013). We compared the reconstructions based on WA.tol.inv and WA.inv and found them to be equivalent and highly correlated (Spearman's rank correlation – r_s =0.91, $p < 0.0001$). It is therefore unexpected that the reconstruction from our chosen WA.tol.inv model does not meet the $p < 0.05$ cutoff whereas the one based on WA.inv does. In addition, the reconstructions based on both models mirror NMDS coordinate one scores, suggesting they are adequately representing the data structure. Although the randomTF function in palaeoSig is now being used routinely to test peatland and lake transfer functions reconstructions (e.g. Amesbury et al., 2013; Upiter et al., 2014), we question its usefulness in this context. It is a statistical tool for testing the amount of variance explained by the transfer function compared to randomly generated models. It is thus a null model to test if the patterns observed are stronger than expected by chance, without the need for ecological information. The large shift in our data at *c.* AD 1400, coincident with the onset of the Little Ice Age, is obviously a real shift in the testate amoebae community reflecting climate-driven hydrological change in the peatland yet our preferred reconstruction (WA.tol.inv) does not meet the arbitrary $p < 0.05$ cut-off. Our results suggest that a detailed understanding of taxon autecology is as important as statistical testing for judging the robustness of quantitative palaeoenvironmental reconstructions.

The use of 'one off' WTD measurements in testate amoeba studies has been debated (Bobrov et al., 1999; Booth, 2008). However, it has been suggested that one-off water-table measurements have been shown to be adequate to drive a hydrological gradient for testate amoebae transfer function development (Woodland, 1996; Charman et al., 2007; Booth, 2008). Several authors have indicated that such measurements are sound as long as times of extreme weather conditions (e.g. prolonged rain or drought) are avoided (Charman et al., 2007; Booth et al., 2008; Swindles et al., 2009; Payne, 2011). Nonetheless, reconstructions based on one-off water-table measurements cannot be related to absolute values, such as mean annual water table. We suggest that such reconstructions should only be interpreted as semi-quantitative measures of directional changes in peatland water table.

Future studies can use this transfer function to examine Holocene ecohydrological changes in the peatlands of the Abisko region as well as elsewhere in Arctic Europe. The transfer function will also prove useful for examining peatland responses to rapid climate change in the Arctic during the twentieth century. Several testate amoebae transfer functions now exist from across the globe (Charman et al., 2007; Lamentowicz et al., 2008; Swindles et al., 2009; Amesbury et al., 2013; Lamarre et al., 2013; Turner et al., 2013; Swindles et al., 2014; Van Bellen et al., 2014). There is now an opportunity to compare and combine these data to examine the ecology of testate amoebae across the globe and develop models that contain suitable analogues for all taxa across wide ecohydrological and climatological gradients.

Conclusions

1. We present ecological data on testate amoebae in permafrost peatlands in the Abisko region, Arctic Sweden and demonstrate their utility as palaeohydrological indicators. The first testate amoeba-based transfer function for palaeohydrological reconstruction from the intensely-studied Abisko region is presented and rigorously tested.
2. The model is applied to a short core from the Stordalen mire. The reconstruction suggests a large shift in WTD occurring at the time of the onset of the Little Ice Age. Our work shows that testate amoebae have great potential for tracing ecohydrological changes in permafrost peatlands to better understand future change in northern regions.

Acknowledgements

GTS, JLC and CW conceived the idea. GTS carried out fieldwork, laboratory and statistical analyses and wrote the paper; MJA carried out statistical analysis and developed the transfer function; TET; carried out laboratory analysis; JLC and CW helped run the field campaign; CR carried out laboratory analysis; DM provided expertise on climate change in the Abisko region; TPR assisted with taxonomy; JMG provided expertise in permafrost dynamics; LP provided expertise in chronology; UK provided data from the field sites; MG provided the Arctic Canada transfer function; DJC provided the European transfer function; JH provided expertise in peatland ecohydrology. All authors contributed to the final paper. We thank the Worldwide University Network (WUN) for funding this project (Project: Arctic Environments, Vulnerabilities and Opportunities). An undergraduate student, Rachel Wiley, was funded by a Royal Geographical Society Fieldwork Apprenticeship and is thanked for her assistance in the field and laboratory. The School of Geography (University of Leeds) is thanked for additional funding for 'Enhancing the Student Experience'. The River Basins Processes and Management cluster and Ecology and Global Change research clusters at the University of Leeds are thanked for funding helicopter time. We acknowledge the Abisko Scientific Research Station for assistance with field logistics, and Kallax Flyg AB for helicopter support. We thank Gabriel Mangan

for providing a reconstruction on our data using the Canadian model and Steve Pratte for assisting with ^{210}Pb interpretation.

Figure captions

Figure 1. Study sites in the Abisko region, subarctic Sweden.

Figure 2. Photographs of peatlands in the Abisko region. A – Thermokarst pool in intact palsa with characteristic cracking around the pool margins (Craterpool); B – Wet area in peatland no longer containing permafrost (Stordalen); C – Subarctic fen (Eagle); D – Decaying palsa mire with bare peat surfaces adjacent to Arctic fen (Electric).

Figure 3. Percentage abundance of testate amoebae in the Abisko contemporary samples ranked by observed water-table depth (selected taxa are illustrated).

Figure 4. NMDS ordination of Abisko contemporary samples (Bray Curtis distance). All measured environmental variables have been fitted. Species full names are shown in Table 2. Site codes are as follows: C – Crash; E – Eagle; I – Instrument; L – Electric; M – Marooned; N – Nikka; P – Craterpool; R – Railway; S – Stordalen. Environmental variables include water-table depth (WTD), moisture content (MC), electrical conductivity (COND), pH, dissolved oxygen (DO), loss-on-ignition (LOI).

Figure 5. Graph of observed versus model-estimated water-table depth for (a) complete dataset; (b) screened dataset.The results are for the model based on based on WA.tol.inv.

Figure 6. Percentage testate amoebae data from the Stordalen peat profile with water table reconstructions based on the new transfer function from Subarctic Sweden, and published models from temperate Europe (Charman et al., 2007) and Subarctic Canada (Lamarre et al., 2013). Errors are based on 999 bootstrap cycles. Calibrated ^{14}C and ^{210}Pb dates are shown. Chronological data are presented in Supplementary file 7.

Figure 7. Scatterplots of observed WTDs from independent contemporary samples from Stordalen against model-predicted values. Predictions are based on the new transfer function from Subarctic Sweden and published models from temperate Europe (Charman et al., 2007) and Subarctic Canada (Lamarre et al., 2013). Linear regression lines with coefficients of determination (R^2) and *p* values are also shown.

Table 1. Site information. Negative water-table values indicate the height of surface ponding.

Table 2. Taxon codes, authorities and information on abundance in the Abisko peatlands (full dataset).

Table 3. Ordination statistics from NMDS, envfit and pCCA. Significance *p* values are based on 999 permutations. In the pCCA single environmental variables were included in the analysis and all other variables were partialled out.

Table 4. The performance statistics for the transfer function models. Values in sections A and B are from leave-one-out cross validation.

Supplementary file 1. Tolerance-optima statistics from the improved transfer function model based on WA.tol.inv.

Supplementary file 2. Sampling distribution of the complete dataset divided into 12 segments. Lines show segment-wise RMSEP for the three best performing models.

Supplementary file 3. Plot showing effect of spatial autocorrelation on R^2 on all model types by deleting sites at random (open circles), from the geographical neighbourhood of the test site (filled circles) or that are most environmentally similar (crosses) during cross-validation (cf. Telford and Birks 2009). Note y-axes are on different scales.

Supplementary file 4. Test of the transfer function reconstruction using the randomTF test for the WA.tol.inv model.

Supplementary file 5. Comparing the WA.tol.inv and WA.inv based reconstructions along with NMDS analysis of the testate amoebae data from the Stordalen core. Percentage abundance for the key testate amoeba taxa of *Archerella flavum* and *Trigonopyxis arcula* type are also shown.

Supplementary file 6. Percentage testate amoebae data from the independent contemporary samples from Stordalen with WTD reconstructions based on the new transfer function from Subarctic Sweden, and published models from temperate Europe (Charman et al., 2007) and Subarctic Canada (Lamarre et al., 2013). Errors are not presented for diagrammatic clarity. The samples are in WTD order.

Supplementary file 7. Chronological information for the Stordalen peat profile.

References

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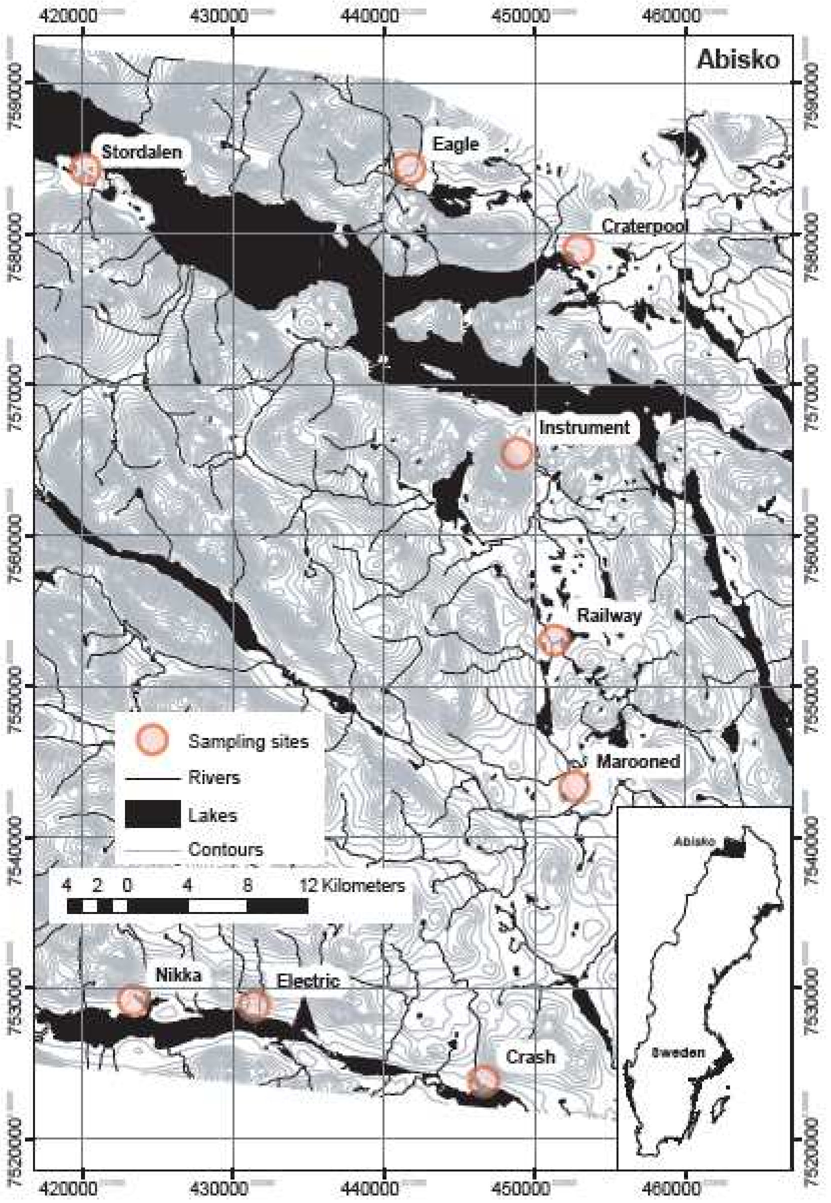
Fig 1


Abisko
420000
430000
440000
450000
460000
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7580000
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7560000
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7540000
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Eagle
Craterpool
Instrument
Railway
Marooned
Nikka
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Crash
Sampling sites
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Lakes
Contours
4 2 0 4 8 12 Kilometers
Abisko
Sweden

Fig 2

Fig 3

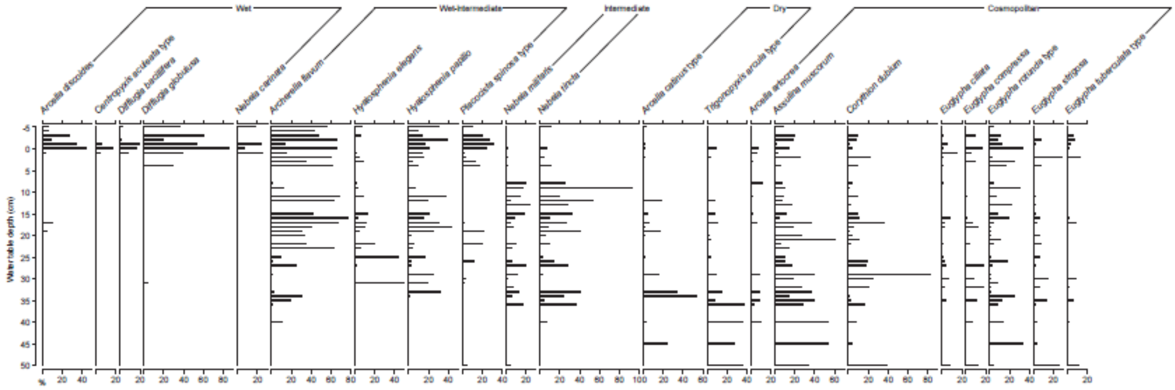
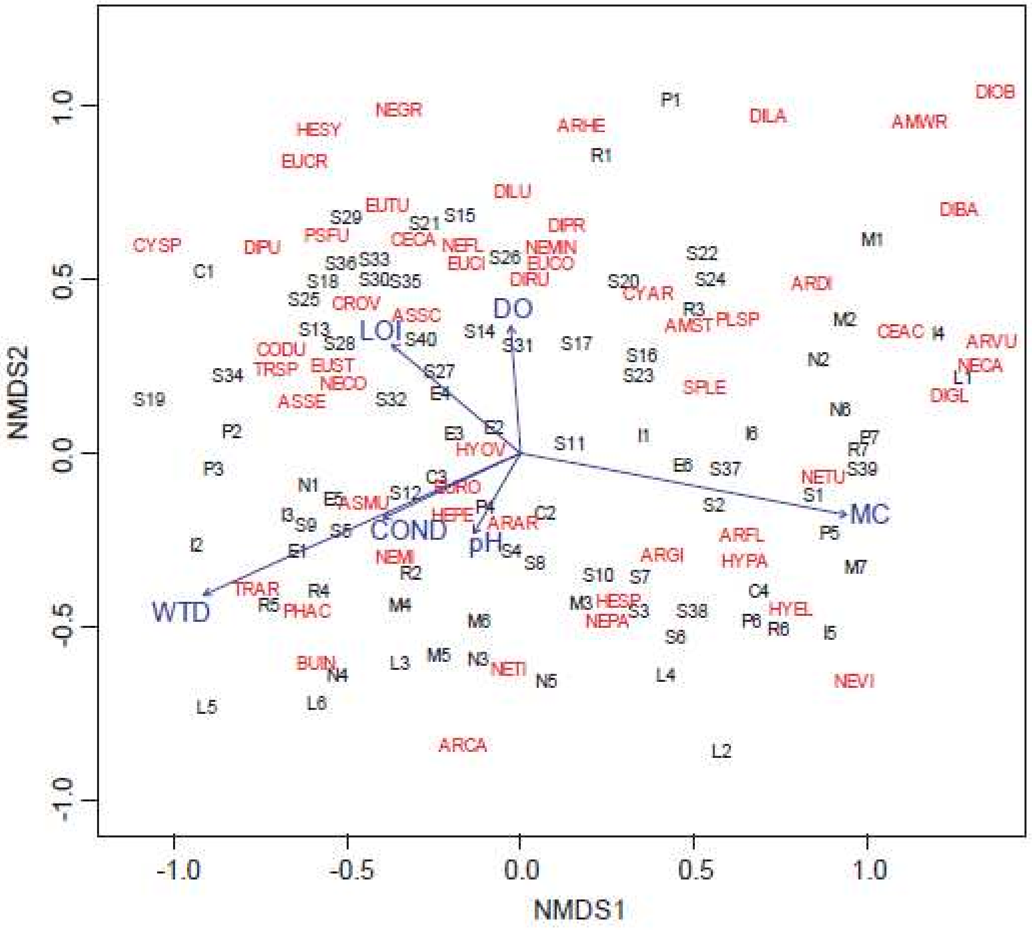

Wet
Wet-intermediate
Intermediate
Dry
Cosmopolitan
Arcella discoides
Centropyxis aculeata type
Difflugia bacillifera
Difflugia globulusa
Nebela carinata
Archerella flavum
Hyalosphenia elegans
Hyalosphenia papilio
Placocista spinosa type
Nebela militaris
Nebela tincta
Arcella catinus type
Trigonopyxis arcula type
Arcella arenaria
Assulina muscorum
Corythion dubium
Euglypha ciliata
Euglypha compressa
Euglypha rotunda type
Euglypha strigosa
Euglypha tuberculata type
Water table depth (cm)
-5
0
5
10
15
20
25
30
35
40
45
50
%
20
40
60
80
100

Fig 4


DIOB
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CYSP
DIPU
PSFU
CECA
NEFL
DIPR
NEMN
M1
S22
C1
S36
S33
EUCI
S26
EUCO
S18
S30
S35
DIRU
S20
S24
ARDI
CYAR
S25
CROV
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R3
PLSP
AMST
M2
CEAC
I4
ASSC
S13
LOI
S28
S40
S14
S31
S17
ARVU
CODU
S16
N2
S34
TRSP
EUST
S27
S23
L1
NECA
NECO
SPLE
DIGL
S19
ASSE
S32
E4
N6
P2
E3
E2
S11
I1
I6
P7
R7
HYOV
P3
E6
S37
NETU
S39
N1
C3
EURO
S1
E5
ASMU
S12
S2
MC
I3
S9
HEPE
P4
ARAR
C2
S5
COND
ARFL
P5
I2
pH
S4
E1
S8
ARGI
HYPA
NEMI
M7
R2
S10
S7
TRAR
R4
C4
WTD
R5
PHAC
M4
M3
HESP
S3
S38
HYEL
NEPA
M6
P6
R6
I5
M5
BUIN
L3
N3
N4
NETI
N5
L4
NEVI
L5
L6
ARCA
L2
1.0
0.5
0.0
-0.5
-1.0
NMDS2
-1.0
-0.5
0.0
0.5
1.0
NMDS1

Fig 5

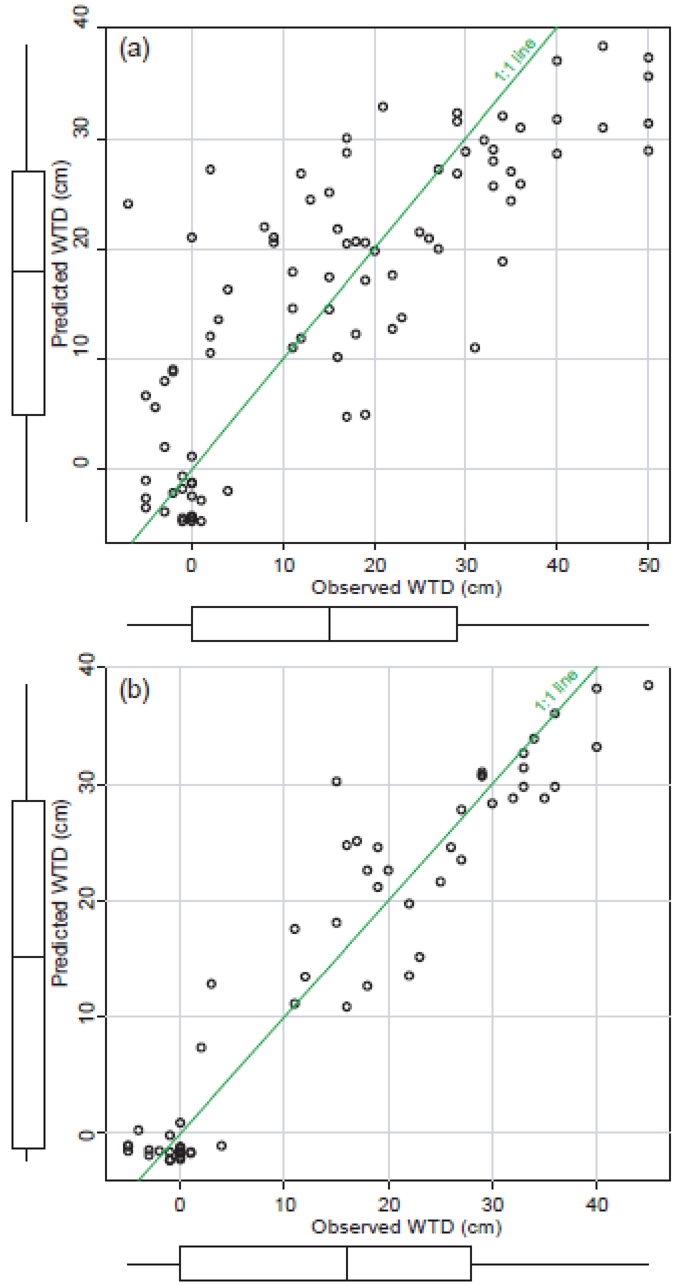
(a)
1:1 line
Predicted WTD (cm)
0
10
20
30
40
Observed WTD (cm)
0
10
20
30
40
50
(b)
1:1 line
Predicted WTD (cm)
0
10
20
30
40
Observed WTD (cm)
0
10
20
30
40

Fig 6

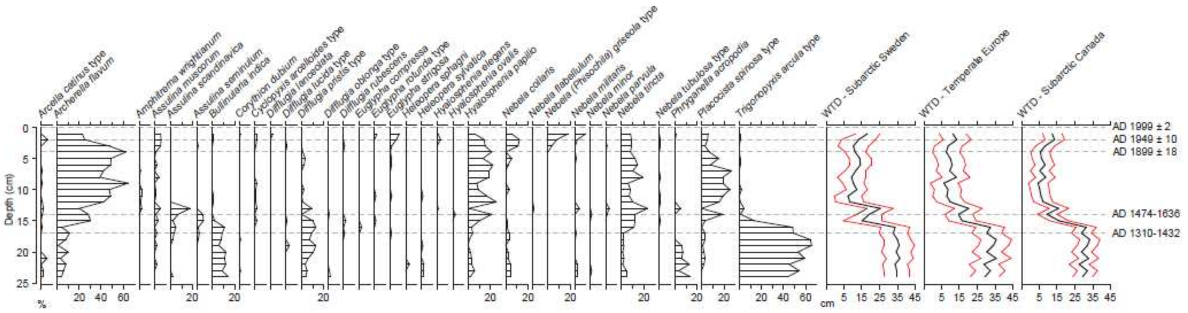
Arcella catinus type
Archerella flavum
Amphitrema wrightianum
Assulina muscorum
Assulina scandinavica
Assulina seminulum
Bullinularia indica
Corythion dubium
Cyclopyxis arcelloides type
Difflugia lanceolata
Difflugia lucida type
Difflugia pristis type
Difflugia oblonga type
Difflugia rubescens
Euglypha compressa
Euglypha rotunda type
Euglypha strigosa
Heleopera sphagni
Heleopera sylvatica
Hyalosphenia elegans
Hyalosphenia ovalis
Hyalosphenia papilio
Nebela collaris
Nebela flabellulum
Nebela (Phisochila) griseola type
Nebela militaris
Nebela minor
Nebela parvula
Nebela tincta
Nebela tubulosa type
Phryganella acropodia
Placocista spinosa type
Trigonopyxis arcula type
WTD - Subarctic Sweden
WTD - Temperate Europe
WTD - Subarctic Canada
Depth (cm)
0
5
10
15
20
25
%
20 40 60
20
20
20
20
20
20
20
20
20 40 60
cm
5 15 25 35 45
5 15 25 35 45
5 15 25 35 45
AD 1999 ± 2
AD 1949 ± 10
AD 1899 ± 18
AD 1474-1636
AD 1310-1432

Fig 7

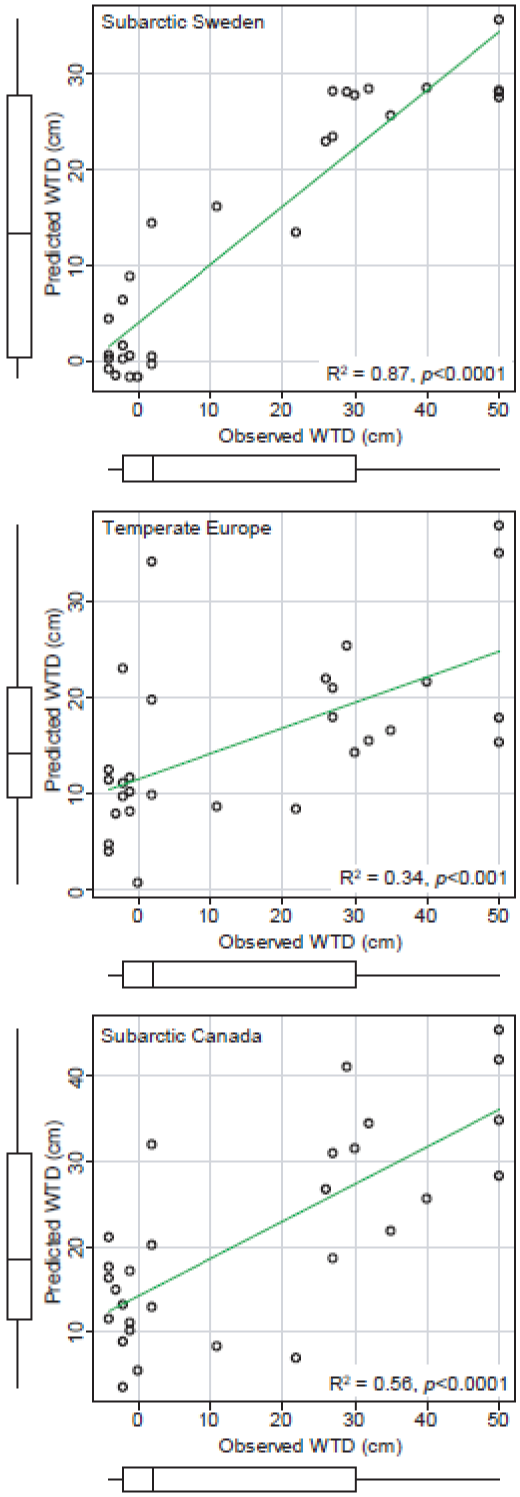
Subarctic Sweden
R² = 0.87, p<0.0001
Predicted WTD (cm)
0
10
20
30
Observed WTD (cm)
0
10
20
30
40
50
Temperate Europe
R² = 0.34, p<0.001
Predicted WTD (cm)
0
10
20
30
Observed WTD (cm)
0
10
20
30
40
50
Subarctic Canada
R² = 0.56, p<0.0001
Predicted WTD (cm)
10
20
30
40
Observed WTD (cm)
0
10
20
30
40
50

Table 1

Site name	Codes	Latitude (°N)	Longitude (°E)	Peatland type	Number of samples	Water table depth range (cm)	pH range
Crash	C1-4	67°49'27.8"	19°43'55.1"	Topogenous peatland	4	2 to 25	4.98 - 6.29
Craterpool	P1-7	68°19'10.1"	19°51'27.2"	Palsa	7	-5 to 45	3.76 - 4.77
Eagle	E1-6	68°21'56.5"	19°35'02.9"	Fen and bog	6	0 to 29	4.52 - 6.74
Electric	L1-6	67°51'56.1"	19°22'06.4"	Palsa	6	0 to 45	3.66 - 6.95
Instrument	I1-6	68°11'52.4"	19°45'56.2"	Palsa	6	0 to 36	3.43 - 5.32
Marooned	M1-7	67°57'24.0"	19°59'11.4"	Fen and bog	7	-1 to 29	3.24 - 4.21
Nikka	N1-6	67°52'02.2"	19°10'42.5"	Fen and bog	6	-1 to 40	4.02 - 5.27
Railway	R1-7	68°05'12.6"	19°49'52.9"	Palsa	7	0 to 40	3.25 - 6.35
Stordalen	S1-40	68°21'24.3"	19°02'53.5"	Palsa and fen	40	-7 to 50	2.99 - 3.80

Table 2

Code	Taxon	Authority	in n samples	Max %
AMST	*Amphitrema stenostoma*	Nusslin 1884	2	1.1
AMWR	*Amphitrema wrightianum*	Archer 1869	2	1.9
ARAR	*Arcella artocrea*	Leidy 1876	23	11.3
ARCA	*Arcella catinus type*	Penard 1890	23	53.8
ARDI	*Arcella discoides type*	Ehrenberg 1843	25	44.7
ARGI	*Arcella gibbosa type*	Penard 1890	4	14.2
ARHE	*Arcella hemisphaerica*	Perty 1852	4	37.4
ARVU	*Arcella vulgaris*	Ehrenberg 1830	5	59.6
ARFL	*Archerella flavum*	Archer 1877; Loeblich and Tappan 1961	58	77.1
ASMU	*Assulina muscorum*	Greef 1888	69	60.4
ASSC	*Assulina scandinavica*	Penard 1890	7	2.7
ASSE	*Assulina seminulum*	Ehrenberg 1848	21	12.2
BUIN	*Bullinularia indica*	Deflandre 1953	14	21.0
CEAC	*Centropyxis aculeata type*	Ehrenberg 1838	10	17.9
CECA	*Centropyxis cassis type*	Wallich 1864	6	4.4
CODU	*Corythion dubium*	Taranek 1871	46	82.5
CROV	*Cryptodifflugia oviformis*	Penard 1890	22	41.1
CYAR	*Cyclopyxis arcelloidestype*	Penard 1902	20	35.9
CYSP	Cyphoderia spp.	Schlumberger 1845	2	17.6
DIBA	*Difflugia bacillifera*	Penard 1890	9	20.0
DIGL	*Difflugia globulosa*	Dujardin 1837; Penard 1902	17	86.3
DILA	*Difflugia lanceolata*	Penard 1890	1	0.6
DILU	*Difflugia lucida type*	Penard 1890	5	4.9
DIOB	*Difflugia oblonga type*	Ehrenberg 1838	1	4.8

DIPR	*Difflugia pristis type*	Penard 1902	15	2.4
DIPU	*Difflugia pulex*	Penard 1902	11	3.0
DIRU	*Difflugia rubescens*	Penard 1891	1	2.2
EUCI	*Euglypha ciliata*	Ehrenberg 1848	26	15.0
EUCO	*Euglypha compressa*	Carter 1864	28	18.4
EUCR	*Euglypha cristata*	Leidy 1874	1	1.0
EURO	*Euglypha rotunda type*	Wailes and Penard 1911	59	34.0
EUST	*Euglypha strigosa*	Ehrenberg 1872; Leidy 1878	39	28.7
EUTU	*Euglypha tuberculata type*	Dujardin 1841	23	13.6
HEPE	*Heleopera petricola*	Leidy 1879	7	4.4
HESP	*Heleopera sphagni*	Penard 1890	2	1.0
HESY	*Heleopera sylvatica*	Penard 1890	1	0.5
HYEL	*Hyalosphenia elegans*	Leidy 1874	25	49.5
HYOV	*Hyalospenia ovalis*	Leidy 1874	22	10.6
HYPA	*Hyalopshenia papilio*	Wailes 1912	54	44.3
NECA	*Nebela carinata*	Leidy 1879	4	25.5
NECO	*Nebela collaris*	Ehrenberg 1848	15	10.6
NEFL	*Nebela flabellulum*	Leidy 1874	1	0.4
NEGR	*Nebela (Phisochila) griseola type*	Wailes and Penard 1911	4	2.7
NEMI	*Nebela militaris*	Penard 1890	39	24.7
NEMIN	*Nebela minor*	Penard 1902	3	0.5
NEPA	*Nebela parvula*	Cash 1908	10	10.0
NETI	*Nebela tincta*	Leidy 1979; Awerintzew 1906	54	93.6
NETU	*Nebela tubulosa type*	Penard 1890	3	1.9
NEVI	*Nebela vitraea*	Penard 1899	1	1.0
PHAC	*Phryganella acropodia*	Hertwig and Lesser 1874; Cash and Hopkinson 1909	23	10.8

PLSP	*Placocista spinosa type*	Penard 1899	27	31.2
PSFU	*Pseudodifflugia fulva type*	Archer 1870	8	5.5
SPLE	*Sphenoderia lenta*	Schlumberger 1845	3	1.8
TRAR	*Trigonopyxis arcula type*	Penard 1912	30	38.4
TRSP	*Trinema spp.*	Penard 1890	22	37.0

Table 3

NMDS and envfit						pCCA	
Variable	NMDS1	NMDS2	R2	Pr(>r)	Significance	Variance explained	Significance
WTD	-0.913	-0.409	0.410	0.001	p < 0.002	17.4%	p < 0.002
MC	0.982	-0.190	0.378	0.001	p < 0.002	19.2%	p < 0.002
COND	-0.901	-0.434	0.078	0.030	p < 0.01	7.6%	p < 0.34
LOI	-0.760	0.650	0.097	0.012	p < 0.01	9.9%	p < 0.07
DO	-0.074	0.997	0.055	0.100	p < 0.1	7.2%	p < 0.36
pH	-0.502	-0.865	0.030	0.255	p < 1	13.8%	p < 0.01

Table 4

A. Model performance for all samples						
	RMSEP	R^2	Average bias	Maximum bias	Skill	n
WA.inv	11.63	0.48	-0.16	18.64	47.34	89
WA.tol.inv	11.56	0.49	0.41	17.94	47.97	89
ML	13.42	0.50	-2.91	13.79	29.92	89
B. Models re-run after removing residuals >20% WTD gradient (improved model)						
	RMSEP	R^2	Average bias	Maximum bias	Skill	n
WA.inv	6.26	0.82	0.10	12.42	82.15	63
WA.tol.inv	5.25	0.87	0.17	8.76	87.31	59
ML	5.56	0.90	-0.41	4.68	89.87	65
C. Performance and reconstruction statistics for improved model						
	RMSEP-LOO	RMSEP-LOSO	SW-RMSEP	palaeoSig *p*-values		
WA.inv	6.26	6.89	6.68	0.03		
WA.tol.inv	5.25	7.49	5.40	0.08		
ML	5.56	11.03	5.40	0.01		

Highlights

- We examine the ecology of testate amoebae in permafrost peatlands
- The first testate amoebae transfer function from Abisko, Sweden is presented
- The transfer function is applied to a short core from the Stordalen mire
- A shift in water table depth occurred at the onset of the Little Ice Age
- Testate amoebae have great potential for tracing changes in permafrost peatlands