



Testing peatland water-table depth transfer functions using high-resolution hydrological monitoring data

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ABSTRACT

Transfer functions are now commonly used to reconstruct past environmental variability from palaeoecological data. However, such approaches need to be critically appraised. Testate amoeba-based transfer functions are an established method for the quantitative reconstruction of past water-table variations in peatlands, and have been applied to research questions in palaeoclimatology, peatland ecohydrology and archaeology. We analysed automatically-logged peatland water-table data from dipwells located in England, Wales and Finland and a suite of three year, one year and summer water-table statistics were calculated from each location. Surface moss samples were extracted from beside each dipwell and the testate amoebae community composition was determined. Two published transfer functions were applied to the testate-amoeba data for prediction of water-table depth (England and Europe). Our results show that estimated water-table depths based on the testate amoeba community reflect directional changes, but that they are poor representations of the real mean or median water-table magnitudes for the study sites. We suggest that although testate amoeba-based reconstructions can be used to identify past shifts in peat hydrology, they cannot currently be used to establish precise hydrological baselines such as those needed to inform management and restoration of peatlands. One approach to avoid confusion with contemporary water-table determinations is to use residuals or standardised values for peatland water-table reconstructions. We contend that our test of transfer functions against independent instrumental data sets may be more powerful than relying on statistical testing alone.

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1. Introduction

Quantitative reconstruction of past environmental variability from fossil data has become increasingly common in palaeoecology since Imbrie and Kipp (1971) first produced a reconstruction of past sea-surface temperature using fossil foraminiferal assemblages. Models for predicting past environmental conditions (so-called 'transfer functions') are firmly based in uniformitarian principles. The relationships between contemporary taxa and environmental variables are modelled and the resultant function is used to

transform fossil data from a biostratigraphic sequence into quantitative estimates of an environmental variable in the past. Transfer functions have been developed for several groups of microfossils to reconstruct a variety of climatic, chemical and hydrological variables (e.g. Imbrie and Kipp, 1971; Fritz et al., 1991; Gasse et al., 1995; Brooks and Birks, 2000; Charman et al., 2007). It has been suggested that the development of such quantitative reconstructions from biological proxies have revolutionised palaeoecology (e.g. Juggins, 2013); however, there have been several recent criticisms of transfer function approaches including the use of niche-based models (Belyea, 2007), spatial autocorrelation (Telford and Birks, 2005; Payne et al., 2012), and the confounding influence of non-causal/secondary variables (Juggins, 2013). It is now imperative that transfer functions are thoroughly and critically tested.

Peatlands accumulated 473–621 Gt of carbon during the Holocene (Yu et al., 2010), and store approximately the same amount of

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carbon as the atmosphere. Although it is established that global peatlands had a net cooling effect on climate through the Holocene (Frolking et al., 2006), there are still major questions over how they will respond to future climate change. This has led to a recent proliferation of studies examining the dynamics of peatlands in terms of carbon-accumulation, hydrology and ecology during the Holocene (e.g. Loisel and Garneau, 2010; van Bellen et al., 2011; Charman et al., 2013; Turner et al., 2014). Testate amoebae (TA) are a group of single-celled organisms that form a shell (their key identification feature – Charman et al., 2000). They are found in abundance on the surface of peatlands and can be well-preserved in Holocene peats (Charman and Warner, 1992; Tolonen et al., 1992, 1994; Charman et al., 2000). TA are sensitive to microenvironmental conditions on peatlands, especially moisture and to a lesser extent pH and water chemistry, and respond rapidly to environmental changes (Woodland et al., 1998; Marcisz et al., 2014). TA-based transfer functions have been key in the reconstruction of hydrological changes (primarily water-table depth) in peatlands across several regions of the world (e.g. Woodland et al., 1998; Booth, 2002; Charman et al., 2007; Lamentowicz et al., 2008a; Swindles et al., 2009; Amesbury et al., 2013; Lamarre et al., 2013; Turner et al., 2013; Swindles et al., 2014). These reconstructions have been used widely as proxy records of Holocene climate change (e.g. Mauquoy et al., 2008; Charman et al., 2009; Swindles et al., 2013).

However, one of the potential problems is that the water-table depths used in such studies typically come from a 'one-off' water-table measurement from the TA sample extraction point. The use of one-off water-table depth measurements in TA studies has been debated previously (Bobrov et al., 1999; Booth, 2008); however, it has been suggested that such measurements are adequate to drive a hydrological gradient for TA transfer-function development (Woodland, 1996; Charman et al., 2007; Booth, 2008). Several authors have argued that one-off measurements are adequate 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; Turner et al., 2013).

One value of water-table depth is produced by the transfer function (i.e. n cm below the peat surface), with sample-specific errors generated through a statistical resampling approach (bootstrapping). However, we know that water tables fluctuate in peatlands and are dynamic (Price, 1992; Evans et al., 1999; Holden et al., 2011). Traditional TA transfer function-generated water-table data may not adequately capture a mean value from a site, and do not account for water-table dynamics (e.g. seasonal or annual variability) which could influence the TA community composition. Here we test the robustness of TA-based transfer functions for water-table reconstruction in peatlands. Previously, model

performance and robustness have been tested using advanced statistical tools (cf. Telford and Birks, 2011; Telford, 2013). Here we take an alternative approach: we use real-world data from independent test sites with high-resolution monitored water-table data to determine the predictive power of two published transfer functions.

2. Materials and methods

We tested two established TA transfer functions – 1. The pan-European transfer function from the ACCROTELM project based on eight raised bogs across Europe (Charman et al., 2007) and 2. A regional transfer function from Northern England based on three blanket peatlands and three raised bogs (Turner et al., 2013). These transfer functions have been used for palaeohydrological reconstruction from fossil data and have provided very similar results (Turner et al., 2013). They were deemed to be appropriate models for our test data in terms of community composition and site characteristics. The models chosen were constructed using weighted averaging-tolerance-downweighted regression with inverse deshrinking as this was found to have very good performance in both cases.

Three independent test datasets were used – 1. Blanket peatlands in the Pennine region of Northern England; 2. An oceanic raised bog in Wales and 3. High-latitude peatlands in Finland (Table 1). These sites were chosen as they have dipwells equipped with pressure transducers providing high-resolution (logged at least once every two hours, but mainly 15-min) peatland water-table data. These data were checked for quality control and a suite of water-table statistics for each point was determined including means, medians, ranges and temporally-constrained measures including water-table depth residence times (Supplementary file 1). These values were calculated as 3-year, 1-year, and summer values (1 year and 3 years) prior to the TA sampling time for each dipwell. Only summer data are available for the sites in Finland as they are frozen during the rest of the year (Supplementary file 1).

Immediately adjacent (<0.5 m) to each dipwell (but away from any areas of trampling or disturbance), a surface sample of *Sphagnum* or other moss was extracted and the TA community composition determined in the laboratory. We analysed the green fraction of the moss (the living plant) and a 1-cm thick section of the brown section to ensure that a sample representing only the very recent period was obtained. TA were extracted using a modified version of Booth et al. (2010). Moss samples were placed in boiling water for 15 min 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. Many testate

Table 1

Site and sample details. The samples with codes in brackets were removed from the analysis as they had very deep water tables (see Fig. 2).

Site	Number of automated dipwells	Codes	Type	Location (decimal degrees)
Keighley Moor (England)	2	B1-2	Blanket peatland	53.850°, -2.034°
Wessenden Moor (England)	1	B3	Blanket peatland	53.569°, -1.919°
Bradfield Moor (England)	6	B4-7 (B20-21)	Blanket peatland	53.420°, -1.678°
Moor House (England)	4	B8-11	Blanket peatland	54.679°, -2.430°
Oakner (England)	8	B12-17 (B22-23)	Blanket peatland	53.599°, -1.972°
Oxenhope (England)	2	B18-19	Blanket peatland	53.791°, -1.970°
Cors Fochno (Wales)	11	R1-11	Raised bog	52.501°, -4.011°
Röyvänsuo (Finland)	1	F1	Sedge fen	65.820°, 27.804°
Marjasuo (Finland)	1	F2	Sedge fen	65.805°, 27.812°
Helvetinjärvi V (Finland)	1	F3	Sedge fen	61.996°, 23.942°
Helvetinjärvi II (Finland)	1	F4	Sedge bog	61.998°, 23.880°
Susimäki (Finland)	1	F5	<i>Vaccinium</i> bog	61.857°, 24.237°

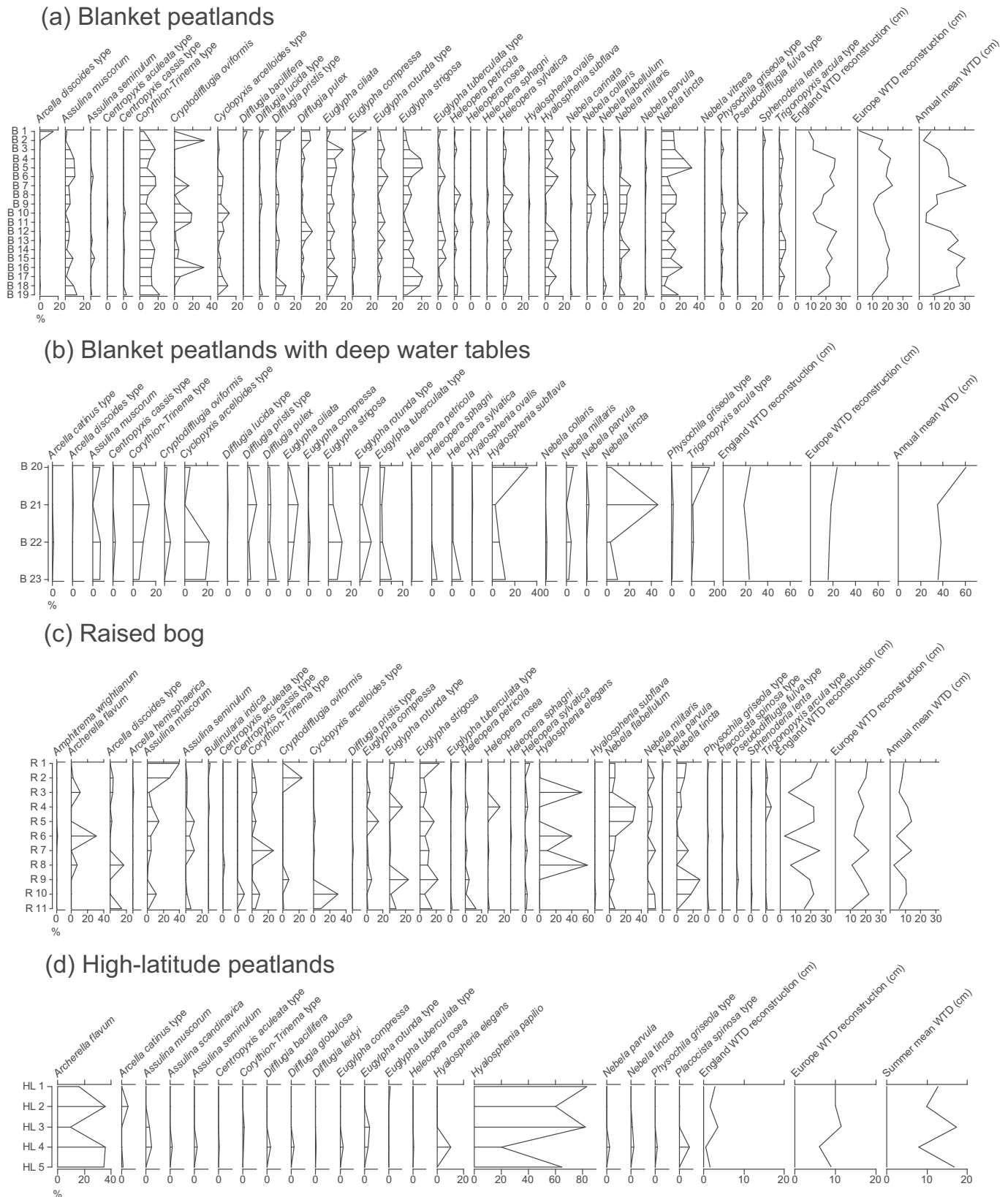


Fig. 1. Percentage testate amoebae data from contemporary samples from (a) blanket peatlands; (b) blanket peatlands with deep water tables (annual mean > 35 cm); (c) a raised bog; (d) high-latitude peatlands. The reconstructed water tables based on the England and European transfer functions are illustrated. The 1-year (or summer in the case of the high-latitude peatland which is frozen for part of the year) mean water-table data from the automated dipwells are also shown. Refer to [supplementary file 1](#) for the bootstrap errors on the reconstructions. The plotting of these samples here in the style of 'pseudo-palaeo' records shows that the transfer functions are identifying directional changes in the profiles; however, magnitudes are not reliable.

amoebae are not classed as true species in a taxonomic sense; rather, identification is based on test characteristics and groups of similar morphospecies (albeit with intraspecific variability) are known as 'types'.

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 400 \times magnification. Identification was aided with reference to several sources (Leidy, 1879; Penard, 1902; Cash and Hopkinson, 1905, 1909; Cash et al., 1915; Deflandre, 1936; Grospietsch, 1958; Corbet, 1973; Ogden and Hedley, 1980; Charman et al., 2000; Meisterfeld, 2001a, 2001b). The taxonomy used is a modified version of Charman et al. (2000), where some 'type' groupings were split to the species level (e.g. *Diffugia globulosa* was split out of *Cyclopyxis arcelloides* type in the case of the England model). However, the taxonomies were harmonised prior to water-table reconstruction. Transfer function-based reconstructions were carried out on the test data and sample-specific errors were calculated using 1000 bootstrap cycles (presented in Supplementary file 1). Statistical analyses were carried out in R version 3.0.2 (R-Core-Team, 2014). As the data are non-normal (based on results of Shapiro–Wilk tests), Spearman's rank correlation was used to determine significant correlations between the monitored water-table statistics and the TA-reconstructed water tables.

To assess the coverage of fossil taxa in the modern calibration set, the maximum abundances of taxa in the modern and fossil dataset were calculated and compared to determine any missing/poor-quality analogues or taxa with poorly-determined optima. Hill's N2 was also calculated to determine rare taxa (defined as $N2 \leq 5$). To compare reconstructed water-table magnitudes with recorded data over a longer timeframe, new fossil TA data from a short core from Moor House blanket peatland, northern England are presented. The core was taken from beside one of the water-table monitoring stations following the coring method of De Vleeschouwer et al. (2010). An outline chronology for the profile was established using spheroidal carbonaceous particles (SCPs) following Swindles (2010).

3. Results

Fig. 1 shows the testate amoebae present in the test data, together with reconstructed water tables from both transfer functions alongside the 1-year annual mean water-table values. Wet indicator taxa in the blanket peatland include *Arcella discoides* type, *Diffugia pristis* type and *Pseudodiffugia fulva* type; dry indicators include *Euglypha strigosa*, *Hyalosphenia subflava* and *Trigonopyxis arcuata* type. In the testate amoebae communities are completely decoupled from the water table, as reflected in the comparison of the monitored and predicted water-table values (Fig. 2). These four samples were excluded from further analyses.

There were several significant correlations between the statistics derived from the monitored water tables and the TA-based water-table reconstructions (Table 2). For example, there is significant correlation between mean annual water table (1 year) and the reconstructions using the European model ($r_s = 0.507$, $p < 0.01$) and England model ($r_s = 0.768$, $p < 0.01$). The correlation coefficients are generally higher for the England model for both the 1-year

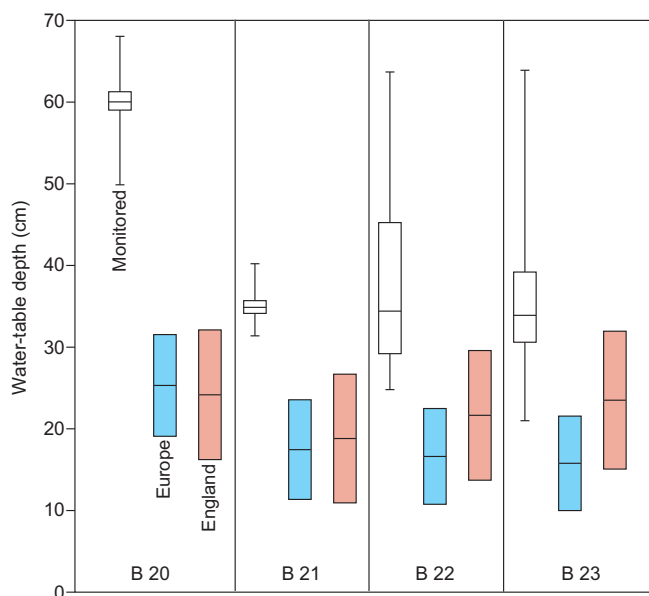


Fig. 2. Boxplots of one-year annual monitored data from four samples from blanket peatlands with very deep water tables (B20 – Loxely 5, B21 – Loxely 6, B22 – Oakner 7, B23 – Oakner 8). The testate-based water-table reconstructions (blue = Europe; pink = England) suggest testate amoebae are de-coupled from water-table depth in these sites. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

annual and summer data. In the 3-year dataset there are a greater number of significant correlations between the indices and the England model (Table 2). These significant correlations and the comparison of the predicted and monitored values illustrate that testate amoeba-based reconstructions do appear to reflect hydrological inter-site variations (Fig. 1, Table 2). However, an examination of the magnitudes suggest that the TA transfer functions poorly represent the annual or seasonal mean or median water-table values for the study sites (Figs. 1 and 3, Table 3). In most cases, both transfer function predictions are drier than the annual and summer measured mean values (i.e. above the 1:1 line in Fig. 3). Such a false over-deepening of the water table is especially apparent in the case of the raised bog samples. However, there are a number of samples from the blanket peatland where the transfer functions under-predict (i.e. less deep than observed) water-table depth. This again may reflect decoupling of the testate amoebae communities from the water table dynamics. The England model has very poor predictive power for the high-latitude samples as it severely under-predicts water-table depth (Figs. 3 and 4). This is due to the dominant taxa in the profile *Archerella flavum* and *Hyalosphenia papilio* being present primarily in very wet samples in the training set (cf. Turner et al., 2013). The more accurate reconstructions for the high-latitude peatlands by the European transfer function probably reflects the inclusion of samples from Estonia and Finland (Charman et al., 2007). These results illustrate the potential of transfer functions based on regional training sets or, alternatively, show that the inclusion of contemporary data from the same region as the fossil data is needed in the case of supra-regional transfer functions.

The variation in predictive power between the two transfer functions may reflect missing taxa or the quality of analogues in the training set (Fig. 5, Table 4). For example, there were several missing analogues in the European model (*Euglypha ciliata*, *Diffugia globulosa*, *Hyalosphenia ovalis*, *Placocista spinosa* and *Sphenoderia lenta*). Although there were no missing analogues in the England model, some taxa probably have poorly-constrained optima (e.g. *Diffugia pulex*, *Hyalosphenia elegans*, *Pseudodiffugia fulva*

Table 2

Correlation statistics (Spearman's rank correlation). The number of samples included in the analysis are shown; B = blanket peatlands; R = raised bog; H = high-latitude peatlands. D represents the water-table level at a given percentage of the time. % values represent the percentage of the time WT within a given depth (in cm) of the peat surface. Significant correlations are given [$**p < 0.01$ (red); $*p < 0.05$ (orange)]. For further information refer to [Supplementary file 1](#).

	Europe reconstruction (WA.tol.inv)	England reconstruction (WA.tol.inv)	n	Samples		Europe reconstruction (WA.tol.inv)	England reconstruction (WA.tol.inv)	n	Samples
Inter-model comparisons									
England reconstruction (WA.tol.inv)	.804**	1.000	35	All					
Annual 1 yr					Annual 3 year				
Mean	.507**	.768**	30	B+R	Mean	0.335	.637**	18	7B+R
Median	.566**	.798**	30	B+R	Median	0.387	.711**	18	7B+R
Max	0.174	.415*	30	B+R	Max	0.212	0.404	18	7B+R
Min	.544**	.767**	30	B+R	Min	0.100	.501*	18	7B+R
Range	-0.205	-0.130	30	B+R	Range	0.325	0.302	18	7B+R
D95	.567**	.785**	30	B+R	D95	0.325	.600**	18	7B+R
D90	.552**	.782**	30	B+R	D90	0.309	.612**	18	7B+R
D75	.551**	.796**	30	B+R	D75	0.337	.645**	18	7B+R
D50	.566**	.798**	30	B+R	D50	0.387	.711**	18	7B+R
D25	.454*	.705**	30	B+R	D25	0.401	.701**	18	7B+R
D10	.384*	.607**	30	B+R	D10	0.354	.550*	18	7B+R
D5	.366*	.591**	30	B+R	D5	0.255	.480*	18	7B+R
IQR	0.030	0.154	30	B+R	IQR	0.118	0.192	18	7B+R
%surface	-.405*	-.713**	30	B+R	%surface	-0.268	-.533*	18	7B+R
%10	-.523**	-.757**	30	B+R	%10	-0.434	-.697**	18	7B+R
%20	-.423*	-.661**	30	B+R	%20	-0.334	-0.448	18	7B+R
%30	-0.156	-.415*	30	B+R	%30	-0.086	-0.346	18	7B+R
%40	-0.109	-0.198	30	B+R	%40	-0.095	-0.254	18	7B+R
%50	-0.157	-0.100	30	B+R	%50	-0.068	-0.167	18	7B+R
Summer 1 year					Summer 3 year				
Mean	.526**	.667**	35	All	Mean	0.369	.493*	23	7B+R+H
Median	.519**	.658**	35	All	Median	0.411	.535**	23	7B+R+H
Max	0.332	.518**	35	All	Max	0.196	0.294	23	7B+R+H
Min	.534**	.654**	35	All	Min	0.187	.518*	23	7B+R+H
Range	0.041	0.091	35	All	Range	0.212	0.163	23	7B+R+H
D95	.598**	.696**	35	All	D95	0.372	.587**	23	7B+R+H
D90	.577**	.693**	35	All	D90	0.335	.544**	23	7B+R+H
D75	.538**	.671**	35	All	D75	0.364	.514*	23	7B+R+H
D50	.519**	.658**	35	All	D50	0.411	.535**	23	7B+R+H
D25	.439**	.594**	35	All	D25	0.358	.432*	23	7B+R+H
D10	.450**	.617**	35	All	D10	0.264	0.386	23	7B+R+H
D5	.449**	.622**	35	All	D5	0.233	0.352	23	7B+R+H
IQR	-0.082	0.060	35	All	IQR	-0.045	0.008	23	7B+R+H
%surface	-0.293	-.414*	35	All	%surface	-0.143	-0.355	23	7B+R+H
%10	-.600**	-.704**	35	All	%10	-.477*	-.566**	23	7B+R+H
%20	-.518**	-.652**	35	All	%20	-0.274	-0.323	23	7B+R+H
%30	-0.209	-.449**	35	All	%30	-0.099	-0.226	23	7B+R+H
%40	-0.179	-0.268	35	All	%40	-0.050	-0.120	23	7B+R+H
%50	0.068	0.136	35	All	%50	-0.188	-0.262	23	7B+R+H

type and *Sphenoderia lenta*) due to under-representation in the training set. Taxa with poorly-constrained optima in the European model include *Arcella catinus* type, *Diffugia bacillifera*, *Diffugia lucida* type and *Nebela collaris*.

4. Discussion and conclusions

There have been several recent studies which have identified problems with transfer function approaches in palaeoecology (Belyea, 2007; Telford and Birks, 2009, 2011; Payne et al., 2012; Velle et al., 2012; Juggins, 2013). The majority of these have used statistical tools to test transfer functions. Instead, we have used independent data sets to test the models, which is an alternative and potentially more powerful test. Here, the comparison of testate

amoeba-reconstructed water tables against high-resolution monitored data for contemporary samples illustrated that the reconstructions poorly represent the water-table magnitudes for the study sites (in terms of true mean, median or residence time-based statistics). However, directional changes in the testate amoeba-based reconstructions do appear to reflect inter-site hydrological variations. Our results show clearly that testate amoeba-based reconstructions can be used to identify past shifts in peat hydrology but reconstructed magnitudes should be interpreted with caution.

To illustrate our contention on the interpretation of water-table magnitudes, a TA profile and water-table reconstruction from Moor House in Northern England is shown in Fig. 6. The water-table reconstruction shows a transition from near surface to deeper water tables at the boundary of the Little Ice Age (LIA) and Current

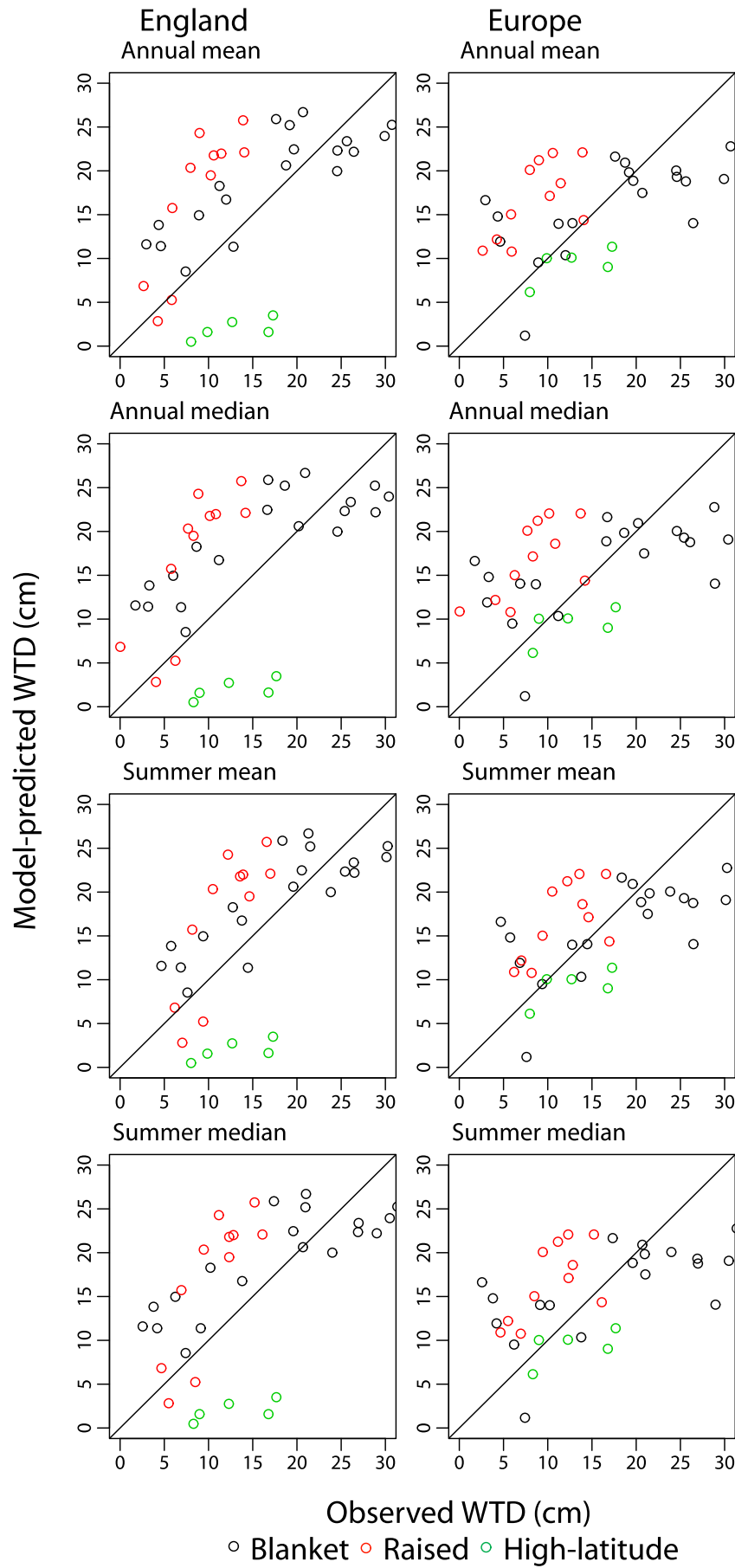


Fig. 3. Scatterplots of model-predicted water-table depth (England and Europe transfer functions) against water-table statistics from the monitoring data (annual and summer mean, and median). The black diagonal lines represent a 1:1 relationship between the two variables, and the peatland types are differentiated by symbol colour.

Table 3
Regression and correlation statistics (see Fig. 4).

Test data	Model	Slope (a)	Intercept (b)	n	R ²	r _s	p-value
All	England	0.59	7.95	35	0.29	0.77	$p < 0.01$
All	Europe	0.31	11.08	35	0.22	0.51	$p < 0.01$
Blanket	England	0.54	10.11	19	0.68	0.74	$p < 0.01$
Blanket	Europe	0.37	9.72	19	0.40	0.61	$p < 0.01$
Raised	England	1.84	0.95	11	0.72	0.85	$p < 0.01$
Raised	Europe	0.75	10.22	11	0.42	0.58	$p = 0.06$
High-latitude	England	0.20	−0.60	5	0.50	0.90	$p < 0.05$
High-latitude	Europe	0.31	5.29	5	0.43	0.70	$p = 0.23$

Warm Period (CWP) at c. 1850. This has been observed in several peatland profiles in the British Isles (e.g. Mauquoy et al., 2008; Swindles et al., 2010; Turner et al., 2014). Such a level of replication suggests that the reconstructed water-table transition is an unambiguous response of peatlands to climate change (e.g. Swindles et al., 2012; Swindles et al., 2013). However, a comparison of the recent part of the reconstruction with the water-table data from beside the coring site suggests that the magnitude of the reconstruction is too dry. In fact, the reconstructed water-table magnitude is equivalent to the maximum water-table depth recorded in the monitoring data (i.e. the end of the whisker of the red boxplot in Fig. 6).

There are probably two reasons for the transfer functions providing predictions that are mainly too dry. Firstly, the field sampling for the development of the two published transfer functions was carried out in the summer season which introduces a warm-season bias. Secondly, not enough time for equilibration of water tables may have been left during sampling leading to water-table data that are artificially too deep. The saturated hydraulic conductivity of peat can vary from $\sim 1 \text{ cm s}^{-1}$ in the uppermost peat to $1 \times 10^{-8} \text{ cm s}^{-1}$ a few tens of cm from the peat surface (Hoag and Price, 1997; Holden and Burt, 2003a; Cunliffe et al., 2013). Thus, when researchers have performed one-off water-table measurements associated with TA sampling, it may be that in some cases the water level in the auger hole or pit had not have risen sufficiently by the time a reading was taken. This problem may be exaggerated when larger holes are dug as a greater volume of water is required to enter the hole. Smearing of the hole sides by spades or augers can also reduce rates of water entry into it. The problem is likely to be greater during summer sampling when water tables are often deeper and more likely to be at depths where the peat has a lower hydraulic conductivity.

Testate amoebae transfer functions now exist from many regions of the world based on one-off water-table measurements (e.g. Charman et al., 2007; Lamentowicz et al., 2008a; Swindles et al., 2009; Amesbury et al., 2013; Turner et al., 2013; Van Bellen et al., 2014). A previous model for British peatlands was developed using mean annual water-table data (Woodland et al., 1998). However, not all the samples in this model were based on sites with high-quality monitored water-table data (some mean annual values were inferred between microforms), and the model suffered from problems of missing/poor analogues as well as some poorly-constrained optima-tolerances; thus, more recent transfer functions are now mostly used.

Several authors have attempted to obtain mean annual water-table data using a method involving the discolouration of PVC stakes or tape (Payne et al., 2006; Swindles et al., 2009; Markel et al., 2010; Amesbury et al., 2013); however, nearly all attempts have failed completely or to some degree. The transfer function of Booth (2008) is the one study where the PVC tape-discolouration method has been used with great success to develop a mean annual water-table transfer function for *Sphagnum* peatlands in the USA. However, the precise relationship of the PVC tape-

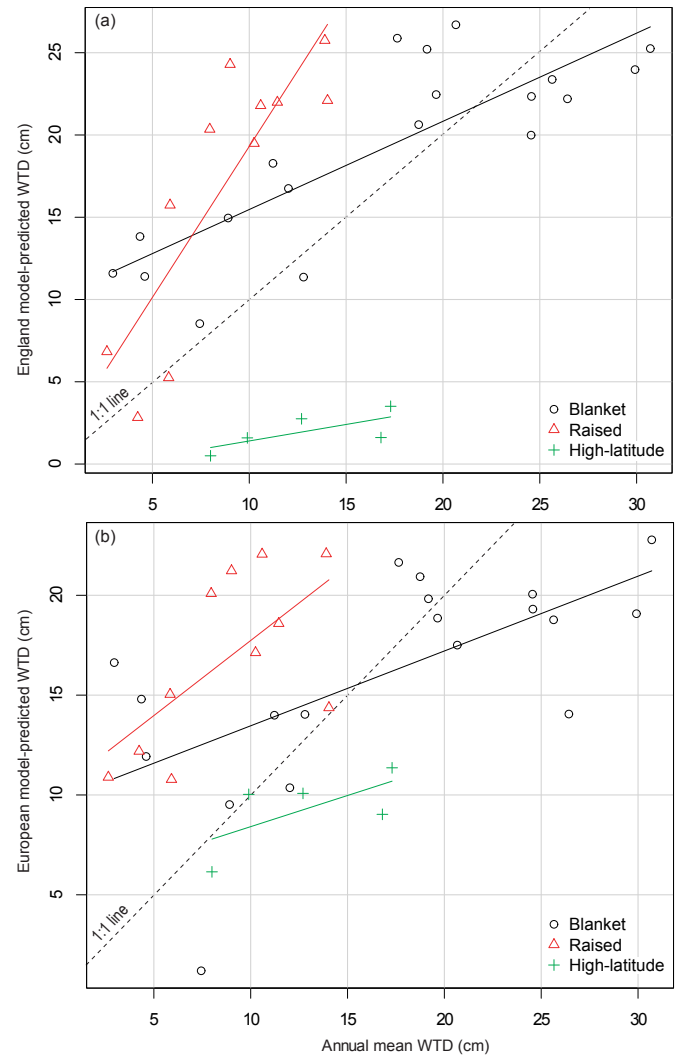


Fig. 4. Scatterplots of model-predicted water-table depth (using the (a) England and (b) Europe transfer functions) against annual mean water-table depth from the monitoring data for the three peatland types. Linear regression lines are shown (see Table 3 for the regression statistics). The black diagonal lines represent a 1:1 relationship between the two variables.

discolouration and water table is still not completely understood (Belyea, 1999; Booth et al., 2005; Schnitchen et al., 2006). It is clear that the best way to achieve high-resolution water-table data is the use of dipwells equipped with logging pressure transducers. However, transfer functions commonly include >100 sample points, thus rendering this approach prohibitively expensive to most researchers.

The decoupling of testate amoebae from very deep water tables partly explain the relatively poor performance of transfer functions at the drier end reported in a number of studies (e.g. Swindles et al., 2009; Van Bellen et al., 2014). Testate amoebae are probably not responding directly to water-table depth, but instead are responding to variables correlated with it (Jassey et al., 2011; Sullivan and Booth, 2011). The very deep water tables at four monitoring points suggest a potentially degraded peatland system at these locations. Indeed, the water table never came within 10 cm of the surface at any point in time for these four points although regular saturation and the development of saturation-excess and near-surface flow during rainfall events is a typical characteristic of fully functioning blanket peat (Holden and Burt, 2003b; Acreman

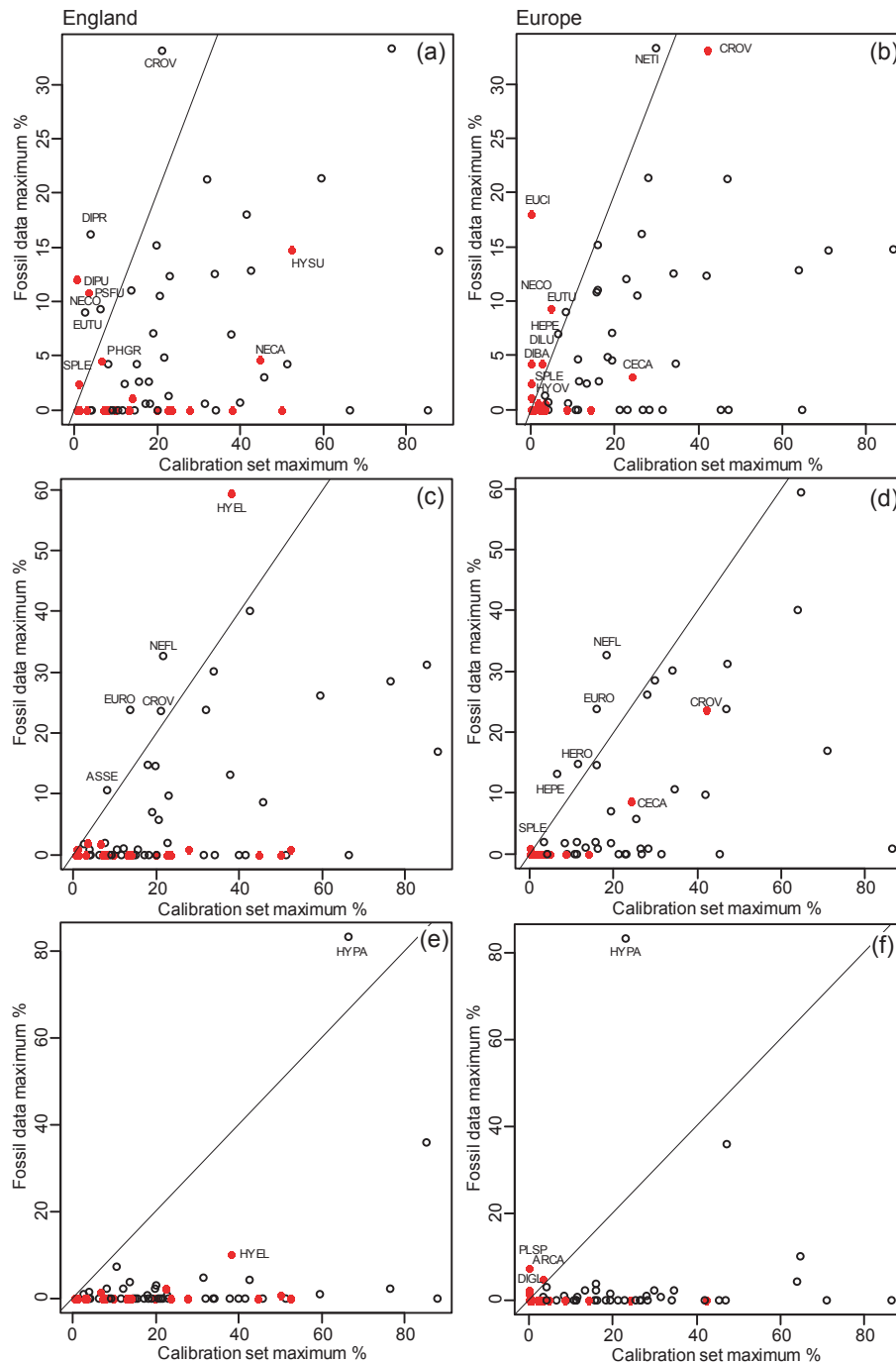


Fig. 5. Maximum abundance of taxa in the calibration (modern) and fossil datasets for testing of analogue quality; (a, b) blanket peatlands; (c, d) raised bog and (e, f) high-latitude peatlands. Taxa with $N2 \leq 5$ are shown by filled red symbols. Abbreviated names are shown for problem taxa (see Table 4 for full names). The black diagonal lines represent a 1:1 relationship between the modern and fossil data. Further interpretation is provided in Table 4. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and Holden, 2013). Thus, the surface moisture content of the peat at these four points may not have been strongly related to the water-table depth and may instead have been more controlled by individual rainfall episodes. Holden et al. (2011) showed that intact blanket peat water tables are strongly controlled by evapotranspiration, with water tables remaining close to the surface for most of the winter and only dropping a few cm in summer during warm, dry conditions. They also showed that for degraded blanket peat, water tables are more strongly controlled by free drainage of water

through the peat, having almost equal levels of variance in both winter and summer.

Unfortunately, there is no simple way to statistically correct transfer function models to mean annual water-table depth or similar measure, due to the variation in accuracy across the hydrological gradient and complexities of community composition (Figs. 3 and 4). Our results may also suggest that the errors generated from bootstrapping are ineffectual as the reconstructions are inaccurate in terms of absolute values. Thus, to avoid confusion

Table 4

Modern analogue quality for the England and Europe transfer function models (refer also to Fig. 5). Three different categories of analogue quality have been determined (in descending order of severity): 1) samples left of the 1:1 line with $N2 \leq 5$; 2) Samples left of the 1:1 line but with no $N2$ problem; 3) Samples right of the 1:1 line with $N2 \leq 5$. Taxon names with an asterisk (*) have no modern analogue in the training set.

	England	Europe
Blanket		
(1) Poorest/Missing analogue $N2 \leq 5$	<i>Diffugia pulex</i> <i>Pseudodiffugia fulva</i> type <i>Sphenoderia lenta</i>	<i>Diffugia bacillifera</i> <i>Diffugia lucida</i> type <i>Euglypha ciliata</i> * <i>Hyalosphenia ovalis</i> * <i>Nebela collaris</i> <i>Sphenoderia lenta</i> *
(2) Poor analogue $N2 > 5$	<i>Cryptodiffugia oviformis</i> <i>Diffugia pristis</i> type <i>Euglypha tuberculata</i> type <i>Nebela collaris</i>	<i>Euglypha tuberculata</i> <i>Heleopera petricola</i> <i>Nebela tinctoria</i>
(3) Reasonable analogue, but $N2 \leq 5$	<i>Hyalosphenia subflava</i> <i>Nebela carinata</i> <i>Physochila griseola</i> type	<i>Centropyxis cassis</i> type <i>Cryptodiffugia oviformis</i>
Raised		
(1) Poorest/Missing analogue $N2 \leq 5$	<i>Hyalosphenia elegans</i>	<i>Sphenoderia lenta</i> *
(2) Poor analogue $N2 > 5$	<i>Assulina seminulum</i> <i>Cryptodiffugia oviformis</i> <i>Euglypha rotunda</i> type <i>Nebela flabellulum</i>	<i>Euglypha rotunda</i> type <i>Heleopera petricola</i> <i>Heleopera rosea</i> <i>Nebela flabellulum</i> <i>Centropyxis cassis</i> <i>Cryptodiffugia oviformis</i>
(3) Reasonable analogue, but $N2 \leq 5$	—	—
High latitude		
(1) Poorest/Missing analogue $N2 \leq 5$	—	<i>Arcella catinus</i> type <i>Diffugia globulosa</i> * <i>Placocista spinosa</i> type*
(2) Poor analogue $N2 > 5$	<i>Hyalosphenia papilio</i>	<i>Hyalosphenia papilio</i>
(3) Reasonable analogue, but $N2 \leq 5$	<i>Hyalosphenia elegans</i>	—

with contemporary site water-table data, we suggest that peatland water-table reconstructions should be converted to residuals or standardised values to avoid confusion with contemporary water-table data with true magnitudes (Fig. 6) (e.g. Swindles et al., 2013). This enables researchers to present a useful index of change along a relative water-table gradient rather than present inaccurate absolute values.

There have been a number of recent studies examining the potential of testate amoebae as management and restoration indicators in peatlands (Buttler et al., 1996; Jauhiainen, 2002; Davis and Wilkinson, 2004; Laggoun-Defarge et al., 2008; Turner and Swindles, 2012; Valentine et al., 2013). To the best of our knowledge, testate amoebae reconstructions have not yet been used in a management/restoration based study. While testate amoebae may provide important ecological information about the state of peatlands, our results suggest that testate amoebae-based reconstructions cannot currently be used to establish site hydrological baselines needed to inform management and restoration policies. To achieve such baselines, a new series of TA transfer functions based on high-quality hydrological data are needed.

Clearly, TA-based transfer functions still offer valuable insights into past environmental changes by helping us identify shifts in environmental conditions as demonstrated by numerous research outputs from several regions on Earth (e.g. Sillasoo et al., 2007; Lamentowicz et al., 2008b; Kokfelt et al., 2009; Swindles et al., 2014; Turner et al., 2014). However, we assert that the interpretation of water-table reconstructions should move away from reporting actual values in most cases and instead focus on directional shifts. Our work highlights that testing transfer functions against independent instrumental data sets is potentially more powerful than relying on statistical techniques alone.

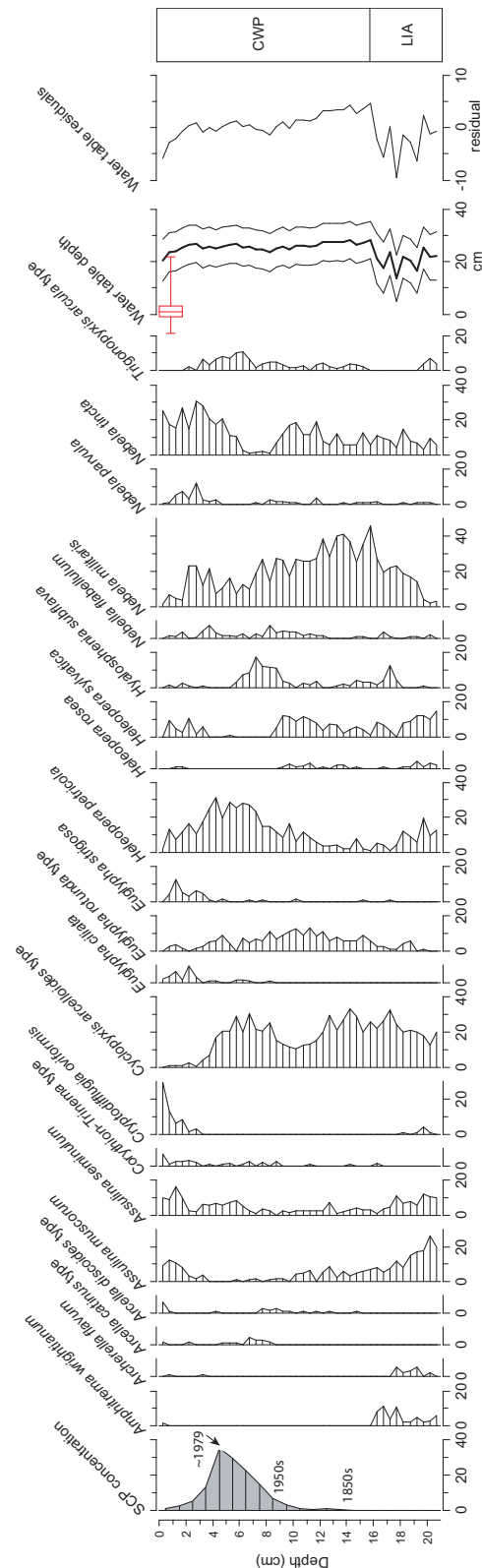


Fig. 6. Percentage testate amoebae data from a core from Moor House blanket peatland, Northern England. Chronological control is achieved through changes in spheroidal carbonaceous particle (SCP) concentration (cf. Swindles, 2010), and water-table depth has been reconstructed using the England model (Turner et al., 2013). Errors on the reconstruction were generated through 1000 bootstrap cycles. The red boxplot illustrates the one-year annual monitored data from a monitoring location beside the coring location. The water-table data is also shown as residual values — one of our recommendations for presentation of water table reconstruction data. The results show a transition from near surface to deeper water tables at the boundary of the little ice age (LIA) and current warm period (CWP) at c. 1850. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quascirev.2015.04.019>.

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