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The performance of single- and multi-proxy transfer functions (testate amoebae, bryophytes, vascular plants) for reconstructing mire surface wetness and pH

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Abstract

Peatlands are widely exploited archives of palaeoenvironmental change. We developed and compared multiple transfer functions to infer peatland depth to the water table (DWT) and pH based on testate amoeba (percentages or presence/absence), bryophyte presence/absence and vascular plant presence/absence data from sub-alpine peatlands in the SE Swiss Alps in order to compare the performance of single-proxy vs. multi-proxy models and assess the performance of presence/absence models.

Bootstrap cross-validation showed the best-performing single-proxy transfer functions for both DWT and pH were those based on bryophytes. The best-performing TF overall were those based on combined testate amoebae %, bryophytes and vascular plants for DWT and on testate amoebae and bryophytes for pH. The comparison of DWT and pH inferred from TA % and presence/absence models showed that the general patterns were similar but the magnitude and timing of some shifts were different.

These results show new directions for palaeoenvironmental research suggesting: 1) that it is possible to build transfer functions which perform well using presence/absence average data, although with some loss of accuracy, 2) supporting the idea that multi-proxy inference models may improve palaeoecological reconstruction. The performance of multi-proxy and single-proxy transfer functions should be further compared in palaeoecological data.

Key words: Peatlands; bryophytes; vascular plants; testate amoebae; transfer function; quantitative palaeoecology; monitoring; water table depth; pH

Introduction

Testate amoebae (Protists) and plant macrofossils are the two most commonly used proxies for reconstructing Holocene environmental change in peatlands (Booth, 2010; Hughes et al., 2006; Mauquoy et al., 2004). These proxies primarily reflect surface wetness and pH and can be used to study mire development, climate change, and human impacts (e.g. drainage, grazing). The two proxies complement each other well in palaeoecological studies (Mauquoy and van Geel, 2007; Mitchell et al., 2008) and also have a strong potential for use in the biomonitoring and conservation management of peatlands (Lavoie et al., 2001). Most studies on peatland testate amoeba ecology highlight the importance of surface wetness, and water table depth or some related variable almost invariably emerges as the strongest environmental variable explaining the testate amoeba community data (Booth, 2008; Charman et al., 2007; Swindles et al., 2009). Relationships to water chemistry have also been documented but have been much less studied, and focused mostly on pH (Lamentowicz et al., 2008; Mitchell et al., 1999; Opravilova and Hajek, 2006; Tolonen et al., 1992). Despite the importance of wetland plants in community ecology (Bridgham et al., 1996; Wheeler and Proctor, 2000), studies providing quantitative inferences on the basis of sub-fossil plant remains are rare (Janssens, 1983; Kuhry et al., 1993; Väliranta et al., 2007).

The use of multiple proxies in the same record is generally believed to lead to more accurate and robust palaeoenvironmental reconstruction (Birks and Seppa, 2010; Caseldine and Gearey, 2005; Charman et al., 1999; Long et al., 1996). The general rationale for this is that while each proxy has its limitations a signal is more likely to be accurate if several proxies show the same trend. Combining different proxies in a synthetic way (e.g. in a single transfer function) is an alternative option. This option may be especially pertinent where proxies differ slightly in their response (Lamentowicz et al., 2010b) or are useful for different parts of a gradient (Gehrels et al., 2001). Previous studies have examined the combined use of testate amoebae, diatoms, and foraminifera (Gehrels et al., 2001) and diatoms and foraminifera (Kemp et al., 2009) for reconstructing past sea-level changes, and of chironomids, diatoms, and chrysophytes for reconstructing alkalinity, DIC, altitude, pH and dissolved CO_2 in mountain lakes (Thompson et al. (2008). This multi-proxy approach has not been trialled for the peatland archive but may offer improved reconstructions.

This study is a continuation of earlier work on the same material, derived from sub-alpine mires of SE Switzerland (Upper Engadine valley). We developed a testate-amoeba-based transfer function for inferring depth to the water table (DWT) and applied it in a palaeoecological study covering the instrumental period AD 1864–2003 (Lamentowicz et al., 2010b) and the last millennium (van der Knaap et al., 2011). We also studied the relationships among testate amoebae, bryophytes, vascular plants, and hydrochemical variables (Lamentowicz et al., 2010a). One outcome of the latter study was that the three categories of organisms had somewhat different, though overlapping responses to environmental gradients; species-environment correlations were higher for testate amoebae than for bryophytes and vascular plants and the individual environmental variables explained different proportions of the variance. Transfer functions combining two or three proxies in a multi-proxy model would therefore be ecologically justifiable and given the differing responses, might offer superior performance. Here we therefore follow-up to assess if multi-proxy models (all possible combinations of testate amoebae, bryophytes and vascular plants) would outperform single-proxy models.

Sites and methods

Lamentowicz *et al*. (2010a) provided a full description of study sites, location map, and field and laboratory methods. Summary information on the sites is given in Table 1. Field sampling was done over a three-day period in August 2007 (97 plots) in the sub-alpine belt of the Upper Engadin valley, SE Swiss Alps (average coordinates 46°27’00’’ N; 9°46’30’’ E; elevation range 1810–1864 m a.s.l.). The sampled locations cover a wide range of surface moisture, trophic states, and vegetation types. The largest mire studied is Mauntschas, a *Sphagnum* mire at the valley bottom surrounded by natural conifer forest that includes minerotrophic mire, sloping fen, *Sphagnum fuscum* hummocks, and ombrotrophic mountain-pine bog. The peatlands near Maloja Pass lie on the side of the valley bottom and are surrounded by non-natural *Pinus mugo* forest. They are poor fens dominated by *Sphagnum fallax*, *Carex rostrata*, and *Eriophorum angustifolium*. Inn Fen is a peaty meadow along the river Inn, dominated by sedge vegetation and with scattered *Alnus incana* and *Salix* trees; the samples are mainly vascular-plant detritus. The mires of Lej da Staz, Lej Marsch, and Lej Nair lie adjacent to small lakes close to the valley bottom and are surrounded by natural conifer forest. Lej Marsch and Lej da Staz mires represent typical examples of terrestrialisation with floating *Sphagnum* mats near the lakeshore and more stable peat closer to the forest; sampling was done in a transect along this gradient. Lej Nair site is species-rich calcareous sloping fen.

Four data sets were used for numerical analysis: testate amoeba (TA) percentages, TA presence/absence, bryophyte presence/absence, and vascular plant presence/absence. Taxa present in less than three samples were removed from the data sets. A limitation of our study is that we did not have percentage data for bryophytes and vascular plants. There are practical and theoretical reasons for this decision. Obtaining reliable percentage data for bryophytes would have required sampling and identifying about 10’000 samples (ca. 100 per plot x ca. 100 plots). We felt that such an effort was not justified because bryophyte macrofossil data is usually at best estimated on a semi-quantitative scale and there is no direct correspondence between surface cover and macrofossil volume because the different moss species have contrast=ing architecture and decay at different rates. Vascular plants, on the other hand, are typically identified as presence-absence data in macrofossil analyses, and even for this the amount of peat material needed often exceeds what is available, especially for studies aiming at high temporal resolution.

Transfer functions were created separately for DWT (depth to the water table measured at the time of sampling) and pH (measured on water extracted from the same moss samples as those used to extract testate amoebae), using C2 (Juggins, 2003). Data filtering (outlier sample removal), although criticised, is often used in palaeoecology (Booth et al., 2008; Edwards et al., 2004; Wilmshurst et al., 2003; Woodland et al., 1998). The rationale for this, besides improving model performance is that some sampled locations may correspond to unusual situations (e.g. affected by a confounding factor such as plant faeces/urine) that are impossible to model accurately. We filtered the data in a single step by removing outlier samples with residuals higher than the standard deviation of the observed values. This procedure was repeated a second time in three cases (as clear outliers remained): for 1) bryophytes and vascular plants, 2) vascular plants, and 3) TA presence/absence. Transfer functions were created for each of the four data sets separately and all appropriate combinations of data sets (Table 2).

Combining presence/absence data with percentage data resulted in an imbalanced data set in which the presence was interpreted as 1% cover. To assess how this affected the model performance we compared three options. The first was the original presence/absence (hereafter: 1/0) data. In the second case the data was multiplied by one hundred (hereafter: 100/0). In the third case the total percentage was adjusted to 100% by replacing each presence by 100 divided by the number of species present in a sample [hereafter: (100/n)/0]. Note that the resulting total "percentage" was therefore of 100% for one data set, 200% for two and 300% for the three sets. In this way, each data set was given equal weight in the overall analysis.

The rationale for comparing TA 1/0 and % data sets was to assess how the corresponding reduction in information affected model performance. In very few palaeoecological studies are testate amoeba abundances too low to make calculations of percentages meaningful and in such cases quantitative inference of DWT or other variables is generally not performed (Wehrli et al., 2010). Percentage cover of plants does not directly relate to volumetric percentages in palaeoecology. It should be recognised that apparent presence/absence partly reflects count total for testate amoebae and quadrat size for plants.

Among the available transfer function models weighted averaging with classical deshrinking was found to perform best in the majority of cases, so this was used to compare the performance of the different combinations of proxies. Our goal here was not to find the absolute best model for each combination of proxies but rather to assess in general how different combinations perform. We assessed the performance of the different transfer functions for DWT and pH on the basis of r^2, root mean squared error of prediction (RMESP), average bias and maximum bias all determined by both bootstrap and the recently-proposed leave-one-site-out cross-validation (Payne et al., in press), using R (R Development Core Team, 2010) and the rioja library (Juggins, 2011). We also compared DWT and pH reconstructions from a 1000 years record from Maunstschas mire (REF XX) based on % or 1/0 testate amoebae filtered or raw models to assess what implications the observed differences in model performance would have on palaeoenvironmental reconstruction.

Results

Among single proxy 1/0 models the best performance was found with bryophytes for DWT and TA or bryophytes for pH (Table 2). The use of 1/0 compared to % reduced the performance of TA transfer functions (e.g. for raw models r^2_{boot} respectively 0.53 versus 0.65

for DWT and 0.67 versus 0.73 for pH, Table 2). It is also noteworthy that the TA 1/0 model failed to accurately predict water table depth below 20 cm (Supplementary Figures 3 & 4).

Our results provide support to the idea that multi-proxy transfer functions combining TA and bryophytes or TA, bryophytes and vascular plants outperform single-proxy transfer functions for both raw and filtered data. However, contrary to expectation and to results from single-proxy models, the use of 1/0 TA data resulted in better multi-proxy models in two of the three cases for DWT (unfiltered data, models including vascular plants) and one case for pH (TA and vascular plants) (Table 2). Indeed the best performing DWT model overall with unfiltered data combined TA 1/0, bryophytes and vascular plants. Thus for both DWT and pH either better models could be produced using 1/0 data, or the use of % TA data only marginally improved model performance.

Data filtering (outlier removal) strongly improved the performance of transfer functions, especially for pH (Table 2, Supplementary Fig. 1–11). As for unfiltered data, TA single proxy models performed better when based on % than on 1/0 data. Among the filtered single-proxy models, bryophytes performed best for both DWT and pH. Among the multi-proxy transfer functions, the DWT transfer function based on TA %, bryophytes, and vascular plants performed best (r^2 = 0.87, RMSEP = 4.3 cm). For pH, the best multi-proxy model was based on TA % and bryophytes (r^2 = 0.94, RMSEP = 0.27 pH units).

We next compared model performances based on three transformations: a) the original presence/absence [1/0] data, b) the same data multiplied by one hundred [100/0], and c) replacing each presence by 100 divided by the number of species present in a sample [(100/n)/0] for unfiltered data. When combining TA % data and bryophyte and/or vascular plant data, the use of 100/0 or (100/n)/0 data generally improved model performance. The best overall model for DWT was for TA%, bryophytes and vascular plants 100/0. The best model for pH was for TA 1/0 and bryophytes (100/n)/0 (Supplementary table 2). These models are based on unfiltered (raw) data and could therefore be further improved through filtering (but making direct comparison among models less meaningful).

Evaluating our models using the newly developed LOSO approach led to similar results (Supplementary table 3). In all cases performance was marginally weaker with LOSO than regular bootstrap validation. Models such as pH based on vascular plants with r^2 around

0.4 had no predictive power in this test (RMSEP>standard deviation), while the performance of the best models was less affected.

Implications for palaeoenvironmental reconstruction

The DWT and pH reconstructions for Mauntschas mire for the last millennium using raw and filtered % and 1/0 TA transfer functions illustrate how differences in model performance can potentially affect palaeoenvironmental reconstruction (Figure 1 & 2, Supplementary Figure 12). The major phases are similar, but some quite important differences are also visible. For example using the 1/0 model results in a ca. 2 cm lag (in sample depth) in the timing of the dry shift occurring between 85 and 90cm depth. As this corresponds to a period of low peat accumulation rate this translates into a 200-year difference in the timing of this shift.

Pairwise comparisons between models show that filtering leads to slightoverestimation of DWT for low values and underestimation ofDWT for larger values (i.e. drier conditions are inferred in wet phases and wetter conditions are inferred in dry phases) overall there is a 5.7cm average underestimation for the filtered model compared to the raw model. For pH the effect is an almost constant overestimation of 0.08 pH units for the filtered model as compared to the raw model. For both DWT and pH, 1/0 models yield results, which are in some cases very different from the values produced by the % model (r^2 between values inferred from raw % and 1/0 models = 0.773 and 0.619, for DWT and pH, respectively). The DWT values inferred from the raw 1/0 model were in many cases lower than those from the raw % model, especially for DWT >25 cm (Figure 2). Inferred pH values from the raw 1/0 model were on average 0.29 pH units lower than those obtained from the raw % model.

Discussion

Building models from presence/absence data

The first important result of our study is the good performance of transfer functions based on presence/absence data. In these cases ‘weighted averaging’ is reduced to simple averaging with the average environmental value of taxa occurrence used to represent its optima. This is rarely done, maybe because it is mostly not considered useful although examples do exist, for instance Mezquita et al. (2005), for freshwater ostracods. Given the computational simplicity of this approach our results suggest that this method should be more widely investigated. Presence/absence data may be quicker to obtain than relative abundance data but partly reflects the count total used. The normal count totals for testate amoeba analysis (50-200 individuals) are insufficient to identify all taxa, so the recorded presence/absence of a taxon reflects sampling intensity as well as real presence or absence (Payne and Mitchell 2009; Wall et al. 2010). Future studies would need to assess the count total needed to achieve sufficiently accurate presence/absence data before lower counts, and therefore quicker counting, could be routinely implemented.

The comparison of inferred DWT and pH patterns from Mauntschas mire using % vs 1/0 models shows that it is to possible to infer both variables using 1/0 models. The two types of models however do not yield identical results. In some cases the interpretation could be quite different, if not for the overall patterns at least for the precise timing and the magnitude of changes. As both % TA models perform better than their corresponding 1/0 models these difference suggest that inference from % models is more reliable than for 1/0 models. Nevertheless as % models are not perfect 1/0 models could in some cases be more accurate.

Single-proxy models

The second important, and surprising result is that single proxy DWT and pH models based on TA, were out-performed by models based on bryophytes for filtered data (and also for raw data in the case of DWT). This raises the question of a possible superior performance of models based on percentage bryophyte data. This is however both difficult to achieve (and was beyond the scope of the present study) and potentially of little practical use for several reasons. First, obtaining reliable percentage data for bryophytes is not a simple task, as precise identification requires microscopy analyses, in this case of thousands or tens of thousands of samples for the full data set. Second, supposing that percentage data could be generated for the modern data set these data would not be fully equivalent to the percentage data obtained from macrofossil analyses (as estimated using e.g. the Quadrat and Leaf Count method – Barber et al. 1994) because surface cover does not equate to volume. Further limitations, are the possible differential preservation of bryophyte species and the variable taxonomic resolution that can be achieved in the analysis of fossil material (Janssens, 1983). Nevertheless, these results suggest that there is potential for quantitative reconstruction of DWT and pH based on presence-absence bryophyte data.

Outlier removal

Filtering the data set by removing outlier samples with residuals higher than the standard deviation of the observed values clearly improved the model performance in many cases. However, these apparent improvements in model performance were often at the cost of a considerable reduction in sample number; this number ranged from 2 to 33 depending on the models (supplementary Table 2). While it can be understandable that a few samples represent truly unusual conditions that do not justify inclusion in a transfer function, and their removal from a data set can then be defendable, this cannot possibly be the case for 40% of the samples as in the most extreme case (vascular plant pH model). This shows that outlier removal should preferably not be based on "automatic", apparently objective procedures but rather on a cautious analysis of the community composition and ecological conditions of the sampling location. Where these clearly indicate that the sample may not realistically be modelled accurately by a transfer function this would warrant exclusion. In other cases it is clearly advisable to keep the samples in the model, even if its apparent performance is not ideal.

Applying the raw and filtered models to the palaeoecological record from Mauntschas mire produced little change in reconstructions. The r^2 of inferred values between raw and filtered models were high (0.95 - 0.996). This clearly shows, at least for the data set on which this comparison is based, that model "optimisation" by data filtering has little effect on palaeoenvironmental reconstruction.

Comparing single-proxy and multi-proxy models

We compared the performance of single-proxy and multi-proxy transfer functions for DWT and pH using TA, bryophytes, and vascular plants. The expectation that multi-proxy models out-perform single-proxy models was confirmed for both DWT and pH and for both raw and filtered data.

Compared to other multi-proxy transfer function studies (e.g. Gehrels et al. 2001) the three groups we compare here are very different in their morphology, ecology and life history. Testate amoebae are mostly heterotrophic unicellular protists living in the upper accrotelm; bryophytes and vascular plants are autotrophic and multi-cellular, bryophytes being dependent on the water available at the soil surface and vascular plants actively drawing water from deeper-lying layers. This affects how the different groups respond to environmental change. For example, fluctuations in surface moisture will directly affect testate amoebae and the bryophytes, until the water table drops below ca. 30cm when a further lowering of the water table is unlikely to produce further impacts (Mitchell et al. 1999). A further drop in the water table may however significantly impact vascular plants, many of which extend their root system several decimetres in the soil. This may make combined predictions based on all groups sensitive to a broader hydrological gradient, but also makes interpretation of those results more difficult. For instance while transfer functions for testate amoebae aim to reconstruct water table depth, the transfer functions actually show the hydrological conditions at quite different spatial scales. While amoebae respond to moisture conditions in their immediate (µm^3 scale) vicinity (e.g. water film thickness on a *Sphagnum* leaf), in the case of bryophytes the hydrological sensitivity is likely to be larger on the scale of cms^3 and for vascular plants larger again, on the scale of dm^3. This need not be a concern if hydrology at all these scales is strongly correlated with water table depth, but this represents a source of uncertainty in the results.

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The difference in scale of environmental sensitivity also applies for pH. The pH was measured on the bryophyte in which the testate amoebae live, whereas the rooting zone of vascular plants may be influenced by water of a different pH due to vertical gradients in water chemistry (Mitchell et al., 2000). In line with this, the best pH filtered model was the one based on testate amoeba percentage and bryophyte data. The distribution of pH along the fen-bog gradient is clearly bimodal and this results in generally poor model performance around pH values of 5.0. A notable exception to this is the model combining testate amoebae percentage data and vascular plants (Supplementary figure 10), which is precisely the best performing raw model. This may be explained by the fact that surface pH values of 5.0 correspond to transitional mire where a clear vertical pH gradient develops (Tahvanainen, 2004). Thus under these conditions bryophytes and/or testate amoebae will indicate more acidic conditions (and hence underestimate pH) while vascular plants will indicate less acidic conditions (and hence overestimate pH). This should be especially important in habitats with surface pH around 5.0, where calci-tolerant *Sphagnum* mosses (e.g. *S. contortum, S. warnstorfii*, and *S. teres*) strongly acidify surface waters by releasing organic acids and hence strengthen the vertical pH gradient (Andrus, 1986; Hajkova and Hajek, 2004).

Our results suggest that multiproxy transfer functions may be a useful new technique for palaeoenvironmental reconstruction from peatlands but further work is necessary to understand the sensitivity of these models. Conventional single proxy reconstructions allow the comparison of different reconstructions: where these diverge an informed ecological judgement can be made about which may be more reliable in each specific circumstance. By combining very different groups of organisms in a single model no such judgement can be reached and it is unclear how a combined model would react in a situation where different groups of organisms indicate different conditions. We therefore recommend that both single and multiproxy reconstructions be produced in parallel and multiproxy results treated with caution where there is a divergence in the results of different proxies.

SUMMARY

Over the last 20 years the approach to macrofossil and testate amoeba-based palaeoenvironmental reconstruction in peatlands has become increasingly standardised. Testate amoeba percentage transfer functions are used to quantitatively reconstruct water table (and less frequently pH) changes and ordination techniques used to summarise macrofossil results in a single index assumed to primarily represent a, loosely defined, peatland surface wetness. Our results show that alternative approaches can be applied and may present superior performance. Bryophyte transfer functions can be produced from presence/absence data and perform well in cross-validation. Presence/absence data might allow quicker testate amoeba analysis, but with some loss of information. Multiproxy transfer functions based on more than one group of organisms may out-perform single-proxy transfer functions. These new approaches require further appraisal with palaeoecological data but offer exciting new options that deserve exploration.

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Tables

Note to editors. The tables were prepared in excel and are pasted as images (more readable).

Editable versions are provided separately

Table 1. Location and general characteristics of the studied sites

Site name	Coordinates		Altitude [m a.s.l.]	Depth to water table [cm]			pH			n *
	Latitude	Longitude		Min	Max	Average	Min	Max	Average	
Mauntschas	46°27'27"N	09°51'22"E	1818	-20	41	11.7	3.61	6.98	5.13	39 (3)
Lej da Staz	46°29'50"N	09°52'10"E	1810	0	76	18.4	4.51	6.15	5.24	11 (1)
Lej Marsch	46°28'31"N	09°49'11"E	1813	5	70	33.2	3.72	4.61	4.09	12 (2)
Lej Nair	46°28'13"N	09°49'12.5"E	1864	0.5	27.5	8.1	3.95	6.80	5.5	12 (2)
Inn Fen	46°24'28"N	09°42'10"E	1803	-4	17.5	5.35	5.77	7.12	6.51	13 (3)
Maloja mire	46°24'19"N	09°41'24.3"E	1850	0	22.5	11.38	3.67	4.22	3.86	8

* Number of samples taken; in brackets samples with incomplete measurements

Table 2. Summary performance indicators of the transfer function models (classical weighted averaging) for depth to the water table (DWT) and pH in peatlands of the Eastern Swiss Alps (Engadine valley). For each group of models (singly proxy, combined with presence-absence data, combined including testate amoeba percentage data) the best values are indicated by undelined numbers both for raw and filtered models, the best of the two are bolded (taking into consideration exact values). The best models overall for DWT and pH are indicated in grey background. Raw: unfiltered models, filtered: filtered models (with removal of rare species and outlier samples, see text for details).

		DWT [cm]		pH	
		Raw	Filtered	Raw	Filtered
Models on individual groups					
Bryophytes presence/absence	r^2_{Boot}	0.71	**0.79**	0.67	**0.89**
	RMSEP	9.0	**6.2**	0.71	**0.37**
Vascular plants presence/absence	r^2_{Boot}	0.62	0.66	0.46	0.87
	RMSEP	11.5	7.4	1.08	0.45
Testate amoebae presence/absence	r^2_{Boot}	0.53	0.71	0.67	0.83
	RMSEP	13.2	8.0	0.70	0.46
Testate amoebae percentages	r^2_{Boot}	0.65	0.73	0.73	0.86
	RMSEP	12.2	6.8	0.62	0.43
Multi-group models with presence/absence data only					
Bryophytes & vascular plants	r^2_{Boot}	0.64	0.74	0.55	0.80
	RMSEP	10.8	6.3	0.90	0.53
Testate amoebae & bryophytes	r^2_{Boot}	0.62	**0.83**	0.68	**0.82**
	RMSEP	9.9	**5.2**	0.62	0.47
Testate amoebae & vascular plants	r^2_{Boot}	0.71	0.81	0.75	0.79
	RMSEP	9.3	5.3	0.58	**0.52**
Testate amoebae, bryophytes & vascular plants	r^2_{Boot}	0.73	0.81	0.70	0.75
	RMSEP	7.6	5.4	0.59	0.52
Multi-group models with testate amoeba percentages data					
Testate amoebae % & bryophytes	r^2_{Boot}	0.66	0.78	0.70	**0.94**
	RMSEP	9.1	5.3	0.61	**0.27**
Testate amoebae % & vascular plants	r^2_{Boot}	0.64	0.73	0.68	0.90
	RMSEP	11.0	5.7	0.70	0.37
Testate amoebae %, bryophytes & vascular plants	r^2_{Boot}	0.68	**0.87**	0.71	0.92
	RMSEP	8.7	**4.3**	0.60	0.30

Figures

Figure 1. Reconstruction of depth to water table (DWT) and pH from a 1000 years record from Mauntschas mire, Engadine, Switzerland (van de Knaap et al. 2011) using raw (unfiltered) percentage (thick curves) and presence/absence (thin curves) testate amoeba-based transfer functions. The data are plotted according to sampling depth so as to best show the differences among models. The same data plotted against sample age and using additional models are shown as supplementary material.

Figure 2. Correlation biplots and r^2 comparing reconstructed depth to water table (DWT – A and B) and pH (C and D) from Mauntschas mire, Engadine, Switzerland (van de Knaap et al. 2011), using raw percentage testate amoeba data transfer functions vs. filtered models (outlier removal) (A and C), and raw percentage testate amoeba data transfer functions vs. raw presence/absence models (B and D). The data in biplots B and D corresponds to the curves shown in Figure 1.

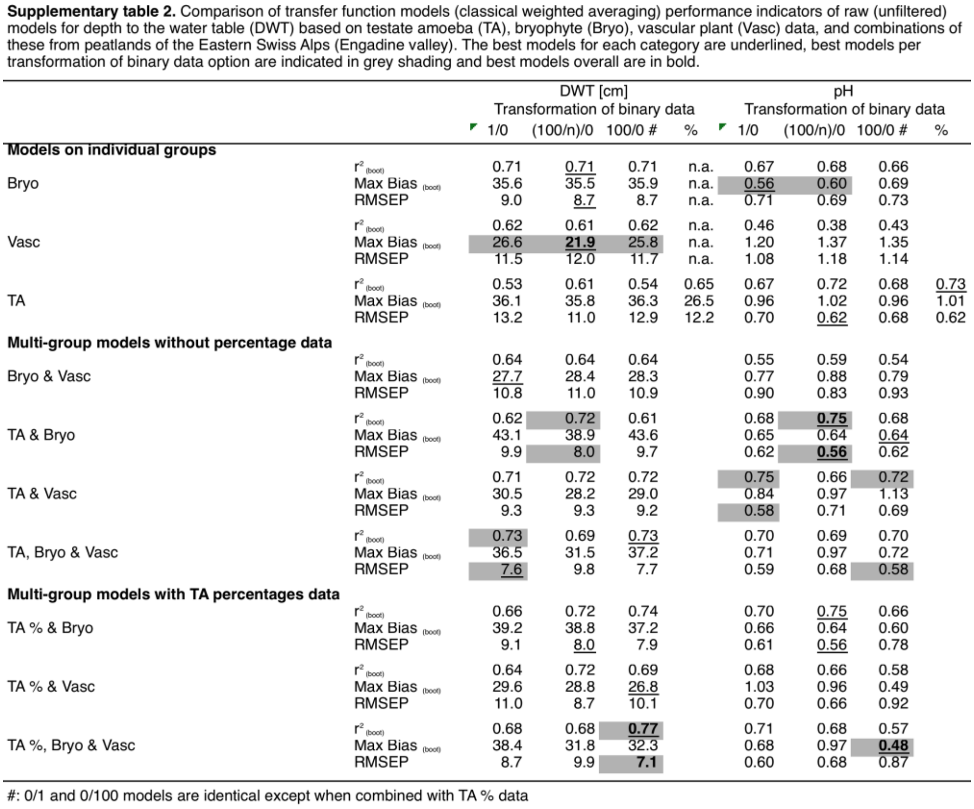
Supplementary online material

3 tables and 12 figures

Supplementary table 1. Summary performance indicators of the transfer function models (classical weighted averaging) for depth to the water table (DWT) and pH in peatlands of the Eastern Swiss Alps (Engadine valley). For each group of models (singly proxy, combined with presence-absence data, combined including testate amoeba percentage data) and for either raw of filtered models, the best values for r^2_{boot}, Maximum Bias $_{Boot}$, and RMSEP are indicated by undelined numbers both for raw and filtered models, the best of the two are bolded (taking into consideration exact values). The best models overall for DWT and pH are indicated in grey background. Raw: unfiltered models, filtered: filtered models (with removal of rare species and outlier samples, see text for details).

		DWT [cm]		pH	
		Raw	Filtered	Raw	Filtered
Models on individual groups					
Bryophytes presence/absence	r^2_{Boot}	0.71	0.79	0.67	0.89
	Maximum Bias $_{Boot}$	35.6	16.2	0.56	0.75
	RMSEP	9.0	6.2	0.71	0.37
	Number of samples	65	62	65	58
	Number of species	12	12	12	11
Vascular plants presence/absence	r^2_{Boot}	0.62	0.66	0.46	0.87
	Maximum Bias $_{Boot}$	26.6	17.8	1.20	**0.28**
	RMSEP	11.5	7.4	1.08	0.45
	Number of samples	82	77	82	49
	Number of species	30	30	30	30
Testate amoebae presence/absence	r^2_{Boot}	0.53	0.71	0.67	0.83
	Maximum Bias $_{Boot}$	36.1	34.8	0.96	0.60
	RMSEP	13.2	8.0	0.70	0.46
	Number of samples	93	74	93	71
	Number of species	69	69	69	69
Testate amoebae percentages	r^2	0.65	0.73	0.73	0.86
	Maximum Bias	26.5	19.4	1.01	0.80
	RMSEP	12.2	6.8	0.62	0.43
	Number of samples	93	81	93	78
	Number of species	69	68	69	69
Multi-group models with presence/absence data only *					
Bryophytes & vascular plants	r^2_{Boot}	0.64	0.74	0.55	0.80
	Maximum Bias $_{Boot}$	27.7	14.8	0.77	0.92
	RMSEP	10.8	6.3	0.90	0.53
	Number of samples	82	78	82	65
	Number of species	42	42	42	42
Testate amoebae & bryophytes	r^2_{Boot}	0.62	0.83	0.68	0.82
	Maximum Bias $_{Boot}$	43.1	12.2	0.65	0.75
	RMSEP	9.9	5.2	0.62	0.47
	Number of samples	65	57	65	54
	Number of species	83	83	83	83
Testate amoebae & vascular plants	r^2_{Boot}	0.71	0.81	0.75	0.79
	Maximum Bias $_{Boot}$	30.5	19.6	0.84	0.71
	RMSEP	9.3	5.3	0.58	0.52
	Number of samples	82	75	82	76
	Number of species	106	106	106	106
Testate amoebae, bryophytes & vascular plants	r^2_{Boot}	0.73	0.81	0.70	0.75
	Maximum Bias $_{Boot}$	36.5	12.7	0.71	0.73
	RMSEP	7.6	5.4	0.59	0.52
	Number of samples	65	63	65	62
	Number of species	105	105	105	103
Multi-group models with testate amoeba percentages data *					
Testate amoebae % & bryophytes (100/0)	r^2_{Boot}	0.66	0.78	0.70	**0.94**
	Maximum Bias $_{Boot}$	39.2	11.0	0.66	0.69
	RMSEP	9.1	5.3	0.61	**0.27**
	Number of samples	65	52	65	45
	Number of species	81	81	81	75
Testate amoebae % & vascular plants (100/0)	r^2_{Boot}	0.64	0.73	0.68	0.90
	Maximum Bias $_{Boot}$	29.6	19.4	1.03	0.76
	RMSEP	11.0	5.7	0.70	0.37
	Number of samples	82	64	82	63
	Number of species	106	102	106	102
Testate amoebae %, bryophytes & vascular plants (100/0)	r^2_{Boot}	0.68	0.87	0.71	0.92
	Maximum Bias $_{Boot}$	38.4	15.3	0.68	0.67
	RMSEP	8.7	4.3	0.60	0.30
	Number of samples	65	50	65	46
	Number of species	105	105	105	103

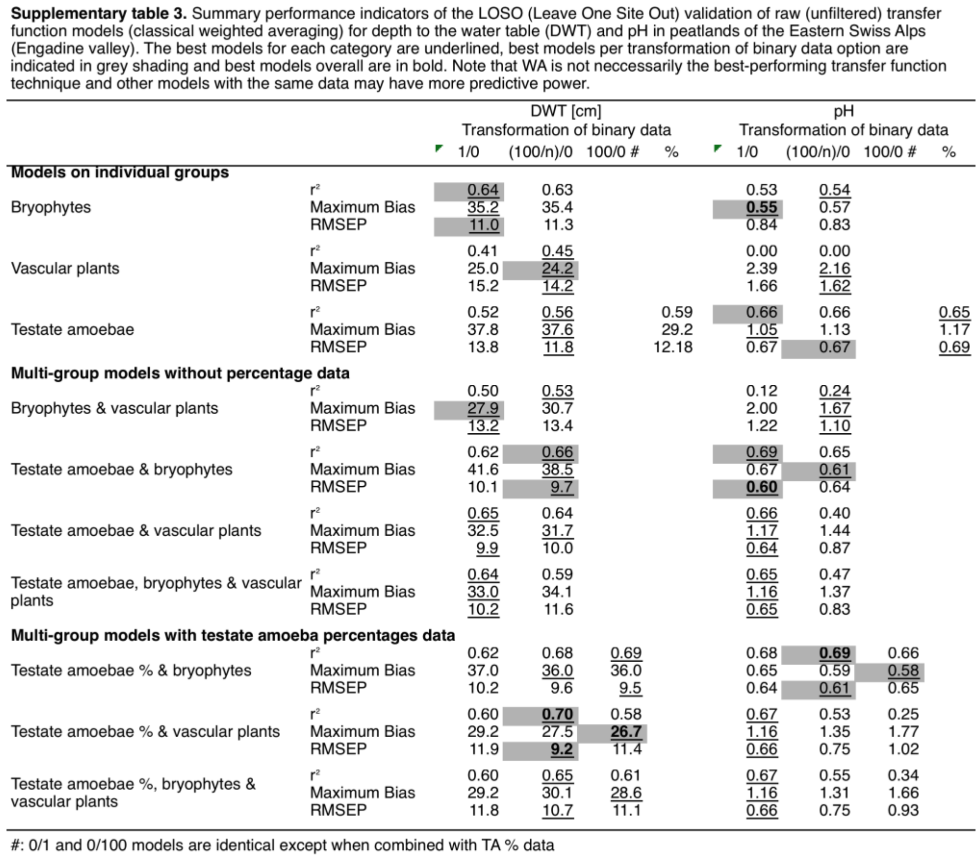
* For models based on presence-absence data, using 0/1 or 0/100 coding does not modify the model performance. In models combining percentage and binary data 0/100 coding of binary data is used.



Supplementary table 2. Comparison of transfer function models (classical weighted averaging) performance indicators of raw (unfiltered) models for depth to the water table (DWT) based on testate amoeba (TA), bryophyte (Bryo), vascular plant (Vasc) data, and combinations of these from peatlands of the Eastern Swiss Alps (Engadine valley). The best models for each category are underlined, best models per transformation of binary data option are indicated in grey shading and best models overall are in bold.

		DWT [cm]				pH			
		Transformation of binary data				Transformation of binary data			
		1/0	(100/n)/0	100/0 #	%	1/0	(100/n)/0	100/0 #	%
Models on individual groups									
Bryo	r^2 (boot)	0.71	0.71	0.71	n.a.	0.67	0.68	0.66	
	Max Bias (boot)	35.6	35.5	35.9	n.a.	0.56	0.60	0.69	
	RMSEP	9.0	8.7	8.7	n.a.	0.71	0.69	0.73	
Vasc	r^2 (boot)	0.62	0.61	0.62	n.a.	0.46	0.38	0.43	
	Max Bias (boot)	26.6	**21.9**	25.8	n.a.	1.20	1.37	1.35	
	RMSEP	11.5	12.0	11.7	n.a.	1.08	1.18	1.14	
TA	r^2 (boot)	0.53	0.61	0.54	0.65	0.67	0.72	0.68	0.73
	Max Bias (boot)	36.1	35.8	36.3	26.5	0.96	1.02	0.96	1.01
	RMSEP	13.2	11.0	12.9	12.2	0.70	0.62	0.68	0.62
Multi-group models without percentage data									
Bryo & Vasc	r^2 (boot)	0.64	0.64	0.64		0.55	0.59	0.54	
	Max Bias (boot)	27.7	28.4	28.3		0.77	0.88	0.79	
	RMSEP	10.8	11.0	10.9		0.90	0.83	0.93	
TA & Bryo	r^2 (boot)	0.62	0.72	0.61		0.68	**0.75**	0.68	
	Max Bias (boot)	43.1	38.9	43.6		0.65	0.64	0.64	
	RMSEP	9.9	8.0	9.7		0.62	**0.56**	0.62	
TA & Vasc	r^2 (boot)	0.71	0.72	0.72		0.75	0.66	0.72	
	Max Bias (boot)	30.5	28.2	29.0		0.84	0.97	1.13	
	RMSEP	9.3	9.3	9.2		0.58	0.71	0.69	
TA, Bryo & Vasc	r^2 (boot)	0.73	0.69	0.73		0.70	0.69	0.70	
	Max Bias (boot)	36.5	31.5	37.2		0.71	0.97	0.72	
	RMSEP	7.6	9.8	7.7		0.59	0.68	0.58	
Multi-group models with TA percentages data									
TA % & Bryo	r^2 (boot)	0.66	0.72	0.74		0.70	0.75	0.66	
	Max Bias (boot)	39.2	38.8	37.2		0.66	0.64	0.60	
	RMSEP	9.1	8.0	7.9		0.61	0.56	0.78	
TA % & Vasc	r^2 (boot)	0.64	0.72	0.69		0.68	0.66	0.58	
	Max Bias (boot)	29.6	28.8	26.8		1.03	0.96	0.49	
	RMSEP	11.0	8.7	10.1		0.70	0.66	0.92	
TA %, Bryo & Vasc	r^2 (boot)	0.68	0.68	**0.77**		0.71	0.68	0.57	
	Max Bias (boot)	38.4	31.8	32.3		0.68	0.97	**0.48**	
	RMSEP	8.7	9.9	**7.1**		0.60	0.68	0.87	

#: 0/1 and 0/100 models are identical except when combined with TA % data



Supplementary table 3. Summary performance indicators of the LOSO (Leave One Site Out) validation of raw (unfiltered) transfer function models (classical weighted averaging) for depth to the water table (DWT) and pH in peatlands of the Eastern Swiss Alps (Engadine valley). The best models for each category are underlined, best models per transformation of binary data option are indicated in grey shading and best models overall are in bold. Note that WA is not neccessarily the best-performing transfer function technique and other models with the same data may have more predictive power.

		DWT [cm] Transformation of binary data				pH Transformation of binary data			
		1/0	(100/n)/0	100/0 #	%	1/0	(100/n)/0	100/0 #	%
Models on individual groups									
Bryophytes	r^2	0.64	0.63			0.53	0.54		
	Maximum Bias	35.2	35.4			**0.55**	0.57		
	RMSEP	11.0	11.3			0.84	0.83		
Vascular plants	r^2	0.41	0.45			0.00	0.00		
	Maximum Bias	25.0	24.2			2.39	2.16		
	RMSEP	15.2	14.2			1.66	1.62		
Testate amoebae	r^2	0.52	0.56		0.59	0.66	0.66		0.65
	Maximum Bias	37.8	37.6		29.2	1.05	1.13		1.17
	RMSEP	13.8	11.8		12.18	0.67	0.67		0.69
Multi-group models without percentage data									
Bryophytes & vascular plants	r^2	0.50	0.53			0.12	0.24		
	Maximum Bias	27.9	30.7			2.00	1.67		
	RMSEP	13.2	13.4			1.22	1.10		
Testate amoebae & bryophytes	r^2	0.62	0.66			0.69	0.65		
	Maximum Bias	41.6	38.5			0.67	0.61		
	RMSEP	10.1	9.7			**0.60**	0.64		
Testate amoebae & vascular plants	r^2	0.65	0.64			0.66	0.40		
	Maximum Bias	32.5	31.7			1.17	1.44		
	RMSEP	9.9	10.0			0.64	0.87		
Testate amoebae, bryophytes & vascular plants	r^2	0.64	0.59			0.65	0.47		
	Maximum Bias	33.0	34.1			1.16	1.37		
	RMSEP	10.2	11.6			0.65	0.83		
Multi-group models with testate amoeba percentages data									
Testate amoebae % & bryophytes	r^2	0.62	0.68	0.69		0.68	**0.69**	0.66	
	Maximum Bias	37.0	36.0	36.0		0.65	0.59	0.58	
	RMSEP	10.2	9.6	9.5		0.64	0.61	0.65	
Testate amoebae % & vascular plants	r^2	0.60	**0.70**	0.58		0.67	0.53	0.25	
	Maximum Bias	29.2	27.5	**26.7**		1.16	1.35	1.77	
	RMSEP	11.9	**9.2**	11.4		0.66	0.75	1.02	
Testate amoebae %, bryophytes & vascular plants	r^2	0.60	0.65	0.61		0.67	0.55	0.34	
	Maximum Bias	29.2	30.1	28.6		1.16	1.31	1.66	
	RMSEP	11.8	10.7	11.1		0.66	0.75	0.93	

#: 0/1 and 0/100 models are identical except when combined with TA % data

Supplementary Figures: captions

Supplementary Figure 1. Observed versus model-predicted values (left) and observed versus residuals (right) of transfer function models of bryophytes for depth to the water table (DWT) and pH.

Supplementary Figure 2. Observed versus model-predicted values (left) and observed versus residuals (right) of transfer function models of vascular plants for depth to the water table (DWT) and pH.

Supplementary Figure 3. Observed versus model-predicted values (left) and observed versus residuals (right) of transfer function models of testate amoeba presence/absence data for depth to the water table (DWT) and pH.

Supplementary Figure 4. Observed versus model-predicted values (left) and observed versus residuals (right) of transfer function models of testate amoeba percentages for depth to the water table (DWT) and pH.

Supplementary Figure 5. Observed versus model-predicted values (left) and observed versus residuals (right) of transfer function models of bryophytes and vascular plants for depth to the water table (DWT) and pH.

Supplementary Figure 6. Observed versus model-predicted values (left) and observed versus residuals (right) of transfer function models of testate amoebae presence/absence data and bryophytes for depth to the water table (DWT) and pH.

Supplementary Figure 7. Observed versus model-predicted values (left) and observed versus residuals (right) of transfer function models of testate amoeba presence/absence data and vascular plants for depth to the water table (DWT) and pH.

Supplementary Figure 8. Observed versus model-predicted values (left) and observed versus residuals (right) of transfer function models of testate amoeba presence/absence data, bryophytes and vascular plants for depth to the water table (DWT) and pH.

Supplementary Figure 9. Observed versus model-predicted values (left) and observed versus residuals (right) of transfer function models of testate amoeba percentages and bryophytes for depth to the water table (DWT) and pH.

Supplementary Figure 10. Observed versus model-predicted values (left) and observed versus residuals (right) of transfer function models of testate amoeba percentages and vascular plants for depth to the water table (DWT) and pH.

Supplementary Figure 11. Observed versus model-predicted values (left) and observed versus residuals (right) of transfer function models of testate amoeba percentages, bryophytes and vascular plants for depth to water table (DWT) and pH.

Supplementary Figure 12. Reconstruction of depth to water table (DWT, A and C) and pH (B and D) from a 1000 years record from Mauntschas mire, Engadine, Switzerland (van de Knaap et al. 2011), plotted against sample depth (A and B) and age (C and D), using raw and filtered percentage (%) and presence/absence (1/0) testate amoeba-based transfer functions. Black lines = raw %, red = filtered %, blue = raw 1/0, green = filtered 1/0.