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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 paleoenvironmental 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 1) compare the performance of single-proxy vs. multi-proxy models and 2) assess the performance of presence/absence models. Bootstrapping cross-validation showing the best performing single-proxy transfer functions for both DWT and pH were those based on bryophytes. The best performing transfer functions overall for DWT were those based on combined testate amoebae percentages, bryophytes and vascular plants; and, for pH, those based on testate amoebae and bryophytes. The comparison of DWT and pH inferred from testate amoeba percentages and presence/absence data showed similar general patterns but differences in the magnitude and timing of some shifts. These results show new directions for paleoenvironmental research, 1) suggesting that it is possible to build good-performing transfer functions using presence/absence data, although with some loss of accuracy, and 2) supporting the idea that multi-proxy inference models may improve paleoecological reconstruction. The performance of multi-proxy and single-proxy transfer functions should be further compared in paleoecological data.

Introduction

Testate amoebae (Protists) and plant macrofossils are the two most commonly used proxies for reconstructing Holocene environmental change in peatlands (Mauquoy et al., 2004; Hughes et al., 2006; Booth, 2010). 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 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 (Charman et al., 2007; Booth, 2008; Swindles et al., 2009). Relationships to water chemistry have also been documented but have been much less studied, and they have focused mostly on pH (Tolonen et al., 1992; Mitchell et al., 1999; Opravilova and Hajek, 2006; Lamentowicz et al., 2008; Hajkova et al., 2011). 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). Most reconstructions using plant remains are indirect, using multivariate methods such as detrended correspondence analysis (DCA) or qualitative interpretations of vegetation type (Birks and Seppa, 2010).

The use of multiple proxies in the same record is generally believed to lead to more accurate and robust paleoenvironmental reconstruction (Long et al., 1996; Charman et al., 1999; Caseldine and Gearey, 2005; Birks and Seppa, 2010). 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.

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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 paleoecological 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 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) 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 Engadine valley, SE Swiss Alps (average coordinates 46°27′00″ N; 9°46′30″ E; elevation range 1810–1864 m asl). 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 a 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 do not have percentage data for bryophytes and vascular plants. In practice, however, most fossil studies have the same limitation.

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 paleoecology (Woodland et al., 1998; Wilmshurst et al., 2003; Edwards et al., 2004; Booth et al., 2008). The rationale for this is that some sampled locations may correspond to unusual situations (e.g., affected by a confounding factor such as faeces/urine), so that their removal results in improved model performance. 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 presence was interpreted as 1% cover. To assess how this affected model performance we compared three options. The first was the original presence/absence (hereafter: 1/0) data. In the second case the data were 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 would affect model performance. In very few paleoecological 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 paleoecology. It should be recognized that apparent presence/absence partly reflects count total for testate amoebae and plot 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

Table 1
Location and general characteristics of the studied sites.

Site name	Coordinates		Altitude [m asl]	Depth to water table [cm]			pH			n [a]
	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

[a] 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 underlined 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					
Bryophyte presence/absence	r^2_{Boot}	0.71	**0.79**	0.67	**0.89**
	RMSEP	9.0	**6.2**	0.71	**0.37**
Vascular plant presence/absence	r^2_{Boot}	0.62	0.66	0.46	0.87
	RMSEP	11.5	7.4	1.08	0.45
Testate amoeba presence/absence	r^2_{Boot}	0.53	0.71	0.67	0.83
	RMSEP	13.2	8.0	0.70	0.46
Testate amoeba 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 and vascular plants	r^2_{Boot}	0.64	0.74	0.55	0.80
	RMSEP	10.8	6.3	0.90	0.53
Testate amoebae and bryophytes	r^2_{Boot}	0.62	**0.83**	0.68	**0.82**
	RMSEP	9.9	**5.2**	0.62	0.47
Testate amoebae and 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 and 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 percentage data					
Testate amoebae and bryophytes	r^2_{Boot}	0.66	0.78	0.70	**0.94**
	RMSEP	9.1	5.3	0.61	**0.27**
Testate amoebae % and 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 and vascular plants	r^2_{Boot}	0.68	**0.87**	0.71	0.92
	RMSEP	8.7	**4.3**	0.60	0.30

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., 2012), using R (R Development Core Team, 2010) and the rioja library (Juggins, 2011). We also compared DWT and pH reconstructions from a 1000-yr record from Mauntschas mire (van der Knaap et al., 2011) based on % or 1/0 testate amoebae filtered or raw models to assess the implications of the observed differences in model performance on paleoenvironmental 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., with raw models r^2_{Boot} was 0.53 vs. 0.65 for DWT and 0.67 vs. 0.73 for pH; Table 2). It is also noteworthy that the TA 1/0 model failed to accurately predict water table depths below 20 cm (Supplementary Figs. 3 and 4).

Our results support 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 both expectation and 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 in 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 Figs. 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 with 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).

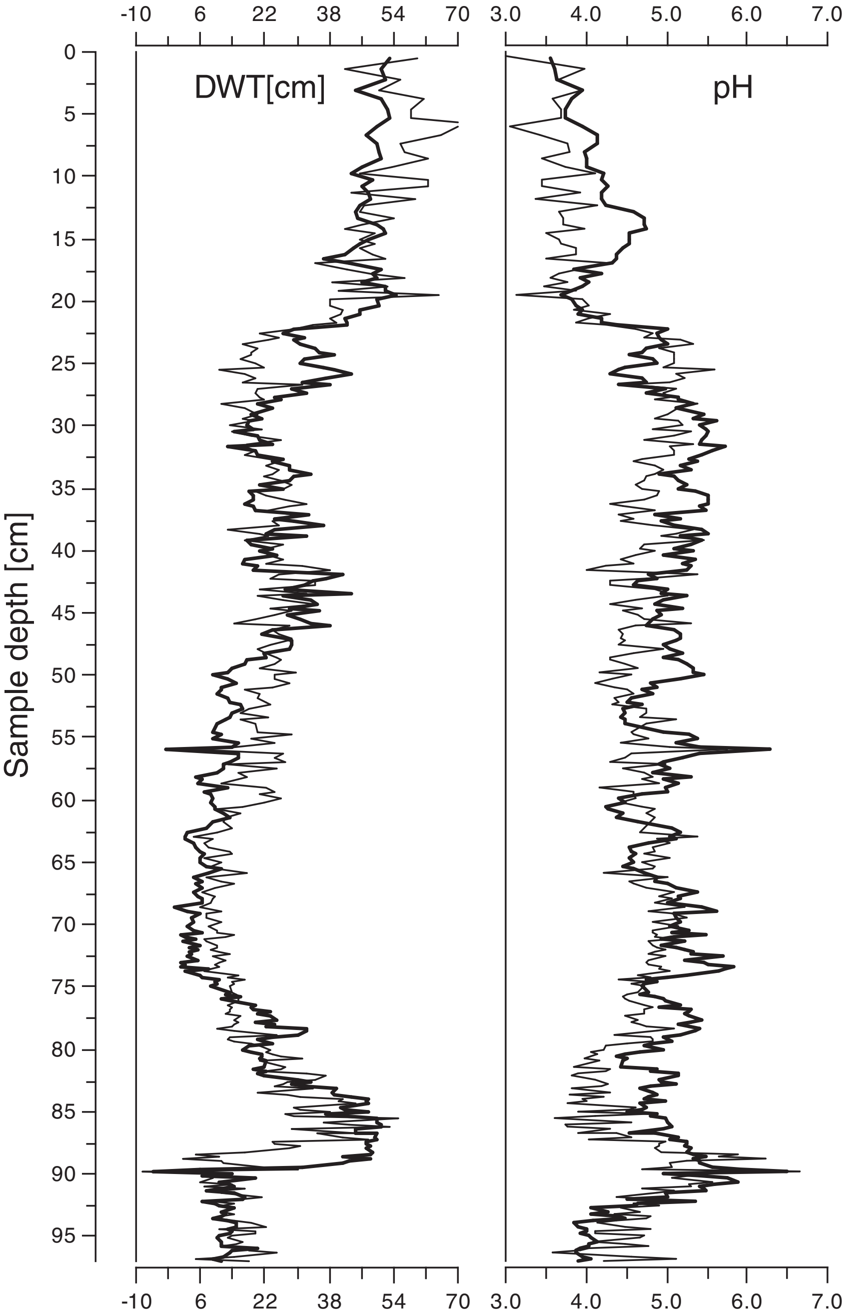

Figure 1. Reconstruction of depth to the water table (DWT) and pH from a 1000-yr record from Mauntschas mire, Engadine, Switzerland (van der Knaap et al., 2011) using raw (unfiltered) percentage (thick curves) and presence/absence (thin curves) testate amoeba-based transfer functions. The data are plotted according to sample 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.

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 paleoenvironmental 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 paleoenvironmental reconstruction (Figs. 1 and 2, Supplementary Fig. 12). The major phases are similar, but some quite important differences are also visible. For example, the 1/0 model results in a ca. 2-cm lag in sample depth of the dry shift occurring between 85 and 90 cm 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 slightly overestimation of DWT for low values and underestimation for larger values. On average, the filtered model underestimates DWT by 5.7 cm compared to the raw model. For pH the overestimation for the filtered model is with 0.08 almost constant compared to the raw model. For both DWT and pH, 1/0 models yield in some cases very different results from the % model (Fig. 2). DWT inferred from the raw 1/0 model was in many cases lower than from the raw % model, especially for DWT > 25 cm (Fig. 2). Inferred pH from the raw 1/0 model was on average 0.29 lower than 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 their

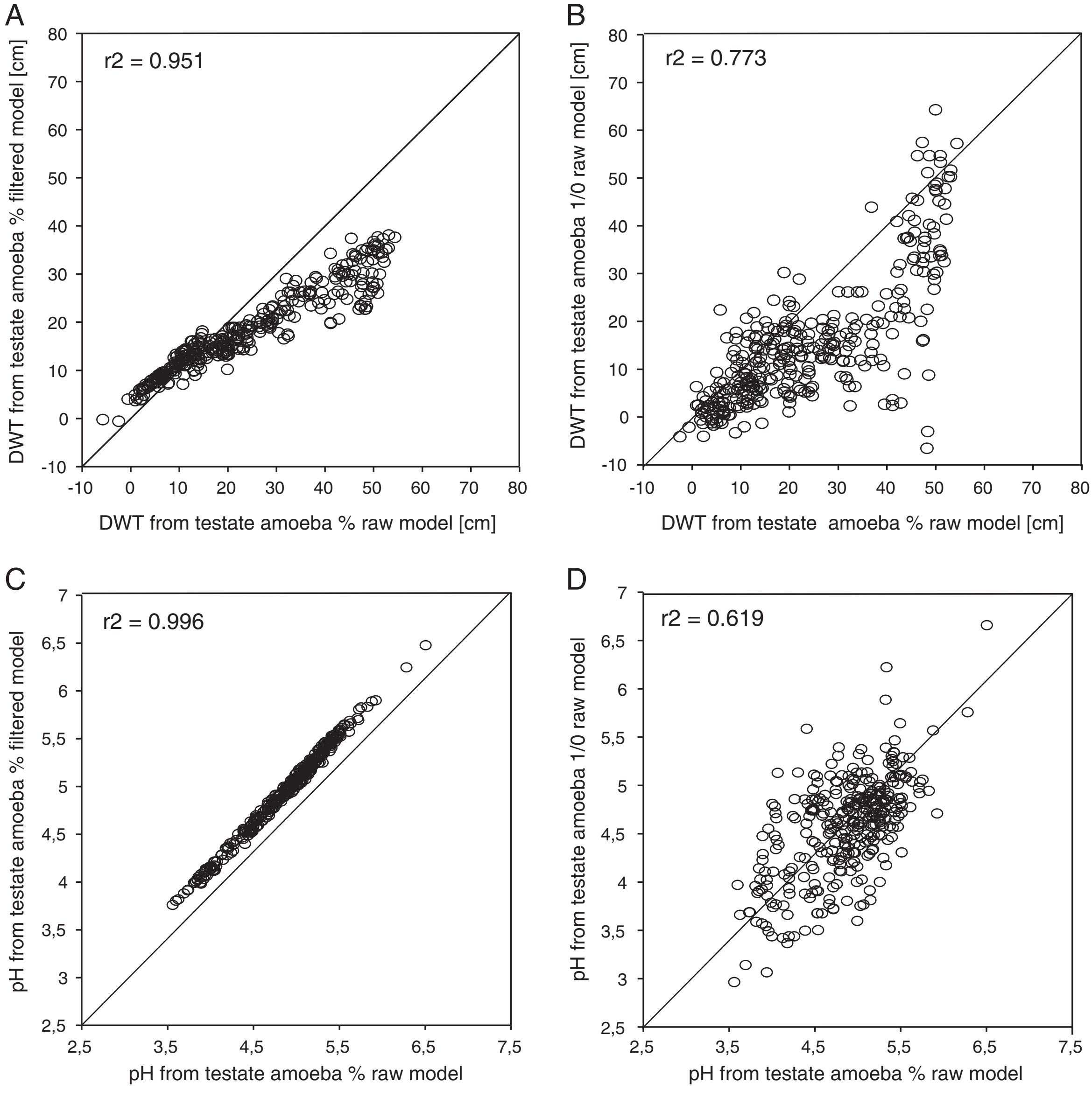

Figure 2. Correlation biplots and r^2 comparing reconstructed depth to the water table (DWT — A and B) and pH (C and D) from Mauntschas mire, Engadine, Switzerland (van der Knaap et al., 2011), using raw percentage testate amoeba data transfer functions vs. filtered models (outlier removal) (A and C),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

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 find 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 total count 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 realistically using 1/0 models. The two types of model did not, however, yield identical results. In some cases the interpretation could be different, not for the overall patterns but for the precise timing and magnitude of changes. As both % TA models perform better than their corresponding 1/0 models, these differences suggest that inference from % models is more reliable than from 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 possibly superior performance of models based on percentage bryophyte data. Bryophyte percentages are, however, both time-consuming to achieve (and not realistic in the present study) and potentially of little practical use for several reasons. First, reliable percentage data for bryophytes are not easy to obtain. Second, modern percentage surface-cover data would differ from the percentages in macrofossil analysis (as estimated with, e.g., the Quadrat and Leaf Count method of Barber et al., 1994). Further limitations are the differential preservation of bryophyte species and the variable taxonomic resolution achieved with fossil material (Janssens, 1983). Nevertheless, our results suggest a 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 observed values clearly improved model performance in many cases. This was, however, often at the cost of a considerable reduction in sample number, ranging from 2 to 33 (Supplementary Table 2). The removal of a few outliers might be defended, but not that of 40% of the samples as in the most extreme case (vascular plant pH model). Outlier removal should therefore not be restricted to automatic, apparently objective procedures but also include a cautious analysis of the community composition and ecological conditions. A clear indication that a sample may not realistically be modelled by a transfer function would warrant its exclusion. In other cases it is advisable to keep the sample in the model, even if its apparent performance is not ideal.

The raw and filtered models yielded for the paleoecological record from Mauntschas mire little difference in the reconstructions. The r^2 of inferred values between raw and filtered models were high (0.95–0.996). This indicates that model optimisation by data filtering may have little effect on paleoenvironmental 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 used 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 bryophytes until the water table drops below ca. 30 cm when a further lowering 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 it also makes interpretation of those results more difficult. Transfer functions aiming to reconstruct water table depth actually show the hydrological conditions at quite different spatial (Mitchell et al., 2000) and temporal (Sullivan and Booth, 2011; Väliranta et al., 2012) scales. While amoebae respond to moisture conditions in their immediate vicinity (μm^3–mm^3 scale, 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 mm^3–cm^3, and for vascular plants larger again, on the scale of cm^3–dm^3. This needs not be a concern if the hydrology at all these scales is strongly correlated but can lead to contradicting results when hummocks develop in otherwise wet habitats (and testate amoebae may indicate drier conditions than vascular plants), or when *S. fuscum* maintains high moisture content in relatively dry sites (in which case testate amoebae would indicate wetter conditions than vascular plants) (Väliranta et al., 2012).

The difference in spatial and temporal scale of environmental sensitivity also applies for pH (Hajkova et al., 2004). 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 data and bryophyte data. The distribution of pH along the fen–bog gradient is clearly bimodal, which results in generally poor model performance around pH 5.0. A notable exception is the model combining testate amoebae percentage data and vascular plants (Supplementary Fig. 10), the best performing raw model. This may be explained by the observation that a surface pH around 5.0 corresponds to transitional mire in which a clear vertical pH gradient develops (Tahvanainen, 2004), so that bryophytes and/or testate amoebae indicate more acidic conditions (and hence underestimate pH) while vascular plants indicate less acidic conditions (and hence overestimate pH). This should be especially important in habitats 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 multi-proxy transfer functions may be a useful new technique for paleoenvironmental 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 that may be more reliable in each specific circumstance. In a single model that combines very different groups of organisms no such judgement can be reached, and it is unclear how a combined model would perform when the different groups of organisms indicate different conditions. We therefore recommend that both single- and multi-proxy reconstructions be developed in parallel and that multi-proxy results be treated with caution when there is a divergence in the results of different proxies.

Conclusion

Over the last 20 years the approach to macrofossil- and testate amoeba-based paleoenvironmental reconstruction in peatlands has become increasingly standardized. Testate amoeba percentage transfer functions are used to quantitatively reconstruct water table (and less frequently pH) and ordination techniques are 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. Multi-proxy transfer functions based on more than one group of organisms may out-perform single-proxy transfer functions. These new approaches require further appraisal with paleoecological data but offer exciting new options that deserve exploration.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.yqres.2012.08.004.

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