Published in Journal of Quaternary Science 25, issue 2, 190-202, 2009
which should be used for any reference to this work

A near-annual palaeohydrological study based on testate amoebae from a sub-alpine mire: surface wetness and the role of climate during the instrumental period

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ABSTRACT: We present the first testate amoeba-based palaeohydrological reconstruction from the Swiss Alps, and the first depth to the water table (DWT) calibration dataset for this region. Compared to existing models, our new calibration dataset performs well (RMSEP = 4.88), despite the length of the water table gradient covered (53 cm). The present-day topography and vegetation of the study mire Mauntschas suggest that it is partly ombrotrophic (large *Sphagnum fuscum* hummocks, one of which was the coring site) but mostly under the minerotrophic influence of springs in the mire and runoff from the surrounding area. Ombrotrophic *Sphagnum fuscum* hummocks developed at the sampling site only during the last 50 years, when testate amoebae indicate a shift towards dry and/or acid conditions. Prior to AD 1950 the water table was much higher, suggesting that the influence of the mineral-rich water prevented the development of ombrotrophic hummocks. The reconstructed DWT correlated with *Pinus cembra* pollen accumulation rates, suggesting that testate amoebae living on the mire and *P. cembra* growing outside of it partly respond to the same factor(s). Finally, temperature trends from the nearby meteorological station paralleled trends in reconstructed DWT. However, contrary to other studies made on raised bogs of northwestern Europe, the highest correlation was observed for winter temperature, despite the fact that testate amoebae would more logically respond to moisture conditions during the growing season. The observed correlation with winter temperature might reflect a control of winter severity on surface moisture during at least the first part of the growing season, through snow melt and soil frost phenomena influencing run-off. More ecohydrological work on sub-alpine mires is needed to understand the relationships between climate, testate amoebae and peatland development.

KEYWORDS: sub-alpine peatland; testate amoebae; pollen; climate; instrumental period; hydrology; winter temperature.

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Introduction

Mires in mountain areas are highly diverse ecosystems (Grünig, 1994; Succow and Joosten, 2001). They exist in various forms – bogs, poor fens and rich fens – and are located in diverse geological settings. Their variable structure is often influenced by bedrock properties, which makes them challenging in ecological and palaeoecological investigations (Hájek *et al.*, 2002; Horsak *et al.*, 2003). Furthermore, climate–hydrology relationships in mountainous areas are very complex, with snow and temperature playing important roles in the hydrology of the soils (Bayard *et al.*, 2005; de Jong *et al.*, 2006).

Most existing palaeohydrological studies are based on northern raised bogs, especially in northern and northeastern Europe (Chambers and Charman, 2004; Chambers *et al.*, 2007; Sillasoo *et al.*, 2007; Swindles *et al.*, 2007; Plunkett and Swindles, 2008) and North America (Booth and Jackson, 2003; Booth *et al.*, 2006). By contrast, southern and central European peatlands have not been studied so extensively, although some of the pioneer work in palaeoecology was done in this region (Roos-Barraclough *et al.*, 2004; Sjögren and Lamentowicz, 2008).

Among the different types of mire, raised bogs are especially valuable for palaeoclimatological research (Charman, 2002), though partly topogenic peatlands such as kettle-hole mires have also proved useful (M. Lamentowicz *et al.*, 2008a). Topogenic mires, however, are challenging to use for palaeoclimatic reconstruction owing to their complex hydrology that is dominated by the groundwater in the catchment, which could be dependent on land-use changes in the past.

Peatlands can provide information about local environmental conditions but also about regional climate (Blackford, 1993; Chambers *et al.*, 1999; Charman, 2002). To understand the modern ecology of a peatland, a variety of palaeoenvironmental studies should be carried out simultaneously, using the multi-proxy approach. Testate amoebae are valuable proxies because they allow quantitative inference of past environmental changes in mires as well as in lakes (Charman, 2001; Mitchell *et al.*, 2008). They proved to be important biotic indicators of changes in surface wetness (Tolonen *et al.*, 1992; Ł. Lamentowicz *et al.*, 2008). Most palaeoecological studies using testate amoebae have been based on *Sphagnum* mires. Testate amoebae are very abundant in *Sphagnum*, they are well preserved in *Sphagnum* peat, and the ecology of species in *Sphagnum*-dominated peatlands is now well known (see Mitchell *et al.*, 2008, for a review).

Knowledge about the modern as well as past hydrology of sub-alpine mires is limited. The hydrology of mountain mires may be more complex than that known from regions such as northeastern Europe where peatlands represent a dominant feature of the landscape and where precipitation is the major factor controlling peatland development. We suppose that in sub-alpine peatlands snow cover, ablation and melting may be decisive factors that are mostly less relevant in northeastern Europe. Testate amoebae from alpine peatlands have not yet been used to reconstruct palaeohydrology. Although there have been attempts to compare the testate amoeba record with climatic data, some at high temporal resolution (Charman, 2007), our study is the first that was made in near-annual resolution.

This study is part of the EU project Millennium, which aims at reconstructing the climate of Europe during the last millennium. Within this project, testate amoebae, pollen and stable isotopes in *Sphagnum* are analysed from a peat core collected in Mauntschas mire, Upper Engadin, Eastern Alps of Switzerland. This paper presents the calibration and validation of the testate amoeba climatic signal for the instrumental period (AD 1864–today), for which an understanding of the local hydrology is essential. This study is related to two other papers from the same project: Goslar *et al.* (2009) on the depth–age modelling of the peat section, and Kamenik *et al.* (2009) on the pollen/climate calibration. This work is part of a series of scientific contributions on Mauntschas mire and is concentrated mainly on the palaeohydrology.

The aims of this study were (a) to provide a new local high-quality testate amoeba calibration dataset for palaeohydrological reconstructions, (b) to reconstruct water table changes since AD 1864 in Mauntschas and (c) to relate this reconstruction to instrumental climate records to assess which climatic variables might have affected surface wetness of the mire. Modern relationships among testate amoebae and their environment, which provide the bases for the depth to the water table (DWT) reconstruction, were studied separately. The development of an amoebae-based DWT training set was based on their well-known response to DWT (Charman, 2001; Booth, 2008; Mitchell *et al.*, 2008). Five aspects make this study especially valuable: (1) the unique near-annual sampling resolution allowed us to investigate the past environmental changes in detail; (2) the availability of instrumental climatic data from a nearby (9 km distant) meteorological station; (3) the high quality of the local training set provided a reliable water table reconstruction; (4) pollen data allowed comparing without the pitfall of circular reasoning the changes in hydrology and vegetation; (5) the unusual setting of the mire, at high elevation, and in a sub-continental climate.

Study site

The study site is Mauntschas mire near St Moritz in the Upper Engadin valley, southeastern Swiss Alps (Swiss coordinates 785.470/151.620, Greenwich 46° 29′ 24.7″ N, 9° 51′ 16.7″ E, 1818 m a.s.l., 10 ha in size) (Fig. 1). Mauntschas is a *Sphagnum* mire situated in the forest-limit ecotone. The mire is located in more continental conditions in comparison to the western and northern parts of Switzerland. No anthropogenic drainage was made in the vicinity of the sampling site, so we assume that the microtopography of this peatland is not disturbed and its present form is the result of natural processes.

The mire lies at the valley bottom and is surrounded by forest growing to a timberline at ca. 2100–2250 m elevation. The forest–mire edge lies about 60 m to the north and west, 200 m south, and 500 m east. The forest around the mire consists of *Picea excelsa* (spruce), *Pinus cembra* (stone pine), and scattered *Larix decidua* (larch). Erect forms of *Pinus mugo* (mountain pine) grow on the mire about 100 m to the southwest. The mire edge has scattered *Salix* (willow) shrubs.

Mauntschas mire is divided into three parts by two frontal moraines (Grünig, 1994). Peat initiation is dated to 11 ^{14}C ka BP. Maximum peat thickness is ~5 m. This peatland is regarded as the most noteworthy mire in the central Alps because of its high biodiversity. It includes many peatland habitat types such as minerotrophic transitional mire, sloping fen and mountain-pine bog. Locally, the floristic composition indicates spring waters rich in calcium (e.g. *Primula farinosa*), whereas other places seem ombrotrophic with hummocks of *Sphagnum fuscum* with *Oxycoccus microcarpus* and *Andromeda polifolia*. Some higher and therefore drier parts of the mire are dominated by *Sphagnum fuscum* and are covered by mountain-pine forest.

The water in the peatland is partly derived from direct precipitation, partly from calcium-rich streams and springs. Plant indicators of minerotrophy are present across all microsites (e.g. *Carex rostrata*, *Molinia coerulea*), even on the higher *Sphagnum*

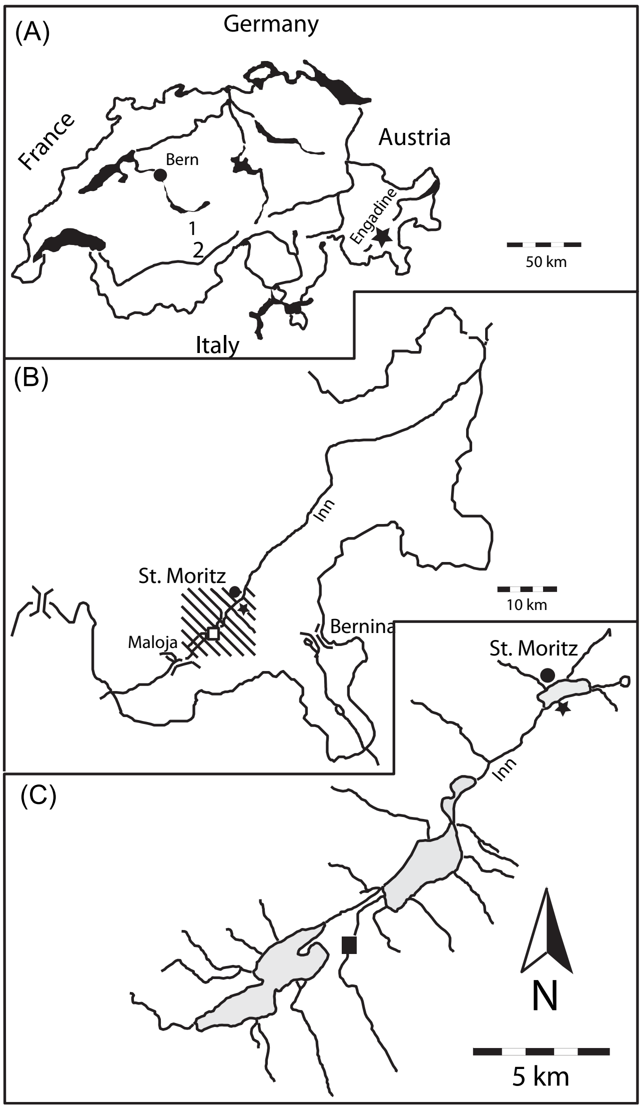

Figure 1 Setting of the study site. The asterisk shows the study site Mauntschas: (A) Switzerland; (B) Engadine region; (C) Upper Engadine. Solid square is climate station at Sils Maria

hummocks. In a transect across the sampling site, the abundance of minerotrophic plant indicators decreases from south to north. This indicates that the minerotrophic water enters the mire in the south of the transect, whereas water surplus leaves the mire on the northern edge lying only slightly lower than both the mire and the adjacent forest.

The coring site on Mauntschas is a *Sphagnum fuscum* hummock 3 m in diameter, ~30 cm high, surrounded by wet brown-moss lawn. On the hummock, abundant low *Empetrum hermaphroditum*, *Vaccinium uliginosum*, *Oxycoccus microcarpus*, *Andromeda polifolia* and (as indicators of minerotrophy) a little non-flowering *Carex rostrata* and *Molinia coerulea* are growing. On other hummocks within 10 m distance, creeping *Juniperus communis* s.l. and small *Pinus mugo* s.l. are also present. The wet lawn that surrounds the hummocks has abundant *Trichophorum cespitosum*, *Carex limosa* and the minerotrophy indicator *C. rostrata*, frequent *Drosera intermedia* and *Trichophorum alpinum*, and occasional *Andromeda polifolia*, but no *Sphagnum*.

Methods

On 6 August 2003, a 130 cm long peat monolith was collected with spades from a *Sphagnum fuscum* hummock in the undisturbed part of Mauntschas. The subsampling of the peat monolith was done in two ways: the peat between 0 and 29 cm was subsampled in unfrozen condition with scissors in Bern, Switzerland, below 29 cm in frozen condition in the Institute of Botany and Landscape Ecology (University of Greifswald, Germany) with the 'Damocles' device (Joosten and de Klerk, 2007).

Subsamples for testate amoeba analysis were prepared with sieving and back-sieving (Hendon and Charman, 1997). The testate amoebae were identified and counted at 200–400× magnification to a total of 150 individuals per subsample whenever possible. Identification was based on the available literature (Grospietsch, 1958; Charman *et al.*, 2000).

The testate amoeba transfer functions were based on a new calibration dataset, combining samples from peatlands of the Upper Engadin collected in August 2007. It was necessary to create this calibration dataset specifically for this site, because the study mire has special features (as described above) absent from mires used in earlier calibration datasets, harbouring testate amoeba species from a wide range of habitats, and species with hitherto unknown ecological demands. A total of 97 moss samples were taken in the field from a variety of habitats, ranging from wet brown-moss and *Sphagnum* lawns to high, dry *Sphagnum* hummocks, in an effort to cover the longest wet–dry and poor–rich gradients. At each sampling site the vascular plants were noted in the field, and the DWT was measured. Based on their well-known response to surface wetness (Charman, 2001; Booth, 2008; Mitchell *et al.*, 2008), the calibration dataset was used for inferring past DWT from testate amoebae.

Six inference models were tested: modern analogue technique (MAT), maximum likelihood (ML), partial least squares (PLS), weighted averaging (WA), tolerance down-weighted averaging (WAtol) and weighted averaging partial least squares (WA-PLS), using the software C2 (Juggins, 2003). Model performance was assessed using root mean squared error of prediction (RMSEP), average bias, maximum bias, and the correlation between observed and predicted values as assessed by bootstrap cross-validation (Crowley, 1992).

Taxa that occurred in fewer than four samples were excluded (Payne *et al.*, 2006). This approach is justified by the observation that a rare species yields insufficient information to model its response realistically. Likewise, samples with rare combinations of testate amoebae and/or environmental characteristics are difficult to model. We therefore optimised the models by removing species or samples with residuals larger than 15 cm (cf. Payne *et al.*, 2006).

Stratigraphic zones among testate amoebae were assessed by optimal sum-of-squares partitioning (Birks and Gordon, 1985; Birks, 1986). The significance of zone boundaries was tested with the broken-stick model (Bennett, 1996).

Pollen was counted to a sum of 308 ± 95 grains (excluding mire plants). Local vegetation changes were described on the basis of the pollen data, and discussed in relation to the reconstructed water table fluctuations. Pollen are presented as accumulation rates (PAR = pollen grains $\mathrm{cm}^{-2}\,\mathrm{a}^{-1}$; also called influx). The use of PAR is preferred above the traditional percentages, because they are quite reliable thanks to the high-resolution timescale (Goslar *et al.*, 2009) and because they provide a better reflection of vegetation change as they are free of percentage effects (Davis and Deevey, 1964; Kuoppamaa *et al.*, 2008; van der Knaap, 2009).

For a comparison with climate data, the irregular time series used for DWT reconstruction were regularised by assigning samples to calendar years (tolerance ± 0.5 a). For calendar years lacking assignments, time series were linearly interpolated. For calendar years with more than one assignment, the respective data were averaged. Because varying temporal resolution and interpolation causes changes in proxy variance (Kamenik *et al.*, 2009), time series were low-pass filtered using a 3-year triangular filter.

Monthly temperature and precipitation data since AD 1864 and monthly snow depth data since AD 1966 were derived from the nearby weather station at Sils Maria (1798 m a.s.l.; 46° 25′ 57.48″ N, 9° 46′ 0.54″ E; 9 km southwest of the study site in the same valley of the Upper Engadin). The SSA-toolkit was used to extract significant trends in seasonal temperature or precipitation time series from Sils Maria (Vautard *et al.*, 1992).

Results

Chronology

The chronology of the upper 100 cm of the profile (encompassing ca. 1 ka) was based on a series of 27 ^{14}C dates (Goslar *et al.*, 2009); 14 of them were measured in the uppermost section, covering the last 300 a (Fig. 2). Age–depth modelling took into account simultaneous shifts in pollen accumulation rates of all major pollen taxa, which indicated sudden changes in peat accumulation rates (Goslar *et al.*, 2009). The 2σ uncertainty of the age–depth model (see Table 3 in Goslar *et al.*, 2009) did not exceed ±2 a in the interval AD 1950–2002, and ±25 a around AD 1850. For the last 150 a, the model was further fine-tuned using larch bud moth events (Kamenik *et al.*, 2009). The final chronology was well supported by a record of spheroidal carbonaceous particles (Kamenik *et al.*, 2009), so its accuracy over the last 150 a is at any level not worse than a few years only.

Testate amoeba transfer functions

We observed a total of 85 testate amoeba taxa in 97 samples. After filtering, the calibration dataset included 68 taxa and 81 samples. The fossil dataset comprised 61 taxa from which 38 were used for DWT reconstruction after filtering rare taxa (which occurred in fewer than four samples) and 129 samples. *Assulina muscorum*, *Centropyxis aerophila* and *Archerella flavum* were the most abundant species in the calibration dataset.

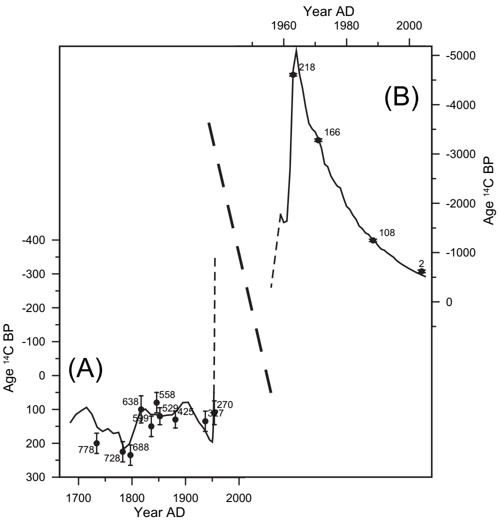

Figure 2 Comparison of ^{14}C dates in the uppermost section of Mauntschas mire with the atmospheric calibration curve during the pre-bomb (A) and post-bomb (B) periods. Numbers near data points denote sample depth (mm)

Table 1 Performance of nine bootstrap-validated transfer-function models

	Boot_R^2	Boot_Ave_Bias	Boot_Max_Bias	RMSEP
MAT	0.78	−0.37	18.90	5.58
PLS comp 1	0.65	−0.02	24.47	7.21
ML	**0.86**	**0.20**	**14.56**	**4.62**
WA_Inv	0.80	0.15	11.99	4.76
WA_Cla	**0.81**	**0.14**	**10.33**	**4.88**
WAtol_Inv	0.84	0.62	11.20	4.69
WAtol_Cla	**0.84**	**0.66**	**9.94**	**4.62**
WA-PLS comp 1	0.75	0.19	11.86	5.33
WA-PLS comp 2	0.78	0.30	12.54	5.11

MAT, modern analogue technique; PLS comp 1, partial least squares, first component; ML, maximum likelihood; WA_Inv, weighted averaging, inverse deshrinking; WA_Cla, weighted averaging, classical deshrinking; WAtol_Inv, tolerance down-weighted averaging, inverse deshrinking; WAtol_Cla, tolerance down-weighted averaging, classical deshrinking; WA-PLS comp 1, weighted averaging partial least squares, first component; WA-PLS comp 2, weighted averaging partial least squares, second component. Boot_R^2 = bootstrapped regression coefficient; Boot_Ave_Bias, bootstrapped average bias; Boot_Max_Bias, bootstrapped maximum bias; RMSEP, root mean square error of prediction. Good results are printed in bold; the best results are underlined.

Classical weighted averaging with and without tolerance down-weighting of rare species (WAtol_Cla, WA_Cla), and the ML model resulted in similar RMSEPs (4.62–4.88). WAtol_Cla had a lower maximum bias than WA_Cla (9.94), which in turn had a substantially lower average bias (0.14). In summary, WAtol_Cla, WA_Cla and ML performed equally well according to error statistics, with WA_Cla having the largest bias at large DWT (Table 1, Fig. 3).

Testate amoebae, water table reconstruction and pollen data

Figure 4 presents the testate amoeba diagram of Mauntschas mire during the instrumental period (AD 1864–2003). Seven biostratigraphic zones were delimited. DWT reconstructions were derived from the WAtol_Cla, WA_Cla and ML models. We decided to use all three models because of similar error statistics (Table 1, Fig. 3). Overall, the highest correlation was recorded between DWT and rates of *Pinus cembra* (Table 2, Figs. 5 and 6).

Zone MA-ta-1 (AD 1864–1934) covered the longest period. The testate amoeba assemblage structure remained generally stable, suggesting a relatively stable habitat in spite of fluctuations in reconstructed DWT: large DWT at AD 1867–1882, small at AD 1882–1895, large at AD 1895–1912, small at AD 1912–1928 and large at AD 1928–1933. The most abundant taxa were *Phryganella acropodia*, *P. paradoxa*, *Trigonopyxis arcula*, *Nebela penardiana*, *Centropyxis aerophila* and *C. platystoma*. Increasing *Trigonopyxis arcula* and *Phryganella acropodia* led to an increase of reconstructed DWT.

The pollen diagram (Fig. 5) shows a high abundance of *Pinus cembra* between AD 1864 and 1893. *Sphagnum* and *Tilletia* were high from AD 1864 to 1867. During the period of large

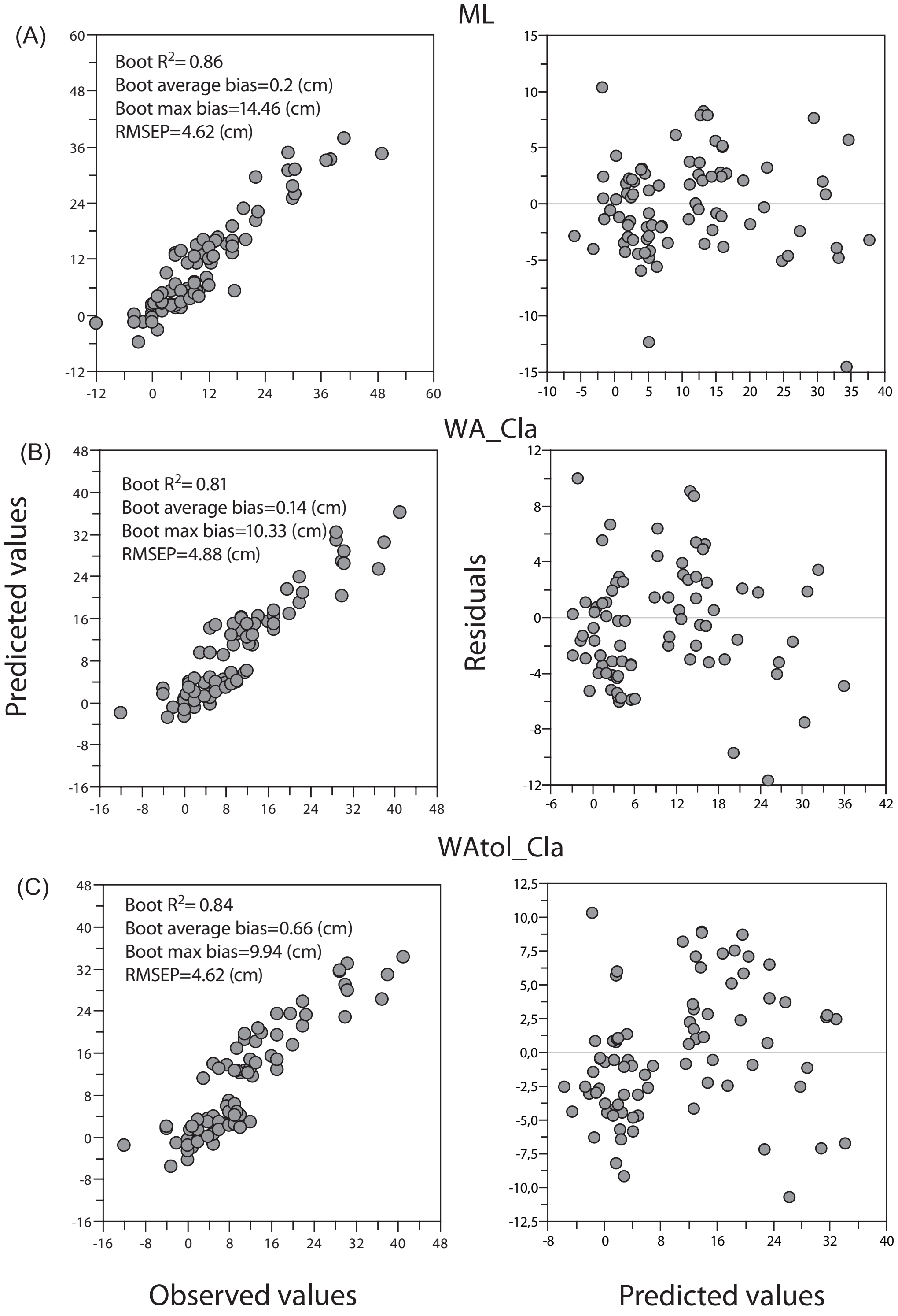

Figure 3 Bootstrap evaluation of testate amoebae/depth to the water table (DWT) transfer functions of three selected inference models, and corresponding error statistics: (A) ML, maximum likelihood; (B) WA_Cla, weighted averaging, classical deshrinking; (C) WAtol_Cla, tolerance down-weighted averaging, classical deshrinking

reconstructed DWT (AD 1867–1882), *Sphagnum* and *Tilletia* markedly decreased. During a shift to small reconstructed DWT (dated AD 1883), *Sphagnum* and *Tilletia* increased again (AD 1882–1889). Shifts in reconstructed DWT around AD 1899 and 1918 coincided with decreasing *Sphagnum* and *Tilletia*.

Zone MA-ta-2 (AD 1934–1954) is characterised by *Centropyxis aerophila*, *Nebela penardiana* and *Phryganella acropodia*. Reconstructed DWT decreased until ca. AD 1940, along with percentage changes of *Centropyxis aerophila* and *Nebela penardiana*. DWT remained small until ca. AD 1950. After 1950, *Nebela speciosa*, *N. tincta*, *Archerella flavum* and *Centropyxis aculeata* became locally extinct, and various *Euglypha* species increased or appeared. Reconstructed DWT increased and remained large until present. *Sphagnum* spores were abundant but *Tilletia* remained low. Any correlation between those two, observed in the deeper peat section, disappeared. *Pinus cembra* pollen gradually increased.

In zone MA-ta-3 (AD 1954–1966), many abundant testate amoeba species typical for mineral-rich habitats disappeared (e.g. *Centropyxis aerophila*, *C. platystoma*, *Nebela penardiana*

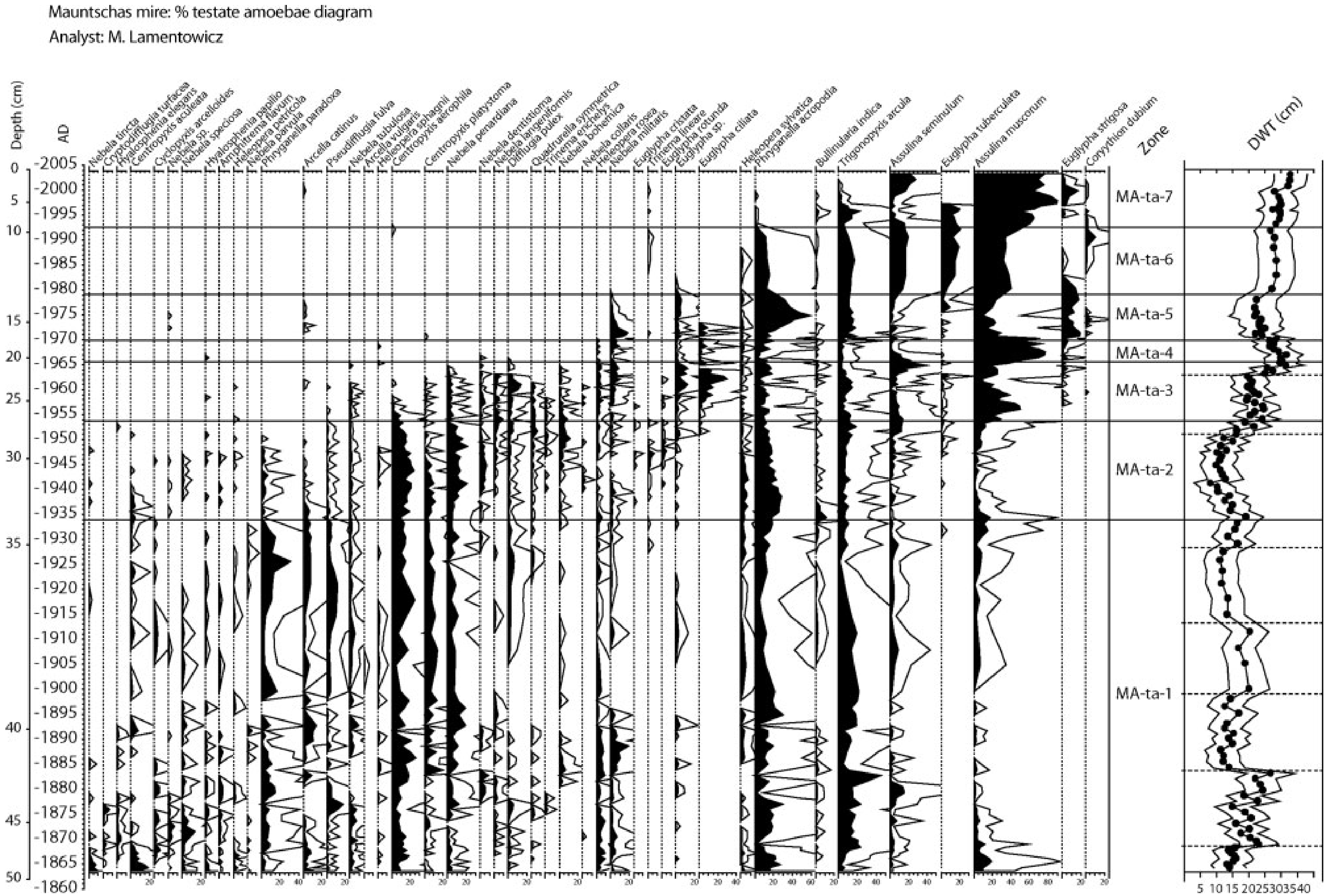

Figure 4 Percentage testate amoebae diagram from Mauntschas mire with the reconstruction of depth to the water table (DWT). Continuous horizontal lines represent statistically significant zone boundaries; dashed lines delimit subjectively marked shifts in mire wetness recorded in the DWT reconstruction

Table 2 Spearman's correlation coefficients for reconstructed depth to water table, trends in measured temperatures (T.) shown in Fig. 6, and *Pinus cembra* pollen accumulation rates (PAR). Correlations for precipitation were insignificant

	T.winter	T.spring	T.summer	T.autumn	PAR
ML	0.689**	0.383**	0.213*	0.446**	0.668**
WA_Cla	0.703**	0.381**	0.175*	0.413**	0.676**
WAtol_Cla	0.615**	0.396**	0.234**	0.451**	0.581**
PAR	0.418**	0.423**	0.251**	0.351**	—

Correlation is significant at.

* $P = 0.05$ (2-tailed); ** $P = 0.01$ (2-tailed).

ML, maximum likelihood; WA_Cla, weighted averaging, classical deshrinking; WAtol_Cla, tolerance down-weighted averaging, classical deshrinking.

and *N. langeniformis*) or declined markedly (e.g. *Heleopera rosea*). Taxa characteristic for acid *Sphagnum* hummocks (*Assulina muscorum* and *A. seminulum*) increased to over 40%. At AD 1963 reconstructed DWT increased dramatically. DWT peaked around the transition to the next zone, AD 1965–1967. Around AD 1960 *Andromeda polifolia* became locally abundant, and soon after *Vaccinium* declined. *Sphagnum* spores peaked. *Pinus cembra* pollen continued to increase.

In zone MA-ta-4 (AD 1966–1970) *Assulina muscorum* (over 60%) and large reconstructed DWT predominated. The diversity within amoebae markedly declined. Over half of the taxa disappeared.

In zone MA-ta-5 (AD 1970–1979) *Phryganella acropodia* reached a maximum (60%), the dryness taxon *Trigonopyxis arcula* increased and *Euglypha strigosa* dominated among the idiosomic taxa. *Assulina muscorum* decreased. Reconstructed DWT levelled off. In 1975, *Pinus cembra* and Cyperaceae pollen and *Sphagnum* spores declined.

Zone MA-ta-6 (AD 1980–1992) had a rising abundance of *Assulina muscorum*, *Euglypha tuberculata* and *Trigonopyxis arcula*, along with a slightly higher, yet stable reconstructed DWT. From the total of 63 testate amoeba taxa only 20 remained in this zone. After 1988 *Pinus* (both types) increased.

In Zone MA-ta-7 (AD 1993–2003) *Assulina muscorum* was the dominant species (over 80%). Only 10 testate amoeba taxa remained. *Andromeda polifolia* had a pronounced maximum. Reconstructed DWT further increased in comparison to zone MA-ta-4. Both types of *Pinus* remained high. *Sphagnum* spores and *Tilletia* had a maximum after 1998.

Reconstructed DWT and climate data

Correlations between DWT and monthly precipitation were insignificant. DWT, however, paralleled trends in air temperature. Correlations between DWT and temperature were highest for winter temperature (Table 2 and Fig. 6). All time series shown in Fig. 6 showed a trend towards higher values in recent decades, but for some the correlation was not stable over time, e.g. DWT *versus* autumn temperature.

Discussion

We present the first testate amoeba-based palaeohydrological reconstruction from the Swiss Alps, and the first calibration dataset for this region. The geographically closest comparable study is that of Mitchell *et al.* (1999) (calibration dataset) and Mitchell *et al.* (2001) (DWT reconstruction of a raised bog, macrofossils and pollen) from the Jura Mountains, in a significantly more oceanic setting and at lower elevation (~1000 m). This study is the first of its type with a nearly annual resolution in peatland. This, in combination with the new training set, allowed us to compare the reconstruction of the water table with instrumental meteorological data.

Calibration dataset

Moisture has long been known to be an important environmental factor that influences the abundance and community structure of testate amoebae in mires (Harnisch, 1948). The new DWT calibration dataset presented here, with its extensive water table gradient (53 cm) and low error of prediction (RMSEP = 4.88), performs well compared to existing calibration datasets (Charman, 1997; Charman and Warner, 1997; Woodland *et al.*, 1998; Bobrov *et al.*, 1999; Wilmshurst *et al.*, 2003; Lamentowicz and Mitchell, 2005; Payne *et al.*, 2006; Charman and Blundell, 2007) (Fig. 7). In most other calibration datasets, a long gradient generates a high RMSEP due to a poorer fit of samples at the dry end of the gradient (Mitchell *et al.*, 1999, 2001). Our models also perform well for dry samples.

Surface wetness and peat development

The dominance of *Sphagnum fuscum* on present-day hummocks in mires of the Upper Engadin valley is intriguing because indicator taxa for ombrotrophic conditions (e.g., *Sphagnum fuscum*, *Oxycoccus microcarpus* and *Andromeda polifolia*) occur intermingled with taxa that indicate mineral-rich water (e.g. *Carex rostrata*, *Eriophorum angustifolium*). Some authors described the parts of mires (including Mauntschas) with *Sphagnum fuscum* hummocks as exclusively ombrotrophic (Held and Wortmann, 1994) and explained the occurrence of plant indicators for minerotrophic conditions on the same hummocks by atmospheric input of cations from non-vegetated surfaces above the tree line. Against this hypothesis is our field observation that all shallow-rooting plants and *Sphagnum fuscum* on the hummocks indicate ombrotrophic conditions, whereas the two minerotrophy indicators are rooting deeply. The patterns on the mire surface rather suggest that the presence of springs in the middle of the mire and runoff from the surroundings (especially during snowmelt) bring sufficient amounts of cations to allow the growth of minerotrophic vegetation in hollows and through hummocks. On this basis Mauntschas should be classified as a transitional bog (Pseudo-Hochmoor in German) *sensu* du Rietz (1954).

An important result of our study is that ombrotrophic *Sphagnum fuscum* hummocks developed at the sampling site only during the last 50 a, when testate amoebae such as *Assulina muscorum* or *Euglypha ciliata* indicated dry and/or acid conditions. It seems that prior to AD 1950, when the water table was much higher (small reconstructed DWT, Fig. 4) and the mire was fed by mineral-rich water (indicated by, for example, *Centropyxis platystoma*, *Nebela penardiana*, *N. langeniformis* and *Heleopera rosea*), such ombrotrophic hummocks could not develop. Indeed, a high calcium content of water in rich fens is believed to prevent *Sphagnum* from becoming dominant (Malmer *et al.*, 1992), while *Sphagnum fuscum* does tolerate moderately dry conditions (Rydin, 1985, 1993). Hence the growth of ombrotrophic *Sphagnum fuscum* hummocks in Mauntschas may have been triggered by moderate drought conditions that would have allowed the calcium content at the surface to decline sufficiently, while the

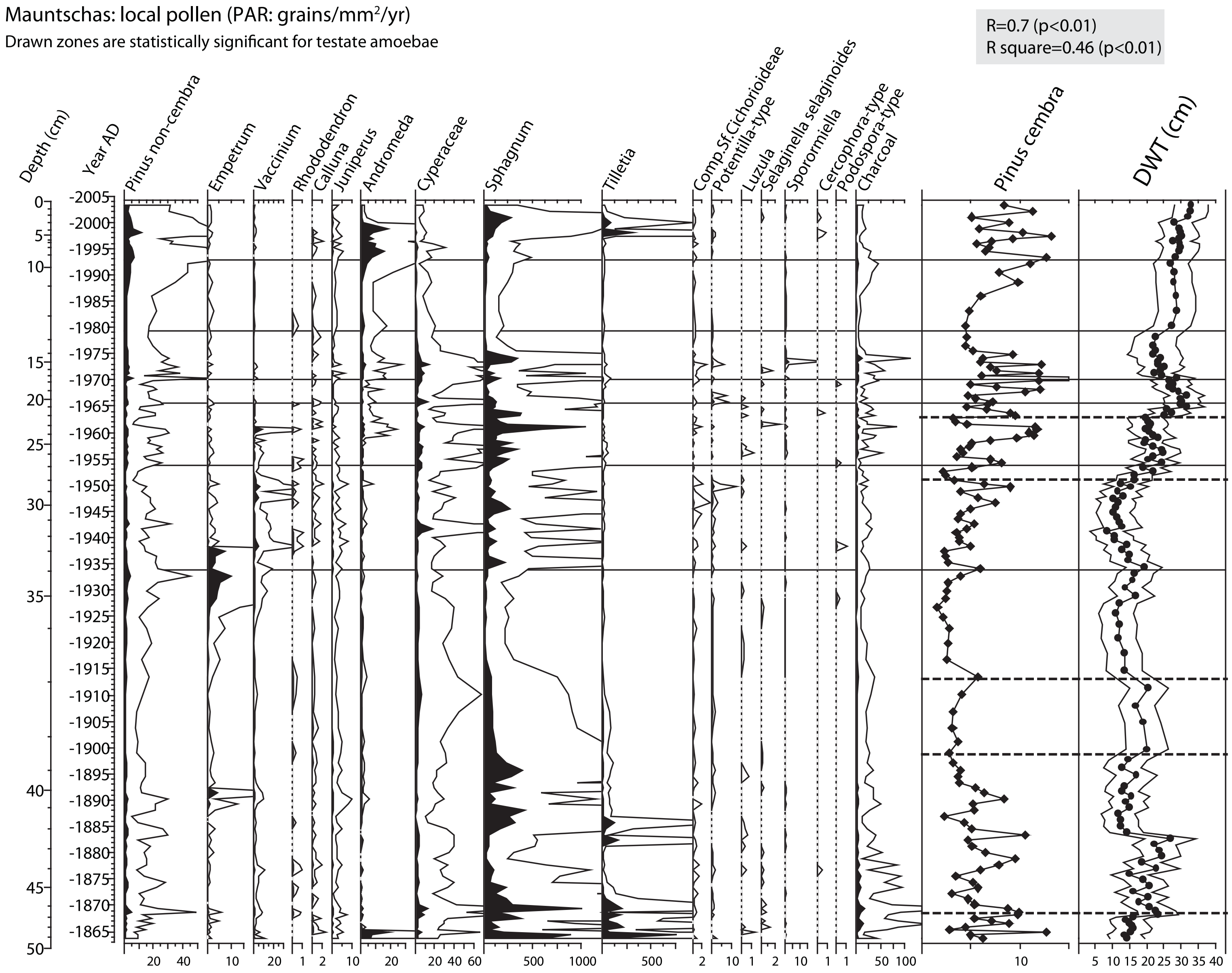

Figure 5 Local pollen accumulation diagram. Continuous horizontal lines represent statistically significant zone boundaries for testate amoebae (see Fig. 4); dashed lines delimit subjectively marked shifts in mire wetness recorded in the DWT reconstruction

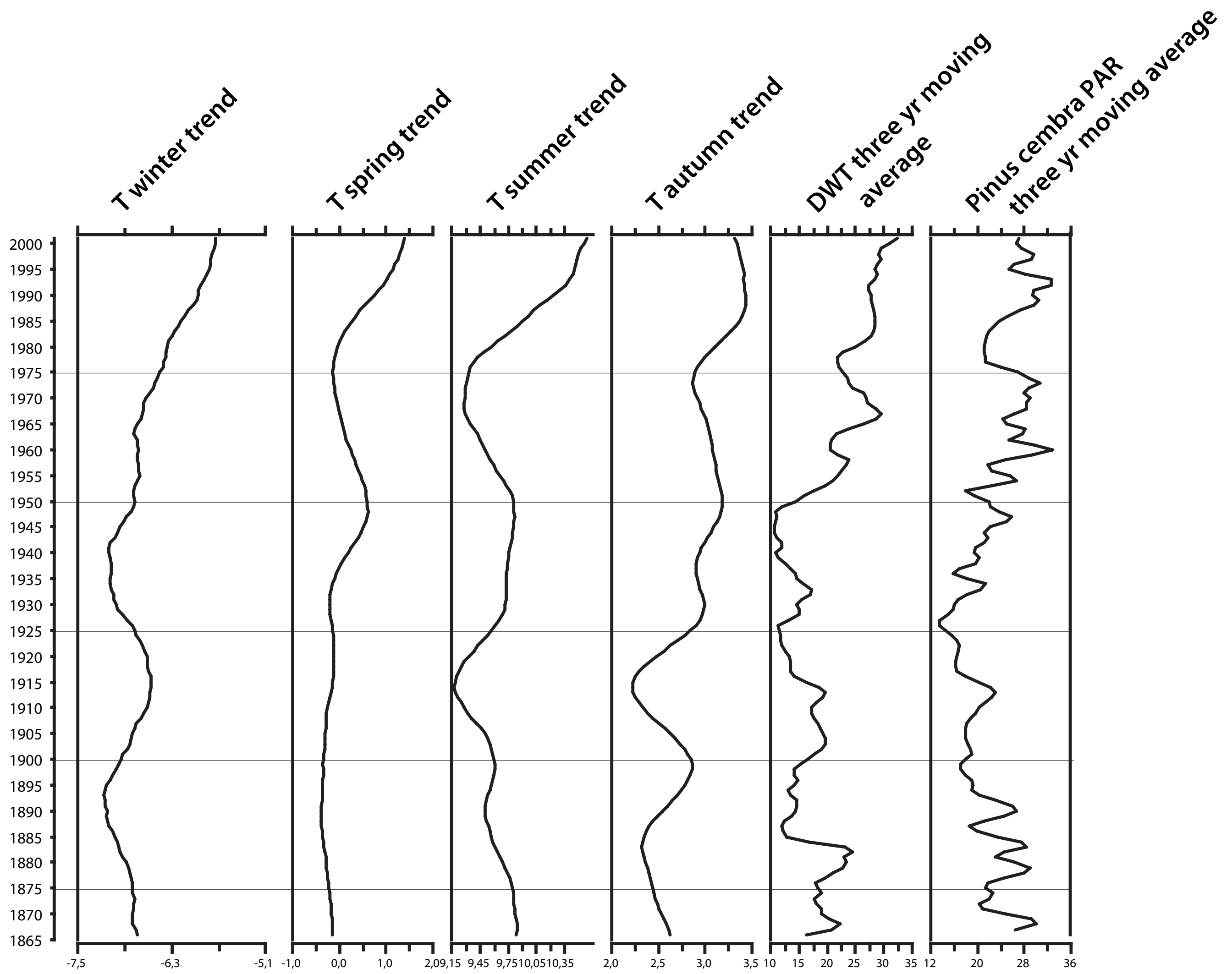

Figure 6 Comparison of DWT changes, *Pinus cembra* pollen, and temperature trends. Temperatures are measured at Sils Maria 9 km from the study site. Trends were calculated with the SSA-toolkit (Vautard *et al.*, 1992)

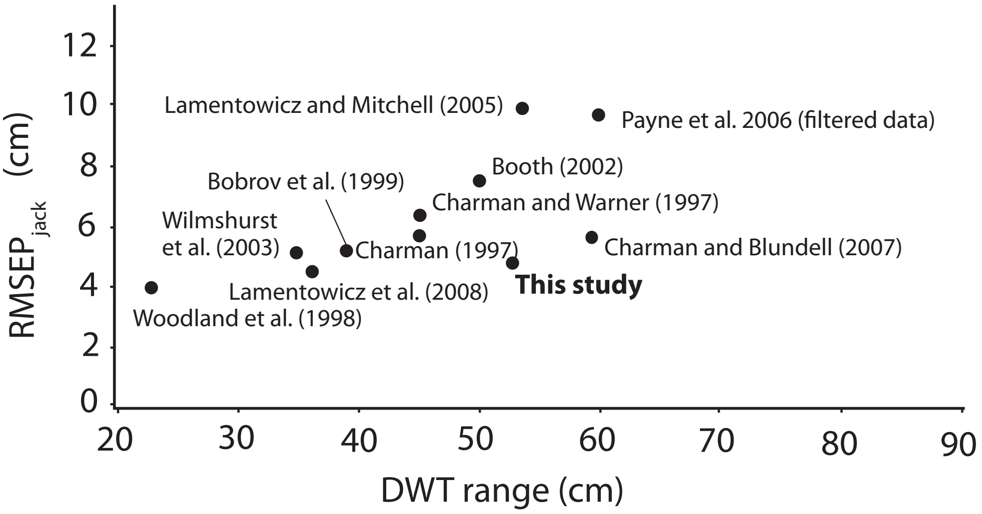

Figure 7 Comparison of gradient lengths and RMSEP (root mean squared error of prediction) of existing testate amoebae–DWT transfer functions. Modified after Payne *et al.* (2006)

moisture content could still have been sufficiently high to support this *Sphagnum* species. This interdependence probably stopped when hummocks grew, thus disrupting their connection to surrounding calcium-rich waters. Part of the major change in reconstructed surface wetness may therefore be attributed to peat growth, showing a transition from primarily minerotrophic to primarily ombrotrophic conditions. Major changes in surface wetness might thus be autogenic (Zobel, 1988; Hughes and Barber, 2004), though the timing of this shift and its correlation with changes in climate are striking.

DWT and nutrient gradients are partly correlated in mires. Therefore part of the fluctuations in the testate amoeba-inferred DWT might also be attributed to changes in nutrient availability. During the DWT increase reconstructed for zone MA-ta-1 (AD 1867–1882), for example, *Nebela penardiana* and *Argynnia* (*Nebela*) *dentistoma* suggested wet phases, but these species are also indicators of heightened trophic state (Ł. Lamentowicz *et al.*, 2008). Some species (e.g. *Centropyxis aculeata*) virtually disappeared at the end of zone MA-ta-1, suggesting a drop of the water table. Local pollen (*Andromeda polifolia*, *Vaccinium*) and modern vegetation indicated a decrease in nutrients.

Surface wetness and vegetation changes

The correlation between *Pinus cembra* pollen and reconstructed DWT suggests that mire moisture and *Pinus cembra* pollen production partly depend on the same factor(s). Pollen may indeed support the testate amoeba-based DWT reconstruction. Changes in *Pinus cembra* pollen values might either be connected with changing temperatures or with human impact on the forest, but the coincidence of water table decrease with *Pinus cembra* pollen increase rather supports a climatic origin. During the last 150 years human impact on the sub-alpine forest has been rather intensive, and the forests around the study site are managed today, so we must take it into consideration. Influence of historical forest transformation on peatlands was also studied in other parts of the world. Warner and other authors found in North America (Warner, 1993; Bunting and Warner, 1998) that deforestation during the European colonisation led to various changes in the peatland ecosystems (e.g. water table increase). Wilmshurst *et al.* (2002) showed that peatlands in New Zealand were affected by change in forest composition, resulting in strong relationships between water table changes and pollen data. Studies in Poland revealed that moisture changes in raised bogs and kettle-hole bogs were correlated with deforestation phases (Lamentowicz *et al.*, 2007a, 2007b, 2008b, 2008c). There are, however, no indications for deforestation around Mauntschas mire, so wetness and vegetation changes in the mire should rather be interpreted in terms of climate change, although we cannot exclude the influence of minor changes in the surrounding forest on the hydrology.

An increase in DWT (i.e. drier conditions) in the cored *Sphagnum* hummock reconstructed for AD 1928, for example, neatly coincided with increasing *Empetrum*, *Vaccinium* and *Pinus* non-*cembra* and declining Cyperaceae indicative of a drier mire over a larger surface than only the cored hummock. In contrast to this, the wet conditions reconstructed for zone MA-ta-2 up to AD 1950 coincided with pollen indicative of dry hummock (presence of the dwarf shrubs *Empetrum*, *Vaccinium*, *Rhododendron* and *Calluna*), so we must assume that dry hummock vegetation was present very close to the coring site but not at it. Our study thus also confirms that the recovered pollen of mire plants does not necessarily reflect hydrological changes at the same local scale as the testate amoebae do. For example, *Empetrum hermaphroditum* is a strong indicator for dry conditions in mire vegetation, but its curve does not follow the DWT estimates. On the other hand, *Andromeda polifolia* pollen follows the expectation of drought indicator with its maximum between AD 1990 and 2000 when the reconstructed water table has its lowest level.

Sphagnum and *Tilletia* spore production seems to be related both to surface wetness and to nutrients. *Sphagnum* may experience stress from minerals during periods of high water tables, and higher spore production may be a response to this. Excessive drought, on the other hand, can inhibit *Sphagnum* spore maturation (Sundberg, 2002). Overall, our results suggest that *Sphagnum* might be affected both by drought stress in warm, dry conditions and by mineral stress in wet conditions. Alternatively, the seemingly complex curve of *Sphagnum* spores might reflect shifts among various *Sphagnum* species having different ecological demands and spore production levels. Likewise, some Cyperaceae may be favoured by drier conditions in bogs (*Eriophorum vaginatum*, *Trichophorum cespitosum*), while others may benefit from wetter conditions and higher mineral supply (*Eriophorum angustifolium*, *Carex rostrata*, *Carex nigra*).

Surface wetness and human impact

Human impact might have been an additional cause of changes in mire surface wetness. The dry phase around AD 1928 described above, for example, might have been related to grazing, as suggested by a single finding of the dung-related fungal spore *Podospora*-type (van Geel, 1986). A possible mechanism is that moderate grazing damages the *Sphagnum* layer in hollows and gullies, resulting in increased runoff and thus a drier peat surface.

Mauntschas was also affected by tourism and sports events. A skiing trail across Mauntschas made for the Olympic Winter Games in AD 1948 was moved to the forest about 5 years ago. Even though the impact might have been minimal because the mire surface was frozen and protected by a thick layer of snow during the ski season and pollen indeed did not indicate any changes in regional vegetation after 1948, the skiing and trampling may have changed the vegetation locally, leading to superficial drainage and lowering of the water table. However, the sampled part of Mauntschas mire lies higher than most of the bog and there are no nearby traces of ditches, peat exploitation or erosion gullies, so we can exclude human impact as the main cause of the water table decrease during the last 150 a.

Surface wetness and climate

The Mauntschas mire peat archive is the first analysed for testate amoebae in near-annual temporal resolution. This approach allowed comparing the instrumental data directly with the palaeoecological reconstruction. This comparison suggests that the relationship between measured climate and peatland wetness is not very tight. One reason for this is likely the complexity of the relationship, as surface wetness is controlled by precipitation amount, seasonality and type (rain or snow), and by temperatures controlling snow-melt, evapotranspiration and run-off depending on frost in the soil. The hydrological buffer provided by the peat body may be another reason. Another possible explanation is that although we have near-annual resolution there is an error associated with each date. According to Goslar *et al.* (2009), the dating error is 1–2 years only after AD 1950, but might be larger before that time. Therefore correlations are more likely to emerge when both the testate amoeba and climatic data are smoothed over several years than by taking the annual resolution data.

Surface wetness is usually the main factor controlling assemblages of testate amoebae (van der Linden *et al.*, 2008). In most northern European raised bogs the water tables are controlled mainly by precipitation (Charman, 2007; Blundell *et al.*, 2008); hence testate amoeba-based water table reconstructions usually correlate with measured precipitation (Charman *et al.*, 2001; Langdon *et al.*, 2003). However, a study from northeastern Europe (Barber and Langdon, 2007) suggests that over centennial timescales summer temperatures are important drivers of the peat-based palaeoclimate record.

The present-day surface pattern of Mauntschas mire suggests that part of the surface water is still derived from outside the mire. The two potential sources would be runoff from the surroundings and springs in the mire (actually observed though not close to the coring locality). This complicates the discussion on climate and its effects on surface wetness. Responses may therefore be rather different from what is observed in truly raised bogs, where most other palaeoecological studies of peatlands were done. One factor is that catchments integrate precipitation over large areas, and precipitation tends to be spatially heterogeneous especially in mountains, so the point measurement of precipitation at the climate station Sils Maria (9 km away) might not reflect faithfully the precipitation regime around Mauntschas mire (Casty *et al.*, 2005). Another factor is that run-off is affected by percolation, retention in soils and uptake by plants in the catchment, and this non-atmospheric water supply modifies the relationship between precipitation and surface wetness. Nevertheless, Hughes and Barber (2004) described sudden, nonlinear changes of mire hydrology to climate change, leading to a reduced influence of minerotrophic water at the mire surface. Over the last 150 a, temperatures in the study area increased (Kamenik *et al.*, 2009), whereas precipitation has not changed (Begert *et al.*, 2005; Casty *et al.*, 2005). Increased pollen from a drought indicator such as *Andromeda* is thus in agreement with an inferred temperature-related drying on the mire.

Charman *et al.* (2004) and Charman (2007) have shown that summer temperature may in a continental setting play an important (though still subsidiary) role in controlling the water table depth of peatlands. Similarly, Schoning *et al.* (2005) observed in the relatively continental setting of central Sweden that the testate amoeba-inferred water table depth correlated best with mean annual temperature. Our results from Mauntschas partly agree with these studies, in that temperature trends paralleled trends in reconstructed DWT. Contrary to these studies, however, the closest similarity was found for temperatures during winter rather than summer. Nevertheless, the testate amoeba-based water table reconstruction can be assumed to reflect the conditions during the season under which these organisms are growing, which is thought to be spring and summer. This implies that winter temperatures are linked with surface wetness of the growing season, but these mechanisms are poorly understood. Useful is the observation by Bayard *et al.* (2005) in the southern Swiss Alps that cold winters prolonged soil frost, and thus blocked downward percolation of meltwater. Similarly, prolonged frost in Mauntschas would reduce the downward percolation of surface water, both on the mire and in the surroundings, thus increasing the runoff onto the mire. Low temperatures during the cold season would thus contribute to increased surface wetness extending into the growing season. Surface wetness would thus depend on a complex interplay between temperature, precipitation, catchment processes and human disturbance on and around the mire (e.g. trampling, artificial drainage or forest management). Especially during the last 100–150 a human impact on the peatland might have been increasing, so it is possible that before AD 1850 wetness changes in Mauntschas had a more natural character. Our ongoing studies on peat layers covering the entire last millennium are aimed to provide more insight into this.

An alternative or possibly complementary explanation for the correlation between testate amoeba-derived DWT and winter temperature relates to the little-studied aspect of winter ecology of soil protozoa. Testate amoeba populations are generally low in spring and increase throughout the growing season. However, in winter the surface of peatlands is not necessarily frozen and is more likely to remain unfrozen if a thick snow cover insulates the soil surface from the cold. Thus a possible explanation for the observed pattern is that during cold winters snow falls early and quickly reaches a thickness sufficient to isolate the surface from the cold. This might allow the testate amoebae to remain active, though perhaps less than during wet and warm spring and autumn weather. A similar observation was made in aspen woodland soils in Alberta, Canada (Lousier and Parkinson, 1984), where even during the cold winters of that region testate amoebae remained active in comparatively drier soils.

Having a local record of climate available measured 9 km distant from the site, we are hesitant to use the global temperature record for quantitative comparison with our results. Nevertheless, it appears that the reconstructed water table fluctuations in Mauntschas are better related to global temperature change (Briffa *et al.*, 2004; Brohan *et al.*, 2006) than to the local temperature record. Especially decrease of the water table ca. AD 1940–1950 matches the global record very well. It is understandable that under the subcontinental climatic conditions of the study region global warming would lead to a water table decrease in peatlands. More studies and methodological progress will be needed to explore and quantify such relationships.

Acknowledgements The study is the part of the European Union project Millennium (SUSTDEV-2004-3.1.4.1). It was further supported by the National Centre of Competence in Research (NCCR) on Climate (Bern, Switzerland). We thank the community of St Moritz and the Department for Nature and Landscape of the Office for Nature and Environment of Canton Grisons (Graubünden) for permission to collect the peat section from Mauntschas mire, and Urs Krähenbühl and Regina Schreier for assistance during fieldwork. Dan Charman is thanked for helpful discussions on the data. We also thank an anonymous reviewer and Dmitri Mauquoy for their very valuable remarks. The pollen data were created in the European Union project PINE (Predicting Impacts on Natural Ecotones), project no. EVK2-CT-2002-00136. Further funding to ML by the Foundation for Polish Science (FNP) (Outgoing Fellowship KOLUMB) and to EM (Swiss NSF project no. 205321-109709/1 and CCES projects RECORD and BigLink) are kindly acknowledged.

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