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Potential implications of differential preservation of testate amoeba shells for paleoenvironmental reconstruction in peatlands

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Abstract Testate amoebae are now commonly used in paleoenvironmental studies but little is known of their taphonomy. There is some experimental evidence for differential preservation of some testate amoeba shell types over others, but it is unclear what, if any impact this has on palaeoenvironmental reconstruction. To investigate this issue we looked at palaeoecological evidence for the preservation of different shell types. We then investigated the possible impact of selective preservation on quantitative palaeoenvironmental inference. We first used existing palaeoecological data sets to assess the vertical patterns of relative abundance in four testate amoeba shell types: (1) shells made of secreted biosilica plates (idiosomes, e.g. *Euglypha*), (2) idiosomes with thick organic coating (*Assulina*), (3) proteinaceous shells (e.g. *Hyalosphenia*), (4) shells built from recycled organic or mineral particles (xenosomes) (e.g. *Difflugia, Centropyxis*). In three diagrams a clear pattern of decay was only observed for the idiosome type. In order to assess the implications of differential preservation of testate amoeba taxa for paleoenvironmental reconstruction we then carried out simulations using three existing transfer functions and a wide range of scenarios, downweighting different test categories to represent the impact of selective test decomposition. Simulation results showed that downweighting generally reduced overall model performance. However downweighting a shell type only produced a consistent directional bias in inferred water table depth where that shell type is both dominant and shows a clear preference along the ecological gradient. Applying a scenario derived from previous experimental work did not lead to significant difference in inferred water table. Our results show that differential shell preservation has little impact on paleohydrological reconstruction from *Sphagnum*-dominated peatlands. By contrast, for the minerotrophic peatlands data-set loss of idiosome tests leads to consistent underestimation of water table depth. However there are few studies from fens and it is possible that idiosome tests are not always dominant, and/or that differential decomposition is less marked than in *Sphagnum* peatlands.

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Further work is clearly needed to assess the potential of testate amoebae for paleoecological studies of minerotrophic peatlands.

Introduction

One of the basic assumptions that needs to be fulfilled if a group of organisms is to be used in paleoecology is that the taphonomy should be well understood (Birks and Birks 1980). Since differential preservation is a reality for all biological proxies to some extent (even pollen) it is important to understand which taxa are more susceptible to preferential decay and what effect this will have on paleoecological interpretation. This is particularly true when direct, quantitative reconstructions are made from fossil assemblages.

Testate amoebae are increasingly used in paleo-environmental studies (Charman 2001). Testate amoebae have been particularly used in palaeoecological studies from peatlands where the hydrological preferences of amoebae species have allowed the use of transfer functions to reconstruct quantitatively past changes in mire wetness, and thereby climate. Testate amoebae have only recently become part of the standard toolkit of paleoecologists and their taphonomy has not been well studied. In contrast to other groups of organisms used in paleoecology for which taphonomy has been studied (Barker 1992; Campbell 1999; Kontrovitz et al. 1998), very little work has been done on testate amoeba taphonomy and its implications for paleoenvironmental reconstruction.

The existence of vertical micro-distribution of testate amoebae in the upper part of *Sphagnum* peatlands in response to micro-environmental gradients has long been established (Bonnet 1958; Booth 2002; Chacharonis 1954, 1956; Meisterfeld 1977; Mitchell and Gilbert 2004). With respect to the fossil communities, Tolonen observed that the siliceous plates (referred to as "idiosomes", e.g. *Euglypha*) are very soluble in peat (Tolonen 1986). Ruzicka (1982) estimated the depth at which 10% of the initial number of testate amoebae tests remained in lake

deposits. The estimated depth varied considerably among taxa that produce proteinaceous tests (e.g. *Hyalosphenia elegans*: 809 cm) and those that build their test from recycled organic and/or mineral particles (referred to as "xenosomes", e.g. *Centropyxis*: 335 cm, *Difflugia*: 232 cm, *Heleopera*: 352 cm) or that use idiosomes (*Euglypha*: 353 cm). More recently, Roe et al. (2002) observed that the abundance of testate amoebae shells decreased sharply in the top 18 cm of saltmarsh sediments and that tests made of idiosomes were less well preserved than those made of xenosomes. Wilmhurst et al. (2003) observed clear differences between modern and fossil communities in peatlands. Wilmhurst et al. (2003) showed that there was good overlap in a detrended correspondence analysis between the position of exclusively modern species and those also present in the fossil record and therefore the observed difference is not due to major ecological shifts but rather to differential preservation. However no attempt has been made to assess quantitatively if there is a systematic bias in shell type with depth within the catotelm peat.

Studies of the decomposition of testate amoeba shells in upland forest litter were carried out by Lousier and Parkinson (1981) and Coûteaux (1992). Lousier and Parkinson (1981) observed high decomposition (74–97% after one week) of shells built from platelets (idiosomes) and lower decomposition (42–68% after one week) for species that build shells from sediment particles (xenosomes). However, Coûteaux (1992) did not observe any significant decay in the course of a five-week long experiment. In a recent study, Swindles and Roe (2007) experimentally tested how different testate amoebae extracted from *Sphagnum* resisted extreme acidic conditions (pH 0.3–0.5). These conditions, which are about three pH units below the lowest values typically observed in ombrotrophic bogs, allowed the authors to observe significant shell decay over a period of only four days. Swindles and Roe observed a relatively wide degree of variability in resistance to decay, even within given genera (e.g. *Assulina, Nebela*) and concluded that this could represent a problem for peat-based palaeoclimate studies. Payne (in press) subjected peat samples to a variety of treatments over a 28-month period. Significant changes were noted in dried samples and samples treated with strong acids, but the possibility of prior differences in the samples

cannot be excluded. Recognising the problem of differential preservation Booth and Jackson (2003) and Booth et al. (2004) excluded taxa not present below the accrotelm from their training set for palaeoenvironmental reconstruction. To date no assessment has been made of the implications of possible differential preservation of testate amoebae tests for paleoenvironmental reconstruction.

The first way to assess if there is indeed a trend for some shell types to be preferentially lost over time is to compare the relative contribution of different shell types to the total community from the surface downwards. However, as pointed out by Swindles and Roe (2007), such a comparison is not necessarily pertinent because the vertical distribution of testate amoeba communities may be due to their response to changes in environmental conditions as well as to differential preservation of shells. An alternative option is to compare the relative percentage of different shell categories in subfossil samples with modern samples from a range of microhabitats. The possible bias here is that the present and past range of microhabitats may be significantly different (e.g. if a broader range of habitats were sampled for the training set and the subfossil sequence only covers part of the ecological gradient).

Despite the wide range of testate amoeba shell types that are expected to differ in their resistance to decay, differential preservation of shells would only matter if the ecological preferences of the different categories of shells were significantly different and this has not been assessed to date with the exception of the study of Wilmhurst et al. (2003). Our goals were therefore (1) to assess if the contribution of different shell types varies with depth using several published and unpublished paleoecological data sets (Lamentowicz 2005; Lamentowicz et al. 2007a, b; Lamentowicz et al. submitted (b); Mitchell et al. 2001), (2) to assess if the ecological preferences of testate amoebae characterized by various categories of shells were significantly different, using data sets currently used for transfer functions (Lamentowicz and Mitchell 2005; Lamentowicz et al. submitted (a); Mitchell et al. 1999; Mitchell et al. 2001; Payne and Mitchell 2007; Payne et al. 2006), and (3) using the same data sets, to assess the performance of models and the bias caused in the inferred water table depth by conducting a theoretical experiment in which we selectively filtered out various proportions of different shell types.

Methods

Data sets

To assess if a pattern of differential preservation existed among the various test types we used three data sets, from Alaska (Jigsaw Lake, Kenai Peninsula, E. Mitchell and K. Kishaba, unpublished data), the Jura Mountains of Switzerland (Praz-Rodet bog) (Mitchell et al. 2001), and Poland (Tuchola mire) (Lamentowicz 2005; Lamentowicz et al. submitted (b)). We also compiled published data from a number of previous studies (see Table 1 for details). While this list is certainly not complete it provides a good impression of the general pattern across many regions and peatland types.

To assess if testate amoebae with different test types also had different ecological preferences, we used data sets from Alaska (Payne et al. 2006), the Jura Mountains of Switzerland and France (Mitchell et al. 1999), and northern Greece (Payne and Mitchell 2007). The final (selected) data were used with the best performing transfer function model; this was a two-component weighted average partial least squares (WA-PLS) model for the Alaskan data and a maximum likelihood (ML) model for the Greek data. For the Jura data the original study only tested simple weighted averaging. Re-analysis in this study showed weighted averaging to be out-performed by a two-component WA-PLS model with a RMSEP$_{jack}$ of 7.7 cm.

Categories of test types and modelling simulations

We divided testate amoebae taxa into four categories on the basis of test construction. The four categories used were:

(1) Idiosomes. This category includes all testate amoebae which produce biosilica or calcite plates but which do not embed the plates in a thick organic matrix. Examples include: *Corythion, Euglypha, Quadrulella, Sphenoderia, Tracheleuglypha* and *Trinema*. Most of these taxa belong to the Euglyphida (testate amoebae with filose pseudopodia).

(2) Idiosomes + organic. This category includes all testate amoebae which produce biosilica or calcite plates and which do embed the plates

Table 1 Data filtering scenarios used to assess the effect of selective loss of certain testate amoeba shell types on inferred depth to water table

Case nr	Fraction of initial population remaining [%]				Case nr	Fraction of initial population remaining [%]			
	Idiosomes	Idiosomes + organic	Protein or calcium	Xenosomes		Idiosomes	Idiosomes + organic	Protein or calcium	Xenosomes
0	100	100	100	100	41	10	60	60	40
1	0	40	40	10	42	10	60	60	60
2	0	40	40	40	43	10	60	90	10
3	0	40	40	60	44	10	60	90	40
4	0	40	60	10	45	10	60	90	60
5	0	40	60	40	46	10	90	40	10
6	0	40	60	60	47	10	90	40	40
7	0	40	90	10	48	10	90	40	60
8	0	40	90	40	49	10	90	60	10
9	0	40	90	60	50	10	90	60	40
10	0	60	40	10	51	10	90	60	60
11	0	60	40	40	52	10	90	90	10
12	0	60	40	60	53	10	90	90	40
13	0	60	60	10	54	10	90	90	60
14	0	60	60	40	55	40	40	40	10
15	0	60	60	60	56	40	40	40	40
16	0	60	90	10	57	40	40	40	60
17	0	60	90	40	58	40	40	60	10
18	0	60	90	60	59	40	40	60	40
19	0	90	40	10	60	40	40	60	60
20	0	90	40	40	61	40	40	90	10
21	0	90	40	60	62	40	40	90	40
22	0	90	60	10	63	40	40	90	60
23	0	90	60	40	64	40	60	40	10
24	0	90	60	60	65	40	60	40	40
25	0	90	90	10	66	40	60	40	60
26	0	90	90	40	67	40	60	60	10
27	0	90	90	60	68	40	60	60	40
28	10	40	40	10	69	40	60	60	60
29	10	40	40	40	70	40	60	90	10
30	10	40	40	60	71	40	60	90	40
31	10	40	60	10	72	40	60	90	60
32	10	40	60	40	73	40	90	40	10
33	10	40	60	60	74	40	90	40	40
34	10	40	90	10	75	40	90	40	60
35	10	40	90	40	76	40	90	60	10
36	10	40	90	60	77	40	90	60	40
37	10	60	40	10	78	40	90	60	60
38	10	60	40	40	79	40	90	90	10
39	10	60	40	60	80	40	90	90	40
40	10	60	60	10	81	40	90	90	60

in a thick organic matrix. One genus is included: *Assulina*. This genus also belongs to the Euglyphida. This genus is well known to palynologists because it is one of the few testate amoebae to resist the acid digestion used in pollen preparations. It is clear from palaeoecological studies that tests of this category are more resistant to decomposition than tests constructed of idiosomes without an organic matrix, so it is important that these groups are separated here.

(3) Protein + calcium. This category includes all taxa that secrete their test but do not build biosilica or calcite. Examples include: *Arcella, Archerella* (syn. *Amphitrema flavum*, the other *Amphitrema* species are in the xenosome categories), and *Hylosphenia*.

(4) Xenosomes. This category includes the taxa that recycle organic or mineral particles from their environment or from their prey and glue these particles together with an organic cement. Examples include: *Amphitrema*, *Centropyxis*, *Cyclopyxis*, *Difflugia*, *Heleopera*, *Nebela*, *Phryganella*, *Pseudodifflugia*. Taxa from the last two categories belong to the Arcellinida, except for the genera *Archerella* and *Amphitrema* whose position in the tree of life is not established.

These groups were initially used to investigate down-core changes in test types in three palaeoecological data-sets. Subsequently the groups were used to investigate how the ecological preferences of testate amoeba taxa vary by test type. Finally, the groups were used in a series of experiments to investigate how selective preservation may affect quantitative inference of mire hydrology. As a first experimental stage each of the four groups was separately down-weighted from 1 (no change) to 0 (100% loss of that type) by increments of 0.1 giving 40 scenarios. As a second experimental stage the groups were filtered simultaneously to give more realistic test decomposition scenarios. Idiosome tests were weighted from 0 to 0.4, idiosome + organic tests from 0.4 to 0.9, protein/calcium tests from 0.4 to 0.9 and xenosome tests from 0.1 to 0.6 giving 81 experimental scenarios (Table 2). Percentages were recalculated after each stage of filtering and the transfer function model applied to the filtered data

set. Bias from the measured DWT values were calculated.

Swindles and Roe (2007) present the results of an experiment applying strong acids to tests. Results demonstrated significant change in some taxa concentrations which the authors suggest can be treated as a preliminary index of test robustness. To test the impact of these changes on inferred DWT values, these weightings were applied to each of the datasets. Taxa not included in the results of Swindles and Roe (2007) were left unchanged.

Results

Patterns of shell type preservation in paleoecological records

The three paleoecological data sets show similarities in that the testate amoebae belonging to the idiosome type rarely or never dominate the community and their contribution to the community seems to decline very fast with depth (Fig. 1). For example in Jigsaw Lake the idiosome type represents 39% of the community in the uppermost sample but then only exceeds 5% in one other sample of the paleoecological record. In Tuchola peatland (Poland) the pattern is similar with 7.7% in the top sample and less than 1% in the paleo samples. In Praz-Rodet, the drop is slower with 35–50% in the top 5 cm, then dropping to below 10% below 15 cm depth and remaining below 3% thereafter. There is no clear pattern for the other three shell types. Data from other published and un-published studies confirm this general pattern (Table 2). Some early references such as Steinecke (1929), Harnisch (1951) are not included because the data are mostly presence-absence or semi-quantitative or idiosome type shells were not recorded. In the latter case the pattern is generally similar although some idiosome types were noted for a few samples from deep peat layers (e.g. >200 cm).

Ecological preferences of testate amoebae differing in test type

In the Jura surface data set (Fig. 2), testate amoebae with idiosome-type shells do not show a clear preference along the water table gradient. They

Table 2 Evidence for idiosome test disappearance in paleoecological records from peatlands

Study reference	Peat depth analysed [cm]	Depth of decline of idiosome shells [cm]	Age AD **	Remarks
Beyens (1985)	430	11	n.a.	*Euglypha ciliata* and *E. rotunda* present only in uppermost sample, *Trinema lineare* present throughout the core with the exception of two samples.
Beyens and Chardez (1987)	200	n.a.	ca. 3850 BP	
Blundell and Barber (2005)	250	70	950	
Booth and Jackson (2003)	190	9	1900	
Booth et al. 2004	500	20	1700	*Physochila griseola & Euglypha* were excluded from the training set
Charman et al. (1999)	400	15	1850	
Charman et al. (2001)	13	8	ca 1950	
Charman et al. (2004)	30	27	1950	
Harnisch (1948)	210	15	n.a.	*Euglypha* only present at 0 cm, absent in next sample (30 cm)
Hendon and Charman (2004)	40	40	1750	
Hendon et al. (2001)—CRM I	200	10	1910	Diagrams plotted against age, depth and age estimated here
Hendon et al. (2001)—CRM II	280	10	1910	Ditto
Hendon et al. (2001)—CRM III	140	n.a.	n.a.	Few shells of idiosome type but some found down to 2/3 of the core depth
Hendon et al. (2001)—CRM IV	230	8	1910	Diagrams plotted against age, depth and age estimated here
Hendon et al. (2001)—TW II	270	25	1880	Ditto
Hughes et al. (2006)	700	20	1900	
Lamentowicz et al. (In press)	100	10	1940	
Lamentowicz—Mukrza*	45	20	1950	
Lamentowicz—Słowińskie Błoto*	100	20	1850	
Lamentowicz—Żabieniec*	125	33	1590	
Langdon and Barber (2005)	300	50	1200	
Langdon and Barber (2005)	500	45	1200	
Langdon et al. (2003)	450	15	1700	
Mauquoy and Barber (2002)				
Mauquoy et al. (2004)	100	13	>1900	*Corythion dubium* only
McGlone and Wilmshurst (1999)	240	20	1900	
Mitchell et al. (2001)	380	50	1800	
Schnitchen et al. (2006)	380	10	1900	
Schoning et al. (2005); (a) Gullbergbymossen	17	15	1970	*Euglypha* only
Schoning et al. (2005); (b) Ätabergsmossen	44	15	1975	*Euglypha* only
Sillasoo et al. (2007)	450	20	1925	
Tolonen (1966a)	450	20	n.a.	
Tolonen (1966b)	400	3	n.a.	
Tolonen (1966b)	350	6	n.a.	
Tolonen (1985)	30–450	20	n.a.	Several cores

Table 2 continued

Study reference	Peat depth analysed [cm]	Depth of decline of idiosome shells [cm]	Age AD **	Remarks
Warner (1990)	80	10	1900	
Warner and Charman (1994)	640	65	>1600	The depth of 65 cm corresponds to the beginning of the historic period
Wilmshurst et al. (2003)	500	150	1000	
Average	270	26	1747	
Minimum	13	3	950	
Maximum	700	150	1975	

* Unpublished data

** Unless otherwise stated; n.a. No dates available

appear to have a bimodal response with peaks at 20 (the highest one) and 40 cm DWT and lower relative abundance at both extremes of the DWT gradient. Testate amoebae with idiosomes + organic type shells (i.e. *Assulina*) peak between 30 and 40 cm DWT, those with protein-type shells are most abundant at the wet end of the gradient (peat around 10 cm DWT), and those with xenosomes-type shells are slightly more abundant in the drier 2/3 of the gradient. In the Alaska data set (Fig. 3) the patterns are quite similar to the Jura except that the protein-type reaches a maximum between 20 and 40 cm rather than at the wettest end of the gradient and the idiosome + organic type has a clearer maximum between 40 and 60 cm. The Greece data set is clearly different from the Jura and Alaska data. Two shell-types strongly dominate the community: the idiosome type and the xenosome type (Fig. 4). The idiosome type shows a clear preference for drier conditions while the xeonosome type is dominant in the wettest end of the gradient.

Model simulations: (1) selective loss of one shell-type

In the Jura data set (Fig. 2), the effect of selective loss of each type on model prediction was mainly apparent for the most extreme cases (100% loss of the type) and for the part of the gradient where the type being down-weighted was most abundant. In a few cases the DWT was overestimated when idiosome-type shells were lost and this effect was clearest for the samples in which this type was most abundant, at a DWT of ca. 20 cm. The opposite effect is observed for the idiosome + organic type with an under-estimation of DWT for observed DWT between 30 and 40 cm. For the protein type DWT is clearly overestimated at the wet end of the gradient when this shell type is lost and the opposite is observed for the xenosome shell type. In the Alaska data set (Fig. 3), the effect of selective loss of each shell type mirrors that observed for the Jura data set. In the Greece data set (Fig. 4), the effect of selective loss of idiosome types is a clear underestimation of the DWT in the dry end of the gradient. In contrast the selective loss of the xenosome type leads to a systematic bias in the predicted DWT. When a bias exists it is always towards higher DWT values (i.e. drier conditions) and at the dry end of the gradient the model performs better (i.e. closer to the 1:1 line of observed vs. predicted DWT) when the xenosome type is lost.

In terms of overall model performance assessed by average bias from measured DWT (Fig. 5) down-weighting shell types generally leads to a reduction in transfer function performance. The principal exception to this is for the xenosome shell type in the Greek data where moderate filtering actually improves model performance, suggesting that taxa with this shell type may be poor hydrological indicators. There is a general relationship between the impact of downweighting and the relative abundance of a shell type. This is illustrated for the idiosome type in Fig. 6 for the three data sets. In all three data sets this relationship was clear at both extremes of the range of relative contribution of the idiosome type shells to the community. However, Fig. 6 shows that in the Jura data even when the idiosome type represents a small proportion of the community (e.g. 10%) their loss may already cause a marked bias in the predicted DWT. In

Fig. 1 Relative abundance profiles of four testate amoeba shell types in three peat profiles
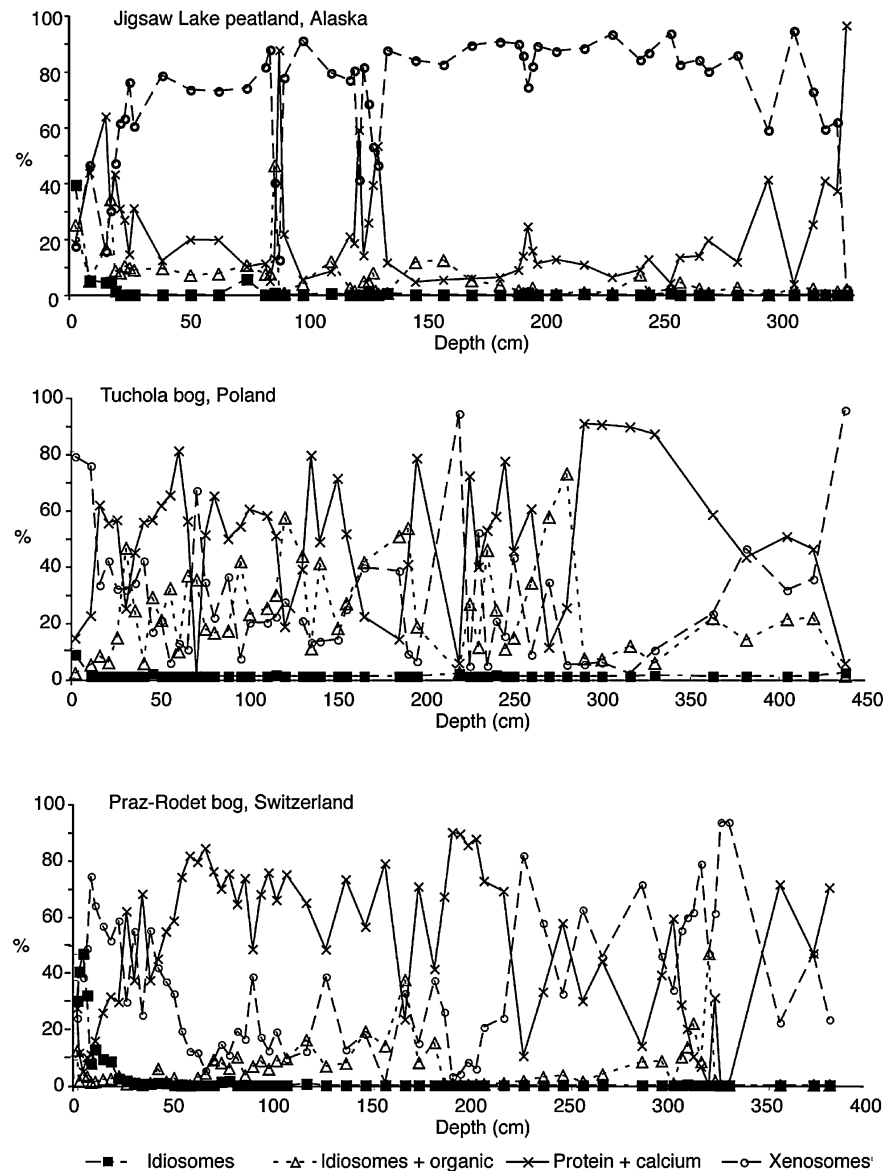
contrast the reverse is observed for the Greece data and the Alaska data represents an intermediate case. In the Jura data, the xenosomes shell type dominates the community and their removal leads to the greatest reduction in model performance (Fig. 5).

Model simulations: (2) scenarios of combined shell loss in the four types

Figure 7 summarises the performance of the transfer functions under 81 different scenarios of differential preservation of the four testate amoeba shell-types. In

the Alaska and Jura data sets all 81 cases perform similar to or worse than the full data set.

In the Jura data set the highest bias (measured as the average bias from measured DWT) is observed for the combination of highest loss of idiosome and xenosome shell-types (56% increase in average bias). Overall, however, the xenosome type affects the performance of the model most.

In the Alaska data set the pattern is similar to the Jura case, but clearer. The loss of the xenosome and idiosome shell-types strongly affects the performance of the model while the protein and idiosome + organic shell-types have little effect. The worst

Fig. 2 Biplots of testate amoeba relative abundance in relation to depth to the water table (DWT) for each of four categories of shell types and effect of selective removal of that shell type on the DWT prediction. Data from *Sphagnum*-dominated peatlands of the Jura Mountains Switzerland and France (Mitchell et al. 1999; Mitchell et al. 2001)
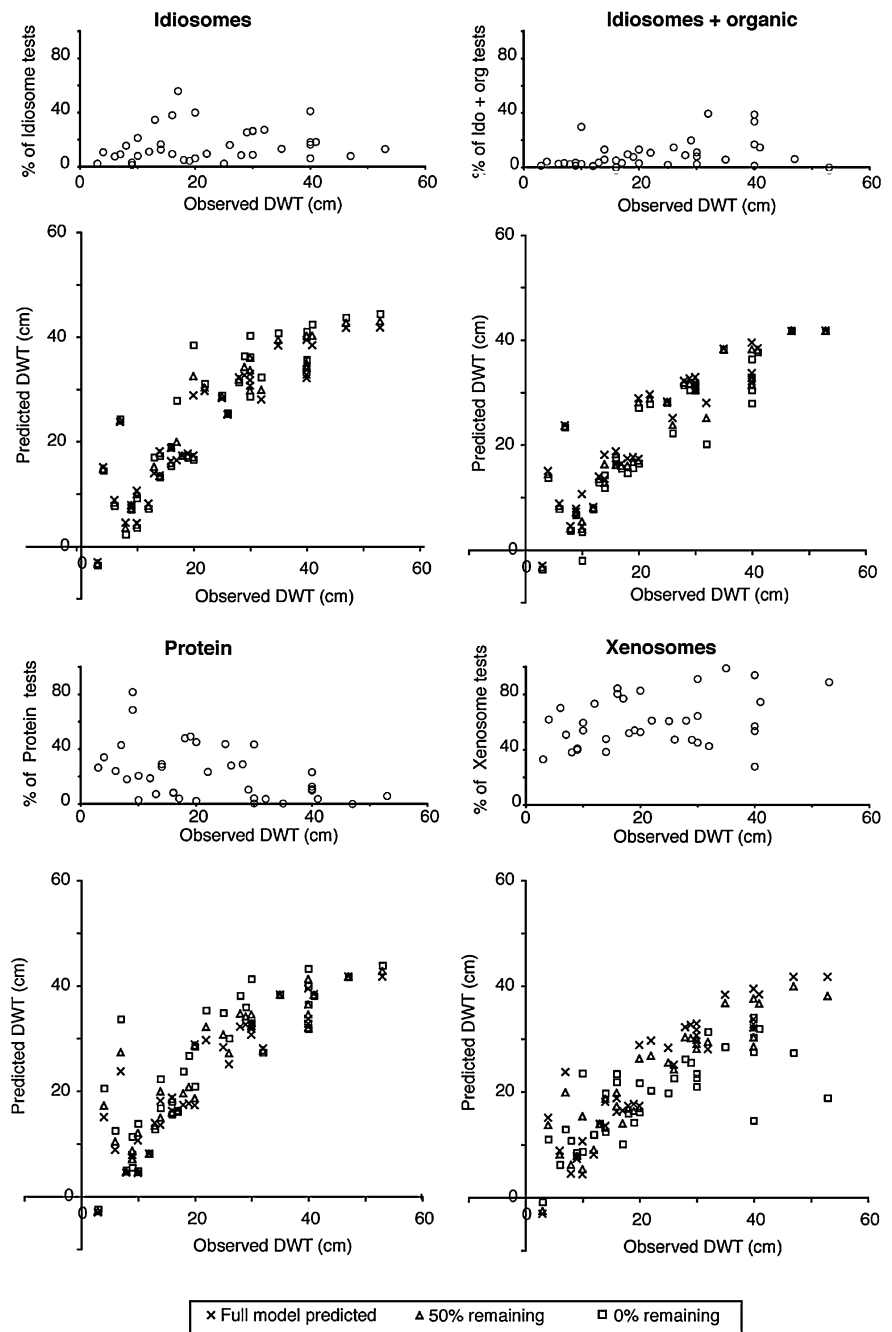

combination of shell loss (highest loss of idiosomes, xenosomes and protein or calcium types) leads to a 63% increase in average bias.

In the Greece data, the loss of idiosome shell types clearly has the strongest effect on model performance. Loss of the xenosome type improves the model performance, but only if a significant proportion of the idiosome type is lost; when 40% of the idiosome type remains, any combination of loss of other shell types does not appear to affect the average model performance significantly. The worst combination (high loss of the idiosome type and low loss of the xenosome type) leads to a 96% increase in average bias while the most favourable combination (high loss of the xenosome type and intermediate loss of the idiosome type) reduces this bias by 15%.

Fig. 3 Biplots of testate amoeba relative abundance in relation to depth to the water table (DWT) for each of four categories of shell types and effect of selective removal of that shell type on the DWT prediction. Data from *Sphagnum*-dominated peatlands of South-Central Alaska (Payne et al. 2006)
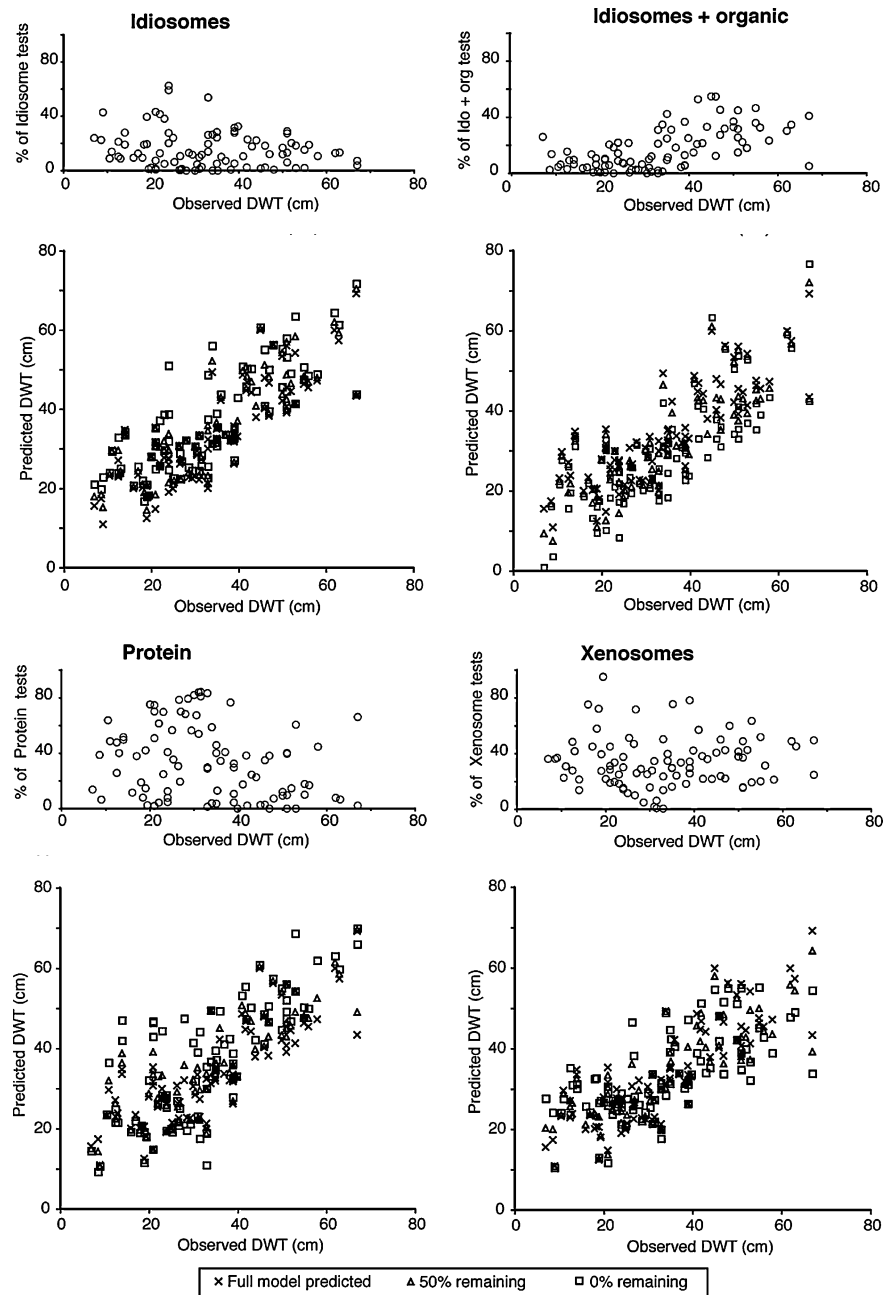
Model simulations: (3) Simulation according to the observations of Swindles and Roe

Using the shell degradation values observed by Swindles and Roe (2007), no significant effect was observed in the predicted DWT (Fig. 8). The changes in relative percentage contribution to the community of individual taxa (±5% at most) were, however, much lower than in our simulations.

Discussion

Patterns of shell type preservation in paleoecological records and implications for model building

The paleo-record clearly suggests that differential preservation exists for the testate amoebae that build their shells from secreted biosilica plates (idiosomes).

Fig. 4 Biplots of testate amoeba relative abundance in relation to depth to the water table (DWT) for each of four categories of shell types and effect of selective removal of that shell type on the DWT prediction. Data from minerotrophic peatlands of Northern Greece (Payne and Mitchell 2007)
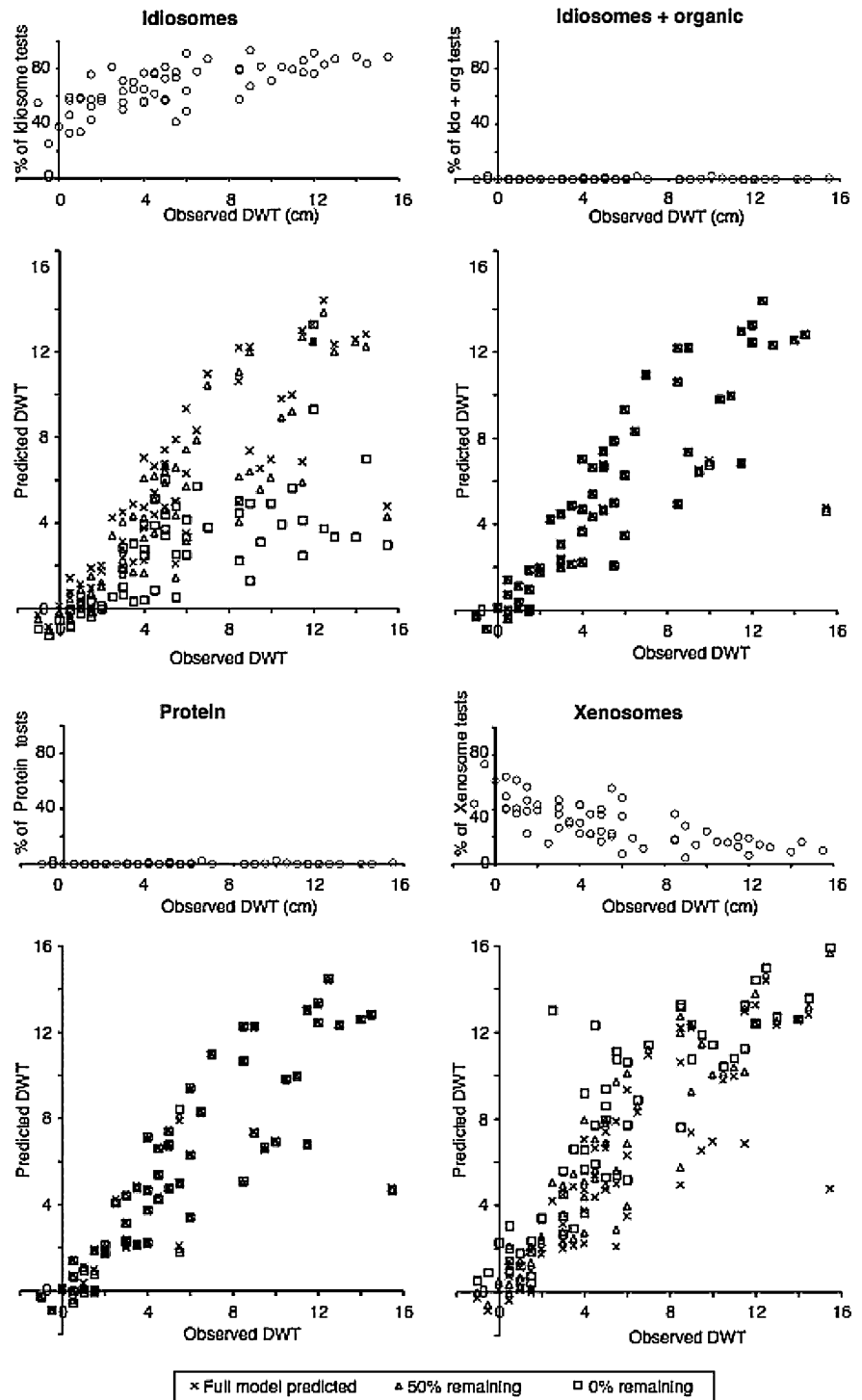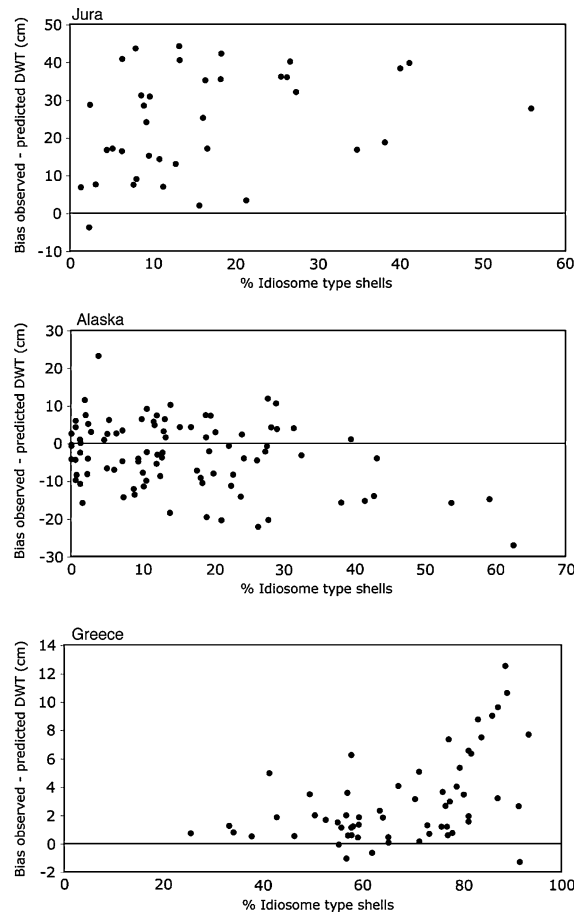

This category corresponds to most of the Euglyphid testate amoebae (genera *Euglypha, Trinema, Corythion, Placocista, Tracheleuglypha*, etc.) with the notable exception of the genus *Assulina*. This

observation, which is in agreement with other studies in peatlands, lakes and saltmarshes (Roe et al. 2002; Ruzicka 1982; Tolonen 1986), leads us to question the inclusion of these taxa in the transfer functions
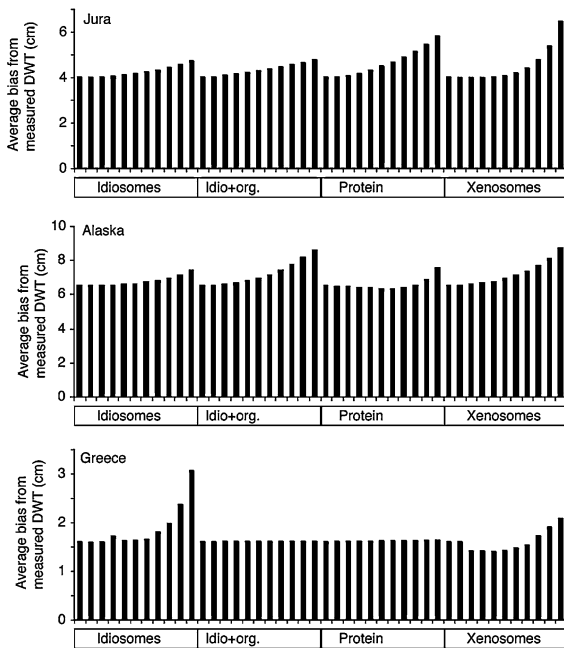
Fig. 5 Average bias from measured depth to water table (DWT) for transfer functions with each of four categories of shell types selectively removed for the three training sets from the Jura Mountains, Alaska and Greece. For each category the first bar corresponds to the full model and subsequent bars represent models with increasing removals of that type (in 10% steps)


Fig. 6 Biplots of the relative percentage of idiosome shell type in the community vs. bias in predicted depth to water table resulting from the total loss of this shell type for three data sets from the Jura Mountains, Alaska and Greece

and indeed in some studies these taxa were excluded (Booth and Jackson 2003; Booth et al. 2004). If they are lost so rapidly, their inclusion in modern training sets and transfer function models will add little to palaeoecological inference. Worse, as these taxa sometimes represent a large proportion of the community (e.g. Greece), including them in the training set will mean that only a small proportion of the total count of testate amoebae which is used to build the transfer function is recovered from peat and the data really useful for building the transfer function may not be sufficient. In our data sets the proportion of this category frequently exceeds 30% of the community in the *Sphagnum* peatlands and is on average 67% of the total in the Greece data set. Model simulations of 100% loss of the idiosome shell-type in the Greece data (Fig. 4) set suggest that paleo-hydrological inference from testate amoebae in these peatlands may underestimate DWT. However, for *Sphagnum* peatlands the preferential loss of idiosome shell-types will not have a significant impact on the inferred DWT.

Ecological preferences of testate amoebae differing in test type and model simulations

The general patterns of ecological optima for the four different shell types are similar for the Jura and Alaska data sets but different for the Greece data set. This can be explained by difference in the types of peatlands studied: *Sphagnum*-dominated peatlands in the first two cases and minerotrophic peatlands in Greece. Minerotrophic peatlands have been much less intensively studied for testate amoeba ecology than *Sphagnum*-dominated mires (Opravilova and Hajek 2006). The improvement of model performance for the Greece data set with preferential loss of the xenosome shell type suggests that some taxa may not have well-defined ecological optima along the

Fig. 7 Summarised performance of the transfer function models with the full data set and 81 simulated cases of differential loss of the four categories of shell type. Shades of grey indicate the percentage of remaining shells for each shell-type. The horizontal line corresponds to the performance of the full data set (far left)
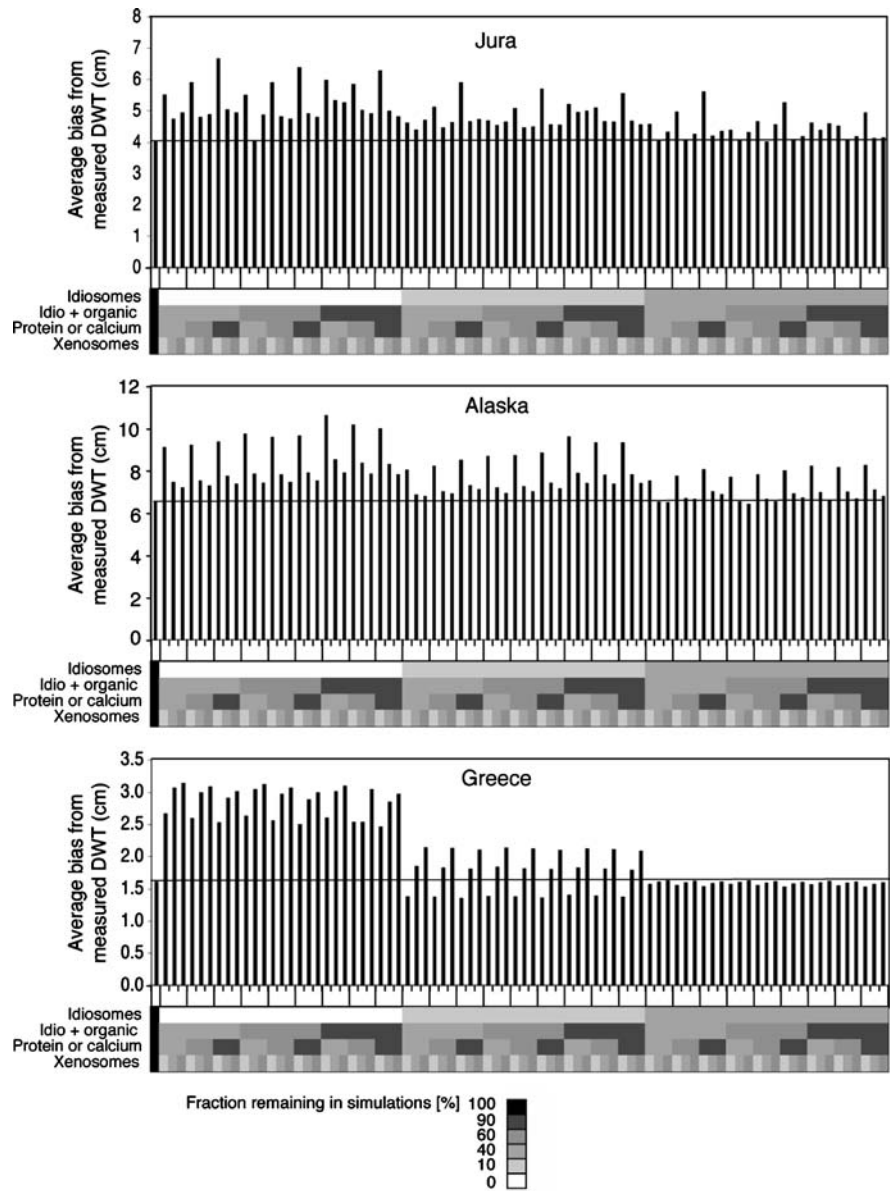
Fig. 8 Biplots of observed vs. predicted depth to water table (DWT) based on testate amoebae in three data sets and effect of differential dissolution of shells (referred to as "limited model") as observed by Swindles and Roe (2007)
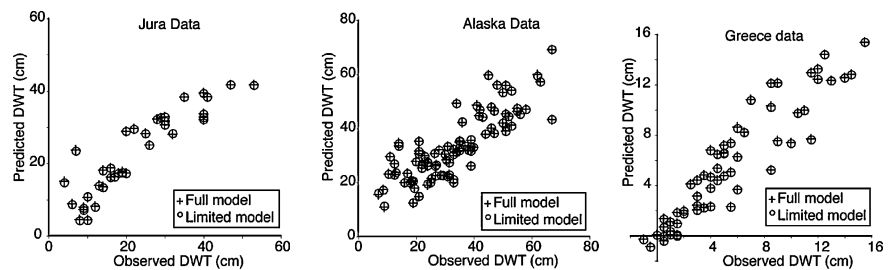
DWT gradient, or that some of the identified morphotypes represent more than one species each with a distinct optimum. Some taxa were especially abundant in a few samples. Such patterns would make modelling their response difficult and this may explain why the model performs better when

xenosome-type shells are preferentially lost. These results call for more studies on the ecology of minerotrophic peatland testate amoebae and also for improvements in the taxonomy (Mitchell et al. 2008).

Implications for the use of testate amoebae in paleoecological studies and suggestions for future studies

According to Swindles and Roe (2007) the differential preservation of testate amoeba represents a particular problem for peat-based palaeoclimate studies. Our results suggest that, at least for *Sphagnum*-dominated peatlands, overall testate amoeba transfer functions are quite robust to even relatively large changes in community structure resulting from differential preservation of different shell types. The scale of change required to produce a significant bias from the full data is considerably greater than that shown experimentally by Swindles and Roe (2007).

For more minerotrophic peatlands such as the Greece data set the situation may not be as favourable as the most sensitive idiosome tests constitute a larger proportion of the community and their loss may lead to a considerable bias in inferred water table. However, existing studies from fens are few in number and it is not certain that idiosome tests always constitute such a high proportion of total tests in such sites, or that differential decomposition is as serious a concern in a less acidic peat environment. Furthermore, by comparison to the Jura and Alaska data, a similar proportional loss of the idiosome shell type caused a comparatively smaller reduction in model performance. It is therefore too early to consider testate amoebae as a lost cause as a paleoecological tool in minerotrophic sedge-dominated peatlands.

A limitation of our study is that we might have lumped in the same category some testate amoeba taxa that differ significantly in their resistance to decay. For example, Swindles and Roe (2007) showed that within given genera (e.g. *Nebela*, *Assulina*) resistance to extreme low pH condition could be different. As such, our simulation experiments might give an over-simplified view of the impact of selective preservation on hydrological inferences. The existing data on testate amoeba shell decomposition is confusing. For example Lousier and

Parkinson (1981) observed high decomposition rates while Coûteaux (1992) did not. An important difference between these two studies is that Lousier and Parkinson (1981) sterilized their samples by heating them to 80°C while Coûteaux used gamma rays and chemical sterilisation. The heat treatment might have weakened the organic cement that keeps the shells in shape and this would have caused a higher than natural decomposition rate. The experimental conditions used by Swindles and Roe (2007) (pH < 1) are also extreme and their results may therefore not correspond to the true pattern of shell decomposition in nature. Additional decomposition experiments, under natural conditions, and including more taxa (especially those with narrow tolerances to relevant environmental variables, i.e., good indicators), might be useful to complete our simulations and provide improved estimates of preservation bias in testate amoeba shells.

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