

TESTATE AMOEBAE AS PALAEOHYDROLOGICAL PROXIES IN SÜRMENE AĞAÇBAŞI YAYLASI PEATLAND (NORTHEAST TURKEY)

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Abstract: Testate amoebae are unicellular micro-organisms whose hydrological sensitivity and good preservation in peats make them valuable proxies for past peatland surface wetness, and therefore climate. Previous testate amoebae transfer functions have been spatially restricted with no studies from Asia. To derive a transfer function, a sequence of samples was extracted from an ombrotrophic peatland in Turkey and amoebae counted. The internal structure of the data was explored using principal components analysis and relationships with the environmental data tested by redundancy analyses. Transfer function models were developed using a variety of techniques. As in other regions, depth to water table is the most important control on amoebae community composition. Transfer function performance was initially poor, primarily due to the inclusion of samples from areas of the site that had been heavily affected by peat cutting and had distinctly different amoebae communities. Model performance is improved by selective sample exclusion, reducing jack-knifed root mean square error of prediction to 7.1 cm. The model was tested using an initial palaeoecological data-set. Overlap with the training set was limited, although a hydrological reconstruction using this model produces similar results to a transfer function derived from northern European peatlands. This study provides the first testate amoebae transfer function from Asia and demonstrates that hydrological preferences of many of the key taxa are consistent across a large area of the Northern Hemisphere. The transfer function will allow detailed palaeoclimate reconstruction from this peatland, adding to our knowledge of Holocene climatic change in southwest Asia.

Key Words: Asia Minor, Paleoclimate, Protists, Transfer function

INTRODUCTION

Peatlands have been shown to archive a continuous, reliable and high-resolution climatic record that has been validated by comparisons among sites, with other proxy records and with instrumental records for the recent past (Baker et al. 1999, Blackford

2000, Charman and Hendon 2000, Hendon et al. 2001, Charman et al. 2004, 2006, Schoning et al. 2005). Studies attempt to reconstruct the palaeohydrology of peatlands, which in ombrotrophic systems is largely determined by the balance between precipitation and evapotranspiration. One of the most important advantages of peatlands as sources of Holocene palaeoclimatic data is their distribution, covering vast areas of the mid to high-latitudes and occurring in isolated locations at altitude around the world. This distribution allows the potential to develop globally integrated networks of Holocene climate records. However, this potential has not been well exploited to date. Studies have concentrated on temperate peatlands in northern and central Europe, North America, and in a small number of locations in New Zealand and South America (Wilmshurst et al. 2003, Mauquoy et al. 2004). In particular, peatland archives have been relatively underexploited in regions that are climatically marginal for ombrotrophic peat growth, where records are likely to be highly sensitive to climatic fluctuations.

In Turkey and the eastern Mediterranean region as a whole, there is meteorological evidence for climatic change since the early twentieth century (Türkeş and Sümer 2004, Türkeş et al. 2007). However, longer-term reconstructions of climate change in the Holocene are of limited number and are spatially and temporally restricted (Bar-Matthews et al. 1998, Goodfriend 1999, Schilman et al. 2001, Stevens et al. 2001, Roberts et al. 2001, 2004, Kashima 2002, Wick et al. 2003, Jones et al. 2005, 2006, Eastwood et al. 2007). Due to generally unfavourable climatic conditions for peat formation and human destruction of mires, Turkish peatlands are rare, covering perhaps 30 Km² (Çaycı et al. 1988, Öz 1996, Byfield and Özhatay 1997). The majority of Turkish peatlands are minerotrophic fens; such ecosystems are considered sub-optimal for palaeoclimate research due to the less direct relationship between climate and peatland hydrology. One large ombrotrophic mire (Sürmene Ağaçbaşı Yaylası peatland) is present with a maximum recorded peat depth of 3.7 m and a good potential to develop a regional climate record.

One of the most well established techniques for palaeoclimatic reconstruction from peatlands is testate amoebae analysis. Testate amoebae are unicellular micro-organisms (protists) that are sensitive indicators of hydrological conditions and are found preserved in peat. The methodology has been particularly developed through the use of transfer function models, which use testate amoebae species data to quantitatively infer water table change over time. These quantitative hydrological reconstructions contrast with the qualitative or at best semi-quantitative reconstructions of peatland surface wetness provided by other techniques such as macrofossil or humification analysis.

Testate amoebae are found in peatlands around the world and although amoebae species may not be entirely cosmopolitan, there is a good deal of similarity in species composition between widely separated sites (Wilkinson 2001, Charman 2001). The hydrological preferences of many taxa are well known and appear consistent across broad geographic regions (Booth and Zygmunt 2005). However, there are notable differences in community composition between studies, and there are several important taxa whose hydrological preferences are still inadequately understood. There have been no previous quantitative studies of testate amoebae in the peatlands of Turkey or Southwest Asia. As the region lies on a different continent from previous studies it is possible that the site may contain amoebae assemblages, and possibly amoebae taxa, not commonly encountered in previous transfer function studies. A study of the modern ecology of

testate amoebae in this site and the development of a transfer function model is therefore an essential pre-requisite to palaeoecological study. The aims of this study are to investigate the testate amoebae community of Sürmene Ağaçaşu Yaylasu peatland, test the hydrological control of amoebae community structure, develop a transfer function model to allow palaeoenvironmental reconstruction, test this model using an initial palaeoecological data-set, and compare the results to those of previous studies.

SITE AND METHODS

Sürmene Ağaçaşu Yaylasu peatland is a large (c. 20 ha) ombrotrophic mire located in northeast Turkey (40°6'N, 40°34'E), 40 km southeast from Trabzon, the regional capital and 10 km south of the Black Sea (Figure 1). The site lies at 2100 m asl. in the Soğanlı Dağ Mountains. Vegetation of the peatland includes *Sphagnum fuscum*, *S. palustre.*, *Carex* spp., and *Nardus stricta* (Byfield and Özhatay 1997). Other plants noted in the field included *Vaccinium uliginosum*, *Potentilla* spp., and bryophytes including *Leucobryum glaucum*, *Rhytidiadelphus squarrosus*, and *Polytrichum longisteum*. The site has been affected by manual peat cutting over at least the last 30 years; cut peat holes are present across much of the site (Payne et al. 2007). Samples were extracted in August 2006 and were taken from three closely adjacent but hydrologically separate peat areas divided by a road and meadowland (Figure 1). These areas are referred to as the eastern, western, and southern sectors; it is unclear whether all three peat areas were once connected. The majority of the samples (38) were taken from the western sector of the site, which has been affected by peat cutting but is generally more intact than the other areas. Smaller numbers of samples were taken from the eastern (8) and southern (7) sectors.

At each sampling point a block of peat approximately 5x5x5 cm was removed from the surface layer. Water table depth was measured by making a small hole adjacent to the sampling point and depth to water table (DWT) measured after leaving the sampling site overnight for the water table to equilibrate. Samples were returned to the laboratory and moisture content and loss on ignition measured by drying the sample at 110°C and then incinerating at 550°C. A 2 cm³ sub-sample was taken from the uppermost 3 cm of the sampling block, disaggregated in 50 ml distilled water and pH measured after one hour. Amoebae were extracted by boiling the sample and then sieving at 15 and 300 µm with the 15>300 µm fraction retained (Hendon and Charman 1997). Slides were prepared by mixing this material with glycerol and examined at 400X magnification. A minimum of 150 amoebae were identified using a range of taxonomic literature (Corbet 1973, Ogden and Hedley 1980, Ogden 1983, Ellison and Ogden 1987, Charman et al. 2000, Clarke 2003). Taxonomy broadly follows Charman et al. (2000) with the exception of a few types that were subdivided: *Cyclopyxis arcelloides* type (into *Cyclopyxis arcelloides*, *Cyclopyxis eurystoma*, and *Phryganella acropodia*), *Corythion-Trinema* type (into *Corythion dubium*, *Trinema complanatum*, and *Trinema enchelys*), *Nebela tubulosa* type (into *Nebela tubulosa* and *Nebela penardiana*), and *Nebela tinctoria* type (which was not differentiated from similar taxa without pores). The taxa referred to as *Arcella catinus* type and *Centropyxis cassis* type by Charman et al. (2000) are referred to here as *Arcella arenaria* type and *Centropyxis aerophila* type reflecting the dominant species.

Ordination was used to investigate the community structure and relationships with the environmental data. As an initial detrended correspondence analysis (DCA) showed

the compositional gradient to be short (< 3 SD), linear methods were more appropriate than their unimodal equivalents. The structure of the data was initially investigated using principal components analysis (PCA) with taxa occurring in four or fewer samples excluded and data log-transformed. The environmental controls on amoebae communities were investigated using redundancy analysis (RDA) with significance testing by Monte Carlo permutation tests (999 permutations). All ordination analyses were carried out in Canoco version 4.53 (ter Braak and Šmilauer 1997-2004).

Transfer function models were developed using weighted average (WA), weighted average partial least squares (WA-PLS), maximum likelihood (ML), partial least squares (PLS), and modern analogue techniques (MAT; Birks 1995) in C² version 1.3 (Juggins 2003). Root mean square error of prediction (RMSEP) was used as the primary indicator of model performance, this was estimated using both jack-knife and boot-strap techniques (1000 cycles). As model performance was initially poor (see results section), data selection was used to improve performance. Taxa occurring in few samples were initially removed; subsequently samples for which the model performed poorly were removed. The samples that were removed were selected using an iterative methodology with residuals re-calculated after every successive phase of data filtering (Payne et al. 2006).

As a test of the efficacy of the transfer function for palaeoenvironmental inference, two of the best-performing models were applied to a sequence of palaeoecological samples. A core was extracted from an uncut area of the western sector of the site and samples extracted every 8 cm. Samples were prepared following Hendon and Charman (1997) and amoebae identified using Charman et al. (2000); a count of 100 tests was targeted. The transfer function was adjusted to account for slight differences in taxonomic approach. The *Cyclopyxis arcelloides*, *Cyclopyxis eurystoma*, and *Phryganella acropodia* types were grouped in the modern data and the *Nebela tincta* and *Nebela parvula* types in the palaeoecological data. As a separate test, a transfer function derived from peatlands in northern Europe was also applied (Charman et al. 2007).

RESULTS

A total of 8,295 amoebae were counted, the most abundant taxa were *Assulina muscorum* (30% of total count) and *Hyalosphenia papilio* (25%; Table 3). Distinct differences were noted between the southern and eastern and the western sectors of the peatland; in particular *H. papilio* was highly abundant in the western sector (35% of total) but was totally absent in the other two areas. The PCA plot (Figure 2) illustrates these differences, with southern and eastern sector samples generally having low scores on axis one and high scores on axis two. RDA shows all the environmental data (DWT, percent moisture, pH, LOI and site sector nominal variables) explain 39% of variance ($P < 0.001$). Depth to Water Table alone explained 16% of variance ($P < 0.001$). With LOI and pH partialled out DWT explained 9.4% of variance ($P < 0.001$).

Using the full data, transfer function model performance was poor with an optimum $\text{RMSEP}_{\text{jack}}$ of 15.2 cm (Table 1). Previous studies have produced models with $\text{RMSEP}_{\text{jack}}$ values below 10 cm. A plot of model predictions against measured values (Figure 3) shows that model performance was particularly poor for some samples at the ends of the water table gradient, and especially one sample (SAY 59) with a water table depth much greater than any of the other samples.

Data selection was used to improve performance of the model. Removing rare taxa resulted in an increase in RMSEP but removing samples with high residuals produced a consistent improvement in model performance. Samples with residuals greater than 14 cm were removed from the data set, reducing $RMSEP_{jack}$ to 7.1 cm. This cut off point amounts to 9% of the total gradient, less than the 20% level applied in several previous studies (Charman 1997, Payne et al. 2006, Charman et al. 2007, Payne and Mitchell 2007); this is largely because the water table gradient was extended by the inclusion of the very dry sample SAY 59 (Table 2). Using data selection usually results in removal of samples from the extremes, reducing the length of the hydrological gradient and thereby reducing the applicability of the model. Here, excluding samples with residuals greater than 14 cm reduces the hydrological gradient by almost 50% from 154 to 79 cm, but this is solely due to removing two samples from the very driest and very wettest locations. The total number of samples included in the model was reduced to 42. Model performance was significantly poorer for the more disturbed eastern sectors of the site. The mean residual for the eastern samples was 13.9 cm compared to 6.9 cm for the western samples. The eastern sector samples are preferentially removed when filtering for high residuals (Table 2). Removing all samples from the eastern sectors of the site reduced $RMSEP_{jack}$ by almost 50%.

Using $RMSEP_{jack}$ to assess model performance the best performing model was a four component PLS model, but when using $RMSEP_{boot}$ to assess performance the best performing model was a ML model. After data filtering a ML model performed best by both measures. Maximum Likelihood models have rarely been tested in testate amoebae transfer function studies. They are distinct from weighted-average based models in that they attempt to directly model the species response curve, rather than approximating this using a weighted average (Birks 1995). The good performance of this model here and in another recent study (Payne and Mitchell 2007) suggest the approach should be more widely tested.

Both the ML and WA-PLS models were applied to a palaeoecological data set and results compared to reconstructions using a northern European transfer function (Charman et al. 2007; Figure 5). Overlap between the modern and palaeoecological data was sub-optimal. Only 14 of the 27 taxa in the palaeoecological data were included in the modern training set, although the exceptions were mostly more minor taxa. Between 70 and 100% of tests were included in the transfer function for each sample (mean 94%). The most abundant taxa not included are *Heleopera sphagni*, *Heleopera sylvatica*, and *Hyalosphenia elegans*. This difference may be because the modern samples did not include the habitats of these taxa, or these taxa have been lost from the site in the past.

Generally similar trends were apparent with both ML and WA-PLS models (Figure 6). From the top of the sequence to 72 cm depth the ML model showed a gradual increase in values while WA-PLS showed short-term variability with no overall trend. From 72 to 120 cm there was a period of higher values. Following this, there was a short period of lower values followed by a resumed increase to a peak at 144 cm and a trough at 152 cm. In the lower portions of the core the ML model showed few trends while the WA-PLS model showed a general increase in values. For the majority of samples, sample specific error estimates were lower with ML than with WA-PLS, supporting the model choice based on modern data. There was broad similarity with the results of the northern European transfer function. The most notable differences were that the northern European

transfer function showed fluctuating values with little overall trend in the upper portions of the core (not shown by the ML model) and a declining trend of values at the base of the core (not shown by either site-specific model). Absolute values were higher with the site-specific model. Results of the WA-PLS model appeared more similar to the northern European transfer function than those of the ML model. This does not necessarily imply superiority; this may simply be due to the greater similarity in model structure.

DISCUSSION

The community compositions in our samples support previous studies in illustrating the cosmopolitan distribution of testate amoebae. The majority of testate amoebae taxa we encountered have frequently occurred in previous transfer function studies from Europe and North America. A few somewhat more unusual taxa are present such as *Nebela tubulata*, *Sphenoderia fissirostris*, *Lesquereusia modesta*, *Lesquereusia epistomium*, and *Tracheleuglypha dentata*. The presence of some of these taxa (particularly the *Lesquereusia* species) may be explained by the changes to the site through peat cutting. *Lesquereusia* species were predominantly found in wet, high-pH samples from the edge of cut holes in the peat surface. A notable absence was *Nebela militaris*, a taxon found in all previous transfer function studies, often in high abundance. Ordination results agree with those of previous studies using similar methodologies in showing hydrology to be the most important control on amoebae community composition. Redundancy analyses showed 9.4% of variance is independently explained by hydrology, comparable to the results of previous studies.

The hydrological optima of testate amoebae taxa (Table 3) showed a good deal of similarity to previous studies. At the wettest end of the gradient were taxa well known for their hydrophilic tendencies such as *Centropyxis aculeata* and *Hyalosphenia papilio*, while at the drier end were taxa believed to be xerophilic such as *Trigonopyxis arcuata* and *Trinema lineare*. Of the more unusual taxa, *Diffflugia pulex* type – an important taxon in many palaeoecological studies – was present in two samples from the drier end of the hydrological gradient (optima 71.7 cm). Although this taxon was very rare its presence is interesting as it contrasts with the lower DWT optima found by Payne and Mitchell (2007) and Charman et al. (2007). *Euglypha cristata* had a relatively high DWT optima (48.1 cm) in contrast to the results from the small number of samples where it was found by Charman et al. (2007) but broadly similar to Payne and Mitchell (2007). *Nebela tubulata* is typical of moderately dry conditions while *Lesquereusia modesta* and *Lesquereusia epistomium* are both found in very wet locations.

Direct comparison of taxa optima with previous work was not possible as studies have adopted different measurement methodologies. All but one study have used one-time water table measurements so values largely reflect weather conditions just prior to the sampling time. Given this situation two approaches are possible to compare optima among studies. Firstly, it is possible to compare the relative positions of taxa optima on the overall hydrological gradient (Booth 2001, Lamentowicz and Mitchell 2005, Payne et al. 2006). Figure 4. shows a comparison of relative DWT optima with selected previous studies. Results for this study generally lie within the range of other studies with the exception of *Centropyxis aculeata*, which has a particularly low DWT optima, and *Euglypha rotunda*, which has a particularly high optima. This approach allows general

comparisons of taxa hydrological preferences but is not ideal as there are real differences in the hydrological range covered by the studies.

An alternative approach is to examine the rank order of taxa on the hydrological gradient (Charman et al. 2000). Table 4 compares rankings between this study and 11 others from previous research in Northern Hemisphere peatlands. Taxa were selected that were present in all studies, were morphologically distinct with minimal opportunity for taxonomic confusion, and for preference, were single species and not groups which may complicate interpretation. Given the broad similarity in peatland types and the general ubiquity of protists, surprisingly few taxa are present in all studies with several common taxa such as *Euglypha rotunda*, *Euglypha strigosa*, and *Nebela militaris* absent from one or more study. The rankings in Table 4 show a good deal of similarity between studies with *Centropyxis aculeata* generally at the wetter end of the spectrum and *Trigonopyxis arcuata* always indicating dry conditions. However there are exceptions. *Hyalosphenia papilio*, which most studies show to be an indicator of wet conditions, is the driest indicator in the Newfoundland study (Charman and Warner 1997). There is little consensus over the indicator value of *Heleopera petricola*, ranging from the second wettest indicator in Russia and Finland to the second driest in the British Isles (Bobrov et al. 1999, Tolonen et al. 1994, Woodland et al. 1998). The similarity between the rankings in this study and previous work can be tested quantitatively using Page's L test (Page 1963). Results demonstrate that the null hypothesis can be rejected; there is a significant relationship between the taxa ranks ($L = 2115$, $P < 0.001$). Although the methodology is comparatively crude this result demonstrates the general similarity in hydrological preferences of the major testate amoebae taxa across a large region of the Northern Hemisphere spanning Alaska to western Russia and Asia Minor. Generally, we have a good knowledge of the hydrological preferences of taxa that are abundant and found at the extremes of the hydrological gradient. However, our knowledge of taxa that are rare or found in intermediate conditions is much poorer.

With the full data set the transfer function model performed comparatively poorly during both cross-validation and palaeoenvironmental reconstruction. This is largely the result of including samples from areas that have been subject to peat cutting. The PCA shows distinct differences between samples from the cut and uncut areas and samples from cut areas of the peatland are preferentially removed in data filtering. Samples were included from regenerating peat in abandoned cuttings and from uncut areas of peat that have been dried out as a result of cutting nearby. Testate amoebae communities from these habitats may not be as sensitive to hydrology as in pristine areas. In uncut areas the amoebae community may not have fully adjusted to the hydrological changes caused by cutting, particularly as samples will integrate amoebae from a period of several years. The plant communities and physical environment of regenerating peat are different from the uncut areas so the controls on amoebae communities may also be different from pristine areas.

Despite imperfect modern analogues, results of palaeoenvironmental reconstruction compare reasonably well with the northern-European model, adding further support to the broad similarity of amoebae hydrological preferences across the northern Hemisphere. Previous studies have used multiple sites to increase the probability of finding good modern analogues for palaeo-amoebae communities. As this is the only ombrotrophic *Sphagnum* peatland currently known in Turkey, there is no option to

include additional sites here. In such instances, comparison with transfer functions from other regions provides a useful means to enhance confidence in the palaeoenvironmental reconstructions produced. These initial palaeoecological results cannot be used for palaeoclimatic inference in the absence of dating evidence. Future work will examine the amoebae palaeoecological record at higher resolution, employ other proxy-records, and radiocarbon date the profile.

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Table 1. Transfer function model performance for full and filtered data with model name abbreviations. Performance assessed by root mean square error of prediction (RMSEP), R^2 , and maximum bias (Max. Bias) estimated by boot-strap and jack-knife techniques. For the full data, additional components in WA-PLS did not outperform WA. Additional components in PLS and WA-PLS were only included if they reduced RMSEP by $> 5\%$. Numbers in bold indicate best performing model.

Model structures						
WA-Tol	Weighted average (tolerance downweighting, inverse deshrinking)					
WA-PLS	Weighted average partial least squares (optimum number of components)					
ML	Maximum likelihood					
PLS	Partial least squares (optimum number of components)					
WMAT	Modern analogue technique (weighted average of 10 closest analogues)					
Full data						
	Jack-knife (leave-one-out) cross validation			Boot-strap cross validation		
	RMSEP	R^2	Max Bias	RMSEP	R^2	Max Bias
WA-Tol	16.6	0.49	96.7	17.0	0.53	95.3
ML	16.5	0.50	78.4	16.5	0.58	79.6
PLS	15.2	0.58	83.9	17.1	0.59	81.4
WMAT	17.6	0.45	89.2	18.6	0.45	89.3
Filtered data						
WA-Tol	8.7	0.71	20.2	9.1	0.73	16.0
WA-PLS	7.6	0.78	25.2	8.3	0.78	25.0
ML	7.1	0.81	21.7	8.1	0.82	21.3
PLS	7.6	0.78	27.9	8.9	0.77	28.5
WMAT	10.4	0.6	24.7	10.8	0.6	24.5

Table 2. Samples removed from data set when filtering for high residuals and possible reasons for poor model performance.

Sample	Possible reason for poor model performance
SAY 6	Very high abundance of <i>Hyalosphenia papilio</i> (90%).
SAY 23	Very high abundance of <i>Hyalosphenia papilio</i> (89%).
SAY 25	Disturbed site on edge of cut hole. Unusual amoebae community with <i>Lesquereusia</i> species.
SAY 30	Unknown.
SAY 31	Unknown.
SAY 43	Regenerating peat.
SAY 48	Regenerating peat. Unusual abundance of <i>Euglypha ciliata</i> (25%).
SAY 50	On edge of peat cutting. Unusual abundance of <i>Trinema lineare</i> (45%).
SAY 51	On site margin (more nutrient-rich?). Unusual abundance of <i>Tracheleuglypha dentata</i> (34%).
SAY 59	On edge of peat cutting. Extremely deep water table.
SAY 60	Very wet sample from cut pool. Unusual abundance of <i>Centropyxis aculeata</i> (31%) and <i>C. arcelloides</i> type (62%).

Table 3. Taxa encountered in this study, abbreviations used, number of occurrences (N), maximum abundance, hydrological optima, and hydrological tolerances calculated by weighted averaging.

Taxon	N	Maximum Abundance (%)	Optima (cm)	Tolerance (cm)
<i>Arcella arenaria</i> Greef 1866 type	7	2	55.6	21.8
<i>Amphitrema flavum</i> (Archer 1877)	3	1	25.6	10.3
<i>Assulina muscorum</i> Greef 1888	52	74	47.7	21.8
<i>Assulina seminulum</i> Ehrenberg 1848	41	75	43.9	10.2
<i>Centropyxis aculeata</i> (Ehrenberg 1830)	3	31	0.6	2.5
<i>Centropyxis aerophila</i> Deflandre 1929 type	26	15	64.0	36.1
<i>Centropyxis ecornis</i> (Ehrenberg 1841)	1	1	55.0	-
<i>Corythion dubium</i> Taranek 1881	39	32	47.5	17.7
<i>Cryptodiffugia oviformis</i> Penard 1890	20	33	36.5	8.1
<i>Cyclopyxis arcelloides</i> (Leidy 1879) type	5	62	1.5	9.0
<i>Cyclopyxis eurystoma</i> (Deflandre 1929) type	10	13	84.3	39.9
<i>Diffugia oblonga</i> Ehrenberg 1838	1	1	12.0	-
<i>Diffugia pulex</i> Penard 1902 type	2	2	71.7	9.2
<i>Diffugia rubescens</i> Penard 1891	2	1	8.9	6.4
<i>Euglypha ciliata</i> (Ehrenberg 1848)	18	25	33.9	22.6
<i>Euglypha compressa</i> Carter 1864	6	1	25.0	14.1
<i>Euglypha cristata</i> Leidy 1874	6	1	48.1	10.2
<i>Euglypha rotunda</i> Wailes 1911	30	29	68.2	32.2
<i>Euglypha strigosa</i> (Ehrenberg 1872)	5	1	28.8	4.6
<i>Heleopera petricola</i> Leidy 1879	4	3	24.6	8.2
<i>Heleopera rosea</i> Penard 1890	34	27	40.4	16.9
<i>Heleopera sylvatica</i> Penard 1890	1	1	81.0	-
<i>Hyalosphenia papilio</i> Leidy 1875	24	94	27.9	10.6
<i>Lesquereusia epistomium</i> Penard 1902	3	11	4.2	2.2
<i>Lesquereusia modesta</i> Rhumber 1895	3	10	3.6	1.8
<i>Nebela dentistoma</i> Penard 1890	8	5	29.1	13.1
<i>Nebela penardiana</i> Deflandre 1936	4	25	12.5	11.4
<i>Nebela tinctoria</i> (Leidy 1879) type	16	13	34.7	17.6
<i>Nebela tubulata</i> Brown 1911	8	6	44.7	12.2
<i>Nebela tubulosa</i> Penard 1890	2	1	29.5	2.1
<i>Phryganella acropodia</i> (Hertwig and Lesser 1874) type	26	9	37.1	15.6
<i>Plagiopyxis cf. callida</i> Penard 1910	5	3	9.6	18.7
<i>Quadrulella symmetrica</i> Wallich 1863	1	6	12.0	-
<i>Sphenoderia cf. fissirostris</i> Penard 1890	18	81	22.7	8.3
<i>Tracheleuglypha dentata</i> Moniez 1888	18	34	32.5	23.3
<i>Trinema complanatum</i> Penard 1890	14	3	67.3	31.9
<i>Trinema enchelys</i> Ehrenberg 1838	1	1	12.0	-
<i>Trinema lineare</i> Penard 1890	19	45	65.1	33.1
<i>Trigonopyxis arcula</i> (Leidy 1879)	3	2	73.9	12.7
<i>Habrotricha angusticollis</i> Murray 1905 ¹	5	3	34.5	22.9

¹ This test-forming bdelloid rotifer is commonly found among testate amoebae communities and has been included in the analyses here.

Table 4. Comparison of rank order of taxa hydrological optima with results of previous studies. Taxa are ranked from 1 in the wettest locations to 8 in the driest.

Location	Reference ¹	<i>Centropyxis aculeata</i> ²	<i>Hyalosphenia papilio</i>	<i>Heleopera petricola</i>	<i>Amphitrem a flavum</i>	<i>Nebela tinctoria</i> ³	<i>Assulina seminulum</i>
Turkey	This study	1	2	3	4	5	6
Alaska, USA	Payne et al. (2006)	3	2	4	1	6	7
United Kingdom	Woodland et al. (1998)	1	2	7	3	4	5
Jura Mountains, France and Switzerland	Mitchell et al. (1999)	3	2	5	1	6	4
Newfoundland, Canada	Charman and Warner (1997)	1	8	2	3	4	5
Minnesota, USA and Ontario, Canada	Warner and Charman (1994)	3	1	4	2	5	6
Ontario, Canada	Charman and Warner (1992)	3	1	4	2	6	8
Finland	Tolonen et al. (1994)	4	3	2	1	8	5
Western Russia	Bobrov et al. (1999)	6	3	2	1	5	4
Michigan, USA	Booth (2001)	1	3	5	2	8	6
Northwest Europe	Charman et al. (2007)	1	4	2	3	7	6
Poland	Lamentowicz and Mitchell (2005)	1	3	4	2	5	6

¹ The studies of Charman (1997) and Payne and Mitchell (2007) are excluded as they have distinctly different amoebae communities; the former is the only study in the southern hemisphere and the later is in more nutrient-rich sites. Booth (2002) does not present optima values.

² May include *Centropyxis hirsuta* in some studies.

³ In this study similar taxa without pores were not differentiated.

Figure 1. Location of Sürmene Ağaçaşlı Yaylası site.

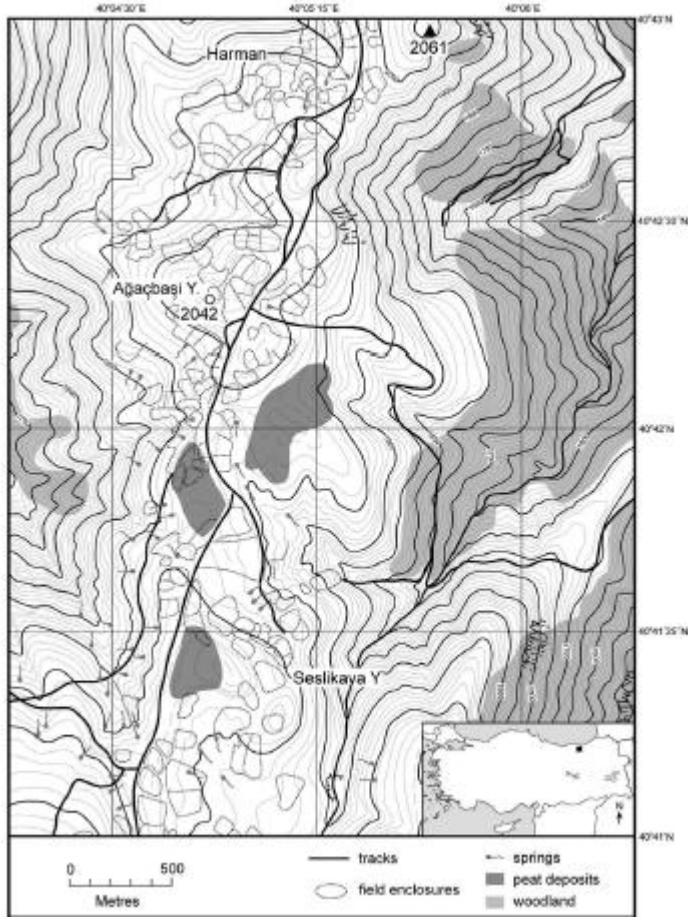


Figure 2. Principal components analysis (PCA) plot of amoebae data. A) Showing samples: western sector samples shown by open squares, eastern sector samples by crosses and southern sector samples by filled squares. B) Showing species.

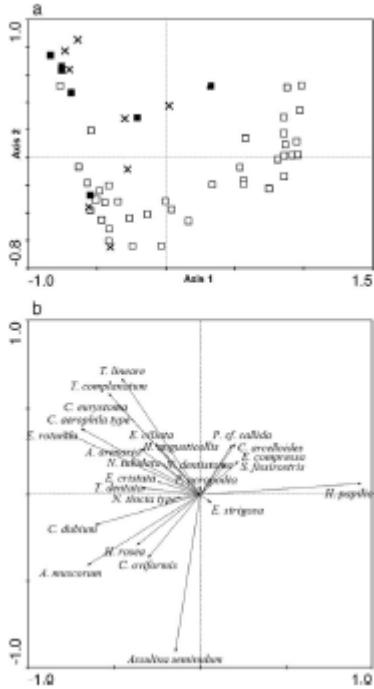


Figure 3. Observed against model predicted depth to water table (DWT) using maximum likelihood model for A) raw and B) filtered data.

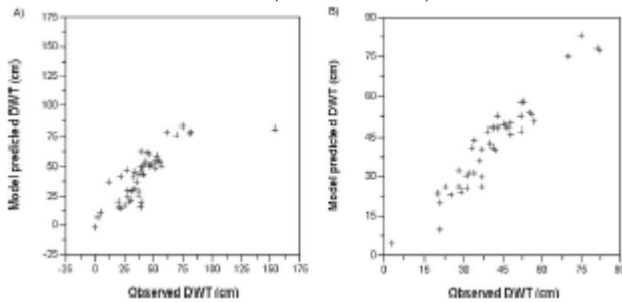


Figure 4. Relative position of selected taxa depth to water table (DWT) optima on the hydrological gradient for this and previous studies.

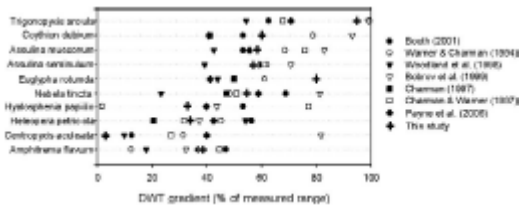


Fig 5. Palaeoecological data from cores at the Sürmene Ağaçbaşı Yaylası site.

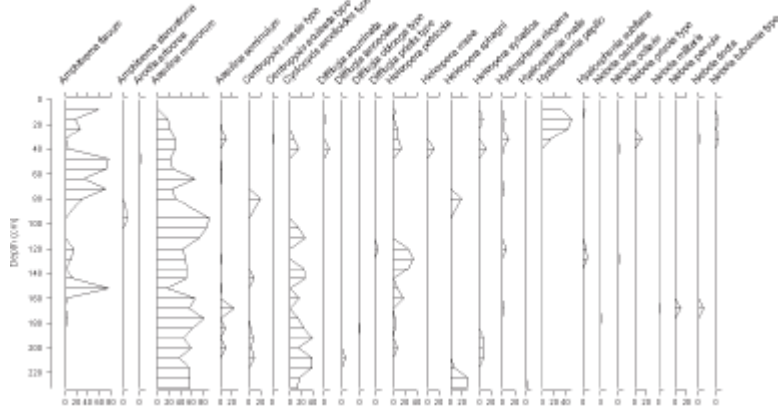


Figure 6. Testate amoebae inferred depth to water table (TI-DWT) reconstructions using the selected ML model and the WA-PLS model for this study and using the northern European model of Charman et al. (2007).

