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TESTATE AMOEBAE AS PALEOCLIMATIC PROXIES IN ROCKY MOUNTAIN PEATLANDS: A CASE STUDY IN THE GREATER YELLOWSTONE ECOSYSTEM.



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✦ ABSTRACT

We investigated the potential of testate amoebae (Protozoa:Rhizopoda) for reconstructing past climate changes in the Rocky Mountain region. Our specific objectives were to determine environmental controls on modern testate amoeba distribution in *Sphagnum*-dominated peatlands of the region, reconstruct past temporal changes in testate amoebae from a *Sphagnum*-dominated peatland in southwestern Yellowstone National Park, and assess relationships between climate variability and testate amoebae for the past century. Our results indicate that substrate moisture is the dominant control on modern testate amoeba distribution in the region, consistent with studies from other regions. Temporal changes in testate amoebae reconstructed from a floating peat mat in the Greater Yellowstone Ecosystem show considerable variability during the past several hundred years, and variability during the past century was correlated with the instrumental record of drought at decadal timescales. The patterns suggest that sensitive paleoclimatic reconstructions are possible from floating mats in the region, and perhaps elsewhere. Testate amoebae from peatlands in the Rocky Mountains show great potential for reconstructing past climate variability, corroborating and extending records inferred from other proxies.

✦ INTRODUCTION

Peatlands are valuable archives of past environmental and climatic variability (e.g. Barber, 1993; Blackford, 2000; Charman, 2002). Continuous records of paleoclimate spanning the mid to late Holocene with multidecadal to centennial-scale temporal resolution have been obtained from peat stratigraphy in various regions of the world, including Europe (e.g., Chambers et al., 1997; Barber et al., 2000, 2003; Hughes et al. 2000; Charman and Hendon, 2000; Langdon et al., 2003), New Zealand (Wilmhurst et al., 2003), and the Great Lakes region of North America (Booth and Jackson, 2003; Booth et al., 2004). These studies typically involve the reconstruction of temporal changes in peatland hydrology, which is controlled by precipitation, evaporation, and temperature (Barber et al., 2000; Charman et al., 2004; Hendon and Charman, 2004). Investigations have focused on *Sphagnum*-dominated peatlands, and in particular, ombrotrophic peatlands such as raised and blanket bogs. Ombrotrophic peatlands derive all moisture from atmospheric sources and contain particularly sensitive records of past climate (Blackford, 1993; Charman, 2002). However, other *Sphagnum*-dominated peatlands have also been shown to contain sensitive records of past climate variability (Anderson, 1998; Hendon et al., 2001; Booth et al., 2004).

Temporal changes in past surface-moisture conditions can be reconstructed from peat stratigraphy using a variety of proxies (Blackford, 1993; Charman, 2002). Testate amoebae, a group of amoeboid protozoans that produce a decay-resistant outer shell, are particularly useful proxies within *Sphagnum*-dominated peatlands, where their distribution is primarily controlled by substrate moisture (Charman, 2001). Relationships between species composition and hydrology have been quantitatively modeled (e.g., Charman and Warner, 1992, 1997; Charman, 1997; Woodland *et al.*, 1998; Mitchell *et al.*, 1999; Booth, 2001, 2002; Wilmhurst *et al.*, 2003). Various modeling techniques have been used to describe relationships between species composition and substrate moisture, particularly water-table depth, and these relationships have been used to reconstruct past moisture fluctuations from subfossil assemblages (Warner and Charman, 1994; Woodland *et al.*, 1998; Hendon *et al.*, 2001; Booth and Jackson, 2003). In North America, paleohydrological applications of testate amoebae have been explored in *Sphagnum*-dominated peatlands of the Great Lakes region (Warner and Charman, 1994; Booth 2001, 2002; Booth and Jackson, 2003; Booth *et al.*, 2004) but modern calibration datasets are needed from other regions and peatland types.

Sphagnum-dominated peatlands are scarce in the Rocky Mountain region, and truly ombrotrophic peatlands are absent (Windell *et al.*, 1986). However, *Sphagnum*-dominated peatlands do occur in isolated topographic and hydrological settings, particularly as floating peat mats on oligotrophic lakes and in areas of relatively acidic groundwater discharge (e.g., 'iron fens'). In this study, we investigated the potential of testate amoebae for reconstructing past environmental and climatic variability in peatlands of the Greater Yellowstone Ecosystem, and elsewhere in the Rocky Mountains. Our primary objectives were to identify environmental controls on testate amoebae within *Sphagnum*-dominated peatlands of the region, and to investigate past temporal changes in the relative abundance of testate amoebae from the sediments of a floating peatland. To assess whether testate amoebae preserved in the sediments of a floating peatland can be used to reconstruct past climate variability, we compare temporal changes in testate amoebae with instrumental climate data for the past century.

◆ STUDY SITES

To locate *Sphagnum*-dominated peatlands in the Rocky Mountain region, data on the distribution of known peatlands and obligate peatland vascular plant species were obtained from the Wyoming Natural Diversity Database, the Rocky Mountain Herbarium, and the Colorado Natural Heritage Program, and compiled with information on the known distribution of *Sphagnum* in Wyoming and Colorado (R.E. Andrus, unpublished data). Fifteen *Sphagnum*-dominated peatlands within Wyoming and Colorado were identified (Figure 1). Five of these peatlands were "iron fens," which are characterized by highly acidic groundwater (pH 3.3-3.4) that is rich in dissolved iron and sulfur (Carsey *et al.*, 1999). The acidic environment in these peatlands supports relatively unique plant communities dominated by *Sphagnum* and other mosses (Carsey *et al.*, 1999). Except for two small peatlands in central Colorado (Henderson A and B), the other peatlands we sampled were floating mats adjacent to or within small lakes (Table 1). There was considerable environmental variation within and between peatlands (Table 1).

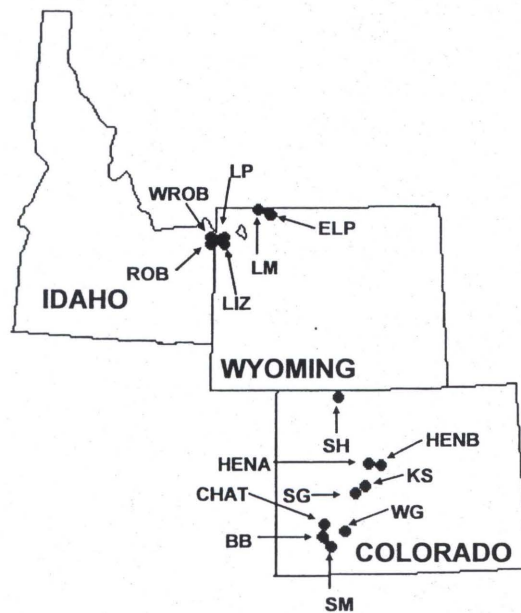


Figure 1. Location of peatlands sampled in the central and southern Rocky Mountains. Peatland abbreviations, and characteristics of each site, are listed in Table 1.

Table 1. Site characteristics, including the location and elevation of each peatland, the range of environmental variables measured (WTD—water table depth; %M—percent moisture; COND—conductivity; BD—bulk density), number of testate amoeba microsites sampled (n), *Sphagnum* species present, peatland type and common vascular plant taxa.

Site Name and Location (UTM)	Elevation (m)	WTD (cm)	%M	pH	COND (µS/cm)	BD (g/cm ³)	n	<i>Sphagnum</i> species	Peatland type and common vascular plant taxa
Burro Bridge Iron Fen (BB) (260067E, 4192065N)	2993	13-50	44.9-75.1	3.0-3.7	880-3400	0.15-0.18	10	<i>S. russowii</i> , <i>S. angustifolium</i>	Iron fen, <i>Carex</i> , <i>Picea</i> , <i>Betula glandulosa</i>
Chatanooga Iron Fen (CHAT) (260288E, 4093778N)	3109	0-50	39.7-79.5	3.3-4.1	220-3600	0.14-0.25	15	<i>S. russowii</i> , <i>S. angustifolium</i> , <i>S. fuscum</i> , <i>S. balticum</i>	Iron fen, <i>Gaultheria</i> , <i>Carex</i> , <i>Betula glandulosa</i> , <i>Picea</i> , <i>Eriophorum</i>
East Lily Peatland (ELP) (602834E, 4978464N)	2469	0-30	49.6-80.6	3.9-5.0	50-400	0.12-0.17	10	<i>S. russowii</i> , <i>S. angustifolium</i> , <i>S. squarrosum</i> , <i>S. warnstorffii</i>	Floating mat around lake, <i>Carex</i> , <i>Chamaedaphne</i> , <i>Salix</i> , <i>Potentilla</i> , <i>Betula glandulosa</i> , <i>Pedicularis</i> , <i>Menyanthes</i> , <i>Drosera</i>
Henderson Park A (HENA) (363680E, 4358463N)	3170	-1-50	61.3-85.4	4.4-5.0	20-1380	0.16-0.30	8	<i>S. platyphyllum</i>	Grounded fen, <i>Carex</i> , <i>Potentilla</i>
Henderson Park B (HENB) (361928E, 4357096N)	3200	2-33	67.1-77.7	3.7-4.9	100-330	0.17-0.25	8	<i>S. russowii</i> , <i>S. platyphyllum</i> , <i>S. warnstorffii</i>	Grounded fen, <i>Carex</i> , <i>Potentilla</i>
Keystone Iron Bog (KS) (323022E, 4303781N)	2865	1-40	51.6-80.5	3.3-3.7	400-2000	0.14-0.29	11	<i>S. russowii</i> , <i>S. teres</i> , <i>S. fimbriatum</i>	Iron fen, <i>Carex</i> , <i>Picea</i> , <i>Pinus contorta</i> , <i>Betula glandulosa</i> , <i>Drosera</i> , <i>Eriophorum</i>
Lilypad Peatland (LP) (499333E, 4889916N)	1948	-4-27	65.3-85.5	3.7-5.6	70-290	0.16-0.31	15	<i>S. squarrosum</i> , <i>S. teres</i> , <i>S. platyphyllum</i>	Floating mat around lake, <i>Potentilla</i> , <i>Menyanthes</i> , <i>Drosera</i> , <i>Carex</i> , <i>Nuphar</i>
Little Moose Lake (LM) (598023E, 4980785N)	2426	1-33	65.1-82.9	4.3-6.1	110-360	0.15-0.21	13	<i>S. russowii</i>	Floating mat around lake, <i>Potentilla</i> , <i>Carex</i> , <i>Drosera</i> , <i>Menyanthes</i> , <i>Salix</i> , <i>Pedicularis</i> , <i>Betula glandulosa</i> , <i>Picea</i> , <i>Eriophorum</i>
Lizard Peatland (LIZ) (498161E, 4888929N)	1942	-2-26	67.4-75.1	4.4-5.8	60-230	0.21-0.33	5	<i>S. squarrosum</i> , <i>S. platyphyllum</i>	Floating mat around lake, <i>Menyanthes</i> , <i>Nuphar</i> , <i>Carex</i>
Robinson Peatland (ROB) (494345E, 4890224N)	1978	-5-13	66.4-83.8	3.4-4.5	10-250	0.13-0.26	15	<i>S. russowii</i> , <i>S. squarrosum</i> , <i>S. platyphyllum</i> , <i>S. fuscum</i> , <i>S. subsecundum</i>	Floating mat within lake, <i>Scheuchzeria</i> , <i>Carex</i> , <i>Dulichium</i> , <i>Drosera</i> , <i>Potentilla</i> , <i>Menyanthes</i>
Shafer Lake (SH) (366148E, 4524837N)	2739	-2-41	48.2-84.6	3.6-5.1	40-450	0.13-0.19	10	<i>S. squarrosum</i> , <i>S. teres</i>	Floating mat around lake, <i>Carex</i> , <i>Menyanthes</i> , <i>Potentilla</i> , <i>Drosera</i>
South Mineral Iron Fen (SM) (260301E, 4188699N)	2908	50	40.9-62.0	2.9-3.6	940-3260	0.15-0.19	8	<i>S. russowii</i> , <i>S. angustifolium</i> , <i>S. fuscum</i>	Iron fen, <i>Carex</i> , <i>Betula glandulosa</i>
Splains Gulch Lake (SG) (319853E, 4300218N)	3164	11-24	68.1-76.3	3.9-4.5	120-500	0.16-0.20	7	<i>S. russowii</i> , <i>S. squarrosum</i> , <i>S. teres</i> , <i>S. fimbriatum</i>	Floating mat around lake, <i>Carex</i> , <i>Potentilla</i>
Wager Gulch Iron Fen (WG) (291681E, 4194722N)	3365	12-50	48.4-72.5	3.1-3.9	700-2500	0.15-0.22	10	<i>S. russowii</i>	Iron fen, <i>Carex</i> , <i>Picea</i> , <i>Salix</i> , <i>Betula glandulosa</i>
West Robinson Peatland (WROB) (494000E, 4890224N)	1978	0-14	69.6-84.2	3.6-4.3	30-70	0.14-0.19	5	<i>S. russowii</i> , <i>S. squarrosum</i> , <i>S. fuscum</i>	Floating mat within lake, <i>Scheuchzeria</i> , <i>Carex</i> , <i>Dulichium</i> , <i>Drosera</i> , <i>Potentilla</i> , <i>Menyanthes</i> , <i>Lycopodium</i>

A sediment core was collected from Robinson Peatland, a floating peat mat in the center of a lake basin in southwestern Yellowstone National Park, in June 2002. Dominant vegetation on the floating mat included *Sphagnum*, *Scheuchzeria*, *Carex*, *Dulichium*, *Drosera*, *Potentilla*, and *Meryanthes*. Open water surrounding the mat was dominated by *Nuphar*, and the surrounding forest was dominated by *Pinus contorta*.

✦ METHODS

Modern calibration dataset

Modern testate amoeba assemblages were collected during June and July of 2002. Collection procedures generally followed previous studies (e.g. Woodland *et al.*, 1998; Mitchell *et al.*, 1999; Booth, 2001, 2002). In each peatland, 5-15 testate amoeba samples were collected in an attempt to represent hydrologic (i.e. wet and dry sites) and biotic (i.e. areas of different vegetation) variability, although we focused on sites where *Sphagnum* was present. At each sampling site, a peat sample was taken by pushing a metal can (11 cm long, 7.5 cm in diameter) with one open end (and a hole in the other end to allow air to escape) into the peat until the top of the can was level with the vegetative surface (about 11 cm deep). This peat sample was sealed and returned to the lab for calculation of bulk density and percent moisture. Modern testate amoeba assemblages were collected by taking approximately 10 cm³ of brown *Sphagnum* (found directly below the green part of the stem, typically 3-6 cm deep) from the edge of the hole left from the peat sample. The brown part of the stem is thought to contain amoebae that are most representative of those found in the fossil record (Warner, 1987), and also contains higher diversity than upper portions of the stem (Booth, 2002; Mitchell and Gilbert, 2004). Depth to water table (cm), conductivity ($\mu\text{S}/\text{cm}$), and pH were measured at each sampling site. Conductivity and pH were measured from as close as possible to the amoeba assemblage, typically by squeezing water from adjacent *Sphagnum*. *Sphagnum* moss samples were collected for species-level identification.

Preparation of peat samples for analyses of testate amoebae generally followed the method of Hendon and Charman (1997). Samples were boiled in 100 mL of distilled water for 10 minutes and then sieved through nested 355- μm and 15- μm filters. Material left in the 15- μm sieve was put into a water solution and centrifuged at 3000 rpm for five

minutes. The supernatant was decanted and the remaining material stained with two drops of safranin-O dye and stored in glycerol. Using a light microscope at 400x magnification, testate amoebae were identified and counted until a total count of at least 150 was reached. Counts of the rotifer *Habrotricha angusticollis* were included in the total amoeba counts, as it is commonly found in association with testate amoebae and has been included in calibration datasets from other regions (Charman, 1997; Charman and Warner, 1997; Booth, 2002). For each sample, the relative abundance of each taxon was calculated as a percentage of the total number of testate amoebae counted. Taxonomy was based solely on test morphology, and follows Charman *et al.* (2000) except as noted in Booth (2002) and Table 2.

Peatland sediment coring

An 89-cm long sediment core was collected approximately 30m from the south-central edge of Robinson Peatland with a 10.2-cm diameter piston corer (Wright *et al.*, 1984). The core was extruded in the field, wrapped in plastic film and aluminum foil, encased in plastic piping, and transported back to the laboratory for analysis. Approximately 2cm³ of peat was collected from each centimeter for testate amoeba analysis. The upper 40 centimeters were analyzed continuously (every cm), and every other centimeter was analyzed below 40cm. Testate amoebae were isolated from peat samples using the same procedures as modern collections.

Analytical methods

Outlier removal

To decrease the influence of anomalous samples, outlier analysis was performed on the dataset using PC-ORD (McCune & Mefford, 1999) and Sørensen's distance measure, removing samples with species data more than two standard deviations from the mean. Three samples from Henderson Peatland A were also removed because of difficulties accurately measuring the water-table depth, which may have been related to the low porosity of a shallow clay/silt subsurface layer that extended from the upland into the edge of the peatland where those samples were collected. Testate amoeba taxa found in fewer than ten samples (*Paraquadrueella irregularis*, *Hyalosphenia elegans*, *Diffflugia acuminata*, *Arcella gibbosa*, *Arcella hemisphaerica*, *Nebela lageniformis*, *Nebela militaris*, *Lesquerusia spiralis*) were removed from the data set prior to analysis. A total of 135 samples and 33 taxa remained (Table 2).

Table 2. Testate amoebae encountered in this study. Taxonomy follows Charman *et al.* (2000) with modifications of Booth (2002) except where noted by asterisks.

Taxon	Abbreviation
<i>Arcella catinus</i> Penard	arccat
<i>Arcella discoidea</i> Ehrenberg type	arcdis
<i>Arcella gibbosa</i> Penard type	arcgib
<i>Arcella hemisphaerica</i> Perty	archem
<i>Arcella vulgaris</i> Ehrenberg	arcvul
<i>Assulina muscorum</i> Greef	assmus
<i>Centropyxis aculeata</i> (Ehrenberg) von Stein type	cenacu
<i>Centropyxis cassis</i> (Wallich) Deflandre type	cencas
<i>Centropyxis platystoma</i> (Penard) Deflandre type	cenpla
<i>Corythion-Trinema</i> type	cortri
<i>Cryptodifflugia oviformis</i> Penard	cryovi
<i>Cyclopyxis kahli</i> Deflandre*	cyckah
<i>Cyphoderia ampulla</i> Ehrenberg*	cypamp
<i>Difflugia acuminata</i> Ehrenberg type	difacu
<i>Difflugia bacillifera</i> Penard	difbac
<i>Difflugia globulosa</i> Dujardin type	difglo
<i>Difflugia lucida</i> Penard type	difluc
<i>Difflugia rubescens</i> Penard	difrub
<i>Difflugia</i> type A	difA
<i>Euglypha cristata</i> Leidy*	eugcri
<i>Euglypha rotunda</i> Wailes and Penard type	eugrot
<i>Euglypha strigosa</i> (Ehrenberg) Leidy	eugstr
<i>Euglypha tuberculata</i> Dujardin type	eugtub
<i>Habrotrocha angustichollis</i> Murray**	habang
<i>Heleopara rosea/petricola</i> Penard/Leidy	hebros
<i>Heleopara sphagni</i> (Leidy) Cash and Hopkinson	helsph
<i>Hyalosphenia elegans</i> Leidy	hyacle
<i>Hyalosphenia papilio</i> Leidy	hyapap
<i>Lesqueresia spiralis/epistomium</i> (Ehrenberg) Bütschli/Penard	lesspi
<i>Nebela collaris</i> (Ehrenberg) Leidy	nebcoll
<i>Nebela lageniformis</i> Penard	neblag
<i>Nebela militaris</i> Penard	nebmil
<i>Nebela parvula</i> Cash and Hopkinson	nebpar
<i>Nebela tubulosa</i> Penard type	nebtub
<i>Nebela vitraea</i> Penard type	nebvitr
<i>Nebela wailesii</i> Deflandre	nebwai
<i>Paraquadrula irregularis</i> (Deflandre) Archer type***	parirr
<i>Pseudodifflugia fulva</i> (Archer) Penard type	pseful
<i>Quadrula symmetrica</i> (Wallich) Schulze	quasym
<i>Sphenoderia lenta</i> Schlumberger	sphlen
<i>Trigonopyxis arcuata</i> (Leidy) Penard type (includes <i>T. minuta</i>)	triacu

*taxonomy follows Ogden and Hedley (1980)

**taxonomy follows Warner and Chengalath (1988)

***taxonomy follows Meisterfeld (2000)

****Similar to *Cyclopyxis arcelloides* type (Booth, 2002), with aperture diameter almost equal to diameter of test, a ragged and uneven aperture margin, and the test usually strongly compressed.

Testate amoebae and environment

To investigate variability in testate amoeba assemblages, and relationships between testate amoeba assemblages and environmental conditions, we used non-metric multidimensional scaling (NMS) (Kruskal, 1964; Mather, 1976; McCune and Grace, 2002). NMS has advantages over other ordination methods because it does not make assumptions regarding underlying species distributions along compositional gradients (McCune and Grace, 2002; Clarke, 1993). We used Sørensen's distance measure in our analyses, along with the automated search feature of PC-ORD (McCune and Mefford, 1999) to identify the best solution and dimensionality. The automated search feature performed 40 runs with real data, each with a random starting configuration and consisting of solutions for 1 through 6 dimensions. Fifty runs with randomized data were then performed and statistics on the final stress at each dimensionality were accumulated. The best solution for each dimensionality was identified by comparing the final stress values.

Developing an age-model for the sediment core

An age model for the sediment core was developed using linear interpolation between an accelerator mass spectrometry (AMS) radiocarbon date at a depth of 88 cm and continuous analyses of ^{210}Pb and ^{137}Cs on the upper 39 cm. The University of Florida performed the analysis of ^{210}Pb and ^{137}Cs . The radiocarbon date was obtained from *Sphagnum* stems and leaves spanning a 1-cm interval of peat. The radiocarbon age was calibrated to calendar-year age using CALIB 4.1 (Stuiver and Reimer, 1993; Stuiver *et al.* 1998).

Comparing temporal changes in testate amoebae with climate data

Fossil testate amoeba assemblages were positioned within the modern sample ordination, using the program PC-ORD and the NMS scores feature (McCune and Mefford, 2002). The procedure allows the fossil samples to be positioned in the original ordination space without altering the position of the original points. Fossil sample scores along each main axis of variation were compared with instrumental climate data, using climate divisions data obtained from the NOAA-CIRES Climate Diagnostics Center, Boulder, Colorado, USA, via the internet (<http://www.cdc.noaa.gov>). Climate division data are monthly averages of instrumental data from regions within states that are thought to be climatically uniform. We used climate division data

from southeastern Idaho (Climate Division #10) for our comparisons. Both the inferred NMS axis data and the climatic data were smoothed to decadal resolution to facilitate comparisons. The smoothing was done with a 10-year moving window, moved in 5-year time steps.

✦ RESULTS AND DISCUSSION

Testate amoeba assemblages and controls on distribution

Testate amoebae of peatlands in the Rocky Mountain region have not been extensively studied. The most recent research dates to the late 1800s (Leidy, 1879; Penard, 1891). This early work suggests that several taxa thought to be quite common in other regions were absent in the Rocky Mountains, including *Hyalosphenia papilio*, *Nebela flabulellum*, and *Assulina seminulum* (Penard, 1891). We did not observe *Nebela flabulellum* or *Assulina seminulum* in our Rocky Mountain samples. However, *Hyalosphenia papilio* occurred in some samples from floating peat mats in northwest Wyoming and adjacent Idaho, though it was absent from other sites. Our data indicate that several other taxa that are common in eastern North America and Europe, including *Amphitrema flavum*, *Amphitrema wrightianum*, *Bulinularia indica*, *Heleopera sylvatica*, *Nebela carinata-marginata* type, and *Nebela griseola*, are probably absent or rare in the Rocky Mountains (Booth and Zygmunt, 2004).

We selected a three-dimensional NMS solution for the ordination of the modern assemblage data from the Rocky Mountains, because additional dimensions resulted in only small reductions in stress. For the final ordination, the solution with the lowest final stress (final stress=18.71, $p < 0.05$) was used, and this solution represented 80% of the variation in the dataset (Table 3). Axis 2 was strongly correlated with most of the environmental variables we measured, including water-table depth, percent moisture, pH, and conductivity (Figure 2, Table 3). Taxa with high scores on this axis, including *Diffflugia globulosa* type, *Arcella vulgaris* type, and *Nebela tubulosa*, tend to be associated with wet habitats, high pH, and low conductivity (Figure

2). Taxa with low scores on this axis, including *Trigonopyxis arcuata*, *Assulina muscorum*, and *Nebela parvula*, are generally associated with dry habitats, low pH, and high conductivity (Figure 2). The patterns along axis 2 are consistent with results from other regions, where substrate moisture and aspects of water chemistry have been identified as the dominant controls of taxa distribution patterns (e.g., Charman and Warner, 1992, 1997; Charman, 1997; Woodland et al., 1998; Mitchell et al., 1999; Booth 2001, 2002). The ecology of individual taxa with respect to moisture conditions is also similar to other regions (Booth and Zygmunt, 2004).

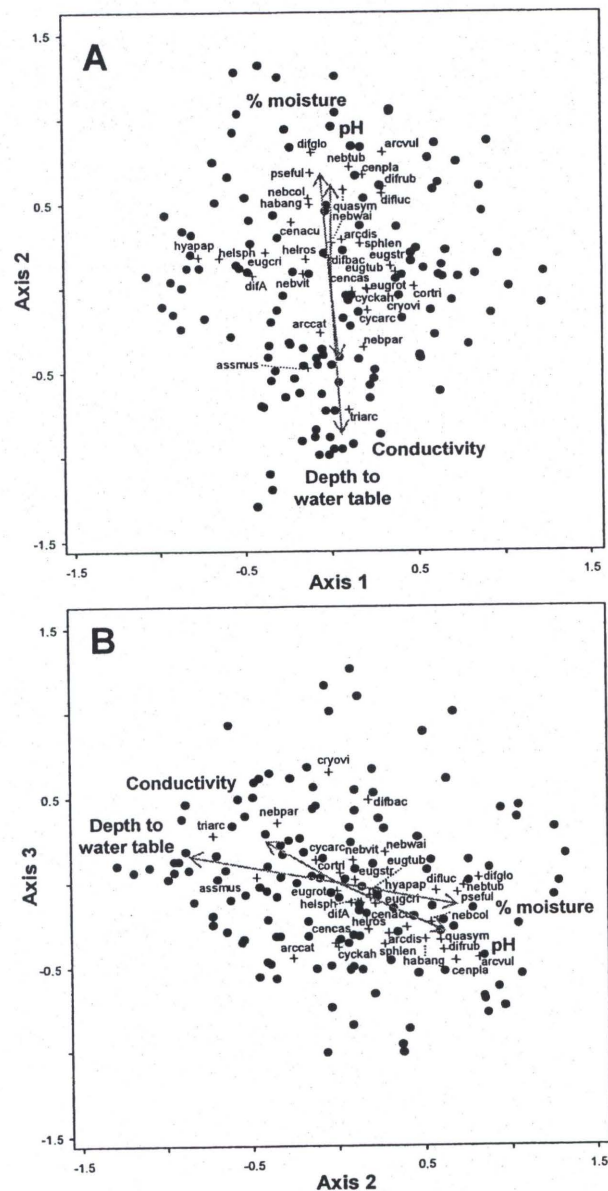


Figure 2. Three-dimensional NMS ordination of modern testate amoeba samples collected in the Rocky Mountains, with sample and species scores for axes 1 and 2 shown in A and scores for axis 2 and 3 shown in B. Abbreviations for species are shown in Table 2. Biplot shows the relative strength of axis-environment correlations, for variables with strong correlations ($r^2 > 0.2$). Axis-environment correlations and percent variance explained are shown in Table 3.

The other two NMS axes were not correlated with any environmental variables we measured. However, each of these axes explains about 20% of the variability in the dataset (Table 3), suggesting that they represent important patterns of variability and that other controls on distribution patterns may exist in the Rocky Mountains. Taxa with high scores along axis 1 include *Corythion-Trinema* type and *Cryptodiffugia oviformis*, and taxa with low scores include *Hyalosphenia papilio* and *Heleopera sphagni*. Taxa with high scores along axis 3 include *Centropyxis platystoma* type and *Arcella catinus*, and taxa with low scores along this axis include *Cryptodiffugia oviformis* and *Diffugia bacilifera*.

Past variability in testate amoebae and environment at Robinson Peatland

Age model

Analysis of ^{210}Pb and ^{137}Cs revealed excess ^{210}Pb present to a depth of 38 cm in the peatland sediment core, and a prominent spike in ^{137}Cs occurred at a depth of about 23 cm (Figure 3). The ^{137}Cs spike is attributable to nuclear weapons testing in the 1960s. Rapid accumulation or mixing occurred between 12 and 19 cm (Figure 3), and the ^{137}Cs peak at 1963 A.D. suggested separate sedimentation rates should be applied above and below this interval. Several models were explored, including constant initial concentration (CIC), constant rate of supply (CRS), and constant flux:constant sedimentation rate (CF:CS) models. A CF:CS model provided the most reliable results (J. Cable, personal communication), and indicates sedimentation rates of 2.97 mm/yr in the upper 12 cm, and 2.80 mm/yr from 19 to 38 cm. Linear interpolation from the basal radiocarbon date suggests an average sedimentation rate of 2.09 mm/yr below 38-cm depth.

Testate amoeba stratigraphy

Depth-to-water-table is an important control on testate amoeba distribution in the Rocky Mountains (Figure 2) and elsewhere (e.g., Woodland et al., 1998; Booth, 2002). Therefore, we expected little temporal variability in the relative abundance of testate amoebae at Robinson Peatland because the floating mat should rise and fall with fluctuations in basin water levels, and hence depth-to-water-table should remain relatively constant. However, the abundance of several taxa varied substantially in the core (Figure 4). Taxa that showed particularly large vertical changes in abundance included *Hyalosphenia papilio* and *Pseudodiffugia fulva* type, which

fluctuated by more than 50% in their relative abundance within the core (Figure 4). Relative abundance of other taxa also varied considerably, particularly taxa with relatively low NMS axis 1 scores in the modern dataset (e.g., *Hyalosphenia papilio*, *Heleopera sphagni*, *Centropyxis aculeata* type). The positioning of fossil samples within the ordination of modern samples indicates a good deal of overlap between modern and fossil samples, although the range of variability is less within the fossil dataset (Figure 5).

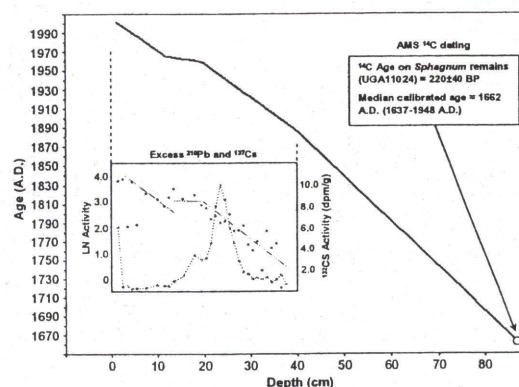


Figure 3. Age-depth model for the Robinson peat core and vertical distribution of excess ^{210}Pb and ^{137}Cs . Note the distinct peak in ^{137}Cs at about 23-cm depth and the apparent event layer between 12 and 19-cm depth, which may have been caused by mixing or rapid deposition. Application of a constant flux:constant sedimentation rate model separately to the periods before and after the event layer gave the most consistent results, suggesting sedimentation rates in the upper 12 cm were about 2.97 mm/yr and about 2.8 mm/yr from 38 to 19 cm depth.

Table 4. Correlations (r) between decadal smoothed instrumental climate data and predicted NMS scores of fossil samples (1895-2002 A.D.). Asterisks denote significance ($p < 0.01$).

Climate variables	Predicted NMS Scores of fossil samples		
	Axis 1	Axis 2	Axis 3
Precipitation			
DJF	0.60*	-0.23	-0.27
JJA	0.59*	0.05	-0.05
Annual	0.58*	-0.15	-0.18
Temperature			
DJF	-0.30	-0.43	0.28
JJA	-0.59*	-0.36	0.61*
Annual	-0.65*	-0.32	0.46
Palmer Drought Severity Index (PDSI)			
DJF	0.77*	-0.01	-0.35
JJA	0.75*	0.08	-0.40
Annual	0.75*	0.03	-0.37

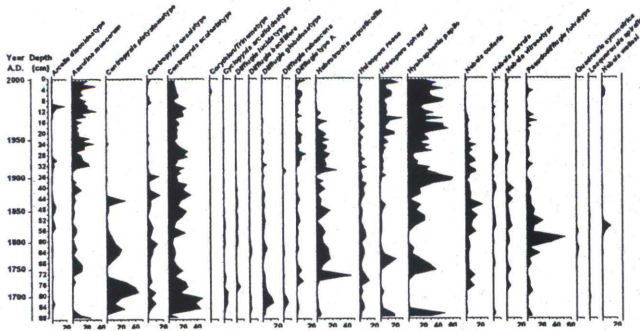


Figure 4. Vertical changes in the relative abundance of testate amoebae in the Robinson peatland sediment core.

A paleoclimate record from a floating peat mat?

We expected that testate amoebae from a floating peat mat would be relatively insensitive to climate variability, because of the stability of water-table depth on the floating mat. However, comparison between instrumental climatic data for the last century and temporal variability in testate amoebae suggests that climatic variation influenced testate amoeba populations at decadal timescales (Table 4). Significant correlations exist between variability along NMS axis 1 and temperature, precipitation, and a commonly used measure of drought, the Palmer Drought Severity Index (PDSI) (Table 4, Figure 6). A correlation between NMS axis 3 scores and temperature also exists (Table 4, Figure 6). However, this correlation appears to be related to the long-term warming trend in temperature during the 20th century, and the long-term trend in the testate amoeba data could conceivably be due to some other long-term process. Temporal variability in testate amoebae along NMS Axis 2 did not show any significant relationships with climate data, even though variability along this axis was correlated with several environmental variables in the modern dataset (Figure 2).

Why is variability along NMS axis 1 correlated with drought during the past century? We hypothesize that, although depth-to-water-table and peat saturation remain constant on floating mats, moisture conditions at and near the peat surface (i.e., the uppermost portions of living *Sphagnum*) are affected by temperature, evaporation, and precipitation. Fluctuations in NMS axis 1 scores appear to be primarily related to changes in the relative abundance of *Hyalosphenia papilio* and *Heleopera sphagni*. These two taxa increase during drier time periods and decrease during wetter time periods. It is probably significant that these two taxa contain symbiotic zoochlorellae, and are typically

concentrated on upper portions of the *Sphagnum* stem (e.g., Heal; 1962; Meisterfeld, 1977; Booth 2002). Moisture content and other properties of the distal portions of *Sphagnum* plants are likely sensitive to seasonal, annual, and decadal variations in climate, and so these microenvironmental variations could drive variations in local testate amoeba populations. Distal *Sphagnum* microenvironments at Robinson Peatland are presumably more favorable for *Hyalosphenia papilio* and *Heleopera sphagni* during dry periods. Although the mechanisms of this relationship remain to be worked out, the strong correlation between the instrumental record and the testate-amoeba record at Robinson Peatland indicates that paleoclimate inferences can be made from floating peat mats in the region.

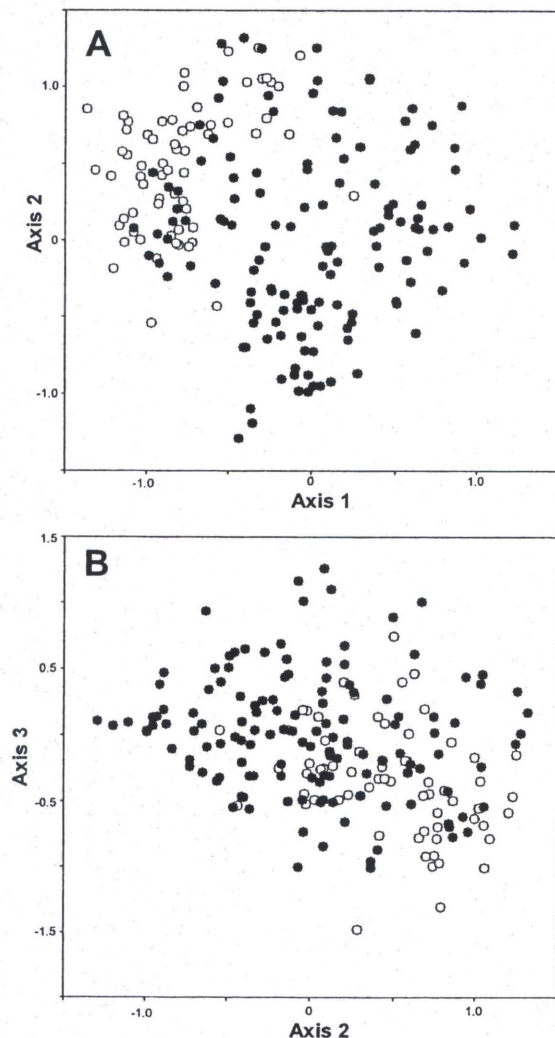


Figure 5. NMS ordination of the modern calibration dataset (closed circles) with predicted scores for fossil samples from Robinson peatland (open circles) for A) axes 1 and 2 and B) axes 2 and 3.

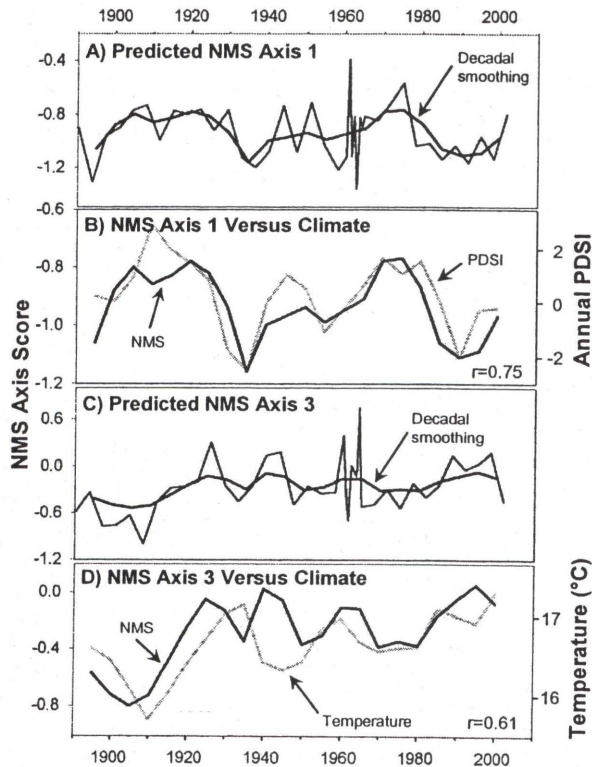


Figure 6. Comparison of the instrumental climatic record with the testate amoeba record of Robinson peatland, for statistically significant correlations (see Table 4). A) Temporal changes in predicted NMS axis 1 scores of testate amoeba samples showing raw data and decadal smoothing. B) Comparison of decadal smoothed NMS axis 1 scores and Palmer Drought Severity Index (PDSI). C) Temporal changes in predicted NMS axis 3 scores of testate amoeba samples showing raw data and decadal smoothing. D) Comparison of decadal smoothed NMS axis 3 scores and temperature.

◆ CONCLUSIONS

Testate amoebae are an underutilized paleoenvironmental proxy, and have great potential for reconstructing past climate variability from peatland sediments of the Rocky Mountain region. As in other studied regions, the dominant controls on species distribution patterns within peatlands of the Rocky Mountains are substrate moisture and water chemistry. A testate amoeba record from a floating peat mat in Yellowstone National Park is correlated with instrumental records of drought during the past century, suggesting strong potential for drought reconstructions at decadal timescales from floating mats in the region, and possibly elsewhere. Assuming suitable sites can be located, testate amoeba-based climatic reconstructions have the potential to extend over longer periods than tree-ring records, and are higher in resolution than those

obtained by plant macrofossils and pollen. Testate amoebae can be used to provide information on past peatland hydrology, which would be particularly useful in the Rocky Mountain region, where water resources are critical for land management.

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