Quaternary Science Reviews 366 (2025) 109491

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

Testate amoebae as paleoenvironmental indicators in peatlands: calibration-dataset synthesis and assessment of modern analogues using the Neotoma Paleoecology Database

Robert K. Booth *, Alexis Stansfield, Erica Cowper, Jared M. Kodero

Department of Earth & Environmental Sciences, 1 West Packer Ave, Lehigh University, Bethlehem, PA, 18015, USA

ARTICLE INFO

Handling Editor: Dr Yan Zhao

Keywords:
Testate amoebae
Peatlands
Paleoecology
Modern analogues

ABSTRACT

Testate amoebae are widely used paleoindicators of past environmental conditions, particularly in peatlands where they have been used as surface-moisture proxies. Modern ecological studies of the past several decades inform the interpretation of stratigraphic records, and increasingly both modern surface-sample datasets and stratigraphic records are being added to publicly available databases like the Neotoma Paleoecology Database. In this paper, we broadly synthesize results of calibration studies during the past ~35 years, and then use data from the Neotoma Paleoecology Database to examine morphospecies-environment relationships in calibration datasets from the northern hemisphere and directly compare subfossil and modern testate amoeba communities to assess the strength of modern analogues for subfossil samples in North American stratigraphic records. Results confirm the consistent and central importance of surface-moisture in controlling testate amoeba communities in peatlands, with similar community-moisture relationships across the Northern Hemisphere. However, many subfossil communities have few good modern analogues, likely due to a combination of factors including differential decomposition of taxa extending beyond the well-documented poor preservation of weakly idiosomic tests. Many subfossil samples contain high abundances and unusual combinations of taxa that are not well represented in modern datasets, and the causes and implications of subfossil communities with poor modern analogues deserve greater attention by the research community. The Neotoma Paleoecology Database is a valuable shared resource, and its continued development will enable the examination of research questions focused on understanding the variability and structure of modern and subfossil testate amoeba communities, as well as moisture reconstructions in both time and space.

1. Introduction

Testate amoebae, a group of single-celled eukaryotes that produce morphologically distinct tests (i.e., shells), are an important and taxonomically rich component of microbial communities in aquatic, wetland, and terrestrial ecosystems (e.g., Arndt, 1993; Mitchell et al., 2008; Wilkinson and Mitchell, 2010; Freitas et al., 2022). Tests are typically between about 20 and 200 μm in length and are made of proteinaceous, siliceous, or calcareous material (e.g., Ogden and Hedley, 1980; Meisterfeld, 2002). Some species incorporate organic or mineral particles from their surroundings into the test. Within wetlands, testate amoebae inhabit standing-water pools, biofilms, the substrate, and the water film on mosses and other vegetation. Testate amoeba community composition is correlated with local environmental conditions, and within peatlands, communities change along moisture and pH gradients (e.g., Mitchell et al., 2008). Similarly, within ponds, lakes, and other aquatic ecosystems, the distribution of testate amoebae is associated with environmental variables like trophic status, hydrology, and water chemistry (e.g., Roe and Patterson, 2006; Escobar et al., 2008; Ju et al., 2014; Siver et al., 2020; Freitas et al., 2022; Sysoev et al., 2024). Sensitivity to environmental conditions, along with the decay-resistant nature of their shells and their short generation times (e.g., Charman, 2001; Mitchell et al., 2008), have led to their use in inferring past environmental conditions from the stratigraphy of subfossil tests preserved in lakes and peatlands (e.g., Qin et al., 2009; Lamentowicz et al., 2015; Magnan et al., 2018; Swindles et al., 2019; Ndayishimiye et al., 2020; Davies et al., 2021; Booth et al., 2023).

Over the past several decades, paleoecological applications of testate

* Corresponding author.
E-mail address: rkb205@lehigh.edu (R.K. Booth).

https://doi.org/10.1016/j.quascirev.2025.109491
Received 27 January 2025; Received in revised form 13 May 2025; Accepted 18 June 2025
Available online 30 June 2025

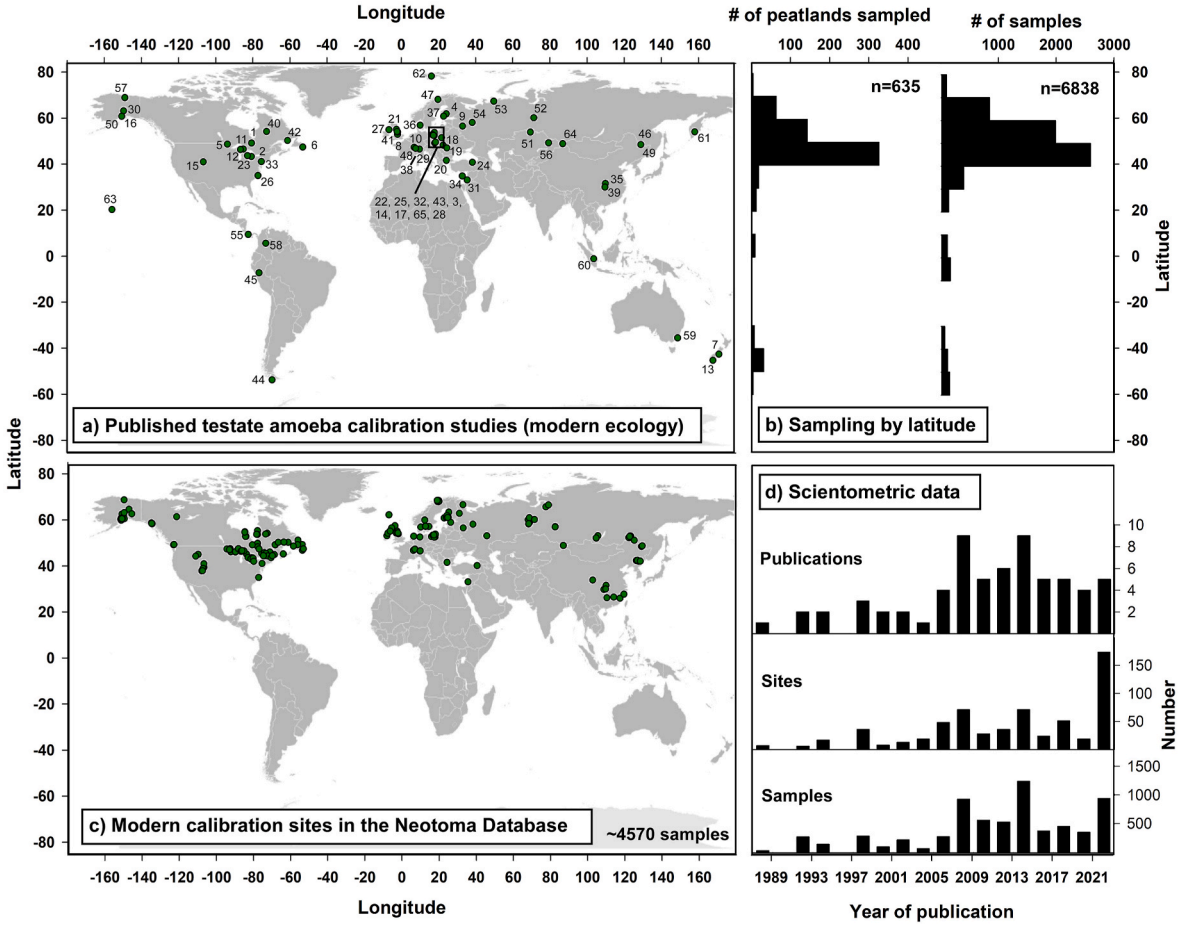

Fig. 1. Calibration studies describing modern testate amoeba communities from peatland surface samples. Published studies that have developed modern calibration datasets are shown in panel a, and the number of sampled peatlands and total number of samples are plotted by latitude in panel b. Individual studies that are shown with numbers on panel a are listed in Table 1. Panel c shows the distribution of peatland surface-samples in the Neotoma paleoecology database as of 2024. Panel d shows scientometric data for the studies in panel a, with numbers of publications, sites, and samples summarized in 2-year bins.

amoebae have motivated the development of numerous surface-sample calibration datasets for paleoenvironmental inference, particularly in peatland environments (Fig. 1, Table 1). These efforts have dramatically expanded our knowledge of modern testate amoeba distribution and community-environment relationships (e.g., Charman and Warner, 1992; Mitchell et al., 1999; Lamentowicz and Mitchell, 2005; Booth, 2008; Markel et al., 2010; Amesbury et al., 2016, 2018; Liu et al., 2019; Barrett et al., 2021, Qin et al., 2021, Sim et al., 2021). Most of these studies have used a morphospecies-based taxonomic approach that relies on test characteristics, because this is what gets preserved in the stratigraphic record (Charman, 2001). Studies have also examined relationships among morpho-functional traits and environmental conditions (e.g., Schönborn and Peschke, 1988; Booth and Meyers, 2010; Fournier et al., 2015; Van Bellen et al., 2017), and results indicate potential paleoenvironmental applications, particularly when combined with morphospecies-based taxonomic approaches (Marcisz et al., 2020; Zhang et al., 2020; Brown et al., 2023; Su et al., 2024). Since the late 1980s, testate amoeba surface-samples have been collected from over 600 peatlands, and quantitative data on community composition has been described within many publications (>65) to develop their use as paleoenvironmental indicators (Fig. 1a). Most of these studies have empirically modelled morphospecies-environment relationships via the development and validation of transfer functions, allowing the estimation of past environmental variables, particularly surface moisture, from subfossil community composition (e.g., Woodland et al., 1998; Booth, 2008; Swindles et al., 2014; Sim et al., 2021). Peatlands of mid-to-high latitudes in the northern hemisphere have been extensively sampled, with significantly less data from the subtropics, tropics and southern hemisphere (Fig. 1b). More than 75 % of modern calibration datasets have been developed within the last ~15 years (Fig. 1d).

Several efforts have brought together regional surface-sample datasets to develop continental-scale transfer functions for peatland paleoenvironmental reconstruction (Amesbury et al., 2016, 2018; Qin et al., 2021). Results of such studies indicate that continental-scale transfer functions can be developed, and hemispheric or global-scale syntheses of training sets may be possible (Amesbury et al., 2018). These and other large-scale efforts can be facilitated by large publicly available datasets, such as those maintained within the Neotoma Paleoecology Database (hereafter referred to as 'Neotoma') (Williams et al., 2018). Neotoma contains surface-sample and stratigraphic datasets from a broad range of paleoecological proxies (e.g., pollen, diatoms, ostracods). The relational database structure of Neotoma allows for taxonomic revision and the accommodation of new types of data, giving it flexibility and agility as research develops over time (Williams et al., 2018). Testate amoeba data are contained within two constituent databases within Neotoma: 1) a modern surface-sample database containing information on the present-day ecology and distribution of taxa, and 2) a database containing stratigraphic records of testate amoebae in peatland and lake cores.

The Neotoma surface-sample database currently contains information on community composition from peatland surface samples, including counts or percentages of individual taxa and measurements of water-table depth and/or pH (Fig. 1c). Potential applications of this large and continually maintained surface-sample database are

Table 1
Studies of testate amoeba ecology focused on the development of calibration datasets for paleoenvironmental inference that were included in this synthesis. Locations of studies are shown on Fig. 1. Latitude and longitude were estimated as the approximate center of the distribution of peatlands sampled in each study. Studies that were in Neotoma, but not used in the initial literature review because they were either unpublished datasets or not explicitly collected as part of a calibration dataset, are denoted with letters.

Study #	Citation	Latitude	Longitude	# of peatlands	# of samples	Data in Neotoma
1	Warner (1987)	43.228	−80.646	7	26	Y
2	Charman and Warner (1992)	49.067	−80.600	1	107	Y
3	Tolonen et al. (1992)	52.474	17.889	5	160	N
4	Tolonen et al. (1994)	61.783	24.294	6	90	Y
5	Warner and Charman (1994)	48.587	−93.572	11	50	Y
6	Charman and Warner (1997)	47.337	−53.017	14	60	Y
7	Charman (1997)	−42.667	171.050	13	57	N
8	Woodland et al. (1998)	52.852	−1.967	9	163	N
9	Bobrov et al. (1999)	56.467	33.047	1	31	Y
10	Mitchell et al. (1999)	47.250	7.000	7	64	Y
11	Booth (2001)	46.470	−84.989	2	74	Y
12	Booth (2002)	46.250	−86.601	11	139	Y
13	Wilmshurst et al. (2003)	−45.320	167.809	19	62	N
14	Lamentowicz and Mitchell (2005)	53.694	17.895	3	45	Y
15	Booth and Zygmunt (2005)	40.869	−106.613	15	136	Y
16	Payne et al. (2006)	60.740	−150.500	9	101	Y
17	Opravilová and Hajek, 2006	49.097	17.986	11	40	N
18	Schnitchen et al. (2006a)	48.180	22.500	13	110	N
19	Schnitchen et al. (2006b)	46.922	24.576	9	40	N
20	Payne and Mitchell (2007)	41.488	24.312	4	60	Y
21	Charman et al. (2007)	55.076	−2.510	8	143	Y
22	Lamentowicz et al. (2007)	52.737	16.756	10	24	Y
23	Booth (2008)	43.610	−82.836	31	369	Y
24	Payne et al. (2008)	40.693	38.335	1	53	Y
25	Lamentowicz et al. (2008)	52.736	16.757	4	30	N
26	Booth et al. (2008)	34.934	−77.104	1	42	Y
27	Swindles et al. (2009)	54.887	−6.549	3	94	Y
28	Mieczan (2009)	51.406	21.760	5	160	N
29	Lamentowicz et al. (2010)	46.475	9.820	6	97	Y
30	Markel et al. (2010)	63.082	−149.528	12	150	Y
31	Payne et al. (2010)	33.067	35.584	2	55	Y
32	Lamentowicz et al. (2011)	52.458	17.298	4	71	Y
33	Sullivan and Booth (2011)	41.039	−75.264	11	72	Y
34	Payne (2011)	34.747	32.898	15	211	N
35	Qin et al. (2012)	31.493	109.997	1	88	Y
36	Turner and Swindles (2012)	53.914	−1.855	3	60	Y
37	Väliranta et al. (2012)	60.783	22.783	2	24	N
38	Mitchell et al. (2013)	46.475	9.820	6	95	N
39	Qin et al. (2013)	29.964	109.753	4	48	Y
40	Lamarre et al. (2013)	54.115	−72.500	18	206	Y
41	Turner et al. (2013)	54.097	−2.175	6	207	Y
42	Amesbury et al. (2013)	50.211	−61.251	18	232	Y
43	Lamentowicz et al. (2013)	52.420	17.365	8	147	Y
44	Van Bellen et al. (2014)	−53.860	−69.576	5	154	N
45	Swindles et al. (2014)	−7.269	−76.542	1	100	N
46	Song et al. (2014)	48.419	129.081	5	46	N
47	Swindles et al. (2015)	68.031	19.766	9	89	Y
48	Koenig et al. (2015)	46.754	7.762	4	84	N
49	Li et al. (2015)	48.417	129.081	3	91	N
50	Fournier et al. (2015)	60.740	−150.500	4	4	N
51	Van Bellen et al. (2017)	53.860	69.576	4	99	N
52	Mazei et al. (2017)	60.117	71.500	13	143	Y
53	Zhang et al. (2017)	67.267	49.883	4	145	N
54	Tsyganov et al. (2017)	58.085	38.242	18	80	Y
55	Swindles et al. (2018)	9.382	−82.366	5	10	N
56	Beaulne et al. (2018)	49.175	79.382	11	72	N
57	Taylor et al. (2019)	68.814	−148.841	5	100	N
58	Liu et al. (2019)	5.543	−72.961	5	107	N
59	Zheng et al. (2019)	−35.650	148.830	8	70	N
60	Krashevska et al. (2020)	−1.200	103.600	1	70	N
61	Payne et al. (2021)	54.000	158.000	16	37	N
62	Sim et al. (2021)	78.183	16.234	5	103	N
63	Barrett et al. (2021)	20.174	−155.738	9	90	N
64	Qin et al. (2021)	48.803	86.930	29	444	Y
65	Šímová et al. (2022)	49.463	18.535	114	264	N
a	Clifford and Booth, unpublished	49.1225	−122.97	6	66	Y
b	Finkelstein & Bunbury, unpublished	52.8449	−83.9264	7	48	Y
c	Roe et al. (2017)	45.6858	−74.0462	3	145	Y
d	Sullivan and Booth (2011)	41.0378	−75.2655	2	66	Y
e	Swindles, unpublished	68.624	−149.583	1	7	Y
f	Talbot, unpublished	45.2729	−75.4687	3	24	Y

(continued on next page)

Table 1 (*continued*)

Study #	Citation	Latitude	Longitude	# of peatlands	# of samples	Data in Neotoma
g	Mallon, unpublished	57.175	12.5975	10	149	Y
h	Lamentowicz et al. (2015)	60.8904	68.6892	1	67	Y
i	Mazei and Tsyganov (2007)	53.01	45.7732	1	38	Y
j	Mazei et al. (2009)	58.0845	38.2417	2	60	Y
k	Mitchell et al. (2000)	52.7973	6.3968	5	78	Y
l	Payne (2010)	56.4517	−5.393	1	50	Y

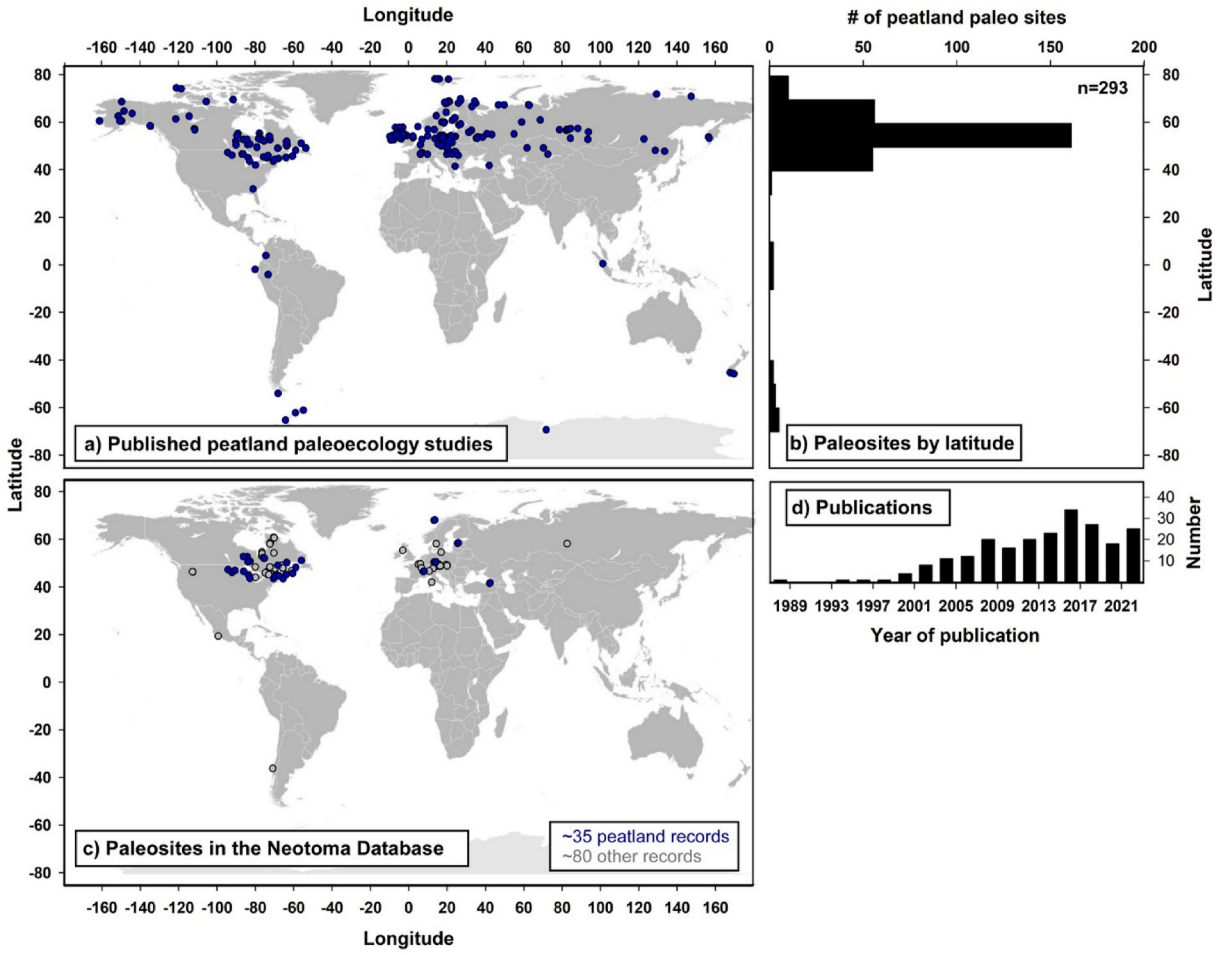

Fig. 2. Published testate amoeba stratigraphic records from peatlands. Distribution of peatlands is shown in panel a, with the number of peatlands plotted against latitude in panel b. Peatland stratigraphic records (blue) and other testate amoeba records, which are mostly from lakes (gray), within the Neotoma paleoecology database are shown in panel c. The frequency of publications since 1988 within 2-year bins is shown in panel d. Names and publications associated with the North American Neotoma records used for the modern-subfossil comparison in this study are listed in Table 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

numerous, and include the examination and modeling of relationships among taxa, morpho-functional traits, and environmental conditions at large spatial and temporal scales, and the assessment of the stability of taxon-environment relationships among regions. Furthermore, the surface-sample data can be used to develop transfer functions at various spatial scales, allowing model development from training sets for individual regions as well as continents, hemispheres, or potentially even global scales.

In tandem with the development of modern calibration datasets from surface samples, an increasing number of Holocene stratigraphic testate amoeba records have been obtained from peatlands over the past several decades, mostly in the northern hemisphere (Fig. 2). In these studies, testate amoebae have served as tools, often used in tandem with other proxies (e.g., plant macrofossils, pollen, geochemistry) to provide insights into a broad range of paleoenvironmental topics, including information about local peatland development and history (e.g., Lamentowicz et al., 2019), factors controlling peatland carbon accumulation (e.g., Charman et al., 2015; Davies et al., 2023), the impact of anthropogenic disturbance and climate change on microbial communities (e.g., Ireland et al., 2014; Amesbury et al., 2017; Zhang et al., 2020), paleoclimatic reconstructions (e.g., Turner et al., 2016; Mackay et al., 2021), and assessing the role of moisture variability in driving ecological change in nearby terrestrial ecosystems (e.g., Clifford and Booth, 2013; Booth et al., 2023).

Regional-scale syntheses of testate amoeba paleoenvironmental records have occurred in a few areas with a high-density of peatland stratigraphic records, focusing on derived variables like water-table depth (e.g., Swindles et al., 2019; Mackay et al., 2021; Zhang et al., 2022). However, broader syntheses of paleoecological records, with respect to both water table depth reconstructions as well as changes in

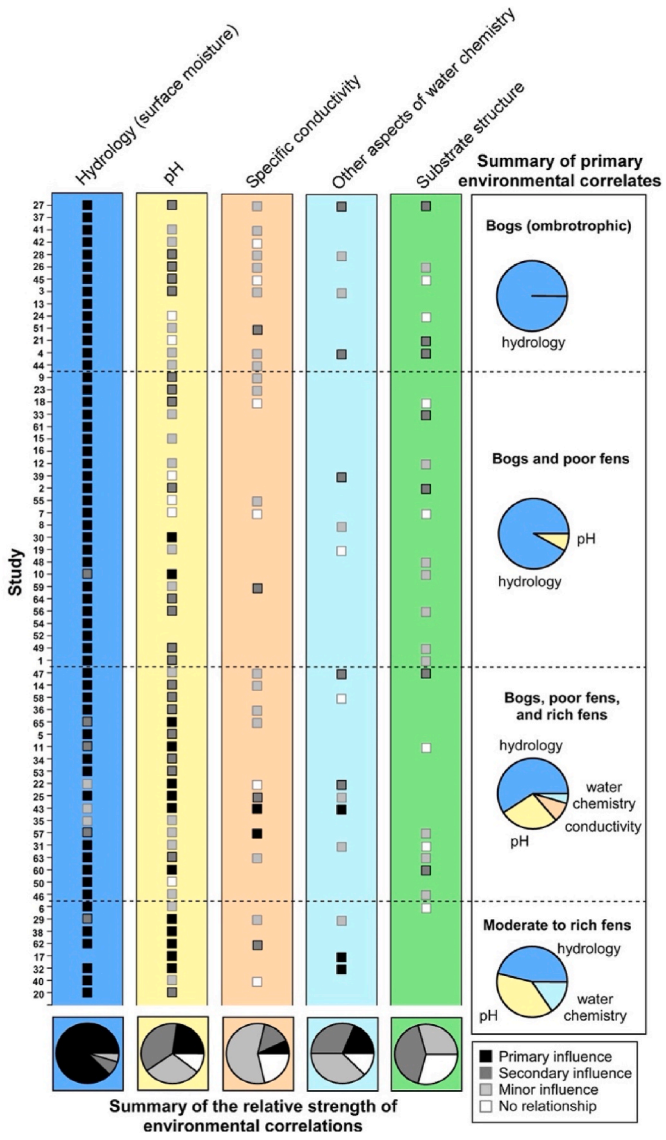

Fig. 3. Summary of the relative strength of environmental factors influencing testate amoeba community composition in surface-sample calibration studies (1987–2022). Squares indicate how important the environmental variable was in explaining testate amoeba community composition, with black squares indicating it was of primary importance, dark gray squares indicating secondary importance, light gray squares indicating a minor relationship, and white squares indicating that no relationship was found. Pie charts along the bottom summarize the importance of each measured variable across all studies, and pie charts along the right summarize the environmental variables of primary importance within studies that sampled different lengths of the peatland trophic gradient. Substrate moisture was measured as either water-table depth or percent moisture, and substrate structure included variables like bulk density, length of live *Sphagnum*, porosity, and organic matter content.

community composition, have been hindered by the relatively small number of stratigraphic datasets that are publicly available in an easily searchable and accessible format. Although the testate amoeba research community has lagged behind other paleoecological research communities (e.g., pollen) in making stratigraphic data publicly available in a centralized database, an increasing number of stratigraphic records are being incorporated into Neotoma (Fig. 2c).

The combined use of large databases, containing both modern and subfossil testate amoebae, may facilitate biogeographic and ecological studies of testate amoebae in both time and space, as well as deeper examination of similarities and dissimilarities between subfossil and modern communities. For example, it has been known for some time that weakly idiosomic tests (WISTs) do not preserve well in many acidic peatlands (Mitchell et al., 2008), although the effect of this on paleoenvironmental interpretations appears small in some records and many studies have removed these taxa from analyses and interpretation (e.g., Booth and Jackson, 2003; Mitchell et al., 2008; Swindles et al., 2020). However, there has not been a systematic assessment of the quality of modern analogues in testate amoeba research like there has been with other proxy types, particularly pollen (e.g., Jackson and Williams, 2004), and such investigations have revealed important insights and uncertainties for paleoenvironmental reconstruction (Overpeck et al., 1985; Williams and Jackson, 2007), and influenced thinking about future changes in the earth system (Jackson and Williams, 2004; Reu et al., 2014; Radeloff et al., 2015). Even beyond the poor preservation of WISTs in testate amoeba stratigraphic records, there may be other causes of differences between modern and subfossil testate amoeba communities, including differential preservation in response to desiccation, decomposition, and peatland acidity (e.g., Swindles and Roe, 2007; Payne, 2007), past environmental conditions outside the range of modern calibration datasets, and/or other ecological dynamics. Furthermore, combinations of taxa that are rarely found in high abundance together in modern surface-samples may characterize some subfossil communities (e.g., Charman et al., 2007; Booth, 2008). Direct comparison of stratigraphic and modern datasets is needed to more fully assess and understand the similarity of modern-subfossil communities, and large datasets are needed to identify broad patterns and extend our knowledge beyond site-specific observations.

In this paper, we first briefly review and discuss peatland testate amoeba ecology with a focus on broadly synthesizing results of calibration studies during the past ~35 years. We then demonstrate the utility of Neotoma by 1) analyzing and discussing modern morphospecies-environment relationships in calibration datasets collectively from the northern hemisphere, and 2) directly comparing subfossil and modern testate amoeba communities to provide an assessment of their similarities and the strength of modern analogues in testate amoeba paleoenvironmental research.

2. Methods

2.1. Synthesis of modern calibration studies

To identify and synthesize studies that have developed calibration datasets for quantitative paleoenvironmental inference, we performed a literature review of studies published prior to 2023 (Table 1). We did not include two continental-scale syntheses in this list (i.e., Amesbury et al., 2016, 2018), as most of the samples included in these were originally published within the regional studies that we reviewed. For each publication, we recorded the environmental measurements that were collected (e.g., water-table depth, pH, specific conductivity), the authors' interpretation of the relative strength of environmental measurements in influencing testate amoeba community composition, and the range of peatland types sampled (e.g., bogs, poor fens, rich fens). To summarize the relative influence of environmental conditions on community composition in each study, we categorically ranked each measured environmental variable based on the authors' descriptions and an inspection of the statistical results, as follows: 1) the most important (i.e., primary) identified environmental control(s), 2) important measured environmental variables, but not as strongly correlated (i.e., secondary), 3) measured environmental variables with a potentially small effect or correlation, and 4) those variables where little-to-no relationship was found with community composition. If transfer functions were developed in the study, we recorded the jackknifed (or bootstrapped, if jackknifed values were not reported) root mean square error of prediction and r-squared value of the best performing transfer function.

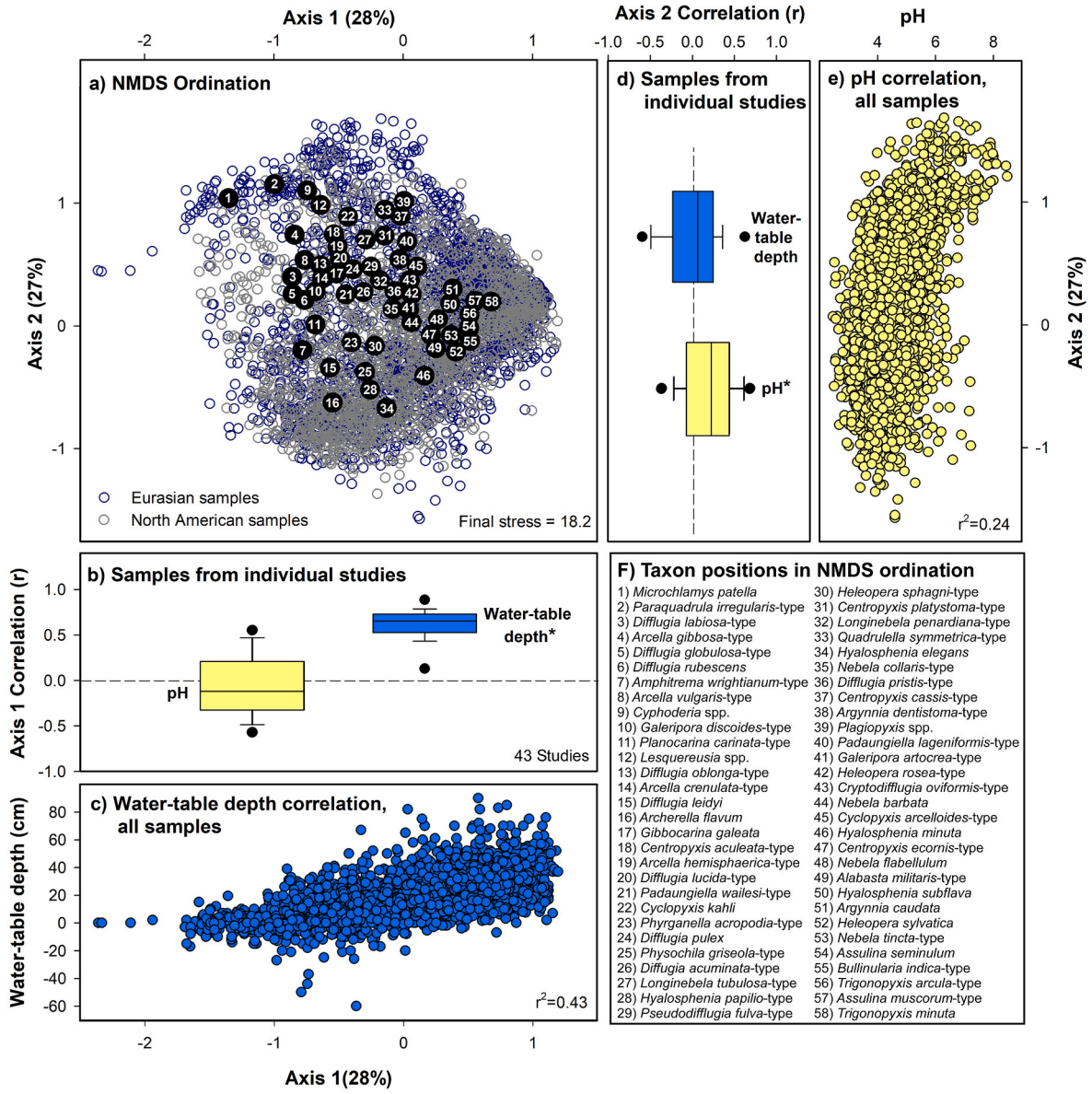

Fig. 4. First two axes of a three-dimensional non-metric multidimensional ordination of testate amoeba communities, excluding weakly idiosomic taxa (WISTs), and environmental correlations using the surface-sample dataset of the Neotoma Paleoecology Database. Panel a shows sample positions, weighted averages for taxon positions indicated with numbers, and the percent variance represented by each axis shown on the axis labels. Axis correlations with pH and water-table depth for samples from individual studies shown in panel b and d. Boxplots show median (line), 25th percentile (box), 75 % percentile (whiskers), and 95 % percentile (dots). Scatterplots of significant correlations ($p < 0.05$) of axes with environmental variables are shown for the entire dataset in panels c and e. Taxa are listed in their order along the moisture-related axis 1 in panel f.

2.2. Examination of modern morphospecies-environment relationships in the northern hemisphere

All peatland surface-samples in Neotoma (neotomadb.org) as of January 2024 were included in our study. Taxonomic harmonization was applied, similar to the approaches used in other large-scale studies (Amesbury et al., 2016, 2018; Qin et al., 2021), and this resulted in the establishment of 58 morphologically defined taxa (Appendix A). After taxonomic harmonization, rare taxa that were present in less than 50 samples were removed from subsequent analyses. We also first removed WIST taxa, given the strong evidence that these do not preserve well in many peatland environments (e.g., Mitchell et al., 2008; Swindles et al., 2020; Sim et al., 2021). After WIST and rare taxon removal, samples with less than 50 total individuals were removed from further analysis and the relative abundance of each taxon was calculated for the remaining samples. The final dataset for analysis included 4012 samples from over 240 sites in the northern hemisphere. Water-table depth and pH measurements were available for 3880 and 3637 of these samples, respectively. Non-metric multidimensional scaling (NMDS), using PC-Ord Software, was used to investigate testate amoeba community composition (McCune and Mefford, 2018). Pearson correlations were calculated between sample axis scores and water-table depth and pH measurements to provide a sense of the direction and strength of these variables in relation to the main gradients of community composition (McCune and Grace, 2002). Environmental correlations were also calculated independently using only the samples from each individual study contained within Neotoma.

2.3. Comparison of stratigraphic and modern communities: assessing modern analogues

Peatland stratigraphic records of testate amoebae contained within

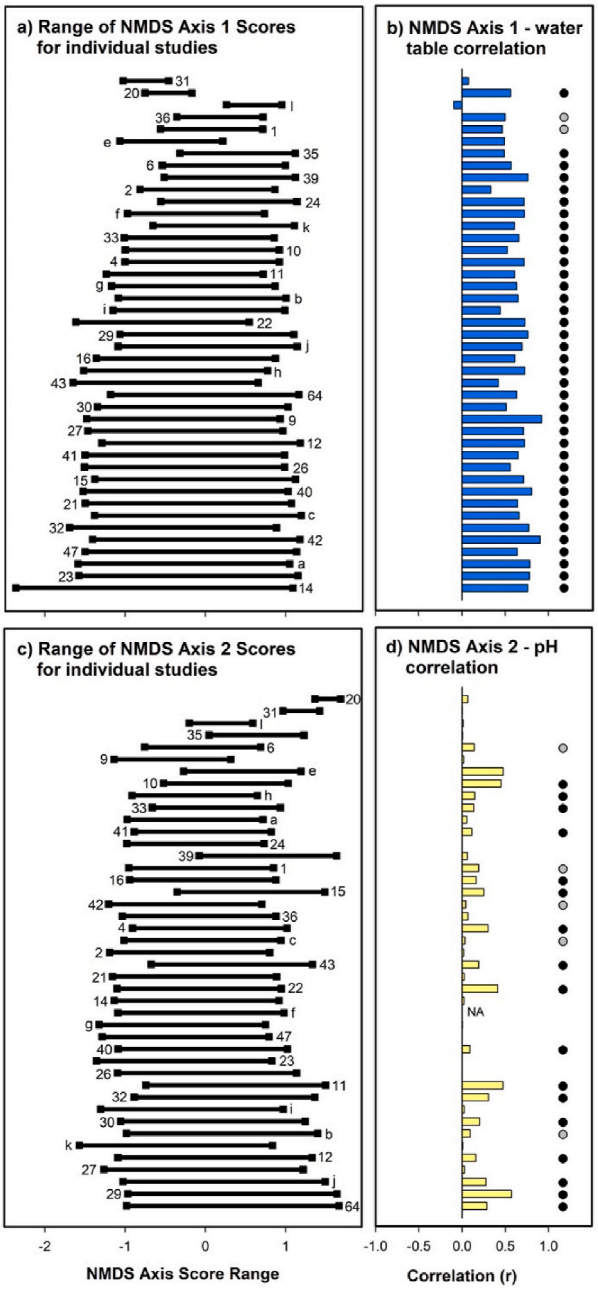

Fig. 5. Length of the compositional gradients along NMDS axis 1 and 2 (panels a and c) for the surface samples of each modern study in Neotoma. Numbers refer to studies listed in Table 1. Correlations between NMDS axis 1 and water table depth for the samples of each study are shown in panel b. Correlations between NMDS axis 2 and pH for the samples of each study are shown in panel d. Significance of correlations is indicated with gray ($p < 0.05$) or black ($p < 0.01$) circles.

Neotoma as of January 2024 were used for our analyses. Several European sites contained only counts for two taxa (*Archerella flavum* and *Assulina muscorum*), or very few samples, so we did not include European stratigraphic samples in this analysis. We applied the same taxonomic harmonization and taxon-removal approach that was used for the modern samples (Appendix A). The final analyzed dataset consisted of 2401 stratigraphic samples from 28 sites in North America (Table 2). We categorized stratigraphic samples based on age or depth, as reported in Neotoma, with samples from the upper 2 cm of each record considered "modern," samples less than approximately 100 years old (1900 CE) considered "recent," and samples older than this considered "subfossil."

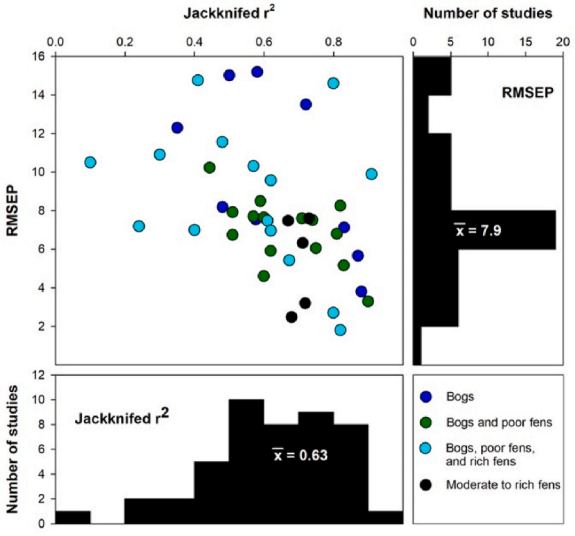

Fig. 6. Summary of transfer function cross-validation statistics for water-table depth from the literature, including root mean square error of prediction (RMSEP) and jackknifed r^2, for the individual studies shown in Table 1.

Modern, recent, and subfossil samples were compared using NMDS, and indicator species analysis was performed using PC-ORD software to identify taxa that differed in frequency and/or abundance in modern versus subfossil samples (Dufrêne and Legendre, 1997; McCune and Mefford, 2018). Indicator values were calculated based on frequency and abundance in the two groups, with Monte Carlo tests ($n = 5000$) to assess significant differences ($p < 0.01$). Morphospecies richness and Shannon diversity were also compared between subfossil and modern datasets, with significant differences assessed through Mann-Whitney Rank Sum tests.

To further assess the degree to which subfossil samples have good modern analogues, the number of modern analogues was determined for each stratigraphic subfossil sample in the dataset. To do this, we calculated a Bray-Curtis dissimilarity matrix with all modern samples, using PC-Ord software (McCune and Mefford, 2018). We defined the critical dissimilarity for the identification of modern analogues using a low percentile of the distribution of pair-wise dissimilarities in the surface-sample dataset, an approach previously used to establish similarity-thresholds for modern analogues (Simpson, 2012). Four percentiles (1, 2.5, 5, 10) were explored as thresholds, reflecting a range of possible values to assess the number of modern analogues for each subfossil sample. Bray-Curtis dissimilarity values were calculated between each subfossil sample and every sample in the modern dataset. The percent of subfossil samples with >0, >10, >20, and >50 modern analogues was calculated for each similarity threshold. To explore and describe the community composition of samples with few good modern analogues, a cluster analysis of subfossil samples with less than 10 good modern analogues, using Edwards and Cavalli-Sforza's chord distance, was performed using TILIA software (Grimm, 2015).

3. Results and discussion

3.1. Synthesis of testate amoeba calibration studies

Quantitative ecological studies of the past several decades, mostly undertaken to inform paleoenvironmental interpretations, have confirmed observations of earlier researchers (e.g., Jung, 1936; Heal, 1961) regarding the importance of surface moisture in controlling the community composition of testate amoebae in peatlands (Fig. 3). These studies have revealed that substrate moisture is a particularly important influence on testate amoeba communities in oligotrophic (i.e.,

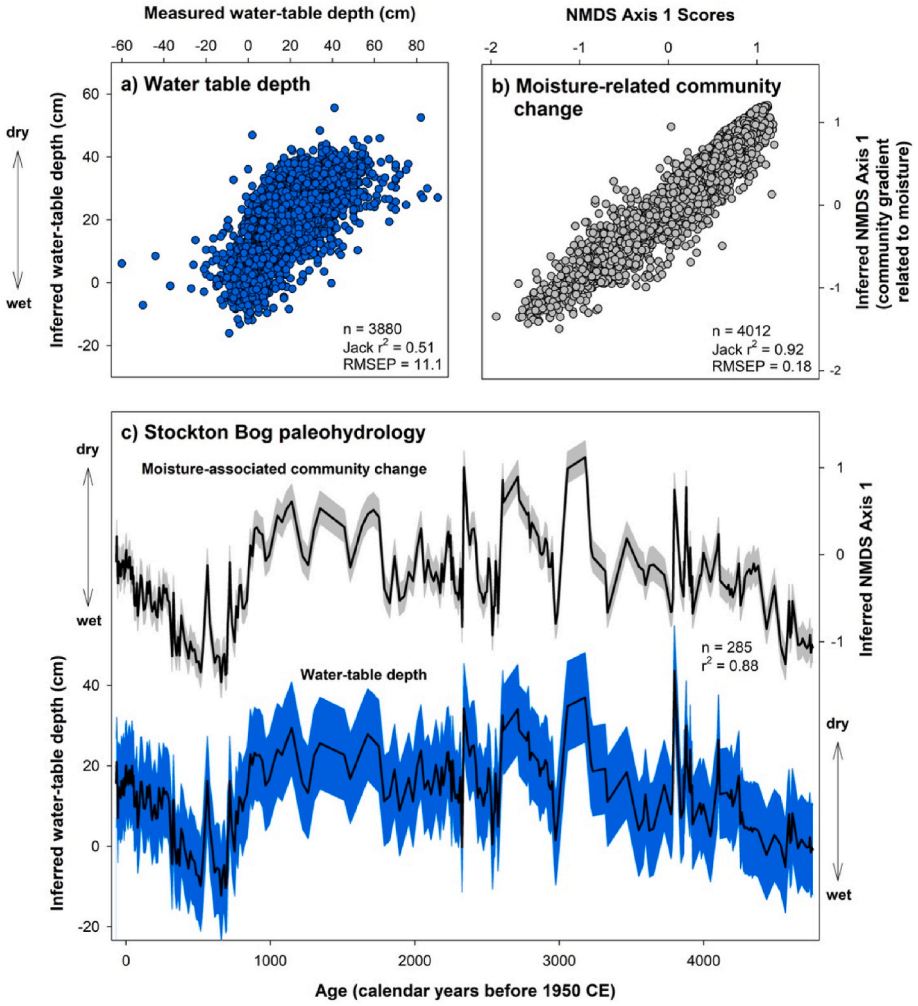

Fig. 7. Cross validation and application of transfer functions for water-table depth and an index of moisture-related community change (NMDS axis 1 from Fig. 4), using North American modern samples from Neotoma. A weighted average partial least squares (2 component) model was used, as this is a commonly applied model in many studies. Cross validation biplot of measured versus inferred water-table depths is shown in panel a, and panel b shows a biplot of calculated versus inferred NMDS axis 1 scores, which represents the community gradient associated with moisture from Fig. 4. Panel c shows testate amoeba-based reconstructions for a subfossil dataset from Stockton Bog in Wisconsin (data from Neotoma). The upper plot shows a reconstruction of the index of moisture-associated community change, with sample-specific bootstrapped uncertainty estimates (n = 1000). The lower plot shows a water-table depth reconstruction using the same subfossil data and the transfer function shown in panel a, also with bootstrapped uncertainty estimates (n = 1000).

low-nutrient), *Sphagnum*-dominated peatlands (i.e., bogs and poor fens). In fact, in low-nutrient and acidic conditions, substrate moisture has been identified as the primary control on morphospecies distribution with few exceptions (Fig. 3). Other environmental factors like pH, water chemistry, and/or characteristics of the substrate (e.g., bulk density, vegetation) have been identified as secondary controls on community composition in oligotrophic peatlands (Fig. 3), and may influence relationships with moisture (e.g., Booth and Sullivan, 2011; Halaś et al., 2023). However, in more nutrient-rich peatlands, or when a more complete fen-to-bog gradient has been sampled, studies have found pH and other aspects of water chemistry to sometimes be equally and occasionally even more important than substrate moisture in controlling morphospecies distribution and abundance (Fig. 3). This is not surprising given the large differences in testate amoeba communities between oligotrophic and nutrient-rich environments. However, the central importance of substrate moisture is highlighted by the fact that over 87 % of the studies during the past 35 years have identified moisture as a primary influence on community composition, regardless of geographic location (Fig. 3).

3.2. *Challenges with merging regional calibration datasets*

Despite the clear relationship between surface moisture and testate amoeba communities in individual studies, a potential challenge for merging peatland calibration datasets has been combining water table measurements made in different seasons, years, and locations. Most calibration datasets have made one-time measurements of water-table depth (i.e., measured on the day of sampling), although the collected testate amoeba communities likely integrate several years of test accumulation. Measuring water-table depths in some peatlands has been particularly problematic during dry seasons or years (Booth, 2008), because these measurements are usually made by digging holes and measuring the water level; however, water levels within these holes may not reach equilibrium with the surrounding peat for a long time because of the often low-hydraulic conductivity of deeper peats. Furthermore, water-table depths within *Sphagnum*-dominated peatlands often vary by more than 40 cm during the growing season (Booth et al., 2005), so measurements made at different times of year are not directly comparable. Only a few studies have been able to obtain average water-levels or other measurements that likely reflect the long-term or growing

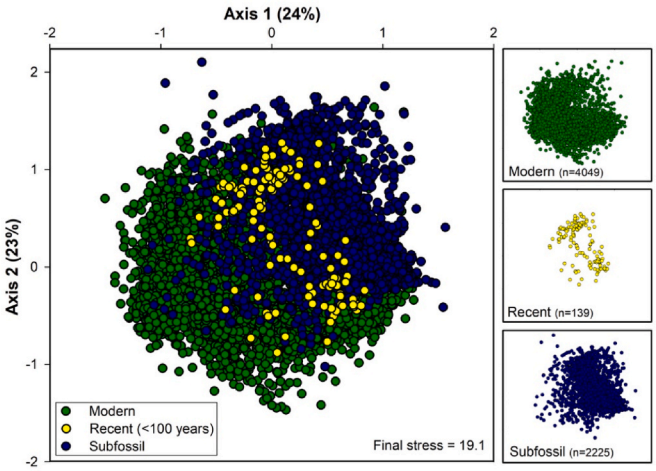

Fig. 8. First two dimensions of a three-dimensional NMDS ordination of modern, recent, and subfossil data from Neotoma, with side panels added to better see the distribution of the three types of samples in the ordination space. The variance represented by each axis is shown on the axis labels.

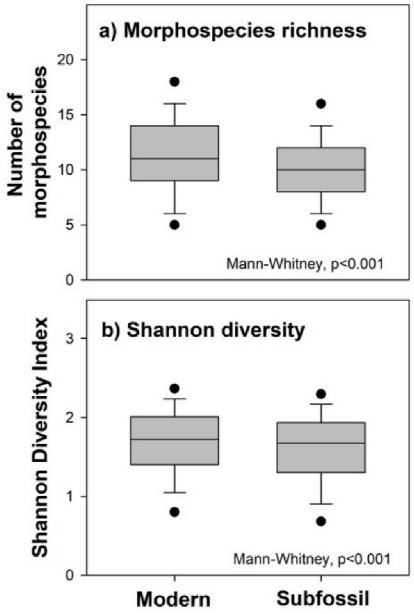

Fig. 9. Comparison of taxonomic a) richness and b) diversity between modern and subfossil samples in Neotoma.

season hydrological conditions (e.g., Woodward et al., 1998; Booth, 2008).

Some studies may also have differed in how they have recorded water-table depth values at the ends of the moisture gradient, although this has not always been well described in publications. For example, some studies have truncated measurements on the dry end of the gradient, with water-table depth values greater than a particular threshold (in some cases 50 cm), all assigned the same maximum value (e.g., Booth, 2002). A similar truncation on the wet-side of the gradient may have occurred in a few studies (R. Payne, personal communication 2010); regardless though, when samples and environmental measurements from multiple studies conducted in different years and seasons are combined for collective analysis, there is much uncertainty introduced into the description and comparability of the moisture gradient.

3.3. Collective analysis of surface-sample datasets using the Neotoma paleoecology database

Despite issues with one-time measurements of environmental conditions, collective analysis of the surface samples from Neotoma revealed significant correlations between community composition and both water-table depth and pH measurements (Fig. 4). A three-dimensional NMDS solution represented 70 % of the variability in the community data, and samples from North America and Eurasia overlapped considerably in the ordination space, attesting to the broad similarity in peatland testate amoeba communities across the Northern Hemisphere at the somewhat coarse taxonomic resolution of this study (Fig. 4a). Typical indicators of drier peatland conditions, like *Trigonopyxis* spp., *Bullinularia indica*-type, and *Nebela tincta*-type, are positioned on the right side of NMDS axis 1, whereas wetter taxa like *Amphitrema wrightianum*-type and several *Difflugia* and *Arcella* are positioned on the left side of NMDS axis 1 (Fig. 4a–f). Taxa more common in higher pH and nutrient-rich fen environments, such as *Paraquadrula irregularis*-type and *Cyphoderia* spp. are positioned high on NMDS 2 (Fig. 4a–f).

Amesbury et al. (2018) noted the similarity in the ecological niche of taxa between North America and Europe, and our analysis suggests that similar relationships exist with moisture across the Northern Hemisphere at the taxonomic resolution of our synthesis (Figs. 4 and 5). When correlations were calculated between the NMDS axis 1 scores and water-table measurements of the samples independently for each individual study in Neotoma, almost all studies had a positive correlation, indicating that patterns of community turnover are not only similar among studies, but these patterns have similar relationships with substrate moisture across regions (Fig. 4b and 5a). The few studies with lower correlations between community composition and water-table depth generally analyzed a very short portion of the total compositional gradient (Fig. 5a and b). Several of these studies were not collected explicitly for paleoenvironmental inference, including an experimental study on acid deposition that captured short water-table depth and compositional gradients (Payne, 2010), and a study from a drained and disturbed peatland (Payne et al., 2010) (Fig. 5a and b). Positive correlations between NMDS axis 2 scores and pH were also found for the samples from most studies (Fig. 5d), suggesting that general patterns of community changes along pH gradients are also broadly similar in the Northern Hemisphere at the taxonomic resolution of the dataset. These results further support the interpretations of individual, regional studies of the past several decades (Fig. 3), and attest to the primary influence of surface moisture on testate amoeba composition, with a secondary influence of pH particularly when a more complete bog-to-fen gradient is sampled (Fig. 5).

Although the major patterns of community change in the individual studies attest to the similarity of testate amoeba community gradients along moisture and pH gradients in the northern hemisphere, it must be remembered that these measurements are acting as proxy variables for complex environmental and habitat gradients (Mitchell et al., 2008). Causal relationships underlying the correlations are not well established, although analysis of morpho-functional trait distributions suggest causal relationships in some cases (e.g., Fournier et al., 2015; Marcisz et al., 2020). Also, other factors can affect testate amoeba community composition (Fig. 3) and the influence of these factors may affect some peatlands more than others, and may have varied in the past, so caveats and caution are needed when interpreting paleoecological records; of course, this is not unique to testate amoeba records (Juggins, 2013). Environmental conditions may also mediate or influence the response of testate amoeba communities to surface moisture. For example, different moss species create different microenvironments for microorganisms and can influence the magnitude of seasonal moisture variability experienced by testate amoebae, and may also affect moisture sensitivity (Sullivan and Booth, 2011, Halaś et al., 2023). However, the consistent importance of moisture in controlling testate amoeba

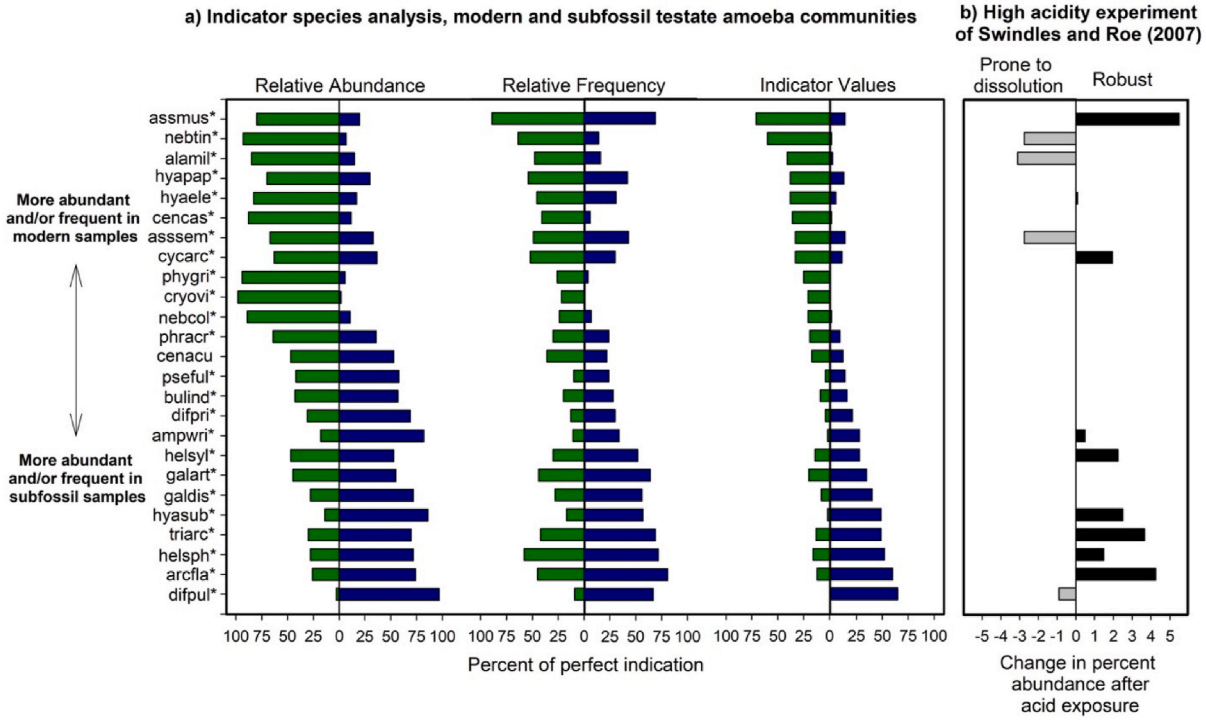

Fig. 10. Results of indicator species analysis comparing the abundance and frequency of common taxa in modern and subfossil samples. Taxa are indicated by the first three letters of the genus followed by the first three letters of the specific epithet. Green bars indicate the relative abundance, relative frequency, and indicator value for taxa in modern samples, and blue bars indicate the relative abundance, relative frequency, and indicator value for taxa in subfossil samples. Relative abundance is expressed as the average abundance of a given taxon in the group divided by the average abundance of that taxon in all samples. Relative frequency is the percent of samples in a group where a taxon is present. Indicator values combine the values for frequency and relative abundance. Asterisks indicate results of Monte Carlo significance test for differences in the indicator value between subfossil and modern samples ($p < 0.01$). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

communities in peatlands across the northern hemisphere is unusual when compared to the diversity of environmental controls affecting other paleoecological proxies. For example, diatoms have been used to reconstruct over 25 different environmental variables (Juggins, 2013) suggesting a broad range of environmental controls that vary across lake types and regions; similarly, the environmental controls on chironomids vary locally and regionally (e.g., Luoto et al., 2016).

Our results are based on a taxonomically harmonized, morphospecies approach consistent with what has been widely applied in peatland paleoenvironmental work over the past several decades (e.g., Woodland et al., 1998; Charman et al., 2007; Amesbury et al., 2016, 2018; Qin et al., 2021). The striking similarity of community changes associated with water-table and pH and gradients across nearly all studies (Fig. 5) provides compelling support for paleoenvironmental work using this taxonomic framework. However, some of the morphospecies used here and in most other Quaternary applications certainly represent diverse collections of species, with potentially different biogeographic distributions and ecology. Future work with increased taxonomic precision would potentially provide valuable insight into regional and local differences, improved distribution models, and may lead to refinement of our knowledge of community-environment relationships.

3.4. *Paleoenvironmental inference using northern hemisphere surface-sample dataset*

Most quantitative studies of the past several decades have developed and cross-validated transfer functions for water-table depth, reporting root mean square error of prediction (RMSEP) and jackknifed (or bootstrapped) r^2 values to assess the performance of these transfer functions. A variety of transfer function models have been employed (e.g., weighted averaging, weighted average-partial least squares, maximum likelihood), and techniques to account for spatial autocorrelation and other issues have been proposed (Payne et al., 2012). Although many studies have focused on identifying best-performing models, performance is often relatively similar across different model types and the interpretation of reconstructions using different models has generally been similar (Booth, 2008; Amesbury et al., 2018). In our review of the literature, the average RMSEP and jackknifed r^2 values for water-table depth across all studies was 7.9 cm and 0.63 respectively, although these are likely somewhat inflated due to spatial autocorrelation (Payne et al., 2012). Studies that included the widest range of peatland types had the greatest variation in performance statistics (Fig. 6).

Despite the challenges of merging regional datasets, continental-scale transfer functions have been successfully developed with one-time measurements of water tables collected in different studies (Amesbury et al., 2016, 2018; Qin et al., 2021). Broader syntheses are also likely possible given the similarity in results based on the application of different continental-scale models; for example, Amesbury et al. (2018) found that applying North American and European transfer functions to the same subfossil record resulted in nearly identical reconstructions. Although our study demonstrates that transfer functions based on samples from the entire northern hemisphere can be developed (Fig. 7a), combining many regional datasets clearly introduces uncertainty into the characterization of the moisture gradient, increasing error estimates for subfossil reconstructions, and potentially masking significant, moisture-related testate amoeba community changes. Not surprisingly, a transfer function based on all the northern hemisphere samples in Neotoma (Fig. 7a), does not perform as well in cross validation as most regional datasets (Fig. 6). However, a clear trade-off exists between using a continental or hemispheric transfer function and a training set based on a local or regional study, given that large

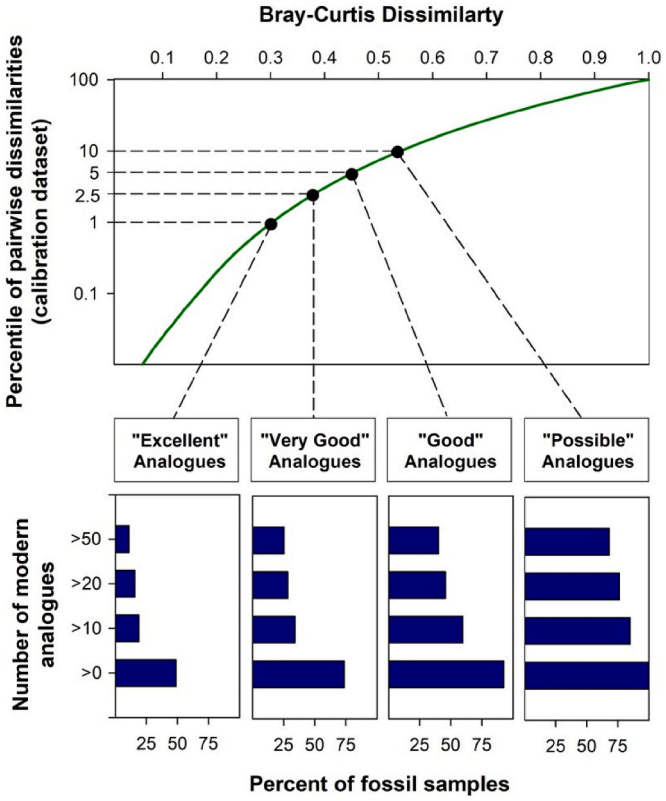

Fig. 11. Percent of subfossil samples across the 28 North American sites with different numbers of modern analogues, using four different similarity thresholds.

datasets contain significantly more information on community structure and a larger number of potential modern analogues. However, regional or local datasets likely have better characterization of the moisture gradient, since measurements were more likely made as part of single field campaign, and often these studies have greater taxonomic precision and may require less taxonomic harmonization than a large dataset compiled from many studies.

Unlike many other biological proxy reconstructions (e.g., pollen inferred temperature or precipitation, diatom inferred pH) the absolute values of water-table depth are rarely interpreted in testate amoeba paleoenvironmental applications; instead, the focus has been on relative changes (e.g., wetter, drier). In fact, several studies have argued for the use of z-scores in moisture reconstructions instead of absolute water table values (Swindles et al., 2015; Amesbury et al., 2016). Given this relative interpretation of water-table depths and the recognized error introduced through the merging of water-table depth measurements from regional datasets, the direct reconstruction of water-table depth using a large hemisphere-spanning dataset may not be ideal. A case can be made that when using large calibration datasets compiled from multiple studies, focusing on changes in the testate amoeba communities themselves might be a more straightforward, even if less quantitative, way to infer past relative changes likely linked to changing surface moisture. A simple way to do this would be to estimate the position for subfossil samples along the community gradient(s) described through ordination of modern samples, given the positive correlation between these community changes and measured water-table depths (Fig. 4). As an example, using the NMDS axis 1 scores and testate amoeba data from the modern samples in Neotoma, NMDS axis 1 scores could be estimated for subfossil samples using a weighted average or one of the many similar transfer-function models (Fig. 7). Many other multivariate approaches could be explored to reconstruct an index of 'moisture-related community change' like that shown in Fig. 7, and although not as quantitative as direct moisture estimates, approaches like this would not directly use the measured water-tables and the uncertainty associated with one-time measurements would not affect interpretation.

Subfossil reconstructions and cross validation of transfer functions for water-table depth and moisture-related community change, based on the northern hemisphere surface samples in Neotoma, reveal very similar patterns (Fig. 7). Not surprisingly, the cross-validation statistics for the reconstruction of moisture-related community change are quite high, and likely not realistic, given that the community gradient was first described by NMDS on the entire dataset (Fig. 7b). However, reconstructions based on stratigraphic data from Stockton Bog in Wisconsin (Booth et al., 2023), are quite similar using the two methods and practical interpretation of the record in terms of changing moisture would be the same (Fig. 7c). The water-table depth reconstruction has higher uncertainty relative to the variance in the record, and at least some of this uncertainty results from the previously discussed problems created by combining water-table measurements collected in different studies at different times of year. Although uncertainty estimates for the moisture-associated community change approach do not reflect real uncertainty in the estimation of surface-moisture, they potentially provide a means of assessing times of significant community changes along the community gradient most likely associated with moisture (Fig. 7c). Such an approach should also be coupled with careful consideration of the actual community changes, avoiding the pitfall of uncritically accepting quantitative estimates of the water-table depth (Charman et al., 2007). Given the tradeoffs between using local or regional calibration datasets, versus hemispheric or even global training sets, the application of local or regional transfer functions along with community-based approaches using large datasets like Neotoma might best inform interpretations. Coupling these approaches with multi-proxy studies (e.g., plant macrofossils, geochemistry) may also aid interpretation and validation efforts.

3.5. *Comparing modern and subfossil testate amoeba communities*

A combined NMDS of subfossil and modern testate amoeba communities indicates that subfossil and modern samples often differ in composition, with many subfossil samples occupying space in the ordination where modern samples are not well represented and vice versa (Fig. 8). Recent stratigraphic samples, less than about 100 years old, tend to be comprised of communities positioned between modern and subfossil samples in the ordination space (Fig. 8). WISTs were not included in these analyses, so the differences in modern and subfossil communities are not related to their well-documented poor preservation in acidic peatlands. There are several possible hypotheses to explain differences in modern and subfossil peatland testate amoeba communities, including, 1) differential preservation of taxa in the subfossil record, 2) differences in the amount of time integrated by subfossil and modern samples, and/or 3) real differences in the composition of past and present testate amoeba communities, likely resulting from differences in past and modern environmental conditions.

Comparing the compositional differences of modern and subfossil communities may help assess the relative importance of these hypotheses. For example, morphospecies richness and diversity are slightly greater in modern versus subfossil samples (Fig. 9), consistent with a potential effect of decomposition removing or decreasing the abundance of more fragile taxa. Furthermore, these patterns don't appear consistent with differences in the amount of time integrated by modern versus subfossil samples; if that were the case, we might expect the subfossil samples to have greater diversity given that they generally incorporate more years of changing environmental conditions. However, differences in time integration cannot be completely ruled out as a source of some differences between modern and subfossil communities, because the effects of this are potentially superimposed on the effects of differential decomposition.

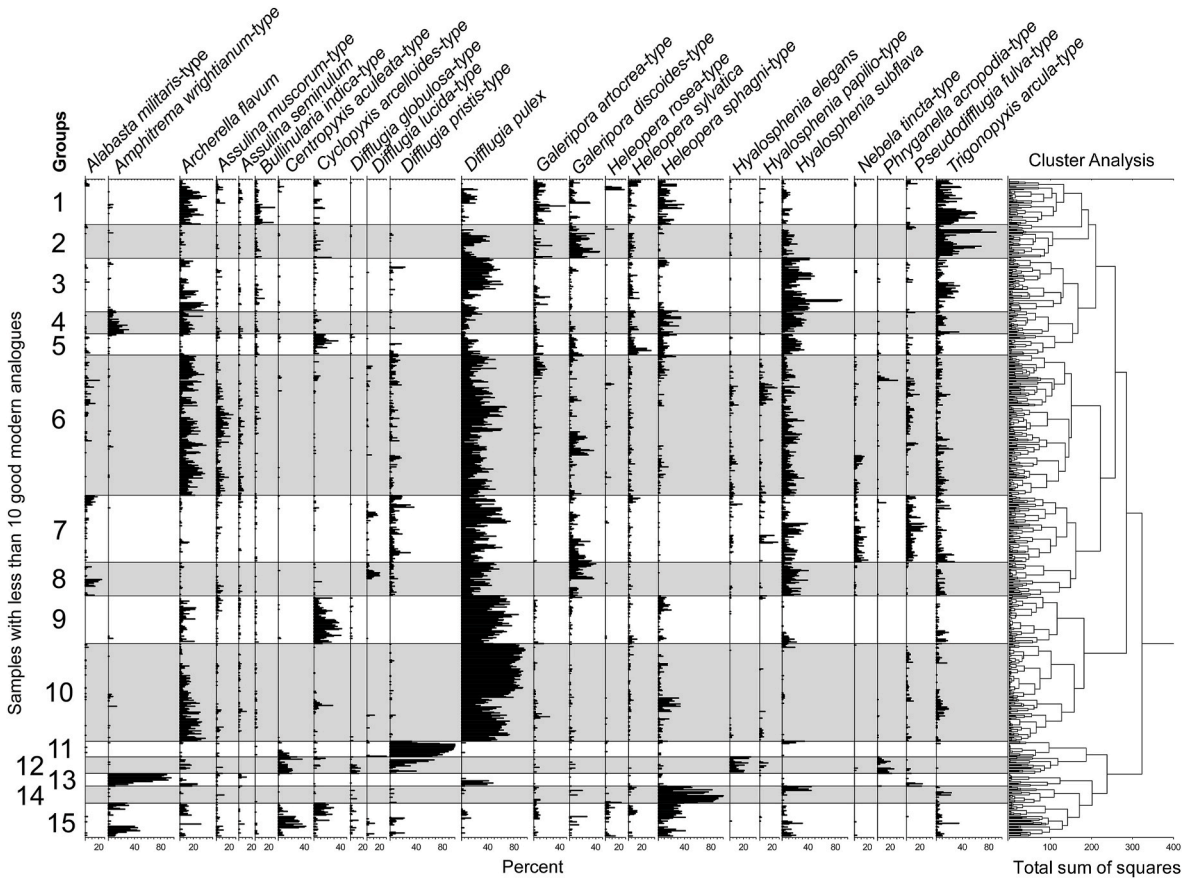

Fig. 12. Cluster analysis of subfossil samples across the 28 North American sites with less than 10 good modern analogues. The relative abundance of taxa present in at least 65 of these 668 samples are shown. Informal groups based on cluster analysis are described in Table 3.

The results of indicator species analysis comparing subfossil and modern communities, when viewed alongside previous experimental work, also tends to support the idea that differential decomposition is a likely cause of some differences (Fig. 10). Taxa more abundant in modern samples include several morphospecies that may be less resistant to microbial decomposition and more prone to dissolution based on experimental work (Fig. 10) (Swindles and Roe, 2007; Payne, 2007). For example, Swindles and Roe (2007) after treating samples with strong acid, found that *Nebela tincta*, *Alabasta militaris*, and *Assulina seminulum* were all prone to dissolution, and Payne (2007) found that the tests of *Hyalosphenia elegans* were sensitive to desiccation, with destruction of tests similar in magnitude to that experienced by *Euglypha rotunda*, a WIST taxon. Subfossil samples in Neotoma tended to have higher relative abundance of *Difflugia pulex*-type, *Archerella flavum*, *Heleopera sphagni*, *Trigonopyxis arcula*, *Hyalosphenia subflava*, *Galeripora discoides*, *Galeripora artocrea*, and *Amphitrema wrightianum* (Fig. 10). Many of these taxa were found to be robust to acid treatment in the experiment of Swindles and Roe (2007), consistent with differential decomposition of other taxa as a potential cause of their increased relative abundance in subfossil samples. Hendon and Charman (1997) and Magnan et al. (2021) found that taxa resistant to the chemicals used in pollen analysis, like *Archerella flavum*, *Galeripora discoides*, and *Assulina muscorum,* became over-represented on pollen slides because of the loss of more fragile taxa and the inter-dependence of percentage data. In our analysis, *Archerella flavum* and *Galeripora discoides* were both found to be more abundant in subfossil samples (Fig. 10).

However, not all differences between subfossil and modern communities can be explained by differential preservation. For example, *Assulina muscorum* is commonly encountered in stratigraphic records and is relatively resistant to acid and chemical treatments (Hendon and Charman, 1997; Magnan et al., 2021; Swindles and Roe, 2007); however, although we found its frequency was similar between modern and subfossil samples, it reached much higher abundance in some modern samples (Fig. 10). *Assulina muscorum* is a widely distributed taxon that reaches peak abundance in dry habitats (Fig. 4). Its higher abundance in modern samples might be due to greater sampling from drier habitats in the modern dataset, whereas very dry conditions might be underrepresented in the subfossil dataset because of poor peat preservation. Interestingly though, Swindles and Roe (2007) found that *Assulina seminulum*, a related taxon with a similar test construction to *Assulina muscorum*, was prone to dissolution when exposed to acid (Fig. 10).

The high abundance of some taxa in stratigraphic samples, like *Difflugia pulex*, has been noted before, in both North American and European records, because of the lack of good modern analogues for these subfossil samples (e.g., Charman et al., 2007; Booth, 2008; Mitchell et al., 2008; Sullivan and Booth, 2011; Amesbury et al., 2013; Lamarre et al., 2013; Magnan and Garneau, 2014). However, the causes for its high abundance in some subfossil communities and its relatively low abundance in surface samples remain unclear. The taxon was found to be slightly prone to acid dissolution (Swindles and Roe, 2007) and its abundance was significantly reduced by the chemical treatments used in pollen analysis (Magnan et al., 2021), so differential preservation is not a likely cause. Booth (2008) speculated that perhaps the taxon occupies lower portions of the *Sphagnum* stem and gets under-sampled in modern studies. Another hypothesis is that abundant *Difflugia pulex* may reflect the prevalence of environmental conditions on peatlands that are not as common today, and Charman et al. (2007) speculated that its high abundance in many mid-Holocene European records might have been related to more intense desiccation at the peatland surface by wind and/or insolation.

Table 2
North American stratigraphic records from Neotoma that were used in modern-subfossil comparison.

Site Name	Publication	Lat	Long	number of samples
Baie	Magnan and Garneau (2014)	49.094	−68.243	112
Burnt Village	Mackay et al. (2021)	51.127	−55.927	30
Frambois	Mackay et al. (2021)	45.722	−60.552	33
Hole	Booth et al. (2006)	47.308	−94.232	113
HRST1301	Davies et al. (2021)	50.766	−82.779	28
HRST1302	Davies et al. (2021)	50.626	−83.893	45
HRST1304	Davies et al. (2021)	50.592	−83.864	60
Jefferys	Mackay et al. (2021)	48.213	−58.820	31
Lebel	Magnan and Garneau (2014)	49.098	−68.222	146
Minden	Booth and Jackson (2003)	43.604	−82.864	184
Pointe des Morts	Magnan and Garneau (2014)	50.264	−63.669	58
Mosaik	van Bellen et al. (2011)	51.982	−75.402	68
Petite Bog	Charman et al. (2015)	45.144	−63.942	40
Plaine	Magnan and Garneau (2014)	50.267	−63.533	131
ROFT19	Davies et al. (2021)	52.750	−86.200	20
ROFTGH27	Davies et al. (2021)	52.790	−86.170	24
Saco	MacKay et al. (2021)	43.555	−70.472	27
South Rhody	Booth et al. (2004)	46.566	−86.075	162
Sterne	van Bellen et al. (2011)	52.044	−75.173	54
Stockton	Booth et al. (2023)	46.927	−90.556	285
Sydney	Charman et al. (2015)	44.387	−69.788	36
VC04-06	Bunbury et al. (2012)	52.710	−84.180	52
Villagedale	Mackay et al. (2021)	43.520	−65.532	24
Lac Le Caron	van Bellen et al. (2011)	52.290	−75.838	129
Irwin Smith	Booth et al. (2012)	45.027	−83.610	188
Sidney	Clifford and Booth (2013)	44.387	−69.788	134
Great Heath	Clifford and Booth (2013)	44.720	−67.833	90
Hornet	Tweiten et al. (2009)	46.077	−92.121	97

3.6. How good are modern analogues for peatland paleoenvironmental work?

Differences between modern and subfossil testate amoeba communities suggest that a more thorough assessment of modern analogues in testate amoeba research is needed, like there has been for other some other proxy types (e.g., Overpeck et al., 1985; Jackson and Williams, 2004; Williams and Jackson, 2007). Although our present analyses only used North American stratigraphic records, the results support the previous observations of poor subfossil-modern community overlap in individual stratigraphic records in many locations (e.g., Charman et al., 2007; Mitchell et al., 2008; Wilmshurst et al., 2003; Schnitchen et al., 2006b; Booth et al., 2023), and suggest that many subfossil testate amoeba communities lack good modern analogues (Fig. 11). For example, using the typical thresholds of similarity that have been employed for other paleoindicator groups (Simpson, 2012), less than 50 % of the analyzed subfossil samples across the 28 North American records have more than 20 good or very good modern analogues (Fig. 11). While there is abundant evidence from multi-proxy studies, multi-site syntheses, and instrumental comparisons that most testate amoeba reconstructions are robust reflections of moisture variability at the peatland surface (e.g., Charman, 2007; Chambers et al., 2012; Swindles et al., 2019), the implications of poor modern analogues for interpretating past communities and moisture reconstructions have not been fully evaluated. Differential decomposition is likely a contributor for the lack of modern analogues, so interpreting recent changes in communities and moisture spanning the catotelm-acrotelm boundary (i.e., transition between the lower more humified peat and partially decomposed upper peat) should be particularly cautious because the effects of differential preservation over this depth interval would be most pronounced.

Table 3
Summary of characteristics of subfossil testate amoeba communities with less than 10 good modern analogues, based on the cluster analysis of these samples shown in Fig. 12.

Group Number	Subfossil Community	General Characteristics of Subfossil Community
1	*Archerella flavum-Trigonopyxis arcula*	Co-dominated by *Archerella flavum* and *Trigonopyxis arcula*-type, which have optimal abundance on opposite sides of the moisture gradient in modern studies. Communities also tend to include abundant *Heleopera sphagni*-type, *Bullinularia indica*-type, and/or *Galeripora artocrea*-type.
2	*Trigonopyxis arcula – Galeripora discoides*	Co-dominated by *Trigonopyxis arcula*-type, *Galeripora discoides*-type, and *Difflugia pulex*. Moderate amounts of *Hyalosphenia subflava* occur in most samples.
3	*Hyalosphenia subflava – Difflugia pulex*	Abundant *Hyalosphenia subflava*, co-dominant with *Difflugia pulex* in many samples.
4	*Hyalosphenia subflava – Amphitrema wrightianum*	Co-dominated by *Hyalosphenia subflava*, *Amphitrema wrightianum*-type, *Archerella flavum*, and *Heleopera sphagni*-type.
5	*Hyalosphenia subflava – Cyclopyxis arcelloides*	Co-dominated by *Hyalosphenia subflava* and *Cyclopyxis arcelloides*-type. Moderate amounts of *Heleopera sylvatica* and *Heleopera sphagni*-type.
6	*Difflugia pulex – Archerella flavum*	Abundant *Difflugia pulex* with *Archerella flavum* and *Hyalosphenia subflava*.
7	*Difflugia pulex – Pseudodifflugia fulva*-type	Abundant *Difflugia pulex*, with *Pseudodifflugia fulva*-type, *Difflugia pristis*-type, and *Hyalosphenia subflava*. *Galeripora discoides*-type and *Nebela tincta*-type abundant in some samples.
8	*Hyalosphenia subflava – Galeripora discoides*	Co-dominated by *Hyalosphenia subflava*, *Galeripora discoides*-type, and *Difflugia pulex*.
9	*Difflugia pulex – Cyclopyxis arcelloides*	Abundant *Difflugia pulex* with *Cyclopyxis arcelloides*-type.
10	*Difflugia pulex*	Very abundant *Difflugia pulex*. In some samples, *Difflugia pulex* is dominant with *Archerella flavum*.
11	*Difflugia pristis*	Very abundant *Difflugia pristis*-type.
12	*Difflugia pristis – Hyalosphenia elegans*	Abundant *Difflugia pristis*-type, *Hyalosphenia elegans*, *Centropyxis aculeata*-type, and *Phryganella acropodia*-type.
13	*Amphitrema wrightianum*	Very abundant *Amphitrema wrightianum*
14	*Heleopera sphagni*	Very abundant *Heleopera sphagni*, with *Hyalosphenia subflava* co-dominant in some samples.
15	*Centropyxis aculeata – Heleopera sphagni*	Co-dominated by *Centropyxis aculeata*-type, *Heleopera sphagni*-type, and *Cyclopyxis arcelloides*-type. Some samples have high abundance of *Amphitrema wrightianum*.

As previously discussed, many subfossil samples with few good modern analogues appear to be dominated by taxa that are not well-represented in modern datasets (e.g., *Difflugia pulex*); however, others contain unusual combinations of taxa (Fig. 12, Table 3) and similarly unusual assemblages have also been described outside of North America (e.g., Schnitchen et al., 2006b; Charman et al., 2007; Mitchell et al., 2008). For example, subfossil communities with abundant *Galeripora discoides*-type and *Hyalosphenia subflava,* as well as communities with abundant *Difflugia pulex* and *Pseudodifflugia fulva*-type (groups 7 and 8 in Fig. 12 and Table 3), have been described from peat sequences in both North America and Europe (e.g., Booth and Jackson, 2003; Charman et al., 2007). Charman et al. (2007) noted that these taxa were abundant in settings with higher water tables but also can survive relatively lower moisture, and Sullivan and Booth (2011) found that these taxa are

indicative of settings with high-moisture variability. Interestingly, these taxa also characterize quite a few other subfossil communities with poor modern analogues, and are found in association with a range of different communities (Table 3, Fig. 12). More modern analogues for the unusual subfossil communities described in Fig. 12 and Table 3 may exist, perhaps in conditions or habitats outside the range typically represented in calibration datasets (Schnitchen et al., 2006b; Mitchell et al., 2008). Despite the large number of modern samples collected and analyzed over the past several decades, additional sampling in under-sampled settings may reveal more modern analogues and inform our interpretation of unusual subfossil communities.

3.7. Conclusions

Our literature review and synthesis of regional testate amoeba calibration studies over the past several decades confirms the primary importance of surface moisture in controlling testate amoeba community composition, and the collective analysis of surface samples using Neotoma further indicates that the patterns of community changes along moisture gradients are similar throughout the northern hemisphere. The consistent importance of surface moisture across such a large geographic expanse is unusual among paleoecological proxies and provides strong support for the use of testate amoebae as qualitative and quantitative moisture indicators in paleoenvironmental and environmental contexts, particularly in oligotrophic peatland settings with little variability in pH.

However, our analyses also reveal that a significant number of subfossil samples have few good modern analogues, and understanding the causes of differences between modern and subfossil samples is critically important to paleoenvironmental interpretations. Our results suggest that some differences may be due to differential decomposition, indicating that this problem may extend beyond WIST taxa. Although differential preservation of WISTs has been found to generally have minor impacts on many moisture reconstructions (Mitchell et al., 2008; Swindles et al., 2020), the effects of poor preservation of other taxa on water-table depth reconstructions have not been assessed. Nearly eighteen years ago, Mitchell et al. (2008) noted that there was a major gap in our understanding of testate amoeba taphonomy; however, only a handful of experimental and observational studies since then have examined taphonomic processes that transform living testate amoeba communities into subfossil assemblages. Much work on testate amoeba taphonomy remains.

However, differential decomposition alone cannot fully explain modern-subfossil community dissimilarities. Subfossil communities that are dominated by taxa not well represented in modern datasets or unusual combinations of taxa have been noted in the literature before (e.g., Booth and Jackson, 2003; Charman et al., 2007; Booth, 2008; Mitchell et al., 2008; Sullivan and Booth, 2011; Amesbury et al., 2013; Lamarre et al., 2013; Magnan and Garneau, 2014; Booth et al., 2023), but their causes are still not well understood and need greater examination. More experimental and observational work is clearly needed, including modern ecological studies in unusual or under-sampled peatland settings. The emerging research on morpho-functional trait distributions (e.g., Fournier et al., 2015; Marcisz et al., 2020) may also provide insights, as the direct comparison of morpho-functional traits between subfossil samples with good and poor modern analogues may also point to potential causal factors. Multi-proxy studies of stratigraphic intervals dominated by subfossil samples with poor modern analogues may also reveal whether unusual environmental conditions characterized these time periods. Taphonomic processes may also vary along the bog-to-fen nutritional gradient, and fen environments have been relatively understudied in both modern and stratigraphic contexts. The analysis of large subfossil and modern datasets, like that contained in Neotoma, will be an important component to this work, allowing generalization of widely observed subfossil-modern differences. An obvious next step would be to compare modern analogues for stratigraphic records outside of North America with modern surface samples.

Neotoma is a research community-curated database that has become a repository for paleoecological data of many kinds, supporting research at the intersection between geology and ecology (Williams et al., 2018). The two analyses presented in this paper demonstrate the potential utility of the database for testate amoeba research; however, there are many other possible applications and questions that could be explored, particularly with the incorporation of additional stratigraphic and modern datasets into the database. The Neotoma testate amoeba databases have substantially grown over the past several years; however, many modern datasets (Fig. 1) and a large number of stratigraphic records (Fig. 2) have not yet been incorporated. Incorporation of morpho-functional trait data into Neotoma is also likely possible, and would potentially enhance this growing area of research (e.g, Marcisz et al., 2020; Zhang et al., 2020). Much work remains to be done to develop and expand the applicability and value of this important shared resource.

Author contributions

RKB designed the study, performed the analyses, and wrote the paper. AS provided editorial comments on the manuscript. RKB, AS, EC, and JMK performed the literature-based data compilation of modern ecological calibration publications.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This research was supported by the National Science Foundation (EAR-1948386, EAR-2410963). We are sincerely grateful to all the researchers that have contributed their data to the Neotoma testate amoeba database. The paper was improved by the comments of two anonymous reviewers.

Appendix A. Taxonomic harmonization for taxa in greater than 50 Neotoma samples, not including WIST taxa

Taxon used in this study	Included taxa within Neotoma
Alabasta militaris-type	*Alabasta militaris*-type, *Alabasta militaris*
Amphitrema wrightianum-type	*Amphitrema wrightianum*, *Amphitrema stenostoma*
Arcella crenulata-type	*Arcella crenulata*, *Arcella mitrata*
Arcella gibbosa-type	*Arcella gibbosa*, *Arcella gibbosa*-type, *Arcella conica*, *Arcella costata*, *Arcella intermedia*
Arcella hemisphaerica-type	*Arcella hemisphaerica*, *Arcella hemisphaerica*-type, *Arcella rotundata*, *Arcella rotundata* var. *aplanata*
Arcella vulgaris-type	*Arcella vulgaris*, *Arcella vulgaris*-type, *Arcella bathystoma*, *Arcella megastoma*
Archerella flavum	*Archerella flavum*

(*continued on next page*)

(*continued*)

Taxon used in this study	Included taxa within Neotoma
Argynnia caudata	*Argynnia caudata*
Argynnia dentistoma-type	*Argynnia dentistoma*-type, *Nebela vitraea*, *Nebela vitraea*-type, *Nebela dentistoma*, *Nebela dentistoma*-type
Assulina muscorum-type	*Assulina muscorum*, *Assulina scandinavica*
Assulina seminulum	*Assulina seminulum*
Bullinularia indica-type	*Bullinularia gracilis*, *Bullinularia indica*
Centropyxis aculeata-type	*Centropyxis aculeata*, *Centropyxis aculeata* var. *discoides*, *Centropyxis aculeata* var. *gibbosa*, *Centropyxis aculeata* var. *minor*, *Centropyxis aculeata* var. *oblonga*, *Centropyxis aculeata*-type, *Centropyxis delicatula*, *Centropyxis gibba*, *Centropyxis hirsuta*, *Centropyxis spinosa*
Centropyxis cassis-type	*Centropyxis aerophila*, *Centropyxis aerophila sphagnicola*, *Centropyxis aerophila*-type, *Centropyxis cassis*, *Centropyxis cassis*-type, *Centropyxis orbicularis*, *Centropyxis sphagnicola*, *Centropyxis sylvatica*
Centropyxis ecornis-type	*Centropyxis ecornis*, *Centropyxis ecornis*-type, *Centropyxis ecornis* var. *quadripannosa*, *Centropyxis laevigata*
Centropyxis platystoma-type	*Centropyxis constricta*, *Centropyxis platystoma*, *Centropyxis platystoma*-type
Cryptodifflugia oviformis-type	*Cryptodifflugia oviformis*, *Cryptodifflugia oviformis*-type, *Cryptodifflugia compressa*, *Cryptodifflugia apiculata*-type, *Cryptodifflugia minuta*
Cyclopyxis arcelloides-type	*Cyclopyxis arcelloides*, *Cyclopyxis arcelloides*-type, *Cyclopyxis eurystoma*
Cyclopyxis kahli	*Cyclopyxis kahli*
Cyphoderia spp.	*Cyphoderia*, *Cyphoderia ampulla*, *Cyphoderia ampulla*-type, *Cyphoderia calceolus*
Difflugia acuminata-type	*Difflugia acuminata*, *Difflugia acuminata*-type, *Difflugia angulostoma*-type, *Difflugia elegans*, *Difflugia bacillariarum*, *Difflugia bacilliarium*-type
Difflugia globulosa-type	*Difflugia brevicola*, *Difflugia globulosa*, *Difflugia globulosa*-type, *Difflugia urceolata*, *Difflugia urceolata*-type
Difflugia labiosa-type	*Difflugia labiosa*-type, *Difflugia amphora*, *Netzelia oviformis*-type, *Netzelia oviformis*, *Netzelia tuberculata*
Difflugia leidyi	*Difflugia leidyi*
Difflugia lucida-type	*Difflugia lucida*-type, *Difflugia lucida*, *Difflugia glans*, *Difflugia avellana*, *Difflugia lithophila*-type, *Difflugia mica*
Difflugia oblonga-type	*Difflugia oblonga*, *Difflugia oblonga* var. *bryophila*, *Difflugia parva*, *Difflugia bacillifera*, *Difflugia bacillifera*-type, *Difflugia gassowski*, *Difflugia gassowskii/longicollis*, *Difflugia paulii*, *Difflugia lacustris*, *Difflugia lanceolata*, *Difflugia oblonga*-type, *Difflugia pyriformis*, *Difflugia viscidula*
Difflugia pristis-type	*Difflugia pristis*, *Difflugia pristis*-type, *Difflugia penardi*
Difflugia pulex	*Difflugia pulex*
Difflugia rubescens	*Difflugia rubescens*
Galeripora artocrea-type	*Arcella arenaria*, *Arcella arenaria*-type, *Arcella artocrea*, *Arcella artocrea*-type, *Arcella catinus*, *Arcella catinus*-type
Galeripora discoides-type	*Arcella discoides*, *Arcella discoides*-type, *Arcella discoides foveosa*, *Arcella polypora*
Gibbocarina galeata	*Nebela galeata*, *Nebela galeata*-type
Heleopera rosea-type	*Heleopera petricola* var. *amethystea*, *Heleopera rosea*, *Awerintzewia cyclostoma*
Heleopera sylvatica	*Heleopera sylvatica*
Helepera sphagni-type	*Heleopera sphagni*, *Heleopera sphagni*-type, *Heleopera picta*, *Heleopera petricola*, *Heleopera petricola*-type
Hyalosphenia elegans	*Hyalosphenia elegans*
Hyalosphenia minuta	*Hyalosphenia minuta*
Hyalosphenia papilio-type	*Hyalosphenia ovalis*, *Hyalosphenia papilio*
Hyalosphenia subflava	*Hyalosphenia subflava*
Lesquereusia spp.	*Lesquereusia*, *Lesquereusia epistomium*, *Lesquereusia modesta*-type, *Lesquereusia spiralis*, *Lesquereusia spiralis*-type
Longinebela penardiana-type	*Gibbocarina gracilis*, *Gibbocarina gracilis*-type, *Nebela penardiana*-type, *Longinebela penardiana*
Longinebela tubulosa-type	*Nebela tubulata*, *Nebela tubulosa*, *Nebela tub*ulosa-type
Microchlamys patella	*Microchlamys patella*
Nebela barbata	*Nebela barbata*
Nebela collaris-type	*Nebela bohemica*, *Nebela bohemica*-type, *Nebela collaris*, *Nebela collaris*-type, *Nebela tincta* var. *major*
Nebela flabellulum	*Nebela flabellulum*
Nebela tincta-type	*Nebela minor*, *Nebela minor*-type, *Nebela parvula*, *Nebela tincta*-type, *Nebela tincta*
Padaungiella lageniformis-type	*Nebela lageniformis*, *Padaungiella lageniformis*-type
Padaungiella wailesi-type	*Nebela wailesi*-type, *Nebela wailesii*
Paraquadrula irregularis-type	*Paraquadrula irregularis*, *Paraquadrula*
Phryganella acropodia-type	*Phryganella acropodia*, *Phryganella acropodia*-type, *Phryganella hemispherica*, *Phryganella nidulus*, *Phryganella paradoxa*
Physochila griseola-type	*Nebela tenella*, *Physochila griseola*, *Physochila griseola*-type
Plagiopyxis spp.	*Plagiopyxis* spp., *Plagiopyxis callida*, *Plagiopyxis callida*-type, *Plagiopyxis declivis*
Planocarina carinata-type	*Planocarina carinata*, *Planocarina carinata*-type, *Planocarina marginata*
Pseudodifflugia fulva-type	*Pseudodifflugia fulva*-type
Quadrulella symmetrica-type	*Quadrulella symmetrica*, *Quadrulella symmetrica*-type
Trigonopyxis arcula-type	*Trigonopyxis* spp., *Trigonopyxis arcula*, *Trigonopyxis arcula* var. *major*, *Trigonopyxis arcula*-type
Trigonopyxis minuta	*Trigonopyxis minuta*

Data availability

A link to the data and/or code is provided as part of this submission.

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