Davies, M. A., Blewett, J., Naafs, B. D. A., & Finkelstein, S. A. (2021). Ecohydrological controls on apparent rates of peat carbon accumulation in a boreal bog record from the Hudson Bay Lowlands, northern Ontario, Canada. *Quaternary Research*, 104, 14-27. <https://doi.org/10.1017/qua.2021.22>

Peer reviewed version

License (if available):
CC BY-NC-ND

Link to published version (if available):
[10.1017/qua.2021.22](https://doi.org/10.1017/qua.2021.22)

[Link to publication record in Explore Bristol Research](#)
PDF-document

This is the author accepted manuscript (AAM). The final published version (version of record) is available online via Cambridge University Press at <https://www.cambridge.org/core/journals/quaternary-research/article/abs/ecohydrological-controls-on-apparent-rates-of-peat-carbon-accumulation-in-a-boreal-bog-record-from-the-hudson-bay-lowlands-northern-ontario-canada/DEA1C4CE2C3FB725DDCF13C7493395D7>. Please refer to any applicable terms of use of the publisher.

University of Bristol - Explore Bristol Research

General rights

This document is made available in accordance with publisher policies. Please cite only the published version using the reference above. Full terms of use are available: <http://www.bristol.ac.uk/red/research-policy/pure/user-guides/ebr-terms/>

**Ecohydrological controls on apparent rates of peat carbon accumulation in a boreal bog
record from the Hudson Bay Lowlands, northern Ontario, Canada**

Marissa A. Davies^a, Jerome Blewett^b, B. David A. Naafs^b, Sarah A. Finkelstein^{a*}

^aDepartment of Earth Sciences, University of Toronto, 22 Ursula Franklin Street, Toronto,
Ontario, M5S 3B1, Canada

^bOrganic Geochemistry Unit, School of Chemistry, School of Earth Sciences, and Cabot
Institute, University of Bristol, Cantock's Close, Bristol, BS8 1TS, United Kingdom

*Corresponding author email address: sarah.finkelstein@utoronto.ca (S.A. Finkelstein).

(RECEIVED October 16, 2020; ACCEPTED March 3, 2021)

Abstract

A multiproxy Holocene record from a bog in the Hudson Bay Lowlands, northern Ontario, Canada, was used to evaluate how ecohydrology relates to carbon accumulation. The study site is located at a somewhat higher elevation and on coarser grained deposits than the surrounding peatlands. This promotes better drainage and thus a slower rate of carbon accumulation relative to sites with similar initiation age. The rate of peat vertical accretion was initially low as the site transitioned from a marsh to a rich fen. These lower rates took place during the warmer temperatures of the Holocene thermal maximum, confirming the importance of hydrological

controls limiting peat accretion at the local scale. Testate amoebae, pollen, and plant macrofossils indicate a transition to a poor fen and then a bog during the late Holocene, as the carbon accumulation rate and reconstructed water table depth increased. The bacterial membrane lipid biomarker indices used to infer paleotemperature show a summer temperature bias and appear sensitive to changes in peat type. The bacterial membrane lipid biomarker pH proxy indicates a rich to a poor fen and a subsequent fen to bog transition, which are supported by pollen, macrofossil, and testate amoeba records.

Keywords: Peatland; Paleoecology; Carbon accumulation; Pollen; Macrofossils; Testate amoebae; Biomarkers; brGDGTs; Holocene

INTRODUCTION

Peatlands are a significant component of the global carbon cycle and provide important archives of terrestrial environmental change. They currently store around one-third of the soil carbon pool under anoxic conditions that inhibit the decomposition of plant biomass (Gorham, 1991; Yu et al., 2010; Nichols and Peteet, 2019). Thus, the development of boreal peatlands following the retreat of the Fennoscandian and Laurentide Ice Sheets had a net cooling effect over the Holocene owing to slow but persistent carbon drawdown (Frolking and Roulet, 2007). However, whether peatlands will remain an active sink towards the end of the century is debated (Gallego-Sala et al., 2018; Loisel et al., 2021). Climate is a fundamental control on long-term peat carbon accumulation rates (CARs). Warmer temperatures can cause increased CARs owing to enhanced net primary productivity, provided that the water table remains sufficiently high to slow decomposition (Ise et al., 2008). Increased precipitation can promote higher CARs in peatlands

by supporting high water table positions. But when moisture availability is not the limiting factor of peat growth, changes in CARs due to moisture changes are likely secondary in importance to the effects of temperature (Charman et al., 2013; Gallego-Sala et al., 2018; Morris et al., 2018). While climate remains a fundamental control when considered in syntheses of many sites over large spatial scales (Gallego-Sala et al., 2018; Morris et al., 2018; Nichols and Peteet, 2019), landscape position, hydrology, and vegetation dynamics at the local scale significantly influence below-ground carbon densities and CARs (Packalen et al., 2016). Preserving the capacity of peatlands to take up carbon is an emerging management concern, and understanding the roles of hydrological and ecological factors in promoting the most effective carbon burial is critical for land use planning, especially under the warmer and often drier climates that northern peatland regions are experiencing due to anthropogenic climate change (McLaughlin et al., 2018).

Paleoecological records document long-term changes in the composition of vegetation communities forming peat deposits. These changes include rich to poor fen and fen to bog transitions, both of which can occur owing to autogenic plant succession, as peat accumulates and the surface becomes isolated from the water table, or to external drivers impacting effective moisture or nutrient availability at the peatland surface (Loisel and Bunsen, 2020). Fen to bog transitions are associated with an increase in *Sphagnum* vegetation and/or other bog indicators and a decrease in pH and nutrient status, which together influence organic matter quality, peat type, and carbon dynamics, including methane emissions (Loisel et al., 2014). Here, we investigate the timing and potential drivers of rich to poor fen and fen to bog transitions and their impacts on apparent CARs at a boreal bog site in the southern Hudson Bay Lowlands (HBL) of northern Ontario, Canada.

The HBL region of Canada is one of the world's largest continuous peatlands (Riley, 2011), with a current peat carbon pool of ~30 Pg C (Packalen et al., 2014). Rapid rates of glacial isostatic adjustment since the retreat of the Laurentide Ice Sheet during the early to mid-Holocene resulted in an uplift chronosequence of new surfaces available for peatland initiation (Andrews and Peltier, 1989). Therefore, the initiation and subsequent hydrology of all HBL peatlands are highly influenced by isostasy (Glaser et al., 2004), with fens dominating the coast on more recently emerged substrates and *Sphagnum* bogs more abundant inland on older surfaces (Holmquist and MacDonald, 2014). Furthermore, Morris et al. (2018) used modelled data to estimate the mid-Holocene paleoclimate in the HBL and inferred a key role for the temperature driving peat initiation. Therefore, initiation of peatlands in the HBL, and subsequent trajectories of peat and carbon accumulation, are tied to hydrological changes caused by both climate and regional uplift, highlighting the complex feedback specific to this region (Packalen and Finkelstein, 2014; Packalen et al., 2016; Morris et al., 2018).

Paleoecological records from HBL peat cores confirm that autogenic succession, climate, hydrology, and regional uplift have all played a role in vegetation dynamics and peat carbon accumulation throughout the Holocene (Bunbury et al., 2012; O'Reilly et al., 2014; Bysouth and Finkelstein, 2020). Because of the proximity of the decaying Laurentide Ice Sheet, orbitally controlled temperature maxima were delayed in the HBL region into the mid-Holocene (7—5 ka; Glaser et al., 2004; Viau and Gajewski, 2009) compared with other boreal regions (~11—9 ka; Renssen et al., 2009; Yu et al., 2010). Warmer temperatures during the regional Holocene thermal maximum (HTM) are associated with higher apparent peat CARs at some sites in the HBL and adjacent regions (van Bellen et al., 2011a; Bunbury et al., 2012; Holmquist and MacDonald, 2014; O'Reilly et al., 2014; Packalen and Finkelstein, 2014; Packalen et al., 2014,

2016; Bysouth and Finkelstein, 2020). However, these high CARs are often associated with early successional stages of peat (typically fens), and there is not always a clear increase in CARs with warmer temperatures, suggesting that peatland vegetation dynamics and local hydrology also play a role in long-term carbon dynamics in these areas (van Bellen et al., 2011a; Bunbury et al., 2012; Packalen and Finkelstein, 2014; Bysouth and Finkelstein, 2020).

Neoglacial cooling over the last four millennia (Viau and Gajewski, 2009; Hargan et al., 2020) is generally associated with lower rates of peatland initiation and lower apparent CARs in some HBL peat records (Kettles et al., 2000; Bunbury et al., 2012; O'Reilly et al., 2014; Packalen and Finkelstein, 2014; Bysouth and Finkelstein, 2020). In several records, the slowdown in peat CARs is associated with a shift from fen to bog conditions after 2500 cal yr BP. However, there is significant variability in the timing of this transition (Bunbury et al., 2012; Holmquist and MacDonald, 2014; Bysouth and Finkelstein, 2020). Thus, ecohydrological processes must be considered in addition to regional climate to determine the drivers of this change (Loisel and Garneau, 2010; Bunbury et al., 2012). This is particularly relevant in the HBL because of the dynamic landscape resulting from ongoing isostatic uplift (Glaser et al., 2004). Further, the HBL is characterised by a mosaic of peatland types in close proximity that have considerable variability in carbon densities (Packalen et al., 2016), suggesting that factors other than climate are needed to complete our understanding of carbon dynamics in this region. However, the density of available peat core data on paleovegetation and CARs remains low relative to the size of the HBL.

Ecohydrological conditions in peatlands can be reconstructed using a variety of proxies, including pollen and non-pollen palynomorphs, plant macrofossils, lipid biomarkers, and testate amoebae. A multiproxy approach is effective, as it allows for the comparison of independent

environmental records that each have limitations (Blundell and Barber, 2005). Here, we integrated testate amoebae, plant macrofossils, and pollen to identify transitions in peatland type and relate these transitions to changing rates of peat vertical accretion and carbon accumulation. Further, we use bacterial branched glycerol dialkyl glycerol tetraethers (brGDGTs) and peat-specific calibrations to reconstruct local pH and temperature (Naafs et al., 2017, 2019) and archaeal isoprenoidal glycerol dialkyl glycerol tetraethers (isoGDGTs) to explore changes in the archaeal community in relation to trends in CARs (Yang et al., 2019; Blewett et al., 2020). Although br- and isoGDGTs have been used for more than a decade on mineral soils (Weijers et al., 2007), their application to peat is relatively limited to date (e.g., Weijers et al., 2011; Zheng et al., 2020). Therefore, our approach provides an independent verification of the reconstructions derived from membrane lipids in peat to better understand their applicability in northern peatland regions.

Overall, this study uses these multiple proxies to (1) compare Holocene CARs before and after the transitions from rich to poor fen and from poor fen to bog in a record that is characterised by lower than average peat depths for the region; (2) determine how those shifts relate to water table depth (WTD; testate amoebae), pH (brGDGTs), vegetation (pollen and plant macrofossil), and regional climatic changes; and (3) evaluate the utility of brGDGT temperature reconstructions under changing environmental conditions.

METHODS

Study site and sampling

The study site (HRST 13-01; 50.7656°N; 82.7794°W; elevation ~168 m asl; Fig. 1) is located on the southern margin of the HBL ecozone of Canada (Ecological Stratification Working Group,

1995). The surrounding region is underlain by Paleozoic carbonates and Mesozoic sandstones and shales; immediately underlying the peat are near-shore marine sands, drumlins, and till deposits, which make up the interfluvial terrain (Fig. 1; Norris, 1986; Barnett et al., 2012; Bajc and Yeung, 2017). The study site is located on a slight upland of the interfluvial between the Albany and Moose River basins and is situated near the limit of an early Holocene marine incursion (i.e., the Tyrrell Sea; Fig. 1; Barnett et al., 2012; Bajc and Yeung, 2017).

The HBL region has a humid microthermal Arctic climate (Martini, 2006). The total annual precipitation at the closest weather station to the study site (Smoky Falls; Fig. 1) is 850 mm. The mean annual temperature is 0.7°C, with the highest daily average in July (17.6°C) and the lowest in January (-18.7°C). Average daily temperatures are below freezing for six months of the year (Government of Canada, 2020). The landscape across the HBL is mainly covered by coastal wetlands and interior peatlands, and organic-rich soils therefore predominate (>90% wetland coverage; Sims et al., 1979; Riley, 2003, 2011). Boreal and subarctic forests and tundra are also found in the region (Riley, 2003). Permafrost is mainly found along the coastal margin, with decreasing coverage southward and towards the interior (Riley, 2003). The study site is presently a bog, with local vegetation predominantly consisting of *Sphagnum* spp., with *Kalmia polifolia*, *Rhododendron groenlandicum*, *Vaccinium* spp., *Picea mariana*, and occasional *Larix* and Cyperaceae. There is no permafrost in the vicinity.

Two complete peat core sequences, taken 30 cm apart, were collected in July 2013 using a 50-cm Russian peat corer (hereafter referred to as “Core 1” and “Core 2”). These were combined into a composite record with sufficient material for a multiproxy analysis. One 10 × 10 × 16 cm (length × width × depth) surface monolith was taken using a square shovel directly adjacent to the coring site to further supplement the uppermost portion of the record. The two

sequences were 130 and 139 cm in length and had organic-inorganic contacts at the same depth (126 cm). The peat depth at the site was representative of the local site but is lower compared with a series of other bog sites in the HBL region (234 ± 56 cm; Packalen et al., 2016). The WTD was within 5 cm of the surface at the time of sampling; porewater conductivity and pH were measured at two points (58 and 64.3 μ S; 3.6 and 3.8, respectively). Cores were stored at 4°C at the University of Toronto until analysis.

Chronology and peat properties

An age-depth model (Fig. 2) was developed with radiocarbon ages from both cores (Table 1) and the surface age (-63 cal yr BP) using rbacon for R (Bayesian age-depth modelling (Blaauw and Christen, 2011)). Calibration of conventional ^{14}C ages to calendar (cal) years was performed using the IntCal13 calibration curve (Reimer et al., 2013). Individual age calibrations for each radiocarbon date in Table 1 were performed using OxCal version 4.3 (Bronk Ramsey, 2009). Two radiocarbon ages were measured at the Illinois State Geological Survey (Champaign, Illinois, USA; Core 1), and four were measured at the Lalonde AMS Laboratory (Ottawa, Ontario, Canada; Core 2). Radiocarbon dates taken from similar depths in each of the cores were approximately coeval, thus dates were combined to create a composite chronology. For loss-on-ignition (LOI) analysis, peat samples of 5–15 cm^3 ($n = 31$; continuous 4-cm sampling; Core 1) were dried at 95°C, ignited at 550°C for 4 h and at 950°C for 2 h to estimate organic matter and carbonate content (Heiri et al., 2001). Ash-free bulk density (AFBD) was calculated as dry mass (g) divided by wet volume (cm^3) and multiplied by the organic matter content (%). The apparent CAR was calculated using an estimated carbon content (50%) multiplied by AFBD (g cm^{-3}) and the modelled accretion rate (cm/yr), after Chambers et al. (2010).

Plant macrofossils were analysed from a selection of the >300- μ m fractions of the testate amoebae and pollen samples (N = 26; Core 2) to determine peat composition. Samples were poured into gridded petri dishes and examined at 40 $\times$ magnification on a stereomicroscope. Macrofossils were assigned to one of four major groups (Ericaceous roots and leaves, herbaceous plant fragments, *Sphagnum* stems and leaves, unidentifiable organic material (UOM)) in 12 randomly selected 1.5 $\times$ 1.5 cm quadrats; percent cover was estimated for each type (quadrat method; Mauquoy et al., 2010). Rare macrofossils encountered in each sample (i.e., *Carex* seeds and *Sphagnum* capsule opercules) were recorded as present but not included in the percent cover estimates. Because of the variability and large number of pieces of UOM that could occur in samples, only pieces that occupied the majority (>50%) of a 0.15 $\times$ 0.15 cm square within the ocular grid were counted. Distinguishing major peat macrofossil groups was performed referencing Lévesque et al. (1988).

Testate amoeba and pollen analysis

Peat subsamples of 1–2 cm³ were taken every 2–5 cm (n = 50; Core 2 and monolith) for enumeration of testate amoebae and pollen. The sampling resolution was varied along the core with the aim to reach a temporal resolution of <250 years between samples. Further, additional samples were added in the upper portion to increase resolution where testate amoebae were well preserved (<100 years between samples). Samples were boiled for 10 min, sieved to retain the 15- to 300- μ m fraction, and mounted in glycerol (Booth et al., 2010). For samples with a low pollen concentration on the microscope slides (N = 27) and a significant mineral content (N = 3), additional treatments (10% HCl, 10% KOH, acetolysis, and HF if visible silicates) were performed to obtain sufficient pollen and spore counts. *Lycopodium* tablets (1 tablet/cm³; batch

no. 3862, N = 9666) were added to each sample to estimate concentrations for determining counting thresholds.

For testate amoebae, a minimum of 150 tests was counted for samples with a concentration >5000 tests/cm³. If the concentration was <5000 tests/cm³, one slide was investigated, and any tests encountered were counted. For pollen, a minimum of 300 non-*Sphagnum* grains/spores was counted for samples with a concentration of $>10,000$ pollen/spores per cm³. If $<10,000$ pollen/spores per cm³, a minimum of 100 pollen/spores was counted, including at least 50 non-*Sphagnum* grains. Taxonomic identification of testate amoebae was performed by referencing Ogden and Hedley (1980), Booth (2008), and Charman et al. (2000). Taxonomic identification of pollen and spores was performed by referencing McAndrews et al. (1973). Select non-pollen palynomorphs (fungal and algal groups) were counted referencing van Geel (1978), van Geel et al. (1980), and Pals et al. (1980). Counts were performed at 400 $\times$ using a Zeiss Axio Imager A1 microscope. Zonation of the core was based on the pollen data and was performed using optimal splitting by information content and significance tested using the broken stick model (Bennett, 1996), using only taxa $>1\%$ of the assemblage. Zones for the testate amoebae and lipid biomarker datasets were also tested using the same method, and two subzones were added to the stratigraphy where there were significant shifts in these assemblages that were not identified in the pollen assemblages. We tested for stratigraphic congruence of the pollen and testate amoeba assemblages using Procrustes analysis on ordination sample scores (see Supplementary Materials and Supplementary Fig. S1).

The WTD was reconstructed using testate amoeba assemblages and a transfer function containing modern samples from the study region (see Supplementary Materials; Amesbury et al., 2018). Taxonomic harmonisations included combining *Trignopyxis arcuata* and *T. minuta*

types and removing *Lesquereusia modesta* type (found at <1% and in only one sample) from the fossil data. Although *Pyxidicula* sp. A was important in the fossil assemblages (up to 30%), *Pyxidicula* species are inconspicuous and thus can be overlooked in testate amoeba counts (Ogden, 1987). Because they are not well represented in the modern dataset (Amesbury et al., 2018), *Pyxidicula* sp. A was removed from the fossil dataset for the reconstruction. Reconstructed WTDs are plotted as z-scores, with higher values corresponding to drier relative conditions (see Supplementary Materials; Swindles et al., 2015).

Lipid analysis

A total of 17 samples were taken every 5–12 cm for isoGDGT and brGDGT lipid analysis (Core 1). Each sampling interval spanned 2–5 cm and was dependent on peat availability. Samples were freeze-dried, and lipids were extracted as outlined in Naafs et al. (2017). Approximately 1.0 g of bulk peat was microwave extracted in a 9:1 (v:v) mixture of dichloromethane (DCM) and methanol (MeOH). Samples were heated to 70°C over 10 min (1000 W) and held at this temperature for 10 min (1000 W) before a gradual 20-min cooling. They were then centrifuged for 3–5 min at 1700 rpm; the supernatant was collected, and an additional 10 ml of DCM:MeOH (9:1 v:v) was added to the remaining peat. This peat-solvent mixture was subsequently centrifuged as above, with this process repeated up to six times to maximise the yield of extractable lipids. The combined supernatants yielded a total lipid extract (TLE), which was concentrated using rota-evaporation. To remove particulates, a 25% aliquot of the TLE was passed through a 2-cm silica column using DCM:MeOH 9:1 (v:v). This aliquot was dried under a gentle flow of N₂ and redissolved in hexane:*iso*-propanol (99:1 v:v) and filtered through a 0.45-µm PTFE filter.

Lipids were dissolved in 100 µl of hexane:*iso*-propanol (99:1 v:v) and analysed via high-performance liquid chromatography–atmospheric pressure chemical ionization–mass spectrometry (HPLC-APCI-MS) on a ThermoFisher Scientific Accela Quantum Access triplequadrupole mass spectrometer at the University of Bristol, United Kingdom. Following the established method of Hopmans et al. (2016), normal phase separation was achieved using two Acquity UPLC BEH HILIC columns (150 mm × 2.1 mm, 1.7 µm, Waters, Eschborn, Germany). The injection volume was 15 µl. In order to increase sensitivity and reproducibility, the mass spectrometer was operated in selective ion monitoring mode, scanning for the following ions: *m/z* 1302, 1300, 1298, 1296, 1294, 1292, 1050, 1048, 1046, 1036, 1034, 1032, 1022, 1020, 1018, 744, and 653. The resultant chromatograms were integrated manually using the Xcalibur software. Daily analyses of inhouse standards indicate that the instrumental error is <0.1 for the GDGT-based indices.

The distribution of brGDGTs was used to calculate three peat-specific indices for paleoenvironmental reconstruction: CBT_{peat} , IR_{6me} , and MBT'_{5ME} (Naafs et al., 2017). CBT_{peat} refers to the proportion of brGDGTs with cyclopentane moieties (i.e., b:1 and c:2 cyclopentane moieties) over those that contain none (a:0 cyclopentane moieties):

$$CBT_{peat} = \log \left(\frac{Ib + IIa' + I Ib + I Ib' + IIIa'}{Ia + IIa + IIIa} \right) \quad (1)$$

The peat-specific calibration (Naafs et al., 2017) was then used to quantify paleo-pH:

$$pH = 2.49 \times CBT_{peat} + 8.07 \quad (n = 51, R^2 = 0.58, RMSE = 0.8) \quad (2)$$

The IR_{6me} ratio, which reflects the ratio between the 5- and 6-methyl brGDGTs (denoted with a ‘ symbol) was also used as a pH indicator in this study (De Jonge et al., 2014):

$$IR_{6me} \quad (3)$$

$$= \left(\frac{IIa' + IIb' + IIc' + IIIa' + IIIb' + IIIc'}{IIa + IIa' + IIb + IIb' + IIc' + IIIa + IIIa' + IIIb + IIIb' + IIIc + IIIc'} \right)$$

272 The MBT'_{5ME} index reflects the proportion of tetramethylated (I) to 5-methyl penta-(II) and
 273 hexamethylated (III) brGDGTs (De Jonge et al., 2014):

$$MBT'_{5ME} = \left(\frac{Ia + Ib + Ic}{Ia + Ib + Ic + IIa + IIb + IIc + IIIa} \right) \quad (4)$$

274 The peat-specific calibration (Naafs et al., 2017) was used to reconstruct the mean annual air
 275 temperature (MAAT):

$$MAAT_{peat}(^{\circ}C) = 52.18 \times MBT'_{5ME} - 23.05 \quad (n = 96, R^2 = 0.76, RMSE = 4.7)$$

277 However, MAAT_{peat} reconstructed using this index can be biased to summer temperatures in
 278 high-latitude peatlands (Naafs et al., 2017), and the magnitude of Holocene-scale temperature
 279 changes is generally within the 4.7°C error of the calibration (Naafs et al., 2017). Thus, we
 280 present this index in the context of a multiproxy study to explore its applicability in Holocene
 281 peat sequences from this region.

282

283 RESULTS

284 Chronology, peat properties, and carbon accumulation

285 The basal sediments below the peat boundary consist of poorly sorted sands to clays. Larger
 286 pebbles are also found within the matrix. Grains are generally subangular to subrounded. Basal
 287 radiocarbon dating of the peat section indicates the onset of peat accumulation at ~7600 cal yr
 288 BP. The age-depth model returns a mean rate of vertical peat accretion of 0.02 cm/yr (Figs. 2 and
 289 3), with very low rates (<0.007 cm/yr) between initiation and 3900 cal yr BP (105 cm). Vertical
 290 accretion increases between 3900 and 1500 cal yr BP (~0.01–0.02 cm/yr; 105–65 cm) and

transitions to the highest rates (>0.03 cm/yr) in the upper samples dating from ~ 1500 cal yr BP to the present (Fig. 3).

Bulk density (BD) is similar from peat initiation through to 40 cm (600 cal yr BP). BD then decreases after 40 cm because of the minimally decomposed *Sphagnum* in the uppermost portion of the record. Percent organic matter remained high after 121 cm ($>90\%$; 6500 cal yr BP; Fig 3), and carbonates as estimated from LOI were $<1\%$ through the entire record. Upon peat initiation, the core is characterised by herbaceous peat until 95 cm (3100 cal yr BP), followed by a mixed *Sphagnum*-herbaceous peat until 63 cm (1500 cal yr BP). After 63 cm, the core is characterised by *Sphagnum* peat for the rest of the record (Fig. 3). Notable exceptions are the increased presence of *Sphagnum* stems and leaves within the herbaceous peat (125–115 cm) and the increase in herbaceous plant fragments within the *Sphagnum* peat interval (30–10 cm).

The mean apparent CAR for 31 peat samples in the HRST 13-01 record was 12 ± 9 g C/m²/yr (mean $\pm$ SD). From peat initiation to ~ 1500 cal yr BP (63 cm), CAR remains generally <15 g C/m²/yr. An increase in CAR to maximum values (up to 34 g C/m²/yr) then occurs between 65 and 35 cm (1500–760 cal yr BP), driven by an increase in the rate of peat vertical accretion after 1500 cal yr BP. After 35 cm (760 cal yr BP), CAR decreases to the top of the core (<10 g C/m²/yr) with a decrease in peat bulk density.

Microfossil and geochemical proxies

At HRST 13-01, 40 testate amoeba taxa, one rotifer taxon, and 35 pollen and spore taxa were identified (Fig. 4, Supplementary Figs. S2 and S3, Supplementary Table S1). Pollen and spores were well preserved and abundant throughout, while testate amoebae were absent for most of the lower portion of the record, apart from between 125 and 115 cm (7600–5600 cal yr BP), where

they were found in conjunction with a small peak in *Sphagnum* macrofossils in a section otherwise dominated by herbaceous peat (Figs. 3 and 4). A consistent presence of testate amoebae occurs above 85 cm (2600 cal yr BP), corresponding to an increasing abundance of *Sphagnum* stems and leaves within the mixed *Sphagnum*-herbaceous peat interval (95–63 cm; 3100–1500 cal yr BP). The isoGDGT record is dominated by isoGDGT-0, which is common in peatland settings (Fig. 5; Sinninghe Damsté et al., 2002; Naafs et al., 2019; Blewett et al., 2020). The pollen and testate amoeba records in Zones 3 and 4 are significantly congruent (Procrustes analysis; $m_{12}^2 = 0.8287$; $p = 0.018$; see Supplementary Materials), signifying that the shifts in the pollen record are related to local environmental changes. The residuals of the sample scores from the Procrustes analysis ranged from 0.02 to 0.28, with the lowest values (<0.1 ; below the first quartile) occurring between 40 and 20 cm (Fig. 4 and Supplementary Fig. S1).

Four biostratigraphic zones were delineated based on the microfossil and geochemical analyses (Figs. 4 and 5, Table 2). Zone 1 (marsh) is contained below the peat boundary in inorganic sediments, with a high bulk density and low organic matter (>126 cm; Fig. 3). Testate amoebae are absent (Fig. 4). Pollen and spore assemblages are characterized by marsh taxa, including Cyperaceae, Chenopodiaceae, and *Equisetum*, and a mixed tree pollen assemblage of *Picea*, *Pinus*, and *Larix* (Fig. 4 and Supplementary Fig. S2). Asteraceae pollen is also abundant ($>5\%$; Fig. 4) and could further indicate marsh conditions, as species such as *Senecio congestus* can dominate marshes in the modern coastal setting of the HBL, where marshes develop into fens between beach ridges (Riley 2003, 2011). The *Sphagnum* spore abundance is also relatively high (20%). Reticulate algae (cf. *Closterium idiosporum* zygospores [HdV-60]), ferns (Polypodiaceae and Pteridophyta), and *Nuphar* are also present in this interval (Fig. 4 and Supplementary Fig. S2).

The onset of Zone 2 (126–95 cm; 7600–3100 cal yr BP; rich fen) corresponds to the establishment of a peat-forming wetland, with organic matter content >50% and the shift to herbaceous peat (Fig. 3). Pollen assemblages show an increase in regional tree pollen (*Picea* and *Pinus*) as marsh taxa decline. *Sphagnum* continues to have a relatively high abundance at the start of the zone but decreases after 115 cm (5600 cal yr BP). Ericaceae pollen also continues to be present in this zone (Fig. 4). Testate amoebae are absent other than in a short interval corresponding to increased *Sphagnum* in the macrofossil record (~125–115 cm), where they were found at low concentrations (<5000 tests cm⁻³; Fig. 4 and Supplementary Fig. S2). The brGDGT ratios (CBT_{peat} and IR_{6me}) indicate a near neutral pH. Crenarchaeol is also present in low amounts (Fig. 5).

Zone 3 (95–35 cm, 3100–760 cal yr BP; poor fen) is characterized by an increasing relative abundance of *Sphagnum* remains within the mixed *Sphagnum*-herbaceous peat of the interval (Fig. 3), increasing rates of peat vertical accretion, and the appearance of testate amoebae in higher concentrations (Fig. 4). The pollen assemblage is characterised by an increase in *Betula* at the base of the zone. Ericaceae and Cyperaceae pollen increase and decrease, respectively, at the subzonal boundary (63 cm; 1500 cal yr BP; Fig. 4). Further, the subzonal boundary marks an increase in *Ambrosia* type and a more consistent presence of *Artemisia* and Chenopodiaceae (Supplementary Fig. S2), which could indicate regional disturbance (e.g., Klinger and Short, 1996; Glaser et al., 2004; O'Reilly et al., 2014). Fungal remains also become more consistently present in this zone, while reticulate algae become absent (Fig. 4 and Supplementary Fig. S2). At the subzonal boundary (63 cm; 1500 cal yr BP), the testate amoeba assemblage shifts from the predominance of *Amphitrema wrightianum* type to *Archerella flavum*, with decreases in both taxa, and increases in *Diffflugia pulex* type and *Hyalosphenia subflava* and

Heleopera sylvatica in the upper portion of the zone. The testate amoeba assemblage shifts are associated with a transition from lower to higher depths to the water table and therefore drier conditions (Fig. 4 and Supplementary Fig. S2). Further, the isoGDGT assemblage shifts at the subzonal boundary, with a decrease in isoGDGT-1 and crenarchaeol and an increase in isoGDGT-2 and isoGDGT-3 (Fig. 5). The subzonal boundary is also characterised by an increase in the MBT'_{5ME} ratio. The IR_{6me} ratio and pH reconstruction also decrease towards the subzonal boundary, with IR_{6me} reaching 0 at 70 cm (1700 cal yr BP; Fig. 5); taken together, these changes suggest a shift from a rich fen to a poor fen.

Zone 4 (35–0 cm; 760 cal yr BP to present; bog phase) is defined by a shift in testate amoeba composition to *Alabasta militaris*, *Diffflugia pulex*, *Arcella catinus*, and *Cyclopyxis arcelloides* types and to *Hyalosphenia subflava*, with sustained drier conditions and the establishment of bog conditions at the site. *Pyxidicula* sp. A is also a significant portion of the assemblage. Species from the *Nebela* and *Euglypha* genera also appear in this zone (Supplementary Fig. S2). The pollen record has a shift to the highest percentage of Ericaceae as well as a shift to an increased *Sphagnum* abundance. The Procrustes analysis shows that the testate amoeba and pollen assemblages have the lowest sum of squares residuals over the lower boundary of Zone 4, indicating a high concordance in the assemblage changes for these records (Fig. 4). Increases in crenarchaeol correspond to increases in herbaceous material and Cyperaceae pollen between 30 and 10 cm. The subzonal boundary is associated with a shift to an increased percentage of Ericaceae roots and leaves in the peat composition, an increase in *Alabasta militaris* and *Diffflugia pristis* type, and a decrease in *Hyalosphenia subflava*, *Diffflugia pulex* type, and *Pyxidicula* sp. A.

DISCUSSION

Peat initiation and wetland succession

Marsh and rich fen stages (Zones 1 and 2; 7600–3100 cal yr BP)

Land emergence in the region occurred between 8500 and 8000 cal yr BP, as dated by field-based and modelled uplift chronologies (Dyke et al., 2003; Peltier et al., 2015), and climate was suitable for peat development from the time of land emergence (growing season temperature $>0^{\circ}\text{C}$ after 8.5 ka; Morris et al., 2018). Peat initiation at the HRST 13-01 site, however, did not occur until at least ~ 400 yr later (Fig. 3). Basal sediments from the site indicate the establishment of a non-peat-forming marsh following land emergence. *Sphagnum* macrofossils (Fig. 3) and spores (Fig. 4) are also present within the inorganic sediments, indicating that the site was transitioning to a fen ecosystem. Peat accumulation was occurring by 7600 cal yr BP, with pollen, plant macrofossils, and brGDGT indices holistically indicating the establishment of a rich fen ecosystem with Cyperaceae and Ericaceae and neutral to alkaline pH (Fig. 5).

Higher relative abundances of Ericaceae, *Larix*, and *Betula* pollen in the early portion of the record (Fig. 4; Zone 1) are similar to other available records from the HBL, which suggest a regional succession from herbs and grasses to shrubs, followed by the establishment of a *Picea*-dominated landscape with decreased marine influence and wetland succession (i.e., coastal marshes to interior fens and bogs; McAndrews et al., 1982; Klinger and Short, 1996; Kettles et al., 2000; Hargan et al., 2020). Rare grains of more southern tree pollen taxa at this site (i.e., *Acer*, *Juglans*, *Quercus*, and *Tsuga*; Supplementary Fig. S2) reflect its proximity to the margin of the HBL ecoregion (~ 85 km from the site; Fig. 1). The record also has *Ambrosia*-type pollen throughout (Supplementary Fig. S2). *Ambrosia* is not found in the HBL (Riley, 2003, 2011). Therefore, its pollen changes are interpreted here as indicators of long-distance transport from

regions where disturbance has occurred, as in previous studies (Klinger and Short, 1996; O'Reilly et al., 2014; Kettles et al., 2000; Glaser et al., 2004).

Upon the establishment of a peat-forming rich fen at 7600 cal yr BP, the record is characterised by exceptionally slow rates of peat vertical accretion (<0.007 cm/yr) until 3900 cal yr BP (Fig. 3). These slow rates are likely related to underlying topographic controls on local hydrology and vegetation type. The site is located on a slight upland between the Moose and Albany River watersheds and is underlain by sand to gravel beach deposits and glacial tills (Fig. 1) that could have promoted drainage and made the site prone to drying (Elmes and Price, 2019). Evidence for drier conditions from the paleoecological record includes the presence of Ericaceae pollen (Fig. 4) and wood fragments (Table 1), suggesting the local presence of woody plants. There is also a higher relative abundance of crenarchaeol in the deepest part of the peat core. Crenarchaeol is a biomarker produced by ammonium oxidising Thaumarchaeota; they require oxygen and are more abundant in dry soils (Sinninghe Damsté et al., 2002; Zheng et al., 2015; Naafs et al., 2019). However, the presence of algal microfossils (cf. HdV-60) suggests that very wet and/or submerged conditions may have also occurred at the site during portions of the rich fen zone (van Geel et al., 1980). The brGDGT pH proxy suggests near alkaline conditions (Fig. 5), which supports sustained groundwater discharge to the site. Therefore, the site may have experienced changes in hydrological conditions that were dependent on seasonal and/or annual changes in groundwater flow (Elmes and Price, 2019). The coarse-grained substrate during times of lower groundwater discharge would have increased the potential exposure of any accumulated peat to oxygenation and subsequent decomposition. Further, herbaceous peat characterises the interval and is also less recalcitrant than other peat types. Therefore, peat type could have further contributed to the low rates of vertical peat growth (Laiho, 2006). Finally, along with varying

groundwater conditions, spatial heterogeneity in terms of surface microforms and vegetation at the site could also have contributed to the variability of the ecological indicators in this interval (e.g., Belyea and Baird, 2006).

Testate amoebae are also found infrequently within the herbaceous-dominated peat, only occurring in two samples with a higher *Sphagnum* macrofossil abundance (125–115 cm; Fig. 4). The varying *Sphagnum* macrofossil abundance in this interval is likely related to changing hydrological conditions at the site and/or spatial heterogeneity of vegetation, as mentioned above. The general coincidence with *Sphagnum* peat for the testate amoebae record may be related to both the initial environment and the taphonomy. Although more diverse in general owing to the higher mineral and nutrient content, minerotrophic fen systems tend to be dominated by herbaceous material and brown mosses, which are more prone to drying, resulting in a less stable habitat for testate amoebae and therefore smaller populations (Lamentowicz et al., 2011). *Sphagnum*, however, can retain moisture within specialised water cells, providing more consistent moisture availability, and thus testate amoebae are more often found in *Sphagnum*-dominated portions of paleoecological records (Lamentowicz et al., 2011). Organic-rich or more alkaline systems, such as the study site, can promote the dissolution of silica in peatlands (Bennett et al., 1991), thus negatively impacting the preservation of testate amoebae with siliceous tests. Siliceous testate amoebae, such as *Diffflugia* and *Centropyxis*, tend to be most diverse in fen systems owing to a higher silica availability; therefore, communities in fen ecosystems may be more prone to dissolution and preservation biases (Lamentowicz et al., 2011). At HRST 13-01, there is a notable absence of *Centropyxis* taxa (Supplementary Fig. S2) in the lower portion of the core, despite being common in rich fen stages in peatland records (Bunbury et al., 2012; Lamentowicz et al., 2013; Bysouth and Finkelstein, 2020). Therefore, the

poor preservation of testate amoebae supports the interpretation of drier and alkaline conditions in the lower portion of the core.

Sustained rich fen conditions at the site until 3200 cal yr BP take place in the context of warmer temperatures associated with the regional timing of the Holocene thermal maximum in the mid-Holocene (8000–5000 cal yr BP), followed by cooling in the late Holocene and transition to the Neoglacial (4000–2500 cal yr BP; Viau and Gajewski, 2009; Hargan et al., 2020). The mid-Holocene differed from the late Holocene because the incursion of dry Pacific and Arctic air masses was less frequent, leading to increased summer precipitation, as inferred from eastern North American $\delta^{18}\text{O}$, charcoal, and pollen records (Edwards et al., 1996; Carcaillet and Richard, 2000; Moos and Cumming, 2011). However, there was reduced overall moisture availability during the mid-Holocene in northern Ontario and Quebec because of warmer temperatures driven by insolation, resulting in a higher evaporative demand, as shown by lower regional lake levels and pollen records (Payette and Fillion, 1993; Moos and Cumming, 2011; Karmakar et al., 2015). Thus, we expect that the HRST 13-01 site would show increased rates of peat vertical accretion during the warmer conditions and longer growing season of the mid-Holocene (Charman et al., 2013; Packalen and Finkelstein, 2014; Gallego-Sala et al., 2018) (higher rates have been recorded at this time for some fen sites in the HBL and northern Quebec regions; see Glaser et al., 2004; van Bellen et al., 2011a; O'Reilly et al., 2014; Packalen and Finkelstein, 2014; Bysouth and Finkelstein, 2020). However, since there are low rates of accumulation at HRST 13-01 at this time, the local topography, underlying surficial deposits, and hydrological conditions at the site appear to be critical in suppressing the rates of peat vertical accretion, despite favourable climatic conditions for peat growth. Further, if drainage and groundwater discharge were especially sensitive to climatic changes in the region surrounding

the site, the relatively drier conditions of the mid-Holocene may have further promoted decomposition in this interval (Bragazza et al., 2016; Elmes and Price, 2019). An increase in peat vertical accretion takes place after 3900 cal yr BP within the rich fen zone (Fig. 3). This major change occurs within the same biostratigraphic zone, suggesting a limited impact of differences in vegetation type, organic matter quality, or peat recalcitrance on the rate of peat accretion in this record. Instead, this may further indicate that the transition to the cooler and relatively wetter conditions of the late Holocene in eastern Canada promoted vertical peat growth at the site by sustaining higher water tables.

Poor fen stage (Zone 3, 3100–760 cal yr BP)

A shift to higher shrub cover with an increased relative abundance of *Betula* pollen, the appearance of testate amoebae, increases in *Sphagnum* macrofossils, a transition to a mixed *Sphagnum*-herbaceous peat, and a transition from neutral to acidic pH as reconstructed by brGDGTs mark a shift from a rich to a poor fen and the transition to Zone 3. *Betula* is interpreted to be a more local successional signal, as lake records from the region indicate that the landscape transitioned to a *Picea*-dominated forest with shoreline regression and wetland succession between 6500 and 6000 cal yr BP (McAndrews et al., 1982; Friel et al., 2014; Hargan et al., 2020). Further, the shift to a *Picea*-dominated landscape surrounding the site in the HRST 13-01 record does not coincide with this shift in *Betula*; instead, it is seen earlier, at the boundary between Zones 1 and 2 (7600 cal yr BP). The testate amoeba assemblages for most of Zone 3 are dominated by *A. wrightianum* type, an indicator of wet conditions (Charman et al., 2000; Lamarre et al., 2013) that has been found in modern poor fen sites in the HBL (Amesbury et al., 2018) and moderately rich fen sites in northern Quebec (Loisel and Garneau, 2010; van Bellen et

al., 2011b). At the subzonal boundary (63 cm; 1500 cal yr BP), fungal groups are also more consistently abundant, signifying oxygenated conditions in the surface peat (Yeloff et al., 2007), and Ericaceae pollen increases in relative abundance (Fig. 4). The fungal groups are also often associated with Ericaceae and *Sphagnum* species (HdV-13 and HdV-27, respectively; Fig. 4), further supporting the local presence of these vegetation types. Increases in the relative abundance of isoGDGTs-2 and -3 and the gradual disappearance of crenarchaeol also occur after the subzonal boundary. These biomarkers could reflect archaeal membrane adaptation in response to increasingly acidic conditions, which has been demonstrated to occur in peats (Blewett et al., 2020), and/or increases in the bog-dwelling acidophilic, nonmethanogenic taxa such as Thermoplasmatales (Yang et al., 2019). Furthermore, 6-methyl brGDGTs, which are associated with a neutral pH (Naafs et al., 2017), disappear from the record ($IR6_{me} = 0$) before the subzonal boundary. Thus, the isoGDGT records also support the inferred trophic changes through Zones 3–4.

At other sites in the HBL and adjacent regions, cool Neoglacial conditions under sufficient moisture have been linked to slower rates of peat accretion due to lower net primary productivity (Kettles et al., 2000; Loisel and Garneau, 2010; Bunbury et al., 2012; Packalen and Finkelstein, 2014; Bysouth and Finkelstein, 2020). At HRST 13-01, however, the establishment of *Sphagnum*, which is more resistant to decay than herbaceous vegetation, promoted an increase in peat accretion. The shift from rich to poor fen-like conditions after 3100 cal yr BP is likely the result of both hydrologic and autogenic changes. Slower rates of isostatic uplift (Andrews and Peltier, 1989) would have promoted more stable hydrologic regimes in the HBL landscape, allowing the potential establishment of a local divide and water table mounds to sustain peat accretion (Glaser et al., 2004). The shift from a rich to a poor fen takes place in the context of

cooler conditions and increased moisture availability, with reduced evaporative demand at the regional scale (Moos and Cumming, 2011; Hargan et al., 2020). More moisture availability at the site would have also promoted peat accretion by limiting decomposition, thus promoting autogenic processes, whereby continued accumulation would lead to reduced groundwater flow and subsequent isolation from groundwater influence (Glaser et al., 2004).

Bog stage (Zone 4, 760 cal yr BP–present)

The fen to bog transition at 35 cm (760 cal yr BP) is marked by a decrease in Cyperaceae, an increase in Ericaceae pollen, a shift to bog-indicator testate amoeba taxa, and an acidic pH (minima ~4) as reconstructed by brGDGTs (Figs. 4 and 5). The boundary is also where the Procrustes analysis shows the highest congruence between pollen and testate amoeba records (Fig. 4 and Supplementary Fig. S1), suggesting coincident shifts in vegetation at the surrounding site and testate amoeba communities at the coring location. Further, there is a shift from generally wet indicators to taxa that have a wider tolerance to drier and more variable hydrological conditions across the boundary (i.e., *Diffflugia pulex* type and *Hyalosphenia subflava* (Booth, 2008; Loisel and Garneau, 2010; Sullivan and Booth, 2011), suggesting a shift to a precipitation-controlled and therefore ombrotrophic setting (Fig. 4). Variable hydrological conditions are also supported by the shifting abundances of herbaceous materials, Cyperaceae pollen, and crenarchaeol in this interval (Zone 4; Figs. 3–5). The fen to bog transition at HRST 13-01 occurs towards the end of the Medieval Climate Anomaly (MCA; 1000–600 cal yr BP; Mann et al., 2009), which could suggest that climate played a role in promoting the shift to ombrotrophy, as has been recorded in other regions (Loisel and Bunsen, 2020). However, the abundance of *Sphagnum* since the poor fen stage and a higher vertical peat accretion also would

have helped to acidify and isolate the site from the groundwater table (Rydin and Jeglum, 2013). Therefore, the shift to ombrotrophy could also be caused by autogenic processes.

Validation of peat-specific brGDGT-based proxies for temperature and pH in peats

The MBT'_{5ME} ratio, which has been used to infer MAAT in modern and ancient peats (Naafs et al., 2017, 2018; Zheng et al., 2017) generally increases up-core at HRST 13-01. This trend is likely partly due to a bias towards summer temperatures in the acrotelm, as found in other high-latitude peats (Naafs et al., 2017). For example, the MBT'_{5ME} ratio for the uppermost sample results in a reconstructed MAAT of $15 \pm 4.7^\circ\text{C}$, much higher than the actual MAAT of 1°C . However, the reconstruction is consistent with the mean summer temperature of 18°C at the closest weather station (Smoky Falls; Fig. 1; Government of Canada, 2020). The MBT'_{5ME} values might also be influenced by changes in peat type, with higher MBT'_{5ME} values for *Sphagnum*-dominated peat (Fig. 3). This is consistent with findings from Weijers et al. (2011), which demonstrated that reconstructed temperature shifts in an ombrotrophic bog in the Jura Mountains were impacted by the changing trophic status of the site.

At HRST 13-01, the CBT_{peat} ratio used to reconstruct the pH also follows vegetation shifts, and the reconstructed pH values are well within the ranges expected for the paleowetland types inferred from the macro- and microfossil proxies, corroborating other studies that have used brGDGTs as a pH proxy in peat (Weijers et al., 2011; Nichols et al., 2014; Zheng et al., 2018). Thus, we further highlight the utility of brGDGT peat-based pH proxies for identifying shifts in rich to poor fen and fen to bog transitions, which are important for confirming successional pathways and impacts on peat accretion and carbon accumulation.

Controls on apparent rates of carbon accumulation

The average CAR for HRST 13-01 is 12 ± 9 g C/m²/yr, which is low compared with other bogs in northern Ontario and Quebec (range 15–25 g C/m²/yr; van Bellen et al., 2011a; Bunbury et al., 2012; Holmquist and MacDonald, 2014; Packalen and Finkelstein, 2014) and with bogs in a synthesis of circumboreal northern peatlands (23 ± 2 g C/m²/yr; mean $\pm$ SE; Loisel et al., 2014). Paleoeological studies of other HBL fens and bogs have suggested that fen cores can have a greater carbon content than bog cores dominated by *Sphagnum* peat (Bunbury et al., 2012; O'Reilly et al., 2014; Bysouth and Finkelstein, 2020), although multisite comparisons of *Sphagnum* and non-*Sphagnum* peat within HBL peat cores are lacking. Multisite comparisons of peat types within peat cores for southern Patagonia have shown instead that *Sphagnum* peat is often associated with a higher CAR than fen peat (Loisel and Bunsen, 2020). In the HRST 13-01 record, the highest CARs take place in the upper part of the poor fen zone and the lower part of the bog zone where *Sphagnum* is abundant. Thus, CAR is not neatly constrained by peatland type; rather, it reaches maximum values when rates of peat vertical accretion are elevated, bulk densities are >0.1 g cm⁻³, and vegetation type is resistant to decay.

In terms of climatic controls on CARs, a series of paleoeological records from the HBL region and adjacent boreal shield show an increased CAR between 6.5 and 4 ka, coincident with the regional HTM (van Bellen et al., 2011a; Bunbury et al., 2012; Holmquist and MacDonald, 2014; O'Reilly et al., 2014; Packalen and Finkelstein, 2014; Bysouth and Finkelstein, 2020). A sustained low CAR in the early part of the HRST 13-01 record, despite regional warming and potentially enhanced primary production, suggests that the local hydrological regime and underlying glacial deposits limited any climatic enhancement of carbon accumulation and instead resulted in the observed very low rates of peat accretion. Further, the warmer

temperatures of the mid-Holocene may have had a larger effect at HRST 13-01 than at other localities by having a stronger control on the local hydrological conditions because of better drainage, which promoted drier conditions and enhanced decomposition. CARs at HRST 13-01 in the late Holocene are strongly tied to a shift to lower bulk densities towards the top of the core, suggesting that vegetation composition and its decomposability are more important factors locally than centennial-scale shifts in climate, such as the MCA, which have been associated with higher CARs at other HBL sites (Bunbury et al., 2012).

CONCLUSIONS

This multiproxy paleoecological record demonstrates the importance of local ecohydrological changes in apparent Holocene CARs in HBL peatlands. Site HRST 13-01 is unusual compared with other regional paleoecological records with similar initiation ages (Glaser et al., 2004; Bunbury et al., 2012; O'Reilly et al., 2014; Bysouth and Finkelstein, 2020) because less peat accumulated; as a result, the average apparent CAR is lower than regional and circumboreal means (Packalen and Finkelstein 2014; Loisel et al., 2014). These lower rates likely reflect the site's physiographic setting on a modest upland and overlying coarse-grained glacial deposits that likely promoted better drainage. As carbon density is variable across the HBL (Packalen et al., 2016), the analyses from HRST 13-01 provide insight into peatland development in areas where peat depths are lower but initiation ages are relatively old for the HBL. The multiple proxies allowed for a division of the record into successional stages, from a marsh to a rich and then a poor fen and finally to a bog. Comparisons between these transitions show that the rates of peat vertical accretion and carbon accumulation were not closely tied to peatland type but related to broad vegetation classes and their decomposability. Low rates of vertical accretion despite the

warmer climate of the HTM suggest that hydrological conditions were of greater importance locally. Vertical accretion rates increased after 3900 cal yr BP but are not directly associated with a shift in peatland type, suggesting that Neoglacial cooling may have promoted a lower evaporative demand and therefore wetter conditions needed to sustain higher rates of peat accretion. Finally, we show a summer bias in the brGDGT indices used to reconstruct paleotemperature, as reported at other high-latitude peatlands. Finally, we demonstrate that the brGDGT proxy for pH is a useful tool for indicating rich to poor fen transitions, as the proxy was consistent with plant macrofossil, pollen, and testate amoeba records.

DATA AVAILABILITY

All data associated with this article (pollen; non-pollen palynomorph, plant macrofossil, and testate amoeba assemblages; radiocarbon dates; LOI; and brGDGT biomarker abundances) are available in the Neotoma Paleoecology Database (<http://www.neotomadb.org/>; Williams et al., 2018), archived with the site name “HRST1301” (site 27270).

ACKNOWLEDGMENTS

We thank P. Barnett for invaluable guidance in the field, many discussions on the geological and geomorphic setting, and help with drafting Figure 1; A. Dalton and M. Nguyen for field assistance; J. Palozzi for laboratory assistance; and R.K. Booth, E. Grimm, J. Williams, and N. Cullen for assistance with uploading the datasets to the Neotoma database. We also thank J. Loisel and two anonymous reviewers for their feedback that helped improve this manuscript. Funding for this project was provided by grants from the Natural Sciences and Engineering Research Council of Canada (NSERC) and support from the Ontario Ministry of Northern

Development and Mines and the Ontario Ministry of Natural Resources and Forestry to S. Finkelstein, and a NSERC postgraduate scholarship (NSERC PGS-D) and Canadian Quaternary Association (CANQUA) Alexis Dreimanis Award to M. Davies. J. Blewett is supported by a NERC GW4+ doctoral training partnership studentship from the Natural Environment Research Council (NE/L002434/1) and is thankful for the support and additional funding from CASE partner Elementar UK Ltd. B.D.A. Naafs acknowledges funding through the Royal Society Tata University Research Fellowship. NERC (Reference: CC010) and NEIF (www.isotopesuk.org) are thanked for funding and maintenance of the LC-MS instrument used for this work.

REFERENCES

- Amesbury, M.J., Booth, R.K., Roland, T.P., Bunbury, J., Clifford, M.J., Charman, D.J., Elliot, S., *et al.*, 2018. Towards a Holarctic synthesis of peatland testate amoeba ecology: development of a new continental-scale palaeohydrological transfer function for North America and comparison to European data. *Quaternary Science Reviews* 201, 483–500.
- Andrews, J.T., Peltier, W.R., 1989. Quaternary geodynamics in Canada. In: Fulton, R.J. (Ed.), *Quaternary Geology of Canada and Greenland*. Geological Survey of Canada, Ottawa. pp. 541–572.
- Bajc, A.F., Yeung, K.H., 2017. Surficial Geology of the Smoky Falls Area Southwest, Northern Ontario. Map P3754, Preliminary Map Series. Ministry of Energy, Northern Development and Mines, Sudbury, Ontario, Canada.
- Barnett, P.J., Yeung, K.H., McCallum, J.D., 2012. Surficial Geology of the Smoky Falls Area Northeast, Northern Ontario. Map P3748, Preliminary Map Series. Ministry of Energy, Northern Development and Mines, Sudbury, Ontario, Canada.

659 Belyea, L.R., Baird, A.J., 2006. Beyond “the limits to peat bog growth”: cross-scale feedback in
660 peatland development. *Ecological Monographs* 76, 299–322.

661 Bennett, K.D., 1996. Determination of the number of zones in a biostratigraphical sequence. *New*
662 *Phytologist* 132, 155–170.

663 Bennett, P.C., Siegel, D.I., Hill, B.M., Glaser, P.H., 1991. Fate of silicate minerals in a peat bog.
664 *Geology* 19, 328–331.

665 Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an
666 autoregressive gamma process. *Bayesian Analysis* 6, 457–474.

667 Blewett, J., Naafs, B.D.A., Gallego-Sala, A.V., Pancost, R.D., 2020. Effects of temperature and
668 pH on archaeal membrane lipid distributions in freshwater wetlands. *Organic*
669 *Geochemistry* 148, 104080. [https://doi: 10.1016/j.orggeochem.2020.104080](https://doi.org/10.1016/j.orggeochem.2020.104080).

670 Blundell, A., Barber, K., 2005. A 2800-year palaeoclimatic record from Tore Hill Moss,
671 Strathspey, Scotland: the need for a multi-proxy approach to peat-based climate
672 reconstructions. *Quaternary Science Reviews* 24, 1261–1277.

673 Booth, R.K., 2008. Testate amoebae as proxies for mean annual water-table depth in *Sphagnum*-
674 dominated peatlands of North America. *Journal of Quaternary Science* 23, 43–57.

675 Booth, R.K., Lamentowicz, M., Charman, D.J., 2010. Preparation and analysis of testate
676 amoebae in peatland environmental studies. *Mires and Peat* 7, 2. [http://www.mires-and-](http://www.mires-and-peat.net/pages/volumes/map07/map0702.php)
677 [peat.net/pages/volumes/map07/map0702.php](http://www.mires-and-peat.net/pages/volumes/map07/map0702.php).

678 Bragazza, L., Buttler, A., Robroek, B.J.M., Albrecht, R., Zaccone, C., Jassey, V.E.J.,
679 Signarbieux, C., 2016. Persistent high temperature and low precipitation reduce peat
680 carbon accumulation. *Global Change Biology* 22, 4114–4123.

681 Bronk Ramsey, C., 2009. Bayesian analysis of radiocarbon dates. *Radiocarbon* 51, 337–360.

682 Bunbury, J., Finkelstein, S.A., Bollmann, J., 2012. Holocene hydro-climatic change and effects
 683 on carbon accumulation inferred from a peat bog in the Attawapiskat River watershed,
 684 Hudson Bay Lowlands, Canada. *Quaternary Research* 78, 275–284.

685 Bysouth, D., Finkelstein, S.A., 2020. Linking testate amoeba assemblages to paleohydrology and
 686 ecosystem function in Holocene peat records from the Hudson Bay Lowlands, Ontario,
 687 Canada. *The Holocene* 31, 457–468.

688 Carcaillet, C., Richard, P.J.H., 2000. Holocene changes in seasonal precipitation highlighted by
 689 fire incidence in eastern Canada. *Climate Dynamics* 16, 549–559.

690 Chambers, F.M., Beilman, D.W., Yu, Z., 2010. Methods for determining peat humification and
 691 for quantifying peat bulk density, organic matter and carbon content for palaeostudies of
 692 climate and peatland carbon dynamics. *Mires and Peat* 7, 7. [http://www.mires-and-](http://www.mires-and-peat.net/pages/volumes/map07/map0707.php)
 693 [peat.net/pages/volumes/map07/map0707.php](http://www.mires-and-peat.net/pages/volumes/map07/map0707.php).

694 Charman, D.J., Beilman, D.W., Blaauw, M., Booth, R.K., Brewer, S., Chambers, F.M., Christen,
 695 J.A., *et al.*, 2013. Climate-related changes in peatland carbon accumulation during the
 696 last millennium. *Biogeosciences* 10, 929–944.

697 Charman, D.J., Hendon, D., Woodland, W., 2000. *The Identification of Testate Amoebae*
 698 *(Protozoa: Rhizopoda) in Peats*. Quaternary Research Association, London.

699 De Jonge, C., Hopmans, E.C., Zell, C.I., Kim, J.-H., Schouten, S., Sinninghe Damsté, J.S., 2014.
 700 Occurrence and abundance of 6-methyl branched glycerol dialkyl glycerol tetraethers in
 701 soils: implications for palaeoclimate reconstruction. *Geochimica et Cosmochimica Acta*
 702 141, 97–112.

703 Dyke, A.S., Moore, A., Robertson, L., 2003. *Deglaciation of North America*. Geological Survey
 704 of Canada Open File 1574. Natural Resources Canada, Ottawa.

705 Ecological Stratification Working Group, 1995. Terrestrial Ecozones and Ecoregions of Canada:
706 A National Ecological Framework for Canada. 1:7500000. Agriculture and Agri-Food
707 and Environment Canada, Ottawa.

708 Edwards, T.W.D., Wolfe, B.B., MacDonald, G.M., 1996. Influence of changing atmospheric
709 circulation on precipitation $\delta^{18}\text{O}$ -temperature relations in Canada during the Holocene.
710 *Quaternary Research* 46, 211–218.

711 Elmes, M.C., Price, J.S., 2019. Hydrologic function of a moderate-rich fen watershed in the
712 Athabasca oil sands region of the western Boreal plain, northern Alberta. *Journal of*
713 *Hydrology* 570, 692–704.

714 Friel, C.E., Finkelstein, S.A., Davis, A.M., 2014. Relative importance of hydrological and
715 climatic controls on Holocene paleoenvironments inferred using diatom and pollen
716 records from a lake in the central Hudson Bay Lowlands, Canada. *The Holocene* 24, 295–
717 306.

718 Frohking, S., Roulet, N.T., 2007. Holocene radiative forcing impact of northern peatland carbon
719 accumulation and methane emissions. *Global Change Biology* 13, 1079–1088.

720 Gallego-Sala, A.V., Charman, D.J., Brewer, S., Page, S.E., Prentice, I.C., Friedlingstein, P.,
721 Moreton, S., *et al.*, 2018. Latitudinal limits to the predicted increase of the peatland
722 carbon sink with warming. *Nature Climate Change* 8, 907–913.

723 Glaser, P.H., Hansen, B.C.S., Siegel, D.I., Reeve, A.S., Morin, P.J., 2004. Rates, pathways and
724 drivers for peatland development in the Hudson Bay Lowlands, northern Ontario,
725 Canada. *Journal of Ecology* 92, 1036–1053.

726 Gorham, E., 1991. Northern peatlands: role in the carbon-cycle and probable responses to
727 climatic warming. *Ecological Applications* 1, 182–195.

728 Government of Canada, 2020. Canadian Climate Normals: 1981–2010 Climate Normals and
 729 Averages (accessed October 15, 2020).
 730 https://climate.weather.gc.ca/climate_normals/index_e.html.
 731 Government of Ontario, 2020. Provincial Digital Elevation Model: North (CGVD28). Ontario
 732 Ministry of Natural Resources and Forestry, Ottawa.
 733 Hargan, K.E., Finkelstein, S.A., Rühland, K.M., Packalen, M.S., Dalton, A.S., Paterson, A.M.,
 734 Keller, W., Smol, J.P., 2020. Post-glacial lake development and paleoclimate in the
 735 central Hudson Bay Lowlands inferred from sediment records. *Journal of*
 736 *Paleolimnology* 64, 25–46.
 737 Heiri, O., Lotter, A.F., Lemcke, G., 2001. Loss on ignition as a method for estimating organic
 738 and carbonate content in sediments: reproducibility and comparability of results. *Journal*
 739 *of Paleolimnology*, 101–110.
 740 Holmquist, J.R., MacDonald, G.M., 2014. Peatland succession and long-term apparent carbon
 741 accumulation in central and northern Ontario, Canada. *Holocene* 24, 1075–1089.
 742 Hopmans, E.C., Schouten, S., Sinninghe Damsté, J.S., 2016. The effect of improved
 743 chromatography on GDGT-based palaeoproxies. *Organic Geochemistry* 93, 1–6.
 744 Ise, T., Dunn, A.L., Wofsy, S.C., Moorcroft, P.R., 2008. High sensitivity of peat decomposition
 745 to climate change through water-table feedback. *Nature Geoscience* 1, 763–766.
 746 Karmakar, M., Laird, K.R., Cumming, B.F., 2015. Diatom-based evidence of regional aridity
 747 during the mid-Holocene period in boreal lakes from northwest Ontario (Canada). *The*
 748 *Holocene* 25, 166–177.

749 Kettles, I.M., Garneau, M., Jetté, H., 2000. *Macrofossil, Pollen, and Geochemical Records of*
750 *Peatlands in the Kinosheo Lake and Detour Lake Areas, Northern Ontario*. Natural
751 Resources Canada, Ottawa.

752 Klinger, L.F., Short, S.K., 1996. Succession in the Hudson Bay lowland, northern Ontario,
753 Canada. *Arctic and Alpine Research* 28, 172–183.

754 Laiho, R., 2006. Decomposition in peatlands: reconciling seemingly contrasting results on the
755 impacts of lowered water levels. *Soil Biology and Biochemistry* 38, 2011–2024.

756 Lamarre, A., Magnan, G., Garneau, M., Boucher, E., 2013. A testate amoeba-based transfer
757 function for paleohydrological reconstruction from boreal and subarctic peatlands in
758 northeastern Canada. *Quaternary International* 306, 88–96.

759 Lamentowicz, M., Galka, M., Milecka, K., Tobolski, K., Lamentowicz, B., Fialkiewicz-Koziel,
760 B., Blaauw, M., 2013. A 1300-year multi-proxy, high-resolution record from a rich fen in
761 northern Poland: reconstructing hydrology, land use and climate change. *Journal of*
762 *Quaternary Science* 28, 582–594.

763 Lamentowicz, M., Galka, M., Rusińska, A., Sobczyński, T., Owsiany, P.M., Lamentowicz, M.,
764 2011. Testate amoeba (Arcellnida, Euglyphida) ecology along a poor-rich gradient in
765 fens of western Poland. *International Review of Hydrobiology* 96, 356–380.

766 Lévesque, P.E.M., Dinel, H., Larouche, A., 1988. *Guide to the Identification of Plant*
767 *Macrofossils in Canadian Peatlands*. Ministry of Supply and Services Canada, Ottawa.

768 Loisel, J., Bunsen, M., 2020. Abrupt fen-bog transition across southern Patagonia: timing,
769 causes, and impacts on carbon sequestration. *Frontiers in Ecology and Evolution* 8.
770 <https://doi.org/10.3389/fevo.2020.00273>.

771 Loisel, J., Gallego-Sala, A.V., Amesbury, M.J., Magnan, G., Anshari, G., Beilman, D.W.,
 772 Benavides, J.C., *et al.*, 2021. Expert assessment of future vulnerability of the global
 773 peatland carbon sink. *Nature Climate Change* 11, 70–77.

774 Loisel, J., Garneau, M., 2010. Late Holocene paleoecohydrology and carbon accumulation
 775 estimates from two boreal peat bogs in eastern Canada: potential and limits of multi-
 776 proxy archives. *Palaeogeography Palaeoclimatology Palaeoecology* 291, 493–533.

777 Loisel, J., Yu, Z., Beilman, Camill, P., Alm, J., Amesbury, M.J., Anderson, D., *et al.*, 2014. A
 778 database and synthesis of northern peatland soil properties and Holocene carbon and
 779 nitrogen accumulation. *The Holocene* 24, 1028–1042.

780 Mann, M.E., Zhang, Z.H., Rutherford, S., Bradley, R.S., Hughes, M.K., Shindell, D., Ammann,
 781 C., Faluvegi, G., Ni, F.B., 2009. Global signatures and dynamical origins of the Little Ice
 782 Age and Medieval Climate Anomaly. *Science* 326, 1256–1260.

783 Martini, I. P., 2006, The cold-climate peatlands of the Hudson Bay Lowland, Canada: brief
 784 overview of recent work, *in* Martini, I. P., Martínez Cortizas, A., and Chesworth, W.,
 785 eds., *Peatlands: Evolution and Records of Environmental and Climate Changes*: Elsevier,
 786 Amsterdam, pp. 53-83.

787 Mauquoy, D., Hughes, P.D.M., Van Geel, B., 2010. A protocol for plant macrofossil analysis of
 788 peat deposits. *Mires and Peat* 7, 6. [http://www.mires-and-](http://www.mires-and-peat.net/pages/volumes/map07/map0706.php)
 789 [peat.net/pages/volumes/map07/map0706.php](http://www.mires-and-peat.net/pages/volumes/map07/map0706.php).

790 McAndrews, J.H., Berti, A.A., Norris, G., 1973. *Key to the Quaternary Pollen and Spores of the*
 791 *Great Lakes Region*. Royal Ontario Museum, Toronto.

792 McAndrews, J. H., Riley, J. L., and Davis, A. M., 1982, Vegetation history of the Hudson Bay
793 Lowland: A postglacial pollen diagram from the Sutton Ridge: *Le Naturaliste Canadien*
794 109, 597-608.

795 McLaughlin, J., Packalen, M., Shrestha, B., 2018. *Assessment of the Vulnerability of Peatland*
796 *Carbon in the Albany Eodistrict of the Hudson Bay Lowlands, Ontario, Canada to*
797 *Climate Change*. Science and Research Branch, Ontario Ministry of Natural Resources
798 and Forestry, Peterborough, Canada.

799 Miola, A., 2012. Tools for non-pollen palynomorphs (NPPs) analysis: a list of Quaternary NPP
800 types and reference literature in English language (1972–2011). *Review of Palaeobotany*
801 *and Palynology* 186, 142–161.

802 Moos, M.T., Cumming, B.F., 2011. Changes in the parkland-boreal forest boundary in
803 northwestern Ontario over the Holocene. *Quaternary Science Reviews* 30, 1232–1242.

804 Morris, P.J., Swindles, G.T., Valdes, P.J., Ivanovic, R.F., Gregoire, L.J., Smith, M.W., Tarasov,
805 L., Haywood, A.M., Bacon, K.L., 2018. Global peatland initiation driven by regionally
806 asynchronous warming. *Proceedings of the National Academy of Sciences* 115, 4851–
807 4856.

808 Naafs, B.D.A., Inglis, G.N., Blewett, J., McClymont, E.L., Laurentano, V., Xie, S.C., Evershed,
809 R.P., Pancost, R.D., 2019. The potential of biomarker proxies to trace climate, vegetation,
810 and biogeochemical processes in peat: A review. *Global and Planetary Change* 179, 57–
811 79.

812 Naafs, B.D.A., Inglisab, G.N., Zheng, Y., Amesbury, M.J., Biestere, H., Bindler, R., Blewett, J.,
813 *et al.*, 2017. Introducing global peat-specific temperature and pH calibrations based on
814 brGDGT bacterial lipids. *Geochimica et Cosmochimica Acta* 208, 285–301.

815 Naafs, B.D.A., Rohrsen, M., Inglis, G.N., Lhteenoja, O., Feakins, S.J., Collinson, M.E.,
816 Kennedy, E.M., *et al.*, 2018. High temperatures in the terrestrial mid-latitudes during the
817 early Palaeogene. *Nature Geoscience* 11, 766–771.

818 Nichols, J., Peteet, D., 2019. Rapid expansion of northern peatlands and doubled estimate of
819 carbon storage. *Nature Geoscience* 12, 917–921.

820 Nichols, J.E., Peteet, D.M., Moy, C.M., Castaneda, I.S., McGeachy, A., Perez, M., 2014. Impacts
821 of climate and vegetation change on carbon accumulation in a south-central Alaskan
822 peatland assessed with novel organic geochemical techniques. *The Holocene* 24, 1146–
823 1155.

824 Norris, A.W., 1986. Review of Hudson Platform Paleozoic stratigraphy and biostratigraphy. In:
825 Martini, I.P. (Ed.), *Canadian Inland Seas*. Elsevier, Amsterdam, pp. 17–42.

826 Ogden, C.G., 1987. The fine structure of the shell of *Pyxidicula operculata*, an aquatic testate
827 amoeba (Rhizopoda). *Archiv fr Protistenkunde* 133, 157–164.

828 Ogden, C.G., Hedley, R.H., 1980. *An Atlas of Freshwater Testate Amoebae*. Oxford University
829 Press, Oxford, UK.

830 O’Reilly, B.C., Finkelstein, S.A., Bunbury, J., 2014. Pollen-derived paleovegetation
831 reconstruction and long-term carbon accumulation at a fen site in the Attawapiskat River
832 watershed, Hudson Bay Lowlands, Canada. *Arctic, Antarctic, and Alpine Research* 46, 6–
833 18.

834 Packalen, M.S., Finkelstein, S.A., 2014. Quantifying Holocene variability in carbon uptake and
835 release since peat initiation in the Hudson Bay Lowlands, Canada. *The Holocene* 24,
836 1063–1074.

837 Packalen, M.S., Finkelstein, S.A., McLaughlin, J.W., 2014. Carbon storage and potential
838 methane production in the Hudson Bay Lowlands since mid-Holocene peat initiation.
839 *Nature Communications* 5, 4078. <https://doi.org/10.1038/ncomms5078>.

840 Packalen, M.S., Finkelstein, S.A., McLaughlin, J.W., 2016. Climate and peat type in relation to
841 spatial variation of the peatland carbon mass in the Hudson Bay Lowlands, Canada.
842 *Journal of Geophysical Research-Biogeosciences* 121, 1104–1117.

843 Pals, J.P., Vangeel, B., Delfos, A., 1980. Paleoecological studies in the Klokkeweel Bog near
844 Hoogkarspel (prov. of Noord-Holland). *Review of Palaeobotany and Palynology* 30,
845 371–418.

846 Payette, S., Filion, L., 1993. Holocene water-level fluctuations of a subarctic lake at the tree line
847 in northern Québec. *Boreas* 22, 7–14.

848 Peltier, W.R., Argus, D.F., Drummond, R., 2015. Space geodesy constrains ice-age terminal
849 deglaciation: the global ICE-6G_C (VM5a) model. *Journal of Geophysical Research:*
850 *Solid Earth* 120, 450–487.

851 Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., Buck, C.E.,
852 *et al.*, 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years
853 cal BP. *Radiocarbon* 55, 1869–1887.

854 Renssen, H., Seppä, H., Heiri, O., Roche, D.M., Goosse, H., Fichet, T., 2009. The spatial and
855 temporal complexity of the Holocene thermal maximum. *Nature Geoscience* 2, 411–414.

856 Riley, J.L., 2003. *Flora of the Hudson Bay Lowland and its Postglacial Origin*. National
857 Research Council of Canada, Ottawa.

858 Riley, J.L., 2011. *Wetlands of the Ontario Hudson Bay Lowland: A Regional Overview*. Nature
859 Conservancy of Canada, Toronto.

860 Rydin, H., Jeglum, J.K., 2013. *The Biology of Peatlands*. 2nd ed. Oxford University Press,
861 Oxford, UK.

862 Sims, R.A., Riley, J.L., Jeglum, J.K., 1979. *Vegetation, Flora, and Vegetational Ecology of the*
863 *Hudson Bay Lowland: A Literature Review and Annotated Bibliography*, Report 0-X-
864 297. Canadian Forestry Service, Sault Ste. Marie, Canada.

865 Sinninghe Damsté, J.S., Schouten, S., Hopmans, E.C., van Duin, A.C.T., Geenevasen, J.A.J.,
866 2002. Crenarchaeol: the characteristic core glycerol dibiphytanyl glycerol tetraether
867 memberane lipid of cosmopolitan pelagic crenarchaeota. *Journal of Lipid Research* 43,
868 1641–1651.

869 Sullivan, M.E., Booth, R.K., 2011. The potential influence of short-term environmental
870 variability on the composition of testate amoeba communities in sphagnum peatlands.
871 *Microbial Ecology* 62, 80–93.

872 Swindles, G.T., Holden, J., Raby, C.L., Turner, T.E., Blundell, A., Charman, D.J., Menberu,
873 M.W., Kløve, B., 2015. Testing peatland water-table depth transfer functions using high-
874 resolution hydrological monitoring data. *Quaternary Science Reviews* 120, 107–117.

875 van Bellen, S., Dallaire, P.L., Garneau, M., Bergeron, Y., 2011a. Quantifying spatial and
876 temporal Holocene carbon accumulation in ombrotrophic peatlands of the Eastmain
877 region, Quebec, Canada. *Global Biogeochemical Cycles* 25, GB2016.
878 <https://doi.org/10.1029/2010gb003877>.

879 van Bellen, S., Garneau, M., and Booth, R. K., 2011b. Holocene carbon accumulation rates from
880 three ombrotrophic peatlands in boreal Quebec, Canada: Impact of climate-driven
881 ecohydrological change: The Holocene 21, 1217-1231.

882 van Geel, B., 1978. A palaeoecological study of Holocene peat bog sections in Germany and the
 883 Netherlands, based on the analysis of pollen, spores and macro- and microscopic remains
 884 of fungi, algae, cormophytes and animals. *Review of Palaeobotany and Palynology* 25,
 885 1–120.

886 van Geel, B., Bohncke, S.J.P., Dee, H., 1980. A palaeoecological study of an upper late glacial
 887 and Holocene sequence from “de borchert”, The Netherlands. *Review of Palaeobotany*
 888 *and Palynology* 31, 367–448.

889 Viau, A.E., Gajewski, K., 2009. Reconstructing millennial-scale, regional paleoclimates of
 890 boreal Canada during the Holocene. *Journal of Climate* 22, 316–330.

891 Weijers, J.W.H., Schouten, S., van den Donker, J.C., Hopmans, E.C., Damste, J.S.S., 2007.
 892 Environmental controls on bacterial tetraether membrane lipid distribution in soils.
 893 *Geochimica et Cosmochimica Acta* 71, 703–713.

894 Weijers, J.W.H., Steinmann, P., Hopmans, E.C., Schouten, S., Sinninghe Damsté, J.S., 2011.
 895 Bacterial tetraether membrane lipids in peat and coal: testing the MBT–CBT temperature
 896 proxy for climate reconstruction. *Organic Geochemistry* 42, 477–486.

897 Williams, J.W., Grimm, E.C., Blois, J.L., Charles, D.F., Davis, E.B., Goring, S.J., Graham,
 898 R.W., *et al.*, 2018. The Neotoma Paleoecology Database: a multiproxy, international,
 899 community-curated data resource. *Quaternary Research* 89, 156–177.

900 Yang, H., Xiao, W., Słowakiewicz, M., Ding, W., Ayari, A., Dang, X., Pei, H., 2019. Depth-
 901 dependent variation of archaeal ether lipids along soil and peat profiles from southern
 902 China: implications for the use of isoprenoidal GDGTs as environmental tracers. *Organic*
 903 *Geochemistry* 128, 42–56.

- Yeloff, D., Charman, D., van Geel, B., Mauquoy, D., 2007. Reconstruction of hydrology, vegetation and past climate change in bogs using fungal microfossils. *Review of Palaeobotany and Palynology* 146, 102–145.
- Yu, Z.C., Loisel, J., Brosseau, D.P., Beilman, D.W., Hunt, S.J., 2010. Global peatland dynamics since the last glacial maximum. *Geophysical Research Letters* 37, 5. <https://doi.org/10.1029/2010gl043584>.
- Zheng, Y., Fang, Z., Fan, T., Liu, Z., Wang, Z., Li, Q., Pancost, R.D., Naafs, B.D.A., 2020. Operation of the boreal peatland methane cycle across the past 16 k.y. *Geology* 48, G46709.46701. <https://doi.org/10.1130/G46709.1>.
- Zheng, Y., Li, Q., Wang, Z., Naafs, B.D.A., Yu, X., Pancost, R.D., 2015. Peatland GDGT records of Holocene climatic and biogeochemical responses to the Asian monsoon. *Organic Geochemistry* 87, 86–95.
- Zheng, Y., Pancost, R.D., Liu, X., Wang, Z., Naafs, B.D.A., Xie, X., Liu, Z., Yu, X., Yang, H., 2017. Atmospheric connections with the North Atlantic enhanced the deglacial warming in northeast China. *Geology* 45, 1031–1034.
- Zheng, Y., Pancost, R.D., Naafs, B.D.A., Li, Q., Liu, Z., Yang, H., 2018. Transition from a warm and dry to a cold and wet climate in NE China across the Holocene. *Earth and Planetary Science Letters* 493, 36–46.

FIGURE CAPTIONS

Figure 1. (color online) Map of study location in the Hudson Bay Lowlands (HBL), northern Ontario, Canada (A, C), and image of HRST 13-01 (B). The HBL outline is after the Canadian Hudson Plains ecozone from Ecological Stratification Working Group (1995); the Quaternary

features are from Barnett et al. (2012) and Bajc and Yeung (2017); the digital elevation model is from Government of Ontario (2020).

Figure 2. Output from rbacon of the Bayesian age-depth model for HRST 13-01, the HBL, northern Ontario, Canada (Blaauw and Christen, 2011). The red dotted line is the weighted mean age for a given depth, and the gray region surrounding the curve represents the 95% confidence interval; acc. = accumulation; mem. = memory. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Figure 3. (color online) Peat properties and plant macrofossils at HRST 13-01, the HBL, Ontario, Canada. Depth is the primary y-axis.

Figure 4. (color online) Pollen and spore, non-pollen palynomorph (NPP; fungi and algae), and testate amoeba assemblages from HRST 13-01, the HBL, northern Ontario, Canada. Taxa present in this diagram are >10% of their given assemblage. Depth is the primary y-axis. Gray exaggeration is 5×. WTD = water table depth. The pollen sum used to calculate the percentages includes all pollen and spore taxa minus *Sphagnum* spores. *Sphagnum* spore and NPP sums are the pollen sum plus the respective taxa included in each category. The testate amoeba (TA) sum includes all taxa minus the rotifer taxon. The rotifer sum was calculated like the *Sphagnum* and NPP sums, using the TA sum as the base. The gray dashed and solid lines in the Procrustes residuals indicate the first, median, and third quartile values from left to right. The samples that fell below the first quartile are highly congruent, suggesting that the pollen and testate amoeba records are responding to a similar local environmental driver (ombrotrophy). The *Picea* curve

indicates sample depths, and the dashed lines represent the samples that had low pollen concentrations and therefore lower counts (see “Methods” for details). The numbers listed after the NPPs are the type numbers, after Miola (2012).

Figure 5. (color online) The relative abundance of isoprenoidal glycerol dialkyl glycerol tetraethers (isoGDGTs) and proxy ratios of branched (brGDGTs) (see “Methods” for details) at HRST 13-01, the HBL, northern Ontario, Canada. Depth is the primary y-axis. Gray exaggeration is 10×.

Figure 1.

Figure 2.

Figure 3.

Figure 5.

Table 1. AMS radiocarbon (^{14}C) ages from HRST 13-01, Hudson Bay Lowlands, northern Ontario, Canada.

Core	Depth (cm)	Radiocarbon Age (^{14}C yr. BP)	Material	Cal BP 2 σ range	Lab ID
2	22-23	356 $\pm$ 21	<i>Sphagnum</i> leaves/stems	490-420 (47.6%) 400-320 (47.8%)	UOC-5126
1	59-60	1555 $\pm$ 25	Cyperaceae leaves	1530-1390 (95.4%)	A2884
2	64-65	1427 $\pm$ 24	<i>Sphagnum</i> leaves/stems	1360-1290 (95.4%)	UOC-5127
2	101-104	3399 $\pm$ 24	Herbaceous leaves	3700-3580 (95.4%)	UOC-5128
2	122-124	6069 $\pm$ 28	Wood fragments	7000-6850 (93.9%)	UOC-5129
1	123-124	6440 $\pm$ 30	Cyperaceae leaves	7430-7290 (95.4%)	A2883

Table 2: Zonation summary for HRST-1301, Hudson Bay Lowlands region, Ontario, Canada

Zone	Depth (cm)	Age (cal yr BP)	Wetland Successional Stage	Description	
				Regional Vegetation	Local Site Conditions
1	>126	>7600	Marsh	Lower tree pollen relative abundances, indicates a landscape of mixed shrubs/trees (<i>Picea</i> , <i>Pinus</i> , <i>Larix</i> , Ericaceae)	Poorly sorted inorganic sediments with a size range of clays to sands; testate amoebae are absent; pollen assemblage consists of marsh and open water indicators including Cyperaceae, <i>Equisetum</i> , <i>Nuphar</i> , and ferns (Polypodiaceae and Pteridophyta). Algal non-pollen palynomorphs, <i>Sphagnum</i> spores and Asteraceae pollen are also abundant (>5%).
2	126-95	7600-3100	Rich fen	Establishment of <i>Picea</i> – dominated landscape with regression of the coastline and establishment of peat accumulation	Herbaceous peat; testate amoebae absent or rare; pH is near neutral, as inferred by brGDGT assemblages; pollen assemblage includes <i>Sphagnum</i> and Cyperaceae
3	95-35	3100-760	Poor fen		Mixed <i>Sphagnum</i> /herbaceous peat; testate amoebae indicate wet conditions at the start of the zone and transition to drier conditions with an assemblage shift at the subzonal boundary; brGDGT proxy indicates that pH transitions from neutral to acidic; pollen assemblage records increases in <i>Betula</i> and Ericaceae and a decrease in Cyperaceae
4	760-0	760 to present	Bog		<i>Sphagnum</i> peat; testate amoebae indicate generally lower water table depth; brGDGT-inferred pH is acidic; the pollen assemblage shifts to high Ericaceae and <i>Sphagnum</i> abundance

Supplementary Material for Davies et al. “Eco-hydrological controls on apparent rates of peat carbon accumulation in a boreal bog record from the Hudson Bay Lowlands, Canada”

1. PRINCIPAL COMPONENTS AND PROCRUSTES ANALYSIS

The sample scores of a principles component analysis (PCA) for samples common to the pollen and testate amoeba datasets (N= 28; Fig. S1) were tested for congruence using Procrustes analysis in the ‘vegan’ package in R (Figure S1; Oksanen et al., 2018). The datasets were converted to proportions and square root transformed prior to PCA analysis to minimize variance. Procrustes analysis rescales and rotates the sample scores of one of the ordination datasets to minimize the sum of squares of the Euclidean distances between the two configurations. A sum of squares value of zero represents perfect alignment (Peres-Neto and Jackson, 2001). This technique has been used to compare multivariate ecological and environmental datasets in both modern (Bunbury et al., 2020) and paleoecological settings (Forcino et al., 2015). We selected the target ordination in the Procrustes analysis to be the testate amoeba dataset, as we wanted to test whether the vegetation (pollen dataset) was responding to local environmental conditions (testate amoeba dataset). We scaled the configurations to equal dispersion (i.e. unit variance; symmetric = TRUE in the ‘procrustes’ function in vegan) before rotation. The Procrustes sum of squares (m_{12}) significance was tested with 999 permutations on a symmetric rotation (Peres-Neto and Jackson, 2001). For the testate amoeba dataset, the PC1 ($\lambda=0.1468$) and PC2 ($\lambda=0.08726$) axes explained 41% and 24% of the variance, respectively. For the pollen dataset, the PC1 ($\lambda=0.02139$) and PC2 ($\lambda=0.00862$) axes explained 45% and 18% of the variance, respectively.

Figure S1. Procrustes analysis of the PCA axis scores for the testate amoeba and pollen datasets (N=28). Labels indicate the position of the samples in the pollen ordination and the arrows indicate the sample position in the testate amoeba ordination. The red arrows indicate the samples that had residuals that were less than the first quartile of the dataset (sample residual <0.1), which was used in this study to indicate samples that were highly congruent. The solid axes lines (black) indicate the rotation of the pollen dataset needed to minimize the sum of squared difference between the two ordinations.

2. POLLEN AND TESTATE AMOEBEA RECORDS

A total of 40 testate amoebae and 35 pollen and spore taxa were identified at Site 13-01. Rare and infrequent taxa not included in Figure 4 of the main text are found in Figure S2 (<10% of the assemblage). Figure S2 also shows the absolute water table depth reconstruction and the reconstruction error. Images of *Pyxidicula* sp. A are found in Figure S3.

Figure S2. Pollen and spore, non-pollen palynomorph (NPP; fungi and algae), and testate amoeba assemblages of HRST 13-01, Hudson Bay

Lowlands region, Canada. Taxa present in this diagram were <10% of their given assemblage. Depth is the primary y-axis for this figure. Grey exaggeration is 10x. WTD: water table depth (larger numbers indicate drier conditions). The pollen sum used to calculate the percentages included all pollen and spore taxa, minus *Sphagnum* spores. *Sphagnum* spore and NPP sums were the pollen sum plus the respective taxa included in each category. The testate amoeba (TA) sum included all taxa minus the rotifer taxon. The rotifer sum was calculated like the *Sphagnum* and NPP sums, using the TA sum as the base. Numbers listed after the NPPs are the type numbers after Miola (2012). The shaded grey region of the water table depth curve is the reconstruction standard error of prediction (SEP).

42

Figure S3. *Pyxidicula* sp. A of HRST 13-01. **A.** Oblique view showing the extension of the test wall or lip seen in some specimens (sample from depth 4-5 cm; 400x magnification). **B.** Aboral view showing the areolar surface texture (sample from depth 18-19 cm, 1000x magnification in oil immersion) **C.** Lateral view showing the test thickening towards the aperture (sample from depth 30-31 cm, 400x magnification) **D.** Aboral view showing the extension of the test wall or lip seen in some specimens (sample from depth 11-12 cm, 400x magnification).

3. WATER TABLE DEPTH RECONSTRUCTION MODEL SELECTION

The wa.inv.tol model of Amesbury et al. (2018) was selected as it included samples from the Hudson Bay Lowlands and the range of percentages for each taxon were suitable analogues for the site samples (i.e. the maximum percentages in the modern dataset were higher than the recalculated fossil percentages, tested using the ‘coverage.plot’ function in the ‘palaeoSig’ package in R; (Telford, 2015)). Sample standard errors and model performance statistics were generated using bootstrap simulations (1000

iterations; Amesbury et al. (2018)). The model was run in the 'rioja' package in R (Juggins, 2017). The WTD reconstruction values were converted to a Z score using 'R.basic' package in R (Bengtsson, 2013) to demonstrate the relative shifts in species assemblages related to hydrology without assigning an absolute value to the data, as although shown to represent directional changes in water table well, absolute values from transfer functions should be interpreted with caution (Swindles et al., 2015).

4.. TAXONOMIC AUTHORITIES FOR THE TESTATE AMOEBA TAXA

A total of 40 testate amoebae and one rotifer were found at site HRST 13-01. Taxonomic authorities and summary data (minimum, maximum, total number of samples, average abundance) for each taxon are shown in Table S1.

Table S1. Taxonomic authorities for the testate amoeba taxa found at Site HRST 13-01. Summary values are based on the 28 samples with counts of > 150 tests. N = number of occurrences. Percentages calculated for minimum (min), mean, and maximum (max) relative abundances are based on all 28 samples.

Taxon	Authority	N	%		
			Min	Mean	Max
<i>Alabasta militaris</i> type	(Penard, 1890)	20	0	3.7	16.5
<i>Amphitrema wrightianum</i> type	Archer, 1869	11	0	4.8	30.7
<i>Arcella artocrea</i>	Leidy, 1876	20	0	1.9	8.7
<i>Arcella catinus</i> type	Penard, 1890	23	0	1.7	10.6
<i>Arcella discoides</i> type	Ehrenberg, 1843	28	1.1	5.6	16.2
<i>Arcella vulgaris</i> type	Ehrenberg, 1830	6	0	0.4	3.3
<i>Archerella flavum</i>	(Archer, 1877)	18	0	8.8	65.9
<i>Assulina muscorum</i>	Greef, 1888	17	0	2.2	10.3
<i>Assulina seminulum</i> type	(Ehrenberg, 1848)	16	0	1.5	8.6
<i>Bullinularia indica</i>	(Penard, 1907)	23	0	1.5	5.8
<i>Centropyxis aculeata</i> type	(Ehrenberg, 1830)	1	0	0.0	0.4
<i>Centropyxis cassis</i> type	(Wallich, 1864)	1	0	0.0	0.4
<i>Centropyxis ecornis</i> type	(Ehrenberg, 1841)	2	0	0.0	0.5
<i>Corythion-Trinema</i> type	Tarànek, 1881; Dujardin, 1841	2	0	0.0	0.4
<i>Cyclopyxis arcelloides</i> type	(Penard, 1902)	20	0	2.3	15.6
<i>Diffflugia globulosa</i> type	Dujardin, 1837	1	0	0.0	0.7
<i>Diffflugia lucida</i> type	Penard, 1890	1	0	0.0	0.6
<i>Diffflugia pristis</i> type	Penard, 1902	19	0	5.6	27.7
<i>Diffflugia pulex</i> type	Penard, 1902	26	0	14.9	47.5
<i>Euglypha rotunda</i> type	Wailes, 1911	3	0	0.1	1.0
<i>Euglypha tuberculata</i> type	Dujardin, 1841	6	0	0.3	2.9
<i>Gibbocarina (Nebela) tubulosa</i> type	(Penard, 1890)	1	0	0.0	0.7
<i>Heleopera petricola</i>	Leidy, 1879	4	0	0.1	1.0
<i>Heleopera rosea</i>	Penard, 1890	1	0	0.0	1.1
<i>Heleopera sphagni</i>	(Leidy, 1874)	21	0	4.5	13.2
<i>Heleopera sylvatica</i>	Penard, 1890	28	1.3	10.6	33.2
<i>Hyalosphenia elegans</i> type	Leidy, 1874	10	0	0.5	4.0
<i>Hyalosphenia minuta</i>	Cash, 1892	5	0	0.1	1.0
<i>Hyalosphenia papilio</i>	Leidy, 1875	14	0	0.9	6.0
<i>Hyalosphenia subflava</i>	Cash and Hopkinson, 1909	27	0	13.3	46.8
<i>Lesquereusia modesta</i> type	Rhumbler, 1895	1	0	0.0	0.6
<i>Nebela collaris-bohemica</i> type	(Ehrenberg, 1848); (Tarànek, 1882)	3	0	0.0	0.5
<i>Nebela flabellulum</i>	Leidy, 1874	2	0	0.1	2.0
<i>Nebela tinctoria-parvula</i> type	(Leidy, 1879); Cash & Hopkinson, 1909	9	0	0.6	3.2
<i>Phryganella acropodia</i> type	(Hertwig and Lesser, 1874)	13	0	0.9	10.6
<i>Pseudodiffugia fascicularis</i> type	Penard, 1902	3	0	0.0	0.5
<i>Pseudodiffugia fulva</i> type	(Archer, 1870)	18	0	2.2	13.6
<i>Pyxidicula</i> sp. A	Ehrenberg, 1838	20	0	6.7	29.0
<i>Trigonopyxis arcula</i> type	(Leidy, 1879)	25	0	2.0	5.9
<i>Trigonopyxis minuta</i> type	Schönborn & Peschke, 1988	24	0	2.1	7.1

REFERENCES CITED

- Amesbury, M.J., et al., 2018. Towards a Holarctic synthesis of peatland testate amoeba ecology: Development of a new continental-scale palaeohydrological transfer function for North America and comparison to European data. *Quaternary Science Reviews* 201, 483-500, doi: 10.1016/j.quascirev.2018.10.034.
- Bengtsson, H., 2013. R.basic: [R] Class Library - Stand-alone basic functions, R Package version 0.53.0., <http://www.braju.com/R/>
- Bunbury, J., Fisher, R.G., Blumenstein, T., 2020. Anthropogenic and climate change impacts on lake-water chemistry over the past 20 years, Upper Midwest, United States. *Physical Geography* 41, 433-450, doi: 10.1080/02723646.2019.1674556.
- Forcino, F.L., Ritterbush, K.A., Stafford, E.S., 2015. Evaluating the effectiveness of the Mantel test and Procrustes randomization test for exploratory ecological similarity among paleocommunities. *Palaeogeography, Palaeoclimatology, Palaeoecology* 426, 199-208, doi: 10.1016/j.palaeo.2015.03.023.
- Juggins, S., 2017. rioja: Analysis of Quaternary Science Data, R Package Version 0.9-15.1, <http://cran.r-project.org/package=rioja>
- Miola, A., 2012. Tools for non-pollen palynomorphs (NPPs) analysis: A list of Quaternary NPP types and reference literature in English language (1972-2011). *Review of Palaeobotany and Palynology* 186, 142-161, doi: 10.1016/j.revpalbo.2012.06.010.
- Oksanen, P., et al., 2018. vegan: Community Ecology Package, R Package version 2.5-2., <https://CRAN.R-project.org/package=vegan>
- Peres-Neto, P.R., Jackson, D.A., 2001. How well do multivariate data sets match? The advantages of a Procrustean superimposition approach over the Mantel test. *Oecologia* 129, 169-178, doi: 10.1007/s004420100720.
- Swindles, G.T., Holden, J., Raby, C.L., Turner, T.E., Blundell, A., Charman, D.J., Menberu, M.W., Kløve, B., 2015. Testing peatland water-table depth transfer functions using high-resolution hydrological monitoring data. *Quaternary Science Reviews* 120, 107-117, doi: 10.1016/j.quascirev.2015.04.019.
- Telford, R.J., 2015. palaeoSigs: Significance tests of quantitative palaeoenvironmental reconstructions, R package version 1.1-3, <http://cran.r-project.org/package=palaeoSigs>