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Keywords:	testate amoeba, Neoglacial, methane, plant macrofossils, Little Ice Age

Poor fen succession over ombrotrophic peat related to late-Holocene increased surface wetness in subarctic Quebec, Canada

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Abstract

Northern peatlands act as archives of environmental change through their sensitivity to water balance fluctuations, while being significant contributors to global greenhouse gas dynamics. Subarctic fens in northeastern Canada are characterized by a dominance of pools and flarks. We aimed to reconstruct the late-Holocene hydrological conditions of these fens to establish the timing of the initiation of pool and flark formation and possible linkages with climate. Testate amoebae and plant macrofossils from five cores, sampled in three fens, were analyzed to infer water tables with chronologies based on ^{14}C and ^{210}Pb dating. All sites showed presence of relatively dry, ombrotrophic conditions with abundant *Picea* from 5000 cal a BP, followed by a first shift to wet, poor fen conditions with pool and flark development around 3000 cal a BP and a subsequent wet shift after ~800 cal a BP. These trends coincide with previously observed Neoglacial and Little Ice Age cooler and wetter conditions and therefore climate may well have been a dominant factor in the initiation and development of pools and flarks over the late-Holocene. The effect of anticipated climate change on subarctic peatlands remains unclear, although wetter conditions might enhance pool expansion to the detriment of terrestrial components.

Key words: testate amoeba, Neoglacial, methane, plant macrofossils, Little Ice Age.

Introduction

Peatlands are defined by the accumulation of organic matter under anoxic conditions, which over millennia results in the creation of stratigraphic archives as they expand vertically and laterally under the influence of autogenic and allogenic factors. Typically, peat accumulation starts under minerotrophic conditions either by the infilling of an aquatic ecosystem, or by the growth of *Sphagnum* over soils through paludification. As accumulation continues, the peatland surface becomes isolated from groundwater supply until eventually precipitation represents the only source of water to the vegetation. This transition is normally present in stratigraphies from ombrotrophic peatlands, often referred to as the fen-bog transition, and its timing may be either autogenically or allogenically influenced (Hughes and Dumayne-Peaty, 2002). Changes in peatland stratigraphy have been of scientific interest as these ecosystems constitute both historic records of environmental and climate change (Aaby, 1976; Barber *et al.*, 1994) and important stores of organic carbon (Gorham, 1991). Because of this sensitivity to environmental change and the high carbon sequestration potential peatland ecosystems represent an important feedback mechanism for climate change (Yu, 2011). Peatlands generally act as sinks for carbon dioxide (CO_2) and sources of methane (CH_4) (Frolking and Roulet, 2007), yet greenhouse gas budgets are highly variable depending on the hydrological and trophic state of the peatland or, more specifically, surface microtopography (Waddington and Roulet, 1996).

In eastern Canada, the distribution of peatland types is related to important longitudinal and latitudinal climatological gradients. The subarctic fens of the Laforge region (54°N; 72°W), located within the La Grande Rivière watershed, have developed at the northern limit of the ombrotrophic peatland distribution, persisting under similar climatic conditions to previously studied patterned fens of western Labrador (Foster *et al.*, 1988). Due to their ecotonal location, these ecosystems are likely to be less resilient to future climate change and therefore their ecohydrological dynamics deserve particular attention (e.g. Tahvanainen, 2011; Weckström *et al.*, 2010). The subarctic fens in the Laforge region are characterized by an important presence of pools and waterlogged flarks, accounting for 35-42% of the surface (Cliche Trudeau *et al.*, 2012; Tardif *et al.*, 2009). Previous studies suggested that water tables have risen during the recent millennia (~3000 cal a BP) and subsequently since the Little Ice Age (LIA), causing important tree mortality and pool expansion to the detriment of terrestrial microforms (Arlen-Pouliot, 2009; Tardif *et al.*, 2009). Cliche Trudeau *et al.* (2012) quantified seasonal CH_4 fluxes for different microforms in Laforge region fens, concluding that pools occupy 42% of the surface, yet account for 79% of CH_4 emissions. As a result, shifts in microform distribution are of major concern considering peatland carbon feedback to climate change. A more detailed image of centennial to millennial peatland CH_4 emissions, for instance, may contribute to the understanding of late-Holocene increases in atmospheric CH_4 concentrations, the forcing of which has been much debated (e.g. Korhola *et al.*, 2010; MacDonald *et al.*, 2006; Ruddiman *et al.*, 2011; Singarayer *et al.*, 2011; Yu, 2011).

In this study, testate amoebae were used as a proxy for paleohydrological conditions. Testate amoebae are single-celled protists that live in the uppermost layer of the acrotelm. They rapidly respond to hydrological shifts while being abundant and diverse (often >20 identifiable species per subsample) and their shells ('tests') are generally well preserved in peat. As testate amoeba presence is related to the position of the water table, past water table levels may be inferred from their fossil assemblages. Over the last two decades, several transfer functions have been created to infer past water tables covering the major part of the global peatland distribution (Booth, 2008; Charman *et al.*, 2007; Lamentowicz *et al.*, 2008; Payne *et al.*, 2008; Warner and Charman, 1994; Wilmshurst *et al.*, 2003). Although the environmental control on amoeba communities may be more complicated in fens due to the presence of a minerotrophic influx, testate amoebae have been successfully used to quantify water table variations in these ecosystems as well (Payne, 2011).

The objective of this study was to reconstruct the hydrological history of the peatlands of the Laforge region using testate amoeba and plant macrofossil analyses. Specifically, we aimed to identify the timing of the hydrological shift from ombrotrophic to poor minerotrophic conditions and test the linkage with Neoglacial cooler and wetter conditions. A transfer function built from a testate amoeba training set covering sites from Quebec (between 45-55°N) was used to infer water table levels (Lamarre *et al.*, accepted). Moreover, plant macrofossils were identified, representing an independent record of changes in hydrology that supports the testate amoeba-inferred reconstructions.

Study region

The Laforge region is located in the *Picea*-dominated lichen-woodland biome of northeastern Canada (Fig. 1; Saucier *et al.*, 1998) where mean annual temperature (MAT) averages -4.3°C with a mean annual precipitation (MAP) of 738 mm (Fig. 2; interpolated means of 1971–2003 NLWIS data; Hutchinson *et al.*, 2009). The short growing season (mean of 153 days for 2009-2010; Cliche Trudeau *et al.*, 2012) is characterized by an average of 1400 degree-days above 0°C. Poor fens are the regionally dominant peatland type in this region. Three representative fens were selected for this study after extensive aerial survey (Fig. 1): Aeroport (54°06'02"N; 72°30'59"W; 3.0 ha), Ours (54°02'56"N, 72°27'25"W; 1.6 ha; 8 km southeast of Aeroport fen) and Abeille (54°06'52"N; 72°30'01"W; 3.5 ha; 2 km northeast of Aeroport fen). Present-day vegetation is characterized by *Sphagnum cuspidatum*, *Gymnocolea inflata*, *Vaccinium oxycoccos* and *Carex* spp. in wet flarks, *Sphagnum cuspidatum*, *Chamaedaphne calyculata*, *Vaccinium oxycoccos*, *Drosera rotundifolia* and *Carex* spp. on strings and *Sphagnum fuscum*, *Empetrum nigrum*, *Rubus chamaemorus* and *Picea mariana* on ridges and near the forest edge (Cliche Trudeau *et al.*, 2012).

Material and methods

Fieldwork

A total of six cores from three fens were extracted from lawns using a box corer with a 10 × 10 cm cross section. One core from Abeille peatland showed contamination and was therefore discarded. To determine core length, we referred to chronologies of Arlen-Pouliot (2009), which showed that 1 m of peat represented ~5000 years. As we focused on the period from the mid-Holocene onwards, we estimated 1 m of peat to be sufficient. Collected monoliths were packed in plastic, aluminium foil and polyvinyl chloride tubes and stored in a cold chamber at 4°C until analysis. Prior to analyses, cores were sectioned into 1-cm slices.

Stratigraphic analyses

Testate amoeba sample preparation followed the method of Hendon and Charman (1997) with *Lycopodium* spores added to 1- or 2-cm^3 subsamples to calculate total amoeba concentrations, with the exception of core Aero1, for which no concentrations were calculated. We aimed for total counts of 150 individuals, yet some were limited to <40 individuals due to poor amoeba preservation and high amounts of highly decomposed organic matter in the amoeba size fraction. Following the recommendations of Payne and Mitchell (2008), water table depths were not inferred for such low counts as they may be unreliable, and we suggest that reconstructions based on <75 amoebae should be interpreted with caution. After initial analyses of the section <355 µm of cores Aero1 and Ours1, 212-µm sieves were used in the preparation of subsamples from Aero5, Ours4 and Abeille5 to facilitate counting. By this means we excluded as much fine-fraction organic matter as possible from our slides while retaining most, if not all, amoebae. Analyses were performed at intervals varying between 1 and 4 cm. Species presence was expressed as a percentage of the total count. Taxonomy follows Charman *et al*. (2000), modified by Booth (2008).

For the identification of plant macrofossils, subsamples of 5 cm^3 were heated in 5% KOH solution and then rinsed through 150- or 170-µm sieves. A binocular microscope was used for the identification of peat-forming vegetation and abundance was expressed as volume percentages or counts; the identification of *Sphagnum* spp. and other bryophytes was performed with a microscope (×40-100). Vascular plant species were determined using guides by Grosse-Brauckmann (1986), Lévesque et al. (1988) and Montgomery (1977). Bryophytes were identified using Crum and Anderson (1979-1980) and Mogensen (1986). The reference collection of fossil and modern material of the Laboratoire de paléoécologie terrestre, Centre d'Études Nordiques at Université Laval was used for validation of the identification of certain vascular plants and bryophytes. Nomenclature follows Marie-Victorin (1995) for vascular plants and Crum and Anderson (1979-1980) and Ireland (1982) for bryophytes. Stratigraphic diagrams were created with C2 version 1.7.2 (Juggins, 2007). Stratigraphic zones were identified by visual interpretation of variations in both plant macrofossil and testate amoeba assemblages.

Transfer function

In order to infer water table depths from testate amoeba assemblages a transfer function was developed from a total of 206 surface peat samples collected from 18 peatlands across the Quebec boreal and subarctic regions (Lamarre *et al.*, in press). We used a weighted average model with tolerance downweighting and classical deshrinking. Water table positions were expressed as depths relative to the peatland surface (WTD), i.e. negative values indicate standing water.

Chronologies

A total of 30 samples were submitted to Keck-CCAMS facility (Irvine, USA), Beta Analytic Inc. (Miami, USA) and IsoTrace Laboratory (University of Toronto, Canada) for accelerator mass spectrometry radiocarbon dating (Table 1). Only *Sphagnum*, leaves or seeds of Ericaceae and conifers were dated, and in rare cases charcoal fragments.

To accurately represent the acrotelm, additional ^{210}Pb dating through α-spectrometry was performed at GEOTOP-Université du Québec à Montréal. Prior to chemical treatments, rootlets were removed from the bulk peat. Chemical treatments included hydrofluoric acid (HF) addition to remove eventual mineral material. Ages were obtained from ^{210}Po activity using the constant rate of supply model (Appleby and Oldfield, 1978). Further details on the applied ^{210}Pb-dating methods can be found in Ali *et al*. (2008).

Age determinations from ^{14}C and ^{210}Pb dating were merged to create chronologies using Clam (Blaauw, 2010) in R (R Development Core Team, 2009). As coring was performed in 2005 (Aero and Ours cores) and 2010 (Abeille5), ages of either -55 or -60 cal a BP were applied to the surface of cores. Loess regression was applied for all cores, except for Aero5 and Ours4, which were modelled by a smooth spline; a minimum of 1000 iterations was set for the construction of chronologies. Loess and smooth spline regression models resulted in more natural accumulation models than those obtained from piecewise linear interpolation, especially for the basal parts of cores Aero5 and Ours4.

Results

Chronologies

Chronologies indicate relatively low rates of peat accumulation typical for subarctic peatlands, with an average sample time span of 45 a cm^{-1} (σ=6.0) (Fig. 3). In cores Aero5, Ours1 and Ours4, peat accumulation rates were higher prior to 4000 cal a BP, whereas the age-depth relationships of Aero1 and Abeille5 were close to linear.

Ecohydrological reconstructions

Detailed stratigraphic analyses show that all coring sites were dominated by ombrotrophic conditions before ~3000 cal a BP (Fig. 4a-e and Tables 2-6; complete diagrams as supplementary Figs. S1 and S2). During this period, local vegetation was dominated by *Sphagnum fuscum* and *Picea mariana* and dominant amoebae were *D. pulex* and *Archerella flavum* indicating water table depths were generally >5 cm below the surface. After 3000 cal a BP, all sites were subject to rising water tables and, although timing of the event is variable, flarks or shallow pool conditions became general between 3000 and 2000 cal a BP with increases in *Sphagnum majus*, *Sphagnum fallax*, *Larix laricina* and Herbaceae in the vegetation assemblages and *A. wrightianum* in the amoeba composition. Moreover, episodic presence of minerotrophic species such as *Sphagnum subsecundum*, *Drepanocladus revolvens* and *Calliergon stramineum* suggest poor fen conditions that generally persisted locally until ~1500 cal a BP (Fig. 5).

After 1490-1310 cal a BP, the two cores from Aeroport fen show a decrease in surface wetness (Fig. 4a-b; Fig. 5). At the same time, reconstructions in Ours fen do not indicate drier conditions in Ours4 whereas in Ours1 late-Holocene reconstructions are hampered by very low amoeba concentrations (<3000 cm^{-3}) and negligible accumulation with only 8 cm of peat accumulated between 2010 and 340 cal a BP (Fig. 5). In Abeille5, water tables during this period could not be inferred due to relatively low amoeba concentrations (<4000 cm^{-3}; Fig. 5).

After this slightly drier period, a return to wet flark conditions is generally observed at most sites ~900 cal a BP, at least at those where water tables could be confidently quantified. *S. majus*, *S. fallax* and amoeba *A. wrightianum* reappear as the dominant species in the vegetation assemblages. Finally, another dry shift has been recorded after ~AD 1880, with slightly decreasing water tables in four cores, as indicated by shifts in both testate amoeba assemblages (decreasing relative presence of *A. wrightianum*) and local vegetation (increases in lawn-associated *Sphagnum magellanicum* to the detriment of *S. fallax* and *S. majus*).

Discussion

The evolution of the subarctic poor fens in the Laforge region can be subdivided into five key periods: 1) a mid-Holocene dry *Picea*-*S. fuscum* bog period (>3000 cal a BP); 2) Neoglacial wet, herbaceous poor fen conditions (3000-1500 cal a BP); 3) An early-Medieval period with low test concentrations and poor WTD estimates (~1500-900 cal a BP); 4) LIA wet poor fen conditions (900 cal a BP-AD 1880) and 5) 20th century decreasing water tables (Fig. 6a).

Testate amoebae as proxies in subarctic fens

Inferring water tables from testate amoeba assemblages in fens may be precarious, as their sensitivity to water table may vary between peatland types (Payne, 2011). In our study, a poor preservation of idiosome tests (testate amoebae that produce biosilica or calcite plates, e.g. *Euglypha*, *Corythion-Trinema* and *Assulina* spp.; Mitchell *et al.*, 2008) causes a relative enrichment in hydrophilous *A. wrightianum* below a depth of ~20 cm (Fig. 4a-e), possibly resulting in an overestimation of water levels before the 20th century. Despite a possible effect of differential preservation, plant macrofossils also suggest drier conditions over the 20th century, with an increasing presence of *Sphagnum rubellum*, *S. fuscum* and *S. magellanicum* to the detriment of hydrophilous *S. majus* and *S. fallax*, as well as a decrease in herbaceous species. Payne (2011) suggested that transfer functions should not be used to cover the fen-bog transition as the amoeba sensitivity to hydrological change may differ between these trophic states. As both testate amoeba and plant macrofossil analyses were applied here, the amoeba-inferred water tables could also be validated by local vegetation reconstructions. We showed that WTD reconstructions are warranted through the association with local plant communities from macrofossils. For instance, the periods dominated by hydrophilous *A. wrightianum* generally coincided with an abundance of Herbaceae and a local presence of *S. majus* and *S. fallax*, two species that are exclusively found in wet flarks and hollows (Fig. 4a-b, d-e; Bastien and Garneau, 1997). At the other end of the humidity spectrum, dominance of *D. pulex* and *Trigonopyxis arcula* closely corresponds with the presence of ridge-forming *S. fuscum*.

Due to the apparent close relationship between ecohydrological history and late-Holocene climate variability (Viau and Gajewski, 2009), we considered the northeastern Canada climate regime fluctuations to explain the reconstructed trends.

Laforge fen hydrology and late-Holocene climate

Testate amoeba and plant macrofossil analyses show that the three studied peatlands developed from dry, ombrotrophic bogs and evolved into wet, poor fens. Moreover, decreasing accumulation rates were associated with the transition to fen ecosystems. This transition was initiated ~3000 cal a BP, with generally highest water tables between 2500 and 1500 cal a BP and 800 and 200 cal a BP (Fig. 6a). Whereas before 4000 cal a BP water table positions varied between those associated with high hummocks or forest edges (Aero1) and wet flarks or hollows (Ours1, Aero5), all cores registered shifts to wetter conditions that persisted during the major part of the late-Holocene. Although the spatially punctual nature of cores may not entirely cover the spatiotemporal complexity of peatlands, we feel that the increase in surface wetness as shown by cores ~3000 cal a BP is most likely associated to a shift in surface microtopography. Moreover, the use of multiple cores per peatland allows for a control at the ecosystem scale.

The reconstructed change from ombrotrophic to minerotrophic conditions is quite atypical, because peatlands generally form under minerotrophic conditions and eventually shift to ombrotrophy (Charman, 2002), yet some reversals have been recorded (Charman, 1995). General models of accumulation assume that long-term peatland development eventually results in the isolation from regional groundwater influence after which ombrotrophic conditions prevail (Hughes and Dumayne-Peaty, 2002). Long-term peat accumulation has even been suggested as a purely autogenic cause for long-term drying, decreasing accumulation rates and shifting vegetation assemblages in continental peatlands (Belyea and Clymo, 2001; Yu *et al.*, 2003). The "inversed" hydroseral succession as observed in the studied region, i.e. from bog to fen conditions, may be related to the biogeographic position of these peatlands at the ecotone of ombrotrophic and minerotrophic systems. Low rates of peat accumulation, with only ~1 m of peat accumulated over ~5000 years, show that the balance between production and decay in these peatlands may be easily disrupted, and therefore ecosystem hydrology may be particularly sensitive to external forcing.

The Neoglacial has been identified as one of the major climatic periods of the Holocene (Wanner *et al.*, 2011), characterized primarily by decreasing northern hemisphere summer temperatures after 4500 cal a BP forced by decreasing insolation. Gradual cooling resulted in decreasing forest productivity and increases in fire and aeolian activity in northern Quebec (Arseneault and Sirois, 2004; Filion, 1984; Kerwin *et al.*, 2004). In addition, due to combined effects of cooling and increases in fire frequency, tree regeneration was limited, leading to an opening of the forest-tundra around ~3500 cal a BP (Asselin and Payette, 2005; Payette and Gagnon, 1985). Finally, frost heave (palsa) formation in subarctic Quebec peatlands started after ~3200 cal a BP, showing that frozen peat could persist during the growing season (Payette and Rochefort, 2001) while peat and carbon accumulation rates decreased in boreal ombrotrophic peatlands (Beaulieu-Audy *et al.*, 2009; van Bellen *et al.*, 2011a; van Bellen *et al.*, 2011b). Palsa formation was important between 1500 and 1000 cal a BP and during the LIA (Asselin and Payette, 2006; Couillard and Payette, 1985; Payette and Rochefort, 2001). Quantitative temperature and precipitation reconstructions using pollen data by Viau and Gajewski (2009) support inferences drawn from these studies, identifying the Neoglacial as a period with cooler summer conditions, while annual precipitation increased (Fig. 6b). Moreover, besides some shorter term variability, cooling was relatively gradual starting ~3000 cal a BP and continuing until the LIA, although punctuated by the Medieval Climate Anomaly (globally starting ~1000 cal a BP; Mann *et al.*, 2009). Long-term trends in annual precipitation are less clear, but abrupt increases in precipitation were found between 3000-2700 cal a BP, 2000-1700 cal a BP and 800-600 cal a BP (Viau and Gajewski, 2009).

Considering the current biogeographical location of the Laforge peatlands (Fig. 2) we hypothesize that Neoglacial cooling negatively affected peatland productivity. Cooler summers, combined with increases in annual precipitation, may thus be a plausible cause for the reversal of the trophic state of these peatlands (Fig. 6a-c). In addition, local groundwater input probably increased as evapotranspiration from adjacent uplands declined with cooling and after the opening of tree covers (Asselin and Payette, 2005). The poor preservation of testate amoebae between 1500 and 900 cal a BP may be related to enhanced peat decomposition, which may be the result of either extremely dry or wet surface conditions. Reconstructions from Aeroport fen show that water tables decreased locally after ~1500 cal a BP, yet aquatic plant macrofossils as *S. fallax* and *Menyanthes trifoliata* appear in other cores (Fig. 4d-e). Climatic warming associated with the Medieval Climate Anomaly seems an unlikely cause for the observed changes, as this event started not earlier than 1100 cal a BP in northeastern Canada (Payette and Delwaide, 2004; Viau and Gajewski, 2009).

The subsequent LIA cooling corresponds to slightly higher test concentrations and strongly increasing water table levels as precipitation likely increased and summer temperature decreased, reducing evaporation and growing season length (Fig. 6a-c). Finally, a trend of decreasing water table levels was reconstructed after ~AD 1880 as suggested by both testate amoeba assemblages and plant macrofossils. Interestingly, a 20th century water table drop is inconsistent with previous research, which showed that northern Quebec lake and bog water tables actually rose over the 20th century, likely resulting from increases in precipitation (Bégin, 2001; Loisel and Garneau, 2010; van Bellen *et al.*, 2011b). Post-LIA warming caused an increase in the length of the growing season that may have enhanced peat accumulation which contributed to the apparent drop in water level. In this specific hydroclimatic context, the recent warming trend (Payette *et al.*, 2004) may have been determinant for local ecohydrology rather than increases in precipitation (Fig. 6c). This corresponds with Dissanska *et al.* (2009) who did not register a significant increase in pool size over the second half of the 20th century using an aerial photo survey.

Potential subarctic fen impact on greenhouse gas budgets

The studied peatlands are currently located near the cold/wet limit of the northern hemisphere peatland distribution when plotted in the MAT/MAP-defined climate space (Fig. 2). Patterned fens, with abundance of flarks and pools, currently persist in northern Finland (“aapa” fens), Labrador (Foster *et al.*, 1988), central Canada ("northern ribbed fens"; Zoltai *et al.*, 1988), central Sweden (Foster and Fritz, 1987) and northern Scotland (Charman, 1995). The limits of the peatland distribution in this climate space may reflect critical MAT and MAP conditions for potential peat accumulation. Considering the position of the Laforge region near the cold/wet limit, Neoglacial and LIA cooling conditions with increases in effective moisture probably resulted in a reduced accumulation potential during these periods. However, the climate space presented by Yu *et al.* (2009) is a simplified representation of local climate conditions, because seasonal averages or other specific variables, e.g. photosynthetically active radiation and growing degree-days above zero (Flanagan and Syed, 2011; Frolking *et al.*, 1998) may well be as important as MAT and MAP.

Ecohydrological history of patterned peatlands has been studied notably in Labrador, where Foster *et al*. (1988) dated the initiation of pool development ~3260-3860 cal a BP (3210-3430 ^{14}C a BP). In central Sweden, Foster and Fritz (1987) dated peat underlying pool sediments at 3410 and 3510 ^{14}C a BP, indicating that pool formation did not occur before ~3480-3960 cal a BP. Furthermore, Charman (1995) reconstructed peatland development in maritime northern Scotland, showing that poor patterned sedge fens developed over ombrotrophic Ericaceae peat ~2850 cal a BP (~2750 ^{14}C a BP), possibly as a result of climate change. Much attention has been given to global increases in oceanic bog water tables due to cold/wet climate conditions ~2800 cal a BP (e.g. Chambers *et al.*, 2007; Charman *et al.*, 2006; van Geel *et al.*, 1996), yet these are often associated with decreases in solar activity at a centennial scale (Mauquoy *et al.*, 2008), rather than the long-term Neoglacial trend. Nevertheless, centennial-scale climatic change may still be sufficient to shift the ecosystem into a different state. Once this new state is established, the peatland may be less sensitive to subsequent climatic variability, preventing a return to the initial state. The pool and flark microforms found in the Laforge region may show such stability, a characteristic that has already been reported by Foster and King (1984).

Combining the results from our study and that of Cliche Trudeau (2011) and Cliche Trudeau *et al*. (2012), we suggest that a general expansion of flarks and pools in the Laforge peatlands caused an enhanced flux of CH_4 and CO_2 to the atmosphere. Interestingly, the globally reconstructed timing of ~3000 cal a BP for flark and pool initiation in patterned fens coincides with the more pronounced increase in global atmospheric CH_4 concentrations (Brook *et al.*, 2000). Although we do not pretend patterned fen dynamics played a significant role in the global atmospheric CH_4 rise, we suggest future studies focus on pool and flark development in other boreal and subarctic regions around the onset of Neoglacial cooling.

In line with the trend observed since the end of the LIA, 21st century global warming combined with increases in precipitation (IPCC, 2007) might enhance the potential for accumulation and related CO_2 uptake of lawns and ridges as registered by Cliche Trudeau (2011) and Pelletier *et al*. (2011) in the boreal region. Increases in growing season temperature would generally increase the potential for *Sphagnum* productivity, yet specific microtopography resilience needs to be considered as well. Pools and flarks may respond differently to global warming, with enhanced local decomposition (Karofeld *et al.*, 2008) and even higher emissions of CO_2 and CH_4.

Considering the sensitivity of the Laforge peatlands and their important potential feedback to climate change due to the abundance of aquatic microtopes, future research needs to focus on developmental history of different types of peatlands to elucidate their specific past and future role in global greenhouse gas budgets.

Conclusion

The patterned fens in the Laforge region, presently characterized by an important presence of pools and flarks, have developed from ombrotrophic conditions. Two major periods of increases in water table heights have been identified, an initial increase starting ~3000 cal a BP and a subsequent one starting at the onset of the LIA ~800 cal a BP. The former coincides with the onset of Neoglacial cooler and wetter conditions, which represents a major climatic shift as registered by various climatic and environmental reconstructions (Allard and Seguin, 1987; Payette and Gagnon, 1985; Viau and Gajewski, 2009). Moreover, the second regional water table increase during the LIA corresponds to data from Arlen-Pouliot (2009). As a precipitation increase by itself may not have been important enough to increase water levels, we suggest that the surface moisture excess may have been positively influenced by a decrease in evaporation. Our results do not indicate an increase in water tables during the 20th century, probably influenced by important warming and higher productivity. High-resolution paleoecological analyses, combined with detailed aerial images to cover spatial variability in microtopography (Dissanska *et al.*, 2009) may be highly useful to increase the understanding of future peatland dynamics and carbon sequestration under changing climate regimes.

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Table 1: Radiocarbon dating sample details and inferred ages from CLAM (Blaauw, 2010). Eric = Ericaceae.

Core	Depth (cm)	Dated material	^{14}C age (a BP)	2σ range (cal a BP)	Age (cal a BP)	Lab code
Aero1	35-36	*Sphagnum*	1480 ± 15	1298-1374	1336	UCIAMS-101740
	49-50	Eric leaves	2060 ± 40	1852-2033	1942	Beta-226438
	62-63	*Sphagnum*; Eric leaves	2485 ± 15	2511-2718	2611	UCIAMS-101741
	78-79	*Picea* leaves	3490 ± 15	3661-3790	3725	UCIAMS-39594
	95-96	*Sphagnum*	4500 ± 25	4858-5093	4973	UCIAMS-101742
	109-110	*Picea* leaves	4790 ± 60	5389-5785	5558	TO-12792
Aero5	34-35	*Picea*/Eric leaves	965 ± 15	625-752	689	UCIAMS-39014
	50-51	*Picea* seeds/Eric leaves	1810 ± 40	1728-1899	1810	Beta-224987
	68-69	*Sphagnum*	3075 ± 20	3078-3221	3147	UCIAMS-101743
	74-75	*Sphagnum*	3285 ± 20	3441-3577	3511	UCIAMS-35983
	86-87	*Sphagnum*	3800 ± 15	3896-4099	4018	UCIAMS-101744
	109-110	*Sphagnum*	3830 ± 50	4221-4664	4471	TO-12796
Ours1	24-25	Eric/*Picea* leaves	2180 ± 15	2043-2242	2161	UCIAMS-101745
	35-36	*Picea* fragments	2885 ± 20	2926-3239	3013	UCIAMS-35981
	48-49	*Sphagnum*	3825 ± 15	3932-4208	4074	UCIAMS-39035
	72-73	Eric/*Picea* leaves; Eric seeds	4360 ± 15	4851-4955	4905	UCIAMS-101746
	87-88	*Picea*/Eric/*Carex* leaves	4555 ± 15	5112-5301	5222	UCIAMS-39033
	109-110	*Picea*/Eric leaves	4810 ± 60	5310-5660	5527	TO-12787
Ours4	27-28	*Picea*/Eric leaves	1130 ± 15	820-938	883	UCIAMS-39031
	42-43	*Sphagnum*	2470 ± 15	2169-2376	2277	UCIAMS-101747
	49-50	*Sphagnum*	2740 ± 40	2776-2948	2861	Beta-226441
	58-59	*Sphagnum*	3325 ± 15	3457-3581	3521	UCIAMS-101748
	74-75	*Sphagnum*	4055 ± 15	4278-4508	4405	UCIAMS-39034
	104-105	*Sphagnum*	4250 ± 50	4732-5302	4927	TO-12790
Abeille5	23-24	Eric seeds; Eric/*Picea* leaves	150 ± 20	39-78	58	UCIAMS-102297
	36-37	*Carex* seeds; Charcoal	910 ± 20	701-867	790	UCIAMS-102298
	51-52	*Picea*/Eric leaves	1770 ± 20	1596-1700	1650	UCIAMS-102299
	64-65	*Sphagnum*	2265 ± 15	2224-2333	2291	UCIAMS-101749
	79-80	*Sphagnum*	2905 ± 20	2898-3017	2967	UCIAMS-102300
	98-99	Charcoal	3430 ± 15	3622-3814	3673	UCIAMS-101750

Table 2: Zonation details for Aero1.

Zone	Depth (cm)	Age (cal a BP/AD)	Description
Aero1-a	108-79	5530-3800	Dry *Sphagnum fuscum*-wood (*Picea*) peat. Initial relatively high accumulation rates decreased after ~4900 cal a BP, when tree presence culminated. Dominance of *Trigonopyxis arcula* and *Arcella catinus* in amoeba assemblages.
Aero1-b	79-65	3800-2800	Dry *S. fuscum*-wood (*Picea*) peat. Abundance of *Difflugia pristis* and *Arcella catinus*. Slight presence of *Calliergon stramineum* may suggest more minerotrophic conditions.
Aero1-c	65-34	2800-1280	Abundance of *Sphagnum majus*, *Sphagnum fallax, Larix* and *Amphitrema wrightianum* indicates the presence of a wet and more minerotrophic conditions suggested by the presence of *Sphagnum subsecundum* and *Drepanocladus revolvens*.
Aero1-d	34-26	1280-750	A ~500 year period of drier conditions is identified by increases in *Archerella flavum* and *Heleopera sphagni*.
Aero1-e	26-10	750-AD 1940	Return to wet conditions with *A. wrightianum* and *S. majus*.
Aero1-f	10-0	AD 1940-present	Slight decrease in water tables with dominance of *Sphagnum magellanicum* and disappearance of *A. wrightianum*.

Table 3: Zonation details for Aero5.

Zone	Depth (cm)	Age (cal a BP/AD)	Description
Aero5-a	109-92	4470-4200	Wet hollow conditions were present during this period, as indicated by a dominance of *Amphitrema wrightianum* and *Sphagnum majus*. Accumulation rates were high with sample time spans <10 a cm^{-1}.
Aero5-b	92-71	4200-3340	Water tables decreased at the start of this period, as indicated by the presence of *Sphagnum fuscum*, *Difflugia pulex, Picea mariana* needles and *Cenococcum* sclerotia.
Aero5-c	71-45	3340-1460	Herbaceae peat with *Sphagnum subsecundum* and *S. majus* suggests minerotrophic conditions. Hydrophilous *A. wrightianum* presence culminates ~2050 cal a BP.
Aero5-d	45-36	1460-820	Water tables decrease rapidly while *S. fuscum* reappears. *Cenococcum* sclerotia and decreasing presence of *A. wrightianum* confirm dry conditions on the site.
Aero5-e	36-20	820-AD 1890	Herbaceae peat with *S. majus* and *Sphagnum magellanicum* indicates a return to wet hollow conditions.
Aero5-f	20-0	AD 1890-present	Presence of dry lawn conditions as shown by *S. fuscum* and the quasi-disappearance of *A. wrightianum*.

Table 4: Zonation details for Ours1.

Zone	Depth (cm)	Age (cal a BP/AD)	Description
Ours1-a	109-98	5530-5400	*Sphagnum fuscum* peat with *Archerella flavum* and *Heleopera sphagni* indicates low hummock, ombrotrophic conditions.
Ours1-b	98-63	5400-4690	Unstable hydrological conditions with ligneous and herbaceous peat, as *Sphagnum* disappears. *Picea* needles indicate episodically nearby presence of trees.
Ours1-c	63-50	4690-4190	High presence of Herbaceae and wet hollow conditions are reconstructed for the latter part of this period while *Amphitrema wrightianum* becomes highly dominant.
Ours1-d	50-23	4190-2010	After a short decrease in water table ~3820 cal a BP, as indicated by *H. sphagni* and *Cenococcum* sclerotia, water tables remain at the surface, while *Picea* and *Chamaedaphne calyculata* persist locally. Hydrophilous *A. wrightianum* culminates ~3490 cal a BP.
Ours1-e	23-13	2010-1820 AD	Accumulation rates are very low over the entire period, resulting in sample time spans of >200 a cm^{-1}. Testate amoeba concentrations are too low for WTD reconstructions. Local vegetation shifts from ligneous to Herbaceae dominance.
Ours1-f	13-0	1820 AD-present	Herbaceae peat with water table depths >10 cm below the surface as *A. wrightianum* declines.

Table 5: Zonation details for Ours4.

Zone	Depth (cm)	Age (cal a BP/AD)	Description
Ours4-a	104-76	4930-4480	Local vegetation is characterized by *Sphagnum fuscum* with presence of *Picea mariana* and *Archerella flavum* suggesting dry lawn conditions. Peat accumulation rates are initially high as indicated by sample time spans of <10 a cm^{-1}.
Ours4-b	76-62	4480-3780	Hydrological conditions are highly variable, although *S. fuscum* and *P. mariana* remain general during this period. Amoeba assemblages are characterized by *Difflugia pulex*. Sample time spans increase to ~60 a cm^{-1}.
Ours4-c	62-45	3780-2540	Transitional conditions with gradually rising water tables. The period starts with deep water tables and *D. pulex* as dominant species with a gradual increase towards wet hollow conditions with *Sphagnum fallax*.
Ours4-d	45-34	2540-1530	After culmination of *Amphitrema wrightianum* ~2320 cal a BP, dry surface conditions are present with *D. pulex*.
Ours4-e	34-8	1530-AD 1940	Wet hollow conditions persist during the entire period. *S. fallax*, *Sphagnum majus* and *Larix laricina* are locally present. Towards the end of the period, the site is characterized by minerotrophic conditions as indicated by *Sphagnum subsecundum*.
Ours4-f	8-0	AD 1940-present	Water tables slightly decline during the 20th century, with increasing presence of *Sphagnum magellanicum* to the detriment of *S. fallax*.

Table 6: Zonation details for Abeille5.

Zone	Depth (cm)	Age (cal a BP)	Description
Abeille5-a	98-78	3670-2930	Ligneous peat with *Sphagnum fuscum* and *Picea mariana* indicates local deep water tables. Abundant charcoal and *Cenococcum* sclerotia support the interpretation of this period as being generally dry yet fluctuating.
Abeille5-b	78-64	2930-2290	The local vegetation opens up as a wet hollow develops. Ligneous species decline drastically. *Sphagnum* spp. become more important, while water tables decrease after ~2750 cal a BP. Amoeba assemblages shift between domination of *Difflugia pulex* to *Archerella flavum*.
Abeille5-c	64-49	2290-1550	Water tables rapidly increase and remain at the surface as indicated by *Amphitrema wrightianum*, *Sphagnum majus* and *Sphagnum recurvum* type
Abeille5-d	49-29	1550-280	Herbaceae dominate the local vegetation while *Sphagnum* disappears. The occasional presence of *Sphagnum subsecundum* and *Menyanthes trifoliata* suggest minerotrophic flark conditions.
Abeille5-e	29-0	280-present	*Sphagnum rubellum* appears locally, indicating lawn conditions after AD 1760. A decline in water level is reconstructed since AD 1940.

Fig. 1: Location of the Laforge region, studied peatlands and core positions. Peatland photos courtesy of K. Chokmani (INRS, Quebec City, Canada) and M. Garneau.

Fig. 2: Marginal position of the Laforge region within the northern hemisphere peatland climate space (Yu *et al.,* 2009), © American Geophysical Union, 2009, reproduced/modified with permission.

Fig. 3: Age-depth models based on results from ^{14}C and ^{210}Pb dating.

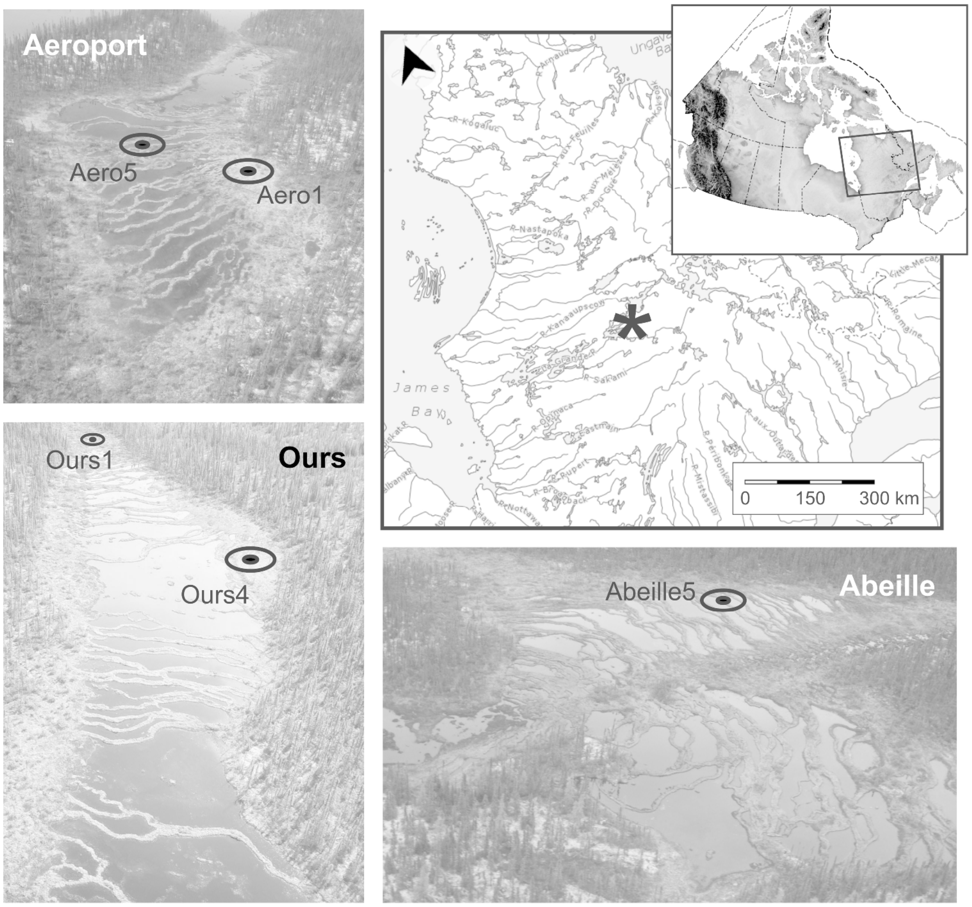
Fig. 4: Testate amoeba, inferred water table depths and plant macrofossil records for a) Aero1; b) Aero5; c) Ours1; d) Ours4 and e) Abeille5. Testate amoebae presence is expressed as percentage values of the total count. Plant macrofossils are quantified by volume percentages and counts. Rare taxa (<1% presence) are identified by "+"-symbol. *Sphagnum* species percentages are relative to total *Sphagnum* presence. Water table depths inferred from amoeba counts inferior to 40 are displayed as dashed lines. Stratigraphic zones are separated by dashed lines and identified at the right end of each figure.

Fig. 5: Inferred water table depths and associated errors for each core. Unreliable WTD reconstructions are indicated by a grey line. Thick dashed lines represent the peatland surface. Vertical arrows show the timing of a shift in trophic state based on plant macrofossil analyses.

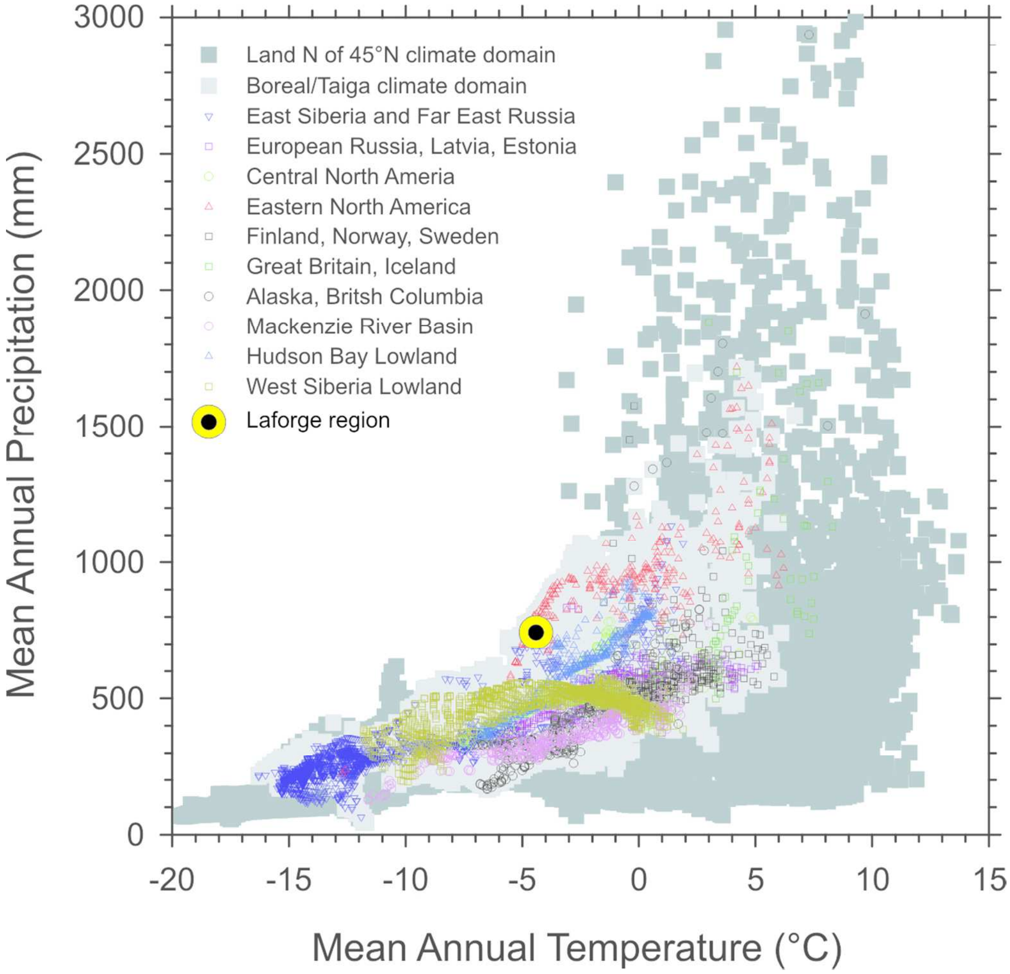
Fig. 6: Synthesis of Laforge fen reconstructed water tables and climate reconstructions since 4000 cal a BP: a) Laforge water table depths pooled in 200-year bins, representing medians, upper and lower quartiles and outliers; b) mean July temperature and mean annual precipitation anomalies in northern Quebec (50–70°N, 65–80°W; data from Viau and Gajewski (2009); © American Meteorological Society, reprinted with permission); c) Precipitation-temperature residuals of z-scores recalculated from Viau and Gajewski (2009).

Fig. S1: Complete testate amoeba records for a) Aero1; b) Aero5; c) Ours1; d) Ours4 and e) Abeille5.

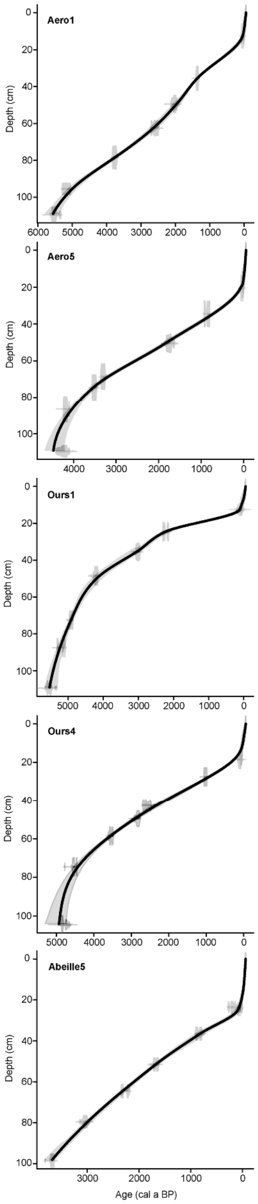
Fig. S2: Complete plant macrofossil records for a) Aero1; b) Aero5; c) Ours1; d) Ours4 and e) Abeille5. Rare taxa (<1% of sample volume) are identified by "+"-symbol.



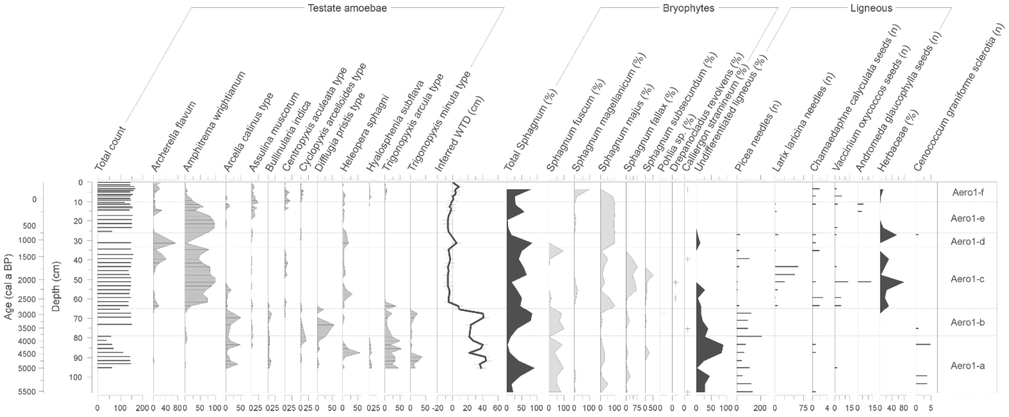
Location of the Laforge region, studied peatlands and core positions. Peatland photos courtesy of K. Chokmani (INRS, Quebec City, Canada) and M. Garneau



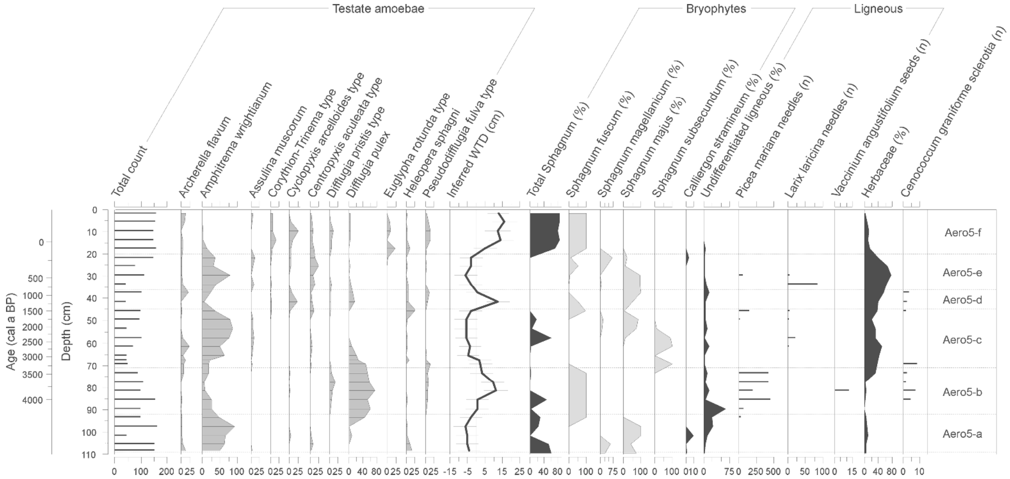
Marginal position of the Laforge region within the northern hemisphere peatland climate space (Yu *et al.*, 2009), © American Geophysical Union, 2009, reproduced/modified with permission.



Age-depth models based on results from ^{14}C and ^{210}Pb dating.
254x1205mm (300 x 300 DPI)



Testate amoeba, inferred water table depths and plant macrofossil records for a) Aero1; b) Aero5; c) Ours1; d) Ours4 and e) Abeille5. Testate amoebae presence is expressed as percentage values of the total count. Plant macrofossils are quantified by volume percentages and counts. Rare taxa (<1% presence) are identified by "+"-symbol. *Sphagnum* species percentages are relative to total *Sphagnum* presence. Water table depths inferred from amoeba counts inferior to 40 are displayed as dashed lines. Stratigraphic zones are separated by dashed lines and identified at the right end of each figure.



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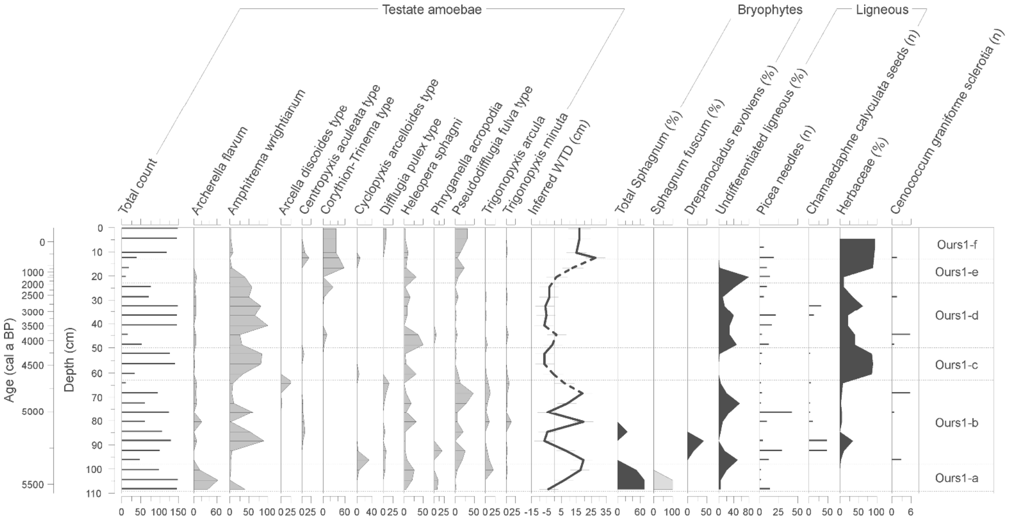

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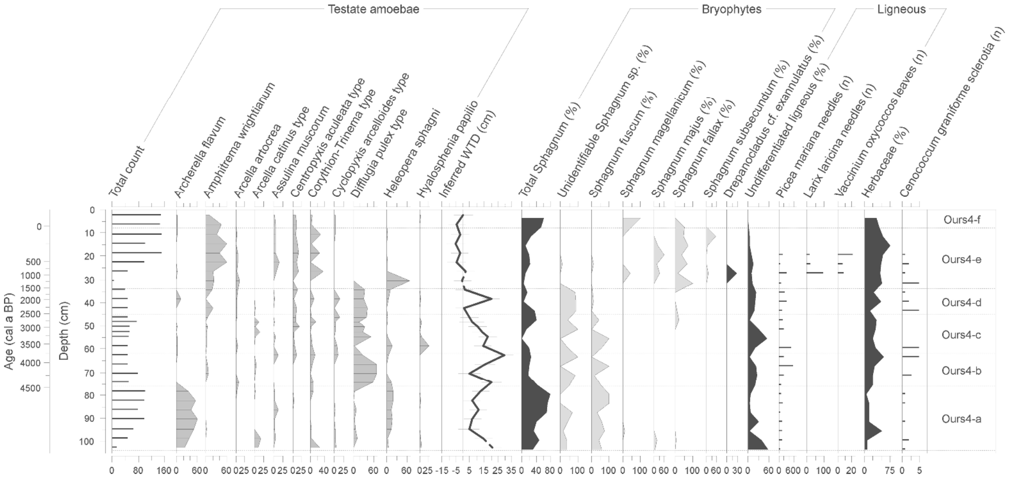

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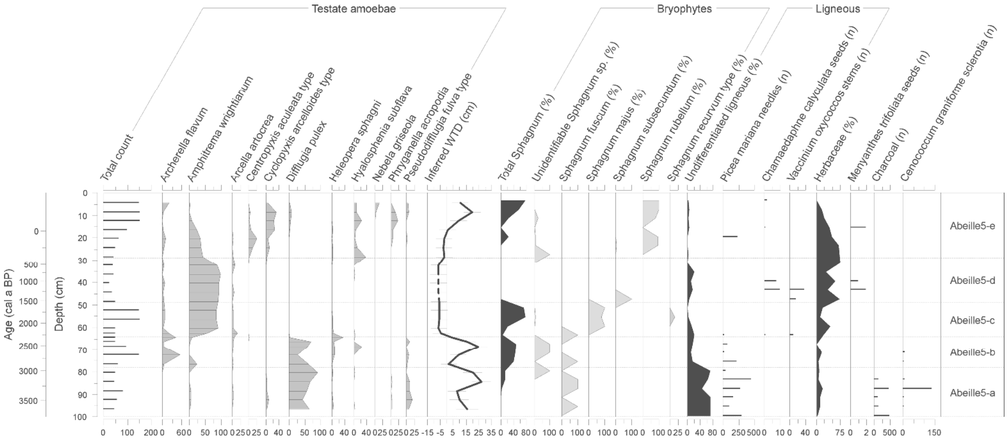

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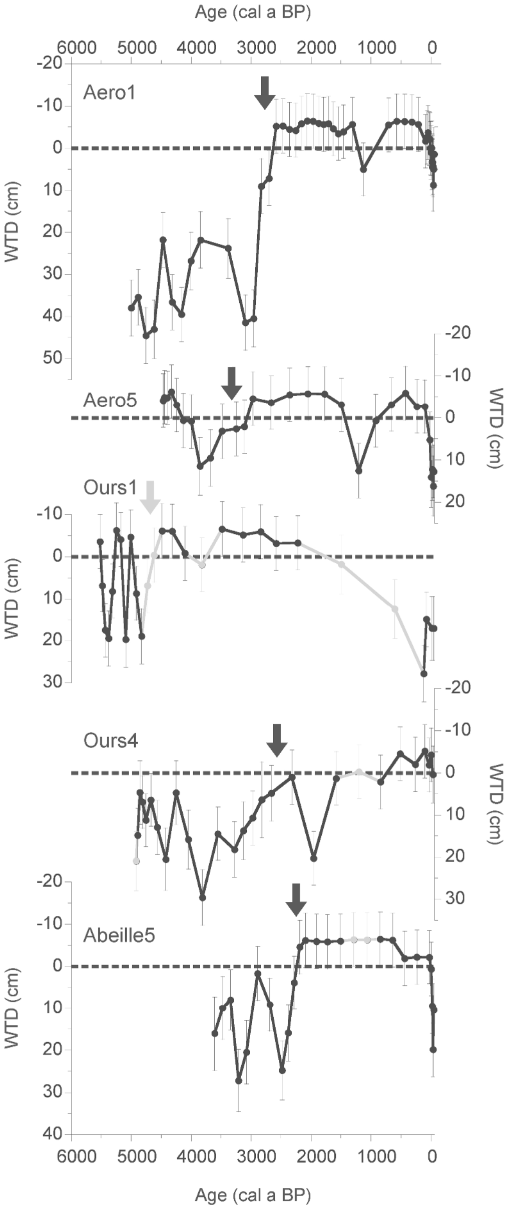
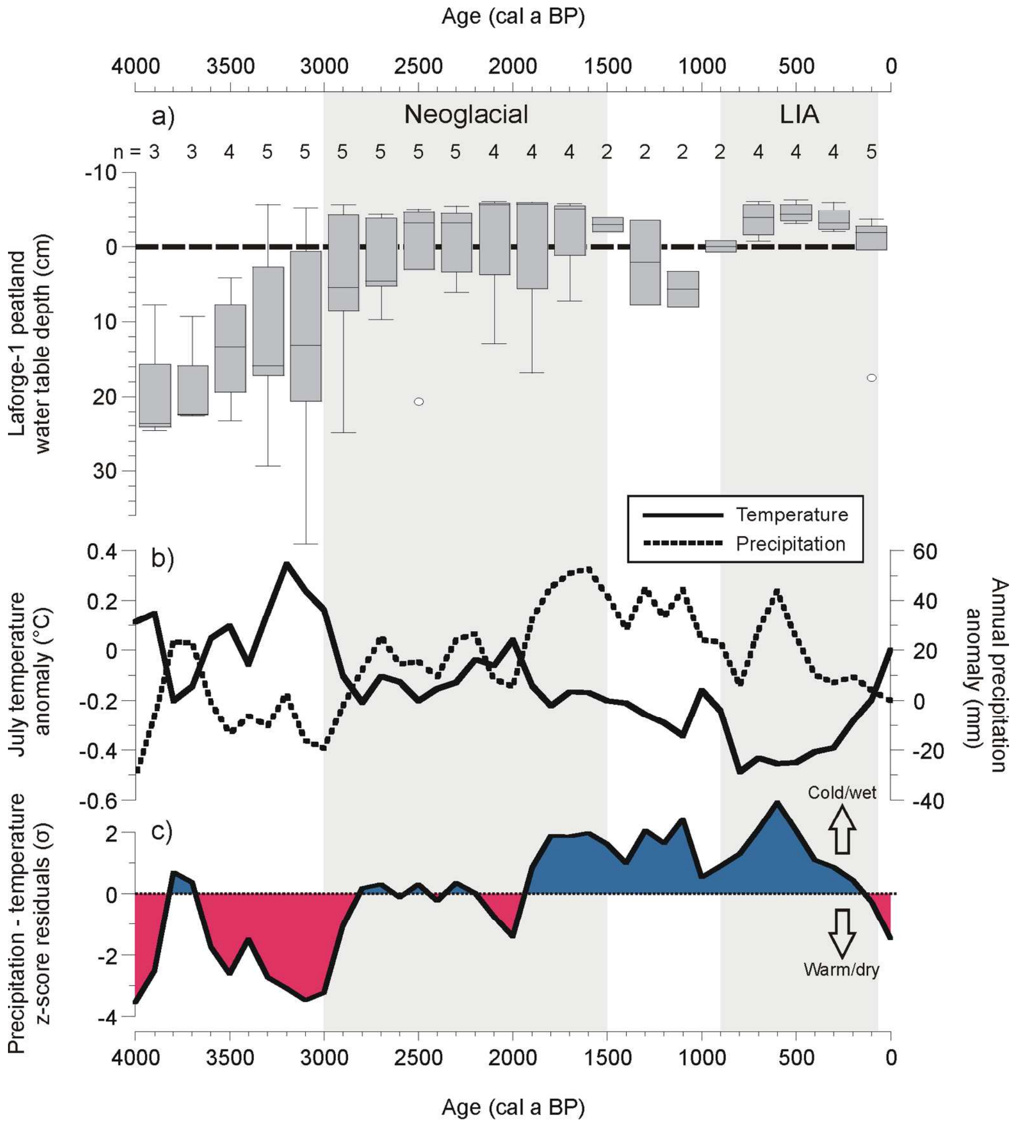
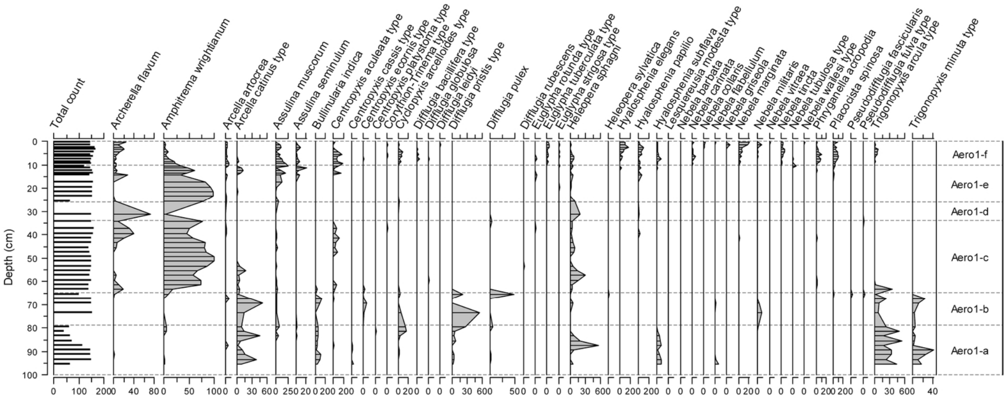


Inferred water table depths and associated errors for each core. Unreliable WTD reconstructions are indicated by a grey line. Thick dashed lines represent the peatland surface. Vertical arrows show the timing of a shift in trophic state based on plant macrofossil analyses.



Synthesis of Laforge fen reconstructed water tables and climate reconstructions since 4000 cal a BP: a) Laforge water table depths pooled in 200-year bins, representing medians, upper and lower quartiles and outliers; b) mean July temperature and mean annual precipitation anomalies in northern Quebec (50–70°N, 65–80°W; data from Viau and Gajewski (2009); © American Meteorological Society, reprinted with permission); c) Precipitation-temperature residuals of z-scores recalculated from Viau and Gajewski (2009).



Complete testate amoeba records for a) Aero1; b) Aero5; c) Ours1; d) Ours4 and e) Abeille5.
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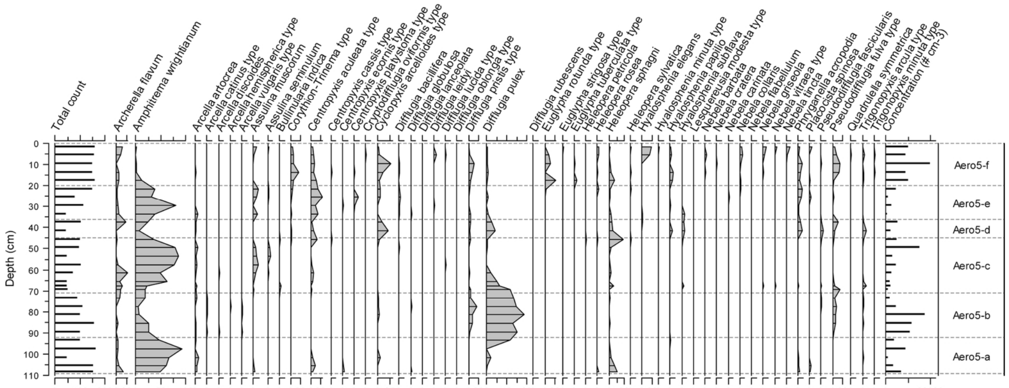
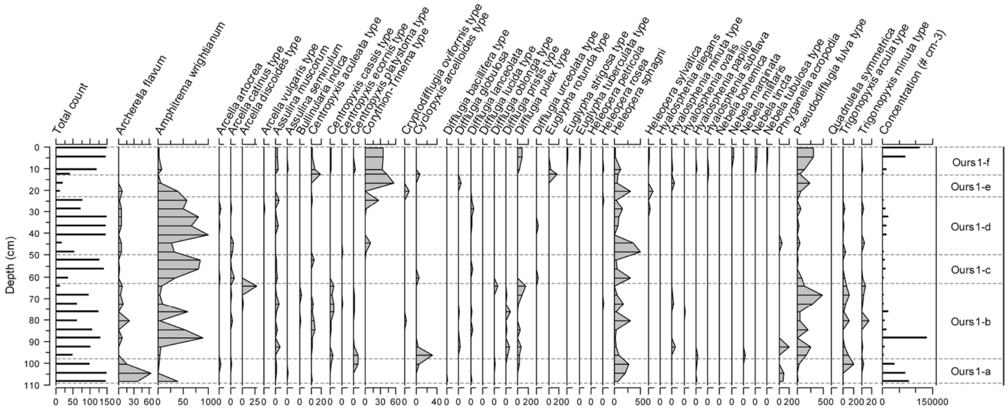


Complete testate amoeba records for a) Aero1; b) Aero5; c) Ours1; d) Ours4 and e) Abeille5.
159x63mm (300 x 300 DPI)



Complete testate amoeba records for a) Aero1; b) Aero5; c) Ours1; d) Ours4 and e) Abeille5.
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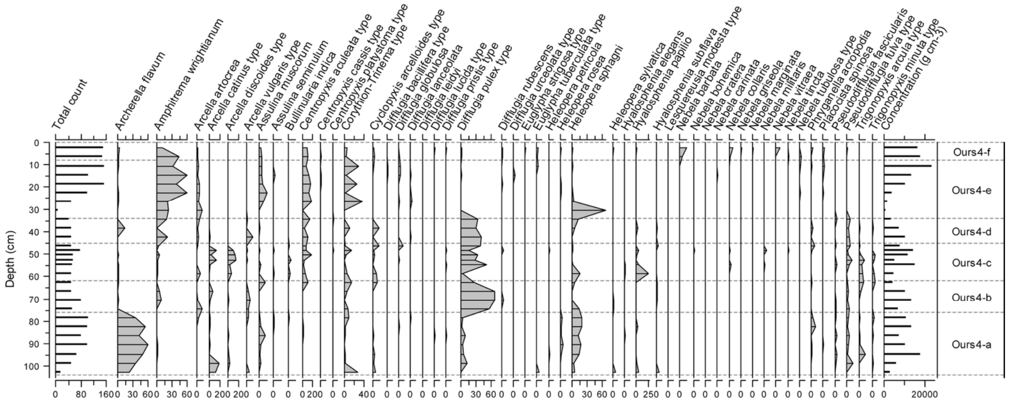

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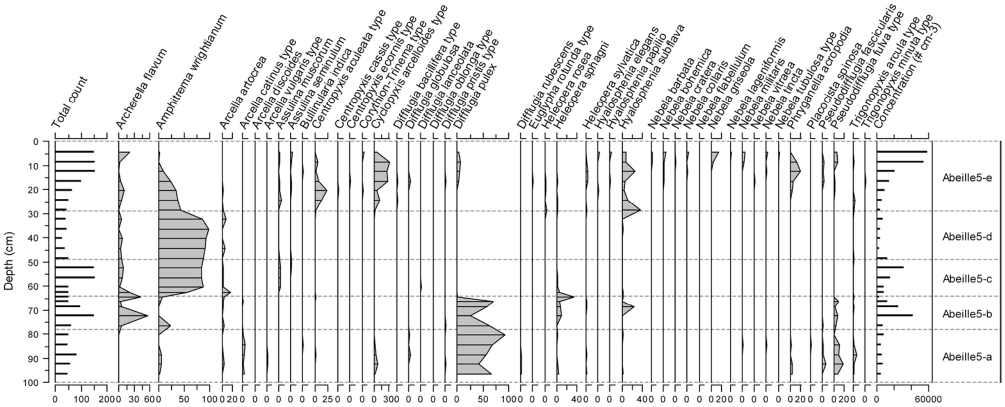
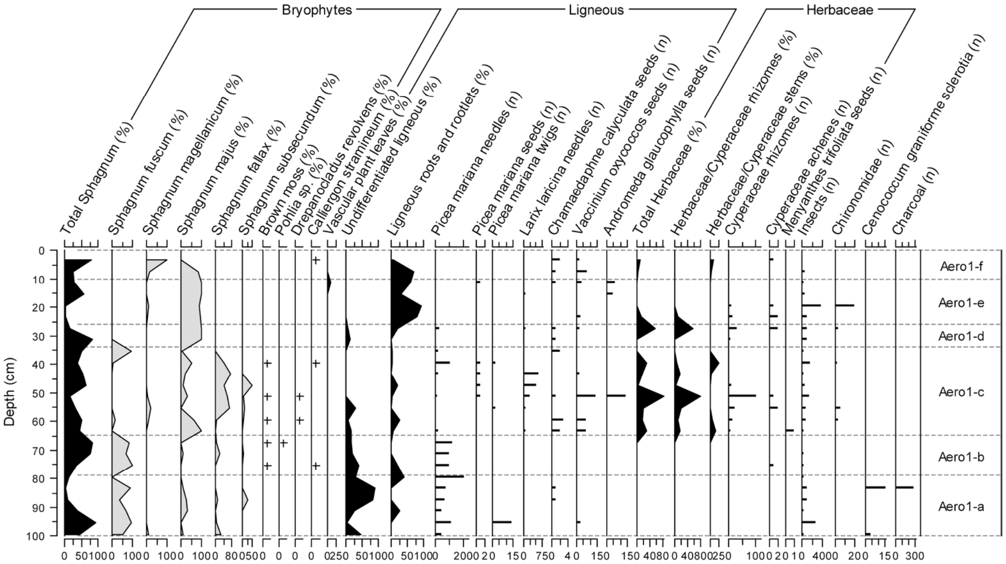
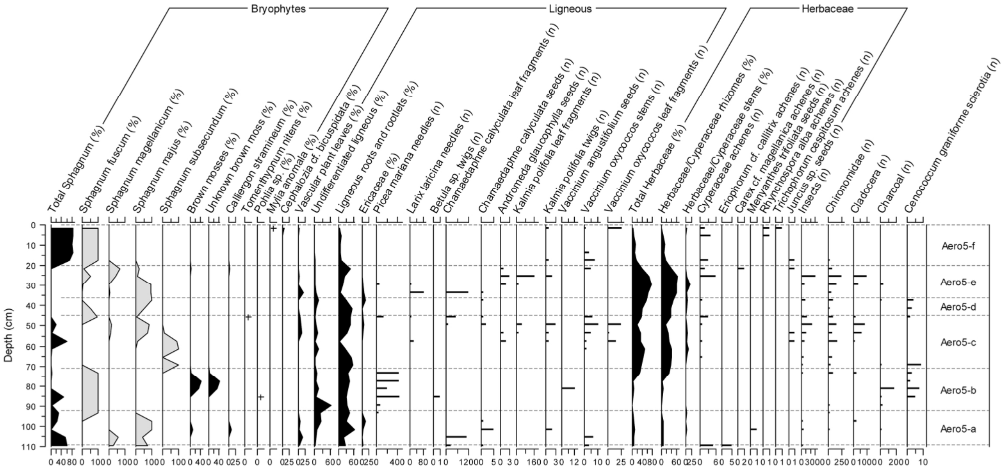


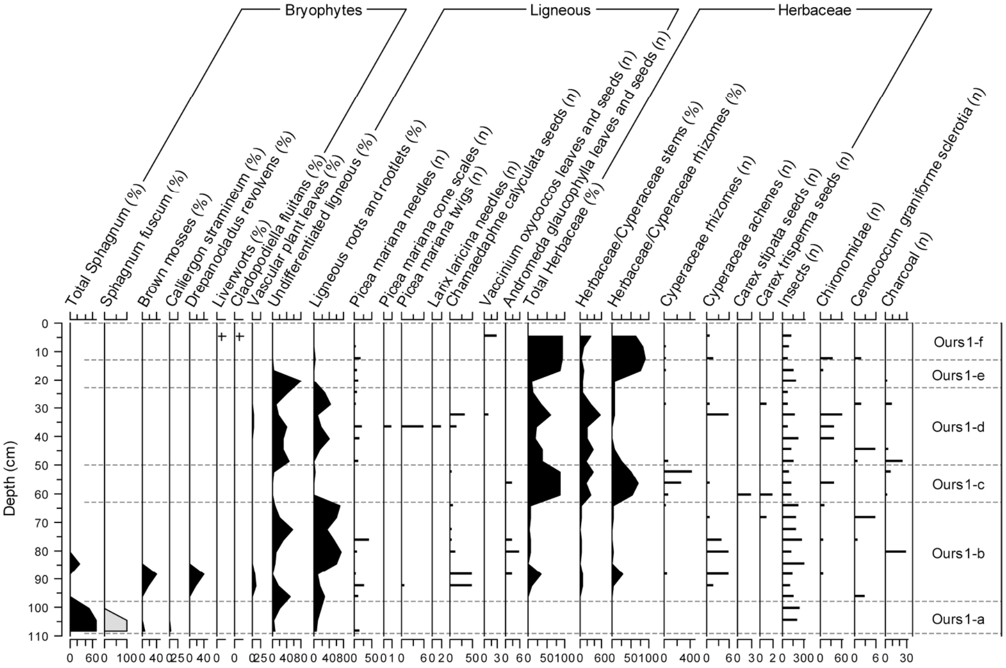
Complete testate amoeba records for a) Aero1; b) Aero5; c) Ours1; d) Ours4 and e) Abeille5.
156x63mm (300 x 300 DPI)



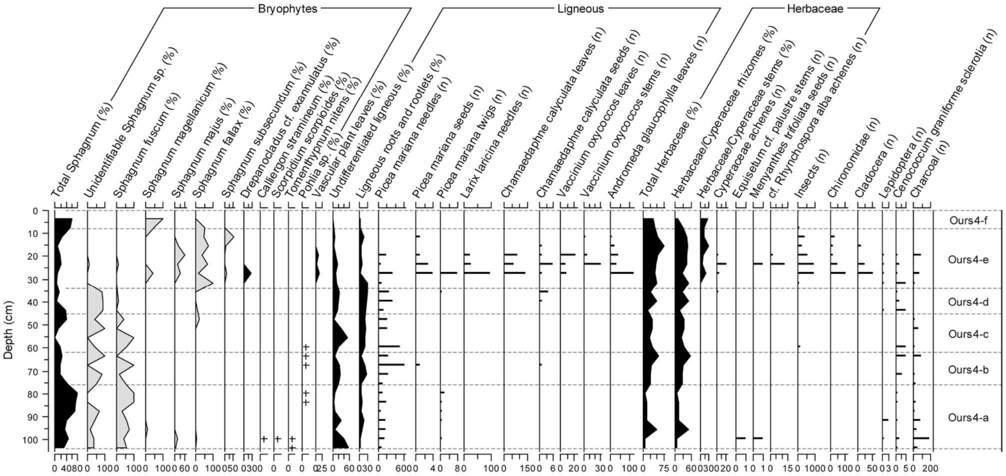
Complete plant macrofossil records for a) Aero1; b) Aero5; c) Ours1; d) Ours4 and e) Abeille5. Rare taxa (<1% of sample volume) are identified by "+"-symbol.
183x102mm (300 x 300 DPI)



Complete plant macrofossil records for a) Aero1; b) Aero5; c) Ours1; d) Ours4 and e) Abeille5. Rare taxa (<1% of sample volume) are identified by "+"-symbol.
196x91mm (300 x 300 DPI)



Complete plant macrofossil records for a) Aero1; b) Aero5; c) Ours1; d) Ours4 and e) Abeille5. Rare taxa (<1% of sample volume) are identified by "+"-symbol.
198x131mm (300 x 300 DPI)



Complete plant macrofossil records for a) Aero1; b) Aero5; c) Ours1; d) Ours4 and e) Abeille5. Rare taxa (<1% of sample volume) are identified by "+"-symbol.
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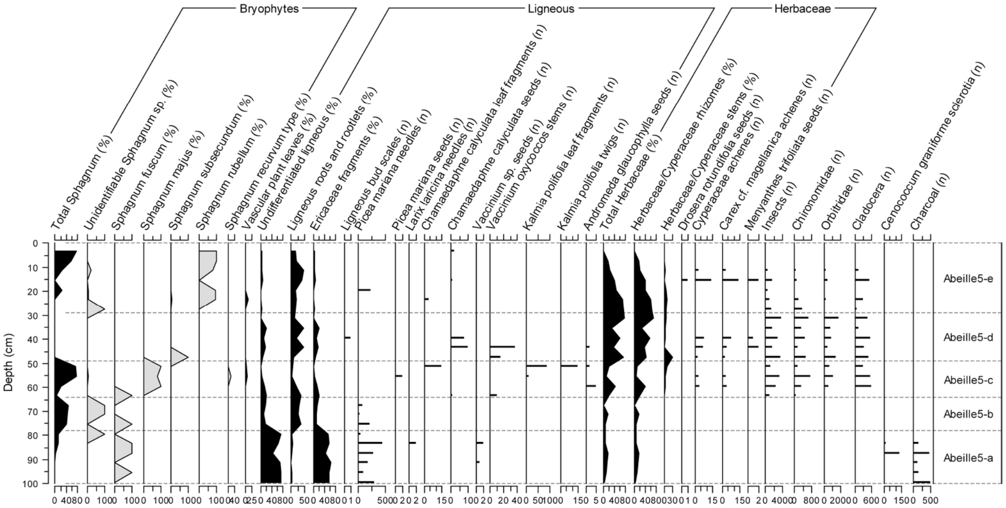

Complete plant macrofossil records for a) Aero1; b) Aero5; c) Ours1; d) Ours4 and e) Abeille5. Rare taxa (<1% of sample volume) are identified by "+"-symbol.
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