

Holocene vegetation dynamics and hydrological variability in forested peatlands of the Clay Belt, eastern Canada, reconstructed using a palaeoecological approach

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Forested peatlands are widespread in boreal regions of Canada, and these ecosystems, which are major terrestrial carbon sinks, are undergoing significant transformations linked to climate change, fires and human activities. This study targets millennial-scale vegetation dynamics and related hydrological variability in forested peatlands of the Clay Belt south of James Bay, eastern Canada, using palaeoecological data. Changes in peatland vegetation communities were reconstructed using plant macrofossil analyses, and variations in water-table depths were inferred using testate amoeba analyses. High-resolution analyses of macroscopic charcoal >0.5 mm were used to reconstruct local fire history. Our data showed two successional pathways towards the development of present-day forested peatlands influenced by autogenic processes such as vertical peat growth and related drying, and allogenic factors such as the occurrence of local fires. The oldest documented peatland initiated in a wet rich fen around 8000 cal. a BP shortly after land emergence and transformed into a drier forested bog rapidly after peat inception that persisted over millennia. In the second site, peat started to accumulate from ~5200 cal. a BP over a mesic coniferous forest that shifted into a wet forested peatland following a fire that partially consumed the organic layer ~4600 cal. a BP. The charcoal records show that fires rarely occurred in these peatlands, but they have favoured the process of forest paludification and influenced successional trajectories over millennia. The macrofossil data suggest that *Piceamariana* (black spruce) persisted on the peatlands throughout their development, although there were periods of more open canopy due to local fires in some cases. This study brings new understanding on the natural variability of boreal forested peatlands which may help predict their response to future changes in climate, fire regimes and anthropogenic disturbances.

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Forested peatlands are widespread in boreal regions of North America, and these ecosystems are major natural carbon sinks that are sensitive to climate change, increasing fire risks and human disturbances (Zoltai & Martikainen 1996; Lavoie *et al.* 2005a; Kurz *et al.* 2013; Turetsky *et al.* 2015). In the Hudson-James Bay Lowlands, the combination of relatively cool and humid climate conditions, flat topography, and poorly drained fine-grained sediments promoted extensive peatland development resulting in one of the largest peat basins worldwide (Gorham 1991; Gorham *et al.* 2007). In the Clay Belt, south of James Bay, forested peatlands and paludified forests dominated by *Picea mariana* (black spruce) are currently dominant ecosystems that are subjected to widespread harvesting activities (Lavoie *et al.* 2005b; Simard *et al.* 2009).

The development of forested peatlands results from the accumulation of thick organic layers over mineral soils usually through the process of paludification from primary or secondary successions (Lavoie *et al.* 2005b). In the Clay Belt, many peatlands that are forested nowadays formed initially in treeless low-lying areas from primary

succession over moist mineral soils shortly following land emergence (Le Stum-Boivin *et al.* in press). The long-term successional dynamics associated with the development of forested peatlands through this process of primary paludification have rarely been investigated from a palaeoecological perspective in the boreal biome of northeastern America.

Most previous studies have used a chronosequence (space-for-time substitution) approach to document the influence of paludification on the long-term dynamics of boreal coniferous forests in eastern Canada. In mesic post-fire forest stands, paludification during secondary succession is typically associated with an invasion of sphagnum over feather mosses, an opening of the canopy and a decline in stand productivity, often leading to the formation of forested peatlands (Lecomte *et al.* 2006a, b; Fenton *et al.* 2007; Simard *et al.* 2007; Bergeron & Fenton 2012). The development of *Sphagnum*-dominated peatlands from formerly forested uplands involves a rise in water table above the mineral soil and an increase in soil moisture, which suppresses tree regeneration and makes these

ecosystems less vulnerable to fire (e.g. Fenton & Bergeron 2006; Simard *et al.* 2007; Terrier *et al.* 2014).

Paludification is primarily influenced by internal factors and abiotic site features such as topography and drainage, but the rate of peatland initiation and expansion in northern regions has also been linked to climate change over the Holocene (Yu *et al.* 2009; Korhola *et al.* 2010). Fire frequency and severity also play an important role in the process of peat accumulation through paludification (Bauer *et al.* 2003; Crawford *et al.* 2003; Kuhry & Turunen 2006). Although the impact of fire severity on paludification dynamics has been previously described in coniferous forests on mesic sites (e.g. Lecomte *et al.* 2006b), the role of fire on millennial dynamics of black spruce peatlands remains largely unknown. Forested ombrotrophic peatlands (bogs) are susceptible to fires due to the relatively high woody biomass and low water-table levels in these environments (Kuhry 1994; Zoltai *et al.* 1998), in contrast to treeless and wetter peatlands, which are rarely affected by fires (Magnan *et al.* 2012, 2014).

Overall, little is known about the dynamics of forested peatlands since the onset of peat formation after the withdrawal of proglacial lakes in the James Bay area. For example, it is unknown if black spruce-*Sphagnum* stands have persisted in these ecosystems throughout their Holocene development. Moreover, the long-term interactions between hydrological variability, vegetation successions and local fire dynamics have rarely been investigated in boreal forested peatlands. This lack of knowledge limits our ability to project the response of these ecosystems to future changes in fire regimes associated with climate change. Also, it is essential to better understand the past natural vegetation dynamics and disturbance regimes in forested peatlands to support forest ecosystem management strategies in the boreal biome (Gauthier *et al.* 2009).

The main objective of this study is to improve understanding of the millennial-scale dynamics of forested peatlands on the Clay Belt of western Québec. More specifically, we aim to (i) understand ecological and hydrological dynamics of peatland formation through primary or secondary paludification, (ii) document the long-term successional pathways leading to the development of present-day forested peatlands, and (iii) improve knowledge of the interactions between water-table variability, vegetation dynamics and fire occurrence throughout the development of these peatlands. In order to achieve these goals, we used a palaeoecological approach combining macrofossils (plants and charcoal) and testate amoebae (Protozoa: Rhizopoda) to infer past water-table variations and to reconstruct local-scale vegetation and fire dynamics in peatlands. Over the last decade, many studies in boreal peatlands of eastern Canada have combined macrofossils and testate amoeba data to reconstruct ecohydrological dynamics in relation to climate and fire over millennial time scales (e.g. Loisel & Garneau 2010; van Bellen *et al.* 2011, 2013; Peros *et al.* 2016; Garneau *et al.* 2017). All these studies focussed on open non-forested peatlands and to our knowledge, such

multi-proxy palaeoecological reconstructions have never been conducted in forested peatlands.

Material and methods

Study area and sites

Two forested ombrotrophic peatlands (bogs) were selected for palaeoecological and palaeohydrological reconstructions. Villebois (latitude 49°25'16"N, longitude 79°00'11"W) and Lili (49°10'19"N, 70°22'08"W) peatlands are located in the Clay Belt of boreal western Québec in eastern Canada, within the *Picea mariana*-feather moss bioclimatic domain (Saucier *et al.* 2009; Fig. 1). In this region, the topography is flat, and the surface deposits are dominated by poorly drained clayey soils left by proglacial Lake Ojibway (Vincent & Hardy 1977). The average slope of the mineral deposit underneath the peatlands was evaluated at <1% at Villebois and 1–2% at Lili (Le Stum-Boivin *et al.* in press; Fig. S1).

Prior to the selection of the two coring sites, plant macrofossil composition of basal peat cores was analysed to determine the spatial extent of the two types of paludification in relation to basin topography (Le Stum-Boivin *et al.* in press; Fig. S1). The selected coring sites on the two peatlands have a similar peat thickness (~1.4 m) but initiated from different paludification processes. At Villebois, the coring site is located in a topographical depression where the basal peat sections are mainly composed of brown mosses and sedges indicating that peat formation started directly on wet clayey deposits following land emergence (i.e. primary paludification). The Lili core was retrieved in a section of the peatland formed by secondary paludification into a former coniferous forest deduced from macrofossil assemblages dominated by black spruce and wood remains in the basal peat section (Fig. S1).

At Villebois, the present-day tree cover at the coring location is relatively open and dominated by *Picea mariana* with sporadic presence of *Larix laricina* (tamarack). *Rhododendron groenlandicum* dominates the shrub layer, and *Sphagnum fuscum* is the main bryophyte. At Lili, the study site is characterized by a relatively dense cover of *Picea mariana* with an understorey dominated by *Sphagnum angustifolium/fallax* and ericaceous shrubs (mostly *Kalmia angustifolia* and *Rhododendron groenlandicum*) (Fig. 2).

The regional climate is sub-polar, subhumid continental, with mean annual temperature and precipitation of 0.5 °C and 907 mm, respectively, recorded at the nearest weather station of Val-Saint-Gilles (MDDELCC 2017). The regional fire cycle was evaluated at ~400 years after 1920 (Bergeron *et al.* 2004).

Fieldwork

The two forested peatlands were first localized using ecoforestry maps and aerial photographs (Ministère des

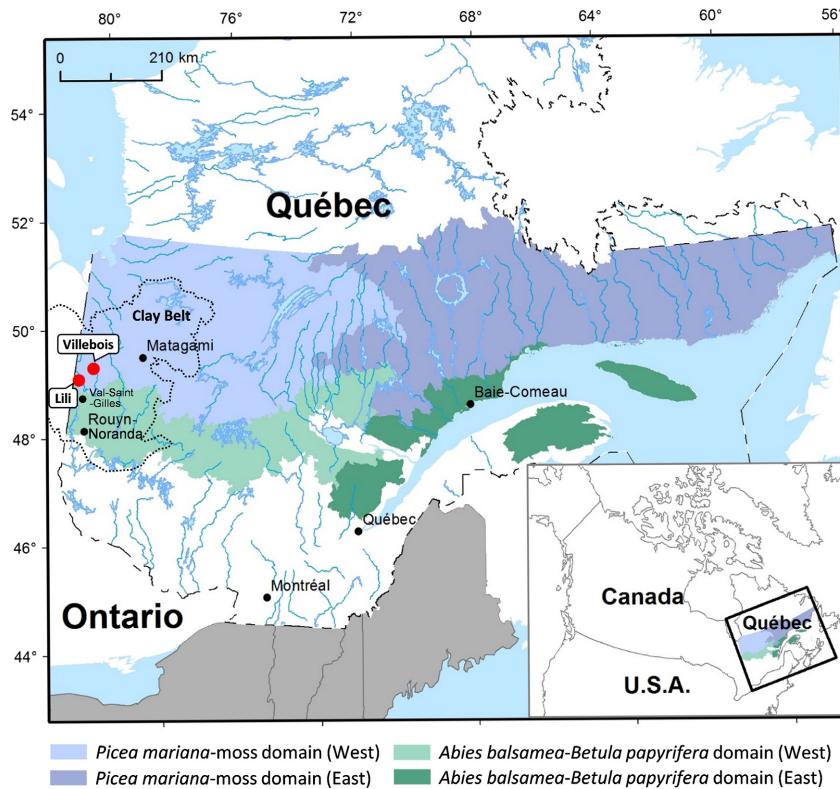


Fig. 1. Location of the two studied forested peatlands of the Clay Belt, in the black spruce-feather moss bioclimatic domain of western Québec in eastern Canada. [Colour figure can be viewed at www.boreas.dk]

Forêts, de la Faune et des Parcs du Québec, MFFP). At each site, peat thickness was measured at 5-m intervals using an Oakfield probe along transects covering a range of tree density. The peat cores were collected using a Box corer (Jeglum *et al.* 1992) for the upper first metre, and a modified Russian corer (Jowsey 1966) was used for deeper peat horizons. The peat cores were wrapped in cellophane and aluminium foil, transported in polyvinyl tubes and stored in a refrigerator at 4 °C before being analysed.

Macrofossil analyses

Plant macrofossils were analysed at 4-cm intervals along each peat core. Peat samples of 4 cm³ were prepared and analysed following standard procedures (Mauquoy *et al.* 2010). Peat subsamples were gently boiled with 5% KOH for 10 min and washed through a 125-µm mesh sieve. Fossil plant remains were identified in a gridded Petri dish with a binocular microscope at a 10 to 40× magnification using identification guides (Lévesque *et al.* 1988; Mauquoy & Van Geel 2007) and the reference collection of plant macrofossils from meridional and boreal Québec (Garneau 1995). The abundance of bryophytes and the main peat components (e.g. ligneous, Cyperaceae, *Sphagnum*) were expressed as volume percentages, and the vascular plants (e.g. needles, seeds, leaves) were represented in numbers per sample. Nomenclature follows Hill *et al.*

(2006) for bryophytes and Marie-Victorin (1995) for vascular plants.

In each sample, about 50 *Sphagnum* leaves were selected randomly and identified at the lowest taxonomic level possible (species or section) with an optical microscope at magnifications between 100 and 400× using the identification guide for *Sphagnum* of Laine *et al.* (2009). Sphagna were identified at the species level only when stemleaves were present. The degree of decomposition of the fossil plant remains was evaluated visually and estimated with an index from 0 (completely undecomposed peat) to 10 (completely decomposed undistinguishable plant remains). The macrofossil diagram zonation was established objectively using stratigraphically constrained cluster analyses (CONISS) with the Rioja package in R (Juggins 2015). The delimitation of some zones was then slightly adjusted to take into consideration important changes in peat properties and shifts in water-table depth (WTD). Macrofossil diagrams were plotted using C2 software version 1.7.2. (Juggins 2007).

Macroscopic charcoal particles >0.5 mm, which are reliable indicators of local fires (Ohlson & Tryterud 2000), were analysed at 1-cm intervals along the two cores. The extraction and analysis of charcoal followed a modified version of the protocol of Hörnberg *et al.* (1995) described in Magnan *et al.* (2012). Peat samples (1 cm³) were boiled for 10 min in a solution of 10% KOH and sieved through a 0.5-mm mesh screen. The charcoal

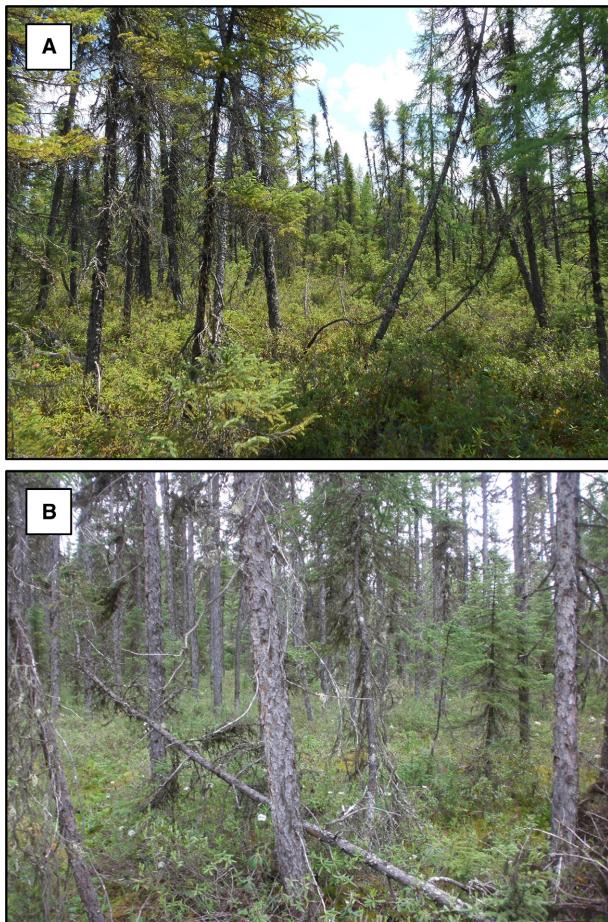


Fig. 2. Photographs of the coring site in the two studied forested peatlands of the Clay Belt. A. Villebois. B. Lili. [Colour figure can be viewed at www.boreas.dk]

fragments were counted in a Petri dish under a stereomicroscope (10 to 20 \times magnification). Charcoal particles were counted in two size classes (0.5–2 and >2 mm). The identification of local fire events was based on the occurrence of distinct peaks of macrocharcoal >0.5 mm and the presence of large charcoal fragments >2 mm, which are unlikely to be transported over long distances (Ohlson & Tryterud 2000).

Testate amoebae and water-table depth reconstruction

Testate amoeba analyses were performed at 4-cm intervals on 1-cm³ peat subsamples along the two peat profiles. Tests were extracted from the peat following the protocol described in Booth *et al.* (2010). Peat samples were boiled in distilled water for 10 min then washed through 250- and 15- μm sieves. The residual material between the two sieves was mounted on glass slides and analysed under an optical microscope at 400 \times magnification. A total count of at least 100 tests was reached for most samples except for some highly decayed woody layers in which the test concentration was very low. For these samples, a mini-

mum of 50 tests was considered reliable for the WTD reconstructions, although the values must be interpreted more cautiously for these levels (Payne & Mitchell 2009).

Long-term WTD variations were reconstructed using a weighted average tolerance downweighting model from a modern data set comprising 260 surface samples of testate amoebae, combining the data from non-forested open peatlands of eastern Canada (Lamarre *et al.* 2013) and the forested peatlands of the Clay Belt (Beaulne *et al.* 2018). Water-table depth values are relative to the peatland surface, and hence higher WTD values represent drier surface conditions. Water-table depth reconstructions from testate amoebae are presented alongside the macrofossil data, and the two proxies are described together in the results in order to facilitate the interpretations of local changes in both hydrological and ecological conditions.

Peat properties

Peat bulk density and ash (mineral) content were measured on 1-cm³ peat samples at every centimetre along both cores following the protocol described in Chambers *et al.* (2011). Dry bulk density (g cm^{-3}) was measured after overnight drying at 105 °C, and organic matter density (g cm^{-3}) and mineral contents were determined using loss-on-ignition at 550 °C for 4 h in a furnace.

Multivariate analyses

In order to explore latent environmental gradients and associations between taxa in the plant macrofossil data, detrended correspondence analyses (DCAs) were performed with Canoco 5.0 software (Ter Braak & Šmilauer 2012). Plant taxa with fewer than three occurrences in the fossil assemblages were excluded from the ordination, and rare taxa were downweighted. In order to help interpret the underlying environmental gradient influencing the plant macrofossils, important variables related to vegetation composition such as organic matter density, mineral content, charcoal concentration, WTDs and peat accumulation rates (PARs) were fitted as passive variables in the ordination.

Chronologies

A total of 17 samples of selected fossil plant remains were pretreated at the radiochronology laboratory of the Center for Northern Studies (Université Laval, Québec, Canada) and submitted to the Keck-CCAMS laboratory (University of California, Irvine, USA) and Center for Applied Isotope Studies (University of Georgia, Athens, USA) for accelerator mass spectrometry (AMS) radiocarbon dating (Table 1). Radiocarbon dates were conducted on the levels corresponding to important transitions in the vegetation composition and local fire events detected from charcoal analyses. Chronologies were developed using Bayesian age-depth modelling with

BACON (Blaauw & Christen 2011) in R software version 2.14.0 (R Development Core Team 2011). The modern post-bomb ^{14}C dates were calibrated using CALIBomb (Reimer *et al.* 2004) with the Northern Hemisphere Zone 1 dataset (Hua *et al.* 2013). The age of the peatland surface was set at -65 cal. a BP, which corresponds to the year of the coring in 2015. All ages are presented in calibrated years before present (i.e. AD 1950) rounded to the nearest decade.

Results

Peat-core chronology

The results of radiocarbon dating and the calibrated ages are presented in Table 1. In the Villebois core, the age-depth model shows very rapid PARs during the early developmental stage of the peatland with an average of 0.89 mm a^{-1} between 8000 and 7530 cal. a BP followed by

a slowdown to 0.22 mm a^{-1} between 7530 and 6560 cal. a BP (Fig. 3). A period with very low PAR from 6560 to 3480 cal. a BP (0.016 mm a^{-1}) is recorded between the two levels dated at 77 and 72 cm. Peat accumulation has been variable and remained relatively low over the last ~ 3500 years (0.21 mm a^{-1}). In the Lili core, PARs were stable and very high between 5240 and 3570 cal. a BP (0.46 mm a^{-1}) and decreased significantly over the last 3570 years to an average of 0.19 mm a^{-1} (Fig. 3). The very high rates of peat accumulation recorded in the last ~ 50 years (upper 30 cm) in the two cores ($\sim 6 \text{ mm a}^{-1}$) correspond to the poorly humified aerobic peat layer (acrotelm) comprising living bryophytes.

Plant macrofossils and water-table reconstructions from testate amoebae

The plant macrofossil data show the local vegetation successions in both the ground layer and the above-

Table 1. Radiocarbon dates and calibrated ages.

Core	Depth (cm) ¹	Laboratory number ²	Material dated ³	^{14}C date \pm error (a BP)	2 σ range (cal. a BP)	Median age probability (cal. a BP)
Lili	32–33	UCIAMS-186704 ULA-6783	<i>Sphagnum</i> ; <i>Picea</i> (need., twigs, bark); Ericaceae (lvs.)	Post-bomb	(−7.5)–(−5.6)	−6
	41–43 ¹	UCIAMS-171030 ULA-5902	<i>Picea</i> (char. need., sds.) <i>Larix</i> (char. need.); conifer char. bark; Ericaceae (char. lvs.)	600 \pm 15	548–646	606
	54–55	UCIAMS-189159 ULA-6918	<i>Sphagnum</i> ; <i>Picea</i> (need., twigs); Conifer periderm	2230 \pm 15	2157–2322	2219
	67–68	UCIAMS-183257 ULA-6672	<i>Sphagnum</i> ; <i>Picea</i> (need., twigs); <i>Larix</i> (need., twigs, bark); Ericaceae (lvs.)	3340 \pm 15	3512–3634	3580
	97–98	UCIAMS-174833 ULA-6150	<i>Larix</i> and <i>Picea</i> (need. and twigs)	3830 \pm 20	4151–4346	4214
	120–121 ¹	UCIAMS-171031 ULA-5903	Char. conifer bark	4080 \pm 20	4448–4796	4564
	144–145	UGAMS-24329 ULA-5864	<i>Picea</i> , <i>Abies</i> , <i>Larix</i> (need.); Conifer periderm	4550 \pm 25	5057–5316	5157
	28–29	UCIAMS-186705 ULA-6784	<i>Sphagnum</i>	Post-bomb	(−17.7)–(−13.4)	−16
	44–45 ¹	UCIAMS-170231 ULA-5904	<i>Picea</i> (char. need., stems); <i>Larix</i> (char. need.); Conifer (char. bark)	640 \pm 20	558–663	592
	53–54 ¹	UCIAMS-174834 ULA-6151	Charcoal, <i>Picea</i> (char. need.); <i>Sphagnum</i>	1920 \pm 20	1822–1920	1868
Villebois	61–62 ¹	UCIAMS-183259 ULA-6674	<i>Picea</i> (char. need., bark); <i>Larix</i> (bark); <i>Sphagnum</i>	2240 \pm 15	2159–2331	2222
	66–67 ¹	UCIAMS-189156 ULA-6915	<i>Picea</i> (char. need.)	3110 \pm 15	3254–3377	3342
	72–73 ¹	UCIAMS-174835 ULA-6152	<i>Sphagnum</i> ; <i>Picea</i> (needles, char. twigs); Ericaceae (lvs.)	3315 \pm 20	3477–3592	3531
	77–78 ¹	UCIAMS-174836 ULA-6153	<i>Sphagnum</i> ; <i>Picea</i> (need., bark, char. twigs)	5755 \pm 20	6494–6633	6551
	98–99	UCIAMS-174826 ULA-6147	<i>Sphagnum</i>	6650 \pm 20	7491–7574	7534
	120–121	UCIAMS-174837 ULA-6154	<i>Larix</i> need.	6890 \pm 20	7672–7784	7711
	139–141	UCIAMS-170211 ULA-5866	Ericaceae (lvs.)	7200 \pm 20	7964–8036	8001

¹Dated charcoal layers (i.e. local fire events).

²UCIAMS = University of California; UGAMS = University of Georgia; ULA = Université Laval.

³char. = charred; lvs = leaves; need. = needles; sds. = seeds.

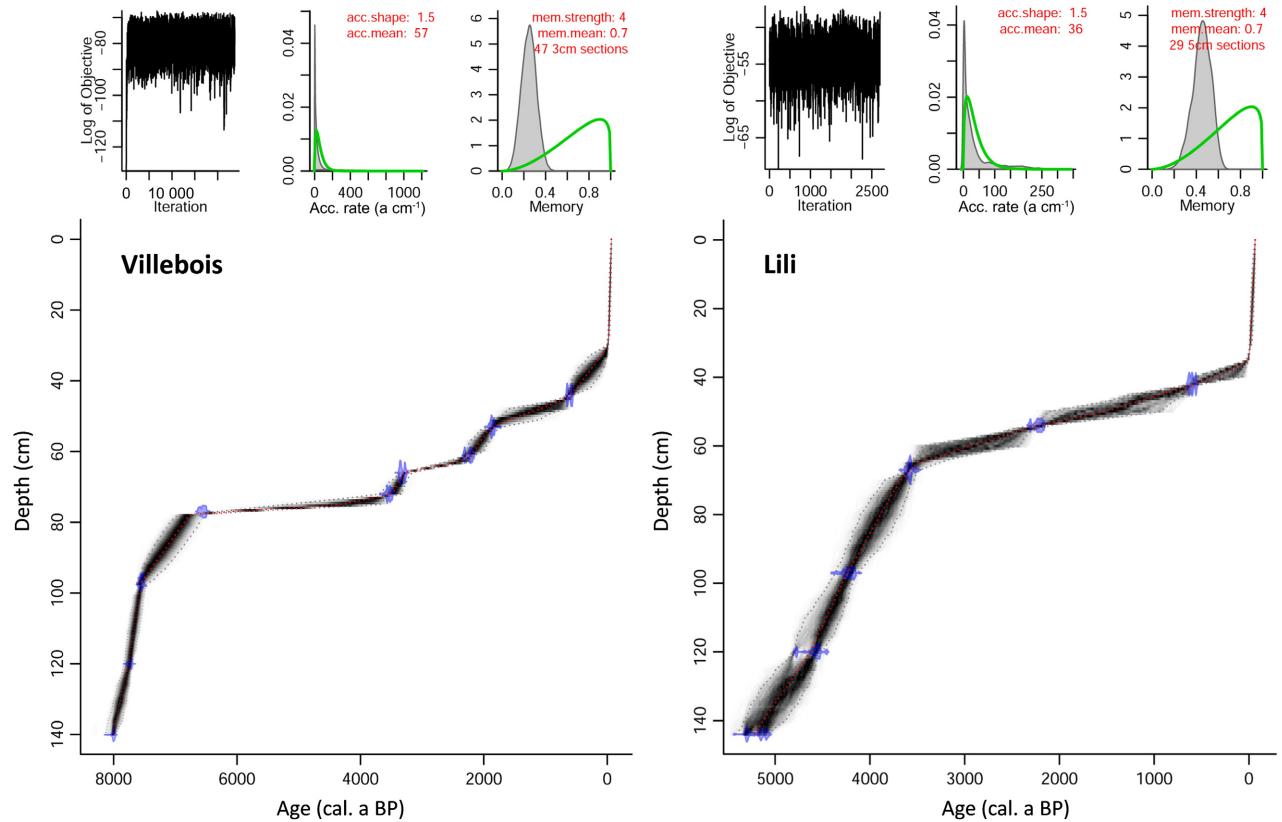


Fig. 3. Age-depth models for the two peat cores developed using a Bayesian approach with BACON software (Blaauw & Christen 2011). Dotted grey lines show 95% confidence intervals. Default settings were used for the memory strength (*mem.strength* = 4), memory mean (*mem.mean* = 0.7) and shape (*acc.shape* = 1.5). [Colour figure can be viewed at www.boreas.dk]

ground communities (e.g. shrubs and trees) throughout the development of Villebois and Lili peatlands (Figs 4, 5). The WTD reconstructions obtained from the testate amoebae records (Figs S2, S3) are presented in the macrofossil diagrams and reflect past fluctuations in peatland surface wetness. A total of six assemblage zones were defined in both cores, which corresponds to the main developmental stages of the peatlands since their initiation (Figs 4, 5). The main characteristics of the macrofossil assemblage zones are summarized in Tables 2 and 3.

Villebois peatland

Zone VI: 140–124 cm. – Peat accumulation started around 8000 cal. a BP in a wet rich minerotrophic environment (fen) colonized by brown mosses (*Calliergon giganteum*, *C. stramineum*, *Drepanocladus* spp.) and sedges (*Carex* spp.) that persisted until 7770 cal. a BP (Fig. 4; Table 2). The absence of conifer remains in the basal peat suggests that the site was not forested initially. Moreover, the testate amoeba assemblages dominated by *Centropyxis aculeata* (Fig. S2) reveal the existence of near-surface water tables (WTD < 10 cm).

Zone V2: 124–108 cm. – The fen was rapidly colonized by *Larix laricina* (high numbers of needles and twigs),

<250 years following peat inception, while the moss *Tomentypnum nitens*, a common hummock-forming species in rich fens (Gignac *et al.* 1991), became dominant in the ground layer between 7770 and 7620 cal. a BP. The peat accumulation rates were particularly high in the tamarack fen (1.07 mm a^{-1}).

Zone V3: 108–76 cm. – After 7620 cal. a BP, the peatland surface became drier (shift to high WTD values inferred from a dominance of *Trigonopyxis* spp. and *Assulina muscorum*). This corresponds with the local establishment of *Picea mariana* (needles and twigs) accompanied by *Sphagnum* sect. *Acutifolia* (mainly *Sphagnum capillifolium*), which indicates the development of a forested bog. This period with high dominance of sphagna (7620–5950 cal. a BP) is characterized by lower peat decay and lower organic matter density. A charcoal layer is identified at the top of this zone and was dated at 6550 cal. a BP and corresponds to the oldest local fire event recorded in this peatland.

Zone V4: 76–44 cm. – The abundance of *Sphagnum* spp. declined drastically from around 5950 cal. a BP; conifer remains are dominant and the ectomycorrhizal fungus *Cenococcum*, indicative of dry conditions, is found in many levels. A total of five distinct charcoal peaks

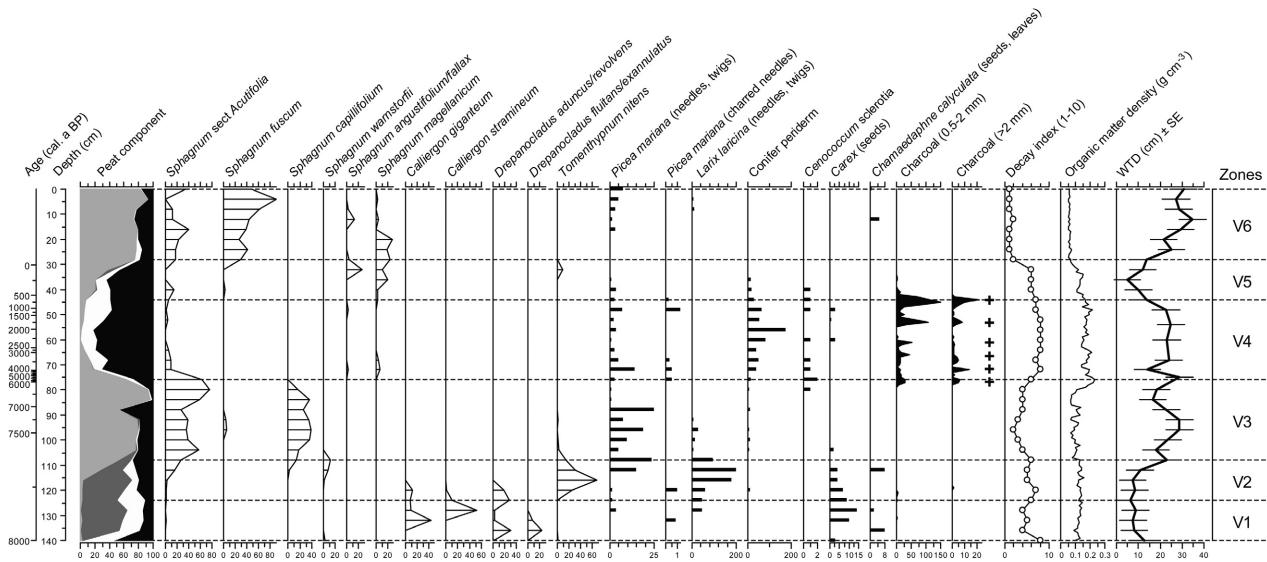


Fig. 4. Plant macrofossil diagram of Villebois showing the data in percentages (silhouettes) and in counts (black bars). The main peat components in cumulative percentages are shown in the left column: *Sphagnum* (light grey), non-*Sphagnum* mosses (dark grey), Cyperaceae (white) and ligneous remains (black). The water table depth (WTD) reconstruction from the testate amoebae record is shown on the right (higher values indicate drier conditions). The charcoal record (1-cm intervals) is presented, and the local fire events are indicated by the + signs. The organic matter density and the visual decay index are also plotted.

corresponding to local fire events are recorded in this zone and were radiocarbon dated at 3530, 3340, 2220, 1870 and 610 cal. a BP. During this period, the peatland was dominated by woody vegetation, water tables remained low (dry bog surface), and peat decomposition was high as suggested by high organic matter density (mean: 0.18 g cm^{-3}) and decay indices (7–8).

Zone V5: 44–28 cm and Zone V6: 28–0 cm. – The most recent fire event dated at ~600 cal. a BP, comprising the highest numbers of charcoal particles in the record, is followed by the establishment of *Sphagnum magellanicum* and a shift to wet conditions (low WTD values) that lasted until ~AD 1970. The decline in the abundance of conifer macrofossils suggests a transition to more open

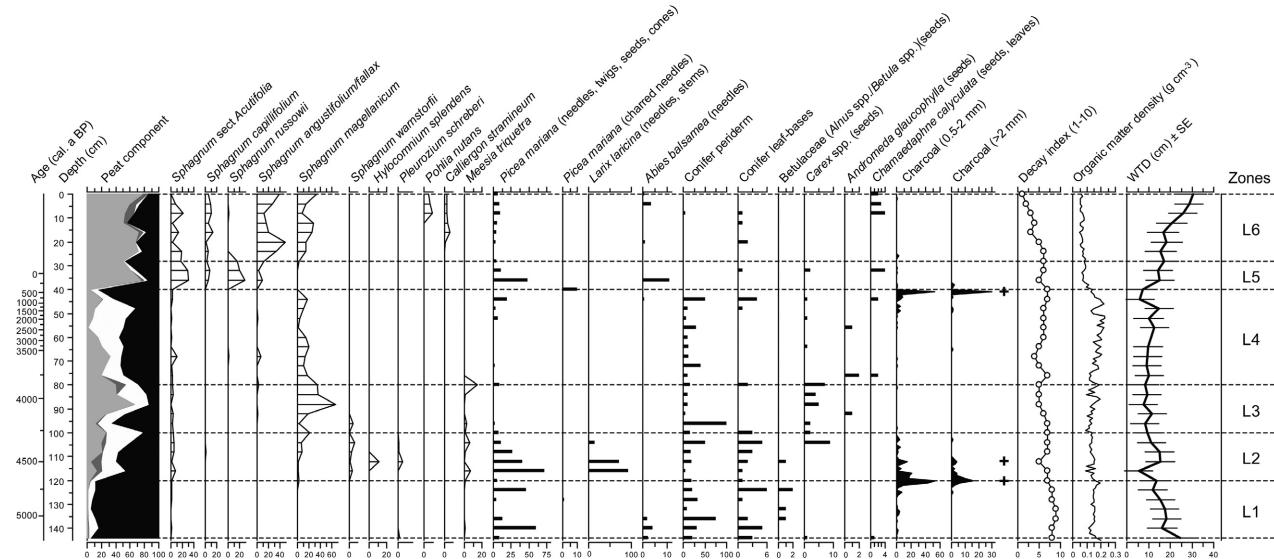


Fig. 5. Plant macrofossil diagram of Lili showing the data in percentages (silhouettes) and in counts (black bars). The main peat components in cumulative percentages are shown in the left column: *Sphagnum* (light grey), non-*Sphagnum* mosses (dark grey), Cyperaceae (white) and ligneous remains (black). The water table depth (WTD) reconstruction from the testate amoebae record is shown on the right (higher values indicate drier conditions). The charcoal record (1-cm intervals) is presented, and the local fire events are indicated by the + signs. The organic matter density and the visual decay index are also plotted.

Table 2. Characteristics of the fossil assemblage zones for Villebois.

Zone	Depth (cm)	Age (cal. a BP/AD)	Main macrofossils	Main testate amoebae taxa	Mean WTD (cm)	Mean PAR (mm a ⁻¹)
V1	140–124	8000–7770	<i>Calliergon</i> spp., <i>Drepanocladus</i> spp., <i>Carex</i> spp.	<i>Centropyxis</i> spp., <i>Cyclopyxis arcelloides</i> , <i>Phryganella acropodia</i>	9.3	0.70
V2	124–108	7770–7620	<i>Larix laricina</i> , <i>Sphagnum warnstorffii</i> , <i>Tomentypnum nitens</i> , <i>Carex</i> spp.	<i>Centropyxis aculeata</i> , <i>Cyclopyxis arcelloides</i> , <i>Hyalosphenia elegans</i>	8.3	1.07
V3	108–76	7620–5950	<i>Picea mariana</i> , <i>Sphagnum capillifolium</i>	<i>Assulina muscorum</i> , <i>Hyalosphenia papilio</i> , <i>Trigonopyxis</i> spp.	22.5	0.19
V4	76–44	5950–600	<i>Picea mariana</i> , conifers, charcoal, <i>Cenococcum</i>	<i>Arcella catinus</i> , <i>Heleopera rosea</i> , <i>Hyalosphenia subflava</i> , <i>Trigonopyxis arcula</i>	22.9	0.06
V5	44–28	600–AD 1970	<i>Sphagnum magellanicum</i> , <i>S. angustifolium/fallax</i>	<i>Amphitrema wrightianum</i> , <i>Centropyxis aculeata</i> , <i>Phryganella acropodia</i>	10.3	0.26
V6	28–0	AD 1970 to present	<i>Sphagnum fuscum</i> , <i>Picea mariana</i>	<i>Assulina muscorum</i> , <i>Diffugia pulex</i> , <i>Hyalosphenia papilio</i> , <i>Nebela militaris</i>	26.4	6.09

forest canopy. Over the last ~50 years, *Sphagnum fuscum*, a late successional species typical of drier microforms in bogs (Laine *et al.* 2009), established and became dominant in the bryophyte layer. This coincides with an important water-table drawdown (WTD values >20 cm) when black spruce recolonized the bog recently.

Lili peatland

Zone L1: 144–120 cm. – The basal sediment is composed of highly decayed ligneous remains of conifers. The organic layers started to accumulate on the mineral soil within a mesic forest dominated by *Picea mariana* between 5240 and 4640 cal. a BP (Fig. 5; Table 3). Some needles of *Abies balsamea* were found at the bottom of the core, suggesting that this species was present in the initial forest but disappeared <200 years after peat inception.

The testate amoebae record (Fig. S3) shows a gradual rise of the water table within the organic horizons during the first 600 years of peatland development.

Zone L2: 120–100 cm. – A distinct high charcoal peak corresponding to a local fire dated at 4640 cal. a BP was followed by the re-establishment of black spruce accompanied by *Larix laricina*. Following this fire, particularly wet surface conditions were inferred from testate amoebae (high abundance of *Phryganella acropodia* and *Hyalosphenia papilio*) as the site was gradually invaded by sphagna (*Sphagnum magellanicum* and *S. warnstorffii*) and the moss *Meesia triquetra* was found in some levels. A distinct charcoal peak identified around 4500 cal. a BP (depth: 112 cm) coincides with the local disappearance of *L. laricina*, the presence of a few remains of feather mosses (*Hylocomnium splendens* and *Pleurozium schreberi*) and a

Table 3. Characteristics of the fossil assemblage zones for Lili.

Zone	Depth (cm)	Age (cal. a BP/AD)	Main macrofossils	Main testate amoebae taxa	Mean WTD (cm)	Mean PAR (mm a ⁻¹)
L1	144–120	5240–4640	<i>Picea mariana</i> , <i>Abies balsamea</i>	<i>Centropyxis</i> spp., <i>Phryganella acropodia</i> , <i>Trigonopyxis</i> spp.	17.3	0.40
L2	120–100	4640–4290	<i>Picea mariana</i> , <i>Larix laricina</i> , <i>Sphagnum warnstorffii</i> , <i>Meesia triquetra</i> , charcoal	<i>Centropyxis</i> spp., <i>Hyalosphenia papilio</i> , <i>Phryganella acropodia</i>	12.2	0.57
L3	100–80	4290–3890	<i>Sphagnum magellanicum</i> , <i>Carex</i> spp.	<i>Centropyxis</i> spp., <i>Heleopera sphagni</i> , <i>Hyalosphenia papilio</i>	9.4	0.50
L4	80–40	3890–390	<i>Sphagnum magellanicum</i> , conifers	<i>Archerella flavum</i> , <i>Centropyxis</i> spp., <i>Heleopera rosea</i> , <i>H. sphagni</i>	9.9	0.11
L5	40–28	390–AD 1970	<i>Sphagnum russowii</i> , <i>Picea mariana</i>	<i>Diffugia pulex</i> , <i>Nebela militaris</i> , <i>Pseudodiffugia fulva</i>	12.4	0.29
L6	28–0	AD 1970 to present	<i>Sphagnum angustifolium/fallax</i> , <i>S. capillifolium</i> , <i>S. magellanicum</i> , <i>Picea mariana</i>	<i>Assulina muscorum</i> , <i>Diffugia pulex</i> , <i>Nebela militaris</i>	21.7	6.09

slight water-table lowering. The abundance of black spruce macrofossils declined gradually between 4640 and 4290 cal. a BP as the peatland surface became wetter (dominance of *Centropyxis* spp. and *Phryganella acropodia*).

Zone L3: 100–80 cm. – *Sphagnum magellanicum* was dominant between 4290 and 3890 cal. a BP along with sedges (*Carex* spp.). The water-table levels were relatively high and stable, inferred from high abundance of *Centropyxis aculeata* and *Hyalosphenia papilio* in the testate amoebae record. The sporadic presence of the moss *Meesia triquetra* suggests the persistence of relatively nutrient-rich conditions locally.

Zone L4: 80–40 cm. – After 3890 cal. a BP, *Sphagnum magellanicum* persisted in the ground layer while the water tables remained near the surface and the abundance of conifers remained low. *Picea mariana* re-established on the bog around 2000 cal. a BP when a shift towards slightly lower water tables is recorded, and the high organic matter density suggests high peat decay. This was followed by a local fire event (high charcoal peak) dated at ~600 cal. a BP, which coincided with a transition towards a high *Sphagnum* abundance.

Zone L5: 40–28 cm and **Zone L6:** 28–0 cm. – *Sphagnum russowii* invaded the bog surface under the *Picea mariana* canopy between ~400 cal. a BP and ~AD 1970 and multiple *Sphagnum* species (*S. capillifolium*, *S. angustifolium/falax* and *S. magellanicum*) established locally over the last ~50 years. A gradual drying of the bog surface over the last ~100 years is inferred from increasing abundance of *Nebela militaris* and *Difflugia pulex*.

Ordination of plant macrofossil data

The DCA ordination of macrofossil assemblages shows, for the two cores, coherent associations between the taxa and a good separation between the different assemblage zones identified (Fig. 6). The cumulative variance explained by axis 1 and axis 2 is 40.4% for Villebois and 45.6% for Lili. The main axis of variability (axis 1) primarily reflects a hydrological and trophic gradient from wet and minerotrophic (fen) communities on the right (high values) to drier nutrient-poor ombrotrophic and more forested environments on the left (low values). The WTD and the mineral content are mainly correlated with axis 1. The charcoal concentration in peat is associated with a high abundance of wood remains but is not clearly correlated with the variables considered. The PAR is mainly related to axis 1 and reflects a higher decomposition of older peat samples on the right side of the ordination (higher organic matter density) and poorly decayed lawn and hummock-forming sphagna with high vertical growth (*S. capillifolium* and *S. fuscum*) on the left, which are abundant in recent upper peat layers. A

significant fraction of the variability in the macrofossil data is explained by axis 2. The position of the taxa along axis 2 seems to reflect an underlying gradient of conifer density and canopy openness with the shade-tolerant species *Sphagnum capillifolium* and *Sphagnum russowii* positioned at the upper end of the gradient (positive scores) and the species intolerant to shade such as *S. magellanicum* found at the lower end (negative scores).

Discussion

Ecological and hydrological contexts of peat inception

In the two studied sites, the peatland formed through paludification resulting from primary or secondary vegetation successions (Fig. 7). These two types of paludification are confounded in the present-day regional landscape of the Clay Belt, and their spatial extent is primarily controlled by edaphic, topographical factors and related drainage potential (Lavoie *et al.* 2005b; Simard *et al.* 2007; Laamrani *et al.* 2015; Le Stum-Boivin *et al.* in press).

At the Villebois site, peat started to accumulate around 8000 cal. a BP within a rich fen dominated by brown mosses over the moist clayey deposit surface shortly after the drainage of proglacial Lake Ojibway that occurred around 8200 cal. a BP (Roy *et al.* 2011). This process of primary paludification was favoured by poor drainage in slight topographical depressions that induced waterlogged soil conditions and fast organic matter build-up, hence preventing the establishment of trees (Lavoie *et al.* 2005b; Simard *et al.* 2007).

At the Lili site, located higher upslope along the topographical transect (Fig. S1), the peatland developed from ~5200 cal. a BP in a formerly mesic black spruce forest stand through secondary succession. This type of paludification was previously attributed to the gradual accumulation of organic layers and the concomitant rise of the water table, which can occur through natural forest succession in the prolonged absence of fire over poorly drained clayey soils (Simard *et al.* 2009). Peat accumulation over forested uplands is often favoured by the lateral expansion of neighbouring peatland primarily controlled by the degree of slope and the rates of peat growth (Kuhry & Turunen 2006). In boreal northern regions, widespread forest paludification was also favoured by a shift towards colder and moister climate conditions and a related decrease in fire occurrence from the Middle Holocene onwards (Korholola 1995, 1996; Weckström *et al.* 2010; Payette *et al.* 2013; Ruppel *et al.* 2013; Schaffhauser *et al.* 2016).

Successional pathways and water-table variability

The palaeoecological data show two different successional pathways towards the formation of the present-day spruce-*Sphagnum* forested peatlands in the Clay Belt (Figs 6, 7). The development of the Villebois peatland

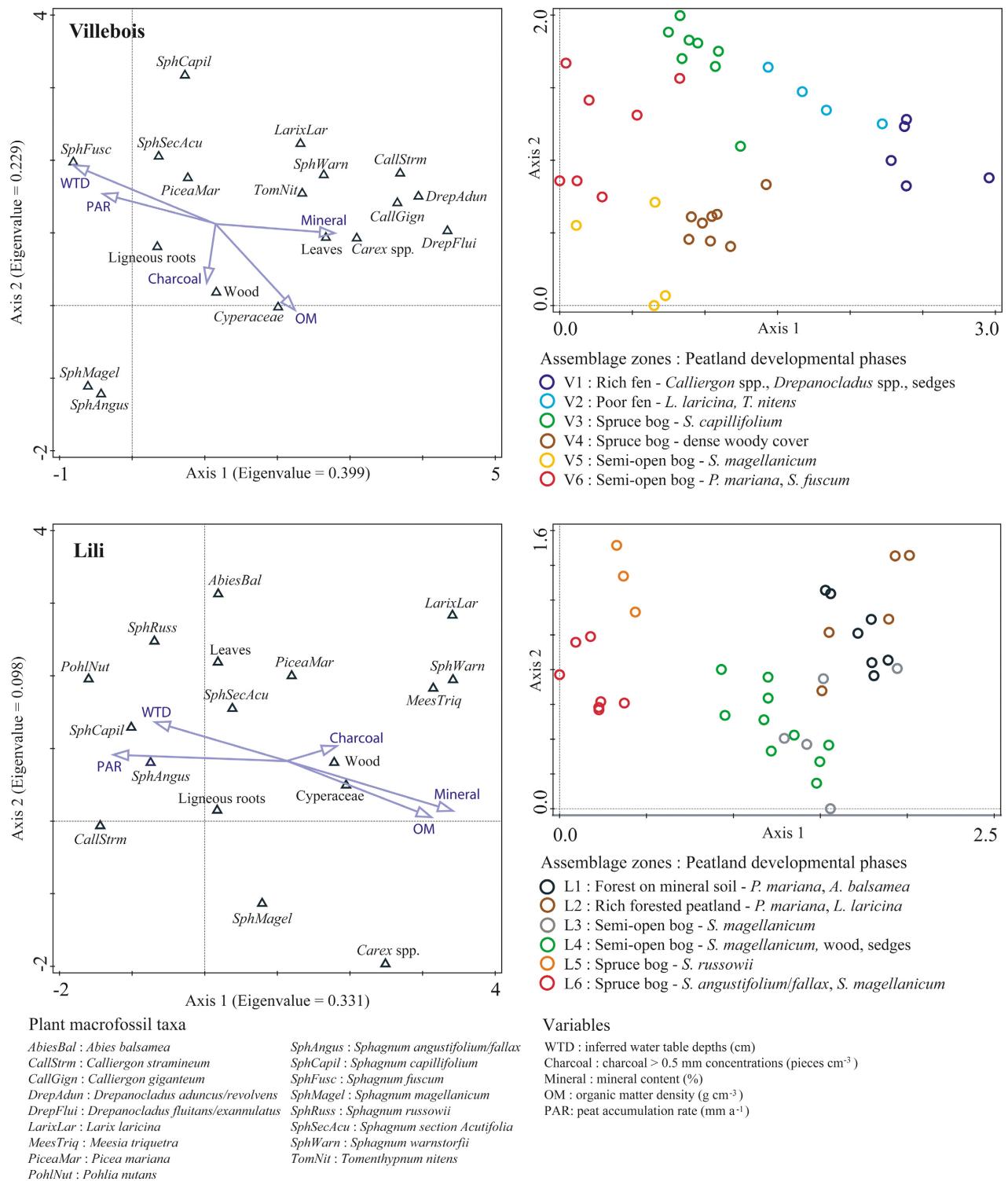


Fig. 6. Biplots of DCA axis 1 and axis 2 of the plant macrofossil assemblages showing the ordination of the taxa (left) and the samples (right) for the two studied cores Villebois and Lili. The variables (Charcoal, WTD, Mineral, PAR and OM) are passively fit in the ordination, and the vectors indicate their relationship with the vegetation assemblages. [Colour figure can be viewed at www.boreas.dk.]

follows a hydroseral succession from wet rich to poor fen, to a dry bog, as commonly observed in the boreal biome (e.g. Bauer *et al.* 2003; Glaser *et al.* 2004; van Bellen

et al. 2011; Lavoie *et al.* 2013; Magnan *et al.* 2014). The surface drying and the shift to ombrotrophy may have been primarily driven by autogenic vertical peat growth

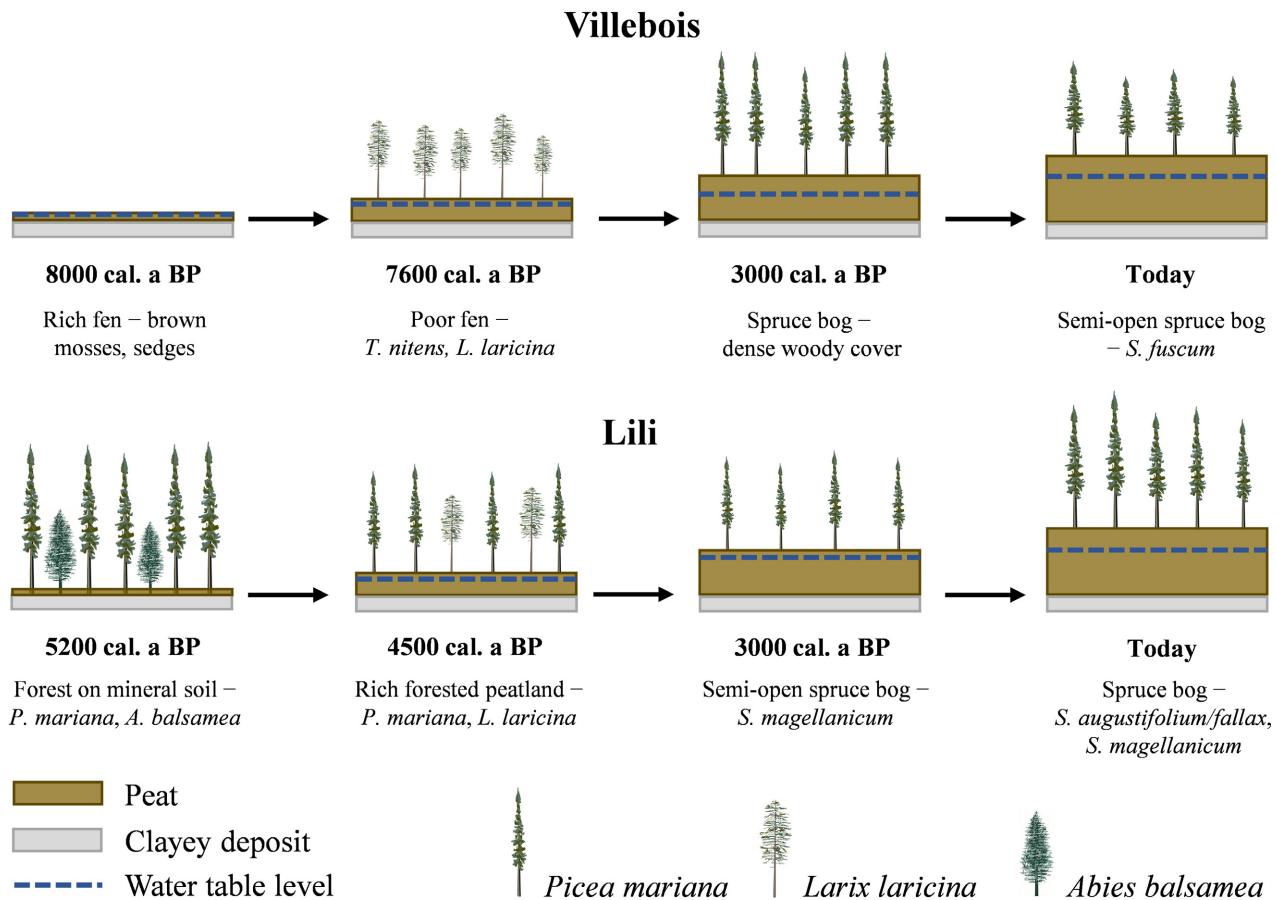


Fig. 7. Schematic representation of long-term successional trajectories and variations in water-table levels throughout the development of the two studied peatlands. Villebois developed through primary paludification on moist clayey soils without an initial forest. At Lili, the peatland initiated over a formerly mesic coniferous forest through secondary paludification. [Colour figure can be viewed at www.boreas.dk]

that gradually raised the peatland surface above the influence of the mineral-rich groundwater (Yu *et al.* 2003; Kuhry & Turunen 2006; Yu 2006). At Villebois, the rapid transformation of the wet and treeless rich fen (Zone V1) into a dry spruce bog (Zone V3) occurred <400 years after peat inception and was favoured by very high peat accumulation rates (Fig. 4; Table 2), which probably caused an apparent lowering of the water-table level relative to the surface. The high plant productivity and peat growth within the early fen were probably stimulated by warm summer conditions at the beginning of the Holocene thermal maximum (Viau *et al.* 2006), while the bryophytes growing on the wet clayey mineral were receiving high nutrient inputs.

The shift towards drier peatland surfaces from 7770 cal. a BP at Villebois coincides with the colonization of *Larix laricina*, a common pioneer species in fens well adapted to waterlogged conditions (Burns & Honkala 1990). The establishment of tamaracks on the peatland may have lowered the water table through enhanced evapotranspiration, which rapidly created suitable conditions for the establishment of *Picea mariana* around 7600 cal. a BP. The growth of black spruce on the peatland seems to have

further deepened the water table (Zone V3). This drying coincides with the establishment of *Sphagnum capillifolium*, a shade-tolerant species (Hayward & Clymo 1983) very common in dense paludified black spruce forests (Fenton *et al.* 2007). Black spruce presence was maintained throughout the development of the bog from 7600 cal. a BP onward while the peat surface remained particularly dry (Zones V3 and V4), but conifers declined following a considerable rise of the water table around 500 cal. a BP (Zone V5; Fig. 4). The recent expansion of *Sphagnum fuscum* followed the decline in black spruce and coincides with the relatively dry conditions and high peat accumulation rates locally (Zone V6). *S. fuscum* is a shade-intolerant species (Gignac 1992) and a late successional sphagnum in forested peatlands usually associated with high levels of canopy openness and a lower water table (Fenton & Bergeron 2006; Fenton *et al.* 2006).

At Lili, the macrofossil data show a rapid shift from a coniferous forest on mineral soil (Zone L1) to a wet forested peatland with species indicative of nutrient-rich conditions (Zone L2) such as *Sphagnum warnstorffii* and *Meesia triquetra* (Gignac *et al.* 1991). This is followed by the development of a semi-open forested bog with a

ground cover dominated by *Sphagnum magellanicum* (Zones L3 and L4). This contrasts with previous post-fire chronosequence studies in paludified stands of the Clay Belt that documented a successional sequence from feather mosses (mainly *Pleurozium schreberi*) to shade-tolerant sphagna (mainly *S. capillifolium*), followed by the establishment of heliotrophic species (e.g. *Sphagnum magellanicum*) as the forest canopy opens up and the soil moisture increases (Fenton & Bergeron 2006; Bergeron & Fenton 2012). At the Lili site, feather mosses were probably present in the ground layer of the initial mesic coniferous forest but are absent from the macrofossil record (Zone L1) most likely due to high litter decay (high decay index values).

At Lili, peat started to accumulate over a residual forest organic layer (~25 cm thick) left by a probable low-severity fire while the water table was already close to the surface (Zone L2; Figs 5, 7). These conditions accelerated paludification and resulted in the establishment of *Sphagnum* species usually found at a later successional stage (e.g. *Sphagnum magellanicum*). The vegetation dynamics documented at Lili differ from those observed over relatively dry exposed mineral soils after high-severity fires, where feather mosses establish and dominate the forest floor under a dense black spruce canopy (e.g. Fenton *et al.* 2009; Fenton & Bergeron 2013). At the Lili site, *Picea mariana* re-established locally on the remaining organic deposits after fire but the presence of *Larix laricina*, a conifer intolerant of shade (Burns & Honkala 1990), suggests that the canopy was relatively open and that the stand was already in an advanced state of paludification (Zone L2; Fig. 7). The conifers gradually declined between 4640 and 4290 cal. a BP as peat was accumulating rapidly (mean PAR: 0.57 mm a⁻¹) in the post-fire forest stand. The shift to near-surface water tables probably reflects reduced evapotranspiration due to the opening of the canopy and a decline in forest productivity (Simard *et al.* 2007). The establishment of *Sphagnum magellanicum*, a shade-intolerant species typically found in illuminated habitats (Fenton & Bergeron 2006), corresponds with a significant decline in the abundance of black spruce between 4300 and 2000 cal. a BP indicating a more open canopy on the bog (Zones L3 and L4; Figs 5, 7). The local re-establishment of black spruce over the last ~2000 years was favoured by a slight drying of the bog surface, a decline in sphagna and the accumulation of more humified peat layers, which created more favourable conditions for tree growth (Fig. 5).

The macrofossil records suggest that *Picea mariana* persisted on these two peatlands during most of their Holocene development (Figs 4, 5, 7). This contrasts with studies in maritime regions in eastern Canada showing that paludified forests on well-drained deltaic sands transformed into non-forested *Sphagnum* bogs during the mid-Holocene that persisted over millennia (Payette *et al.* 2013; Magnan *et al.* 2014). This regional difference in vegetation dynamics probably reflects a

pervasive influence of the continental climate on the bogs in western boreal Québec where higher evapotranspiration potential under warmer summers favours low water-table levels that promote tree growth.

Influence of fire on millennial peatland dynamics

Our data suggest that fires have played a role in the process of paludification at Lili. At this site, the transformation of the coniferous forest into a forested peatland was accelerated by a fire that only partially consumed the organic layer. Previous studies showed that a low depth of burn negatively affects post-fire tree regeneration and results in more open forest stands, which further promotes paludification (Fenton *et al.* 2005; Lecomte *et al.* 2005, 2006a; Simard *et al.* 2007; Johnstone *et al.* 2010). At Lili, the high soil moisture (high water tables) in the paludified forest when the fire occurred seems to have prevented a deep burning of the organic layer up to the mineral soil (Terrier *et al.* 2014). Moreover, the removal of conifers by fire may have reduced evapotranspiration rates causing a temporary rise of the water table and an increase in available light, which promoted *Sphagnum* growth (Crawford *et al.* 2003; Fenton *et al.* 2005; Fenton & Bergeron 2006, 2007).

The charcoal records show relatively low fire frequency in the two peatlands with only three distinct local fire events in Lili over the last ~5200 years and a total of six fires since 8000 cal. a BP in Villebois. This corroborates results of other studies in boreal Québec showing that forests on thick organic layers (>50 cm) can escape fire for millennia due to wet soil conditions (e.g. Ouarmim *et al.* 2015). However, some fires seem to be responsible for significant shifts in vegetation communities and water table levels in the studied peatlands. At Villebois, the presence of multiple charcoal layers between 6000 and 600 cal. a BP coincides with a major decline in *Sphagnum* and very low peat accumulation rates suggesting that some peat layers were lost by combustion. The recurrence of fire was highest on the peatland between ~3500 and ~600 cal. a BP, when five local fire events were recorded (Zone V4; Fig. 4). The susceptibility of the peatland to fire may have increased due to autogenic-driven drying and the related increase in aboveground biomass. However, charcoal reconstructions from nearby sites (<20 km from Villebois peatland) also suggested higher fire frequencies during the late Holocene (Carcaillet *et al.* 2001; Ali *et al.* 2008) although a decrease in fire frequency is documented in the boreal biome of northeastern America during this period (Ali *et al.* 2012; Remy *et al.* 2017).

Our data suggest that the presence of black spruce was an important factor allowing fire propagation in these peatlands. At Lili, the absence of local fires between 4300 and 600 cal. a BP is explained by the low abundance of conifers and wet soil conditions, which must have prevented the spread of fire at the coring site. The most recent fire dated at 600 cal. a BP occurred shortly after the local re-establishment of black spruce (Zone L4). In Villebois, all

the fires occurred under particularly dry peat surface conditions while the bog was dominated by ligneous vegetation (Zone V4; Fig. 4).

The most recent fire on the Villebois bog dated at 600 cal. a BP marks a transition towards near-surface water tables and a decline in black spruce (Zone V5). Surface fires in peatlands can trigger a shift to wet conditions due to reduced evapotranspiration by ligneous vegetation and/or the combustion of upper peat layers, which lowers the surface closer to the water level (Tuittila *et al.* 2007; Välijärvi *et al.* 2007; Wieder *et al.* 2009; Sillasoo *et al.* 2011). Forested peatlands are probably more likely to be affected by deep burning than open peatlands due to the higher abundance of woody biomass and drier peat surface conditions.

Although some local fires seem to have slowed down peat accumulation in the forested bog, the removal of conifers by episodic fires probably favoured the persistence of these ecosystems in the landscape over the Holocene. The opening of the forest cover created by fire increases surface wetness and light availability, which is beneficial for *Sphagnum* growth. In the absence of fire, black spruce would probably have gradually invaded the bogs in maintaining favourable growth conditions by further lowering water tables and inhibiting *Sphagnum* growth.

Recent ecohydrological changes

The two studied bogs have experienced a substantial lowering of water tables and a shift in sphagna communities over the last ~50 years (Zones V6 and L6; Figs 4, 5). Drier surface conditions in these forested peatlands may be due in part to enhanced evapotranspiration losses under warmer summer conditions documented in recent decades in western Québec (Housset *et al.* 2015). In the two studied sites, the rapid vertical growth of poorly decayed *Sphagnum* peat after the last local fire (~600 cal. a BP) has probably caused an apparent drying in disconnecting the peatland surface from the water table. Recent changes in bryophyte cover and related water-table drawdown have been documented in other pristine boreal bogs of continental western Canada and were attributed to regional climate warming affecting both plant productivity and surface wetness (e.g. Bauer *et al.* 2009; van Bellen *et al.* 2018; Magnan *et al.* 2018).

The fate of forested peatlands under projected climate change and modifications in fire regimes remains largely unknown. A significant warming during the summer and an increase in the frequency and severity of fires is projected by the end of the 21st century for the boreal regions of eastern Canada (Bergeron *et al.* 2010; Girardin *et al.* 2013), which would reduce paludification rates (Lafleur *et al.* 2015; Terrier *et al.* 2015). The enhanced evapotranspiration potential under a warmer climate could deepen water tables and increase tree density in peatlands. These conditions would increase the vulnera-

bility of peatland ecosystems to fire and have major impacts on their vegetation and carbon dynamics (Camill *et al.* 2009; Turetsky *et al.* 2011; Heijmans *et al.* 2013).

Conclusions

In this study, we have combined plant macrofossil and testate amoeba data to provide new insights into the dynamics of forested peatlands over millennial time scales. The palaeoecological data showed two successional pathways leading to the formation of forested peatlands in the Clay Belt, in eastern Canada. The oldest documented peatland initiated through primary paludification in a wet topographical depression rapidly after land emergence around 8000 cal. a BP. At this site, the trajectory of vegetation succession involves the transformation of a rich treeless fen into a dry black spruce forested bog <400 years after peat inception driven by fast peat build-up. In contrast, the other peatland site, located in a better drained location, has undergone a secondary succession with a gradual conversion of a mesic black spruce forest to a wet forested peatland favoured by a fire that partially consumed the organic layers. Fire rarely occurred in the forested peatlands in the past and these ecosystems have escaped fire for up to several thousand years. However, some local fire events have significantly impacted their ecological and hydrological dynamics. The macrofossil data suggest that black spruce has persisted over the long-term development of the bogs but also show variations in the conifer canopy due to autogenic peat growth, water-table fluctuations and the occurrence of local fires.

Our palaeoecological reconstructions show the complexity of local-scale vegetation and hydrological dynamics in forested peatlands in response to internal and external factors, which could not have been captured using a chronosequence approach. Different successional pathways can occur at the landscape scale even within a single forested peatland depending on site-specific factors such as edaphic conditions, topographical position and local fire history. In forested peatlands, the shifts in water-table levels and bryophyte communities seem to be primarily driven by internal dynamics and stochastic processes such as the removal of conifers by fires and the related decrease in evapotranspiration and increased light availability. More research will be needed to evaluate how variations in conifer density influence the hydrology and the bryophyte cover in forested peatlands in order to better assess the impacts of climate change, fire cycle and logging on the future dynamics of these ecosystems.

This study brings new understanding on natural disturbance and vegetation dynamics in boreal forested peatlands. These results can help in improving ecosystem-based management strategies that aim at reducing the gap between managed and natural forests to maintain their biodiversity and ecological functions. Furthermore, improved knowl-

edge of the resilience and vulnerability of forested peatlands may improve our ability to predict their response to future changes in climate and fire regime.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at <http://www.boreas.dk>.

Fig. S1. Topographical position of the two long peat cores presented in this study (black rectangles) along the transects studied by Le Stum-Boivin *et al.* (in press).

Fig. S2. Testate amoebae diagram of Villebois core showing the relative abundance (%) of all taxa identified.

Fig. S3. Testate amoebae diagram of Lili core showing the relative abundance (%) of all taxa identified.