

1 **Recent Vegetation Dynamics and Hydrological Changes in Bogs Located in an**
2 **Agricultural Landscape**

3 Stéphanie Pellerin^{1*}, Martin Lavoie², Arnaud Boucheny¹, Marie Larocque^{3,4}, Michelle
4 Garneau^{4,5,6}

5 ¹ Institut de recherche en biologie végétale, Université de Montréal and Jardin botanique de
6 Montréal, Montréal, Qc, Canada.

7 ² Département de géographie and Centre d'études nordiques, Université Laval, Québec, Qc,
8 Canada

9 ³ Département des sciences de la Terre et de l'atmosphère, Université du Québec à Montréal,
10 Montréal, Qc, Canada

11 ⁴ GEOTOP – Geochemistry and Geodynamics Research Center, Université du Québec à
12 Montréal, Montréal, Qc, Canada

13 ⁵ Département de géographie, Université du Québec à Montréal, Montréal, Qc, Canada

14 ⁶ Chair on Peatland Ecosystems Dynamics and Climatic Change, Université du Québec à
15 Montréal, Montréal, Qc, Canada

16

17 *Corresponding author:

18 e-mail: stephanie.pellerin.1@umontreal.ca

19 phone: 514-872-2829

20 fax: 514-343-2288

21

22 **Abstract**

23 This study aims to reconstruct the recent dynamics of two bogs located in an agricultural
24 landscape and to determine which factors favour tree expansion, the most salient change recently
25 reported in treeless peatlands. The vegetation and hydrological dynamics of the bogs as well as
26 land use changes in the vicinity were reconstructed using a combination of paleoecological,
27 paleohydrological, and historical approaches. It was hypothesized that upland deforestation
28 indirectly induced atmospheric mineral dust deposition on sites, thus increasing nutrient
29 availability and triggering forest expansion. Results indicated that a widespread, but
30 asynchronous tree expansion occurred in both bogs during the 20th century. However, no
31 evidence suggesting that nutrient enrichment favoured the phenomenon was found. Forest
32 expansion seems rather to have been favoured by drying of the peat surface, as a decrease of the
33 water table depth coincided with the beginning of the forest encroachment on both sites. This
34 drying correlated with the establishment of an *in situ* artificial drainage ditch on one site and with
35 agricultural development in the catchment of the other. Local historical factors of each site
36 apparently override regional factors such as climate anomalies or upland deforestation in
37 explaining rapid, abrupt changes in bogs.

38 **Keywords** Human disturbance, Peatland, Plant macrofossil, Testate amoebae, Tree
39 encroachment, Vegetation shift

40

41 **Introduction**

42 Peatlands are wetlands formed through the accumulation of partially decayed organic material
43 (peat); they represent 50–70% of global wetland resources (Chapman et al. 2003). These
44 ecosystems are important for biodiversity conservation, climate regulation and human welfare.
45 For instance, owing to their peat accumulation processes, peatlands play an important role in the
46 global carbon (C) cycle, having accumulated approximately 600 GtC during the Holocene (Yu et
47 al. 2010). They also store fresh water and help regulate regional hydrologic fluxes (e.g., Levison
48 et al. 2014). Furthermore, they support specialized flora adapted to harsh prevailing conditions,
49 notably acidic and water logged soils. In temperate regions, their flora contrasts sharply with
50 surrounding environments and contributes to increased regional diversity (Ingerpuu et al. 2001).
51 The maintenance of the above functions and services is nevertheless threatened when peatland
52 plant communities are altered. With intensification of the human footprint on these ecosystems,
53 it becomes crucial to better understand the factors driving their compositional and structural
54 changes through time, in order to better protect them.

55 Increases in woody plant cover and density on historically treeless or sparsely treed sites is one
56 of the most drastic changes recently reported in ombrotrophic peatlands (bogs) of northern
57 Europe (Freléchoux et al. 2000; Linderholm and Lein 2004; Kapfer et al. 2011) and North
58 America (Pellerin and Lavoie 2003; Berg et al. 2009; Talbot et al. 2010; Ireland and Booth 2012;
59 Pasquet et al. 2015). Although the progression of bog communities from *Sphagnum* to tree
60 dominated has been considered as a natural stage of wetland succession (e.g., Mitsch and
61 Gosselink 1986), the results of recent studies indicate that direct and indirect anthropogenic
62 disturbances favour the current phenomenon. Indeed, human-induced drainage, eutrophication,
63 fire and contemporary climate change (warmer and/or drier climatic conditions) are the main

64 factors usually pinpointed to explain the present-day woody encroachment in bogs, through their
65 influence on water and nutrient availability (e.g., Frankl and Schmeidl 2000; Linderholm and
66 Leine 2004; Pellerin and Lavoie 2003; Berg et al. 2009; Pasquet et al. 2015). For example, using
67 paleoecological techniques, Ireland and Booth (2012) have shown that the shift from *Sphagnum*
68 to white pine (*Pinus strobus*) dominance on a floating kettle peatland in north-western
69 Pennsylvania (USA) coincided with enhanced nutrient availability due to an increase of mineral
70 dust deposition that concurred with upland deforestation by European settlers (ca. 1900). Using
71 similar techniques, Pellerin and Lavoie (2003) attributed the recent (20th century) tree expansion
72 (*Pinus banksiana* and *Picea mariana*) in bogs of southeastern Québec (Canada) to the impact of
73 combined fire and drainage disturbances associated with short dry climatic periods. In Europe,
74 the recent pinewood development on bogs in the Jura Mountains has also been linked to artificial
75 drainage and peat cutting (Freléchoux et al. 2000).

76 The aims of this study were 1) to reconstruct the recent dynamics of two bog zones located in a
77 large wetland complex in southern Québec (Canada), and 2) to determine which factors
78 influenced tree expansion on those sites. The vegetation and hydrological dynamics of the bogs
79 were reconstructed using a combination of paleoecological, paleohydrological, and historical
80 approaches. As the study sites are located in protected areas, and in accordance with Ireland and
81 Booth (2012), it is hypothesized that upland deforestation indirectly induced peat sediment
82 enrichment through an increase of atmospheric mineral dust deposition rich in nitrogen and
83 phosphorous, triggering forest expansion on the sites.

84

85 **Methods**

86 Study Area

87 The Lanoraie Wetland Complex is located 40 km northeast of Montréal, on the north shore of the
88 St. Lawrence River, southern Québec (Canada), and covers an area of 76 km² (Fig. 1). Inherited
89 from the St. Lawrence River paleochannels, the complex lies over low-permeability clayey silts
90 of the Champlain Sea and is bordered by deltaic terrace sands (Rosa and Larocque 2008).
91 Organic accumulation began around 7400 cal BP (Comtois, 1982), and peat thickness ranges
92 between 0.3 and 8.4 m (Rosa et al. 2009; Tousignant et al. 2010). The complex is mainly
93 composed of forested fens dominated by *Acer rubrum*, *Alnus incana* subsp. *rugosa* and *Ilex*
94 *verticillata*. Scattered areas of bogs are also present, and dominated by *Picea mariana*, *Larix*
95 *laricina*, ericaceous shrubs (mostly *Chamaedaphne calyculata*, *Kalmia angustifolia*,
96 *Rhododendron groenlandicum* and *Vaccinium angustifolium*) and *Sphagnum* mosses (mostly
97 *S. capillifolium*, *S. fallax* and *S. magellanicum*). Swamps and riparian marshes occur along the
98 four rivers that run through the complex (Fig. 1). The complex is part of a vast hydrosystem
99 composed of five catchment areas where surface water and groundwater are intensively used for
100 drinking water purposes and irrigation (Bourgault et al. 2014).
101 European settlement in the region began around 1630 (Morneau et al. 2012). However, the
102 region remained sparsely populated until 1850, when agricultural activities began to increase.
103 Land clearance peaked around 1940-50 with the mechanization of drainage and agricultural
104 practices, and during this period, summer aeolian erosion events were frequent (Morneau et al.
105 2012). Today, less than 10% of the lands surrounding the complex are forested. The region has a
106 strong agricultural vocation with approximately 85% of the territory used for agriculture, mainly
107 fruit and vegetable production.

108 The lands surrounding the wetland complex have been transformed by human activities, and the
109 complex itself has also been highly disturbed, mainly in the forested swamps at its margins.
110 Since the beginning of European settlement, the complex has been used for wood gathering,
111 especially *Thuja occidentalis* trees, which were used for posts and fences (Tousignant et al.
112 2010). Over the last 100 years, approximately 28% of the complex's area has been converted to
113 agricultural use or housing (Tardy and Pellerin 2006). Moreover, it is now partitioned by several
114 roads, highways, railroads and power line rights-of-way, while about 200 irrigation reservoirs
115 and drainage ditches have been built in and around it. According to a recent study of its present-
116 day vegetation patterns (Tousignant et al. 2010), anthropogenic disturbances (agriculture,
117 drainage, logging, transportation infrastructures) had detrimental effects on the richness of
118 bryophyte and peatland species (i.e., species that occur always, preferably or frequently in
119 peatlands), but favoured grasses as well as non-peatland and exotic species diversity. In 1994,
120 approximately 4 km² were set aside to ensure long-term protection, with the creation of the
121 Tourbières-de-Lanoraie Ecological Reserve by the Government of Québec (Fig. 1). Additional
122 areas have been protected since then by a local non-governmental conservation organization
123 (Fig. 1).

124 The regional climate is temperate and continental. The mean annual air temperature (1915–2010)
125 at the nearest meteorological station (Joliette; 15 km) is 5.5 °C, and varies from a minimum of
126 3.2 °C in 1926 to a maximum of 7.9 in 2010 (see Online resource 1 for complete climatic data).
127 Mean annual precipitation is about 910 mm (20% of which falls as snow), and varies from a
128 minimum of 567 mm (1953) to a maximum of 1346 mm (1981). The mean annual potential
129 evapotranspiration is 588 mm and varies from 528 mm (1926) to 642 mm (2010). Mean
130 temperature, total precipitation and potential evapotranspiration time series show a statistically

131 significant increase trend (Mann-Kendall test; $p < 0.001$).

132 Coring Sites and Peat Extraction

133 In 2010, two 1-meter long cores were collected using a Box corer ($100 \times 8 \times 8$ cm; Jeglum et al.
134 1992) in two protected ombrotrophic sectors of the complex (Fig. 1). Both cores were extracted
135 from a small hollow in a *Sphagnum*-dominated environment surrounded by a dense cover of
136 ericaceous shrubs and a semi-open forest canopy of *Larix laricina* and *Picea mariana*. Following
137 extraction, the sediments were wrapped in cellophane and aluminium foil for transport to the
138 laboratory, where they were stored at 4°C until analysis.

139 The Ecological Reserve coring site (ER; $45^{\circ}59'26.5''\text{N}$, $73^{\circ}18'00''\text{W}$) is located in the Point-du-
140 Jour River catchment near the junction with the St. Joseph River catchment, and about 240 m
141 south of a railway constructed between 1847 and 1850, and abandoned in 1894. A large
142 (~ 1.5 m), deep (~ 2 m) artificial drainage ditch was dug in the southwestern part of the sector
143 (about 1000 m from the coring site) at the end of the 1960s (Fig. 1). The St. Jean coring site (SJ)
144 is located in the headwaters of the St. Jean River catchment ($45^{\circ}59'46.6''\text{N}$, $73^{\circ}13'22.8''\text{W}$), and
145 about 30 m from an unpaved road and a large (~ 1.5 m), deep (~ 2 m) artificial drainage ditch dug
146 in the 1980s (Fig. 1).

147 Chronology

148 For each core, one sample (consisting of a few mg dry weight of bulk sediments) from 46 cm
149 (ER site) and 50 cm (SJ site) was submitted for accelerator mass spectrometry (AMS)
150 radiocarbon dating (Table 1). One sample was pre-treated and prepared at Laval University's
151 ^{14}C Laboratory and dated at the Keck-Carbon Cycle AMS facility (University of California,
152 Irvine). The other sample was dated at the Beta Analytic laboratory (Florida). The two

153 radiocarbon dates (^{14}C yr BP) were calibrated (cal yr BC/AD) using the CALIB 6.0.1 program
154 (Stuiver and Reimer 1993) and the INTCAL09 dataset (Reimer et al. 2009). Calibrated dates
155 were rounded to the nearest 10 years using a 2-sigma cal age range. A ^{210}Pb chronology was also
156 obtained for each core at 4 cm-intervals from the surface to 50 cm downcore. Measurements
157 were performed on an alpha-spectrometer at GEOTOP Research Center (Université du Québec à
158 Montréal, Montréal). For each level, a dry 0.5 g subsample was analyzed for ^{210}Pb activity after
159 spiking with a ^{209}Po yield tracer. The constant rate of supply model was applied to calculate age
160 (Appleby and Oldfield 1978; Appleby 2004). Results are presented in calibrated years (years
161 AD; Table 2).

162 Macrofossil Analysis

163 First, both cores were cleaned and cut into contiguous 1-cm thick slices. Since the aim of our
164 study was to reconstruct vegetation changes following the onset of anthropogenic activities in
165 the vicinity of the wetland complex, analyses and results described in this paper are restricted to
166 the upper 50 cm of each core (data and results from 50 to 100 cm are available in Boucheny
167 2014). Intervals of 1 cm were used for macrofossil analysis. For each level, a 20-cm³ subsample
168 was prepared according to Bhiry and Fillion (2001). Macroremains were separated from the
169 organic matrix by boiling the material for about 3 min in a weak 5% KOH solution to induce
170 deflocculation. The material was then wet-screened through a series of sieves of 0.850, 0.425 and
171 0.180 mm mesh. The percentage of volume occupied by each of the different botanical groups
172 (wood remains, roots and rootlets, herbaceous plants, brown mosses, *Sphagnum*, ericaceous
173 plants) was first estimated. Then, remains of vascular plants were picked out, identified and
174 counted using a stereomicroscope at 4 to 40× magnification (results were expressed in number of
175 macrofossils per 20 cm³ of sediments).

176 Testate Amoebae Analysis and Water Table Level Reconstruction

177 Subsamples of 2 cm³ were taken for testate amoebae analysis at 2 cm-intervals. Standard
178 methods were used to isolate testate amoebae from the organic matter (Hendon and Charman
179 1997; Charman et al. 2000; Booth et al. 2010). Subsamples were boiled in distilled water
180 (10 min) and then screened through a series of sieves with 0.350 and 0.150 mm mesh. Residual
181 material was stained, mounted on glass slides and analyzed under a microscope
182 (400× magnification). For each level, at least 150 tests (shells) were identified and counted
183 (Payne and Mitchell, 2009). Test identification was performed using the Charman et al. (2000)
184 identification key with the modifications suggested by Booth and Sullivan (2007). The relative
185 abundance of each taxon was calculated as a percentage of the total count. Past water table
186 depths (cm) were inferred using a transfer function developed by Lamarre et al. (2013).
187 Diagrams were built with the most abundant observed species throughout both cores.

188 Organic Matter, Nitrogen and Phosphorus Analyses

189 Subsamples (2 cm³) were taken from both cores at regular intervals (2 cm) and analyzed for
190 percent-weight organic matter by loss-on-ignition (550 °C; Heiri et al. 2001). To measure
191 nitrogen (N) and phosphorus (P) contents, supplemental subsamples of 1- cm³ were collected.
192 Subsamples were subjected to a wet digestion procedure based on the method developed by
193 Parkinson and Allen (1975). Total N concentrations were quantified using flow injection analysis
194 (FIA QuikChem4000, Lachat Instruments Division, Milwaukee, USA), and total P with an
195 inductively coupled plasma optimal emission spectrometer (Optima 4300 DV ICP, PerkinElmer
196 Instruments, Norwalk, USA). Analyses were performed at Laval University's *Laboratoire de*
197 *pédologie forestière*.

198 Aerial Photograph Analyses

199 To assess recent tree encroachment history on the two studied bogs, we used grey-scale aerial
200 photographs from 1933, 1964, 1979, 1997 and 2012. Aerial photographs were selected based on
201 cloud-free conditions and absence of distortion. All photos were digitized and georeferenced
202 using QGIS (QGIS, Open Source Geospatial Foundation Project, Beaverton, OR, USA). Sectors
203 surrounding the coring point that showed no obvious signs of extensive tree cutting since 1933
204 were first delineated (ER: 67.5 ha; SJ: 250 ha). Forested areas in these sectors were then
205 manually delineated on each aerial photo based on colour, brightness, contrast and texture.
206 Forested areas roughly correspond to those with more than 35% coverage of tall trees (>2 m;
207 S. Pellerin, unpublished data). Automatic methods, such as thresholding, were not suitable due to
208 high variability in the background colour of the photos (especially with the oldest photos). Visual
209 interpretation of vegetation structure was confirmed by stereoscopic viewing of all aerial
210 photographs.

211 The perimeters of disturbed surfaces (agricultural lands, tree cutting areas, roads, etc.) and
212 drainage ditches located within or bordering the peatlands were then digitized on each
213 georeferenced photograph. The percentage of disturbed surfaces and ditch density (m/ha) within
214 a radius of 500 m from each coring site were then calculated.

215 **Results**

216 Vegetation History and Human Disturbances

217 For the ER site, a radiocarbon date of 1860 AD (mid-point age) was obtained at a depth of 46 cm
218 while ^{210}Pb results indicated a date of 1907 AD at 24 cm. For the SJ site, a radiocarbon date of
219 1660 AD (mid-point age) was obtained at a depth of 50 cm while ^{210}Pb results indicated a date of

220 1880 AD at 32 cm (Tables 1 and 2; Fig. 2).

221 In both cores, *Sphagnum* remains were abundant throughout the record, suggesting ombrotrophic
222 conditions (Fig. 2). Remains of ericaceous shrubs (mainly *Chamaedaphne calyculata*, *Kalmia*
223 *angustifolia* and *Rhododendron groenlandicum*; data not shown) increased in abundance towards
224 the top of both cores, with a similar pattern for *Larix laricina* needles in the SJ core and brown
225 mosses (mainly *Polytrichum strictum*) in the ER core. The percentage of volume occupied by
226 roots and rootlets (mainly monocots roots) was quite high at the bottom of the ER core. This
227 section of the core corresponds to the fen/bog transition (see Boucheny 2014 for complete
228 macrofossil results). In the ER, the percentage of volume occupied by roots and rootlets (mainly
229 dycots roots) peaked between 24 and 16 cm and between 10 and 8 cm. These peaks likely
230 correspond to the rooting zones of present-day shrubs and trees and to those that established at
231 the beginning of the 1990s.

232 The increase of shrub (both sites) and tree (SJ) remains concurred with the increase of tree cover
233 (according to aerial photograph analyses) on both sites (Fig. 2). Widespread forest expansion has
234 indeed occurred in both sectors since 1933 (Fig. 3). In the ER sector, the percentage of the area
235 occupied by forest increased from 4 to 45% between 1933 (year of the older aerial photograph)
236 and 2012 (the most recent photograph), which represents an overall gain of 27 ha of forest
237 habitat. The tree cover increase accelerated after 1979. During the same time period, disturbed
238 areas have increased from 10 to 30%, and artificial drainage density from 4.3 to 6.3 m/ha (Fig.
239 2). In the SJ sector, the percentage of the area occupied by forest increased from 44 to 95%
240 between 1933 and 2012, representing an overall gain of 143 ha of forest habitat (Fig. 3).
241 Disturbed areas have increased from 32 to 71%, and artificial drainage density from 7.8 to 9.0
242 m/ha (Fig 2).

243 Inferred Water Table Depths

244 Testate amoebae were identified throughout both cores (Fig. 4). As living tests were found in the
245 uppermost 10 cm, their assemblages have not been interpreted as a record of past hydrological
246 changes.

247 At ER, a gradual rise of the water table from 29 cm (ca. 1840 at 50 cm depth) to 13 cm (ca. 1900
248 at 28 cm depth) was inferred with the decline of *Hyalosphenia subflava* and *Cyclopyxis*
249 *arcelloides*. This was followed by a relatively stable water table (mean 20 ± 0.8 cm) recorded
250 between 28 and 14 cm depths (ca. 1900 to 1970) and characterized by the co-dominance of
251 *Diffflugia pristis*, *D. pulex*, *Hyalosphenia subflava* and *Nebela militaris*. Finally, a decline of the
252 water table from 21 to 35 cm was registered between 14 cm (1970) and 10 cm (1985) depths,
253 associated with the decline of *D. pristis*, *D. pulex* and *N. militaris*, and the increase of *Trinema-*
254 *Corythion*, *Assulina muscorum* and *C. arcelloides*. The mean inferred WTD was 32 ± 3.7 cm
255 during this last period.

256 At SJ, the inferred water table was relatively stable (15 ± 2.8 cm) between 50 and 20 cm depths
257 (ca. 1660 to 1946). This period is characterized by a high abundance of *Diffflugia pulex*, a species
258 with a wide tolerance to surface wetness level (Lamarre et al. 2013), and other species associated
259 to similar conditions (e.g., *Archerella flavum*, *Cyclopyxis arcelloides*, *Pseudodiffflugia fulva*).
260 This period was followed by a decrease of the water table from 20 to 10 cm depths (1946
261 to 1988) inferred by the abundance of *Hyalosphenia subflava* and the co-occurrence of *Nebela*
262 *militaris*, *Heleopera sylvatica*, *Trigonopsis arcula* and *D. pristis*.

263 Organic Matter, Nitrogen and Phosphorus Contents

264 Organic matter content was high (> 94%) and quite stable along both cores (Fig. 5).

265 Concentrations of peat N ranged from 0.99 to 2.03% (mean: 1.34%) in the ER core and from
266 0.89 to 2.07% (mean: 1.27%) in the SJ core. In the ER core, concentrations of N were lower than
267 the mean, from the top of the core to 37 cm depth (ca. 1880) with the exception of a small
268 increase at 9 cm depth. In the SJ core, concentrations of N were lower than the mean from the
269 top of the core to 17 cm depth (ca. 1970) as well as from 31 to 36 cm depth (ca. 1886 to 1835).
270 In the ER core, P concentrations remained relatively stable from the bottom up to 20 cm (ca.
271 1943) ranging from 0.06 to 0.09% (mean: 0.08%), after which they increased up to the surface
272 (ranging from 0.10 to 0.57%; mean: 0.18%). Concentrations of peat P ranged from 0.04 to 0.08%
273 (mean: 0.06%) in the SJ core and were stable throughout.

274 **Discussion**

275 Disentangling drivers of vegetation changes in peatlands during recent centuries is a challenge,
276 as natural drivers can be confounded with *in situ* and regional anthropogenic factors. A
277 multi-proxy approach, as used in this study, is expected to facilitate the task by making it
278 possible to explore several drivers acting at different temporal and spatial scales (Pellerin and
279 Lavoie 2003; van der Linden and Van Geel 2006; Lamentowicz et al. 2008; Ireland and Booth
280 2012). Overall, the paleoecological and historical analyses showed that tree encroachment on
281 both sites began recently (last 100-50 years) but was not synchronous. This suggests that the
282 factors driving the phenomenon are different at ER and SJ, even though they are situated in
283 proximity to each other (5.7 km). This general result concurs with a previous study conducted in
284 16 bogs of southeastern Québec, that concluded that local historical factors of each site (e.g., fire,
285 drainage) override regional factors (e.g. climate anomalies, upland deforestation) in explaining
286 rapid and abrupt changes (Pellerin and Lavoie 2003).
287 In a recent Pennsylvania study, Ireland and Booth (2012) showed that upland deforestation by

288 European settlers indirectly induced enrichment of organic deposits due to increased deposition
289 of atmospheric mineral dust rich in nitrogen, phosphorus and potassium and likely caused tree
290 encroachment in a kettle peatland. It was hypothesized that a similar phenomenon occurred on
291 the studied sites, as they were both affected by a very low level of direct human disturbances.
292 However, there was no evidence to support this in the present study. Nitrogen content was lower
293 in both sites following the onset of upland deforestation (1850), while phosphorus content
294 remained relatively stable at the SJ site. At the ER site, a sharp increase in phosphorus content
295 was only registered at the top of the core (ca. 1995-2000), i.e., much later than the peak of
296 upland deforestation. This increase is likely related with the conversion of agricultural practices
297 from tobacco to potato in the vicinity of the ER site (Morneau et al. 2012). Phosphorus loss
298 (through runoff or soil aeolian erosion) in areas of potato production is indeed a widespread
299 concern, because potatoes are a high P-demanding crop that uses applied P inefficiently, leading
300 to frequent over-application of P to crop fields (Ruark et al. 2014).

301 Trees or shrubs encroachment in peatlands has often been ascribed to warmer and/or drier
302 climatic periods (e.g., Birks 1975; Pilcher et al. 1995; Berg et al. 2009). Such conditions are
303 known to favor the lowering of the water table and facilitate the survival and growth of trees in
304 waterlogged ecosystems. In SJ, the beginning of the water level drawdown and of the forest
305 expansion (ca 1946) occurred during a period of low annual precipitation and of high potential
306 evapotranspiration (Online resource 1). In ER, the beginning of the water table drawdown
307 (ca. 1970) and of forest expansion (ca. 1979) occurred rather during a period of high annual
308 precipitation and of average level of potential evapotranspiration. Although we cannot rule out
309 that the climate have contributed to enhance tree expansion, the fact that the tree encroachment
310 and water level drawdown were not synchronous on both studied sites despite close proximity,

311 suggest that climate was likely not the main factor initiating the phenomenon. A more detailed
312 climatic analysis combined with tree rings analyses would be needed to evaluate adequately the
313 influence of climate on the observed changes. An alternative explanation for tree encroachment
314 could be related to gradual drying of the peat deposits associated with *in situ* drainage or by the
315 development of agriculture and associated drainage network on mineral soils in the surrounding
316 catchment. Several paleoecological and ecological studies have indeed shown increased tree or
317 shrub density following the establishment of drier conditions induced by artificial drainage (e.g.,
318 Pellerin and Lavoie 2003; Linderholm and Leine 2004; Talbot et al. 2010; Pasquet et al. 2015).
319 The ditch density measured on both study sites of the Lanoraie Wetland Complex is quite low
320 (<10 m/ha), and much lower than the level of 200 m/ha recommended to spur tree growth in
321 bogs (Roy et al. 2000). However, on both study sites, a decrease of the water table depth
322 (inferred from testate amoebae) coincides with the beginning of forest encroachment. At the SJ
323 site, the water table began to decrease around 1946, i.e. three decades before the drainage ditches
324 in the bog were dug (1980s). However, this water level drawdown matches the peak of
325 agricultural activities and ditch digging mechanization in the area (Morneau et al. 2012). This
326 suggests that the main driver of the tree encroachment in this site was the gradual drying of the
327 peatland surface due to a change in the regional hydrology associated with an intensification of
328 modern agricultural activities on adjacent mineral soils. *In situ* ditches and climate
329 warming/drying may have facilitated further tree expansion and eventually impeded the return to
330 previous open *Sphagnum*-dominated state. At the ER site, forest cover expansion (ca. 1979)
331 occurred much later than the peak of agriculture (ca. 1950), but only ca. 15 years after a large,
332 deep artificial drainage ditch was dug in the southwestern part of the sector (Fig. 2). This lag is
333 likely associated to the time needed for a tree to be distinguishable on an aerial photograph

334 following its establishment. Consequently, human-induced drainage likely triggered tree
335 encroachment in the sector, an assertion supported in part by the fact that forest expansion began
336 near the ditch (see Fig 1).

337 **Conclusion**

338 This multi-proxy approach reveals that the recent tree encroachment in the two studied bogs was
339 triggered by a drying of the bog surface likely caused by a combination of both *in situ* and
340 regional anthropogenic drainage. Although climate warming/drying could have contributed to
341 the tree encroachment, its effect does not appear to be dominating. Contrary to the prediction,
342 upland deforestation seems to have had no or little effect on woody encroachment, as no
343 evidence was found of nutrient enrichment concurrent with this transformation of the landscape.
344 Whatever the underlying causes of the forest expansion in the two studied bogs, the phenomenon
345 is expected to cause deleterious effects on the diversity and functioning of these protected sites.
346 For instance, a recent study on the flora of these sites showed that forested bog habitats were
347 characterized by fewer true ombrotrophic species, such as *Sphagnum magellanicum*, *S.*
348 *angustifolium* and *Kalmia angustifolia* and more minerotrophic, non-peatland or exotic species,
349 such as *Calamagrostis canadensis*, *Osmundastrum cinnamomeum*, *Oxalis stricta* and *Solidago*
350 *rugosa*, than open bog sectors (Tousignant et al. 2010). Moreover, the observed plant succession
351 toward a globally more forested system may create conditions that will hamper peat
352 accumulation, notably through the decrease in *Sphagnum* growth under forest cover (Eppinga et
353 al. 2009). Finally, this study shows that the vegetation dynamics of even preserved bogs located
354 in humanized landscapes are sensitive to activities in the surrounding catchments, but that the
355 local history of disturbances seems more influential than the regional setting.

356 **Acknowledgements**

357 Funding for this study was provided by the Fonds de recherche Nature et technologies (Team
358 grant to M. Larocque and S. Pellerin), the Natural Sciences and Engineering Research Council of
359 Canada (Discovery grant to S. Pellerin: RGPIN-2014-05367), the Friends of the Montréal
360 Botanical Garden and the *Ministère du Développement durable, de l'Environnement et de la*
361 *Lutte contre les changements climatiques du Québec*. Our thanks to the Quebec Centre for
362 Biodiversity Science for providing grants to A. Boucheny, as well as E.R. Robert, C. Michaud
363 and H. Asnong for their technical contributions, A. Lamarre for testate amoebae analyses, K.
364 Grislis for English revision and two anonymous reviewers for comments on a previous version of
365 the manuscript.

366 **References**

- 367 Appleby PG (2004) Chronostratigraphic techniques in recent sediments. In: Last WM, Smol JP
368 (eds.) Tracking environmental change using lake sediments. Basin analysis, coring, and
369 chronological techniques, vol. 1. Kluwer Academic Publishers, Dordrecht, pp 171-203.
- 370 Appleby PG, Oldfield F (1978) The calculation of lead-210 dates assuming a constant rate of
371 supply of unsupported ^{210}Pb to the sediment. *Catena* 5: 1-8. doi: 10.1016/S0341-
372 8162(78)80002-2
- 373 Berg EE, McDonnell Hillman K, Dial R, DeRuwe A (2009) Recent woody invasion of wetlands
374 on the Kenai Peninsula Lowlands, south-central Alaska: a major regime shift after 18 000
375 years of wet *Sphagnum*-sedge peat recruitment. *Canadian Journal of Forest Research* 39:
376 2033-2046. doi: 10.1139/X09-121
- 377 Bhiry N, Filion L (2001) Analyse des macrorestes végétaux. In: Payette S, Rochefort L (eds.)
378 *Écologie des tourbières du Québec-Labrador*, Presses de l'Université Laval, Sainte-Foy, pp
379 259-273.

380 Birks HH (1975) Studies in the vegetational history of Scotland. IV. Pine stumps in Scottish
381 blanket peats. *Philosophical Transactions of the Royal Society of London* 270: 181–226.

382 Booth RK, Lamentowicz M, Charman DJ (2010). Preparation and analysis of testate amoebae in
383 peatland palaeoenvironmental studies. *Mires and Peat* 7: Article 02, 1-7.

384 Booth RK, Sullivan M (2007). Key of testate amoebae inhabiting *Sphagnum*-dominated
385 peatlands with an emphasis on taxa preserved in Holocene sediments. Lehigh University,
386 Bethlehem.

387 Boucheny A (2014) Dynamique végétale récente du complexe tourbeux des Tourbières-de-
388 Lanoraie (Québec). Dissertation, Université de Montréal.

389 Bourgault MA, Larocque M, Roy M (2014) Simulation of aquifer-peatland-river interactions
390 under climate change. *Hydrology Research* 45: 425-440. doi:10.2166/nh.2013.228

391 Charman DJ, Hendon D, Woodland WA (2000) The identification of testate amoebae (Protozoa:
392 Rhizopoda) in peats. Technical Guide No. 9, Quaternary Research Association.

393 Chapman S, Buttler A, Francez A, Laggoun-Defarge F, Vasander H, Schloter M, Combe J,
394 Grosvernier P, Harms H, Epron D, Gilbert D, Mitchell E (2003) Exploitation of northern
395 peatlands and biodiversity maintenance: a conflict between economy and ecology. *Frontiers in*
396 *Ecology and the Environment* 1: 525-532. doi: 10.2307/3868163

397 Comtois P (1982) Histoire holocène du climat et de la végétation à Lanoraie (Québec). *Canadian*
398 *Journal of Earth Sciences* 19: 1938-1952. doi: 10.1139/e82-172

399 Eppinga MB, De Ruiter PC, Wassen MJ, Rietkerk M (2009) Nutrients and hydrology indicate
400 the driving mechanisms of peatland surface patterning. *The American Naturalist* 173: 803-
401 818. doi: 10.1086/598487.

402 Frankl R, Schmeidl H (2000) Vegetation change in a south German raised bog: ecosystem

403 engineering by plant species, vegetation switch or ecosystem level feedback mechanisms?
404 Flora 195: 267-276.

405 Freléchoux F, Buttler A, Schweingruber FH, Gobat JM (2000) Stand structure, invasion, and
406 growth dynamics of bog pine (*Pinus uncinata* var. *rotundata*) in relation to peat cutting and
407 drainage in the Jura Mountains, Switzerland. Canadian Journal of Forest Research 30: 1114-
408 1126. doi: 10.1139/x00-039

409 Heiri O, Lotter AF, Lemcke G (2001) Loss on ignition as a method for estimating organic and
410 carbonate content in sediments: reproductibility and comparability of results. Journal of
411 Paleolimnology 25: 101-110. doi: 10.1023/A:1008119611481

412 Hendon D, Charman DJ (1997) The preparation of testate amoebae (protozoa: Rhizopoda)
413 samples from peat. The Holocene 7: 199-205. doi: 10.1177/095968369700700207

414 Ingerpuu N, Vellak K, Kukk T, Partel M (2001) Bryophyte and vascular plant species richness in
415 boreo-nemoral moist forests and mires. Biodiversity and Conservation 10: 2153-2166. doi:
416 10.1023/A:1013141609742

417 Ireland AW, Booth RK (2012) Upland deforestation triggered an ecosystem state-shift in a kettle
418 peatland. Journal of Ecology 100: 586-596. doi: 10.1111/j.1365-2745.2012.01961.x

419 Jeglum JK, Rothwell RL, Berry GJ, Smith GKM (1992) A peat sampler for rapid survey.
420 Technical Note, Canadian Forestry Service, Saut-Sainte-Marie.

421 Kapfer J, Grytnes JA, Gunnarsson U, Birks HJB (2011) Fine-scale changes in vegetation
422 composition in a boreal mire over 50 years. Journal of Ecology 99: 1179-1189. doi:
423 10.1111/j.1365-2745.2011.01847.x

424 Lamarre A, Magnan G, Garneau M, Boucher É (2013) A testate amoeba-based transfer function
425 for paleohydrological reconstruction from boreal and subarctic peatlands in northeastern

426 Canada. *Quaternary International* 306: 88-96. doi:10.1016/j.quaint.2013.05.054

427 Lamentowicz M, Milecka K, Gałka M, Cedro A, Pawlyta J, Piotrowska N, Lamentowicz L, Van
428 der Knapp WO (2008) Climate and human induced hydrological change since AD 800 in an
429 ombrotrophic mire in Pomerania (N Poland) tracked by testate amoebae, macro-fossils, pollen
430 and tree rings of pine. *Boreas* 38: 214-229. doi: 10.1111/j.1502-3885.2008.00047.x

431 Levison J, Larocque M, Fournier V, Gagné S, Pellerin S, Ouellet MA (2014) Dynamics of a
432 headwater system and peatland under current conditions and with climate change.
433 *Hydrological Processes* 28: 4808-4822. doi: 10.1002/hyp.9978.

434 Linderholm HW, Leine M (2004) An assessment of twentieth century tree-cover changes on a
435 southern Swedish peatland combining dendrochronology and aerial photograph analysis.
436 *Wetlands* 24: 357-363. doi: 10.1672/0277-5212(2004)024[0357:AAOTCT]2.0.CO;2

437 Mitsch WJ, Gosselink JG (1986) *Wetlands*. Van Nostrand Reinhold. New York.

438 Morneau J, Lanthier P, Brouillette N (2012). *Histoire de Lanaudière*. Presses de l'Université
439 Laval, Québec.

440 Parkinson JA, Allen SE (1975) A wet oxydation procedure for the determination of nitrogen and
441 mineral nutrients in biological material. *Communications in Soil Science and Plant Analysis*
442 6: 1-11. doi: 10.1080/00103627509366539

443 Pasquet S, Pellerin S, Poulin M (2015) Three decades of vegetation changes in peatlands isolated
444 in an agricultural landscape. *Applied Vegetation Science* 18: 220-229. doi:
445 10.1111/avsc.12142

446 Payne RJ, Mitchell EAD (2009) How many is enough? Determining optimal count totals for
447 ecological and palaeoecological studies of testate amoebae. *Journal of Paleolimnology* 42:
448 483-495. doi: 10.1007/s10933-008-9299-y

449 Pellerin S, Lavoie C (2003) Reconstructing the recent dynamics of mires using a multi-technique
450 approach. *Journal of Ecology* 91: 1008-1021. doi: 10.1046/j.1365-2745.2003.00834.x

451 Pilcher JR, Baillie MGL, Brown DM, McCormac FG, MacSweeney PB, McLawrence AS (1995)
452 Dendrochronology of subfossil pine in the north of Ireland. *Journal of Ecology* 83: 665–671.

453 Reimer PJ, Baillie MGL, Bard E et al (2009) IntCal09 and Marine09 radiocarbon age calibration
454 curves, 0–50,000 years cal BP. *Radiocarbon* 51: 1111-1150.

455 Rosa E, Larocque M (2008) Investigating peat hydrological properties using field and laboratory
456 methods: application to the Lanoraie peatland complex (southern Quebec, Canada).
457 *Hydrological Processes* 22: 1866-1875. doi: 10.1002/hyp.6771

458 Rosa E, Larocque M, Pellerin S, Gagné S, Fournier B (2009) Determining the number of manual
459 measurements required to improve peat thickness estimations by ground penetrating radar.
460 *Earth Surface Processes and Landforms* 34: 377-383. doi: 10.1002/esp.1741

461 Roy V, Plamondon AP, Bernier PY (2000) Draining forested wetland cutovers to improve
462 seedling root zone conditions. *Scandinavian Journal of Forest Research* 15: 58-67. doi:
463 10.1080/02827580050160475

464 Ruark M, Kelling K, Good L (2014) Environmental concerns of phosphorus management in
465 potato production. *American Journal of Potato Research* 91: 132-144. doi: 10.1007/s12230-
466 014-9372-1

467 Stuiver M, Reimer PJ (1993) Extended ¹⁴C database and revised CALIB radiocarbon calibration
468 program. *Radiocarbon* 35: 315-330.

469 Talbot J, Richard PJH, Roulet NT, Booth RK (2010) Assessing long-term hydrological and
470 ecological responses to drainage in a raised bog using paleoecology and a hydrosequence.
471 *Journal of Vegetation Science* 21: 143-156. doi: 10.1111/j.1654-1103.2009.01128.x

472 Tardy G, Pellerin S (2006) Complexe tourbeux du delta de Lanoraie. Délimitation révisée et état
473 de situation. Institut de recherche en biologie végétale, Montréal.

474 Tousignant ME, Pellerin S, Brisson J (2010) The relative impacts of human disturbances on the
475 vegetation of a large wetland complex. *Wetlands* 30: 333-344. doi: 10.1007/s13157-010-
476 0019-9

477 van der Linden M, van Geel B (2006) Late Holocene climate change and human impact recorded
478 in a south Swedish ombrotrophic peat bog. *Palaeogeography, Palaeoclimatology,*
479 *Palaeoecology* 240: 649-667. doi:10.1016/j.palaeo.2006.03.039

480 Yu Z, Loisel J, Brosseau DP, Beilman DW, Hunt SJ (2010) Global peatland dynamics since the
481 last glacial maximum. *Geophysical Research Letters*. doi:10.1029/2010GL043584

482

483 Table 1. Radiocarbon dates of the cores collected from the Lanoraie Wetland Complex.

Site and depth (cm)	Laboratory number	Material dated	¹⁴ C date (years BP)	2 σ age range (years BC/AD)	Mid-point (years BC/AD)
RE-46	UCIAMS-121089 ULA-3937	Peat	135 ± 15	1832 – 1885 AD	1860 AD
SJ-50	UCIAMS-121088 ULA-3936	Peat	125 ± 20	1642 – 1676 AD	1660 AD

484

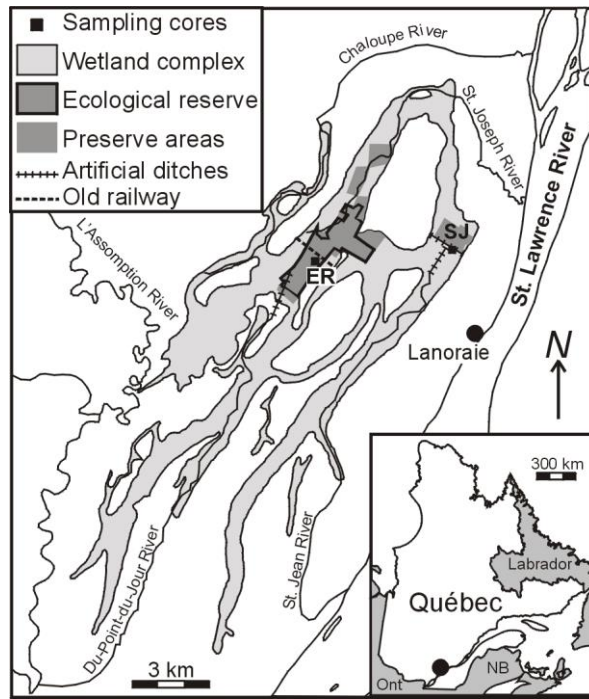
485

486 Table 2. ^{210}Pb concentrations and dates from the upper part of the peat cores collected from the
 487 Lanoraie Wetland Complex.

Site and depth (cm)	Material dated	^{210}Pb concentration (dps/g)	Year AD
RE-0.5	Peat	13.960	2005
RE-4.5	Peat	22.320	2000
RE-8.5	Peat	27.219	1990
RE-12.5	Peat	19.476	1979
RE-16.5	Peat	23.043	1962
RE-20.5	Peat	16.400	1943
RE-24.5	Peat	15.989	1907
SJ-0.5	Peat	14.353	2006
SJ-4.5	Peat	21.885	2001
SJ-8.5	Peat	19.558	1993
SJ-12.5	Peat	21.042	1986
SJ-16.5	Peat	26.921	1970
SJ-20.5	Peat	15.310	1946
SJ-24.5	Peat	10.827	1913
SJ-28.5	Peat	2.033	1892
SJ-32.5	Peat	1.488	1880

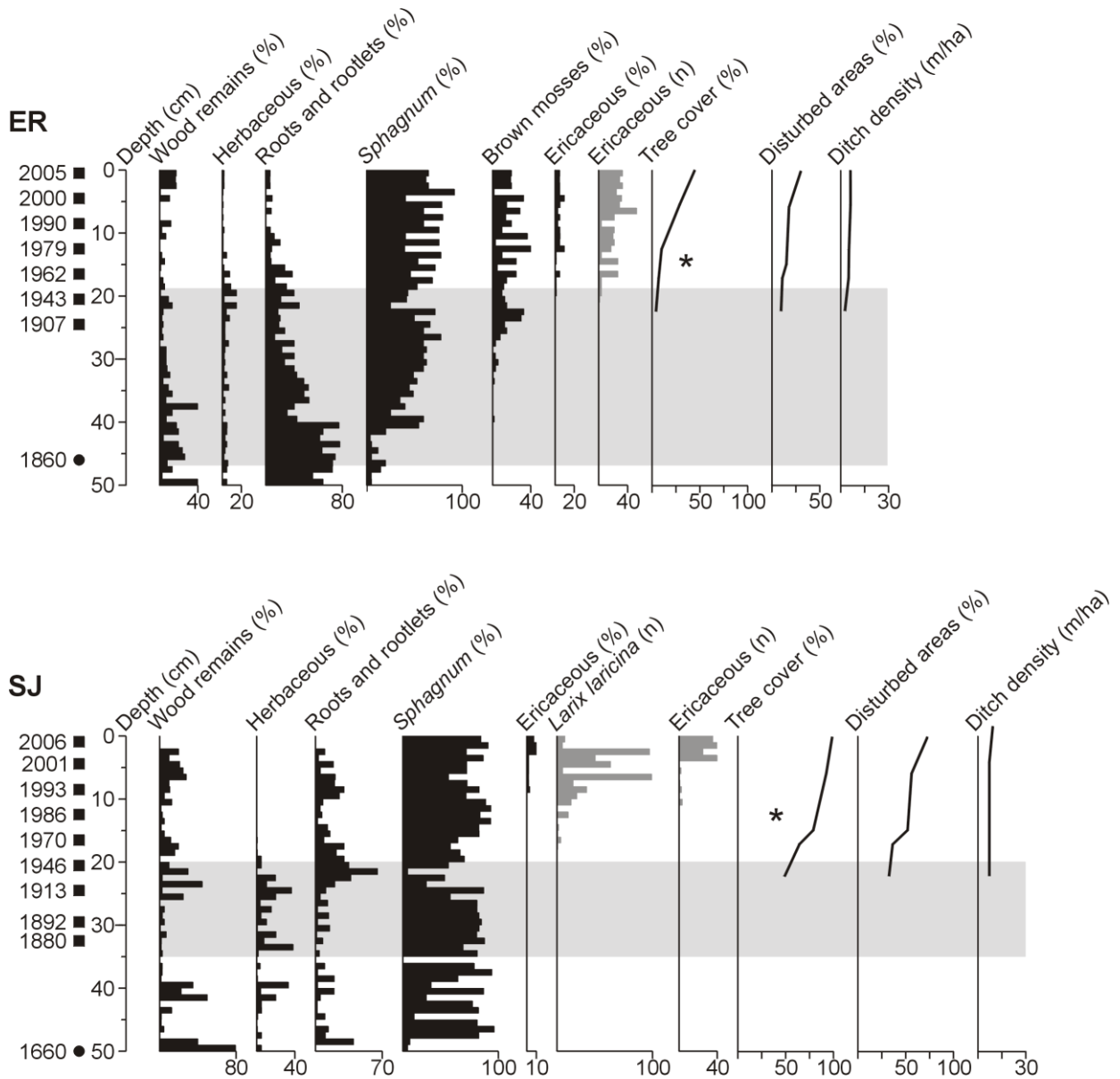
488

489 **Fig. 1** Location of the Lanoraie Wetland Complex (southern Québec, Canada) and of the two
490 coring sites: Ecological Reserve (ER) and St. Jean (SJ).



491

492 **Fig. 2** Macrofossil diagrams (black bars = botanical groups expressed as percentage of organic
 493 matter volume; grey bars = number of vascular plant macrofossils/20 cm³, selected taxa only) for
 494 the Ecological Reserve (ER) and St. Jean (SJ) cores. Grey bands begin at 1850 and end at 1950,
 495 corresponding respectively to the onset of agricultural activities and maximum deforestation in
 496 the area (Morneau et al. 2012). Evolution of the tree cover on the sites according to aerial
 497 photograph analyses is also shown, along with percentage of disturbed areas and ditch density in
 498 a radius of 500 m of the coring point. The asterisks indicate the approximate date when the main
 499 ditches were dug. Chronological data are shown on the left axis (black squares = ²¹⁰Pb; black
 500 circles = ¹⁴C).
 501

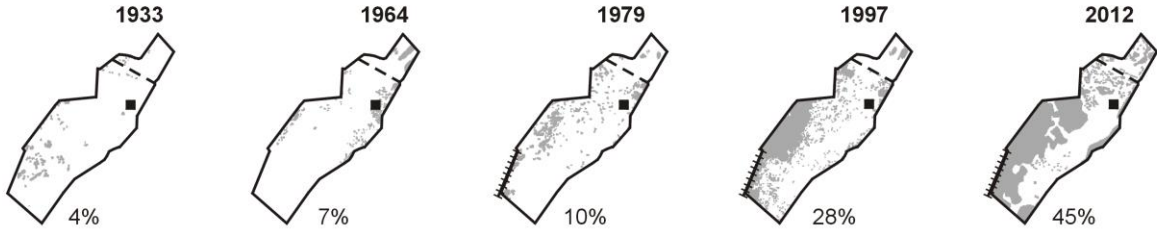


502

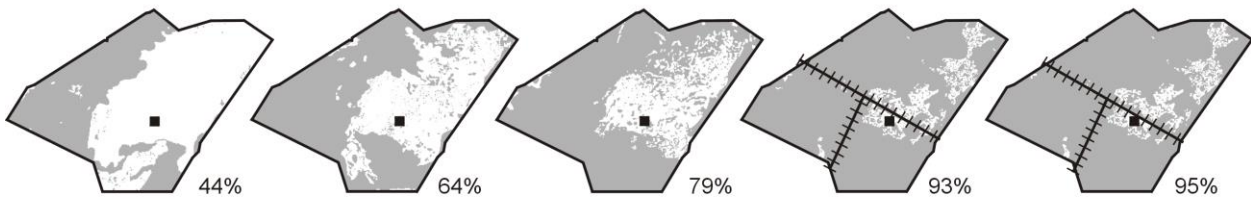
503

504 **Fig 3** Spatiotemporal evolution of the forest cover (grey areas) of the Ecological Reserve (ER)
505 and St. Jean (SJ) sectors of the Lanoraie Wetland Complex (sites are not to scale), reconstructed
506 from aerial photographs. Percentage of the bog area covered by forest is indicated for each year.
507

ER (67.5 ha)



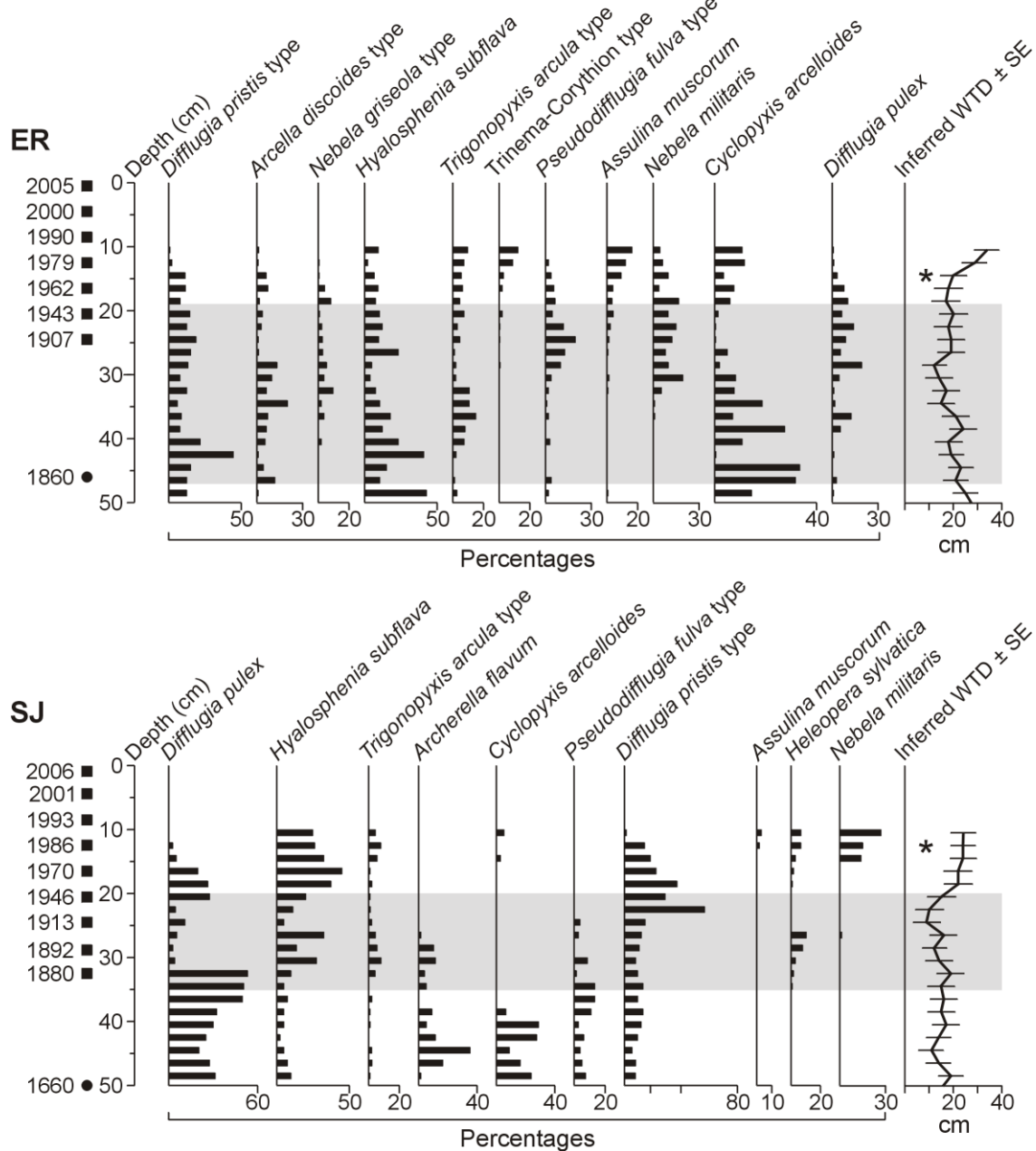
SJ (250 ha)



■ Sampling sites Artificial ditches - - - Old railway

508

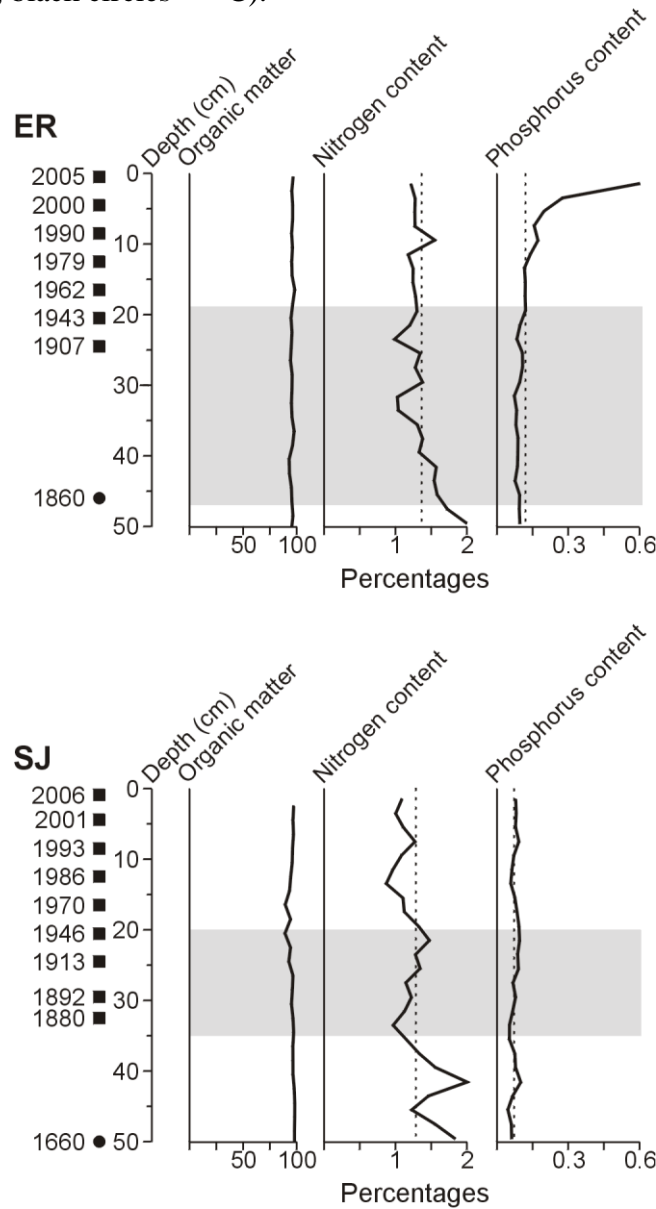
509 **Fig. 4** Testate amoebae diagrams (selected taxa only) and inferred water table depth (WTD \pm
 510 standard error [SE]) for the Ecological Reserve (ER) and St. Jean (SJ) cores. Living tests were
 511 found in the uppermost 10 cm of both cores; their assemblages have thus not been interpreted as
 512 a record of past hydrological changes. Grey bands begin at 1850 and end at 1950, corresponding
 513 respectively to the onset of agricultural activities and maximum deforestation in the area
 514 (Morneau et al. 2012). The asterisks indicate the approximate date when the main ditches were
 515 dug. Chronological data are shown on the left axis (black squares = ^{210}Pb ; black circles = ^{14}C).



516

517

518 **Fig. 5** Changes in organic matter, nitrogen and phosphorus contents (dashed lines = mean level)
 519 through time for the Ecological Reserve (ER) and St. Jean (SJ) cores. Grey bands begin at 1850
 520 and end at 1950, corresponding respectively to the onset of agricultural activities and maximum
 521 deforestation in the area (Morneau et al. 2012). Chronological data are shown on the left axis
 522 (black squares = ^{210}Pb ; black circles = ^{14}C).



523

524

