



Weichselian Lateglacial environmental and vegetation development in the Moervaart palaeolake area (NW Belgium); implications for former human occupation patterns



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ABSTRACT

In this paper, a detailed vegetation and environmental reconstruction for the Lateglacial interstadial in the Moervaart area (NW Belgium) is discussed, in relation to former human occupation patterns. This reconstruction is based on a multi-disciplinary research carried out on calcareous deposits of a large palaeolake (~25 km²). The combination of physical (magnetic susceptibility, micromorphology, organic matter, calcium carbonate), botanical (pollen, macrofossils, diatoms), zoological (chironomids, molluscs, ostracods) and chemical analyses (stable carbon and oxygen isotopes) allowed for a highly detailed reconstruction of the lake ecosystem and vegetation surrounding the lake. The chronology of the lake record was provided by radiocarbon dating and comparison with the nearby Rieme sites and regional biostratigraphy.

During the Bølling phase, the Moervaart palaeolake formed as result of a major rise of the groundwater table in the area. Water level rise continued during the early Allerød phase and a rich water flora and fauna developed in the lake. From this period onwards, the area provided a suitable landscape for the *Federmesser* Culture hunter-gatherers with fresh drinking water, extensive and fertile woodlands and lake edges for wild game hunting, plant gathering and fowling. Water levels rose to a maximum at the end of the early Allerød. Thereafter, an outlet for the lake was formed in the east. As a result, water levels gradually decreased during the middle to late Allerød and eventually the Moervaart lake turned into a swamp and ceased to exist. In combination with the prevailing colder conditions, this led to a marked population decrease with probably temporary abandonment of the region.

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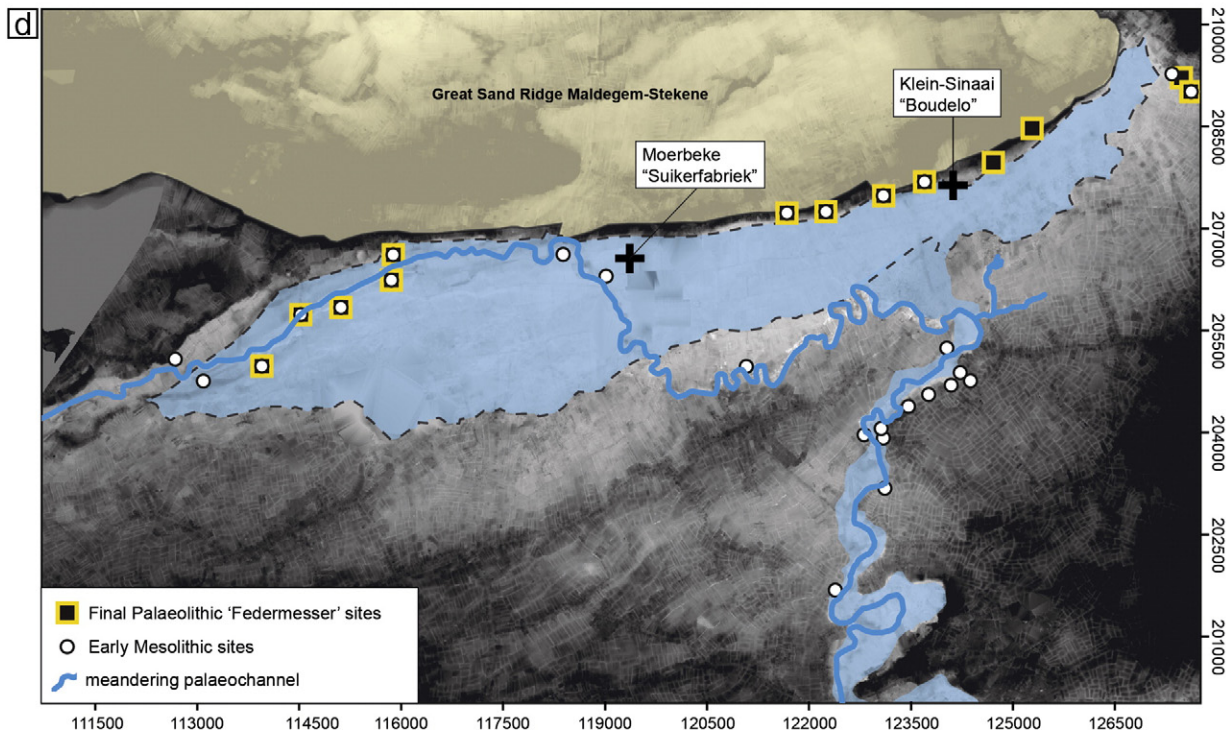
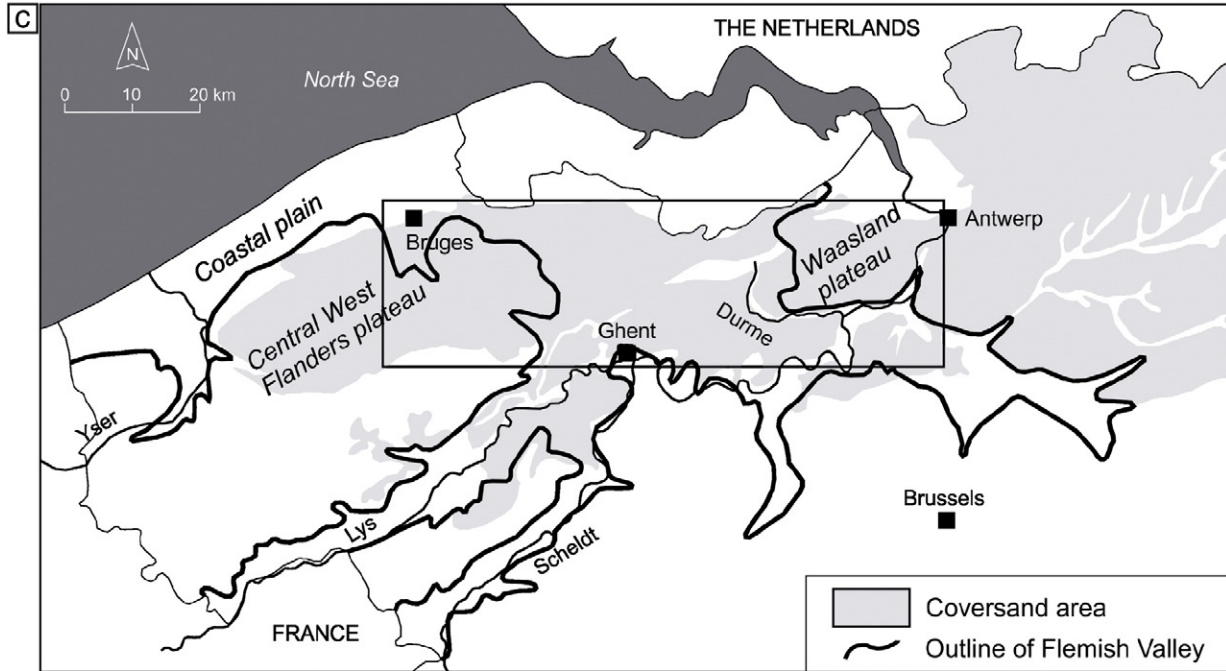
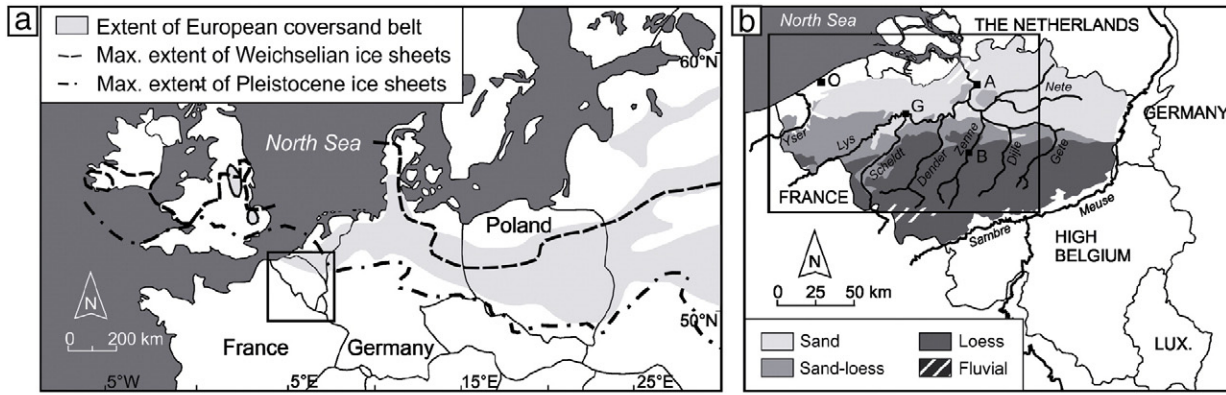
1. Introduction

This paper concentrates on the Moervaart region situated in the sandy lowland of NW Belgium at the southern margin of the Great NW European Plain (Fig. 1a–d). The area is known for its numerous high-resolution and high-quality palaeoenvironmental archives dating to the Lateglacial, Early Holocene and later time-periods (Crombé et

al., 2011). The region has been subject of a multi-disciplinary research project that focused on understanding the geomorphological (Werbrouck et al., 2011; Crombé et al., 2013), hydrological (De Smedt et al., 2011, 2012; Zwertvaegher et al., 2013) and palaeoecological development (Demiddele et al., 2016). Within this project, a trench was excavated providing the investigation of a high-quality lacustrine sediment record from the large palaeolake that existed during the Lateglacial in the centre of the Moervaart depression (Fig. 1d). Recently, results from this multi-disciplinary research project were integrated, showing a direct link between vegetation development and climatic changes that occurred during the Lateglacial period (Bos et al., 2017). In the current paper, we use these data to provide a detailed reconstruction of regional and local vegetation development, as well as lake ecosystem changes.

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The region was densely populated during the Lateglacial and Early Holocene, as indicated by the large number of prehistoric sites, dating from the Lateglacial (Final Palaeolithic, ca. 14,000–13,000 cal BP) and Early Holocene (Mesolithic, ca. 10,700–6500 cal BP) (Fig. 1d). Especially the high density of *Federmesser* Culture sites consisting of temporary campsites along the northern bank of the Moervaart palaeolake is striking (Crombé et al., 2011, 2013, 2014, Fig. 1d). However, evidence of human presence during the colder Younger Dryas stadial and Preboreal is scarce (Crombé et al., 2013; Crombé and Robinson, 2017).

Our aim is to reconstruct the Lateglacial lake ecosystem in relation to changes in climate and the surrounding landscape and to gain insight into the impact of vegetation and environmental changes on past human occupation patterns.

2. Study area

The Moervaart region is characterised by a complex and dynamic palaeolandscapes. The most important features of this region are (Fig. 1d): (1) an extensive coversand ridge, i.e., the Great Coversand Ridge of Maldegem–Stekene (80 km long, locally 3 km wide, height 5–15 m a.s.l., average elevation ca. 3–4 m) (De Moor and Heyse, 1978; Verbruggen et al., 1996; Crombé et al., 2012), including numerous shallow dune-slacks and ponds; (2) a ca. 25 km² large but shallow freshwater inland lake, i.e., the Moervaart palaeolake (length: ~15 km, width: ~2.5 km) immediately south of the Great Coversand Ridge (Heyse, 1979, 1983); and (3) a deep meandering palaeochannel of the Kale (upper course) or Durme (lower course) River, a tributary of the River Scheldt.

3. Material and methods

The multi-disciplinary research was carried out on deposits collected from a trench that was dug across the deepest part of the Moervaart depression (Moerbeke “Suikerfabriek”, Fig. 1d). Detailed sampling information and methodology are discussed in Bos et al. (2017) and given in the Supplementary data. Samples for most proxies were collected from the master sequence, enabling direct comparison between the different proxies. Two complementary sequences, S2 and S4 (visually correlated to the master sequence), retrieved respectively 12 m and 14.5 m north of the master sequence, were sampled for ostracod and mollusc analyses (Fig. 2).

The lithology of the sequence was described in Bos et al. (2017) (Fig. 2). To aid this visual description, magnetic susceptibility (κ) was measured at 2.5 mm intervals. Minerogenic, organic and CaCO₃ contents were measured on samples with a 1 cm resolution. In addition nine samples were collected from the different layers for micromorphological analysis. Stable carbon (¹³C) and oxygen (¹⁸O) isotope analysis was performed on valves of *Candona candida*.

Botanical proxies that were analysed include plant macroremains, microfossils (pollen and spores) and diatoms. Samples for botanical macroremains were collected at selected intervals in relation to AMS ¹⁴C dating. Microfossil samples were collected at 1–5 cm intervals and diatom samples at 2 cm intervals. In addition to these botanical proxies, a number of zoological analyses were performed. These include the study of chironomids, molluscs and ostracods. Fossil remains of chironomid larvae were analysed at a 4–8 cm resolution. Mollusc and ostracod sampling was carried out continuously and each bulk sample matched

one specific stratigraphic unit. Sample preparation of the different proxies is described in detail by Bos et al. (2017) and in the Supplementary data.

Chronology of the record was provided by four radiocarbon dates, obtained from dating seeds and fruits of terrestrial plants (Table 1). Furthermore, the Moervaart regional pollen zones were visually correlated to the Lateglacial regional pollen zonation scheme of the Netherlands and northern Belgium (Hoek, 1997). This provided a chronological framework for the sequence (Fig. 3). These pollen zones also could be correlated to the major Lateglacial climatic events, as identified in the Greenland oxygen isotope records (e.g., Rasmussen et al., 2014; see also Bos et al., 2017). We chose to include the Poaceae in the regional pollen sum based on the absence of local grass indicators in the macrofossil record and comparison with other pollen diagrams from the region. However, it should be noted that, in part of the record, wetland taxa contributed to the Poaceae group (see also Van Asch et al., 2012). In the Supplementary data section a further discussion about the pollen sum used is given.

4. Results and interpretation

The Moervaart sequence covers almost the whole Lateglacial Interstadial, with sediment accumulation starting during the late Pleniglacial. In the section below we will refer to the Lateglacial regional pollen zones (Zone 1a, etc.) as established by Hoek (1997) and to the event stratigraphy used by the INTIMATE group (Pleniglacial GS-2, GI-1, etc.) (Rasmussen et al., 2014). Note that the term *Earliest Dryas* mentioned by Hoek (1997) is not used any more as at present day it is considered part of the later Pleniglacial, while the Lateglacial starts with the Bølling warming phase, corresponding to Greenland Interstadial 1e (Hoek, 2008).

4.1. Zone 1a, Pleniglacial (corresponding to GS-2)

4.1.1. Regional vegetation

The basal sediments of the Moervaart master sequence consist of grey sands (Layer A), deposited during the Pleniglacial. At the end of the cold Pleniglacial, vegetation in the Moervaart region was very open and locally bare ground was present on the sandy soils. Trees were absent and long-distance transport of pollen and surface erosion occurred by wind and water. This resulted in the accumulation of sand along with pollen deposition of wind-pollinated trees (*Pinus*), exotic and thermophilous trees (Fig. 4a). The regional vegetation can be characterised as a steppe-tundra, with some shrubs of juniper (*Juniperus*) and many grasses (Poaceae) and heliophilous herbs (e.g., *Artemisia*, *Saxifraga granulata*, *Plantago*, *Amaranthaceae*, *Helianthemum*, *Botrychium lunaria*, *Fabaceae*, *Apiaceae*, *Brassicaceae* and *Ranunculaceae*).

4.1.2. Vegetation, flora and associated fauna in the palaeolake area

At the end of the Pleniglacial, the flora and fauna with ostracods and gastropods indicate that a wet meadow developed in the Moervaart depression, with shallow pools on a sandy bottom in which sedges (Cyperaceae; see also *Clasterosporium caricinum*, Suppl. Fig. 1c), herbs (Asteraceae, *Thalictrum*, *Carex oederi*, *Equisetum* (see also conductive tissue), *Isoetes*, *Selaginella selaginoides*) and some grasses were growing (Fig. 4a, Suppl. Fig. 1a–d). Algae (*Pediastrum*, *Botryococcus*, HdV-128A/B) were present in shallow pools. *Isoetes* points to nutrient-poor

Fig. 1. a. Extent of the European coversand belt. Belgium is indicated by an open square (left). b. Schematic map of Belgium, showing some of the major rivers and the Pleistocene sedimentation areas in N Belgium. G = Ghent, A = Antwerp, B = Brussels and O = Ostend (right). c. Simplified geomorphological map of Sandy Flanders (Derese et al., 2010). The Moervaart study area is indicated by an open square. d. Topography of the Moervaart study area with the maximum extent of the Moervaart depression on the southern edge of the Great Sand Ridge of Maldegem–Stekene. In the central part of the palaeolake (indicated in light blue), manual auger transects and location of the two trenches (Moerbeke “Suikerfabriek” and Klein-Sinaai “Boudelo”) are given. The reconstructed course of the meandering palaeochannel was based on data from corings, EMI and DEM (Lidar, AGIV 2001–2004). Also the distribution of *Federmesser* sites and Early Mesolithic sites are indicated. Figure adapted after Crombé et al. (2013).

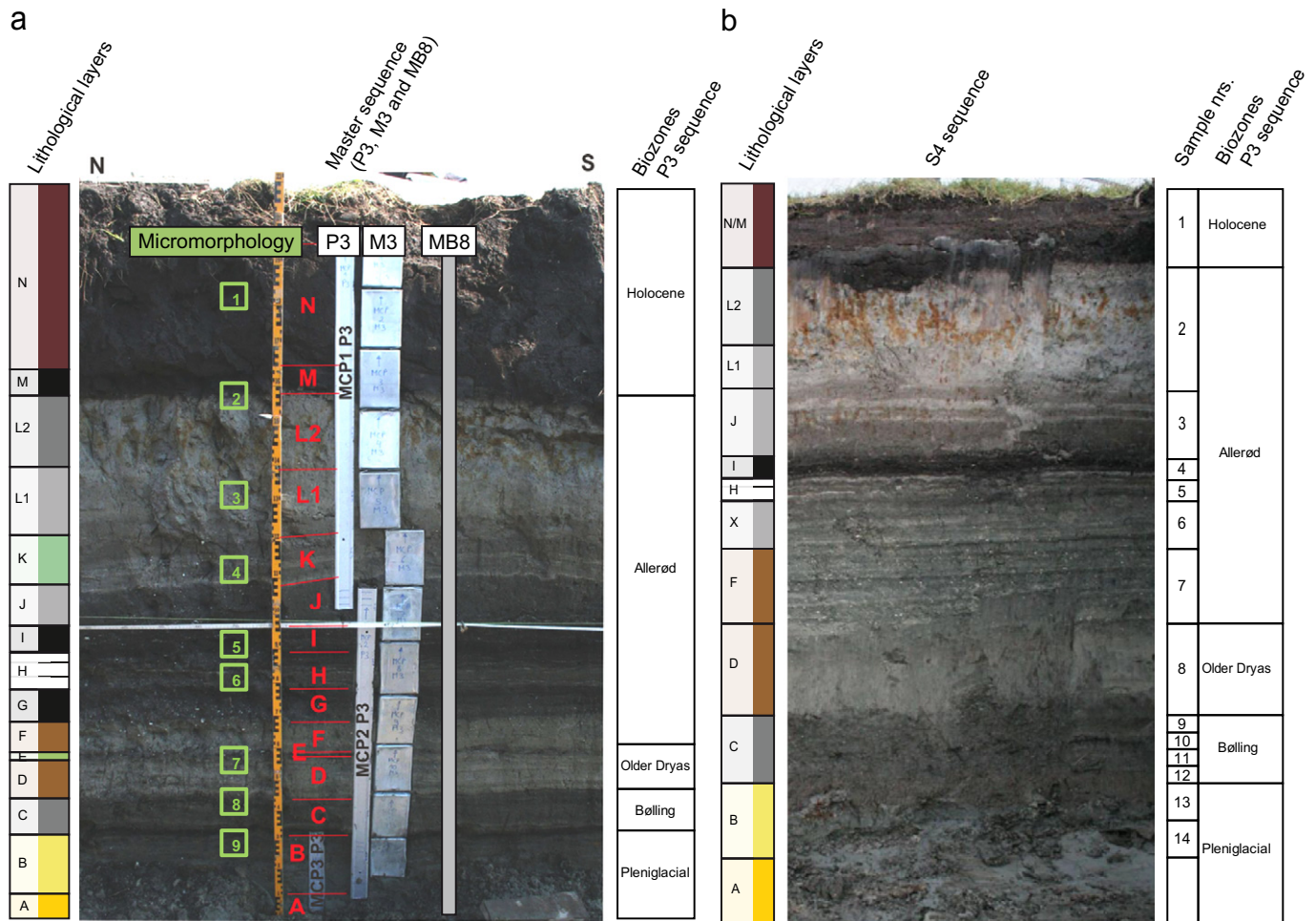


Fig. 2. a. Detail of the sampled layers collected in the Moervaart (P3/M3/MB8) master sequence and micromorphological sampling (green boxes). b. Location of the mollusc and ostracod samples (numbers 1–14) collected from Moervaart S4 sequence and their reference to the lithological Layers A–N in the master sequence. The bottom units 13 and 14 comprise the muddy horizontal trench bottom. Also the biozones based on the pollen data are indicated.

conditions (Van der Meijden, 2005) during the formation of Layer A, indicating the dominance of direct precipitation and absence of lateral groundwater input. Later more calcareous-rich and mesotrophic conditions developed and sandy gyttja was deposited (Layer B). Layers A–B, display the highest magnetic susceptibility.

The ostracod cold-water fauna in the lower Layer B (Fig. 5b) with *Candona candida*, *C. neglecta* and *Tonnacypris tonnensis* in the muddy horizontal trench bottom, suggests a cold and oligotrophic environment (Van der Meeren et al., 2009 and references therein). Ostracod species abundance was low. In the upper Layer B (Figs. 2, 5b) a relatively species-rich community dominated by *Cyclocypris ovum* was established and *C. ovum* and *Cypria ophthalmica* show their highest relative

abundances. Both taxa are very common, *C. ovum* is usually found in the littoral zone of lakes and pools and has a preference for marshy environments (especially reed-belts), while *C. ophthalmica* can occur at all depths (Meisch, 2000).

Also freshwater gastropods (Fig. 5a) were living in the shallow pools. *Gyraulus crista* suggests that these were permanent water bodies. *Gyraulus crista* is followed by *Gyraulus albus* and *Radixa balthica/peregra*, but *G. crista* is the most abundant species in this first phase. *Gyraulus albus* is a pioneer and often appears as one of the first in newly created waters. Furthermore, freshwater bivalves, i.e., *Pisidium milium* and *Pisidium pulchellum* occur. The latter also suggests small and clear water basins (Gittenberger and Janssen, 2004). Diatom shells were

Table 1
AMS ^{14}C dates of the Moervaart master sequence. KIA: Leibniz Labor, Kiel, Germany.

Depth (cm)	Lab. Nr.	Moervaart sample Nr., weight	$\delta^{13}\text{C}$ (‰)	Dated material f. = fruits	Age (^{14}C yr BP)	Age (calendar yr BP)
126.5	KIA-46067	4: 1.03 mg C	-30.49 ± 0.08	<i>Schoenoplectus lacustris</i> f. 14×; <i>Eleocharis palustris</i> f. 1×; <i>Carex</i> cf. <i>rostrata</i> f. 12×	$11,630 \pm 60$	13,550–13,400 (68.3%) 13,580–13,320 (95.4%)
139.5	KIA-46066	3: 1.28 mg C	-19.78 ± 0.10	<i>Schoenoplectus lacustris</i> f. 13×; <i>Carex</i> cf. <i>pseudocyperus</i> f. 1×; <i>Carex</i> cf. <i>rostrata</i> f. 3×; <i>Carex</i> sp. f. 1×	$11,965 \pm 60$	13,940–13,730 (68.3%) 14,020–13,600 (95.4%)
173	KIA-46065	2: 1.69 mg C	-26.19 ± 0.12	<i>Schoenoplectus lacustris</i> f. 9.25×; <i>Carex</i> cf. <i>rostrata</i> f. 12.3×; <i>Lycopus europaeus</i> f. 1×; <i>Potentilla palustris</i> f. 2.5×	$12,240 \pm 60$	14,240–14,040 (68.3%) 14,500–13,950 (95.4%)
186	KIA-46064	1: 1.65 mg C	-25.88 ± 0.13	<i>Schoenoplectus lacustris</i> f. 42×; <i>Carex</i> cf. <i>oederi</i> f. 1×	$12,205 \pm 60$	14,180–14,000 (68.3%) 14,320–13,850 (95.4%)

Age BP	Hoek (1997) Biozones	Bio-stratigraphy	Rieme (Bos et al., 2013)	Moervaart "Suikerfabriek" (this study)	Correlation to event stratigraphy INTIMATE group
11,250	2b	late Allerød			GI-1c
11,500	2a2	middle Allerød			GI-1c
	2a	-----	11,565+/-55	-----	
	2a1	early Allerød	11,625+/-60 11,710+/-55 11,920+/-60	11,630+/-60 11,965+/-60	
11,900					
12,100	1c	Older Dryas	12,110+/-60		GI-1d
			12,205+/-60		
12,450	1b	Bølling		12,240+/-60 12,205+/-60	GI-1e
	1a	Pleniglacial			GS-2

Fig. 3. Uncalibrated ^{14}C dates from the Moervaart master sequence, compared with those from the dune-slacks at Rieme (Bos et al., 2013) and regional biostratigraphy of Hoek (1997). Correlation was made with the event stratigraphy used by the INTIMATE group (Rasmussen et al., 2014).

absent from these basal deposits, while chironomid larvae were scarce and/or badly preserved (Fig. 4b, c).

4.1.3. Human occupation

There is no archaeological evidence for human presence during the late Pleniglacial. The area with open tundra vegetation surrounding the Moervaart depression must have been very unattractive for human occupation. This is fully consistent with other regions in NW Europa, lacking evidence of human activity prior to the Lateglacial.

4.2. Zone 1b, Bølling (corresponding to GI-1e)

4.2.1. Regional vegetation

The increase in shrubs and large amount of heliophilous herbs in the pollen assemblages indicate that during the Bølling a dwarf shrub tundra developed with pioneer herbaceous communities and scattered (dwarf) shrubs of willow (*Salix*), dwarf-birch (*Betula nana*), juniper and sea-buckthorn (*Hippophae rhamnoides*) (Fig. 4a) as a result of climate warming. As a consequence soil formation also could start from this time onward. The large amount of heliophilous herbs recorded in the pollen assemblages suggests that the regional vegetation remained relatively open with locally bare ground on sandy soils. Due to the openness of the landscape, surface erosion by wind and water continued. The dynamic environment and presence of bare, sandy substrates of the coversand areas favoured the germination and growth of juniper and sea buckthorn during the Lateglacial (Hoek, 1997). Both taxa can migrate rapidly as their fruits are spread by birds (Weeda et al., 1987; Bouman et al., 2000). This is reflected by an evident peak in juniper pollen at the start of the Bølling. Sea buckthorn prefers calcareous-rich habitats and can fix free nitrogen from the atmosphere in root nodules (Lotter et al., 2010).

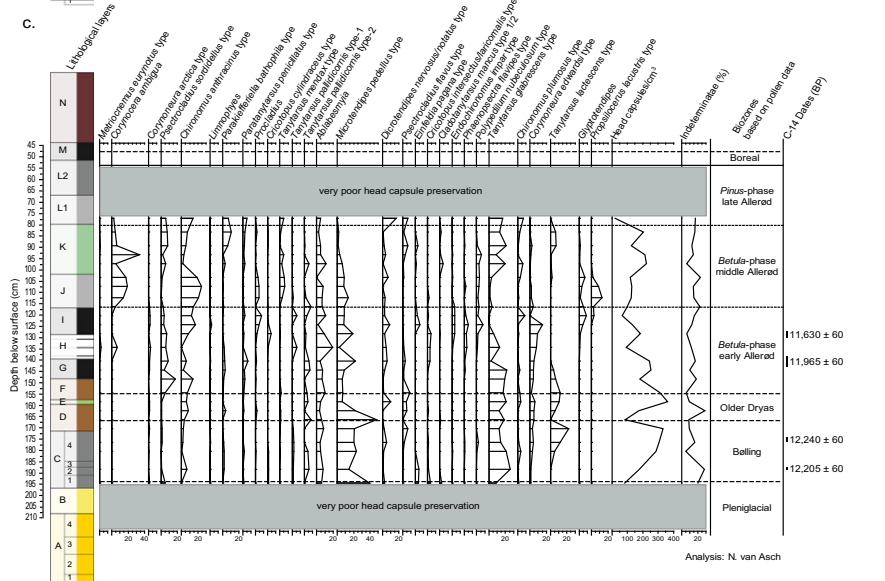
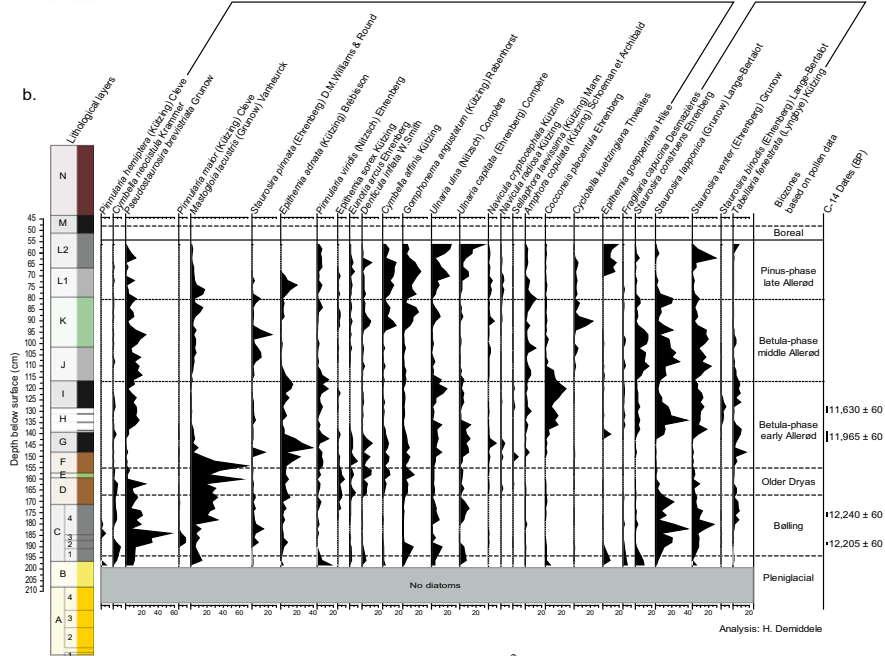
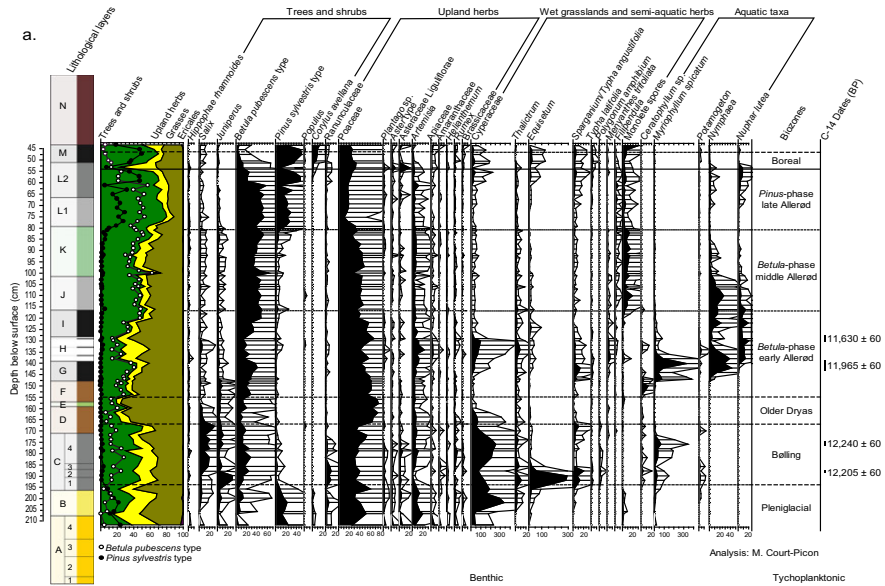
4.2.2. Vegetation, flora and associated fauna in the palaeolake area

Due to climate warming at the start of the Bølling, groundwater inflow to the Moervaart depression probably increased as result of both an increase in effective precipitation and increase in lateral groundwater input from the surrounding sandy ridges (cf. Bohncke, 1993). Melting of surrounding permafrost likely contributed to the groundwater level rise (e.g., Hoek et al., 1999; Hoek and Bohncke, 2002; Bos et al., 2006). This rising groundwater level also resulted in the formation of ponds and dune-slacks on the adjacent Great Sand Ridge of

Maldegem–Stekene at Rieme (Bos et al., 2013) and Wachtebeke (Derese et al., 2010; Crombé et al., 2012). The pollen and macrofossil flora (Fig. 4a and Suppl. Fig. 1a–d) indicate that the vegetation in the Moervaart depression changed from a wet meadow into a shallow lake with swamps along the shores. In this lake, the water table fluctuated throughout the year, with higher groundwater levels during winter and spring. Humic calcareous gyttja with thin peaty lenses was formed (Layer C) and with increasing water depth, lake marls (Layer D). The series of calcareous deposits (Layers C–I) behave entirely diamagnetically, with exception of Layers D and G, where a κ -increase is measured (Fig. 6).

During the Bølling, the increase in botanic taxa in both the pollen and macrofossil record indicates that the vegetation in and around the lake became more diverse. This caused the appearance of a variety of freshwater faunal taxa. A large number of chironomid taxa (*Ablabesmyia*, *Psectrocladius*, *Paratanytarsus*, *Corynoneura*, *Cricotopus*, *Endochironomus*, *Phaenopsectra*, *Polypedilum*, Fig. 4c) and many fresh water gastropods (*Gyraulus crista*, *Radix balthica*, *Lymnaea stagnalis*, *Physa fontinalis*, *Hippeutis complanatus*, *Myxas glutinosa*) and ostracods (*Cyclocypris ovum*) were associated with the increase in aquatic and marsh vegetation (e.g., Hoek et al., 1999; Brooks et al., 2007; Serbruyns, 2010). Aquatic taxa (*Characeae*, *Gloeotrichia*, *Myriophyllum spicatum*, *Ceratophyllum*, *Potamogeton pectinatus*, *Groenlandia densa*, *Ranunculus* subgenus *Batrachium*, *Schoenoplectus lacustris*, *Utricularia vulgaris*) and a large number of algae (*Botryococcus*, *Pediastrum*, *Spirogyra*, *Tetraedon minimum*, *Zygnema* type, HdV-128A/B) developed in the shallow lake. Plants, such as sedges (*Schoenoplectus lacustris*, *Carex rostrata*; *Clasterosporium caricinum*, Suppl. Fig. 1c) and semi-aquatics (*Persicaria amphibium*, *Filipendula*, *Alisma*, *Typha latifolia*, *Equisetum*, *Thalictrum*, *Lycopus europaeus*, *Potentilla palustris*) were growing along the shores. The semi-aquatic and aquatic taxa indicate shallow, mesotrophic and calcareous-rich conditions. The latter is reflected in high CaCO_3 values and presence of calcitic micromass and calcified plant remains in the sediment thin sections (Fig. 7a, b), while the higher organic productivity of the lake is revealed by the elevated LOI values (Fig. 6). Diatom assemblages also suggest a higher trophic lake status at the start of the Bølling (Figs. 4b, 6). The spectrum mentioned above suggests a lake depth of maximal 1 m at the master sampling location (Hannon and Gaillard, 1997).

Gloeotrichia (cyanobacteria) probably played a pioneer role in nutrient (nitrogen-) poor conditions, thanks to its ability to fix nitrogen



and thus making conditions suitable for other aquatic plants (Van Geel et al., 1989). Submerged macrophytes (*Myriophyllum spicatum*, *Ceratophyllum*, *Potamogeton pectinatus*, *Groenlandia densa*) oxygenated the water (Swindells, 1997). Their fast growing ability caused oxygenation levels to increase rapidly, thereby inducing the growth of other macrophytes. The diatom assemblage (Fig. 4b) also suggests oxygenation of the water in a mesotrophic environment (especially during the early Bølling). It consists of species that are predominantly benthic and tychoplanktonic (*Staurosira* and *Staurosirella*, Fig. 4b) taxa that are known to be competitive in shallow, mesotrophic, alkaline and cold environments with possible periods of ice-cover (Lotter and Bigler, 2000).

In the chironomid assemblage, the humic sandy gyttja and peat deposits (Layer C) are dominated by *Microtendipes pedellus* type (~40%), which often occurs in lakes with coarse sediments (Brooks et al., 2007). Other important taxa are *Tanytarsus glabrescens* type and *Tanytarsus lactescens* type, the latter being typical for carbonate lakes (Brooks et al., 2007).

The ostracod assemblage (Layer C, Fig. 5b) with *Cyclocypris ovum* and *Cypridopsis vidua* indicates a well-vegetated, shallow water environment as both species have preference for shallow water bodies with a rich vegetation (Danielopol, 1991; Kiss, 2007). In Layer C, the relatively species-rich community dominated by *Cyclocypris ovum* and *Cypridopsis vidua* slowly disappears and changes towards a *Cypridopsis vidua*-dominated fauna, which could indicate algal mats. This fauna is associated with a marsh environment. The intermediate $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values in combination with a quite large isotopic variability measured in *Candona candida* valves, correspond with the inferred shallow water environment (Figs. 5b, 6).

4.2.3. Human occupation

Despite temperatures rose during the Bølling, there is still no archaeological and botanical evidence for human activities in the Moervaart region. This suggests that the sparsely vegetated landscape was probably still very unattractive for human occupation. The natural resource capacity of the area was probably too low as game, open water and wild edible plants were scarce. In addition, the coversand dunes, which were still in development, were probably not yet suited for settling camp sites (Crombé et al., 2011).

4.3. Zone 1c, Older Dryas (corresponding to GI-1d)

4.3.1. Regional vegetation

During this period, the regional vegetation in the Moervaart area became slightly more open with more bare ground due to a temporary colder and drier climate. Herbaceous communities were present on the sandy soils with typical steppe plants (*Ephedra fragilis*, *Ephedra distachya*, *Artemisia*) and heliophilous herbs (*Helianthemum*, *Gentiana*, *Rumex*, *Asteraceae*, *Caryophyllaceae*, *Amaranthaceae*). The high values of Poaceae and herbs (Fig. 4a) suggest the development of grass-steppe-tundra. Grass communities were present on the coversand ridge, as well as in the low-lying areas around the Moervaart depression. Especially in the lower areas surrounding the Moervaart depression, where swampy conditions prevailed during the Bølling, drier conditions during the Older Dryas led to the expansion of grass vegetation. This can explain the high values of Poaceae pollen in this section of the record. On sandy substrates, *Juniperus* and *Hippophae rhamnoides* remained present. Dwarf shrubs (*Betula nana*, *Salix*) probably inhabited the wetter areas with more organic-rich soils, although dwarf willows also may have been present on coversands. The Great Sand Ridge of

Maldegem–Stekene was probably tree-less and erosion by wind and water occurred especially on the elevated areas. This is indicated by an increase in the magnetic susceptibility in Layers D and E (Fig. 6).

4.3.2. Vegetation, flora and associated fauna in the palaeolake area

During the Older Dryas, a marsh developed in which laminated lake marls (Layers D and F) were deposited. The two layers are separated by a thin humic to peaty marl horizon (Layer E). There is a clear erosive contact between Layers C and D and between Layers D and E, indicating erosion prior to the start of the Older Dryas (and within), resulting from a temporary change to colder climate (Bos et al., 2017).

The aquatic vegetation largely disappeared (Fig. 4a) due to lower water levels as result of a drier climate (Bos et al., 2017). Only submerged specimens of *Ceratophyllum* and Characeae remained present. The presence of abundant Characeae is well documented in the sediment thin sections 7 and 8 (Fig. 7c–d). In the shallow water also algae (e.g., *Botryococcus*, *Pediastrum*, *Spirogyra*, *Tetraedon minimum*, *Zygnema* type, HdV-128A/B) were present, but their values decrease during this period (Suppl. Fig. 1c). The marsh plants (*Typha*, *Equisetum*, *Thalictrum*, *Menyanthes*, Cyperaceae, also indicated by *Clasterosporium caricinum*, Suppl. Fig. 1c) show very low values, equally indicating lower water levels. Along with most macrophytes a number of chironomid, freshwater gastropod and ostracod taxa associated with these plants disappeared or show lower values. In the mollusc assemblage (Fig. 5a), *Gyraulus crista* and *Lymnaea stagnalis* strongly decrease respectively disappear. Although some taxa disappear, the total chironomid abundance (Fig. 4c) increases in the lake marl deposits (Layers E–F). *Microtendipes pedellus* type reaches its highest abundances (of almost 50%) in the early Older Dryas. *Tanytarsus glabrescens* type remains abundant. *Microtendipes* occurs in warmer, low-latitude lakes (Walker et al., 1991), and in the Alps, this taxon is predominantly found in lowland and subalpine lakes (Lotter et al., 1997). The ostracod fauna (Fig. 4b) continues to be dominated by *Cypridopsis vidua*. However, additional taxa appear, including *Cypris pubera* and *Limmocythere inopinata*. The latter is associated with the shallow littoral zone (Meisch, 2000 and references therein) and prefers macrophyte debris and invertebrate faeces as substrate (Benzie, 1989). In the diatom assemblage (Fig. 4b), nearly all benthic and tychoplanktonic *Staurosira* taxa disappear. The biozone is dominated by fresh-brackish taxa (particularly *Mastogloia lacustris*) suggesting a shallower lake (or swamp) (Cumming and Smol, 1993). Besides *M. lacustris*, other benthic species, such as *Cymbella affinis*, *Denticula inflata*, *Epithemia adnata*, *Epithemia sorex*, *Eunotia arcus* and *Gomphonema angustatum* are present. During this period, oxygen and trophic levels decrease and the water becomes less eutrophic (Fig. 6; Demiddele et al., 2016).

4.3.3. Human occupation

During the Older Dryas, there is no archaeological evidence for the presence of hunter-gatherers in the Moervaart area.

4.4. Zone 2a, early and middle Allerød (corresponding to GI-1c)

4.4.1. Regional vegetation

During the early and middle Allerød, vegetation in the coversand area became more diverse, soils continued to form and due to a larger and more varied vegetation cover, more nutrient-rich habitats developed. Tree-birch (*Betula cf. pubescens*) immigrated and expanded (see macroremains, Suppl. Fig. 1d), both in the Moervaart depression as well as on the Great Sand Ridge of Maldegem–Stekene (Bos et al.,

Fig. 4. Diagrams of the Moervaart master sequence, showing the lithological layers and ^{14}C dates. a. Regional and local microfossil diagram. The botanical taxa are arranged stratigraphically and grouped by habitat. Microfossils are shown as curves (%) with an exaggeration of 5×. A selection of curves is displayed. Complete diagrams are displayed in the Supplementary diagrams Fig. 1a–d. b. Diatom diagram showing the depth distributions of the (square root-transformed) counts of the most important taxa. The taxa are arranged stratigraphically and grouped by habitat. Diatoms are shown as curves (%). c. Chironomid diagram showing the relative abundances (%) of the taxa. The zonation in panels b–c is based on the biozones in the P3 sequence. Figure adapted after Bos et al. (2017).

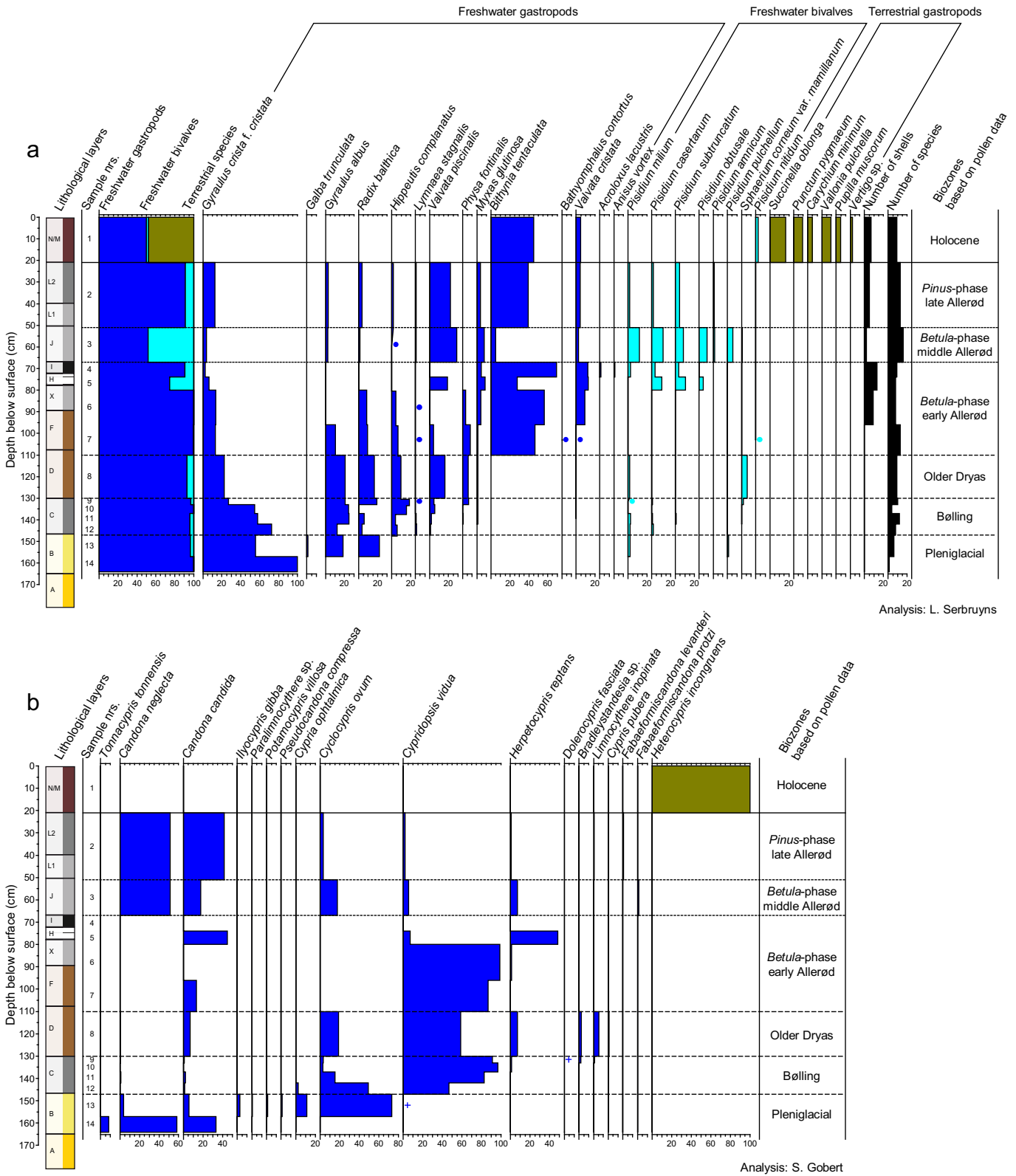


Fig. 5. Mollusc and ostracod diagrams of the S4 sequence. a. Mollusc diagram showing the relative abundances (%) of freshwater and terrestrial molluscs. b. Ostracod diagram showing the counts for each species as a percentage of the total amount of valves identified. Molluscs and ostracods are shown as histograms. All taxa are arranged stratigraphically. Zonation of the diagrams is based on the biozones of the P3 sequence.

Figure adapted after Bos et al. (2017).

2013). On the wetter soils, along lakes, ponds, marshes and slopes of the coversand ridge, birch woodlands and willow shrubs developed. These woodlands remained relatively open and various herbs (Apiaceae,

Geum and *Valeriana*) and shrubs (*Arctostaphylos alpina*) (Suppl. Fig. 1d) were growing in the understory. Juniper, dwarf willow and sea-buckthorn suffered from the competition with *Betula pubescens* for

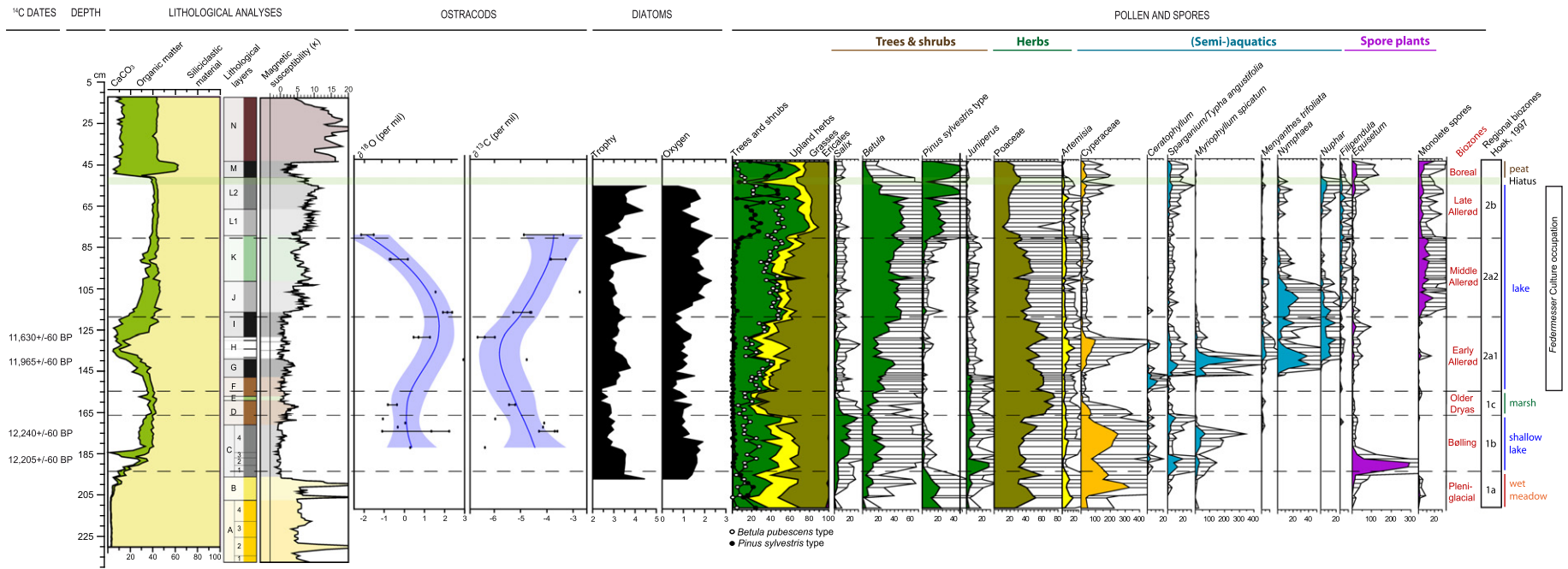


Fig. 6. Summary overview combining a large number of multi-proxy data, e.g., LOI, CaCO₃, lithology, MS, pollen, diatoms (trophy and oxygen) and delta ¹⁸O and ¹³C data measured on *Candona candida* from the Moervaart master sequence. Figure adapted after Bos et al. (2017). Also the Federmesser Culture period is indicated.

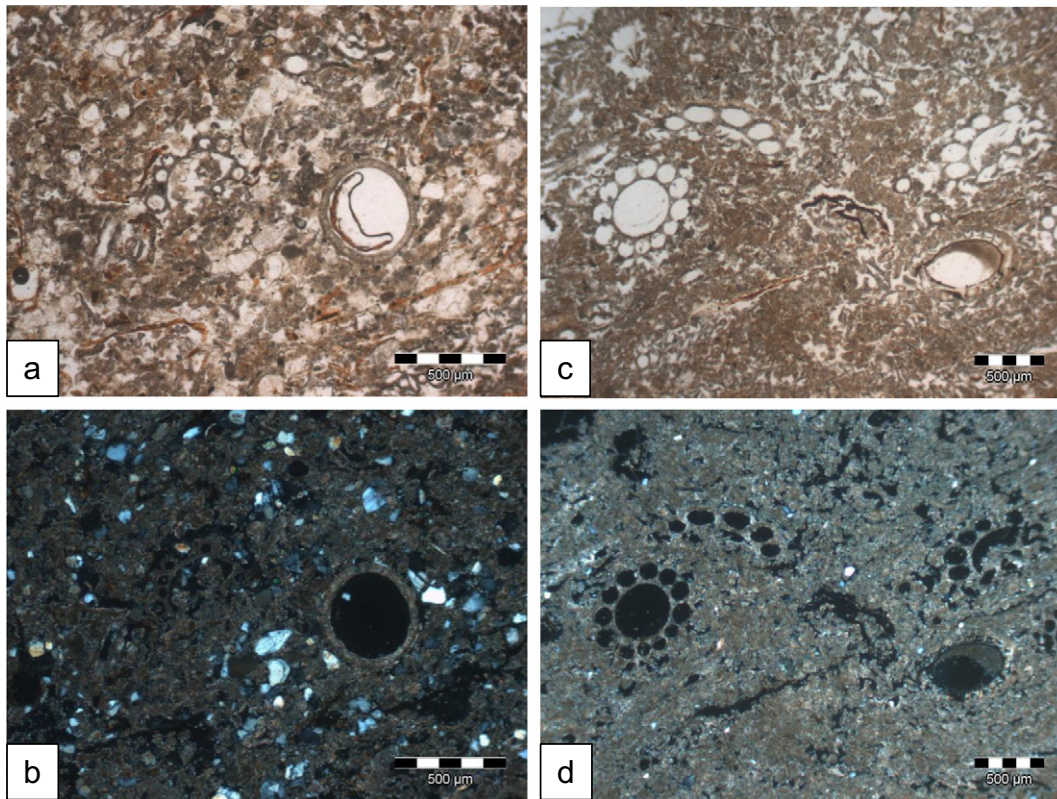


Fig. 7. Micromorphological features. PPL = plane polarised light, XPL = crossed polarisers. a–b. Calcareous micromass and calcified charophyte remnants in thin section 9 (Layer C4–C3–C2; panel a in PPL, panel b in XPL). c–d. Intact and fragmented calcified charophyte oogonia, stems and calcitic micromass in thin section 7 (top Layer ED–basis Layer F; panel c in PPL, panel d in XPL).

light and space, but remained present in shrubs or low vegetation on the more exposed, sandy soils, together with heliophilous herbs. Grass vegetation was still present in the moist areas of the depression. As the grass vegetation was present relatively close to the sampling location, i.e. within the low-lying area south of the coversand edge, this resulted in a high value of Poaceae pollen in the record. Various herbs (*Sanguisorba minor*, *Sanguisorba officinalis*, *Silene*, *Ranunculus*, *Filipendula*, *Botrychium lunaria*, Apiaceae) were present in this grass vegetation. Later, *Populus tremula* (aspen) appeared in the landscape (Fig. 4a). There are, however, no indications that aspen formed an important element in the birch forests along the Moervaart palaeolake, which contrasts with the coversand area of NE Brabant, The Netherlands (Bos, 1998; Bos et al., 2006).

4.4.2. Vegetation, flora and associated fauna in the palaeolake area

4.4.2.1. Zone 2a1, early Allerød (corresponding to GI-1c). During the early Allerød, plant and animal diversity increased with the development of more diverse and nutrient-rich habitats in the wetlands (e.g. lakes, shores, marshes and meadows, Suppl. Fig. 1b). The strong increase in aquatic taxa such as *Ceratophyllum*, *Myriophyllum spicatum* and Nymphaeaceae indicates that a renewed groundwater level rise took place (see also Bos et al., 2017), which was probably related to an increase in lateral groundwater input from the surrounding calcareous sand ridges (favoured by snow-melt) associated with high evapotranspiration in summer. At the same time, ponds and dune-slacks were formed on the Great Coversand Ridge Maldegem–Stekene (Derese et al., 2010; Crombé et al., 2012; Bos et al., 2013). Before and during the early Allerød, the Moervaart palaeolake was a shallow and topographically closed lake (Bos et al., 2017). This is reflected in the good correlation between $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ (Fig. 6). In the west, the Moervaart palaeolake was connected to a network of small and shallow channels, which, combined with the groundwater flow, fed the lake (Crombé et

al., 2013). Decalcification of the higher coversands and local seepage of carbonate-rich groundwater (see seepage indicators: *Utricularia*, *Potamogeton mucronatus*, *Menyanthes trifoliata*, *Hippuris palustris*, *Myriophyllum spicatum*, Characeae, Weeda et al., 1988) brought more carbonate into the lake system, sustaining in the deposition of a second layer of calcareous gyttja (Layer F). From the early to middle Allerød, this process slowed down as clastic inflow and seepage flow were diluted by authigenic lacustrine organic productivity (see high LOI values, Layer I, Fig. 6) and lake levels rose to a maximum. This is reflected in the deposition of more organic-rich deposits, as the deposits change from laminated lake marl (Layer F) to humic (peaty) calcareous gyttja (Layers G–H–I–J).

The lake level rise resulting in a larger lake is well reflected in all biological proxies, while it caused a strong increase in the species richness of botanical taxa (expansion of aquatic and marsh vegetation, Suppl. Fig. 1a, b, d), chironomids, gastropods (appearance of the deepwater species *Bithynia tentaculata*), bivalves (appearance of *Pisidium* species), benthic diatoms and ostracods (increase in *Cypridopsis vidua*) (sensu Hannon and Gaillard, 1997; Hoek et al., 1999; Gittenberger and Janssen, 2004; Bos et al., 2006). Many of the diatoms and faunal taxa are associated with marsh plants and macrophytes. In the botanical assemblages, the increase in species richness is reflected in the (re-)appearance of a large number of marsh taxa (*Schoenoplectus lacustris*, *Carex* spp., *Equisetum*, *Thalictrum*, *Sparganium natans*, *Menyanthes trifoliata*), submerged aquatics (*Ceratophyllum*, *Myriophyllum spicatum*, Characeae, *Potamogeton* spp.), floating-leaved aquatics (*Potamogeton natans*, *Nymphaea alba*, *Nuphar lutea*, including Nymphaeaceae mucilaginous cells, epidermis and trichosclereids, Suppl. Fig. 1c), cyanobacteria (*Gloeotrichia*) and various algae (*Debarya*, *Mougeotia*). The submerged aquatics were confined to the deeper parts of the lake, while in the shallower zones floating-leaved vegetation developed (compare Hannon and Gaillard, 1997). Although the lake was slightly deeper than during the Bølling and Older Dryas, lake depth was probably

max. 2.5 m during the early Allerød. The decrease in Characeae and CaCO₃ content (Layer H) suggests that the lake water was initially calcareous-rich and mesotrophic but later changed to calcareous-poor and meso- to eutrophic. The change in trophic conditions was probably related to the final disappearance of surrounding permafrost (sensu Hoek et al., 1999; Hoek and Bohncke, 2002; Bos et al., 2006), as it is expected that permafrost conditions in the preceding Pleniglacial were similar to the coversand areas of the southern Netherlands.

The increase in species richness and number of individuals in the diatom assemblage (Fig. 4b) is reflected in an increase in bentic and tychoplanktonic species (*Staurosira*, *Staurosirella*, *Cocconeis placentula*, *Epithemia adnata*). *Staurosira* s.l. taxa are fast growing, highly adaptable species associated with disturbances or strongly varying environments (Denys et al., 1990). They often dominated lake environments during the Lateglacial and Early Holocene (Lotter et al., 1997). Their occurrence was associated with an increase in shore plants providing habitats for epiphytic taxa. *Cocconeis placentula* is connected to macrophytes like *Nymphaea* and *Nuphar*. Leaves of these plants likely supported diverse epiphytic diatoms. The diatom assemblage indicates meso- to eutrophic conditions and high but varying oxygen status (Demiddele et al., 2016).

Also the ostracod fauna (Fig. 5b), characterised by *Cypridopsis vidua*, *Herpetocypris reptans* and *Candona candida*, was associated with vegetated littoral marshy environments. Vegetation type and richness also may be the determining factor for the occurrence of *Herpetocypris reptans* (Benzie, 1989; Kùlköylüoglu and Vinyard, 2000), since it prefers *Chara* and *Eleocharis palustris*. Both taxa were present in the lake vegetation (Suppl. Fig. 1d). *Herpetocypris reptans* is usually restricted to the shallow littoral zone (Meisch, 2000). Similar to the diatoms, the ostracod fauna indicates development of a shallow lacustrine habitat with littoral species.

Among the chironomids (Fig. 4b), there are many taxa (*Ablabesmyia*, *Psectrocladius*, *Dicortendipes*, *Glyptotendipes*, *Paratanytarsus*, *Corynoneura*, *Cricotopus*, *Endochironomus*, *Phaenopsectra* and *Polypedilum*) that are associated with macrophytes (Brooks et al., 2007). The humic calcareous gyttja deposits (Layers G–H–I–J) are marked by a strong decrease of *Tanytarsus glabrescens* type, while *T. lactescens* type disappears. A number of taxa temporarily increase (*Cricotopus*, *Endochironomus impar* type, *Phaenopsectra flavipes* type, *Glyptotendipes severini* type), all indicating macrophyte vegetation. Other taxa (*Dicortendipes*, *Tanytarsus pallidicornis* type, *Corynoneura*, *Ablabesmyia*) are present throughout the record. Highest abundances of *Ablabesmyia* (~20%) are reached in the humic calcareous gyttja deposits with sandy layers (Layer H). In these deposits, *Corynocera ambigua* is also present. Both latter taxa also indicate the presence of macrophytes.

In the mollusc fauna, *Bithynia tentaculata* (Fig. 5a) appears and quickly becomes dominant. It is a common species in interglacial and interstadial deposits (Gittenberger and Janssen, 2004). Often only opercula are found because they are composed of calcite, which is stronger and more resistant to degradation than the shell's aragonite (Penkman et al., 2013). The species prefers deep and eutrophic lakes (Hoek et al., 1999). Some taxa, such as *Lymnaea stagnalis* and *Valvata cristata*, reappear during the Allerød. The presence of *V. cristata* points to relatively clear, well-vegetated water and is, like the ostracod *Herpetocypris reptans*, often found living in *Chara* meadows (Hoek et al., 1999). New taxa are *Pisidium* species, *Anisus vortex* and *Acroloxus lacustris*. The latter is a relatively warmth-loving species and often appears during the early Allerød (Hoek et al., 1999). Among the recorded species are many that prefer large surface waters (e.g., *Acroloxus lacustris*, *B. tentaculata*, *Myxas glutinosa* and *Valvata piscinalis*) and/or are associated with floating vegetation (e.g., *Gyraulus crista*, *Myxas glutinosa*, *Hippeutis complanatus*, *Lymnaea stagnalis*, *Physa fontinalis* and *Radix balthica*) (Gittenberger and Janssen, 2004), which supports the interpretation of a large palaeolake with an abundance of aquatic vegetation. At the end of the early Allerød the Moervaart palaeolake reached its largest size and deepest phase. The larger organic productivity of the lake is reflected in a maximum in the organic values (Layer I, Fig. 6).

4.4.2.2. Zone 2a2, middle Allerød (corresponding to GI-1c). During the high water-level phase at the start of the middle Allerød, an outlet was formed for the Moervaart palaeolake, probably due to the incision of the Kale/Durme River (Fig. 1d). This is indicated by a major change in isotopic signature (from relatively high $\delta^{18}\text{O}$ and low $\delta^{13}\text{C}$ in Layers H, I, and J, towards relatively low $\delta^{18}\text{O}$ and high $\delta^{13}\text{C}$ in Layer K, Fig. 6), which suggests a hydrological change from a large lake with a relatively high evaporative surface, towards a slightly smaller lake with an inflow and outflow (Bos et al., 2017). Radiocarbon dates from the basal channel infilling indicate that incision took place before ca. 13,100 cal yr BP (Crombé et al., 2014; Bos et al., in press.). Due to formation and gradual incision of this outlet, lake water levels lowered. The erosional contact between Layers I/J corresponds to the transition of the lake at its deepest point to slightly shallower, and where possibly channels developed in the lake bottom. Increased magnetic susceptibility in Layers J to L2 (Fig. 6) further supports evidence for a lake level decrease, as the abrupt susceptibility rise suggests changing redox conditions resulting in magnetic enhancement. Contact I/J furthermore shows in the south of the trench a gully with sandy infill, 5 to 12 cm deep and a sharp 7 cm deep V-form wedge at the bottom.

The deposits changed from humic, calcareous gyttja (Layer J) into clayey, calcareous gyttja (Layer K). This lithological change is reflected in a decrease in organic matter, an increase in CaCO₃ content, and increasing abundance of Characeae (both *Chara* and *Nitella*) observed both in the macrofossils (Suppl. Fig. 1d) and sediment thin section 4 (transition Layer K/J). It occurs simultaneous with changes in the chironomid, diatom (disappearance *Cocconeis placentula*), mollusc (decrease *Bithynia tentaculata*) and ostracod (increase *Candona neglecta*) taxa, an increase in ferns and semi-aquatics (*Hippuris vulgaris*, *Filipendula*, *Silene*, *Valeriana*, *Sanguisorba officinalis*) and a decrease in floating-leaved vegetation (*Nymphaea alba*, *Nuphar lutea*, see also mucilaginous cells, epidermis, trichosclereids, Suppl. Fig. 1c). The latter disappeared when during the later middle Allerød the lake became too shallow, i.e. <1 m. The presence of *Lemma* (duckweed) suggests that nutrient availability and productivity of the lake water were high (see also trophy, Fig. 6).

In the chironomid record (Fig. 4c), *Corynocera ambigua* strongly increases and reaches a maximum of 34% in Layer K. *Chironomus anthracinus* type (25%) and *Prosilocerus lacustris* type (13%) show a maximum in Layer J. *Chironomus* taxa are abundant in warm, eutrophic lakes where they are mostly confined to the profundal zone but also may be present in the littoral zone and in lakes in subalpine or subarctic environments. They are tolerant of low oxygen and low pH levels (Johnson and Wiederholm, 1989). The diatom assemblage at 120 cm (base of Layer J; Fig. 4b) indicates low oxygen levels. In the overlying calcareous gyttja (Layer K) and lake marl (lower Layer L1), *C. anthracinus* type strongly decreases in abundance, while *P. lacustris* type disappears. These deposits are again dominated by *Tanytarsus glabrescens* type, while *T. lactescens* type and *Parakiefferiella bathophila* type also increase. *Parakiefferiella bathophila* type and most *Tanytarsus* species occur in the littoral zone of relatively warm, productive lakes (Brooks et al., 2007, and references therein), which suggests the presence of a large littoral zone, probably due to a decrease in water depth.

In the ostracod record (Fig. 5b), *Candona* species (*C. candida*, *C. neglecta*) become dominant again. Both species are common in lakes in both the littoral and profundal zones. *Candona candida* prefers muddy bottoms (Kùlköylüoglu and Vinyard, 2000) and its presence was probably connected with deposition of more clayey material. The increase in *Candona neglecta* (Layer J) was associated with a local decrease in aquatic macrophytes as the species prefers sediment without aquatic vegetation (Kiss, 2007). However, freshwater molluscs (*Valvata piscinalis*, *Myxas glutinosa*) (Fig. 5a), as well as the pollen data, suggest that aquatics were still abundant elsewhere in the lake during the deposition of Layer J. Their decrease occurs during deposition of Layers K and L1.

In the mollusc assemblage, the diversity of taxa increases (Fig. 5a). Among the freshwater bivalves many *Pisidium* species appear or

increase in abundance in Layer J. The larger abundance of *Valvata piscinalis* and *Pisidium obtusale* points to shallower water and less eutrophic conditions. Similar conditions were also recorded during the middle Allerød in the southern Netherlands (Hoek et al., 1999).

4.4.3. Human occupation

The landscape, with open forested areas and forest edges (boreal forests) alternated by lakes, ponds and marshes that developed during the early and middle Allerød, was probably very suitable for large herbivores such as elk (Bos et al., 2013). In the Moervaart record, evidence for large herbivore presence around the palaeolake is formed by records of ascospores of coprophilous fungi (*Apiosordaria verruculosa*, *Sordaria* type, *Sporormiella* type, *Podospora* type, see Van Geel et al., 2003; Suppl. Fig. 1d). These suggest that large herbivores foraged the woodlands and used the shores of the palaeolake as watering place. The plentiful presence of permanent open water (= Moervaart lake), with wild game for hunting and plants to gather made the Moervaart lake area for the first time very attractive for (*Federmesser* Culture) hunter-gatherers. They settled along the entire northern bank of the palaeolake, forming an almost continuous site-complex of temporary campsites stretching over ca. 15 km (Fig. 1d). At these locations, settlements were protected from the prevailing winds that generally came from the (north)west (Isarin et al., 1997). At the northern side of the Great Coversand Ridge, the local climate was probably too harsh for human occupation. This is supported by the scarcity of sites on the northern slope of the coversand ridge.

In the Moervaart palaeolimnological record, there is no direct palynological evidence (i.e., opening of forests followed by a regeneration phase with herbs) for human presence during the Allerød period, but the distance over which pollen evidence for human interference in the landscape usually can be traced in the boreal forests is very small, i.e. between 50 and 150 m (Hicks, 1993; Bos and Janssen, 1996). The slightly higher values of microscopic charcoal and ascospores of *Gelasinopora* (Van Geel, 1978) recorded during the middle Allerød clearly points to local fires. At the nearby Rieme site, on the northern side of the Great Sand Ridge of Maldegem-Stekene, indications were found for burning of the reedswamps in combination with the presence of large herbivores (Bos et al., 2013). All this might suggest active burning of the vegetation by *Federmesser* Culture people, i.e. to create openings and induce the growth of herbs and shrubs in order to attract large herbivores (Mellars, 1976; Mellars and Dark, 1998; Bos et al., 2005). Yet, a natural origin of these fires cannot be fully excluded.

4.5. Zone 2b, late Allerød (corresponding to GI-1c/b)

4.5.1. Regional vegetation

The increase in pine pollen during the late Allerød (Fig. 4a) suggests that pine immigrated into the region and birch-pine woodlands formed. Open pine woodlands probably developed on the sandy soils of the Great Sand Ridge of Maldegem-Stekene, where woodlands partly replaced the herbaceous vegetation and shrubs. Some open spots with herbaceous vegetation (*Artemisia*, *Helianthemum*, *Rumex*, *Dipsacus fullonum*, *Amaranthaceae*, *Brassicaceae*, *Asteraceae*) remained present. Birch was growing in open woodlands with an undergrowth of herbs (*Symphytum*, *Valeriana* and *Apiaceae*) and ferns on the slopes of the coversand ridges and along lake shores. Grasslands became less abundant. Wet grasslands on nutrient-poor soils with *Ophioglossum vulgatum*, *Parnassia palustris* developed on the coversand dunes. The high AP (including pine) and low NAP values in the pollen assemblages (Fig. 4a) indicate that the landscape became more densely forested with the change from birch to birch-pine forests. This led to an increase in effective evapotranspiration, resulting in a regional groundwater lowering. This, in combination with the lower lake levels and lake's terrestrialisation process turned the lake into a marsh, which eventually led to the final disappearance of the lake near the end of the Allerød. During this period also other lakes in the region changed into marshy

environments, while nearly all dune-slacks completely dried-out and were covered by thick packets of blown sands, indicating a marked drop of the groundwater level in the sandy lowland region (Denys et al., 1990, 1998; Crombé et al., 2012). This change has been tentatively connected with the Intra Allerød Cold Period or GI-1b, which occurred between 13,261 and 13,049 cal yr BP (Bos et al., 2017).

4.5.2. Vegetation, flora and associated fauna in the palaeolake area

In the Moervaart lake, light grey lake marl (with low LOI and high CaCO₃ values), subdivided into Layers L1 and L2 (oxidation features), was deposited during the late Allerød (Fig. 6). Due to oxidation, chironomid head capsules are badly preserved (Fig. 4c). Both layers show, similar to the underlying Layers J and K, a stronger presence of para- and ferrimagnetic minerals (Fig. 6). During deposition of Layer L1, aquatic vegetation (*Lemna*, *Potamogeton natans*, *Schoenoplectus lacustris*, Characeae) and algae (*Botryococcus*, HdV-128A/B) were present near the master's sample location, indicating nutrient-rich water and, in comparison to the middle Allerød, a slightly deeper lake (water depth 0.5–1 m). This is supported by an increase in the diatom *Cymbella affinis*. During the deposition of Layer L2, Nymphaeaceae (*Nuphar*, *Nymphaea*), *Potamogeton mucronatus* and *Utricularia vulgaris* re-appeared, while Characeae disappeared (Suppl. Figs. 1b, c, d), indicating a change from a slightly deeper lake with submerged taxa to a shallower lake with predominantly floating aquatic taxa. Furthermore, some marsh plants increased in value (*Sparganium*, Cyperaceae, *Equisetum*). This all suggests that water levels further went down and the lake turned into a swamp with several pools of open water in which some floating aquatics persisted. The diatom record confirms this decrease in water level and indicates that oxygen levels gradually decreased (Figs. 4b, 6), while the lifeform remained tychoplanktonic but with less benthic species (Demiddele et al., 2016). Near the end of the late Allerød, diatom species richness decreased and above 56 cm diatoms were absent.

In the ostracod record (Fig. 5b), *Candona* species (*C. candida* and *C. neglecta*) continue to dominate. At the S2 sequence, Layers L1 and L2 were sampled separately, confirming the abundance of *C. candida* and *C. neglecta* ostracods in both units. *Pseudocandona compressa*, which shows a clear preference for the shallow littoral zone, is mainly restricted to Layer L2 (Gobert, 2012). The presence of *Limnocythere inopinata* indicates shallow littoral water and presence of macrophyte debris (Meisch, 2000 and references therein). Among the molluscs, *Bithynia tentaculata* increases (Fig. 5a) and becomes dominant again in Layers L1 and L2. The S2 sequence shows that *B. tentaculata* decreases in abundance in Layer L2, in comparison to Layer L1, while *Pisidium* species become more abundant in Layer L2 (Serbruyns, 2010). Both the ostracod and mollusc taxa thus point to lower lake water levels during the formation of Layer L2.

4.5.3. Human occupation

Hunter-gatherers of the *Federmesser* Culture continued to be present in the Moervaart area during the late Allerød. Palynological evidence for their presence during this period was not found. However, the slightly higher values of microscopic charcoal and finds of *Epilobium* pollen, which may indicate the presence of fireweed (*Epilobium angustifolium*), recorded during the late Allerød, may point to local fires. Fireweed can be a pioneer in localities where (woodland) vegetation is burned or cut down (Van Geel et al., 1981). If these fires were caused by active burning of the vegetation by *Federmesser* Culture people or if they had a natural origin remains unknown. However, in the Moervaart record the microcharcoal is clearly linked to the gradual appearance of pine, a species which is very sensitive to natural burning, e.g., caused by lightning.

Later during the late Allerød, the absence of a large and open deep water lake and the return to a colder climate during the Intra Allerød Cold Period and following Younger Dryas most likely hindered prehistoric man to remain settled in the Moervaart area. Evidence for human presence during the colder Younger Dryas is at present very

limited and not conclusive (Crombé et al., 2011; Crombé and Robinson, 2017). Possibly hunter–gatherers shifted to other areas, which still offered enough drinking water and protection from the cold climate, such as the adjacent Scheldt river (Crombé and Robinson, 2017) and Ardennes (cf. Arts and Deeben, 1981).

4.6. Zone 3, Holocene

The Moervaart lake marls (Layer L2) are discordantly covered by peat (Layer M, Figs. 2, 6). Farther east (Klein-Sinaai “Boudelo” trench, Fig. 1d), the peat deposits are ca. 0.5 m thicker and better preserved, thanks to the overlying Medieval sediments (13th–14th century). A strong decline in magnetic susceptibility marks Layer M, which is overlain by the magnetically enriched plough layer (Layer N, Fig. 6). In the peat, a number of terrestrial gastropod species are recorded (Fig. 5a), pointing to a more terrestrial environment. Chironomids and diatoms are absent from these deposits, which is related to these terrestrial conditions. The only ostracod recorded is *Heterocypris incongruens*, which also occurs in a terrestrial environment, especially in small temporary puddles and seasonal pools in grasslands (Ganning, 1971). Based on the presence of pollen of thermophilous trees and shrubs such as *Corylus*, *Quercus*, *Ulmus* and more upwards *Alnus* and *Cerealia* (cereals), the peat dates to the Boreal, respectively Atlantic (Holocene). This suggests a large hiatus of at least 2000 calendar years between Layers L2 and M.

4.6.1. Human occupation

Hunter–gatherers did not return to the Moervaart area before the Boreal, suggesting that the area was unoccupied for at least 2 millennia. During the Early Holocene, occupation patterns changed markedly as from the Boreal onwards hunter–gatherers settled along the dry banks of the meandering Kale/Durme River (Fig. 1d) that probably had become the sole source of drinking water in the area since all lakes and ponds had vanished long before. However, due to increased evapotranspiration and temperatures the Kale/Durme River was already reduced to a small and shallow stream with either slowly running or stagnant water (Storme et al., 2016; Bos et al., in press.). This suggests that the presence of a water resource in the Moervaart depression formed a principal component in the subsistence strategies of hunter–gatherer communities in the NW Belgian lowland (Crombé et al., 2011; Bos et al., in press.).

5. Conclusions

The Moervaart depression holds a valuable archive of Lateglacial climate and environmental changes. This study showed that changes in the lake–ecosystem were directly linked to changes in the surrounding landscape and climate. The lake formed in a depression south of a large Pleniglacial coversand ridge and infilling started when rising temperatures at the onset of the Lateglacial caused melting of permafrost in the neighbouring region. Carbonates in the coversands surrounding the lake were transported to the lake by groundwater, which led to the formation of calcareous gyttjas. Environmental changes that occurred during the Lateglacial interstadial are clearly reflected in the lithology and chemical and biological composition of the deposits. Combination of the different analyses allowed for the reconstruction of lake level changes, which seemed to be particularly influenced by climate changes.

During the Lateglacial interstadial, vegetation cover increased and the vegetation changed from tundra into boreal forest with birch and pine. In the lake, submerged aquatic plants were subsequently followed by floating aquatic communities which eventually culminated into the development of a shallow swamp. This progressive development was shortly interrupted during the Older Dryas, when swamp conditions returned due to a drier climate. The final drying of the lake near the end of the Allerød caused a hiatus in the record. Water levels increased

again during the Holocene, leading to the formation of peat covering the Lateglacial interstadial lake deposits.

From the start of the Allerød onwards, the area provided a very suitable landscape for the *Federmesser* Culture hunter–gatherers with the nearby Moervaart lake providing drinking water and extensive and fertile woodlands for hunting and gathering. The drying up of the lake and return to a colder climate probably hindered prehistoric man to remain settled in the area. This led to a marked decrease or hiatus in the human occupation and exploitation of the area which lasted more than 2000 yrs.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.revpalbo.2017.09.006>.

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