

Original Article

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**Corresponding author:**

M.T.I.J. Gouw-Bouman,  
Email: [M.Gouw-Bouman@archol.nl](mailto:M.Gouw-Bouman@archol.nl)

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# From lake to river. The Weichselian Lateglacial and early Holocene palaeoenvironmental development of the Moervaart region (northwestern Belgium): a synthesis on vegetation patterns, climate, abiotic landscape and human occupation

Hanneke Bos<sup>1†</sup>, Marjolein Gouw-Bouman<sup>1,2</sup>, Nelleke van Asch<sup>1,3</sup>, Jeroen Verhegge<sup>4</sup> and Philippe Crombé<sup>4</sup>

<sup>1</sup>ADC Archeoprojecten, Amersfoort, the Netherlands; <sup>2</sup>Archol bv, Leiden, the Netherlands; <sup>3</sup>Geofoxx, Oldenzaal, the Netherlands; <sup>4</sup>Ghent University, Department of Archaeology, Ghent, Belgium

## Abstract

In this paper, a synthesis is given of a large multi-disciplinary project, which included physical, botanical, zoological and archaeological studies, accelerator mass spectrometer (AMS) <sup>14</sup>C and Optical Stimulated Luminescence (OSL) dating and chemical analyses from numerous locations in and along the extensive Moervaart palaeolake (NW Belgium), south of the Maldegem-Stekene Coversand Ridge. This rich dataset enabled a detailed reconstruction of climate, vegetation development and human presence in the period from the Weichselian Lateglacial and early Holocene. In addition, this dataset was used to make spatial reconstructions of the vegetation patterns in the direct surroundings of the Moervaart palaeolake for seven time slices and artist impressions for three moments in the archaeological record. These vegetation maps and the high resolution data on climate and the abiotic landscape are compared to former human occupation patterns to give insight in these early human presences in NW Europe.

The first evidence for human presence, after a long period of absence, was found from the Allerød period. During this period, hunter-gatherers of the *Federmesser* culture were present in encampments along the northern shore of the Moervaart palaeolake which had developed during the Bølling period. Both the improving climate and the availability of a fresh water source stimulated human presence. The vegetation transitioned from a tundra landscape in the Bølling period to a boreal forest with birch and pine in the Allerød. During the following cold period of the Younger Dryas, forests retreated and tundra vegetation redeveloped. At the same time, the Moervaart palaeolake and most of the surrounding dune ponds turned dry. Evidence of human presence in the region during the Younger Dryas period is scarce, presumably related to the colder climatic conditions and the strongly reduced availability of fresh water sources. Due to climate warming during the early Holocene, boreal forests expanded again. However, evidence of human occupation of the area remains scarce. The Preboreal forest expansion was shortly interrupted by another cold reversal, the so-called Preboreal Oscillation or 11.4 event. After this event, hunter-gatherers returned to the area, then settling preferably along the dry banks of the Kale/Durme river, a tributary of the Scheldt river, which was the only source of fresh water in the region. During the following Boreal, coniferous forests were gradually replaced by deciduous forests which had developed initially with hazel, elm and oak, but later (Atlantic) also with lime, alder and ash. Hunter-gatherer site-density was highest during the first part of the Boreal, when hazel dominated the landscape. Afterwards, site-density dropped considerably; however, it is not clear whether this reflects a marked population reduction or rather points to changing mobility in response to a changing environment.

## Introduction

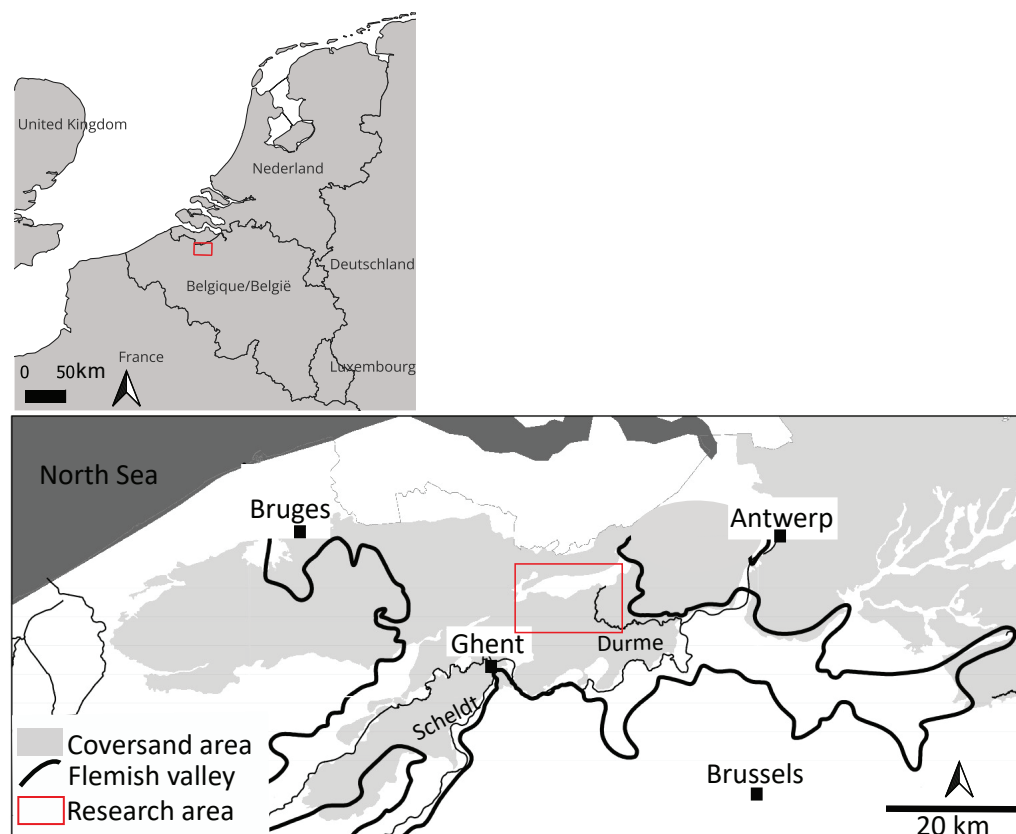
The focus of this paper are the palaeoenvironmental development and past human occupation patterns of the Moervaart region, and specifically the direct surroundings of the Moervaart palaeolake, situated in the sandy lowland of NW Belgium at the southern margin of the NW European coversand belt (Figure 1). During the Late Glacial, several lakes developed in closed local depressions at the southern foot of an

extensive dune complex named the Maldegem-Stekene Coversand Ridge (De Moor & Heyse, 1978). The best-known palaeolake is the one formed in the Moervaart depression, a depression within a former Middle Pleistocene valley (Heyse, 1979). With a total estimated surface of ca. 25 km<sup>2</sup>, it was by far the largest Late Glacial freshwater lake not just in NW Belgium but within the entire NW European coversand region. In addition, the Moervaart palaeolake is one of the few lakes that was intersected by a meandering river channel, which gradually filled with sediments dating to the final phases of the Late Glacial and early Holocene. This combination of lacustrine and riverine soil archives makes the Moervaart region a unique context for studying the palaeoenvironment in a continuous way from the very start of the Late Glacial till the Atlantic period.

Archaeologically, fresh water lakes are important given that they were the focus of occupation by hunter-gatherers of the Final Palaeolithic and Early Mesolithic (Crombé & Robinson, 2017; Crombé *et al.*, 2011; De Bie & Van Gils, 2006; Deeben, 1988; Van Gils & De Bie, 2008; Vanacker *et al.*, 2001; Vanmontfort *et al.*, 2022). It is thus not surprising that over the years, the Moervaart region has received much attention from scientists, including archaeologists, geologists, geomorphologists and palynologists. Research started in the 1960s mainly focusing on the geomorphology and hydrology (De Moor, 1963; Heyse, 1979, 1983), while the investigation of past vegetation remained limited to a few spots and the analysis of fossil pollen (Verbruggen, 1979). After the 1980s, however, environmental research in the Moervaart depression came almost to a standstill until

in 2008 an extensive interdisciplinary research project was granted by Ghent University. This multi-disciplinary research project focussed on understanding the geomorphological, hydrological and ecological evolution of the landscape in relation to former human settlement patterns. Detailed investigations were conducted into the palaeogeomorphology (Crombé *et al.*, 2013; Werbrouck *et al.*, 2011), palaeohydrology (De Smedt *et al.*, 2011, 2013; Zwervaegeher *et al.*, 2013) and palaeoenvironment (Bos *et al.*, 2013, 2017, 2018a, 2018b, 2018c; Crombé *et al.*, 2020; Demiddele *et al.*, 2016; Meylemans *et al.*, 2011a; Storme *et al.*, 2017; van Asch *et al.*, 2024; Zwier, 2018) of the region using state-of-the-art research methods and techniques, such as geophysical survey techniques (mainly EMI), Digital Elevation Modelling (DTM), groundwater modelling (model MODFLOW-96), isotope analyses, OSL and AMS-dating (Crombé *et al.*, 2012, 2014; Derese *et al.*, 2010). Almost simultaneously with the onset of palaeoenvironmental research in the late 20th century, archaeological fieldwork was initiated by amateur-archaeologists who surveyed the Moervaart area in an extensive and systematic way until today (Van Vlaenderen *et al.*, 2006). After four decades, this resulted in the discovery of a very substantial number of prehistoric sites dating to the Late Glacial (Final Palaeolithic) and Early to Middle Holocene (Mesolithic), making the Moervaart region currently one of the archaeologically best documented research areas of northern Belgium and the southern Netherlands (Crombé *et al.*, 2011; Crombé & Verbruggen, 2002).

Since significant changes occurred both in environmental features (climate, landscape and vegetation) as well as



**Figure 1.** Location of the research area within NW Europe and NW Belgium.

human presence, the unique combination of high-resolution palaeo the environment and archaeological data in this area allows for a detailed analysis of the interplay between climate, ecosystem and human behaviour. The present paper synthesises the various multi-proxy studies that were carried out within the Moervaart region, both published and unpublished, and gives an overview of the past environmental development of the area. It also presents for the first time a series of vegetation reconstruction maps as well as artist impressions of the landscape for different timeslices of the Late Glacial and early Holocene.

Using the available palynological studies, detailed geomorphological maps were translated into vegetation reconstruction maps showing the distribution of vegetation units. When compared to archaeological data, these spatial landscape and vegetation reconstructions in combination with the climatic records enabled us to determine the impact of vegetation and environmental changes on past human occupation patterns. Since human presence during this time period is strongly controlled by environmental factors, this study provides useful insight into site selection, settlement systems, landscape exploitation and population density throughout the Late Glacial and early Holocene, and possible changes therein. The ultimate goal of this study is to investigate whether and to what extent ecosystems and hunter-gatherer lifeways during the Late Glacial (Final Palaeolithic) and early to middle Holocene (Mesolithic) were impacted by climatic fluctuations – both the major climatic fluctuations (e.g. Late Glacial and Early Holocene warming, Younger Dryas cooling), as well as centennial scale climatic oscillations (e.g. Bond-cooling events). We expect that the results of the present study will be relevant for future research in other areas of the coversand plain of NW Europe and might contribute to a better prediction of locations of Final Palaeolithic and Mesolithic activities.

## Material and methods

### Research area

The Moervaart region, situated in the centre of the plain of the Flemish Valley, a Pleistocene valley (De Moor & Heyse, 1978), is characterised by a complex and dynamic palaeolandscape. Overall, the area corresponds to a low-lying coversand plain (2–3 m above sea level) with weak microtopography, consisting of narrow and low ridges with a general southwest - northeast (SW-NE) orientation. However, this landscape is interspersed with some striking landscape features that were developed during the Late Glacial, although not all simultaneously. These are (Figure 2):

- 1) An extensive coversand ridge, named the Great Coversand Ridge of Maldegem-Stekene, resulting from aeolian activity during the Weichselian Pleniglacial, and continuing to develop throughout almost the entire Lateglacial (Crombé et al., 2012; De Moor & Heyse, 1978; Verbruggen et al., 1996). Running east-west over ca. 80 km and locally reaching a width of ca. 3 km, it is composed of a complex microrelief of intersecting and overlapping dunes alternated with irregularly elongated depressions and dune slacks. The latter are preserved as organic to peaty layers (palaeosols) within the aeolian sandy deposits, which represent the

bottom of these former dune ponds. The Coversand Ridge of Maldegem-Stekene is characterised by a gentle northern flank and a rather steep and abrupt southern edge, indicating its formation under dominant N(W) wind conditions. OSL dating was used to date the sandy sediments of the Great Coversand Ridge of Maldegem-Stekene (Derese et al., 2010). This indicated that deposition of the sandy sediments occurred especially during the Late Pleniglacial and Older Dryas; however, the bulk of the coversand ridge at Heidebos was probably deposited during the Allerød and/or Younger Dryas (Crombé et al., 2012; Derese et al., 2010).

- 2) An anastomosing river system consisting of numerous interconnected shallow gullies (depth 1.5–2.5 m), situated in the northwestern part of the palaeolake and dating to the early Lateglacial.
- 3) A large but shallow freshwater inland palaeolake, named the Moervaart palaeolake (Heyse, 1979, 1983), which was formed during the Bølling and turned into a marshy depression at the end of the Allerød (Bos et al., 2017, 2018a; Crombé et al., 2013; Zwertvaegher et al., 2013). Covering a surface of ca. 25 km<sup>2</sup>, it is by far the largest inland palaeolake within the Dutch-Belgian lowlands. It is situated along the steep southern edge of the Coversand Ridge of Maldegem-Stekene and most likely was created as the latter blocked the previously open northern exit route for surface waters and groundwater (De Moor & Heyse, 1978; Verbruggen et al., 1996).
- 4) A deep (4–6 m) meandering palaeochannel of the Kale/Durme River, a tributary of the Scheldt River, which cuts through the Moervaart palaeolake sediments from the middle Allerød onwards.

### Multi-proxy sites in the Moervaart region

The research in the Moervaart region resulted in 14 multi-proxy studies where palynology was included covering the time period from the late Pleniglacial up to the Boreal (Figure 2 and Table 1). The sites of Moerbeke 'Moervaart' (1; Verbruggen et al., 1996), Moerbeke 'Suikerfabriek' (2; Bos et al., 2017, 2018a), Moerbeke 'Driehoek' (3; Crombé et al., 2020), Klein-Sinaai 'Boudelo' (4; Bos et al., 2018c), Wachtebeke 'Penen' (8, Suppl. data), Moerbeke Terweststraat (12; Verbruggen 2021) and Moerbeke 'Wulfsdonk' (13; Suppl. data) were all situated along and in the Moervaart palaeolake (Figure 2 and Table 1). Of these sites, most detailed research has been carried out on the Moerbeke 'Suikerfabriek' record (2) that was obtained from the central part of the lake deposits. In the eastern part of the palaeolake, the lake deposits were investigated at Moerbeke 'Driehoek' (3; Crombé et al., 2020) and Klein-Sinaai 'Boudelo' (4; Bos et al., 2018c). In the western part of the Moervaart depression, investigations were carried out on channel infills at Moerbeke 'Wulfsdonk' (13; Suppl. data), Wachtebeke 'Penen' (13; Suppl. data) and channel infills at Moerbeke 'Noord' (7; Meylemans et al., 2011a, 2011b). The site Wachtebeke 'Heidebos' (6; Suppl. data) is located on the southern slope of the coversand ridge Maldegem-Stekene. At this site, thick coversand deposits alternating with thin organic to peaty layers were present (Crombé et al., 2012; Derese et al., 2010). These organic layers were studied for pollen, but this data were never published and are therefore included in the supplementary material. Another palaeoenvironmental study was carried out

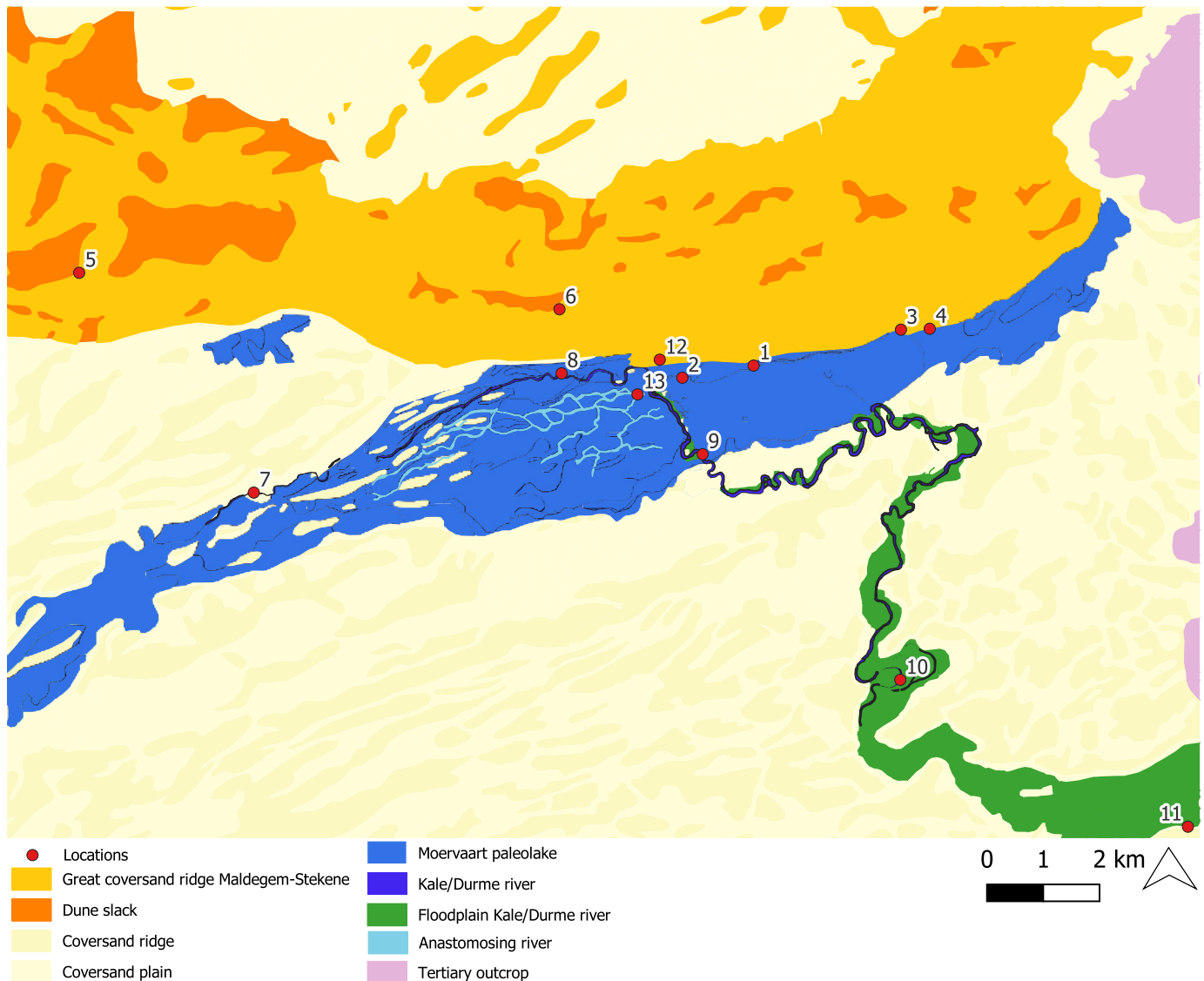
on Lateglacial humiferous to peaty palaeosols on the north-western side of the same coversand ridge: Rieme 'Noord' (5; Bos *et al.*, 2013). From the buried, meandering Kale/Durme River system, four sequences were analysed; from north to south, these were, Moerbeke 'Peerdemeers' (9; Bos *et al.*, 2018b), Daknam 'Broek' (10; van Asch *et al.*, 2024; Zwier, 2018) and Zele 'Hoekstraat' (11; Storme *et al.*, 2017). Further downstream and outside of the research area, the site of Klein 'Broek' is located in a palaeochannel of this meandering river system (14; Storme *et al.*, 2017).

The palynological data from these sites were used to produce new vegetation maps which are presented in this paper. All other data were used to provide information on past environmental and climatic conditions, which were discussed in detail in the original publications. These analyses included sedimentological and physical (organic matter and calcium carbonate, magnetic susceptibility, micromorphological), botanical (macrofossils, diatoms), zoological (ostracods, molluscs, chironomids) and chemical analyses (stable carbon and oxygen isotopes), radiocarbon and OSL dating (Table 1). Applied methodology and detailed

data can be found in the original papers (Table 1). Methods and data for the unpublished pollen records of Wachtebeke 'Heidebos', Wachtebeke 'Penen' and Moerbeke 'Wulfsdonk' can be found in the supplementary information.

#### Human occupation in the Moervaart region

Data on human occupation in the Moervaart region were obtained from fieldwalking surveys, mainly conducted by amateur-archaeologists since the 1980s (Crombé *et al.*, 2013; Van Vlaenderen *et al.*, 2006), archaeological augering and test-pitting (Bats, 2001; Crombé *et al.*, 2013; Van Hoecke *et al.*, 2023) and excavations (De Smedt *et al.*, 2013; Van Hoecke *et al.*, 2023; Vanmoerkerke & De Belie, 1984). These combined researches resulted in the discovery of >100 prehistoric sites, of which 59 could be attributed to a specific time-period and/or prehistoric culture (Table 2). Lacking radiocarbon dates, most of these attributions are based on typological, technological and raw material characteristics of the lithic assemblages (Crombé *et al.*, 2011). As a measure of human presence in the area, the number of sites per archaeological phase



**Figure 2.** General geomorphological map of the research area showing main landscape elements and location of sites of palynological data. For site details see Table 1.

was converted into estimates per 100 calendar years to account for the different duration of each subphase (Figure 3, Table 3), following the method developed by Crombé et al. (2011).

The locations of known sites of human activities were plotted on the vegetation maps, in view of analysing their spatial distribution in relation to changing environment, but were not used as input data for the vegetation reconstruction. The vegetation type and development around archaeological sites is discussed in the result section.

### Vegetation reconstruction maps

Vegetation maps showing the distribution of plant communities were made to visualise the vegetation composition in

the Moervaart region for specific time slices during the Lateglacial and early Holocene. Each time slice reflects a pollen biozone and was selected for a reconstruction map when sufficient palynological datapoints (a minimum of five) for a period were available. All available pollen records reflecting the selected time period were used. All data were derived from lakes, dune slacks (palaeosols) and residual channels, with a total of 14 locations and 19 records (Figure 2; Table 2; see Multi-proxy sites in the Moervaart region). The method used for the reconstruction of the vegetation maps was developed by Van Beek et al. (2015a, 2015b) and is based on the inherent relationship between the abiotic landscape and vegetation development, assuming that these relations are consistent during a specific time period in a relatively

**Table 1.** Palynological data and recorded time interval available from the various sites in the Moervaart region.

| Site nr. | Location and site                            | <sup>14</sup> C (supplementary data) | Zones recorded in the pollen sequence and correlated to Hoek (1997a, 1997b) | Zones recorded in the pollen sequence correlated to ice-core records (Rasmussen et al., 2014) | Used for vegetation map | Published by   | Other proxies  |
|----------|--|--------------------------------------|---|---|-------------------------|--|--|
| 1        | <i>Moerbeke 'Moervaart'</i>                  | Bulk                                 | 1b, 1c, 2a1, 2a2, 2b  | GI-1e, GI-1d, GI-1c3, GI-1c2, GI-1c1, GI-1b   | 1, 2, 3, 4, 5, 7        | Verbruggen, (1979, 1996)                               |  |
| 2        | <b>Moerbeke 'Suikerfabriek'</b>              | AMS                                  | LP/1a, 1b, 1c, 2a1, 2a2, 2b, 5  | GS-2, GI-1e, GI-1d, GI-1c3, GI-1c2, GI-1c1, GI-1b, Holocene                                   | 1, 2, 3, 4, 5           | Bos et al. (2017, 2018a)                               | LOI/CaCO <sub>3</sub> , Magnetic susceptibility, Micromorphology, Diatoms, Ostracods, Molluscs, Chironomids, d13C+d18O |
| 3        | <b>Moerbeke 'Driehoek'</b>                   | NA                                   | 1b, 1c, 2a1, 2a2  | GI-1e, GI-1d, GI-1c3, GI-1c2, GI-1c1  | 1, 2, 3, 4              | Crombé et al. (2020)                                   | LOI/CaCO <sub>3</sub> , Grainsize  |
| 4        | <b>Klein-Sinaai 'Boudelo'</b>                | AMS                                  | 1b, 1c, 2a1, 2a2, 2b, 5, 6  | GI-1e, GI-1d, GI-1c3, GI-1c1, GI-1b, Holocene   | 1, 2, 3, 4, 5, 7        | Bos et al. (2018c)                                     | LOI/CaCO <sub>3</sub> , Grainsize  |
| 5        | <b>Rieme 'Noord'</b>                         | AMS                                  | 1b, 1c, 2a1 (3 records)   | GI-1e, GI-1d, GI-1c3, GI-1c2, GI-1c1  | 1, 2, 3, 5              | Bos et al. (2013)                                      | LOI/CaCO <sub>3</sub> , Chironomids  |
| 6        | <i>Wachtebeke 'Heidebos'</i>                 | AMS                                  | 1b, 1c, 2a, 4c?, 5, 6   | GI-1e, GI-1d, GI-1c, Holocene   | 1, 2, 3                 | Derese et al. (2010), Crombé et al. (2012), this paper | Micromorphology, OSL dating  |
| 7        | <i>Mendonk / Moerbeke 'Noord'</i>            | Bulk                                 | 1b, 1c, 2b-6 (multiple short records)                                       | GI-1c1/1b, Holocene   | 1, 6, 7                 | Meylemans et al. (2011a)                               |  |
| 8        | <i>Wachtebeke 'Penen'</i>                    | AMS                                  | 3a, 3b  | GS-1  | 5                       | this paper   |  |
| 9        | <b>Moerbeke 'Peerdemeers'</b>                | AMS                                  | 3a, 3b, 4a, 4b  | GS-1, 11.4, Holocene  | 6                       | Bos et al. (2018b)                                     | LOI/CaCO <sub>3</sub> , Grainsize, Magnetic susceptibility, Diatoms, Ostracods, d13C+d18O                              |
| 10       | <b>Daknam 'Broek'</b>                        | AMS                                  | 3b, 4a, 4b, 4c, 5, 6  | GS-1, 11.4, Holocene  | 6, 7                    | Zwier (2018)   |  |
| 11       | <i>Zelee 'Hoekstraat'</i>                    | AMS                                  | 4b, 4c, 5, 6  | 11.4, Holocene  | 6, 7                    | Storme et al. (2017)                                   |  |
| 12       | <i>Moerbeke Terweststraat</i>                | AMS                                  | 1b, 1c, 2a1, 2a2 (3 records)  | GI-1e, GI-1d, GI-1c3, GI-1c2, GI-1c1  | 1, 2, 3, 4              | Verbruggen (2021)                                      | LOI/CaCO <sub>3</sub> , OSL dating   |
| 13       | <i>Moerbeke 'Wulfsdonk'</i>                  | AMS                                  | 1b, 1c, 2a1, 2a2  | GI-1e, GI-1d, GI-1c3, GI-1c2, GI-1c1  | 1, 2, 3, 4              | this paper   | LOI/CaCO <sub>3</sub> , Magnetic susceptibility  |
| 14       | <b>Klein 'Broek' (outside research area)</b> | Bulk                                 | 3b, 4b, 4c, 5, 6  | GS-1, 11.4, Holocene  | 6, 7                    | Storme et al. (2017)                                   |  |

The Lateglacial and early Holocene zones described by Hoek (1997a, 1997b) reach from 1 t/m 5. In this table zone number 6 is added representing the Atlantic period following Verbruggen et al. (1996). Sites in bold were included in the regional vegetation overview as discussed in section 'Overview of regional vegetation development'.

**Table 2.** Overview of prehistoric sites within the Moervaart region.

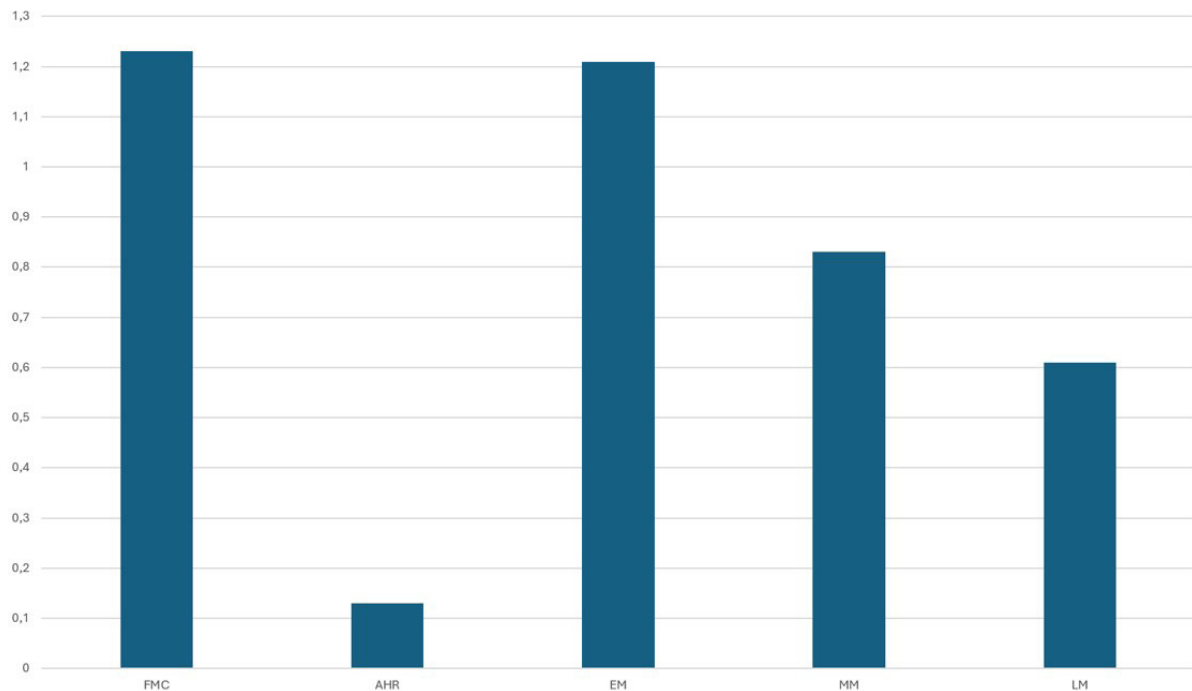
| Site name                       | Latitude      | Longitude    | FMC | AHR | EM | MM | LM |
|---------------------------------|---------------|--------------|-----|-----|----|----|----|
| Daknam 911/912                  | 51°07'28"N    | 3°58'24"E    |     |     | X  |    | X  |
| Daknam Bormte                   | 51°08'19"N    | 3°59'05"E    |     |     | X  |    |    |
| Daknam Werkstede I              | 51°07'26"N    | 3°58'27"E    |     |     | X  |    | X  |
| Eksaarde Fondatie               | 51°09'24"N    | 3°59'50"E    |     |     | X  | X  | X  |
| Kemzeke Moortelbeek I           | 51°11'34.53"N | 4°02'48.38"E | X   |     |    |    |    |
| Kemzeke Moortelbeek II          | 51°11'39"N    | 4°02'43"E    |     |     | X  | X  |    |
| Klein-Sinaai Boudelo            | 51°10'44"N    | 3°59'35"E    | X   |     | X  |    |    |
| Lokeren Eekwijk I               | 51°08'41.01"N | 3°59'02.48"E |     |     | X  |    |    |
| Lokeren Werkstede II            | 51°07'21.29"N | 3°58'16.60"E |     |     |    |    | X  |
| Mendonk 30                      | 51°09'06.33"N | 3°50'23.85"E |     |     | X  | X  |    |
| Moerbeke Suikerfabriek          | 51°10'18"N    | 3°55'22"E    | X   |     | X  |    |    |
| Moerbeke Caudenborn             | 51°10'29"N    | 3°58'13"E    | X   |     |    |    |    |
| Moerbeke Driehoek               | 51°10'41"N    | 3°58'58"E    | X   |     |    |    |    |
| Moerbeke Terwest                | 51°10'22"N    | 3°54'25"E    |     |     |    |    | X  |
| Moerbeke Vossel                 | 51°10'29"N    | 3°57'44"E    | X   |     |    |    |    |
| Sinaai Einde                    | 51°08'47"N    | 3°59'32"E    |     |     | X  |    |    |
| Sinaai Eindeken                 | 51°09'15"N    | 3°59'20"E    |     |     | X  |    |    |
| Sinaai Leebrug II               | 51°09'09"N    | 4°00'9"E     |     |     | X  |    |    |
| Sint-Kruis-Winkel Spanjeveer    | 51°08'55"N    | 3°48'29"E    |     |     | X  | X  | X  |
| Sint-Kruis-Winkel Winkelwarande | 51°09'18"N    | 3°50'03"E    |     |     | X  |    |    |
| Stekene Hazenhoek               | 51°12'17.75"N | 4°01'31.15"E |     |     | X  | X  |    |
| Stekene Heirweg                 | 51°10'53.39"N | 4°00'25.28"E | X   |     |    |    |    |
| Stekene Meulenvijver            | 51°11'11"N    | 4°00'56"E    | X   |     |    |    |    |
| Stekene Molenberg               | 51°12'20.70"N | 4°01'49.74"E |     |     | X  |    | X  |
| Stekene Noordscheidbeek         | 51°13'16.13"N | 3°59'41.27"E |     |     |    | X  | X  |
| Stekene Preikershei             | 51°13'32.68"N | 4°02'41.65"E |     |     |    | X  |    |
| Stekene Vogelzang               | 51°13'12.57"N | 4°01'50.76"E | X   |     |    |    |    |
| Wachtebeke 'T Mat               | 51°09'57"N    | 3°52'50"E    | X   |     | X  |    | X  |
| Wachtebeke Kalve                | 51°10'07"N    | 3°52'47"E    | X   |     | X  |    |    |
| Wachtebeke Kloosterbos          | 51°10'35"N    | 3°50'23"E    |     |     |    |    | X  |
| Wachtebeke Langelede            | 51°11'55.71"N | 3°51'45.40"E |     |     |    |    | X  |
| Wachtebeke Oostdonk             | 51°09'11"N    | 3°51'02"E    | X   |     | X  |    |    |
| Wachtebeke Oudenburgse Sluis    | 51°12'30.34"N | 3°51'27.72"E |     |     | X  | X  |    |
| Wachtebeke Overlede             | 51°09'40"N    | 3°51'35"E    | X   |     |    |    |    |
| Wachtebeke Overslagdijk         | 51°12'28.51"N | 3°52'31.22"E |     | X   | X  |    |    |
| Wachtebeke Potdam               | 51°09'43"N    | 3°52'08"E    |     | X   | X  |    |    |
| Wachtebeke Walderdonk           | 51°10'19"N    | 3°50'31"E    |     |     |    | X  |    |
| Wachtebeke Warande              | 51°09'40"N    | 3°50'44"E    |     |     | X  |    | X  |

FMC = *Federmesser* Culture; AHR = Ahrensburgian Culture; EM = early Mesolithic; MM = middle Mesolithic; LM = late Mesolithic.

uniform area. Therefore vegetation–landscape relations (i.e. what type of vegetation community is present on which landscape unit) derived from single site reconstructions can be used to convert landscape units into vegetation communities in areas outside of the direct surroundings of palynological sampling sites. The method is an interpretative approach and thus takes into account, although non-numerically, the variations in pollen productivity and dispersal characteristics between and per species, and the characteristics of the entire plant community such as landscape openness and structure (e.g. Broström et al., 2004; Bunting & Farrel 2022; Gaillard et al., 2008; Sugita et al., 1999).

Our reconstructions do not show the distribution or absolute coverage of individual species. However, the usage

of plant communities instead of single species minimises potential errors regarding visibility and representation of singular species in the pollen record (Fyfe et al., 2015; Janssen, 1974; Woodbridge et al., 2014). The first step in establishing these vegetation–landscape relations was the development of an overview of regional vegetation development. This regional overview was used to identify the main plant communities present in the region during each time period. These plant communities were allocated to landscape units using their ecological preferences. Using the established links between vegetation units and landscape units, the palaeogeographical maps of the Moervaart region were converted into seven vegetation maps. In addition, three 3D renders or artist impressions of the



**Figure 3.** Number of prehistoric sites per century for different archaeological phases/cultures within the Moervaart region. FMC = *Federmesser* Culture; AHR = Ahrensburgian Culture; EM = early Mesolithic; MM = middle Mesolithic; LM = late Mesolithic.

**Table 3.** Absolute and converted number of prehistoric sites per archaeological phase/culture within the Moervaart region.

| Archaeological phase/culture     | Biozone                        | N of sites | Boundaries cal BP | Duration yr | N of sites/ 100y |
|----------------------------------|--------------------------------|------------|-------------------|-------------|------------------|
| <i>Federmesser</i> Culture (FMC) | Allerød                        | 13         | 13,904–12,846     | 1,058       | 1.23             |
| (Epi)Ahrensburgian Culture (AHR) | Younger Dryas-early Preboreal  | 2          | 12,846–11,350     | 1,496       | 0.13             |
| Early Mesolithic (EM)            | Late Preboreal-1st half Boreal | 23         | 11,350–9,456      | 1,894       | 1.21             |
| Middle Mesolithic (MM)           | 2nd half Boreal                | 10         | 9,456–8,257       | 1,199       | 0.83             |
| Late Mesolithic (LM)             | Atlantic                       | 12         | 8,257–6,300       | 1,957       | 0.61             |

Chronological boundaries are based on Van Maldegem et al. (2021) and Rasmussen et al. (2014).

palaeoenvironment for the early Allerød, Preboreal/Boreal and the Middle Holocene were produced by Ulco Glimmerveen which are also included in this paper.

### Palaeogeographical maps

For each of the investigated time slices, a detailed abiotic landscape map incorporating palaeogeographical, lithological, geomorphological and elevation data was constructed. These maps were used as a base for the vegetation reconstruction maps and are shown in the result section. This data was obtained through:

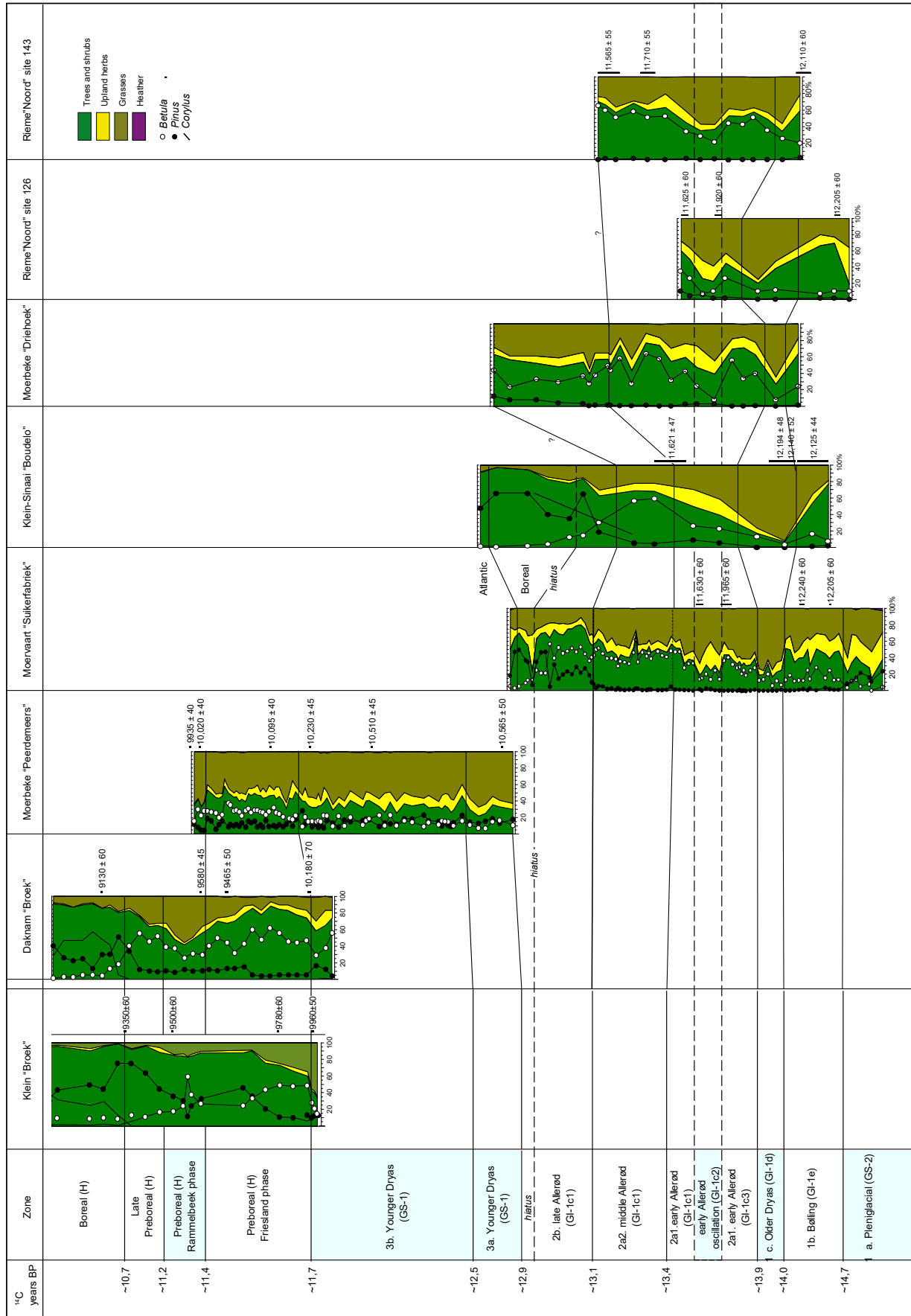
- The geomorphological map of the study region (Heyse, 1979) which was used as a basis for the palaeogeographical maps and adjusted with features identified on the Flemish Light Detection and Ranging (LiDAR)-based Digital Elevation Model (DEM) (Werbrouck et al., 2011).
- In total, 930 manual augerings in north-south transects and several mechanical drillings using Begemann and Nordmeyer HBS-RKR drills at specific sampling

locations added further details to the geological mapping of palaeochannels (Crombé et al., 2013).

- Furthermore, targeted geophysical surveys using a mobile multi-receiver electromagnetic induction instrument for mapping the soil apparent electrical conductivity (ECA), in the central part of the Moervaart palaeolake to determine the position of palaeochannels and distribution of lake sediments (De Smedt et al., 2011, 2013).
- The palaeogeographic insights gained through (bio-)stratigraphic analyses and dating retrieved from the cores and excavated sections were extrapolated to the landform features identified in the geomorphological map, which enabled the determination of the age and distribution of the geological elements in the area and the construction of geomorphological maps for the different time slices.

### Chronology of the vegetation development

Chronology of the records in the Moervaart region was based on radiocarbon dates (Supplementary Table 1) and on the



**Figure 4.** Correlation diagram, showing the relative values of a number of indicator species (*AP*, *Betula*, *Pinus*, *Corylus*, *Ericales*, *Poaceae* and *NAP*) in the main diagrams, plotted on the calibrated time scale.

**Table 4.** Description of the vegetation units and their placement factors identified in the wider Moervaart region during the Bølling to Boreal.

| Vegetation unit  | Landscape unit   |
|--|--|
| <b>Bølling – GI-Ie</b>   |  |
| Open dwarf shrub tundra vegetation with heliophilous herbs                                       | Coversand plains   |
| Open tundra vegetation with heliophilous herbs, bare ground and scattered shrubs such as juniper | Great coversand ridge and coversand ridges                                 |
| Swamp with dwarf birch   | Low areas surrounding Moervaart depression                                 |
| Grassy marsh vegetation with willow and sedges   | Western side Moervaart depression (floodplain river) , dune ponds on ridge |
| Shallow water  | Moervaart depression eastern part  |
| Flowing water  | Anastomosing riversystem   |
| <b>Older Dryas – GI-Id</b>   |  |
| Open tundra vegetation with grasses and scattered shrubs such as juniper                         | Great coversand ridge and coversand ridges                                 |
| Open tundra vegetation with grasses  | Coversand plains   |
| Open tundra vegetation with dwarf birch and willow   | Low areas surrounding Moervaart depression                                 |
| Marsh vegetation intersected by small river channels   | Anastomosing riversystem   |
| Marsh vegetation with grasses and sedges   | Moervaart depression, eastern side   |
| Marsh vegetation with grasses, sedges and willow   | Moervaart depression, western side   |
| Barren ground  | High exposed areas of the Great Coversand ridge                            |
| <b>Early Allerød – GI-Ic3</b>  |  |
| Open birch forest with herbs and shrubs  | Coversand plains   |
| Open vegetation with grasses and herbs, some scattered shrubs                                    | Great coversand ridge and coversand ridges                                 |
| Marsh vegetation with grasses, dwarf birch and willow  | Lake edge and river islands  |
| Flowing water  | Anastomosing riversystem   |
| Water  | Lake and deeper dune ponds on ridge  |
| <b>Middle Allerød GI-Ic1</b>   |  |
| Birch forest with herbs and shrubs   | Coversand plains   |
| Open herbaceous vegetation with grasses and scattered shrubs such of juniper                     | Great coversand ridge and coversand ridges                                 |
| Marsh vegetation with sedges   | River floodplain and former lake   |
| Open shallow water, small islands with marsh vegetation  | Dune ponds on ridge  |
| Flowing water  | Kale/Durme river   |
| Water  | Lake (Moervaart depression)  |
| <b>Late Allerød – GI-Ic1/Ib</b>  |  |
| Open pine forest   | Great coversand ridge  |
| Open birch – pine forest   | Coversand ridges   |
| Open birch forest with herbs and shrubs  | Coversand plains   |
| Herbaceous vegetation with stand of birch and pine   | Dune ponds on ridge  |
| Marsh vegetation with sedges   | Floodplain Kale/Durme river  |
| Marsh vegetation with sedges, small pools of water   | Former lake (Moervaart depression)   |
| Water  | Lake (Moervaart depression)  |
| Flowing water  | Kale/Durme river   |
| <b>Late Preboreal –</b>  |  |
| Pine forest with scattered birch trees   | Great coversand ridge  |
| Birch -pine forest   | Coversand plains and ridges  |
| Birch carr with aspen and ferns  | Floodplain Kale/Durme river  |
| Open grassland   | Former lake (Moervaart depression)   |
| Flowing water  | Kale/Durme river   |
| <b>Boreal</b>  |  |
| Pine forest  | High, dry coversand windward side  |
| Deciduous forest with oak, elm and hazel   | Great coversand ridge leeward side and coversand plains and ridges         |
| Birch carr with aspen  | Floodplain Kale/Durme river  |
| Grassland  | River dune   |
| Grassland with stands of willow carr   | Former lake (Moervaart depression)   |
| Flowing water  | Kale/Durme river   |

biostratigraphy of the pollen diagrams of the available sequences. OSL dates were only performed on the aeolian sediments at Wachtebeke 'Heidebos' (Derese *et al.*, 2010). Radiocarbon dates were converted to calendar years using CALIB 8.2 and the INTCAL20 calibration curve (Reimer *et al.*, 2013; Stuiver & Reimer, 1993; Stuiver *et al.*, 2020). As the number of dates for each record was limited, no age models were constructed. Radiocarbon ages are expressed in  $^{14}\text{C}$  years BP and calibrated ages are reported in cal yrs BP. Each diagram was visually subdivided into regional pollen assemblage zones (= regional PAZ) reflecting the same pollen content and time interval. These PAZs were correlated to the Greenland ice core records (Rasmussen *et al.*, 2014) as well as with the Lateglacial and early Holocene pollen zonation scheme for the Netherlands and northern Belgium (Hoek, 1997a, 1997b), The Holocene PAZ of the the Boreal and Atlantic were compared to Verbruggen *et al.* (1996) and Storme *et al.* (2017) (Table 1). The ages for the established pollen assemblage transitions in the Lateglacial and early Holocene are consistent with Hoek (1997b, 2001), Bos (2007) and Storme *et al.* (2017). This correlation indicates that the Moervaart regional PAZ can be correlated with the established major climatic and environmental events as recorded in the terrestrial and marine records of the North Atlantic region and Greenland oxygen isotope records (Björck *et al.*, 1998; Blockley *et al.*, 2012; Lowe *et al.*, 2001, 2008; North Greenland Ice-Core Project Members, 2004; Rasmussen *et al.*, 2014) and thus results in a robust chronology. When sufficient datapoints – over five sites – per PAZ were available, this biozone was included as a vegetation reconstruction map in this study.

### Overview of the vegetation development

An overview of the regional vegetation development during the Lateglacial and early Holocene is shown in a correlation diagram (Figure 4). This compilation of several pollen diagrams from the region shows the relative values of dominant taxa in the vegetation development (AP, *Betula*, *Pinus*, *Corylus*, Ericales, Poaceae and NAP). The main diagrams were stratigraphically arranged next to the calibrated time scale, using the PAZ-boundaries as markers to show the regional vegetation succession through time. Dated intervals with AMS  $^{14}\text{C}$  are also shown. Pollen diagrams which represent larger time slices of the Lateglacial and/or early Holocene were included and plotted. Pollen diagrams with only a few pollen spectra or large hiatuses were excluded from this overview but were still used for the reconstruction maps. The correlation diagram was subdivided into PAZs (see above), and for all sites, a pollen sum was used defined by Hoek (1997b) which includes all trees, shrubs, upland herbs and grasses. From this dataset, vegetation units present during each investigated time slice were established (Table 4). First, the pollen data were interpreted into terms of plant communities. Pollen records reflect both a regional as well as a local vegetation signal. The local vegetation type and component was identified using the ecological characteristics and the environmental setting of the sample and taken into account when interpreting the data (e.g. Bradshaw & Webb III, 1985; Jackson, 1990; Jacobson & Bradshaw, 1981; Janssen, 1973, 1981, 1984). Secondly, the plant communities were matched to the geomorphological landscape units, using the ecological preferences of these communities (Weeda *et al.*, 2000, 2002, 2003, 2005) and the reconstructed abiotic characteristics of the landscape. When multiple plant communities

match to an abiotic landscape element, the relative abundance of these communities in the pollen record was taken into account as both a measure of the proximity of the plant community to the sampling site as well as an indication of the total acreage of each community.

In addition, the correlation diagram may be used for future biostratigraphic correlation in the Moervaart region. The pollen diagrams were constructed using TILIA (Grimm, 1992–2021). Vegetation development per time period is described in the result section.

## Results and discussion

In this section, the vegetation reconstruction maps and climate conditions are described and the resultant vegetation patterns are compared to habitation patterns. To provide a complete overview of the vegetation development of the region, PAZs for which a vegetation map could not be reconstructed as a result of limited data availability are still, briefly, discussed.

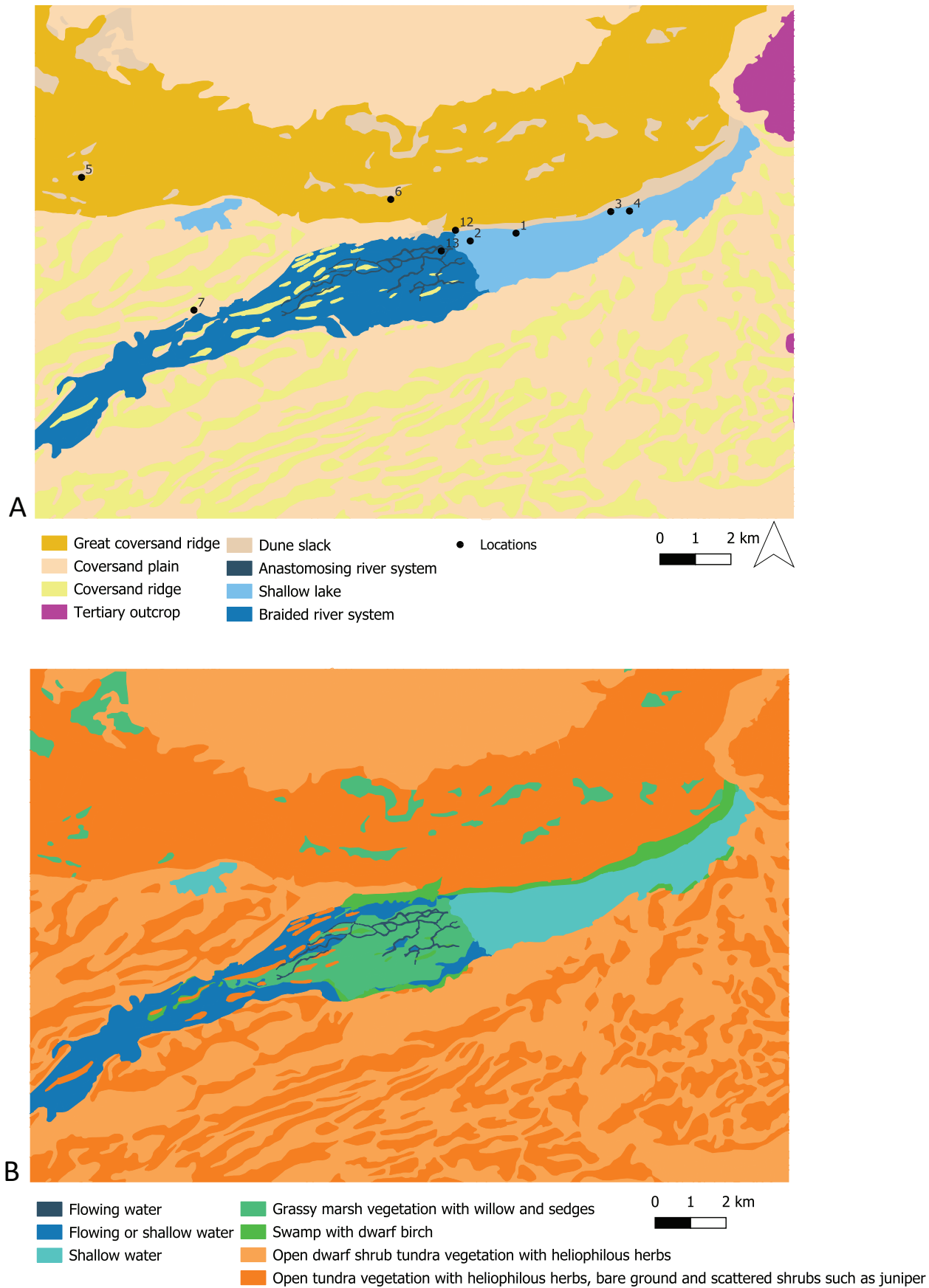
### Pleniglacial (corresponding to GS-2; till ~14,700 cal. yr BP)

There is only one site in the Moervaart region, Moerbeke 'Suikerfabriek' (Bos *et al.*, 2017, 2018b), that reflects the late Pleniglacial vegetation. Therefore no landscape and vegetation map from this period was made. Climate during the late Pleniglacial was cold and dry, as indicated by the botanical and zoological data, with a minimum mean July temperature (MMJT) of 7–8°C (Bos *et al.*, 2017). The landscape was very open with bare ground and steppe-tundra vegetation, consisting of grasses, sedges, heliophilous herbs and some shrubs of juniper (*Juniperus*). In the Moervaart depression, a wet meadow developed with shallow pools. There are no archaeological finds indicating human presence in this period, just like other regions in NW Europe (Deeben & Rensink, 2005; Grimm & Weber, 2008; Stapert, 2005). Climatic and environmental conditions in this area were probably unsuitable for human occupation in the late Pleniglacial.

### Bølling (corresponding to GI-1e; ~14,700 – ~14,000 cal. yr BP)

The Bølling is marked by an increase in both January and July temperatures. Based on chironomids from the Moerbeke 'Suikerfabriek' site, mean July temperatures of ~16–17°C could be inferred for the Bølling, which is in agreement with a plant-based MMJT of 10–16°C (Bos *et al.*, 2017). Rising groundwater levels led to the formation of a shallow lake in the eastern part of the Moervaart depression, that was partly fed by a fluvial anastomosing river system from the western section of the Moervaart depression (Crombé *et al.*, 2013) (Figure 5a and b). This western lake section was further characterised by a marsh vegetation with occasional stands of willow. Increasing groundwater levels in combination with the still limited dune height also resulted in the formation of ponds and dune-slacks extending over large parts of the adjacent Great Sand Ridge of Maldegem-Stekene, as attested at Rieme 'Noord' (Bos *et al.*, 2013) and Wachtebeke 'Heidebos' (Crombé *et al.*, 2012; Derese *et al.*, 2010) in which a marsh vegetation was present.

Dwarf shrub tundra developed in large parts of the research area in this period. In comparison to the sites on the coversand ridge, the sites in the Moervaart depression show higher values of birch pollen, suggesting a larger abundance of dwarf-birch



**Figure 5.** (A) Palaeogeographical map for the Moervaart region depicting the landscape during the Bølling, including locations of palynological data. (B) Vegetation reconstruction map for the Moervaart region depicting the vegetation units present during the Bølling.

vegetation in the depression. Dwarf-birch (*Betula nana*) grows on wet but well-drained areas, often sloping, with a nutrient-poor, acidic soil and is found in arctic/alpine tundra and bogs, swamps and fens (De Groot et al., 1997; Mossberg et al., 1997). In the Moervaart depression, dwarf birch was probably present in swamps along the shallow Moervaart palaeolake. On the sloping soils of the coversand ridge, vegetation was more open, with less shrubs of dwarf-birch and willow and more juniper, heliophilous herbs and bare ground. Especially around the Rieme 'Noord' sites, juniper vegetation strongly expanded on the bare, sandy substrates of the coversand ridge. At Rieme 'Noord' and Wachtebeke 'Heidebos', organic layers in the dune ponds were intercalated with sandy layers, which suggests that deposition of aeolian sands locally continued. The Moervaart palaeolake sites indicate that in the lake, mesotrophic, oxygen-rich and calcareous-rich conditions prevailed (Bos et al., 2017, 2018b, 2018c; Crombé et al., 2020). Plants, such as willow (*Salix*), sedges and semi-aquatics fringed the shores of the Moervaart lake; this small vegetation zone is not included as a separate vegetation unit. During this period, willow was more abundant in the marsh vegetation at the Klein-Sinaai 'Boudelo' site, which is likely related to the location of the site, slightly closer to the lake shore in comparison the other sites in the Moervaart depression.

Even though temperatures had increased, there is so far no evidence of human presence in the area during the Bølling. This is in agreement with other regions within the sandy lowlands of northern Belgium and southern Netherlands (De Bie & Vermeersch, 1998; Kramer, 2012). The sparsely vegetated landscape, in combination with ongoing aeolian activity, was probably still unsuitable for human occupation (Crombé et al., 2011). In addition, the environment was probably still overall too wet for human settlement as the coversand dunes were not yet well-developed and not high and thus dry enough for erecting campsites. Furthermore the lack of good-quality flint and voluminous nodules, essential for the production of long standardised blades typical of the (late) Magdalenian and Creswellian Culture (Pigeot, 1987; Stapert, 1985; Valentin, 2008) might have played a role.

#### **Older Dryas (corresponding to GI-1d; ~14,000 – ~13,900 cal. yr BP)**

The Older Dryas is characterised by a temporary change to colder and drier conditions and corresponds with a centennial-scale cold oscillation (GI-1d) between 14,025 and 13,904 cal yrs BP (14,075–13,954 b2k) in the oxygen isotope record of the Greenland ice-cores (Rasmussen et al., 2014). At the Moerbeke 'Suikerfabriek' site, chironomid-inferred mean July temperatures show a minor decrease to just below 16°C (Bos et al., 2017). In addition, at this site, fossil soil wedges or frost cracks were present in the top of the Older Dryas deposits, which indicate mean annual air temperatures below –1 to 0°C (Huijzer & Isarin, 1997; Maarleveld, 1976) and thus very cold winters. A general lowering of the groundwater occurred in the Moervaart region stimulating wind erosion. This locally led to an increase in the height of the Great Coversand Ridge of Maldegem-Stekene (Crombé et al., 2013; Derese et al., 2010).

The climatic changes resulted in the development of a grass-steppe tundra in the Moervaart region and an increase in barren ground, mainly on the higher coversand ridge (Figure 6a and b). Grass communities expanded both on the coversand ridge, as well as in the lower areas surrounding the Moervaart

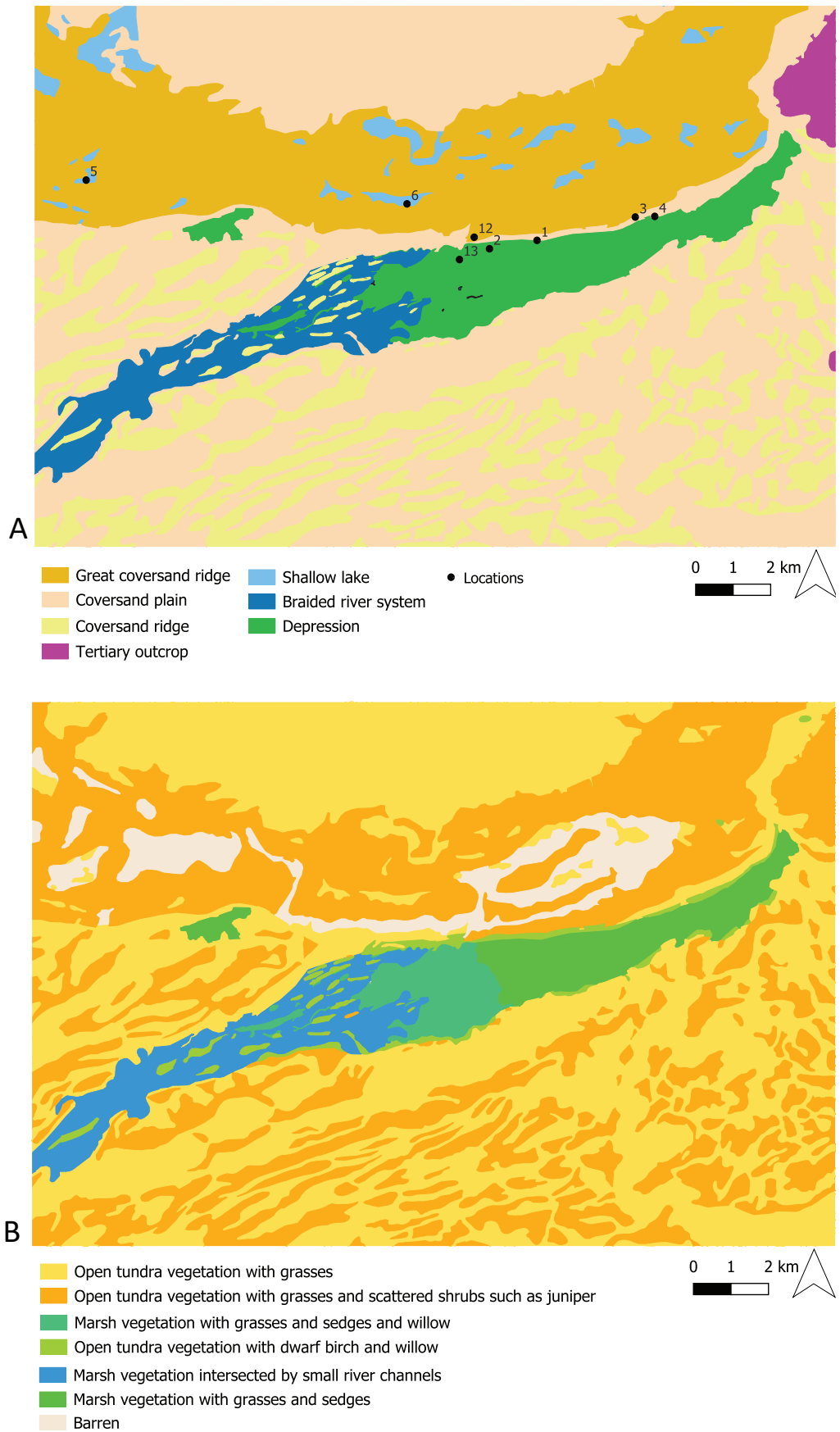
depression. Shrubs, such as juniper, sea buckthorn (*Hippophae*) and scattered dwarf willows, were present on the coversand ridge and were occasionally found in the lower region. Dwarf-birch and willow probably inhabited the wetter areas with more organic-rich soils along the Moervaart depression. Lower lake levels as a result of the drier conditions occurred in the Moervaart palaeolake resulting in the development of marsh vegetation. Water flowed into the depression from the western side via small river channels which gradually disappeared into the marshy environment. At the Moerbeke 'Suikerfabriek' site, a marsh with pools of open water developed and further east, around the Moerbeke 'Moervaart', Moerbeke 'Driehoek', Moerbeke 'Wulfsdonk' and Klein-Sinaai 'Boudelo' sites locally a wet meadow developed. In the ponds and dune-slacks on the Great Sand Ridge of Maldegem-Stekene, at Rieme 'Noord' and Wachtebeke 'Heidebos', water levels also lowered and drier vegetation types developed although the depressions contained a higher portion of willow. Towards the end of the Older Dryas, conditions in the region became wetter.

As climatic and environmental conditions temporarily deteriorated, it is not surprising that there is no evidence for human occupation of the area during the Older Dryas.

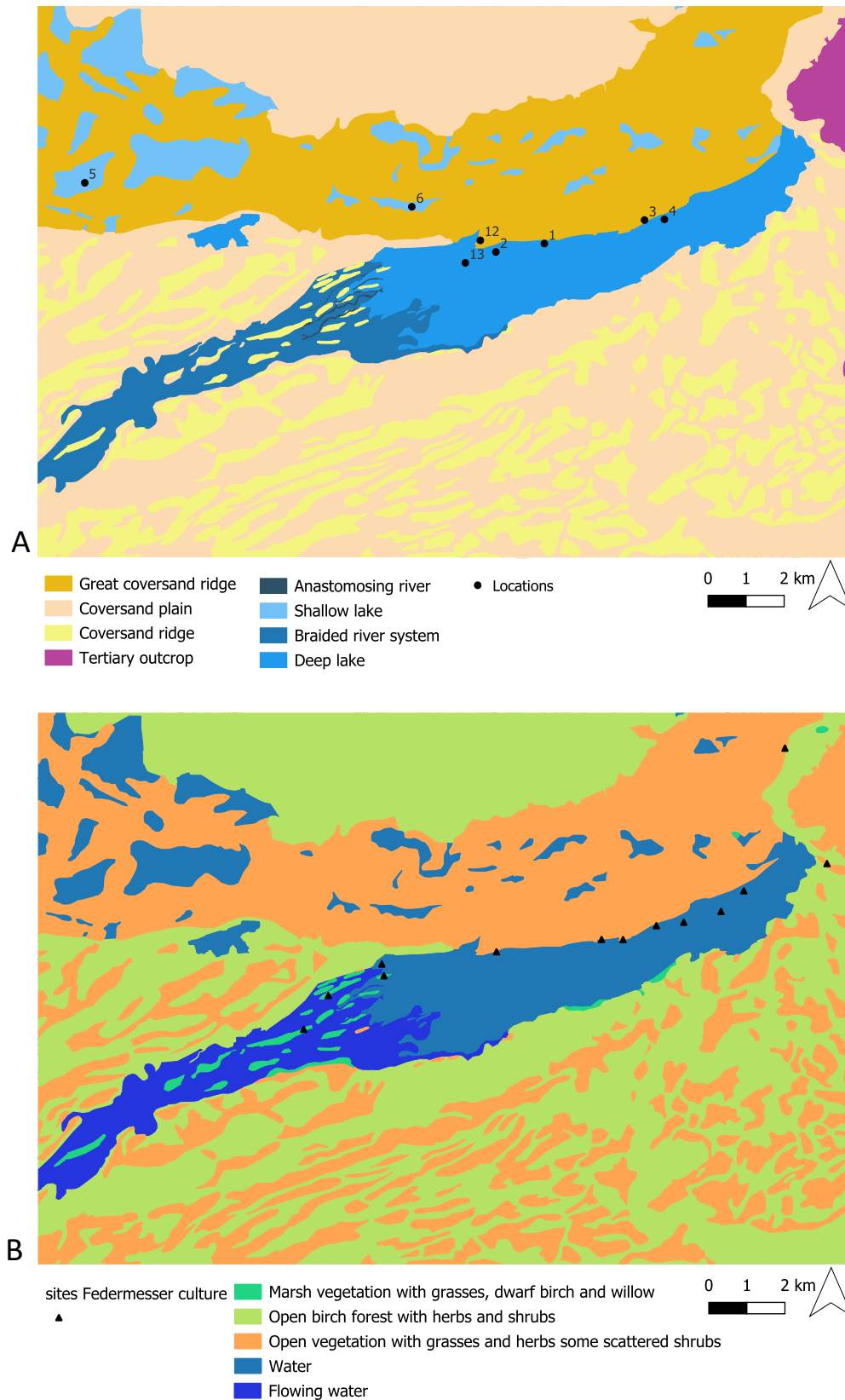
#### **Early Allerød (corresponding to GI-1c3; ~13,900 – ~13,400 cal. yr BP)**

In the early Allerød, temperatures increased again and ground-water levels rose resulting in wetter conditions. Chironomid-inferred July temperatures at the site Moerbeke 'Suikerfabriek' estimate a ~16.5°C in this period (Bos et al., 2017). This is in agreement with a plant-based MMJT of 12–15°C for this site. The renewed groundwater level rise resulted in a deepening of the Moervaart palaeolake as well as a water level rise in the ponds and dune-slacks on the coversand ridge (Bos et al., 2013, 2017; Crombé et al., 2012; Derese et al., 2010; Verbruggen 2021). The lake was fed by anastomosing channels from the west as well as an influx of groundwater from the adjacent coversand ridge (Crombé et al., 2013). At the end of the early Allerød, the Moervaart palaeolake reached its largest and deepest phase (max. 2.5 m at the Moerbeke 'Suikerfabriek' site, Bos et al., 2018a).

The warm and wet conditions promoted soil formation and the development of more nutrient-rich habitats. Tree-birch (*Betula cf. pubescens*) immigrated into the region as seen in both the pollen and macrofossil records and birch woodlands developed (Fig. 7a and b and Fig. 12a). Woodlands remained open with an understorey of various herbs and shrubs. On the more exposed, sandy soils of the Great Coversand Ridge and smaller coversand ridges in the southern part of the area, vegetation was more open consisting of a grass vegetation with a variety of herbs and also with juniper, dwarf willow and sea-buckthorn. The deepening of the Moervaart palaeolake caused an expansion of aquatic vegetation with submerged aquatics in the deeper parts of the lake, while floating-leaved vegetation developed in the shallower zones. The western part of the lake transitioned in an anastomosing river system resulting in more flowing water on this side. In the moist areas of the western Moervaart depression and along the shores of the palaeolake, marsh vegetation and wet meadows with grasses were present. Since this marsh vegetation, which also included sedges and other riparian taxa, formed a relatively small zone, it could not be presented on the vegetation maps as a separate unit. Dwarf birch and willow were also found



**Figure 6.** (A). Palaeogeographical map for the Moervaart region depicting the landscape during the Older Dryas, including locations of palynological data. (B) Vegetation reconstruction map for the Moervaart region depicting the vegetation units present during the Older Dryas.



**Figure 7.** (A) Palaeogeographical map for the Moervaart region depicting the landscape during the early Allerød, including locations of palynological data. (B) Vegetation reconstruction map for the Moervaart region depicting the vegetation units present during the early Allerød, site distribution of the *Federmesser* culture is also shown.

in the swamps along the palaeolake and along the ponds and dune-slacks on the coversand ridge. Along the shores of the ponds and probably the palaeolake, reed swamps were also present; but these vegetation elements were too small to be accurately mapped.

A short and pronounced short-term climatic oscillation is visible within the early Allerød in the records from Moerbeke 'Moervaart', Moerbeke 'Suikerfabriek', Moerbeke 'Driehoek', Rieme 'Noord' and Moerbeke 'Terweststraat' (Table 1; Figure 4). This oscillation likely corresponds with a centennial scale cold oscillation (corresponding to Greenland Interstadial-1c2) in the oxygen isotope record of the Greenland ice-cores (Rasmussen et al., 2014) that was dated between 13,610 and 13,550 cal yrs BP (=13,660–13,600 b2k). This short oscillation is not included as a vegetation reconstruction map since it was not recorded in sufficient records. In the Moervaart 'Suikerfabriek' and Rieme 'Noord' (location 126) records, the base and top of this oscillation were dated, which correspond well with the ages in the ice-core records (Supplementary Table 2, Bos et al., 2013, 2017). The chironomid-inferred temperature curve of Moervaart 'Suikerfabriek' shows a ~2°C temperature decline to ~14.6°C, which is slightly colder than during the Older Dryas (GI-1d). Both the mollusc and ostracod data also point to colder conditions during this period (Bos et al., 2017). In the pollen data, the event is recognised as a distinct dip in the tree and shrub values and a strong increase in herbaceous pollen, especially grasses, sedges and various herbs. This suggests that the landscape temporarily became more open with more barren ground and herb and grass vegetation. Birch trees likely survived in more sheltered areas along the Moervaart palaeolake and on the coversand ridge near Rieme 'Noord' (Bos et al., 2013). The more open vegetation and larger area of barren ground resulted in an increase in aeolian activity which deposited sandy layers in the dune-slacks and ponds on the coversand ridge and in the Moervaart palaeolake. The difference between this oscillation and the Older Dryas (GI-1d) is that during GI-1c2 more heliophilous herbs and less grasses were present in the regional vegetation around the Moervaart palaeolake and that the mean air summer temperatures were probably slightly lower. In contrast to the Moervaart records, in the Greenland ice-cores oscillation GI-1d is much more pronounced than GI-1c2 (Rasmussen et al., 2014).

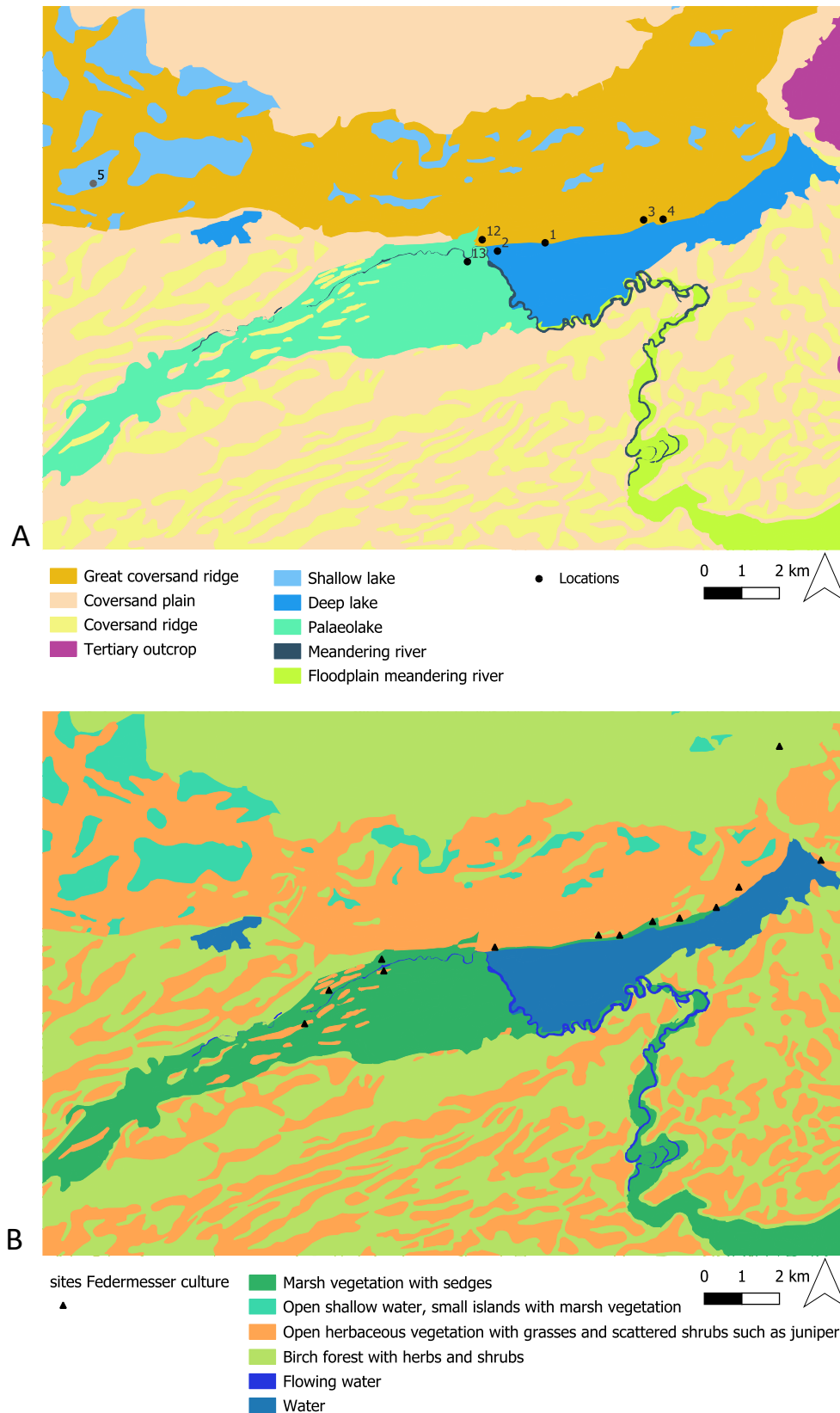
After a very long period of absence during and after the LGM, hunter-gatherers finally returned to the Moervaart region. Remains of the *Federmesser* Culture or Curve-Backed Point Groups, which occupied large parts of the NW-European Plain during the Allerød and locally already from the Older Dryas (Grimm et al., 2020), were collected on at least 13 locations (Crombé, 2020; Crombé & Robinson, 2017). Yet, given the numerous deflation events during and after the Allerød (cf. below), it can be reasonably assumed that there are still sites to be expected underneath aeolian sand deposits. One such site was already fortuitously discovered during the excavation of a Medieval abbey at Klein-Sinaai (Vanmoerkerke & De Belie, 1984). Unfortunately, none of the Moervaart sites have so far been radiocarbon-dated, hindering the development of a fine chronological framework and synchronisation of the *Federmesser* occupation with the climatic and environmental changes during the Allerød. However, within the lithic industries, there are technological indications that these hunter-gatherers were present during almost the entire duration of the Allerød (Crombé & Robinson, 2017). All *Federmesser* sites are situated

along the northern bank of the palaeolake, forming an almost continuous site-complex of temporary campsites stretching over ca. 15 km (Figure 7b). In the central and eastern part of the palaeolake sites are situated along the southern steep edge of the Great Sandridge Maldegem-Stekene, while further west they are positioned within the palaeolake on small levees bordering the anastomosing gullies. On the early Allerød vegetation map, some *Federmesser* sites are plotted in the lake itself. The water level and position of the shoreline of the Moervaart palaeolake fluctuated during the Allerød, and presumably these sites do not correspond to the period of lake high stand as depicted on this map. The total absence of *Federmesser* sites along the southern bank of the Moervaart palaeolake is most likely due to the absence of high and dry-enough coversand dunes close to the lake edge. This overall distribution pattern is very similar to the one observed in other areas of the coversand region, such as the Belgian-Dutch Campine. In the latter area, *Federmesser* sites also tend to cluster along the northern and western banks of former lakes (De Bie & Van Gils, 2006; Deeben, 1988). This is an interesting observation which might guide future surveys in the coversand region of NW Europe.

All sites are located in close proximity to a water source and most likely close to marsh vegetation. The density of *Federmesser* sites along the Moervaart palaeolake is remarkably higher compared to other areas within Sandy Flanders (Crombé et al., 2011), demonstrating the great attraction this extensive palaeolake had on contemporaneous hunter-gatherers. Probably they could return more frequently and/or stay longer along its margins due to its rich and varied ecology, making this palaeolake a kind of persistent place in the sandy lowland within a residential mobility system (Crombé & Robinson, 2017). The region provided *Federmesser* culture hunter-gatherers with permanent drinking water (i.e. Moervaart lake), extensive and fertile woodlands and lake edges for wild game hunting, plant gathering and fowling. Records of ascospores of coprophilous fungi at Rieme 'Noord', Moerbeke 'Suikerfabriek' and Moerbeke 'Driehoek' confirm that large herbivores (game) were present in the region. Large herbivores, including elk, were probably foraging in the meadows and open birch woodlands and used the lakes and ponds as drinking places (Bos et al., 2013; Crombé et al., 2020). The area with open forested areas and forest edges (boreal forests) alternated by lakes, marshes and springs and probably covered in winter by snow, was very suitable for large herbivores such as elk. Finally, settling along the steep southern lake bank also provided some protection against the prevailing winds that generally came from the (north)west (Heyse, 1979; 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.

#### ***Middle Allerød (corresponding to GI-1c1; ~13,400 – ~13,100 cal. yr BP)***

The middle Allerød was most likely a phase of intense wind deflation in the coversand region of NW Belgium (Crombé et al., 2020). Chironomid-inferred temperatures for this period are slightly lower than during the preceding early Allerød,

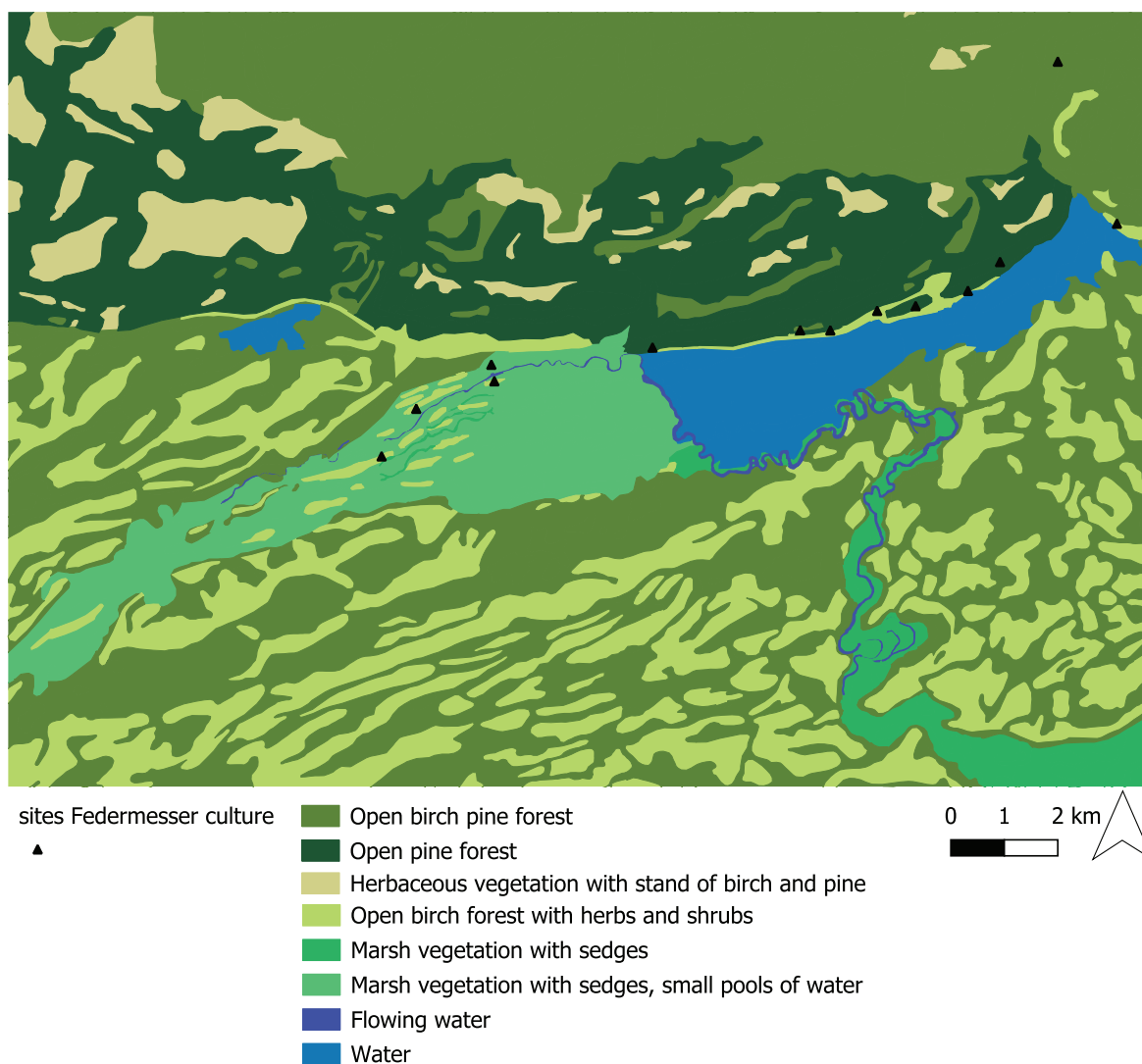


**Figure 8.** (A) Palaeogeographical map for the Moervaart region depicting the landscape during the middle Allerød, including locations of palynological data, sites in grey only used for late Allerød map. (B) Vegetation reconstruction map for the Moervaart region depicting the vegetation units present during the middle Allerød, site distribution of the *Federmesser* culture is also shown.

with an average mean July temperature of  $\sim 14.5^{\circ}\text{C}$  (Bos et al., 2017). On the coversand ridge, organic infilling of the dune-slacks and ponds at Rieme 'Noord' ceased at ca. 13,500 cal yrs BP (Bos et al., 2013). At these locations, only the accumulation of sand continued. Similar observations have been reported from other locations along the Great Coversand Ridge of Maldegem-Stekene (Cromb  et al., 2012). At Moerbeke 'Driehoek', stratified sands were found on top of the lacustrine deposits, dated roughly between 13,400 and 13,100 cal yrs BP (= middle Aller d). A similar deposition of wind-blown sands dating to the middle Aller d on top of an organic layer was observed at Beveren Properpolder 'Zuid' (Verhegge et al., 2020), ca. 25 km northeast of Moerbeke 'Driehoek', on the same Great Coversand Ridge of Maldegem-Stekene. This increase of wind erosion during the middle Aller d was probably not related to a climatic fluctuation, like during the GI-1c2 oscillation. It was, however, most likely caused by an increased occurrence of forest fires in the boreal birch woodlands in the Moervaart region resulting in an opening of the landscape. The slightly higher values of microscopic charcoal (including charred stomata and epidermis from grasses and sedges) and

ascospores of *Gelasinopora* recorded in various sites along the Moervaart palaeolake (i.e. Moerbeke 'Suikerfabriek', Moerbeke 'Driehoek' and Klein-Sinaai 'Boudelo') clearly point to the regular occurrence of fires in the entire research area during the middle Aller d. There is also little evidence which points to controlled fires by *Federmesser* hunter-gatherers; rather it seems that it concerns wildfires which were initiated by lightnings in the birch woodlands. During the high water-level phase of the Moervaart palaeolake, an outlet, the meandering Kale/Durme River was formed in the middle Aller d, at the eastern side of the lake (Figure 2). The increased outflow led to a lowering of the water level in the palaeolake.

During the middle Aller d, the vegetation on the Great Coversand Ridge was probably open, with herbaceous vegetation, grass vegetation and low shrubs of juniper, willow and sea buckthorn (Figure 8a and b). Initially, some birch trees may have survived at more sheltered locations on the Great Coversand Ridge; however, when wind deflation intensified, it is assumed that they probably disappeared from the ridge. On more sheltered locations such as the coversand plains south of the Moervaart depression, birch woodlands could further



**Figure 9.** Vegetation reconstruction map for the Moervaart region depicting the vegetation units present during the late Aller d, site distribution of the *Federmesser* culture is also shown. For palaeogeographical map see Figure 8a.

expand and became less open, while an open herbaceous vegetation type was present at the more exposed higher parts of the landscape. On the shores of the Moervaart palaeolake, a marsh vegetation was present with sedges. The lake during this time period was less deep which resulted in an increase in ferns and semi-aquatics and a decrease in floating-leaved deep water vegetation. Ultimately, the floating-leaved aquatic vegetation with white and yellow water lily (*Nymphaea alba*; *Nuphar lutea*) disappeared at the Moerbeke 'Suikerfabriek', Moerbeke 'Wulfdonk' and Moerbeke 'Driehoek' sites, when the water became too shallow (less than 1 m).

Lacking a fine chronology for the *Federmesser* occupation within the Moervaart region, it remains unclear if or to what extent the lower lake level as a result of increased drainage as well as the natural forest fires of the middle Allerød impacted the lifeways of contemporaneous hunter-gatherers.

#### **Late Allerød (corresponding to GI-1c1/1b; ~13,100 – ~12,900 cal. yr BP)**

Based on the botanical data from the Moervaart records, a MMJT of 12–13°C could be inferred for the late Allerød (Bos et al., 2017), which corresponds to the one chironomid sample from the Moerbeke 'Suikerfabriek', from which a mean July temperature of ~14°C could be reconstructed (Bos et al., 2017). Water level in the eastern part of the Moervaart palaeolake temporarily increased again at the start of the late Allerød, the moment depicted on the reconstruction map. However, the water level did not reach the level of the early Allerød as it was restricted to ca. 0.5 to 1 m depth.

During the late Allerød, Scotch pine (*Pinus sylvestris*) immigrated into the Moervaart region and open pine woodlands developed on the sandy soils of the Great Coversand Ridge, where these woodlands partly replaced the herbaceous vegetation and shrubs (Figure 9). Birch still occurred in open woodlands, with an undergrowth of herbs and ferns, along the shores of the palaeolake and on the coversand plains. On the coversand ridges, pine and birch were probably found in more intermixed open forest. Grasslands became less abundant in the region, although locally some wet grasslands developed on nutrient-poor soils on the coversand dunes. Since these units were small, these were not included on the map. The dune slacks on the ridge had dried-out during this period and were covered by thick packets of blown sands and probably sustained a herbaceous vegetation (Crombé et al., 2012; Denys et al., 1990, 1998).

Increased water levels at the start of the late Allerød are reflected in the temporary re-occurrence of aquatics in the lake vegetation which was fringed by a vegetation of sedges, horsetail, bulrush, cattail and meadowsweet (Bos et al., 2017, 2018a, 2018c). In the western part of the Moervaart depression, a swamp developed, with some pools of open water in which floating aquatics persisted. Towards the end of the late Allerød, not pictured, terrestrialisation led to the final disappearance of the whole Moervaart palaeolake and surrounding ponds. Drainage of the area continued via the Kale/Durme river system. An erosional contact in the palaeolake sequence at the Moerbeke 'Suikerfabriek' and Klein-Sinaai 'Boudelo' sites (Bos et al., 2017, 2018c) suggests the presence of a hiatus at the end of the late Allerød as a result of a lake water drop presumably resulting from the start of a colder climate phase (Figure 4). This change has been tentatively connected with the Intra

Allerød Cold Period or GI-1b (Donnelly et al., 2005; Lotter et al., 1992; Rasmussen et al., 2014), which occurred between 13,261 and 13,049 cal yrs BP (Bos et al., 2017). Lower lake levels at the end of the Allerød, leading to a hiatus, have also been recorded in the southern Netherlands (Bos et al., 2006; Hoek & Bohncke, 2002; Hoek et al., 1999) and in northern France (Deschodt et al., 2009; Magny, 1995, 2001).

Despite the decreasing lake level, hunter-gatherers of the *Federmesser* Culture most likely continued to be present in the Moervaart region. In the Moerbeke 'Suikerfabriek' and Klein-Sinaai 'Boudelo' sites, an increase of microcharcoal points to the higher frequency of fires (Bos et al., 2018a, 2018c). This was likely related to the presence of pine in the region, as the species is very sensitive to burning. This is very similar to other regions in the coversands of NW Europe, where numerous pine charcoal fragments have been found often in close association with the well-known Usselo-soil, dated to the late Allerød and first half of the Younger Dryas (Crombé et al., 2024; Hoek, 1997a; Kaiser et al., 2009; van Hoesel et al., 2012). Therefore, the higher frequency of forest fires was probably not caused by active burning of the vegetation by *Federmesser* Culture people, but rather by the vulnerability of the vegetation to lightning strikes. During the end of the late Allerød, the disappearance of the open water source, in combination with a change to a colder climate during the Intra Allerød Cold Period and following Younger Dryas, most likely led to a partial abandonment of the Moervaart region (c.f. Younger Dryas). This led to a marked decrease in the human occupation and exploitation of the region which lasted almost 1,500 years.

#### **Younger Dryas (corresponding to GS-1; ~12,900 – ~11,700 cal. yr BP)**

As the Moervaart depression and dune-ponds fell dry during the late Allerød and subsequent Allerød-Younger Dryas transition, only few sampling locations in the Moervaart region record the Younger Dryas (Table 1, i.e. Moerbeke 'Peerdemeers', Moerbeke 'Noord', Daknam 'Broek' and Klein 'Broek'). These records are all obtained from channel fills, that belong to the Kale/Durme meandering river system which flowed through the Moervaart depression from west to east. Infilling of this system only started in the Younger Dryas and thus did not record the late Allerød/Younger Dryas transition. The Moerbeke 'Peerdemeers' site starts recording in the later part of the early Younger Dryas. In the Daknam 'Broek', Klein 'Broek' and Moerbeke 'Noord' (MVN-11-B and D) sequences, only the end (of the second part) of the Younger Dryas is represented by a few pollen spectra. It was therefore not possible to make landscape and vegetation maps for this period.

Based on the records of (semi-)aquatic and terrestrial plants from the Moerbeke 'Peerdemeers' site, a MMJT of 12–13°C could be inferred for both the 1st and 2nd part of the Younger Dryas (Bos et al., 2018b), which is consistent with Bos et al. (2007). However, it is usually thought that the first part of the Younger Dryas was wetter and colder, followed by a slightly warmer and drier phase (e.g. Bohncke, 1993; Isarin & Bohncke, 1999). The cold-water ostracods (*Candona neglecta* and *C. candida*) in the Moerbeke 'Peerdemeers' record show a decrease during the Younger Dryas period (Bos et al., 2018b), which may indeed suggest less cold conditions during the second part.

As a result of the colder conditions during the Younger Dryas, vegetation became much more open. The open pine forests that

had developed on the coversand ridge in the late Allerød largely disappeared. Here, bare ground and vegetation with low willow shrubs, grasses and many herbs developed. A decline of the birch forests is also observed. However, birch copses remained and occurred scattered throughout the region. These were mainly found on the moister and more sheltered areas, both on the slopes of the coversand ridges, as well as on the northern banks of the former Moervaart palaeolake and riversides of the meandering Kale/Durme River. On the river floodplain and around the meandering channels, grass vegetation was present on (moderately) nutrient-rich soils. The restricted vegetation also induced renewed aeolian erosion, as attested at several sites (Rieme 'Noord', Wachtebeke 'Heidebos', Moerbeke 'Driehoek') by the presence of several metres of wind-blown sands on top of the Great Coversand Ridge and in former dune-ponds (Crombé et al., 2012). Locally (i.e. at Moerbeke 'Driehoek'), this also led to a southward migration of the Great Coversand Ridge, covering former lacustrine deposits (Crombé et al., 2020).

During the second part of the Younger Dryas (ca. 12,500–11,700/11,800 cal yrs BP), some shrubs of juniper, dwarf birch and heath re-appeared in the vegetation on the (slopes of the) coversand ridge. The increase in Ericales (probably *Empetrum*) in the landscape is typical for the 2nd, slightly warmer and drier part of the Younger Dryas (Bos et al., 2007; Hoek, 1997a, 1997b; Van der Hammen, 1951). Dwarf birch was growing in swamps on the river floodplain and around the meandering palaeochannel near Moerbeke 'Peerdemeers'. Open birch woodlands were present on the northern banks of the former Moervaart palaeolake. When, during the 2nd part of the Younger Dryas, the ground water level slightly lowered due to natural infilling and drier climate, birch woodlands probably also became more abundant on the river floodplains where they partly replaced the grass vegetation and marshes with dwarf birch. During this period, the channel near Moerbeke 'Peerdemeers' was cut off and sandy loam/loamy sand was deposited in the residual channel. In the channel, the water was probably only flowing during periods of high water levels in winter and spring. Records of ascospores of coprophilous fungi at Daknam 'Broek' suggest that large herbivores (game) were foraging the riverbanks and floodplains during the late Younger Dryas.

The combination of a cold climate, more open vegetation, increased aeolian deflation and disappearance of most freshwater reservoirs (lakes and dune ponds), will have created an unsuitable environment for both large herbivores (game) and hunter-gatherers during the Younger Dryas. The open landscape will have facilitated little shelter for camp-sites on the southern side of the coversand ridge. The only source of freshwater will have been the meandering Kale/Durme River, but that already started to fill in during the Younger Dryas. This probably explains the marked reduction in prehistoric sites within the Moervaart area, a phenomenon which was also observed in other parts of the Belgian lowlands (De Bie & Vermeersch, 1998) and surrounding regions, such as northern France (Fagnart & Coudret, 2000, 2019). Compared to the *Federmesser* Culture, site-density in the Moervaart depression drops from 1.23 sites/century to 0.13 sites/century (Figure 3; Tables 2 and 3), indicating that the area was largely abandoned (Crombé, 2019; Crombé & Robinson, 2017). Supposedly game as well as hunter-gatherers shifted to other areas that were less affected and still offered enough drinking water and protection from the cold climate, such as the adjacent Scheldt valley (Crombé & Robinson, 2017) and the Belgian-Dutch Meuse

basin. In the former Schelde valley, currently just four sites can be tentatively attributed to the (Epi)Ahrensburgian Culture (Crombé, 2019), while there are numerous sites in the Meuse basin (Arts & Deeben, 1981; Baales, 1996; Crombé et al., 2024; Dewez, 1974, 1987; Gob, 1988; Niekus et al., 2019). This concentration of sites in the Meuse basin is most likely due to the presence of sheltered contexts (caves and rock shelters) and the continued existence of freshwater lakes in the coversand area, at least during the first half of the Younger Dryas (Bos et al., 2006; Hoek, 1997b).

### **Preboreal (corresponding to the early Holocene; ~11,700 – ~10,700 cal. yr BP)**

In NW Europe, the transition to the Preboreal (Holocene) is characterised by an abrupt warming and increase in precipitation. The Preboreal can be subdivided into the Friesland Phase, Rammelbeek Phase and Late Preboreal (e.g. Behre, 1966, 1978; Bos et al., 2007; Hoek, 1997b; Van Geel et al., 1981). We have chosen to reconstruct a vegetation map for the Late Preboreal since it is most descriptive for the overall vegetation development during the early Holocene but will also describe vegetation development during the Friesland and Rammelbeek Phase. The landscape during the Preboreal became more stable as a result of increasing continuous vegetation cover limiting large-scale soil erosion. The Kale/Durme river channel was relatively stable during this time period.

### **Friesland phase (~11,700 – ~11,400 cal. yr BP)**

The Friesland Phase (11,703–11,400 cal yrs BP) was a period of climate warming and also of an increase in precipitation. The latter is reflected in many lakes and residual channels as a rise in ground- or lake water level (e.g. Bohncke & Wijmstra, 1988; Magny et al., 2007). In the residual channels of the Kale/Durme river, a rise in the water level was also registered. Based on the presence of botanical taxa (*Groenlandia densa*, *Potamogeton mucronatus* and *Ceratophyllum demersum*, e.g. Bell, 1970; Isarin & Bohncke, 1999) in the Moervaart records, a MMJT of 13–16°C is recorded for the Friesland Phase. Similar temperatures were inferred by Bos et al. (2007), which suggest that at the start of the Holocene, MMJTs quickly rose from 12–13°C to 13–16°C. In addition, in the Moerbeke 'Peerdemeers' sequence (Bos et al., 2018b), the coldwater-associated *Candona* species decrease, also suggesting slightly warmer water temperatures during the Friesland Phase.

A temporary increase in juniper is visible at the onset of the Holocene, which is characteristic of the Friesland phase (Bos et al., 2007; Hoek 1997b; Van Geel et al., 1981). This was followed by the development of boreal birch woodlands, similar to other coversand areas in the Netherlands and northern Belgium (compare Hoek, 1997b; Verbruggen et al., 1996). Due to the warmer climate and increasing shade, the habitat of dwarf birch decreased and the species largely disappeared from the region being replaced by birch trees. In the Moervaart region, the boreal woodlands expanded along the riversides of the Kale/Durme River near Daknam 'Broek' and on the southern side of the Great Coversand Ridge of Maldegem-Stekene. Pine trees were largely absent in the regional landscape during the Friesland Phase, although some pines may have survived the Younger Dryas at more sheltered locations. On the coversand ridge, juniper and many typical Late-glacial herbs (such as *Artemisia*) remained present. The former Moervaart palaeolake

remained relatively open with more grass vegetation. Around the residual channels of the Durme river, willow shrubs and marsh plants were present. Records of microcharcoal (epidermis of grasses and sedges) and ascospores of *Gelasinopora* suggest that this vegetation was regularly burned down (van Asch et al., 2024; Zwier, 2018). In the residual channels, more organic-rich deposits accumulated and algae (including diatoms), submerged and floating-leaved macrophytes were growing. A fauna with ostracods, molluscs, chironomids, worms, bryozoans, Trichoptera and fish was present in these waters. The flora and fauna indicate a shallow, predominantly eutrophic, aquatic environment. In the river floodplains, nutrient-poor fens developed whereas a more nutrient-rich vegetation type developed on the drier riverbanks. Records of ascospores of coprophilous fungi at Daknam 'Broek' testify to the presence of large herbivores on the riverbanks and floodplains during this period.

### **Rammelbeek phase (~11,400 – ~11,250 cal. yr BP)**

Early Holocene climate improvement was shortly interrupted by a drier, more continental phase with warm, dry summers and cold winters, the so-called Rammelbeek Phase (ca. 11,400–11,250 cal yrs BP) (Behre, 1966, 1978; Bos et al., 2007; Van Geel et al., 1981). The more continental climate of the Rammelbeek Phase was coeval with cooling (Preboreal oscillation = PBO *sensu* Björck et al., 1996 or 11.4 event *sensu* Rasmussen et al., 2007) in Greenland (Bos et al., 2007; Van der Plicht et al., 2004). During the Rammelbeek Phase, summer temperatures were probably similar to that during the Friesland Phase, but winter temperatures were lower. Taxa such as *Schoenoplectus lacustris*, *Typha latifolia*, *Oenanthe aquatica* and *Lycopus europaeus* (Bell, 1970; Iversen, 1954) suggest a MMJT of 13–16°C (Bos et al., 2018b; Zwier, 2018). During this period, also the mollusc *Bithynia tentaculata* appears, both in the Moerbeke 'Peerdemeers' and Daknam 'Broek' records. The species is frost-sensitive and indicates warmer water temperatures.

During the Rammelbeek phase, forest expansion was temporarily interrupted, and in the Moervaart region, more steppe-like open grassland vegetation with herbs developed as a result of a drier and more continental climate. On the Great Coversand Ridge, juniper and heliophilous herbs were present while pine was largely absent from the region. At ca. 11,418 cal yrs BP, at the start of the Rammelbeek Phase, the palaeochannel near Klein 'Broek' (Storme et al., 2017) east and downstream of the research area was cut off and started to fill in with gyttja, pointing to a deep stagnant water environment. Slightly later, around ca. 11,288 cal yrs BP, also the channel near Zele 'Hoekstraat' (Storme et al., 2017) was abandoned and gyttja started to accumulate. At Daknam 'Broek', alternating sandy and organic layers were deposited during this period indicating drier conditions. Also at many Dutch and northern Belgian sites, a sedimentological change (a lower organic matter content) is visible in the deposits (e.g. Bos et al., 2007; Hoek, 1997b; Hoek & Bohncke, 2002). This was probably caused by a decrease in the biological productivity due to a lowering of the water table in combination with an increase in aeolian activity due to a less forested, more open landscape with soils not completely covered by vegetation. In all the investigated residual channels of the Kale/Durme River reflecting this period (Table 1), an aquatic vegetation with algae and floating and

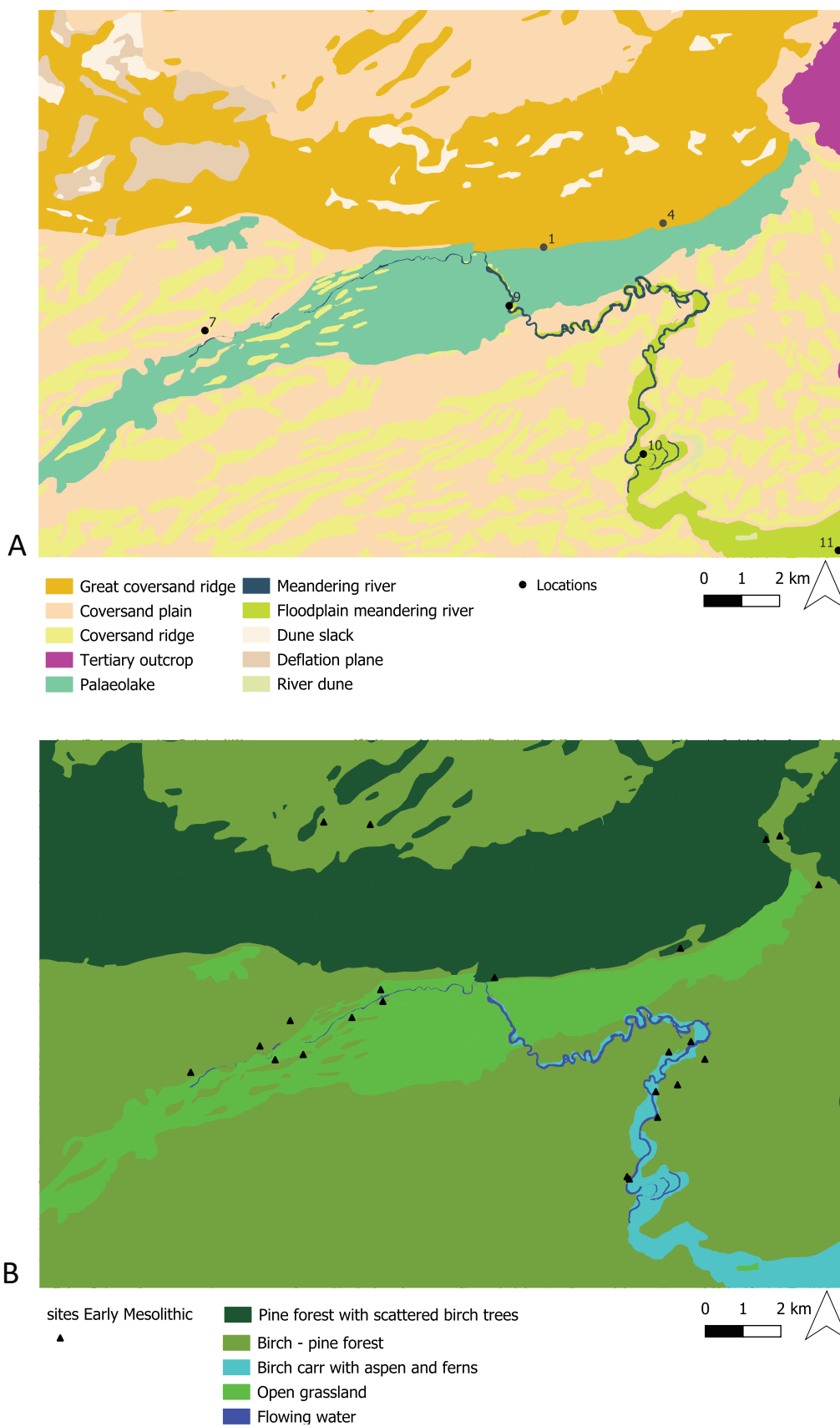
submerged aquatics was present and gyttja is deposited. Nymphaeaceae (especially white water lily), however, were dominant during this period. The dominance of white water lily suggests stagnant water and a water depth less than 3 m in the abandoned residual channels of the Kale/Durme River (Hannon & Gaillard, 1997). The shore vegetation was formed by willows, sedges and semi-aquatic herbs. In the birch woodlands around the residual channels near Wachtebeke 'Penen', Zele 'Hoekstraat' and Klein 'Broek', aspen (*Populus tremula*) became a more important element. The higher values of microcharcoal epidermis of grasses and sedges and ascospores of *Gelasinopora* (van Asch et al., 2024; Zwier, 2018) suggest that due to the drier climate, fires occurred more frequently in the vegetation on the riverbanks and floodplains. Large herbivores were still present in the vegetation near Daknam 'Broek', probably also with elk (see records of *Bombardioidea*, Bos et al., 2005).

### **Late Preboreal (~11,250 – ~10,700 cal. yr BP)**

The dry Rammelbeek phase was followed by a shift to a more humid climate during the Late Preboreal (11,250–10,700 cal yrs BP) (Bos et al., 2007; Van der Plicht et al., 2004). Although the MMJTs were probably similar to the Friesland and Rammelbeek phases.

During the Late Preboreal, a re-expansion of pine in the Moervaart region occurred and gradually boreal woodlands with birch and pine started to develop over large parts of the area (Figure 10a and b, Figure 12b). During this period, pine trees probably largely replaced the open vegetation with juniper and heliophilous herbs on the drier, more sandy substrates of the coversand ridges including the Great Coversand Ridge. These plant taxa probably suffered from the competition with birch and pine for light and space and disappeared from the vegetation as a result of the increasing shade and a more stable environment. On the flanks of the Great Sand Ridge of Maldegem-Stekene, pine was probably found intermixed with birch. Records of microcharcoal (including charred epidermis of grasses and sedges) and ascospores of *Gelasinopora* suggest that fires still occurred in the boreal forests.

On the floodplains and riverbanks of the Kale/Durme residual channels, birch woodlands with aspen and an undergrowth of marsh taxa developed. From this period onwards, grey alder (*Alnus incana*) also became part of the woodland vegetation. Macroremains of grey alder recorded in the Wachtebeke 'Penen' sediments, suggest that grey alder was an important element in the local vegetation on the river floodplain of the Kale/Durme River. During the Late Preboreal, infilling of the residual channels of the Kale/Durme with organic sediments continued and in the marsh vegetation now also ferns became a more important element. At Daknam 'Broek' and Wachtebeke 'Penen', the infilling process was more advanced than at Moerbeke 'Noord' location MVN-11-B, Zele 'Hoekstraat' and Klein 'Broek'. During the Late Preboreal, the open water vegetation was more and more replaced by marsh vegetation with ferns. Aquatic vegetation with pondweed (*Potamogeton*) and white and yellow water lily remained present in the residual channels near Moerbeke 'Noord' location MVN-11-B, Zele 'Hoekstraat' and Klein 'Broek'. In the shallow depression near Moerbeke 'Noord' location MVN-11-D, a willow carr with horsetail formed and peat accumulation started. In areas of the former Moervaart palaeolake not part of



**Figure 10.** (A) Palaeogeographical map for the Moervaart region depicting the landscape during the late Preboreal/Early Boreal, including locations of palynological data, sites in grey only used for late Boreal map. (B) Vegetation reconstruction map for the Moervaart region depicting the vegetation units present during the late Preboreal/Early Boreal, site distribution of early Mesolithic sites is also shown.

the Kale/Durme floodplain, presumably an open grassland vegetation prevailed.

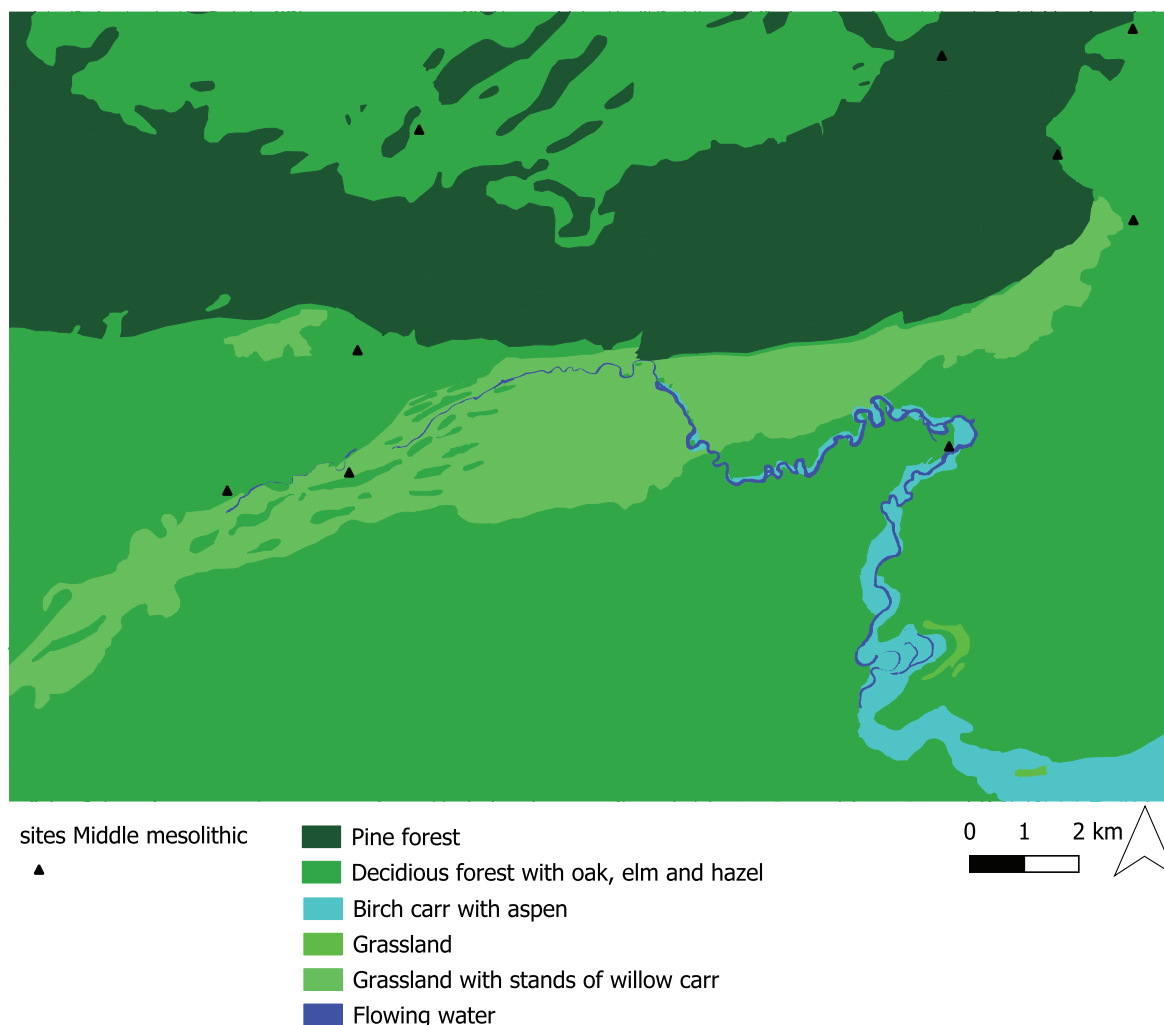
Despite the clear warming and increased availability of edible plants, there is currently little evidence of a massive return of hunter-gatherers during the Preboreal. This correlates well with the data from adjacent study areas, such as northern France (Fagnart & Coudret, 2019) and the Netherlands (Crombé et al., 2014; Niekus, 2019). It is assumed that the cold and dry Rammelbeek oscillation was one of the reasons for the delayed human recolonisation following its partial abandonment during the Younger Dryas; but clearly further research is needed to fully understand this scarcity of sites. Apparently Mesolithic hunter-gatherers did not return to the region before the Preboreal-Boreal transition, after which climate had stabilised and forests had plenty of edible plants, nuts and fruits to offer, amongst which hazelnuts.

#### **Boreal (corresponding to the early Holocene; ~10,700 – ~8,600 cal. yr BP)**

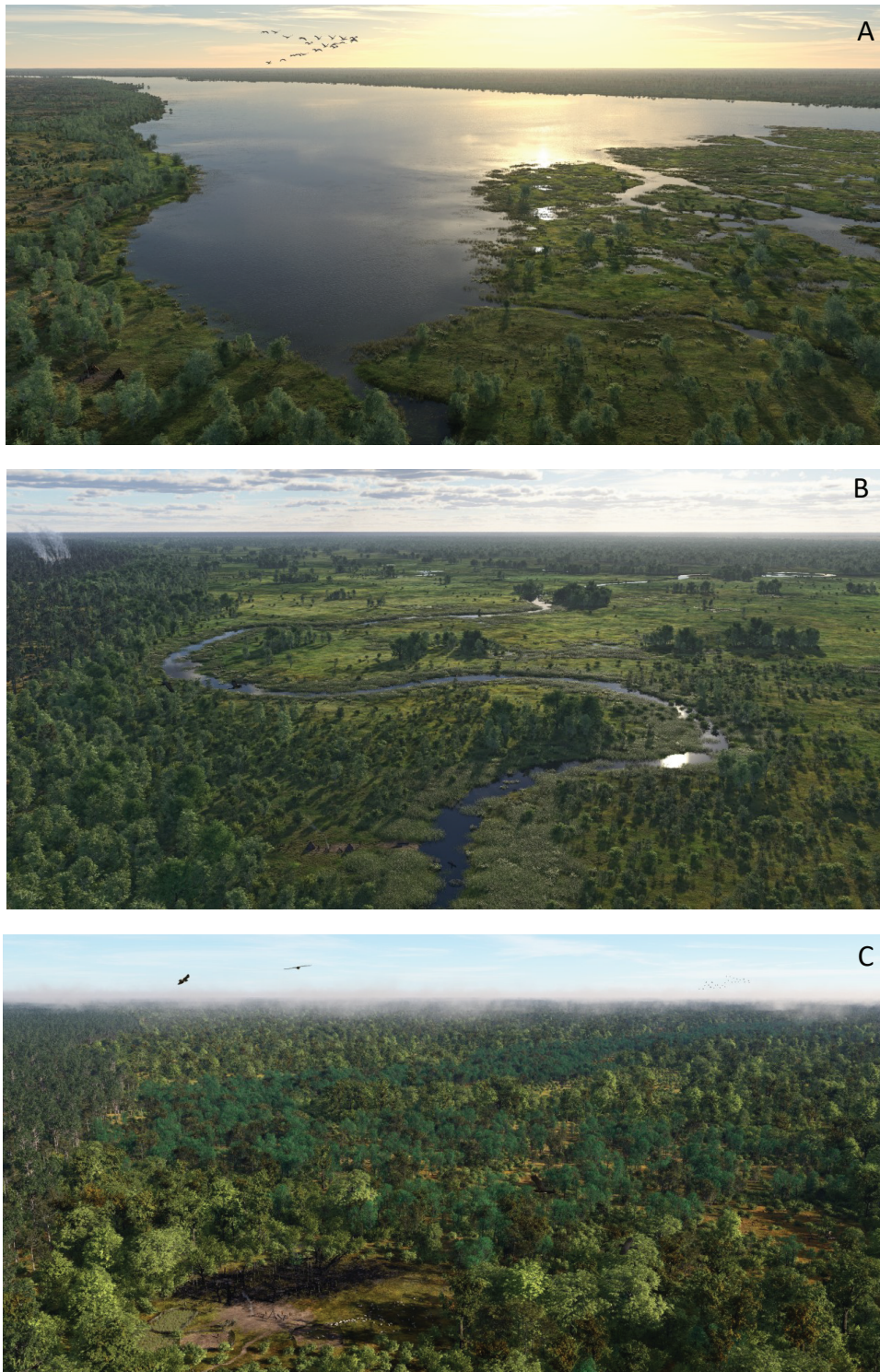
There is no climatological data available from the Moervaart region from this period; but from the Greenland ice core data (Rasmussen et al., 2014), it is known that mean summer

temperatures further increased during the Boreal. Due to the higher temperatures and increased evapotranspiration, the Kale/Durme River at this time was reduced to a small and shallow stream with either slowly running or stagnant water (Storme et al., 2017).

In the pollen diagrams of the Moervaart region, the Boreal is reflected by a sharp rise of hazel (*Corylus avellana*) and the arrival of oak (*Quercus*) at the start, closely followed by elm (*Ulmus*). This is typical for the Sandy Flanders region of which the Moervaart region is part of (Storme et al., 2017; Verbruggen et al., 1996). *Corylus* already started to spread after 11,200 cal. BP, but the main expansion in northern central Europe occurred at ca. 10,800 cal. BP (Theuerkauf et al., 2014). Previously it was suggested that Mesolithic hunter-gatherers could have played an important role in the spread of hazel (e.g. Firbas, 1949; Smith, 1970; Zoller, 1960). However, the expansion of hazel was probably triggered by warming, favoured by a combination of high seasonality, summer drought and frequent fires, which helped hazel to outcompete oak (e.g. Finsinger et al., 2006; Huntley, 1993; Tallantire, 2002; Theuerkauf et al., 2014). The hypothesis is that hazel probably did not enter the pine-dominated woodlands on well drained sandy soils, but that the early stands occurred mainly in the hilliest areas, where



**Figure 11.** Vegetation reconstruction map for the Moervaart region depicting the vegetation units present during the middle to late Boreal, site distribution of middle Mesolithic sites is also shown. For palaeogeographical map see Figure 10a.



**Figure 12.** (A) Artist impression of the landscape and vegetation around the Moervaart paleolake looking in southeastern direction. (© Province of East Flanders; by Ulco Glimmerveen). (A) Situation during the early Allerød. On the left hand side the Great Coversand Ridge of Maldegem-Stekene with an open tundra vegetation present with scattered birch trees and shrubs. On the right hand side the anastomosing river channels are flowing through a marsh into the lake. This Moervaart freshwater lake with its anastomosing channels reached its highest level and extension during this period. In the front left a hunter-gatherer campsite of the *Federmesser* Culture is depicted, erected along the steep and dry southern edge of the Great Coversand Ridge of Maldegem-Stekene, facing the extensive lake. (B) Situation during the Preboreal/Boreal transition. On the left hand side the Great Coversand Ridge of Maldegem-Stekene is covered with dense pine forests with birch forests on the flanks. The meandering Kale/Durme river which cuts through the former palaeolake has already turned into a slow-running and shallow river. In the floodplain a marsh vegetation is present. The coversands to the right of the river are covered by birch forests. Human occupation, illustrated by a camp-site occupied by a few Mesolithic hunter-gatherer families, now focusses on levees and sand dunes along the river, being the only source of freshwater in the wide area. A natural forest fire is burning in the back left (C) Situation during the Atlantic. Large parts of the landscape are covered by a mixed deciduous forest of oak, elm and lime. The Great Coversand Ridge of Maldegem-Stekene is covered with pine forests. The Kale/Durme river is completely abandoned and an alder carr is present in its residual channels. At this point the Moervaart region had hardly any freshwater to offer, contrasting with the water-rich environment of the Lateglacial and early Holocene. Human occupation during the late Mesolithic and subsequent Neolithic concentrated in the few spots that still yielded some drinking water.

hazel could benefit from the warm microclimate of the southern slopes (Theuerkauf et al., 2014). In the Moervaart region, hazel shrub likely expanded from the southern flanks of the coversand ridges, where there was a warm microclimate and less shade.

The vegetation reconstruction map (Figure 11) shows the vegetation during the middle to late Boreal when deciduous woodlands covered large parts of the area. These deciduous woodlands with oak and elm and some hazel were present on the coversand plains and ridges. It is likely that hazel was the most dominant in the vegetation on the southern slopes of these coversand ridges. Furthermore, hazel was probably also present at forest edges together with bracken (*Pteridium aquilinum*). In the undergrowth of the woodlands, shrubs, herbs and ferns were present. During the depicted time frame, woodlands with pine remained dominant on the higher and drier, sandy areas of the Maldegem-Stekene ridge. Small patches of pine could also occur on the smaller coversand ridges south of the Moervaart depression.

On the river floodplains of the Kale/Durme river, birch forests with aspen and grasslands were present. In the Daknam 'Broek' residual channel, the open water vegetation with algae and white water lily disappeared and was replaced by marsh vegetation dominated by ferns. Which is signalling a reduction in water depth, also corresponding to start of peat formation. In the Zele 'Hoekstraat and Klein 'Broek' residual channels, a willow carr vegetation developed with marsh vegetation and ferns in the undergrowth. In these channels, some pools of open water remained with white and yellow water lily. Also in the shallow depression near Moerbeke 'Noord' location MVN-11-D, willow carr vegetation was present. At Moerbeke 'Suikerfabriek' and Klein-Sinaai 'Boudelo', marsh vegetation with ferns was present during the Boreal and peat respectively peaty sand accumulated. Although these two records reflect different moments during the Boreal The higher Non-Arboreal Pollen (NAP) and Poaceae values in the pollen diagrams of these locations suggest that the former Moervaart palaeolake area was probably dominated by grass vegetation rich in herbs and likely more open compared to the Kale/Durme River floodplain.

Continued warming possibly was the main trigger for the marked return of hunter-gatherers to the Moervaart area as was the case in other parts of the sandy lowlands (Crombé et al., 2011; Van Gils & De Bie, 2008; Van Maldegem et al., 2021). In particular, during the first half of the Boreal, corresponding to the early Mesolithic, site-density increased considerably up to 1.21 sites/century (Figure 3; Tables 2 and 3), which is very similar to the situation during the Allerød. Albeit with an interruption of ca. 1.5 millennia during which nearly no habitation was present. Just like in the Allerød, the environment again offered plenty of plant species for consumption, in particular hazel (Crombé et al., 2023), Guelder rose (berries) (*Viburnum opulus*), bulrush (rhizomes) (*Typha*), horsetail (tubers) (*Equisetum*), water lily (seed pods) and nettles (greens) (*Urtica*), but also for the production of tools, such as nets, baskets and strings. Many lithic artefacts from the early Mesolithic display usewear traces linked to the processing of siliceous plants, probably reed, nettles and/or rushes (Crombé & Beugnier, 2013). Although game for hunting was probably present in the region, there is no palynological evidence (i.e. ascospores of dung fungi) for the presence of large herbivores. Yet, the many lithic microliths

found at early Mesolithic sites testify to the continued importance of hunting.

Since all shallow freshwater lakes had permanently disappeared at the Allerød-YD transition, the Kale/Durme constituted the only source of freshwater in the Moervaart region during the early Holocene. This most likely explains the dense clustering of early Mesolithic sites along its banks, even though the Kale/Durme was already reduced to a small and shallow stream with either slowly running or stagnant water (Storme et al., 2017) (Figure 10). This occupation pattern persisted during the later stages of the Boreal, corresponding to the middle Mesolithic (Figure 11), yet site-density dropped markedly to 0.83. This shift of occupation from lake to river banks apparently contrasts with other areas within the Belgian-Dutch coversand region, such as the Belgian Campine, where the banks of former lakes/dune-ponds continued to attract hunter-gatherers during the early Mesolithic (Vanacker et al., 2001). This might imply that, contrary to the coversand area of NW Belgium, freshwater ponds lasted longer in the adjacent Campine area. However, lacking organic sediments dating to the early Holocene in these ponds, this still remains a hypothesis. Recent surveys (Van Gils & De Bie, 2008) have also indicated that early Mesolithic sites are regularly situated on sand ridges bordering small rivers and brooks, suggesting some correspondence with the Moervaart region.

#### **Atlantic (corresponding to the Middle Holocene; ~8,600 – ~5,800 cal. yr BP)**

The climate during the Atlantic (onset 8,600 cal yr BP) was warm and wet. Only a few spectra correspond to this middle Holocene pollenzone since most residual channels of the Kale/Durme river system were completely filled in. In addition, in some river sections, e.g. at Peerdemeers, the upper peat fill was reworked in later times, probably as a result of peat extraction (Jongepier et al., 2011). It was therefore not possible to construct a vegetation map for this time period. However based on the few datapoints and general knowledge of Holocene vegetation development, an artist impression of this time period was constructed (Figure 12c).

The forest expansion which started in the early Holocene continued into the middle Holocene resulting in a densely forested landscape during the Atlantic period. The drier conditions on the Great Coversand Ridge limited the expansion of deciduous forest here, resulting in the continued presence of pine forests on the higher parts of this ridge. On the flanks of this ridge and on the coversand plains and ridges south of the Moervaart depression mixed deciduous forest with oak, elm and lime (*Tilia*) developed. Lime appeared in these forest during the Atlantic. Hazel occurred at the forest edge and in clearings in the forest. These oak forests have spread onto the edge of the former Moervaart paleolake. The former lake itself, including the residual channels of the Kale/Durme river, is largely covered by an alder carr. Alder (*Alnus*) strongly increased during the Atlantic period. In wetter areas in the former floodplain, ferns, grasses and sedges form a more open marsh vegetation. There is no availability of large bodies of water in the region.

During the early Atlantic, corresponding to the late Mesolithic, site-density dropped even further, to 0.61 sites/century (Figure 3). It is assumed that this gradual reduction of sites from the middle to late Mesolithic is not necessarily a

reflection of a population reduction, comparable to the Younger Dryas, but rather testifies of a change in mobility induced by a changing environment (Crombé et al., 2011; Van Maldegem et al., 2021). More specifically, a change is considered from the high residential mobility during the early Mesolithic induced by the random distribution of natural resources to a reduced mobility as resources such as freshwater and the presence of (semi)aquatic edible plants considerably decreased in this region and became more confined during the Atlantic.

## Conclusions

Long-term investment in high-resolution, multiproxy palaeo-ecological research and archaeological surveys has provided a unique opportunity to closely examine ecosystem and human responses to multiple climate changes within the area of the extensive Moervaart freshwater lake. An almost continuous vegetation record encompassing the entire Lateglacial and early Holocene, except for the Allerød-Younger Dryas transition, could be obtained, forming the basis of a series of vegetation maps and artist impressions. By plotting the prehistoric sites on these maps, insights into the way contemporaneous hunter-gatherers adapted their settlement and exploitation systems to changing landscape could be obtained.

The main landscape elements, such as the Great Sand Ridge of Maldegem-Stekene, were established in the Weichselian Lateglacial, but aeolian activities continued to reshape the landscape up until the early Holocene when vegetation cover stabilised the landscape. An interesting outcome of the multiproxy research in the Moervaart area is the observation that aeolian erosion was not restricted to the colder Dryas-phases but was also present during the warm Allerød as a result of either short, abrupt cooling events and/or forest fires. These recurrent deflations resulted in the partial or complete filling of dune ponds and the southwards migration of the Great Sand Ridge of Maldegem-Stekene, which led to a gradual displacement of the northern lake shore, intensively occupied by Final Palaeolithic hunter-gatherers. This offers interesting perspectives for future archaeological surveys, given the potential to find well-preserved sites sealed by aeolian sands.

The vegetation reconstruction shows the development from an open arctic landscape to a forested region, with several temporary reversals as a result of climate oscillations. First evidence of human presence is found from the relatively warm Allerød with the appearance of hunter-gatherers of the *Federmesser* Culture. Shifts to colder and scarcer conditions such as during the Younger Dryas led to the near abandonment of the region. And even though climatic conditions improved at the start of the Holocene, Mesolithic population density did not increase until the climate had stabilized and forests had plenty of edible plants, nuts and fruits to offer, amongst which hazelnuts. One of the main conclusions is thus that re-colonization at the onset of both abrupt warming events, the Lateglacial and early Holocene, shows a surprisingly similar pattern: one of a delayed re-population as there is hardly any evidence of human occupation dated respectively to the Bølling and Preboreal. For the time being this is explained by the lasting unattractive conditions of the landscape which needed time to develop under the warmer conditions, but it is clear that further archaeological and palaeo-environmental research is needed to elucidate this analogous course of events. Re-population after the Last Glacial Maximum (LGM) started not before the

Allerød, when the boreal forests gradually developed and numerous freshwater reservoirs, including the large Moervaart lake and numerous dune ponds came into existence, creating a stable and an ecologically rich and diverse environment. The northern bank of the Moervaart lake was the focus of habitation by *Federmesser* hunter-gatherers, who probably focused on the exploitation of this extensive dry to wet ecotone. The vegetation reconstruction maps show that these campsites were positioned between the lake and the drier Great Coversand ridge in a zone where marsh vegetation was present. This apparently came to a (sudden) end at the Allerød-Younger Dryas transition as a result of a sudden reappearance of extreme coldness and the disappearance of all freshwater reservoirs, probably in combination with frequent and large-scale wildfires during the late Allerød and severe wind activity. Hunter-gatherer populations were severely impacted and forced to move to the river valleys of the Scheldt and possibly the Meuse. This focus on river valleys or water availability continued well into the Mesolithic, when hunter-gatherers returned to the area. This return is presumably related to the warmer climatic conditions during the early Holocene. However, the continuously changing forest composition pushed hunter-gatherers to alter their mobility and exploitation systems in the course of the Mesolithic. The reconstructions show that human presence seems largely linked to shelter and the availability of water and not only climatic conditions and wild resources. Sites are often found at the edge or boundary of vegetation types and thus boundaries between geomorphological elements, these zones provide the highest abundance in species diversity and thus exploitation potential. The presence of a sheltered and dry shore along a freshwater lake during the Allerød provided resources and suitable conditions for the establishment of hunting camps belonging to the *Federmesser* culture, whereas a meandering river channel provided resources for hunter-gatherers during the Boreal. As a result, hunter-gatherers had to shift from lake to river and from high to lower residential mobility in response to changing climate and ecosystems.

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