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III. DYNAMICS

LATE GLACIAL AND EARLY HOLOCENE VEGETATION DEVELOPMENT IN SOUTHEAST DENMARK - PALAEOENVIRONMENTAL STUDIES FROM A SMALL LAKE BASIN CLOSE TO THE PALAEOLITHIC SITE OF HASSELØ

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Eastern Denmark was an important region for the early immigration of humans into southern Scandinavia throughout the late Glacial period. One possible explanation for this is that the landscape provided an especially favourable environment for Palaeolithic hunters. To examine this, the local and regional environment is reconstructed through the analysis of pollen and plant macrofossils from a small kettle hole and discussed in relation to human presence in the region. The kettle hole is situated close to a Palaeolithic occupation site with artefacts belonging to the Federmesser and Bromme Cultures. The lake sediments encompass the Bølling, Allerød, Younger Dryas and the early Preboreal biostratigraphic periods. An increase in charcoal dust at c. 14,000 and 13,900 cal. BP may be related to the occupation site.

It is shown that an ecotone existed between present-day Denmark and northern Germany during a large part of the late Glacial period. Denmark and Germany are separated by a low lying region, which was periodically covered by the Baltic Ice Lake that may have delayed the dispersal of plants from south to north. Areas lying between different habitats are known to have a high biodiversity and this may be why a high frequency of Palaeolithic finds is seen here. It has long been thought that tree birch grew in the Danish region from the beginning of the late Glacial but this study of both local and regional

proxies shows a clear delay of more than 1000 years in the immigration of tree birch.

The investigation also shows a delay of c. 250 years between the climatic transition from GI-1a to GS-1 and the biostratigraphic transition from the Allerød to the Younger Dryas periods. The three ^{14}C ages available from the Danish Bromme Culture are from this transition phase when the birch woodland was becoming more open. The classical partitioning of the Younger Dryas is seen in the pollen analysis as an early dry phase, until c. 12,100 cal. BP, and a wetter later phase. This was most likely due to a change in atmospheric circulation and variations in the extent of sea ice in the North Atlantic. The combined analysis of both pollen and plant macrofossils has led to a detailed and accurate reconstruction of the local environment and, in turn, the preconditions for human presence.

Introduction

The region around Lolland, Falster and southern Zealand in south-eastern Denmark has a relatively high concentration of late Palaeolithic finds from the Hamburg, Federmesser, Ahrensburg and especially Bromme cultures (Pedersen 2009). The region must have been important for humans during the late Glacial period. There is a long history of archaeological research in Denmark so this Pal-

aeolithic 'hot spot' cannot be explained by differences in regional research intensity alone (Petersen 2009). Even though large climatic changes led to enormous environmental variations and transformations of the landscape in the region during the late Glacial (Iversen 1954; Björck et al. 1998), this 'hot spot' was probably mainly due to an enhanced availability of resources.

Pollen based reconstructions of the late Glacial landscape from south-eastern Denmark (e.g. Krog 1954; Fredskild 1975; Kolstrup & Buchard 1982; Kolstrup 1982) have given a well-defined picture of the vegetational development during the late Glacial period in relation to climate, soil development, succession etc. In recent years, however, macrofossil based reconstructions have helped to form a more detailed and sometimes surprising view of the vegetation as compared to those based on pollen alone (e.g. Lidberg-Jönsson 1988; Birks 1993; Birks et al. 2005; Mortensen et al. 2011). One of the major advantages of plant macrofossils over pollen based reconstructions is their better representation of the local environment and their high taxonomic precision. Pollen assemblages are influenced by many factors such as pollen source area, vegetation patchiness and a taxonomic precision often limited to genus level (Prentice 1985; Sugita 1994; Nielsen & Sugita 2005). Reconstructions based on macrofossils are therefore often more diverse and multifaceted than those based on pollen alone (e.g. Birks & Birks 2000; Bos et al. 2006; Hofstetter et al. 2006).

Plants in treeless, arctic environments often produce a limited amount of pollen. Pollen can be transported over long distances from other regions and this 'exotic' fraction can therefore represent a large proportion of the total pollen rain and result in misleading interpretations (see Birks & Birks 2000). A classic example of this effect is seen in the immigration of tree birch, where there is often a significant time difference between when tree birch pollen appears relative to when the first macrofossils are seen. This difference can most likely be attributed to long distance transport of tree birch pollen (Birks 1993; Van Dinter & Birks 1996; Bennike et al. 2004a), which reflects that tree birch produces a wealth of well dispersed pollen.

One of the most important landscape changes is that between open land and woodland, which gives very different flora and fauna. This is especially important in archaeology as hunting strategies differ

with the available prey, which is in turn determined by the type of environment. Only one other well-dated environmental reconstruction of the late Glacial from southern Jutland, Denmark, including both pollen and macrofossils, has been published (Mortensen et al. 2011, 2014a). In southern Jutland tree birch was first established much later than previously thought, in the middle of the Allerød period about 13,500 cal. BP (e.g. Iversen 1954; Kolstrup 1982; Paus 1995), but it is not known whether this was also the case in eastern Denmark. The aim of this project is therefore to use both pollen and plant macrofossils to reconstruct the different environments during the late Glacial period. To this end, a palaeo-lake at Hasselø, south-eastern Denmark, was selected. Small sites such as Hasselø are known to often contain large numbers of well preserved, macrofossils, which allow detailed analysis of the local environment around the lake (Mortensen 2007).

South-eastern Denmark was repeatedly covered by glacial advances from the Scandinavian ice sheet during the last ice age, the Weichselian. The active period of the final glacial advance, the 'Baltic Ice Advance' between 17,000 and 16,000 cal. BP, left a weakly undulating moraine landscape with calcium carbonate-rich, clayey sediments and large quantities of buried dead ice (Bennike & Jensen 1998; Houmark-Nielsen & Kjær 2003; Houmark-Niels-

en et al. 2006; Houmark-Nielsen 2012). As the climate warmed during the late Glacial and early Holocene, the dead ice melted, forming depressions filled with water (kettle holes). Kettle holes are a characteristic feature of the late Glacial and early Holocene and the landscape was littered with numerous lakes and ponds in various stages of infilling. The Hasselø basin is such a kettle hole and was still a small lake during the late Glacial. Several Palaeolithic stray finds have been registered in the area around Hasselø. In 1994 part of the kettle hole was excavated along with a Federmesser/Bromme occupation site (Hasselø Tværvej) around 50 m to the southeast. No *in situ* traces of the occupation site were found in the lake sediments although single flakes of worked flint and bird bones were found in the spoil heaps (Petersen 2006).

The environmental analysis of Hasselø is part of a larger research project examining the immigration and establishment of humans in Denmark and southern Scandinavia relative to the climatic and landscape development of the region (Pedersen 2009; Mortensen et al. 2011, 2014a, 2014b; Fischer et al. 2013a, 2013b).

Site description

Hasselø is situated on Falster, an island in south-eastern Denmark (fig. 1). The present day yearly av-

Table 1. AMS radiocarbon dating of terrestrial plant remains from the Hasselø sediments.

AAR	Meterial (species)	Depth (cm)	δ¹³C (‰ VPDB)	¹⁴C age (¹⁴C yr BP)	Model age (cal. BP, 95.4% probality)
15014	*Dryas* leafs	5.2	-27.73	12226 ±44	14355-13941
15015	*Dryas* leaf and, *Salix* twigs	17.8	-27.68	12223 ±43	14140-13903
15016	*Betula nana* leafs	32.3	-27.71	11945 ±43	13960-13750
15017	*Betula nana* and *Salix* leafs	45.8	-26.89	11955 ±65	13890-13660
15018	*Betula* seeds and leafs	73.5	-26.97	11741 ±44	13685-13415
15019	*Betula pubescens* seeds and catkin scales	88.0	-27.94	11516 ±45	13459-13254
15020	*Salix* leafs	106.3	-28.06	10707 ±39	12710-12554
15021	*Betula nana* and *Salix* leafs	117.0		10340 ±39	12415-12143
15022	Leafs and buds. *Betula nana*, leafs and *Salix* buds	135.7	-28.41	10392 ±40	12339-12051
15013	*Menyanthes*, seeds and bud scales	160.8	-27.55	9660 ±40	11209-10868

Plate 1a & b
a. Excavation of the Hasselø basin with late Glacial sediments in the profile.
b. Lake sediment profile. The thin, dark coloured layers in the lowermost part are rich in in-washed macrofossils. Above these are layers of light coloured, clay and calcium carbonate-rich gyttja followed by darker gyttja dated to the second part of the Allerød. The Allerød layers are overlain by Younger Dryas sediments and then by dark coloured Holocene sediments.
(Photo: Morten Fischer Mortensen)

erage temperature is 8.6 °C (January average 1.4°C, July average 16.9 °C) and the yearly average precipitation is 617 mm (Theilgaard 2006). The basin had an original area of c. 0.05 ha prior to infilling, it was 20-30 m wide and a couple of metres deep and the lake had neither inflow nor outflow. The area is now extensively farmed and the lake sediments are covered by about 2 m of loose, unconsolidated sediments.

Material and methods

Stratigraphy. An around 8 m wide profile of lake sediments was exposed by excavating a trench from near the lake edge onto dry land. The exposed sediments (plate 1a+b) were described in detial. No disturbance such as slumping or deformation was observed. Two overlapping sediment monoliths of 160 x 10 x 10 cm were sampled encompassing the late Glacial and early Holocene sediments. The

Figure 2. Age-depth model for the Hasselø sequence sediments.
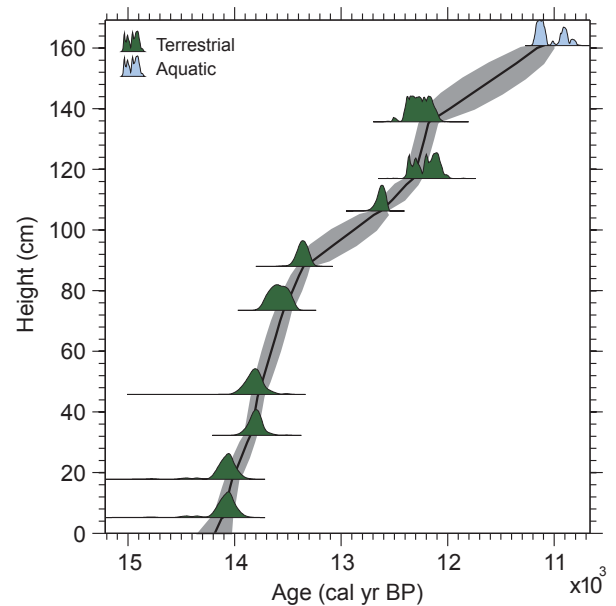
field descriptions were supplemented in the laboratory by descriptions of the monoliths using the Troels-Smith system (Troels-Smith 1955). The organic and calcium carbonate content was estimated at continuous 1 cm resolution by loss-on-ignition (LOI). 2 cm³ of sediment was dried at 105°C for 12 hours (dry weight), and ignited at 550°C for 2 hours (to determine organic content) and at 950°C for 2 hours (to determine calcium carbonate content). Organic and calcium carbonate content are important proxies of biological production and of erosion. No artefacts indicating human activity were found *in situ* in the sediments, even though the lake is situated close to the Federmesser/Bromme Culture occupation site.

Chronology. Terrestrial plant macrofossils from 10 levels sampled during macrofossil analysis were AMS radiocarbon dated. We used deciduous leaf fragments and fruits or twigs in the absence of the former (table 1). Remains of aquatic plants, such as *Potamogeton* sp. (pondweed) and *Batrachium* sp. (water-crowfoot), were not used because of potential hard water effects. Seeds of *Menyanthes trifoliata* (bogbean) were dated from one level (AAR-15013) due to the absence of sufficient terrestrial material *Menyanthes trifoliata* is a wetland plant but photosynthesises atmospheric CO2 and therefore suitable for dating. Material for ¹⁴C determination was selected from the 2 cm contiguous samples and subjected to a standard acid-base-acid treatment to

remove possible contaminants, such as carbonates and infiltrating humic acid. The dating results are reported according to international conventions (Stuiver & Polach 1977) as conventional ¹⁴C dates in ¹⁴C yr BP (before 1950 AD) based on the measured ¹⁴C/¹³C ratio corrected for the natural isotopic fractionation by normalizing the result to the standard δ¹³C value of -25‰ VPDB (Andersen et al. 1989). The dates were calibrated and an age-depth model constructed using OxCal 4.2 (Ramsey 2009) using the radiocarbon calibration curve IntCal09 (Reimer et al. 2009).

Pollen analysis. Pollen was analysed on 34 out of a total of 158 contiguous samples. Pollen preparation followed standard procedures, including KOH, HCl, HF and acetolysis (Fægri & Iversen 1989) and *Lycopodium* (clubmoss) spores were added for the estimation of pollen concentrations (Stockmarr 1971). The residues were mounted in silicone oil. An average of 500 terrestrial pollen grains was counted per sample along with spores, algae and other palynomorphs. All terrestrial pollen and spores were included in the pollen sum. Cyperaceae (sedge) were excluded because of their overwhelming local abundance. Whole slides were analysed to avoid effects of unequal distribution of pollen under the cover slip. Beug (2004) was consulted for general pollen identification, supplemented by the reference collection at the National Museum of Denmark for problematic grains and

Figure 3a and b. Pollen percentage diagram of selected taxa based on the total terrestrial pollen sum but excluding Cyperaceae and spores. 10 x exaggeration is shown by the open outline.

Figure 4a and b. Macrofossil concentrations per 100 ml sediment. The taxa are seeds or fruits unless otherwise indicated. T = macrofossil type.
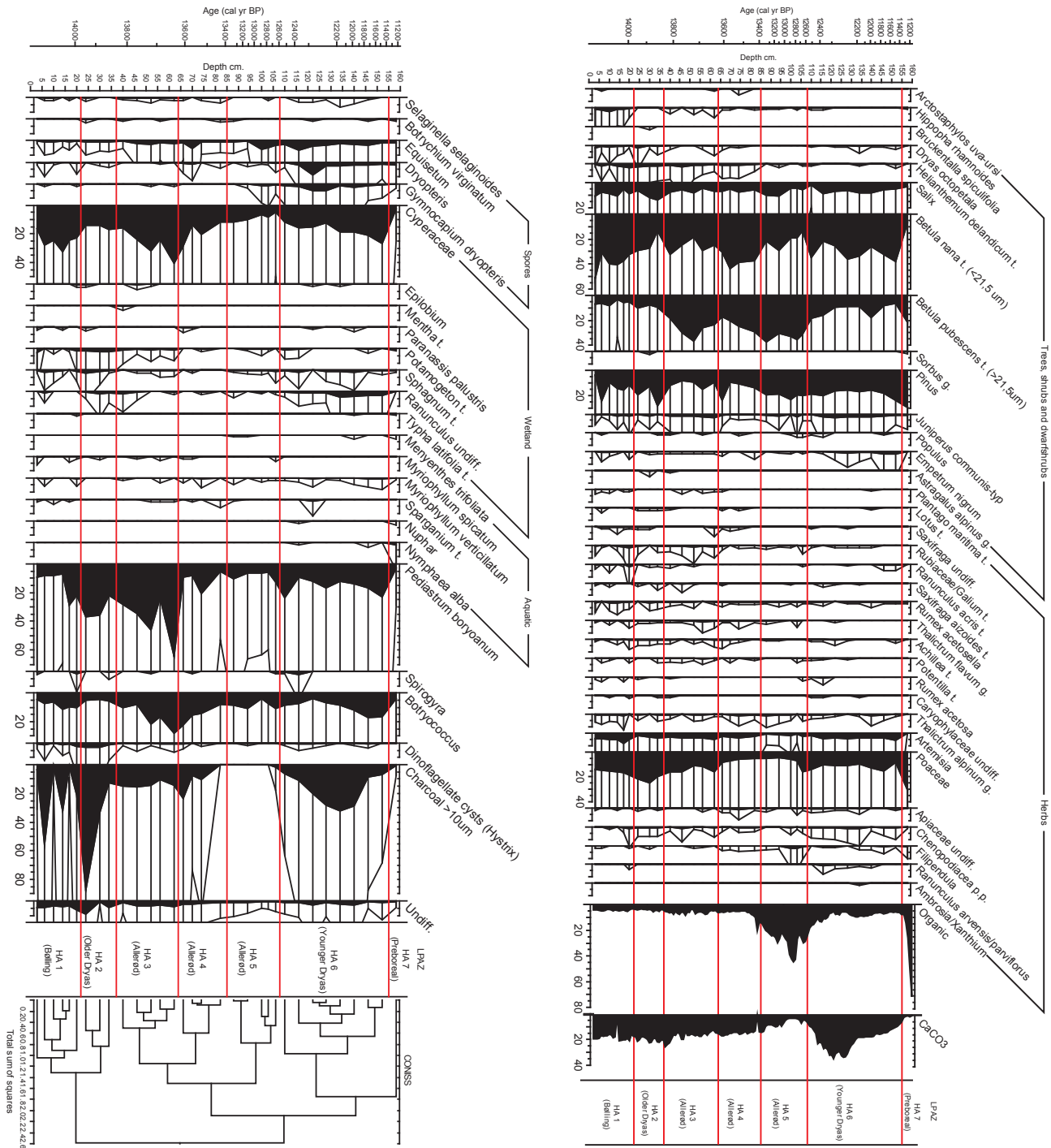
specialist works for the following: Punt and Black-more (1991) and Punt et al. (1995) for *Cerastium cerastoides* g. (starwort mouse-ear), *Thalictrum al-pinum* g. (alpine meadow-rue), *Thalictrum flavum* g. (common meadow-rue), Moore et al. (1991) for *Oxyria* (mountain sorrel), *Equisetum* (horse-tail), Fægri and Iversen (1989) and Moe (1974) for spores, and van Geel (1976) for non-pollen paly-

nomorphs. Although the grain size of *Betula nana* (dwarf birch) tends to be smaller than that of tree birches, an absolute separation is not possible due to their overlapping size distributions (e.g. Birks 1968; Usinger 1977; Andersen 1980). Therefore a fixed threshold at 21.5 μm was used to separate a *Betula nana* type from a tree birch type (e.g. Kolstrup 1982; Karlsdóttir et al. 2007). These measurements supplement the macrofossil analysis, which is a more powerful in the differentiation of *Betula* species. Pollen of thermophilous taxa such as *Alnus* (alder), *Corylus* (hazel), *Picea* (spruce), *Quercus* (oak), *Tilia* (lime) and *Ulmus* (elm) were regarded as redeposited if present in the late-glacial deposits. Charred fragments >10 μm were counted. The pollen and macrofossil data were plotted using the Tilia program (Grimm 2011). Plant nomenclature follows Wisskirchen & Haeupler (1998). CONNIS was used to determine the local pollen assemblage zones by a square root transformation and Edwards and Cavalli-Sforza's chord distance. Trees, shrubs, dwarf shrubs and herbs were used to determine the local pollen assemblage zones (LPAZ) and these were correlated to the regional biostratigraphy as described by Mortensen et al. (2011).

Macrofossil analysis. Macrofossils were analysed on 17 of the 34 levels analysed for pollen. A sediment volume of 100 cm³ from the 2 cm samples was measured by water displacement and samples were then wet sieved through a 0.25 mm mesh. When necessary, sodium pyrophosphate was added to soften the sediment before sieving. Macrofossils were identified and counted at 6.3-60 x magnification. The reference collection at the National Museum of Denmark was consulted for identification together with identification guides (Cappers et al. 2006; Nilsson & Hjelmqvist 1967; Aalto 1970; Katz et al. 1965). Frequency of taxa represented by high numbers of fossils was estimated from quantitative subsamples. The abundances of remains that cannot be counted, including leaf material of *Betula* and *Dryas octopetala* (mountain avens), mosses, twigs, and *Characeae* oospores, were estimated and given the following scores in the further calculations: present (2), rare (4), occasional (10), frequent (25), abundant (100), very abundant (250). Other fossils are presented as numbers per 100 cm³ fresh sediment.

Table 2. Description of the development of pollen, macrofossils and LOI.

Results

The ages of the 10 ¹⁴C dated samples are presented in table 1 and an age-depth model is shown in fig. 2. The age-depth model was developed by employing the depositional model option in OxCal 4.1 with a model parameter k = 100 (Ramsey 2009).

The pollen diagram was divided into seven local pollen assemblage zones (LPAZ HA1 – HA7). This zonation is also used to describe the macrofossil results and the LOI results (table 2). The results of the pollen, macrofossil and LOI analyses are shown in figs. 3a, b and 4a, b.

Discussion
– The open pioneer landscape

Bølling (HA1. *Hippophaë-Betula nana*, 14,200-14,000 cal. BP). This zone is characterized by pollen maxima of *Hippophaë ramnoides* (sea-buckthorn) and *Beula nana* type and a generally high proportion of light demanding (heliophile) taxa (e.g. *Dryas octopetala, Saxifraga* sp. (saxifrage), *Rumex acetosella* (sheeps sorrel), *Thalictrum alpinum, Artemisia* sp. (mugwort) and Poaceae (grass)). The macrofossil assemblage shows that the local vegetation around the lake was also dominated by light demanding pioneer taxa such as *Arctostaphylos alpinus* (mountain bearberry), *Beula nana, Dryas octopetala, Salix herbacea* (dwarf willow) and *Saxifraga* sp. These pioneer taxa are adapted to environments with disturbed soils, water stress and minimal nitrogen content but do not compete well with other plants (Petersen & Vestergaard 2006). The low organic content and high sediment accumulation rate of the sediments show that erosion and soil instability were important factors in the Bølling period (fig. 3a). The distinct dark bands seen in the predominantly minerogenic sediments have a high macrofossil content and were probably formed during the spring snowmelt and/or during heavy rainfall (plate 1b). This kind of unstable environment along with associated weak soil formation and water stress is typical for the early successional phase and is probably one of the main

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LPAZ	Height (cm)	Age (cal BP)	Pollen	Macrofossils	LOI	Regionally periods
HA 7 *Betula pubescens-Pinus-Poaceae*	155-160	11,350-11,100	Dryland: Increase in *Betula pubescens* t. and Poaceae, most other taxa decline	Wet land: *Betula nana* and *Empetrum nigrum*.	Organic content: 75% Increasing $CaCO_3$: 0%	Preboreal
HA 6 *Betula nana-Poaceae-Artemisia*	108-155	12,600-11,350	Dryland: High percentage of *Betula nana* t., along with *Pinus, Juniperus communis, Artemisia sp.*, Chenopodiaceae and Poaceae. Maximums of *Dryopteis* and *Gymnocarpium drypoteris* in the first half. Around the middle of the zone an increase in *Empetrum nigrum* and *Ranunculus* sp. Charcoal increases towards the middle of the zone. Wetland: Cyperaceae increases in the middle of the zone and more aquatic taxa are seen. *Pediastrum* and *Botryococcus* increase through the zone.	Dryland: *Betula nana, Dryas octopetala, Empetrum nigrum* and *Stellaria media* t., along with *Cenococcum geophilum*. Aqatic: *Potamogeton filiformis* and *Batrachium sp.*	Organic content decreases from 25% to 5% followed by relatively stable values c. 10%. $CaCO_3$ increases strongly through the first half of the zones, followed by a decrease.	Younger Dryas
HA 5 *Betula pubescens-Pinus*	85-108	13,400-12,600	Reduction of *Betula nana* t., increase in *Betula pubescens* type and *Pinus*. Low peak of *Juniperus communis*. Low percentages of heliophile taxa such as *Artemisia* and Poaceae. Towards the end of the zone shows a reduction of *Betula pubescens* and an increase in more light demanding taxa such as *Betula nana, Filipendula*, Poaceae, *Gymnocarpium drypoteris*. In the wetland taxa an increase of *Equisetum* is seen in the middle of the zone but otherwise low values. The proportions of aquatic taxa are generally low but *Pediastrum* increases towards the end of the zone.	*Betula pubescens* is seen throughout the whole zone. *Populus temula* and *Betula nana* are also seen in the first part of the zone. Heliophile taxa such as *Selaginella selaginoides* and *Thalictrum alpinum* are also seen in the first part together with *Cladium mariscus*. *Arctstaphylos uva-ursi* found in the last part of the zone. Wet land taxa of *Polamogeton filiformis, Potamogeton natans, Myriophyllum alterniflorum* seen.	The organic content increases strongly until c. 95 cm where a small trough is seen. This is followed by an increase to 100 cm after which it decreases. $CaCO_3$ decreases in the first half to the zone and then remains low.	Allerød
HA 4 *Betula nana-Betula pubescens*	64-85	13,600-13,400	An increase in *Betula nana* type and *Betula pubescens* type, while *Artemisia* and Poaceae decrease together with other heliophile taxa. Cyperaceae pecentages decrease. *Myriophyllum verticillatum* and *Sparganium* aquatic taxa are present and a reduction of *Pediastrum* and *Botryococcus* are seen. Charcoal and hystrix are absent.	First macrofossils of *Betula pubescens*, together with those of *Betula nana*, and *Salix* sp. Wet land taxa of *Carex rostrata, Eleocharis palustris/uniglumis, Parnassia palustris, Selaginella selaginoides* and *Batracium* sp. Macrofossils of *Chara* sp. *Potamogeton filiformis* and *Potamogeton praelongus* also seen.	Organic content c. 7-8% until the end of the zone where it increases markedly. $CaCO_3$: c. 15%.	Allerød
HA 3 *Betula pubescens-Helianthemum*	37-64	13,800-13,600	This zone is characterised by a strong increase in *Betula pubescens* type which peaks in the middle and then decreases to 20 %, along with an increase in *Juniperus communis*. Decreases in *Salix, Betula nana* and *Pinus*. Still many open taxa such as *Dryas octopetala, Helianthemum oelandicum, Rumex acetosella, Thalictrum alpinum* and Chenopodiaceae, alon with relatively high *Artemisia* sp. values. The wetland taxa Cyperaceae and *Equisetum* increase. The aquatic taxa *Myriophyllum spicatum, Myriophyllum verticillatum, Potamogeton, Sparganium* are seen. Maximums of *Pediastrum* and *Botryococcus*.	High counts of *Betula nana* macrofossils. *Artostaphylos uva-ursi, Dryas octopetala* and *Salix herbacea* are also represented. Also seen are macrofossils of *Carex aquatilis, Juncus, Batrachium* sp., *Menyanthes trifoliata, Primula (P. farinosa, P. stricta* or *P. scandinavica), Selaginella selaginoides, Batrachium* sp. *Potamogeton filiformis* and *Potamogeton praelongus.*	Organic content: 7-8% $CaCO_3$: c. 15%	Allerød
HA 2 *Poaceae-Helianthemum*	22-37	14,000-13,800	Increasing percentages of *Salix* and *Pinus*, along with Poaceae. Many open ground taxa such as *Dryas octopetala, Helianthemum oelandicum, Rumex acetosella, Thalictrum alpinum, Artemisia*, Chenopodiaceae. Reduction in Cyperaceae, while the percentage of *Spagnum* spores increase. Maximum of *Pediastrum* while *Botryococcus* decline. Maximums of Hystrix and charcoal.	Dry land taxa dominated by *Betula nana, Dryas octopetala*, and *Salix* sp. Wetland and aquatic taxa of *Juncus* and *Batraschium* sp., *Chara* sp. *Myriophyllum* sp. and *Potamogeton filiformis*.	Organic content generally low at c. 15%. $CaCO_3$: c. 20%	Older Dryas
HA 1 *Hippophaë-Betula nana*	0-22	14,200-14,000	Maximums of *Hippophaë ramnoides* and *Betula nana* t. High percentages of heliophile taxa such as *Dryas octopetala, Helianthemum oelandicum, Empetrum nigrum, Saxifraga* sp., *Rumex acetosella, Thalictrum alpinum, Artemisia* sp., Poaceae and Chenopodiaceae. Wetland taxa are dominated by Cyperaceae which increases from 20 to 35%, followed by a reduction. Aquatic taxa seen are *Myriophyllum spicatum, Myriophyllum verticillatum, Potamogeton* and *Sparganium*. Two small peaks of charcoal are also seen.	Dominated by open ground taxa such as *Artostaphylos alpinus, Betula nana, Dryas octopetala, Salix herbacea* and *Saxifraga* sp. Wet land and aquatic taxa of *Carex aquatilis, Carex nigra, Eleocharis palustris/uniglumis, P palustris, S. selaginoides, Batrachium, Callistriche, Potentilla palustris. Potamogeton filiformis, Potamogeton praelongus* and *Chara* sp.	Organic content generally low at c. 5%. $CaCO_3$: c. 20% and gently rising.	Bølling

reasons why more competitive taxa such as *Betula pubescens* (downy birch) did not arrive earlier.

The vegetation of the Bølling period has previously been described in detail at only one other site in Denmark, Slotseng (Mortensen et al. 2011). Hasselø and Slotseng had similar landscapes with low, open and species-rich vegetation with many dwarf shrubs, herbs and grasses (plate 2a). This would have been an ideal environment for reindeer *Rangifer tarandus* (reindeer) which was characteristic of this period (Aaris-Sørensen et al. 2007). Southern Scandinavia may have been an important reindeer calving region at this time and this was probably the initial reason for human immigration into the region (Aaris-Sørensen et al. 2007; Jensen 2001). With the exception of one, out-of-context, arrow head belonging to the classical phase of the Hamburg Culture (Jensen 2001), the first reliable and well dated traces of humans in Denmark belong to the Havelte phase of the Hamburg Culture (e.g. Holm 1993; Mortensen et al. 2008) and date to the end of the Bølling period (Weber & Grimm 2009; Mortensen et al. 2014b). No traces of the Hamburgian are found at Hasselø. The nearest occupation

sites are situated c. 40 km to the west at Sølbjerg and Krogsbølle on the island of Lolland (Petersen & Johansen 1993, 1996; Petersen 2006; Pedersen 2009). The two small peaks of charcoal seen in the pollen diagram (fig. 3b) could indicate more hitherto undiscovered occupation sites in the area near the lake but the peaks may also represent reworked charcoal from glacial sediments.

Older Dryas (HA2. *Poaceae-Helianthemum*, 14,000-13,800 cal. BP). A continuance of the high proportion of heliophile taxa such as *Dryas octopetala, Helianthemum oelandicum* (hoary rockrose)*, Rumex acetosella, Thalictrum alpinum, Artemisia* and *Chenopodiaceae (goosefoot)* is seen but with an increase in *Salix* (willow), *Pinus* (pine) and Poaceae. The macrofossil assemblage indicates that the local vegetation did not change and continued to be dominated by cold-tolerant pioneer taxa such as *Betula nana*, *Dryas octopetala* and *Salix*.

The Older Dryas (GI-1d) is shown in the isotopic records of Greenland ice cores to be a cold period (Rasmussen et al. 2006) but in north-western Europe this short-lasting period is difficult to see in pollen diagrams. Some pollen records are inter-

Plate 2a & b

a. The open and treeless environment of Hadangervidda, Norway could be similar to the environment in Denmark during the Bølling period.

b. Light, open mountain birch forest *(Betula pubescens* ssp. *czerepanovii*) at Ringebu, Norway. Juniper *(Juniperus communis* ssp. *nana)* and dwarf birch *(Betula nana)* are seen in the undergrowth. The landscape could be similar to the environment around Hasselø during the second part of the Allerød period. (Photo: Morten Fischer Mortensen).

preted as showing a temperature decrease (Iversen 1954; Usinger 1985; de Klerk et al. 2001) while others are interpreted as a pronounced dry period (Kolstrup 1982; Berglund et al. 1994; Mortensen et al. 2011). The Hasselø pollen diagram exhibits a strong decrease in *Hippophaë ramnoides*, a species which cannot tolerate cooler climates. This occurs at the same time as an increase in arid tolerant taxa, especially *Helianthemum oelandicum*, which is characteristic of the Danish Older Dryas. An increase in dinoflagellate cysts (*Hystrix*) indicates an increase in erosion undoubtedly due to the partial fragmentation of the vegetation cover while the decrease in Cyperaceae indicates a drier climate and possibly a lake level lowering.

It is probable that the Older Dryas climate became both colder and drier but since the vegetation was already dominated by cold tolerant taxa, a temperature decrease would not be clearly expressed in the pollen diagram with the exception of the few warmth demanding taxa such as *Hippophaë ramnoides*. It is likely that this is the reason why the Older Dryas is not more strongly expressed in Danish studies. This is in contrast to northern Germany where the Older Dryas is clearly seen despite being situated only 70-80 km from from Hasselø (de Klerk 2002, 2008). This difference also indicates the existence of an ecotone between the two regions with open tundra and pioneer vegetation to the north and a more advanced vegetational development, with the beginning of the spread of tree birch, immediately to the south of Denmark.

The significant charcoal content found in several consecutive samples could however, be an indication of human activity. Charcoal is present from the beginning of the period (c. 14,000-13,900 cal. BP) and could come from the occupation site. These dates fall within the period defined for the spread of the Federmesser Culture (Pedersen 2009; Petersen 2006; Riede & Edinborough 2012) but neither a natural fire sparked by lightning nor redeposited charcoal can be excluded and the association of the charcoal peaks with the occupation site cannot be confirmed. However, if humans were present in the Danish region in the first half of the Allerød, they would have taking advantage of the available resources in the border regions between the open tundra and the open woodland. The most likely objective would have been reindeer, which was the largest prey present at this time (Aaris-Sørensen 2009).

– The open shrub and grassland landscape

Allerød (HA3. *Betula pubescence-Helianthemum*, 13,800-13,600 cal. BP). This zone is characterized by a strong increase in *Betula pubescens* type pollen accompanied by an increase in *Juniperus communis* (juniper) and a simultaneous decrease in *Salix, Betula nana* and *Pinus*. There are still, even in the presence of a strong tree birch increase, many open ground and light demanding taxa represented in the pollen flora, for example, *Dryas octopetala, Helianthemum oelandicum, Rumex acetosella, Thalictrum alpinum,* Chenopodiaceae and *Artemisia* sp. The macrofossil assemblage still shows a domination of pioneer taxa, for example *Betula nana, Arctostaphylos uva-ursi* (bearberry), *Dryas octopetala and Salix herbacea. Betula nana* in particular dominates with *Dryas octopetala* in lower numbers. *Dryas octopetala* is probably reduced due to competition with the more competitive shrubs and tall herbs which are becoming more dominant in the landscape. The *Betula pubescens* pollen type increases to almost 40%, which could indicate a strong increase in tree birch locally. However, in the absence of macrofossils, it is more likely that the high percentages are due to long distance transport of pollen from, for example, northern Germany where tree birch was expanding (de Klerk 2008).

– The first trees

Allerød (HA4. *Betula nana-Betula pubescens*, 13,600-13,400 cal. BP). An increase in *Betula nana* type and *Betula pubescens* type occurs at the same time as a decrease in *Artemisia,* Poaceae and other heliophile taxa. This is a clear indication that more competitive taxa have become locally established in the catchment area. The macrofossil analysis also shows that *Betula pubescens* is now locally present for the first time. The time difference between the distinct increase in tree birch pollen in LPAZ HA3 and its first appearance in the macro-

fossil record is c. 200 years. The most light demanding and least competitive taxa (*Dryas octopetala* and *Salix herbacea)* are now absent while *Betula nana*, a species which can grow in the undergrowth of open woodland and on wet ground, is still present (plate 2b). During this first phase of woodland development, tree birch probably grew in moist, protected areas with the most developed soils, while the drier and more exposed areas remained relatively open. The low organic content in the sediments suggests that there was still a significant input of minerogenic material (fig. 3a). Towards the end of this zone, increased organic content indicates that a birch woodland proper had become established around the lake and that the roots and undergrowth had stabilised the soils.

It has previously been argued that tree birch immigrated into the Danish region as early as during the Bølling period (Iversen 1954; Kolstrup 1982; Paus 1995). There is some support for this from a study on Kullen in southern Sweden where a few tree birch macrofossils were assigned to the Bølling Period (Liedberg-Jonsson 1988). However, we consider this questionable as the sequence was dated using bulk sediment samples with low organic content. The eventual local presence of tree birch southern Sweden needs to be confirmed by new studies using modern dating techniques. The investigations at Slotseng have shown that it arrived much later and it was not until around the middle of the Allerød period (13,500 cal. BP) that the first tree birch macrofossils are found (Mortensen et al. 2011, Mortensen et al. 2014a). The similar age of 13,600 cal. BP at Hasselø confirms the late immigration of tree birch into the Danish region in contrast to what was previously believed. This is also the same time as elk *Alces alces* (elk) immigrated into the region (Aaris-Sørensen 2009).

This change from tundra with dwarf-shrub heaths to birch woodland marks an important environmental change (vegetation, available fauna etc.) and changes in the archaeological material may be expected to demonstrate a shift at the same time.

Allerød (HA5. *Betula pubescens-Pinus*, 13,400-12,600 cal. BP). The beginning of this zone shows a reduction in *Betula nana* type and increases in *Betula pubescens* type and *Pinus*. The double peak of *Betula pubescens* type is caused by a

slight reduction in the woodland associated with the cold Gerzensee Oscillation (Andresen et al. 2000). Macrofossils of *Betula nana*, *Selaginella selaginoides* (lesser clubmoss) and *Thalictrum alpinum* show that the woodland at the beginning of the zone was still open even though heliophile pollen decreases. The lack of *Dryas octopetala* and other heliophile taxa from the macrofossil assemblage in zone HA5 indicates a closing of the woodland, at least around the lake. It is probable that there were open patches on the drier and more exposed areas throughout this period but that these areas lay outside the macrofossil catchment area. The Allerød woodland around Hasselø appears to have been denser than at Slotseng in southern Jutland (Mortensen et al. 2011).

In addition to *Betula pubescens*, the Allerød woodland in eastern Denmark included *Populus tremula* (aspen) and *Juniperus communis* (Hartz 1902; Fischer et al. 2013b), various large willow species such as *Salix* cf. *caprea* (goat willow) (Iversen 1954; Mortensen et al. 2011) and most likely also *Sorbus* (rowan). *Sorbus* is found in the Hasselø pollen assemblage and at a number of other Danish sites and, as it is insect pollinated, the pollen probably came from local populations. *Pinus* macrofossils have not yet been found in Danish late Glacial sediments, even though *Pinus* pollen are abundant in the pollen assemblages and pine was probably not part of the late Glacial woodland of Denmark. The closest find of *Pinus* logs lays 60 km south of Hasselø at Rostocker Heide, northern Germany (Terberger et al. 2004) and a sample has been dated to 11,220±250 BP (13,600-12,600 cal. BP) and thus shows an ecotone between southeast Denmark and northern Germany during the second half of the Allerød period (fig. 6). Even though there was a very strong temperature gradient over Europe (Coop et al. 1998; Renssen & Isarin 2001), average July temperatures of 13-15°C in southern Denmark (Coope et al. 1998) would have been sufficient for the establishment of *Pinus*. Other factors such as dispersion rate and soil formation must account for the delayed immigration of pine to Denmark. The large valley area found between southeast Denmark and northeast Germany may have acted as a barrier. This low lying region was covered either by the Baltic Ice Lake or by large wetland areas and it was subject to large and abrupt lake level changes during

much of the late Glacial (Bennike & Jensen 2013). This may have delayed the north-westerly spread of *Pinus* and although pine can grow on many soil types (Friis-Møller et al. 2010), competition with the already established birch woodland may also have contributed to the delay.

– The Allerød woodland

The reconstruction shows that during the second half of the Allerød south-eastern Denmark was covered by birch woodland with *Populus*, *Juniperus* and probably also *Sorbus* (Iversen 1954; Fischer et al. 2013b). The woodlands were relatively open with *Betula nana, Rubus caesius* (dewberry), *Rubus saxatilis* (stone bramble) and *Urtica dioica* (commen nettle) (e.g. Jensen 1985, Fischer et al. 2013b). The woodland to the west and north probably had more of a mosaic structure with many open areas (Kolstrup 2007; Bennike et al. 2004a; Mortensen et al. 2011), while mixed birch pine woodland were found just south of the Danish region (Usinger 2004; Latalowa & Borowka 2006; de Klerk 2008; Theuerkauf and Joosten 2009). The coast of the Baltic Ice Lake was found to the east (Bennike & Jensen 1998; Bennike et al. 2004b) and the coast of the Yoldia Sea was located near northern Zealand (Houmark-Nielsen & Kjær 2003). The south-eastern Danish region was therefore situated in a zone between several different ecosystems (fig. 6). Such marginal areas are known to have a particularly high biodiversity (e.g. Petersen & Vestergaard 2006) and the numerous available subsistence strategies may explain the especially rich representation of the Bromme Culture in the region. Bones of large game such as *Alces alces, Megaloceros giganteus* (giant deer), *Rangifer tarandus, Ursus arctoc* (brown bear) and *Castor fiber* (beaver) have been found from this period and show that the late Glacial period offered potentially rich hunting grounds. But the picture produced by the known availability of large game animals during the Late Glacial may have coloured our interpretation of the people's total subsistence. The coastal areas would also have offered valuable resources (Fischer et al. 2013a) although the evidence is fragmentary. But we assume that there was a rich bird fauna available for both hunting and for collection of eggs and chicks. Fishing had also been practiced during the Palaeolithic (Gramsch et al. 2013) and the numerous lakes would have provided good fishing opportunities of, for example, pike and perch whose sticky eggs are rapidly spread by water birds. Lastly, the vegetation itself would have been both a food resource (Tyldesley & Bahn 1983; Aura et al. 2005; Revedin et al. 2010) and a material for tool production (e.g. Riede 2012), although wooden tools are almost never preserved.

– The Allerød-Younger Dryas transition

The climate cooling at the end of the Allerød had a strong impact on the vegetational succession of the late Glacial forest. A distinct reorganisation of atmospheric circulation over the northern hemisphere followed by a gradual temperature decline is indicated in the Greenland ice cores (Rasmussen et al. 2006; Blockley et al. 2012). According to the Greenland ice core chronology (GICC05) (Rasmussen et al. 2006; Blockley et al. 2012) the transition from the warm GI-1a interstadial to the colder GS-1 stadial is dated to 12,896 ±138 B2K (12,846 before AD 1950). Temperatures continued to decline until 12,780 B2K (12,730 before 1950 AD), at which time a large and rapid decrease occurred. These changes are not only seen in Greenland ice core proxies but also in records from the whole of the northern hemisphere (e.g. Björck et al. 1996). It is important to stress, however, that although atmospheric circulation, climate and biosphere are linked, the chances can inherently not be synchronous (Rasmusssen et al. 2006).

The temperature decrease between 12,846 and 12,730 cal. BP seen in the ice cores does not appear to have affected the vegetational assemblage at Hasselø, but a decline in the organic content of the lake sediments is seen. This could be due to a transition to a drier climate, which may have led to lowering of the lake level and associated erosion of minerogenic material from the lake margin. There is however, a marked and rapid response of the vegetation to the temperature decline at 12,730 cal. BP. *Betula pubescens* decreases at the same time as an increase in light demanding taxa such as *Betula nana, Filipendula* (meadowsweet), Poaceae and *Gymnocarpium dryopteris* (oak fern). This corresponds with the Allerød-Younger Dryas transition seen at Kråkenes

in western Norway, one of the best dated late glacial lake sequences in Europe. Here the transition is dated to 12,711±52 cal BP (Lohne et al. 2013). This agrees well with a number of annually layered lake sequences in Germany where the transition is dated between 12,679±30 and 12,606±40 varve years BP (Zolitschka et al. 2000, Brauer et al. 2001, Neugebauer et al. 2012). The Allerød type environment continued despite the substantial temperature decrease but it became more fragmented with light open woodland. At c. 12,575 cal. BP, a threshold was reached and the woodland environment and ecosystem collapsed. The fragmentation of the vegetation cover promoted erosion and the deposition of clastic, inorganic sediments.

It has been suggested previously that the Greenland ice core event stratigraphy (Björck et al. 1998) can be broadly correlated to the northern European pollen zones (e.g. Terberger et al. 2009), as the vegetation often responds immediately to climate changes. The Hasselø record also shows a rapid response, but it additionally shows that the late Glacial woodland survived several hundred years after the beginning of the GS-1 cold period. Younger Dryas type vegetation is not evident until 12,575 cal. BP, which is cause for caution when interpreting archaeological data. Figure 5 shows the Danish Bromme Culture ^{14}C ages from Bromme, Fensmark and Trollesgave (Fischer et al. 2013b) and illustrates that the dates lie within GS-1 but also that they all belong to an Allerød environment. The transition between Allerød / Younger Dryas and GI-1a/GS-1 is therefore far from synchronous. This demonstrates that the relationship between ^{14}C ages, human occupation sites and ice core data cannot be used to directly define the local environment. Such conclusions must always come from local/regional climate and environmental reconstructions, especially if the ages lie in the transitional zone between two different climatic regimes.

– The open Younger Dryas landscape

Younger Dryas (HA6. *Betula nana*-Poaceae-*Artemisia*, 12,600-11,350 cal. BP). A vegetational paradigm shift occurs from the open woodland landscape of HA5 to an open landscape with pioneer vegetation in HA6. *Betula pubescens* type pollen decrease while there are generally higher values of *Betula nana* type and *Pinus*, *Juniperus communis*, *Artemisia sp.*, Chenopodiaceae and Poaceae also reach generally higher percentages throughout the HA6 zone. *Dryopteris* and *Gymnocarpium dryopteris* reach their local maxima in the first half of the zone. *Empetrum nigrum* (crowberry), *Rannunculus* sp. (buttercup) and Cyperaceae increase around the middle of the zone.

Macrofossils of *Betula nana*, *Dryas octopetala*, *Empetrum nigrum* and *Stellaria media* (common chickweed) show that the vegetation was replaced by more cold adapted plants. The absence of tree birch indicates an average summer temperature of less than 10°C. The exact limit of tree birch at this time is not known but it probably survived in regions immediately south of Denmark (Usinger 2004; de Klerk 2008). Evidence from lake sequences suggests that the first part of the Younger Dryas was arid and many smaller lakes in northern Germany dried out (Usinger 1981). This was also the case in the south-
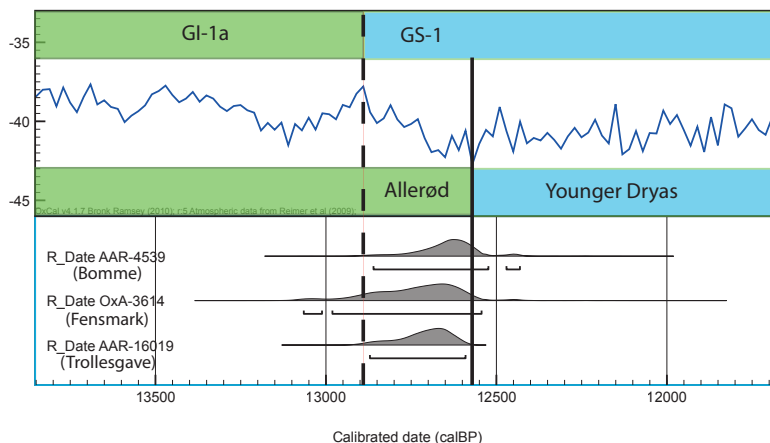
Figure 5. Bromme Culture ages from Denmark (Fensmark Skydebane, Trollesgave, Bromme). The transition from GI-1a to GS-1 (GICC05) is shown by the dashed line and the transition from Allerød to Younger Dryas by the solid line.

Figure 6. Map of southern Scandinavia during the late Allerød period showing the ecotone between the Danish birch forest and the northern German birch/pine forest. The low lying region between Denmark and Germany were flooded during the maximum extent of the Baltic Ice Lake.

ern part Jutland. In the lake sequence from the Slotseng kettle hole (Mortensen et al. 2011) there is a distinct peak of microtephra from the Vedde ash located directly on top of the Allerød layer (Larsen 2014). This indicates that the Slotseng kettle hole dried out and that there was no sedimentation between the end of the Allerød until the deposition of the Vedde ash which are dated to 12,140±40 varve years BP (Lane et al. 2013). This very dry first part of the Younger Dryas was most likely caused by extensive sea ice in the northern North Atlantic. Extended sea ice would have advected the relatively warm and moist air from the Atlantic further south promoting prevailing easterly winds over Scandinavia and leading to a colder, drier climate (Bakke et al. 2009). A shrinking of the sea ice extent after c. 12,150 cal. BP caused the Scandinavian climate to become dominated by westerly, relatively warm and moist winds again pushing the polar front northwards (Bakke et al. 2009) and sedimentation in the Slotseng basin resumed.

This shift corresponds with a rise in *Empetrum nigrum* in Hasselø, dated to c. 12,100 cal. BP, along with increased percentages of Cyperaceae and *Ra-*

nunculus sp. *Batrachium* sp. (water-crowfoot) as seen in the macrofossils, all of which suggest increased precipitation. The increase in *Empetrum nigrum* is well known in pollen diagrams from Denmark, Germany and The Netherlands (e.g. Iversen 1954; Hoek 1997; Usinger 2004; de Klerk 2008) and is interpreted as a response to a more oceanic climate (Usinger 2004; Hoek 1997). No evidence has yet been found in Denmark to indicate the presence of humans during the Younger Dryas, but reindeer was present throughout the period and with them, the possibility of humans. The environmental response and the cold climate during the Younger Dryas may explain the gap in human presence during this period (Petersen 2006), with the exception of sporadic hunting expeditions by groups from the Ahrensburg Culture.

– The Preboreal woodland environment

Early Holocene (HA7. *Betula pubescens-Pinus-Poaceae*, 11,350- cal BP). The beginning of the Preboreal shows an increase in *Betula pubescens* type and Poaceae pollen while almost all other taxa decrease significantly. These changes are a response

to improved growth conditions instigated by the transition to the warmer Preboreal period. The local presence of *Betula nana* and *Empetrum nigrum* is shown by the macrofossil analysis but surprisingly, no macrofossils of *Betula pubescens* were found. Many pollen records show that the Preboreal period in Denmark began with a marked *Juniperus communis* peak. This lasted for a few hundred years, after which tree birch immigrates and rapidly dominates. The juniper peak is not clearly seen in the Hasselø data but this may be due to low sample resolution in this period. However, a diffuse representation of *Juniperus communis* is also seen in other sites from south-eastern Denmark (Jessen et al. 2014) so it may also be due to soil type and associated competitive factors. The delay in the spread of tree birch after the Holocene warming is probably due to the still unstable soils and LOI values indicate continued substantial erosion during the early Preboreal. This is also seen at other sites, e.g. Trollesgave, southern Zealand, where large-scale soil movements have been documented (Fischer et al. 2013b). At Lundby Mose, c. 40 km north of Hasselø, pollen data also show a late immigration of *Betula pubescens* (Jessen et al. 2014). These data from southeast Denmark indicate an actual delay in immigration of tree birch.

Conclusions

Based on the investigation from Hasselø we have established the first well-dated late Glacial biostratigraphy from eastern Denmark covering the period from the Bølling to the early Preboreal.

The vegetation during the Bølling and Older Dryas periods is dominated by pioneer taxa and eastern and western Denmark had similar landscapes.

An ecotone existed between southeast Denmark and northern Germany throughout a large part of the late Glacial. The large lowland area between these two regions, which was periodically covered by the Baltic Ice Lake, may have formed a barrier to spread of plants.

Tree birch did not immigrate to the Danish region until the middle of the Allerød period, c. 13,600 cal. BP, and this late arrival appears to be a general feature of the vegetation development.

It has long been thought that tree birch grew in

the Danish region from the beginning of the late Glacial, but this study of both local and regional proxies shows a clear delay of over 1000 years in the immigration of tree birch.

The Allerød environment collapsed and was replaced by that of the Younger Dryas at c. 12,575 cal. BP, around 300 years after the transition to GS-1. The calibrated ages of the Danish Bromme Culture are positioned within GS-1, but they belong to an Allerød environment.

The Younger Dryas can be divided into two phases. The first part is very cold and arid and is followed by a warmer and more humid phase from 12,100 cal. BP initiating the development of *Empetrum nigrum*-rich heaths.

The early Preboreal is characterized by erosion and soil instability, which may have led to delayed establishment of *Betula pubescens*.

Acknowledgements

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