Vegetation development in south-east Denmark during the Weichselian Late Glacial: palaeoenvironmental studies 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 is 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 between *c.* 14,000 and 13,900 cal. BP may be related to the occupation site. This study shows that an ecotone was positioned between present-day Denmark and northern Germany during a large part of the Late Glacial period. This was especially the case during the Older Dryas and early Allerød periods, when woodland was expanding in northern Germany while the Danish area remained open. Later in the Allerød period, northern Germany seems to have been the northern limit for pine woodland. The low-lying region separating Denmark and Germany was periodically covered by the Baltic Ice Lake and this 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 clearly shows that the immigration of tree birch was delayed by more than 1000 years. 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 is also shown. The three ^{14}C ages available from the Danish Bromme Culture are from this transition phase when the birch woodland was becoming more open. Pollen analysis also shows the classical Younger Dryas cold separated into an early dry phase (until *c.* 12,100 cal. BP) and a later wetter phase. This was most likely due to a change in atmospheric circulation and variation 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.

Keywords: pollen analysis; macrofossil analysis; vegetation development; palaeoenvironment; Late Glacial; Late Palaeolithic; Denmark; Bølling; Allerød; Younger Dryas

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 Palaeolithic '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 1982, Kolstrup and Buchardt 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 with those based on pollen alone (e.g. Lidberg-Jönsson 1988, Birks 1993, Birks et al. 2005, Mortensen et al. 2011, 2014a). Among the major advantages of plant macrofossils over pollen-based reconstructions are 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 and Sugita 2005). Reconstructions including macrofossils are therefore often more diverse and multifaceted than those based on pollen alone (e.g. Birks and 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 and 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. Tree birch produces large amounts of pollen and is well dispersed, and the documented difference can most likely be attributed to the long-distance transport of tree birch pollen (Birks 1993, Van Dinter and Birks 1996, Bennike *et al.* 2004a).

One of the most important landscape changes is that between open land and woodland with their associated different flora and fauna. This is especially important in archaeology as hunting strategies differ with the available prey, which in turn is 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). In southern Jutland, tree birch was first established in the middle of the Allerød period about 13,500 cal. BP (Mortensen *et al.* 2011), much later than previously thought (e.g. Iversen 1954, Kolstrup 1982, Paus 1995). A delay in the expansion of birch is also seen in Schleswig-Holstein (Usinger 1985) but it is not known whether this was also the case in eastern Denmark.

South-eastern Denmark was repeatedly covered by glacial advances from the Scandinavian ice sheet during the last glacial period, 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 and Jensen 1998, Houmark-Nielsen and Kjær 2003, Houmark-Nielsen *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 in previously glaciated regions such as Denmark, and the landscape was therefore 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 sites have been registered in the area around Hasselø since the late 1970s. Most of these sites are situated on low hilltops overlooking the

former freshwater lake of Bredningen. One further low-lying site, Hasselø Tværvej, has attracted attention since its discovery due it being situated by the Hasselø basin. Due to deep ploughing, a rescue excavation was carried out in 1994 (Petersen 2006). The flint inventory at the Hasselø Tværvej site contained several Federmesser points as well as Bromme points (Petersen 2006) and thus confirms the general tendency of Danish Federmesser finds to cluster in two groups of probably different age: an early group associated with late Hamburgian finds (Jels, Slotseng, Sølbjerg) and a late group associated with early Brommian finds (Løvenholm (Madsen 1983), Stoksbjerg Vest (Johansson 2003) and Hasselø Tværvej (Petersen 2006)). Only 50 m separate the kettle hole and the closest of the flint concentrations but, despite an intensive search, only few signs of human activity were seen in a few worked flint pieces, small bone fragments and charcoal which were found in the spoil heaps of the former dead ice lake (Petersen 2006).

The kettle hole was revisited in 2010 to extract sediment samples to reconstruct the environment available for human occupation in the area and possibly to date any human traces in the sediments. This paper focuses on the environmental reconstruction gained from pollen and macrofossil analysis. The results of the occupation site itself will be published at a later date. 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, 2012, Mortensen *et al.* 2011, 2014a, 2014b, Fischer *et al.* 2013a, 2013b).

Site description

Hasselø is situated on Falster, an island in south-eastern Denmark (Figure 1). The present-day annual average temperature is 8.6 °C (January average 1.4°C, July average 16.9 °C) and the annual average precipitation is 617 mm (Theilgaard 2006). The basin had an original area of *c.* 500 square meters 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

A profile of around 8 m in width of lake sediments was exposed by excavating a trench from near the lake edge onto dry land. The exposed sediments (Figure 2a+b) were described in detail. No disturbance such as slumping or deformation was observed. Two overlapping sediment

Figure 1.   Map of southern Scandinavia showing the Allerød distribution of land and sea. The location of Hasselø is shown in red. Six other localities discussed in the text are shown in black (1. Slotseng, 2. Bromme, 3. Trollesgave, 4. Fensmark Skydebane, 5. Lundby Mose, 6. Sølbjerg, 7. Krogsbølle, 8. Rostocker Heide).

monoliths of 160 x 10 x 10 cm were sampled encompassing the Late Glacial and early Holocene sediments. The 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 fired 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 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.

from one level (AAR-15013) due to the absence of sufficient terrestrial material. *M. trifoliata* is a wetland plant but photosynthesises atmospheric CO_2 and is therefore suitable for dating. Material for ^{14}C 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 and Polach 1977) as conventional ^{14}C dates in ^{14}C yr BP (before AD 1950) based on the measured ^{14}C/^{13}C ratio corrected for natural isotopic fractionation by normalizing the result to the standard δ^{13}C value of −25‰ VPDB (Andersen *et al.* 1989). The dates were calibrated and an age-depth model constructed using OxCal 4.2 (Ramsey 2009) and the radiocarbon calibration curve IntCal09 (Reimer *et al.* 2009).

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. (watercrowfoot), were not used because of potential hard water effects. Seeds of *Menyanthes trifoliata* (bogbean) were dated

Pollen analysis

Pollen was analysed for 34 out of a total of 158 contiguous samples. Pollen preparation followed standard procedures, including KOH, HCl, HF and acetolysis (Fægri and 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 were

(a)

(b)

Figure 2.   a) Excavation of the Hasselø basin with the late glacial sediments showing in the profile. b) Lake sediment profile. The thin, dark-coloured layers in the lowermost part are 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.

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 the 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 specialist works for the following: Punt and Blackmore (1991) and Punt *et al.* (1995) for *Cerastium cerastoides* g. (starwort mouse-ear), *Thalictrum alpinum* g. (alpine meadow-rue) and *Thalictrum flavum* g. (common meadow-rue); Moore *et al.* (1991) for *Oxyria* (mountain sorrel) and *Equisetum* (horsetail); Fægri and Iversen (1989) and Moe (1974) for spores; and van Geel (1976) for non-pollen palynomorphs. Although the grain size of *Betula nana* (dwarf birch) tends to be smaller than that of tree birches, absolute separation is not possible due to their overlapping size distributions (e.g. Birks 1968, Usinger 1977, Andersen 1980). Therefore a fixed threshold of 21.5 µm was used to separate a *B. 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 tool 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) was 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 and 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

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

AAR-	Material (species)	Height (cm)	δ^{13}C (‰ VPDB)	^{14}C age (^{14}C yr BP)	Model age (cal. BP, 95.4% probability)
15014	*Dryas* leaves	5.2	−27.73	12,226 ± 44	14,355–13,941
15015	*Dryas* leaves and *Salix* twigs	17.8	−27.68	12,223 ± 43	14,140–13,903
15016	*Betula nana* leaves	32.3	−27.71	11,945 ± 43	13,960–13,750
15017	*B. nana* and *Salix* leaves	45.8	−26.89	11,955 ± 65	13,890–13,660
15018	*Betula* seeds and leaves	73.5	−26.97	11,741 ± 44	13,685–13,415
15019	*Betula pubescens* seeds and catkin scales	88	−27.94	11,516 ± 45	13,459–13,254
15020	*Salix* leaves	106.3	−28.06	10,707 ± 39	12,710–12,554
15021	*B. nana* and *Salix* leaves	117.0	−25.00	10,340 ± 39	12,415–12,143
15022	*B. nana* leaves and *Salix* buds	135.7	−28.41	10,392 ± 40	12,339–12,051
15013	*Menyanthes* seeds and bud scales	160.8	−27.55	9660 ± 40	11,209–10,868

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 cm^3 from the 2 cm samples was measured by water displacement and samples were then wet-sieved through 0.25 mm mesh. Sodium pyrophosphate was added where necessary, to soften the sediment before sieving. Macrofossils were identified and counted at ×6.3–60 magnification. The reference collection at the National Museum of Denmark was consulted for identification, together with identification guides (Katz *et al.* 1965, Nilsson and Hjelmqvist 1967, Aalto 1970, Cappers *et al.* 2006). Frequency of taxa represented by high numbers of fossils was estimated from quantitative subsamples. The amount of remains that could not 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 further calculations: present (2), rare (4), occasional (10), frequent (25), abundant (100), very abundant (250). Other fossils are presented as numbers per 100 cm^3 fresh sediment.

Results and discussion

The ages of the 10 ^{14}C dated samples are presented in Table 1 and the age/depth model is shown in Figure 3. The age/depth model was developed by employing the depositional model option (p-sequence) in OxCal 4.2 with a model parameter k = 100 (Ramsey 2009).

The pollen diagram was divided into seven local pollen assemblage zones (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 Figures 4a, b and 5a, b.

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 *B. nana* type and a generally high proportion of light-demanding (heliophile) taxa (e.g. *D. octopetala*, *Saxifraga* sp. (saxifrage), *Rumex acetosella* (sheep sorrel), *T. alpinum*, *Artemisia* sp. (mugwort) and Poaceae (grasses). 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), *B. nana*, *D. octopetala*, *Salix herbacea* (dwarf willow) and *Saxifraga* sp. These pioneer taxa are adapted to environments with disturbed soils, water stress and minimal
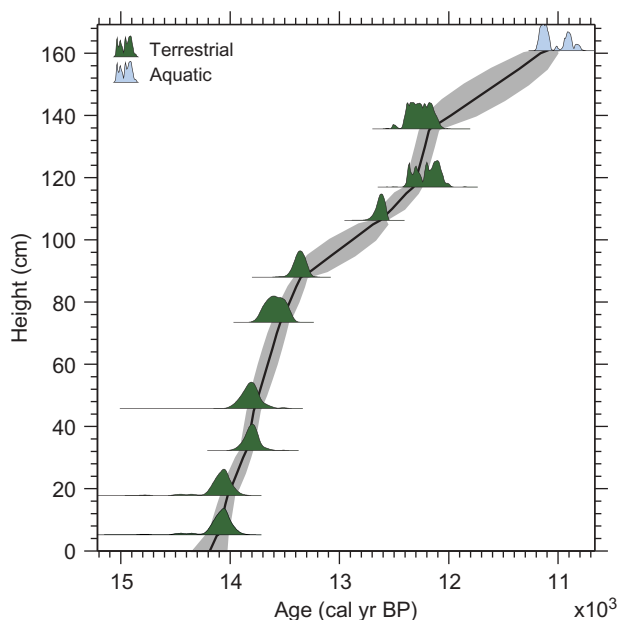

Figure 3. Age/depth model for the Hasselø sediments.

nitrogen content but do not compete well with other plants (Petersen and 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 (Figure 4a). 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 (Figure 2b). 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 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. This would have been an ideal environment for *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 (Aaris-Sørensen *et al.* 2007) and this was probably the initial reason for human immigration into the region (Petersen and Johansen 1993). With the exception of one, out-of-context, arrowhead belonging to the classical phase of the Hamburg Culture (Holm and Rieck 1992), the first reliable and well-dated traces of humans in Denmark are of 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 and Grimm 2009, Mortensen *et al.* 2014b). No traces of the Hamburgian are found at

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

LPAZ	Height (cm)	Age (cal BP)	Pollen	Macrofossils	LOI	Regional period
HA7 *Betula pubescens, Pinus*, Poaceae	155–160	11,350–11,100	Increase in *B. pubescens* t. and Poaceae, most other taxa decline	*B. nana* and *Empetrum nigrum*	Organic content 75%; increasing CaCO$_3$ 0%	Preboreal
HA6 *Betula nana*, Poaceae, *Artemisia*	108–155	12,600–11,350	High percentage of *B. nana* t., along with *Pinus, Juniperus communis, Artemisia sp.*, Chenopodiaceae and Poaceae Maxima of *Dryopteris* and *Gymnocarpium drypoteris* in the first half. Around the middle of the zone an increase in *E. nigrum* and *Ranunculus* sp. Charcoal increases towards the middle of the zone. Wetland: Cyperaceae increase in the middle of the zone and more aquatic taxa are seen. *Pediastrum* and *Botryococcus* increase through the zone	*B. nana, Dryas octopetala, Empetrum nigrum* and *Stellaria media* t., along with *Cenococcum geophilum*. Aquatic: *Potamogeton filiformis*	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
HA5 *B. pubescens, Pinus*	85–108	13,400–12,600	Reduction in *B. nana* t, increase in *B. pubescens* type and *Pinus*. Low peak of *J. communis*. Low percentages of heliophile taxa such as *Artemisia* and Poaceae. Towards the end of the zone there is a reduction in *B. pubescens* and an increase in more light-demanding taxa such as *B. nana, Filipendula*, Poaceae, and *G. drypoteris*. In the wetland taxa an increase in *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	*B. pubescens* is seen throughout the whole zone. *Populus tremula* and *B. 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. A. uva-ursi* found in the last part of the zone. Wetland taxa of *Potamogeton filiformis, Potamogeton natans* and *Myriophyllum alterniflorum* seen	Organic content increases strongly to *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 of the zone and then remains low	Allerød

Table 2. (Continued).

LPAZ	Height (cm)	Age (cal BP)	Pollen	Macrofossils	LOI	Regional period
HA4 *B. nana, B. pubescens*	64–85	13,600–13,400	An increase in *B. nana* and *B. pubescens* types, while *Artemisia* and Poaceae decrease together with other heliophile taxa. Cyperaceae percentages decrease. *Myriophyllum verticillatum* and *Sparganium* aquatic taxa are present and a reduction in *Pediastrum* and *Botryococcus* is seen. Charcoal and hystrix are absent	First macrofossils of *B. pubescens*, together with those of *B. nana* and *Salix* sp. Wetland 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. $CaCO_3$, ca. 15%	Allerød
HA3 *B. pubescens, Helianthemum*	37–64	13,800–13,600	This zone is characterized by a strong increase in *B. pubescens* type which peaks in the middle and then decreases along with an increase in *J. communis*. Decreases in *Salix*, *B. nana* and *Pinus*. Still many open taxa such as *Dryas octopetala*, *Helianthemum oelandicum*, *Rumex acetosella*, *Thalictrum alpinum* and Chenopodiaceae, along with relatively high *Artemisia* sp. values. The wetland taxa Cyperaceae and *Equisetum* increase. The aquatic taxa *Myriophyllum spicatum*, *Myriophyllum verticillatum*, *Potamogeton* and *Sparganium* are seen. Maxima of *Pediastrum* and *Botryococcus*	High counts of *B. nana* macrofossils. *A. uva-ursi*, *D. 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

Table 2. (*Continued*).

| LPAZ	Height (cm)	Age (cal BP)	Pollen	Macrofossils	LOI	Regional period
HA2 Poaceae, *Helianthemum*	22–37	14,000–13,800	Increasing percentages of *Salix* and *Pinus*, along with Poaceae. Many open-ground taxa such as *D. octopetala, H. oelandicum, Rumex acetosella, Thalictrum alpinum, Artemisia,* Chenopodiaceae. Reduction in Cyperaceae, while the percentage of *Sphagnum* spores increases. Maximum for *Pediastrum* while *Botryococcus* declines. Maxima of Hystrix and charcoal	Dominated by *B. nana, D. octopetala* and *Salix* sp. Wetland and aquatic taxa of *Juncus* and *Batrachium* sp., *Chara* sp., *Myriophyllum* sp. and *Potamogeton filiformis*	Organic content generally low at ca. 5%. CaCO₃, *c.* 20%	Older Dryas
HA1 *Hippophaë, B. nana* zone	0–22	14,200–14,000	Maxima of *Hippophaë rramnoides* and *B. nana* t. High percentages of heliophile taxa such as *D. octopetala, H. oelandicum, E. nigrum, Saxifraga* sp., *Rumex acetosella, Thalictrum alpinum, Artemisia* sp., Poaceae and Chenopodiaceae. Wetland taxa are dominated by Cyperaceae which increase 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 *Arctostaphylos alpinus, B. nana, D. octopetala, S. herbacea* and *Saxifraga* sp. Wetland and aquatic taxa of *Carex aquatilis, Carex nigra, Eleocharis palustris/ uniglumis, P. palustris, S. selaginoides, Batrachium, Callitriche, Potentilla palustris, P. filiformis, P. praelongus* and *Chara* sp.	Organic content generally low at *c.* 5%. CaCO₃, *c.* 20% and gently rising	Bølling
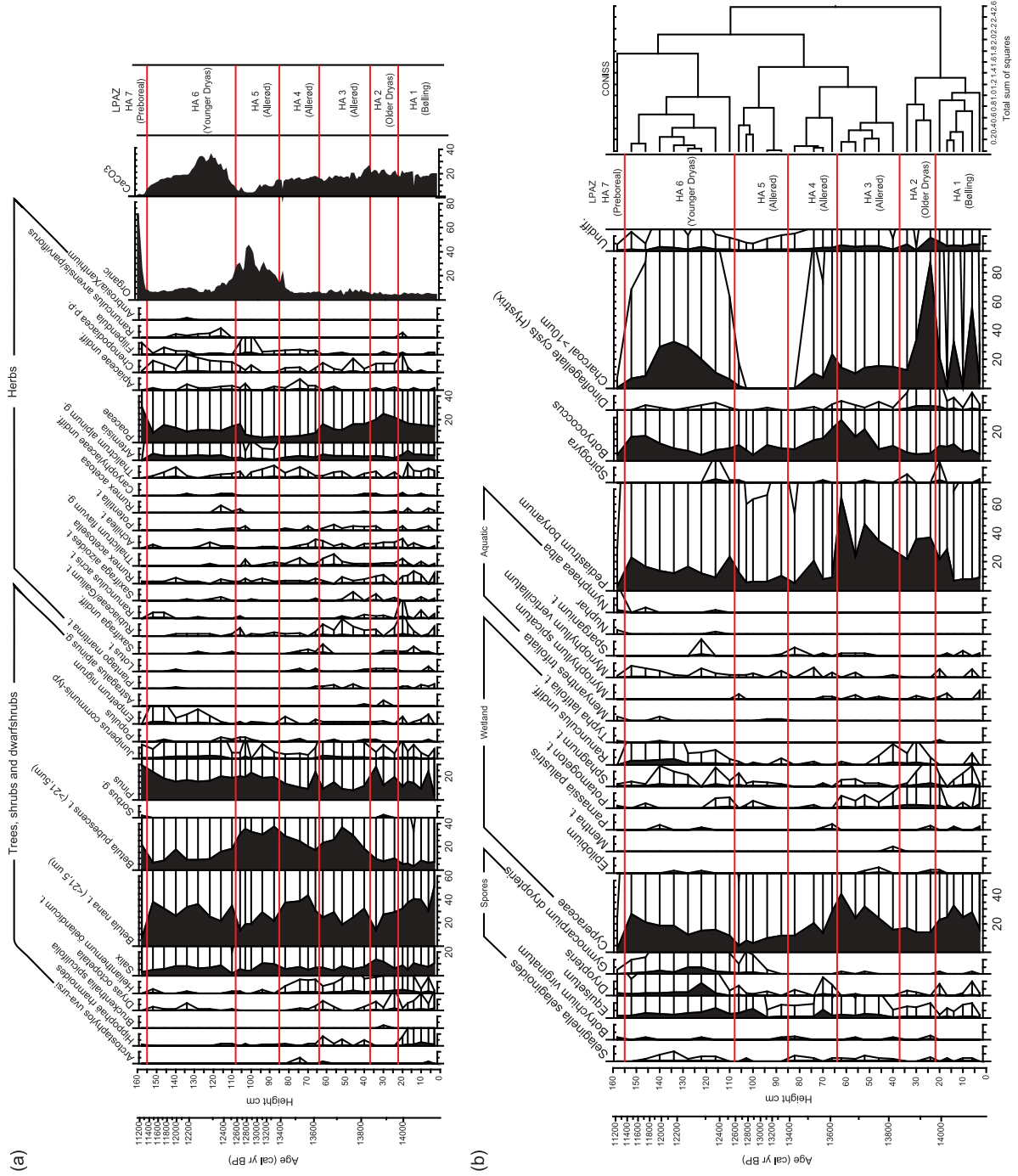
Figure 4. Pollen percentage diagram of selected taxa based on total terrestrial pollen excluding Cyperaceae and spores. ×10 exaggeration is shown by the open outline.

Figure 5. Macrofossil concentrations per 100 ml sediment. The taxa are seeds or fruits unless otherwise indicated. T = macrofossil type.

Hasselø. The nearest occupation sites are situated *c.* 40 km to the west at Sølbjerg and Krogsbølle on the island of Lolland (Petersen and Johansen 1993, 1996, Petersen 2006, Pedersen 2009). The two peaks of charcoal seen in both the pollen percentage and concentration (not shown) diagrams (Figure 4b) could indicate further hitherto undiscovered occupation sites in the area near the lake. However, reworked charcoal from glacial sediments cannot be excluded.

Older Dryas (HA2. Poaceae–Helianthemum, 14,000–13,800 cal. BP)

A continuance of the high proportion of heliophile taxa such as *D. octopetala, Helianthemum oelandicum* (hoary rock-rose), *R. acetosella, T. alpinum, Artemisia* sp. 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 *B. nana, D. octopetala* and *Salix*.

The Older Dryas (GI-1d) is shown in the isotopic records of Greenland ice cores as a cold period (Rasmussen *et al.* 2006) and in chironomid and coleoptera records (Brooks *et al.* 2012, Lemdahl *et al.* 2014) from north-western Europe, but this short-lasting period can be difficult to identify in pollen diagrams. Some pollen records are interpreted 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 *H. ramnoides*, a species which cannot tolerate cooler climates. This occurs at the same time as an increase in arid-tolerant taxa, especially *H. 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 *H. 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 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 high charcoal content found in several consecutive samples (also seen in the concentrations (not shown)) 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 is likely to come from the occupation site, since charcoal from local fireplaces is likely to be represented in the stratigraphy close to late glacial and early Holocene settlements (Bos and Urz 2003, Fischer *et al.* 2013b, Tolksdorf *et al.* 2014). The date around 14,000–13,900 cal. BP falls within the period defined for the spread of the Hamburgian and the Federmesser Cultures (Petersen 2006, Grimm and Weber 2008, Pedersen 2009, Riede and Edinborough 2012). The charcoal peak could represent either an undiscovered occupation site from the Hamburgian culture or a very early occurrence of the Fedemesser culture in the Danish area, although neither a natural fire sparked by lightning nor redeposited charcoal can be excluded. However, if humans were present in the Danish region in the Older Dryas and the first half of the Allerød, they would have taken advantage of the available resources in the border regions between the open tundra and the woodlands. The most likely objective would have been reindeer, which was the largest prey available at this time (Aaris-Sørensen 2009).

The open shrub and grassland landscape

Allerød (HA3. Betula pubescens–Helianthemum, 13,800–13,600 cal. BP)

This zone is characterized by a strong increase in *B. pubescens*-type pollen accompanied by an increase in *Juniperus communis* (juniper) and a simultaneous decrease in *Salix, B. nana* and *Pinus*. There are still, even in the presence of a marked increase in tree birch, many open-ground and light-demanding taxa represented in the pollen flora, for example, *D. octopetala, H. oelandicum, R. acetosella, T. alpinum*, Chenopodiaceae and *Artemisia* sp. The macrofossil assemblage still shows a predominance of pioneer taxa, for example *B. nana, Arctostaphylos uva-ursi* (bearberry), *D. octopetala* and *S. herbacea. B. nana* in particular predominates with *D. octopetala* in lower numbers. *D. octopetala* is probably reduced due to competition with the more competitive shrubs and tall herbs which are becoming more dominant in the landscape. The *B. 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 high percentages are due to long-distance transport of pollen from, for example, northern Germany where tree birch was expanding (de Klerk 2008).

In the transition between HA3 and HA4, *B. pubescens* declines while some of the more heliophile taxa as *D. octopetala, H. oelandicum* and *B. nana* increase slightly. This development has also been recorded in areas further

south where it has been related to cooler climatic conditions (Usinger 1985, Litt *et al.* 2001).

The first trees

Allerød (HA4. Betula nana–Betula pubescens, 13,600–13,400 cal. BP)

An increase in *B. nana* and *B. pubescens* types 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 *B. 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 macrofossil record is *c.* 200 years. The most light-demanding and least competitive taxa (*D. octopetala* and *S. herbacea)* are now absent while *B. nana*, a species which can grow in the undergrowth of open forest and on wet ground, is still present. 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, as has previously been shown at Slotseng in south-west Denmark (Mortensen *et al.* 2011). Similar studies from Germany have shown that birch during the Allerød favoured rich soils (Theuerkauf and Joosten 2012). The low organic content in the sediments suggests that there was still a significant input of minerogenic material (Figure 4a). 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 stabilized 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 (Lidberg-Jönsson 1988). However, these ages are questionable as the sequence was dated using bulk sediment samples with low organic content, and the local presence of tree birch in southern Sweden needs to be confirmed by new studies with the advantage of more modern dating techniques. In Schleswig-Holstein in northern Germany, tree birch is present during the early Allerød period (Usinger 1985). In Denmark, investigations at Slotseng have shown that tree birch arrived much later as the first macrofossils are not found until around the middle of the Allerød period (13,500 cal. BP) (Mortensen *et al.* 2011, 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 *Alces alces* (elk) immigrated into the region (Aaris-Sørensen 2009).

Allerød (HA5. Betula pubescens–Pinus, 13,400–12,600 cal. BP)

The beginning of this zone shows a reduction in *B. nana* type together with increases in *B. pubescens* type and *Pinus*. The double peak of *B. pubescens* type might represent a slight reduction in the woodland associated with the cold Gerzensee Oscillation (Andresen *et al.* 2000). Macrofossils of *B. nana, Selaginella selaginoides* (lesser clubmoss) and *T. alpinum* show that the woodlands at the beginning of this zone were still open even though heliophile pollen decreases. The lack of *D. octopetala* and other heliophile taxa from the macrofossil assemblage in zone HA5 indicates a closing of the woodlands, at least in the area 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 woodlands around Hasselø appear to have been denser than at Slotseng in southern Jutland (Mortensen *et al.* 2011).

In addition to *B. pubescens*, the Allerød woodlands in eastern Denmark included *Populus tremula* (aspen) and *J. 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 and even though *Pinus* pollen is abundant in the pollen assemblages, pine was probably not part of the Late Glacial woodlands of Denmark. The closest find of *Pinus* logs lay 60 km south of Hasselø at Rostocker Heide in northern Germany (Terberger *et al.* 2004), and one sample has been dated to $11,220 \pm 250$ BP (13,600–12,600 cal. BP). This is further indication of an ecotone between south-east Denmark and northern Germany during the second half of the Allerød period (Figure 6). Even though there was a very strong temperature gradient over Europe (Coope *et al.* 1998, Renssen and Isarin 2001), the reconstructed 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 south-east Denmark and north-east Germany may have acted as a barrier. This low-lying region was covered by either the Baltic Ice Lake or large wetland areas during much of the Late Glacial and was subject to large and abrupt lake level changes (Bennike and Jensen 2013). This may have delayed the north-westerly spread of *Pinus* and even though pine can grow on many soil types (Friis-Møller *et al.* 2010), competition with the previously established birch woodlands may also have contributed to the delay.

Figure 6. Map of southern Scandinavia showing the ecotone between the Danish birch forest and the northern German birch/pine forest. The low-lying region between Denmark and Germany was flooded during the maximum extent of the Baltic Ice lake.

The Allerød woodlands

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, Mortensen *et al.* 2014a). The woodlands were relatively open with *B. 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 (Bennike *et al.* 2004a, Kolstrup 2007, Mortensen *et al.* 2011), while mixed birch pine woodlands were found just south of the Danish region (Usinger 2004, Latałowa and Borówka 2006, de Klerk 2008, Theuerkauf and Joosten 2009, 2012). The coast of the Baltic Ice Lake was found to the east (Bennike and Jensen 1998, Bennike *et al.* 2004b) and the coast of the Yoldia Sea was located near northern Zealand (Houmark-Nielsen and Kjær 2003). The south-eastern Danish region was therefore situated in a zone between several different ecosystems (Figure 6). Such marginal areas are known to have a particularly high biodiversity (e.g. Petersen and Vestergaard 2006) and the numerous subsistence strategies available 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 arctos* (brown bear) and *Castor fiber* (beaver) have been found from this period and show that the Late Glacial period offered potentially rich hunting grounds (Aaris-Sørensen 2009). However, besides the known availability of large game animals, a range of other resources may have been part of the subsistence. Although the evidence is fragmentary, the coastal areas would also have offered other valuable resources (Fischer *et al.* 2013a). For example, there would have been a rich bird fauna available for both hunting and the collection of eggs and chicks. Additionally, fishing had also been practised during the Palaeolithic (Gramsch *et al.* 2013) and the numerous lakes would have provided good fishing opportunities, for example, for pike and perch whose sticky eggs are rapidly spread by water birds. Lastly, the vegetation itself would have been both a food resource (Tyldesley and Bahn 1983, Aura *et al.* 2005, Revedin *et al.* 2010) and a material for tool production (e.g. Riede 2012), although wooden tools are rarely preserved in the archaeological record.

The change from tundra to birch woodland marks an important environmental change in the vegetation, available fauna, etc. Humans must have responded to these marked changes in resource availability and the existing data suggests that the occurrence of the Bromme Culture in the Danish area is coincident with the immigration of

woodland (Mortensen *et al.* 2014a). The nature and speed of the human response to environmental change is difficult to determine and requires that the archaeological and environmental data have rigorous chronological resolution over a large geographic area (Birks *et al.* 2014). With these larger and well-established datasets it will be possible to test different hypotheses of human–environment interactions (e.g. Banks *et al.* 2006, 2011).

The Allerød–Younger Dryas transition

Climatic cooling at the end of the Allerød had a strong impact on the vegetational succession of Late Glacial woodlands. A distinct reorganization 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 B2 K (12,846 before AD 1950). Temperatures continued to decline until 12,780 B2 K (12,730 before AD 1950), at which time a large and rapid decrease occurred. These changes are seen not only in Greenland ice core proxies but also in records from the whole of the northern hemisphere (e.g. Björck *et al.* 1996, Rach *et al.* 2014). It is important to stress however, that although changes in atmospheric circulation, climate and the biosphere are linked, the responses are not necessarily synchronous (Rasmussen *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 from 12,879 ± 207. This could be due to a transition to a drier climate which may have led to a 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 12,692 ± 130 cal. BP. *B. pubescens* decreases at the same time as an increase in light-demanding taxa such as *B. nana, Filipendula* (meadowsweet), Poaceae and *Gymnocarpium dryopteris* (oak fern). This corresponds to 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, Rach *et al.* 2014). The Allerød-type environment continued despite the substantial temperature decrease but it became more fragmented with light open

woodland. At *c.* 12,575 ± 74 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 previously suggested 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 woodlands survived several hundred years into 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 7 shows the Danish Bromme Culture ^{14}C dates from Bromme, Fensmark and Trollesgave (Fischer *et al.* 2013b) and illustrates that although all the ages lie within GS-1, they 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 directly to 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 of HA5 to an open landscape with pioneer vegetation in HA6. *B. pubescens*-type pollen decreases while there are generally higher values of *B. nana* type and *Pinus*. *J. communis, Artemisia sp.*, Chenopodiaceae and Poaceae also reach generally higher percentages throughout the HA6 zone. *Dryopteris* and *G. dryopteris* reach their local maxima in the first half of the zone. *Empetrum nigrum* (crowberry), *Ranunculus* sp (buttercup) and Cyperaceae increase around the middle of the zone.

Macrofossils of *B. nana, D. octopetala, E. 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 southern part of Jutland. In the lake sequence from the Slotseng
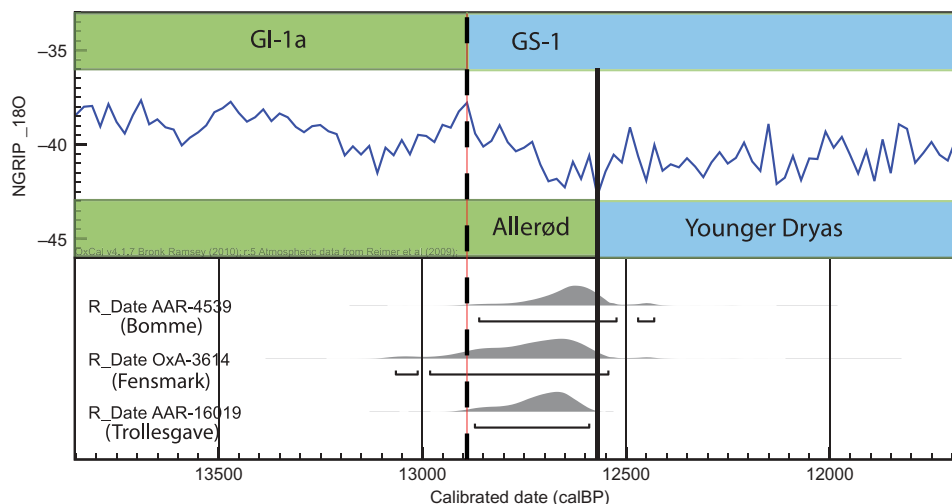
Figure 7. Bromme Culture ages from Denmark (Fensmark Skydebane, Trollesgave, Bromme). The transition from GI-1a to GS-1 (GICC05) is shown by the dotted line. The transition from Allerød to Younger Dryas is shown by the solid line.

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 is 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, Rach *et al.* 2014). 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 *E. nigrum* in Hasselø, dated to *c.* 12,100 cal. BP, along with increased percentages of Cyperaceae and *Ranunculus* sp. (probably water-crowfoot as seen in the macrofossils), all of which suggest increased precipitation. The increase in *E. 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 (Hoek 1997, Usinger 2004). The evidence from Bromme occupation sites suggests year-round presence during the Allerød period while it is thought that the Ahrensburg culture was only occasionally present during the Younger Dryas (Pedersen 2012). This was probably due to the availability of reindeer hunting (Aaris-Sørensen *et al.* 2007, Aaris-Sørensen 2009).

Early Holocene (HA7. Betula pubescens–Pinus-Poaceae, 11,350- cal. BP)

The beginning of the Preboreal shows an increase in *B. 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 *B. nana* and *E. nigrum* is shown by the macrofossil analysis but surprisingly, no macrofossils of *B. pubescens* were found. Many pollen records show that the Preboreal period in Denmark began with a marked *J. communis* peak. This lasted for a few hundred years after which tree birch immigrates and rapidly predominates. 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 *J. 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. LOI values indicate continued substantial erosion during the early Preboreal, and the delay in the spread of tree birch after the Holocene warming is probably due to the ongoing instability of soils. 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 *B. pubescens* (Jessen *et al.* 2014). These data from south-east 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. It is shown that the vegetation during the Bølling and Older Dryas periods is dominated by pioneer taxa and that eastern and western Denmark had very similar landscapes. The high concentration of charcoal between 14,000 and 13,900 cal. BP could suggest a nearby occupation site. During large parts of the Late Glacial an ecotone existed between south-east Denmark and northern Germany. The large lowland area between these two regions, which was periodically covered by the Baltic Ice Lake, may have formed a barrier to the spread of some plants. In comparison to previous work this study of both local and regional proxies shows a clear delay of more than 1000 years between the first late glacial warming and the immigration of the first tree birch. The first trees (birch trees) 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 in the eastern part of Denmark. This forest existed until 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. Based on the pollen assemblage, 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. During the early Preboreal the landscape was characterized by erosion and soil instability, which may have led to delayed establishment of *B. pubescens*.

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