Long-term forest dynamics at Gribskov, eastern Denmark with early-Holocene evidence for thermophilous broadleaved tree species

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Abstract

We report on a full-Holocene pollen, charcoal and macrofossil record from a small forest hollow in Gribskov, eastern Denmark. The *Fagus sylvatica* pollen record suggests the establishment of a small *Fagus* population at Gribskov in the early Holocene together with early establishment of other thermophilous broadleaved trees, including *Quercus* sp., *Tilia* sp. and *Ulmus* sp. The macrofossils contribute to the vegetation reconstruction with evidence for local presence of species with low pollen productivity or easily degraded pollen types such as *Populus*. The charcoal record shows frequent burning during two periods of the early Holocene and from c. 3000 cal. BP to present. The early-Holocene part of the record indicates a highly disturbed forest ecosystem with frequent fires and abundant macrofossils of particularly *Betula* sp. and *Populus* sp. The sediment stratigraphy and age–depth relationships give no clear indication of post-depositional disturbance, although a possible short-lived hiatus occurs around 6500 cal. BP. The early pollen record from thermophilous trees could indicate that there may have been some downwash following sediment desiccation through wood peat layers deposited between c. 6500 and 10,000 cal. BP, but the overall biostratigraphy is consistent with other Danish small hollow records.

Keywords

broadleaved trees, charcoal, Denmark, forest history, macrofossils, pollen analysis

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Introduction

The way in which species distributions respond to variations in climate is of concern, owing to rapid, current climate change. Information about past tree distributions can increase our understanding of climate–vegetation relationships and help refine models that forecast future vegetation responses to climate change (Giesecke et al., 2007; Petit et al., 2008). Many palaeoecological studies have investigated how trees returned to the deglaciated areas of northern Europe during the Lateglacial and early-Holocene climatic warming (Huntley and Birks, 1983; Iversen, 1973). Interpretation of previous research has suggested that species spread with different speeds as rapid migration fronts from southern refugia (Bialozyt et al., 2012; Clark, 1998), and consequently arrived in northern Europe in a predictable and consistent order (Huntley and Birks, 1983; Iversen, 1973). This view has been challenged by evidence for so called ‘cryptic refugia’ (Bhagwat and Willis, 2008; Hu et al., 2009; Magri et al., 2006; Petit et al., 2003; Provan and Bennett, 2008; Stewart and Lister, 2001; Willis et al., 2000). Bennett (1986, 1988) suggested that establishment and first expansion of small outlying tree populations in an already forested landscape occurs at too low population densities to be recorded in conventional pollen data from lakes and peat deposits. Determining the rational limit, in terms of pollen percentage, above which a species is locally present, is problematic, but pollen accumulation rates may provide some additional information, as these are independent of other species in the vegetation, and can be compared to accumulation rates at the distributional limit (Davis et al., 1973; Hicks, 2001). Likewise,

Davis et al. (1991) concluded that small outlying populations are very difficult to detect with pollen data, even with a closely spaced grid of sites, owing to the low pollen representation of small populations. However, the often long, discontinuous tails of thermophilous tree species in regional pollen diagrams pre-dating major population rises have been suggested to reflect early establishment of small outlying populations (e.g. Giesecke et al., 2007; Kullman 1998a, 1998b). Kullman (1998a, 1998b, 2002, 2005, 2008) inferred from macrofossil evidence that both boreal (especially *Picea abies*) and thermophilous broadleaved tree species (*Alnus glutinosa*, *Corylus avellana*, *Quercus robur*, *Tilia cordata* and *Ulmus glabra*) immigrated much earlier to mid and northern Sweden than previously believed based on pollen evidence from regional sites. Segerström and von Stedingk (2003) provided limited pollen support for Kullman’s claims with finds of continuous,

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but low-level occurrences of *Ulmus* pollen back to c. 10,000 cal. BP and discontinuous occurrences of *Quercus* and *Tilia* until 8000–10,000 yr cal. BP in two different mires in Northern Sweden.

The establishment of thermophilous trees requires that climate is suitable for the species. Temperatures increased rapidly during the early Holocene (Johnsen et al., 2001; Seppä and Birks, 2001). Salonen et al. (2011) suggest that the summer temperatures already exceeded present-day values from 11,500 cal. BP onwards in northeast European Russia. A recent study from southern Scandinavia (Brown et al., 2012) showed that both January and July mean temperatures gradually increased during the early Holocene to a maximum between c. 8000 and 4500 cal. BP. In addition, spatiotemporal January and July temperature maps show similar values to the present already by c. 10,000 cal. BP and data suggest the development of a maritime climate in Denmark and southern Sweden c. 9900 cal. BP (Brown et al., 2012). This indicates that climatic conditions for establishment of thermophilous tree species were present in Denmark very early in the Holocene.

Odgaard (2006, 2010) reviewed the arrival order of tree species in Denmark after the last glacial. *Betula* sp., *Salix* sp., *Juniperus communis*, *Populus tremula*, *Sorbus aucuparia* and probably *Pinus sylvestris* arrived during the Lateglacial period. During the early Holocene c. 11,000–8500 cal. BP, *Corylus avellana*, *Ulmus* sp., *Quercus* sp., *Alnus glutinosa*, *Tilia* sp. and *Fraxinus excelsior* arrived in Denmark. *Fagus sylvatica* and *Carpinus betulus* were the last tree species to arrive by natural immigration c. 3500 cal. BP, though one *Fagus* macrofossil pre-dates these records by c. 1000 years (Odgaard, 2010). This and other indications of the difficulty of identifying the precise timing of *Fagus* immigration in a region based on pollen analysis calls on macrofossil evidence as the only indisputable evidence of presence (Rasmussen, 2005). However, owing to the irregular occurrences of macrofossils in sediment records from large sites, the study of pollen and macrofossils from smaller sites might offer a way to cast further light on the discussion of the arrival of tree species in an area.

Pollen and macrofossils from small forest hollows record the vegetation at the stand-scale and are consequently ideal for studying local vegetation succession and the impact of disturbances (Overballe-Petersen and Bradshaw, 2011). The relevant pollen source area for this type of site is interpreted as being c. 20–100 m in radius (Andersen, 1970; Jacobson and Bradshaw, 1981; Prentice, 1985; Sugita, 1994). Small forest hollows thus offer the possibility to reconstruct the surrounding vegetation with high spatial resolution, and consequently to locate and study species dynamics of small founding populations that would be swamped by the large regional signal at conventional palynological sites (Bradshaw, 2007; Davis et al., 1998). In addition, the study of macroscopic charcoal from small forest hollows predominantly reflects the local fire record (Hannon et al., 2000; Higuera et al., 2007). Fire is a disturbance agency in many forest ecosystems either from natural or anthropogenic causes. The expected main factors shaping fire dynamics through time have been climate and the presence of flammable fuel and humans (Bowman et al., 2009; Conedera et al., 2009). In southern Scandinavia the evidence for anthropogenic impact on fires is considered limited to the last two millennia based on palaeoecological charcoal records (Bradshaw et al., 2010), whereas climate and vegetation composition were the most likely fire-regulating agents earlier in the Holocene (Carcaillet et al., 2007).

In the present study, a small forest hollow with a complete Holocene pollen, charcoal and preliminary macrofossil record is studied to explore the establishment of thermophilous broad-leaved tree species in Gribskov, eastern Denmark, and to evaluate the vegetation responses to natural as well as anthropogenic disturbances at the site. We examine the hypothesis that thermophilous tree species (*Alnus*, *Fagus*, *Fraxinus*, *Quercus*, *Tilia* and

Ulmus) were able to track closely their suitable climate and habitats by long-distance founding events from currently known glacial refugia (Petit et al., 2003; Magri et al., 2006; Tzedakis et al., 2002), and establish small founding populations in a scattered pattern over northern Europe, ahead of their main spreading fronts, if the soils and microclimate of the site were favourable for the specific species.

Study area

Site location and setting

Gribskov is a c. 5600 ha cultural forest located north of Copenhagen, northern Zealand, Denmark (Figure 1a). The mean annual temperature in Gribskov is 7.7°C, with four to six months without frost (Laursen et al., 1999). Mean annual precipitation is 697 mm (Frich et al., 1997). The soils are mainly derived from sandy tills formed during the Weichselian ice age, and Holocene peat (Hermansen and Jacobsen, 1998). The topography around the study site is undulating. In AD 2008 the forest cover consisted of approximately 34% introduced conifers, mainly *Picea abies*, and 66% deciduous trees, mainly *Fagus sylvatica*, *Quercus* sp., *Betula* sp. and *Alnus glutinosa* (Rune, 2009).

History

Gribskov has been one of the largest forests in Denmark for many hundred years, and is heavily influenced by people (Rune, 2009). Signs of scattered agriculture within the forest date back 6000 years, and several remains of Middle Ages field systems occur north and east of the study site (Rune, 2009). The site is situated in the southwestern margins of past fields and meadows of a former forest village, Ostrup. The village was abandoned in AD 1717 and its land used for stud farming until AD 1852, when it was turned over to the forest district (Rune, 2009). Inventory data and maps from Gribskov show that in AD 1855–1856 the hollow was surrounded by *Fagus* forest stands to the west and south, aged 50–80 and 150–180 years old, respectively, and that the dry meadow to the north was afforested c. AD 1870–1880.

Study site

The study site is a small forest hollow, named the Gribskov-Ostrup hollow, within a mature *Fagus* stand (56°N, 12°20'E, 44 m a.s.l.) in the northern part of Gribskov (Figure 1b). The treeless part of the hollow is almost circular with a diameter of 20 m. *Alnus glutinosa* grows in the hollow to the north and west, and together with the crowns of the surrounding *Fagus* trees, they leave no opening in the canopy above this part of the hollow. The open part of the hollow is separated from the closed-canopy part by a small ditch and the vegetation is dominated by *Carex* sp. There is a larger, open bog (2.4 ha) c. 300 m west of the site and c. 10 ha open grassland, both dry and wet, located between 300 and 350 m to the east. The study site was selected following the guidelines for size, shape, topography and location in the forest given in Overballe-Petersen and Bradshaw (2011) for the selection of small forest hollows for pollen analysis. It was selected ahead of other promising sites owing to relatively deep sediments with mostly organic content and the presence of visible macrofossils and abundant pollen.

Methods

Pollen

A 240 cm deep sediment core was extracted using a Russian corer (Jowsey, 1966) in October 2007, and subsequently stored at 5°C. Pollen subsamples were taken at 5 cm intervals and prepared

Figure 1. (a) Map showing Denmark, Copenhagen and the location of Gribskov. On the inset coloured map green: forest; white: arable land; orange: cities; blue: water (lakes and the sea); and yellow: coastal sand dunes. An arrow points to the approximate location of the Gribskov-Ostrup hollow. (b) The studied small forest hollow.

using standard techniques (Berglund and Ralska-Jasiewiczowa, 1986). The core was scraped carefully at each sample point to remove any potential surface contamination. *Lycopodium* tablets were added to samples of known volume, allowing pollen concentration and influx to be calculated (Stockmarr, 1971). Pollen grains were identified according to Erdtman et al. (1961), Moore et al. (1991), Fægri and Iversen (1989) and Andersen (1979) and by comparison with the reference collection of the Geological Survey of Denmark and Greenland. The results are presented as percentage data based on the pollen sum from terrestrial plants excluding ferns, algae, wetland species and aquatics (see Figures

3 and 4). Pollen influx records of selected species are presented in Figure 5. The pollen diagrams were drawn using the computer programmes TILIA, TILIA GRAPH and TGView version 2.0.2 (Grimm, 2004). Minor taxa are presented as presence in Table 2.

Plant macrofossils

After subsampling for pollen, plant macrofossil samples of 10 ml were extracted every 5th centimetre. The samples were soaked overnight in 5% NaOH, after which they were washed through a sieve of 500 μ m. Macroremains were identified using plant keys

(Bertsch, 1941) and matched with specimens from a reference collection where possible. The preliminary results are presented as number of specimens per 10 ml of sediment (histograms) or simply as presence (dots) (see Figures 3, 4; Table 2).

Macrocharcoal

Contiguous sediment sample slices for macrocharcoal analyses were taken every 2 cm throughout the core. Subsamples of 2 cm³ from each cm slice were suspended in 20 ml of Calgon and left to disaggregate overnight (Halsall, 2009). Samples were then washed gently through a 125 µm sieve. 5 ml of 6% sodium hypochlorite was added to the material retained in the sieve and the samples were left overnight. The samples were then washed gently through a 125 µm sieve and the material in the sieve was retained. This method is described by Mooney and Radford (2001) and Mooney and Tinner (2010). Samples were quantified by area using the digital-analysis software ImageJ (<http://rsbweb.nih.gov/ij/index.html>) with a threshold of 38.32. A 12.1 megapixel camera was used with a light box (Halsall, 2009). Results are presented as area of particles > 125 µm deposited per square centimetre of sediment per year (see Figure 3).

Dating

Ten samples, two macrofossil wood pieces and eight peat sediment samples (Table 1, Figure 2), were dated using the AMS dating technique at the Radiocarbon Dating Laboratory, Lund University in Sweden. The calibration and age–depth relationship (Figure 2) were calculated using the Calib09 calibration curve (Reimer et al., 2009) and a smooth spline model was applied to the results using the programme CLAM (Blaauw, 2010). The two dates from 105 cm and 116–118 cm were treated as outliers and not included in the smooth spline calculation (Figure 2). Including the two outlying dates in the age–depth model would create a very abrupt change in sedimentation rate, and an anomalous very high peak in total pollen accumulation, suggesting the dates are too old.

Results and interpretation

The pollen, macrofossil and charcoal diagrams in Figures 3 and 4 as well as the influx records in Figure 5 have been subdivided visually into five zones corresponding to major palaeoecological changes. The following descriptions summarize the development

Table 1. Radiocarbon dates from the Gribskov-Ostrup hollow. The measurements were made at the Radiocarbon Dating Laboratory, Lund University, Sweden. The material consisted of eight sediment samples and two wood pieces (sample depths 150 cm and 215 cm). Insufficient individual macrofossils were available for dating.

Lab. number	Sample depth (cm)	¹⁴ C age (yr BP)	Modelled age cal. BP
LuS 8052	15	385 ± 45	654
LuS 8053	35	2205 ± 45	2049
LuS 8054	65	3685 ± 50	4112
LuS 8055	90	5090 ± 50	5911
LuS 8865	94–96	5565 ± 50	6254
LuS 8056	105	6982 ± 50 ^a	6868
LuS 8866	116–118	7530 ± 65 ^a	7488
LuS 8057	150	7890 ± 50	8746
LuS 8058	195	8945 ± 60	10,086
LuS 8059	215	9450 ± 60	10,705

^aOutlying dates, not used in the age–depth model.

Figure 2. The relationship between calibrated years BP (1950) and sediment depth for the site, the Gribskov-Ostrup hollow. A smoothing spline function has been fitted using the likelihood distribution of the calibrated ages of each sample. The grey area on both sides of the curve represents the 95% confidence intervals.

in these zones. The sediment description is given in Table 3 and in the lithology columns of Figures 3 and 4.

Zone I (11,500–9000 cal. BP; depths 240–160 cm): frequent but irregular fire regime; *Betula*–*Pinus*–mixed deciduous forest

In this zone the fire regime is irregular with frequent peaks in charcoal the first c. 1000 years indicating a highly disturbed site with fires of variable size (Figure 3). It reflects the most frequent and widespread burning in the record, whereas the fire record literally disappears in the rest of the zone. The fires in zone I were most likely triggered by natural causes, though minor human fire disturbances of the forest cannot be ruled out. Humans were present in the area of Gribskov since the early Mesolithic times, c. 11,700–5900 cal. BP (www.dkonline.dk, accessed 12 February 2010), but the earliest archaeological findings from the area just around the study site are probably from the Bronze Age, c. 3700–2500 cal. BP (www.kulturarv.dk/fundogfortidsminder/Lokalitet/194855, accessed 3 September 2010).

The macrofossil record, which pre-dates the pollen record, shows that pioneer woodland was established in the area c. 11,200 cal. BP, where *Populus*, *Salix* and high numbers of *Betula* are found (Figure 3). The forest probably consisted of *Betula*, *Pinus*, *Populus*, *Salix*, *Corylus*, and *Quercus*, when the pollen record starts at c. 10,900 cal. BP. The rich macrofossil record of *Populus* documents a much higher abundance in the early woodland than the *Populus* pollen curve suggests, probably owing to relatively low pollen production, easily degraded pollen and possible poor preservation of this taxon in the more minerogenic lacustrine sediments at the base of the core. The macrofossils contribute to reveal the long-term forest dynamics and document that trees were growing close to or actually on the small hollow in zone I. In the top part of zone I, from c. 9500 cal. BP, *Pinus* dominates the tree pollen (Figure 3), which is also seen as rapidly increasing influx values towards the peak c. 9200 cal. BP (Figure 5). At the end of the zone the dominance of *Pinus* is followed by rising values of *Corylus* and a rise in *Quercus* percentages to 15–25%,

Analysts: Mette Venås Overballe-Petersen (pollen), Anne Birgitte Nielsen (pollen), Karen Halsall (charcoal) and Gina E. Hamon (macrofossils)

Figure 3. Pollen (continuous curves) and macrofossils (histograms or dots) of trees and shrubs together with charcoal (histogram) and lithology from the Gribkov-Ostrup hollow. The pollen data are percentages of the terrestrial pollen sum excluding ferns, algae, wetland species and aquatics. The patterned areas show 10x magnifications. The macrofossils are concentration per 10 ml of sediment (histograms) or presence (dots). Abbreviations: b: bud; br: bract; caps: capsule; f: fruit; flr: fruit/bract; flr: flower; l: leaf; n: needle; s: seed; w: wood. The charcoal record is area of particles per square centimetre of sediment per year [(mm²/cm² per yr) x 1000] for charcoal fragments > 125 µm. The lithology is as follows: 0–10 cm humus; 10–99 cm fen fibres, lots of vegetative detritus, little identifiable; 99–100 cm short-lived hiatus; 100–120 cm wood peat; 120–195 mainly wood with some macrofossils; 195–225 cm lacustrine sediments with leaves and some wood; 225–240 cm lacustrine sediment.

Analysts: Mette Venås Overballe-Petersen (pollen), Anne Birgitte Nielsen (pollen) and Gina E. Hannon (macrofossils)

Figure 4. Pollen (continuous curves) and macrofossils (histograms or dots) of selected minor taxa. The pollen data are percentages of the terrestrial pollen sum excluding ferns, algae, wetland species and aquatics. The patterned areas show 10x magnifications. The macrofossils are concentration per 10 ml of sediment (histograms) or presence (dots). Abbreviations: b: bud; br: bract; caps: capsule; f: fruit; f/br: fruit/bract; flr: flower; l: leaf; n: needle; s: seed; w: wood. The lithology is as follows: 0–10 cm humus; 10–99 cm fen fibres, lots of vegetative detritus, little identifiable; 99–100 cm short-lived hiatus; 100–120 cm wood peat; 120–195 cm mainly wood with some macrofossils; 195–225 cm lacustrine sediments with leaves and some wood; 225–240 cm lacustrine sediment.

Figure 5. Pollen accumulation rates (PAR, pollen grains/cm² per year) of *Pinus*, *Tilia*, *Ulmus*, *Fraxinus*, *Quercus* and *Fagus* from the study site in Gribskov, Denmark.

which is contemporary with establishment of *Quercus* reported from elsewhere in Denmark (Andersen, 1989; Odgaard, 1999, 2010). In addition, small but continuous pollen records of *Tilia*, *Ulmus* and *Fraxinus* exist throughout the zone. Andersen (1989) reported on *Ulmus* percentages up to 10% in a small hollow pollen analysis from southern Zealand c. 8000 BP and Odgaard (1999) also found small records of *Ulmus* around 10,000–9000 cal. BP from two lakes in Jutland, Denmark, so these records are plausible. From c. 10,000 cal. BP a small, but continuous record of *Fagus* pollen occurs. This record pre-dates earlier findings of *Fagus sylvatica* in Denmark by at least 5000 years (Odgaard, 2010; Rasmussen, 2005) so needs careful scrutiny.

Zone II (9000–6500 cal. BP; depths 158–100 cm):
irregular fire regime; Corylus-Ulmus-Quercus-
mixed deciduous forest

The fire record of zone II is irregular and almost non-existent for the first c. 900 years until c. 8100 cal. BP, where the only major charcoal peak in this zone appears (Figure 3). This peak could be caused by a local fire, but also possibly by increased inwash of charcoal associated with the so-called 8.2 ka cooling event, which was characterised by a wet climate in Denmark (Hede et al., 2010). The decreases in *Tilia* and *Quercus* pollen at the time could be a response to the short-term climate cooling. The fire record continues to be irregular with no major peaks in the rest of the zone. As for zone I this fire record presumably originated from natural causes.

The pollen record suggests a forest consisting of mixed deciduous species with dominance of *Corylus* and a substantial proportion of *Ulmus* and *Quercus* throughout the zone (Figure 3). The macrofossil record shows *Betula* and *Pinus* still playing a role in the forest, which together with the continuous pollen curves of herbs such as Apiaceae, *Artemisia* type, Cyperaceae, *Filipendula*, Poaceae and *Urtica* could indicate that more open conditions prevailed in the forest (Figures 3 and 4). Another possibility is that these trees and herbs mainly grew at or close to the hollow, which must have created an opening in the canopy at the time, since several macrofossil remains of aquatics and wetland species in zones I and II show that some open pools of water were present at the site in the early Holocene (Figure 4; Table 2). According to the macrofossil record, conditions at the site became dryer between 7000 and 6500 cal. BP (110–100 cm depth) coincidental with a possible hiatus at 99–100 cm depth marking a sediment shift from wood peat to fen peat (Figure 4).

Zone III (6500–4000 cal. BP; depths 98–64 cm):
almost non-existent fire regime; Tilia-Ulmus-
Quercus-mixed deciduous forest

The near absence of evidence for burning during zone III could reflect a change in climatic conditions and/or the management of the area. Further studies would be required to elucidate the reason for this. Among the tree species, *Tilia* pollen dominates through most of the zone with unusually high percentages. *Tilia* was likely the most important canopy tree at this time, as it is a low pollen producer. This is also reflected in the influx values, where *Tilia* shows high values throughout zone III (Figure 5). A major drop in *Tilia* pollen occurs just before c. 4000 cal. BP. Similar declines are recorded in other small forest hollows from eastern Denmark in the period between c. 4000 and 2000 cal. BP (Andersen, 1985, 1989; Hannon et al., 2000). All authors interpret this decline as triggered by anthropogenic activities. *Ulmus* plays a minor role in the forest, but continues its largest abundance throughout this zone (Figure 3), which is also reflected in the pollen influx showing sustained high values in zone III with a peak c. 5000 cal. BP

(Figure 5). At 5900 cal. BP *Ulmus* declines to below half its previous percentage value (from between 4.6 and 6.0% to 1.9%) coinciding with the general *Ulmus* decline in Denmark (Aaby, 1986; Iversen, 1973; Odgaard, 2006, 2010). *Quercus* plays a minor role in the beginning of zone III, but increases constantly throughout the zone to values of c. 30%. *Fagus*, *Fraxinus* and *Alnus* pollen records remain relatively low and the tree species probably play minor roles in the forest during zone III.

Zone IV (4000–1000 cal. BP; depths 62–22 cm):
regular fire regime with irregular minor peaks;
Quercus-Alnus-mixed deciduous forest

From c. 3000 cal. BP a regular fire record with low values restarts, preceded by a drop in the pollen percentages of trees such as *Fraxinus*, *Pinus*, *Tilia* and *Ulmus* c. 3800 cal. BP, and followed by increases in *Quercus*, *Calluna vulgaris* and herb pollen, especially *Plantago lanceolata*, *Rumex acetosella*, *Artemisia* type and *Filipendula* (Figures 3 and 4). These changes are interpreted as anthropogenic related – either resulting from shifting cultivation with fire or grazing. The regular fire regime was very likely linked to human activities such as clearing forest for agriculture and initiating low-intensity fires to improve livestock grazing, which has also been suggested by Andersen (1985, 1989). The charcoal around 32 cm depth (c. 1800 cal. BP) was charred rather than burnt, supporting the interpretation of low-intensity fires. Such burning to improve grazing is also reported from the *Pinus ponderosa* forests of Oregon and Washington in western North America (Langston, 1995). The pollen record shows little evidence for farming in the vicinity of the hollow from 4000 to 2000 cal. BP. The continuous curves of *Secale cereale* and *Hordeum* type start after 2000 cal. BP, with *Triticum* type appearing c. 1000 cal. BP.

The upland forest seems to have been dominated by *Quercus*, which shows high pollen percentages and influx values throughout zone IV (Figures 3 and 5). There is a slightly increasing amount of *Betula* towards the end of the period just before the final rise of *Fagus* began on the border between zones III and IV. *Fagus* already shows increased local presence of 4.2–5.4% in a period of a few hundred years just after 4000 cal. BP. *Pinus*, *Tilia*, *Ulmus* and *Fraxinus* all show low abundances in the zone. The *Tilia* pollen percentages of c. 1.5–3.5% indicate that this low pollen producer probably played a minor role until c. 2000 cal. BP, after which the record almost disappears (Figure 3). The disappearance of *Tilia* from the record coincides with a peak in Poaceae and is followed by minor peaks in *Plantago lanceolata* and *Rumex acetosella* type, suggesting human impact as the cause of the decline in *Tilia* as also argued by Turner (1962) and Björse and Bradshaw (1998). The influx values of *Fraxinus*, *Tilia* and *Ulmus* are also high in this zone until c. 2000 cal. BP indicating that all three species did play a role in the forest during the first c. 2000 years of zone IV (Figure 5). The high proportion of *Alnus* pollen is interpreted as coming from trees growing directly on the small hollow.

Zone V (1000 cal. BP–present; depths 20–0 cm):
regular fire regime with low values; Fagus-Quercus-
Alnus forest

The regular fire regime that started in the previous zone continues with low values during zone V, which begins with a rapid expansion of *Fagus* c. 1000 yr cal. BP leading to dominance among the trees together with *Quercus* (Figure 3). The influx values of *Fagus* are very high in zone V, whereas those of *Quercus* have declined markedly (Figure 5). This is interpreted as *Fagus* trees succeeding *Betula* on abandoned fields cleared by fire in the previous period. Small hollow pollen analyses from two sites on southern Zealand also showed *Fagus* expansion around 1000

Table 2. The remaining taxa identified in the pollen and macrofossil analysis from the Gribskov-Ostrup hollow and not shown in Figures 3 or 4. x describes that the taxon was identified in the specific zone.

Species	Zone I	Zone II	Zone III	Zone IV	Zone V
Pollen					
<i>Acer</i>		x		x	
<i>Alchemilla</i>		x	x	x	
<i>Anemone</i> type				x	x
Asteraceae: <i>Achillea</i> type		x		x	x
Asteraceae: <i>Saussurea</i> type	x	x			x
Asteraceae: <i>Solidago</i> type	x	x		x	x
<i>Botrychium</i>	x			x	
<i>Botryococcus</i>	x				
Brassicaceae	x	x	x	x	x
<i>Caltha</i> type					x
Caryophyllaceae	x			x	
Caryophyllaceae: <i>Dianthus</i> type		x			
<i>Castanea sativa</i>					x
Cereal sp.					x
Chenopodiaceae	x	x	x	x	
<i>Crataegus</i>		x		x	
Dipsacaceae (<i>Succisa</i>)				x	x
Ericaceae					x
<i>Empetrum</i>					x
<i>Equisetum</i>	x				
<i>Frangula alnus</i>	x			x	
<i>Galium</i> type	x		x	x	x
<i>Geranium</i>		x			
<i>Humulus</i> type	x	x		x	
<i>Iris pseudacorus</i> type				x	
<i>Jasione</i>	x	x	x	x	x
Lamiaceae: <i>Mentha</i> type	x	x	x	x	
<i>Lemna</i>	x	x	x	x	
Natural <i>Lycopodium</i>					x
<i>Lysimachia</i> type		x			x
<i>Melampyrum</i>			x		
<i>Myrica gale</i>	x				x
<i>Nuphar</i>		x			
<i>Nymphaea</i>	x				
<i>Ononis</i> type					x
<i>Osmunda</i>					x
<i>Plantago major</i>	x	x	x	x	x
<i>Plantago</i> sp.	x	x	x	x	
<i>Polygonum aviculare</i> type		x		x	x
<i>Polygonum convolvulus</i> type					x
<i>Potamogeton</i>	x	x			
<i>Prunus</i>	x				
<i>Ranunculus acris</i> type	x	x	x	x	x
<i>Ranunculus flammula</i> type	x	x	x		
<i>Ranunculus</i> sp.	x	x	x	x	
Rosaceae	x	x			
<i>Rubus chamaemorus</i>		x			
<i>Rumex acetosa</i> type	x	x	x		x
<i>Rumex</i> sp.	x		x		x
<i>Spergula arvensis</i> type				x	x
<i>Thelypteris palustris</i>	x	x			x
<i>Trifolium</i> type	x			x	x

Table 2. (continued)

Species	Zone I	Zone II	Zone III	Zone IV	Zone V
<i>Typha latifolia</i>	x	x		x	
<i>Vaccinium</i> type	x	x		x	
<i>Valerianella</i>					x
<i>Viburnum</i>	x	x	x	x	
<i>Vicia</i> type		x			
<i>Viscum album</i>		x			
<i>Pediastrum</i>	x				
Macrofossils					
<i>Alisma plantago-aquatica</i> (s)		x			
<i>Ceratophyllum</i> (f)	x				
<i>Lycopus europaeus</i> (nt)		x			
<i>Nymphaea</i> (f)	x				
<i>Oxyria</i> (s)	x				
<i>Potamogeton</i> (f)	x	x			
<i>Rubus</i> agg. (s)			x	x	x
<i>Sphagnum</i> (l)					x
<i>Typha</i> (s)		x			
<i>Viola</i> (s)	x				

years ago following human disturbance (Andersen, 1989; Hannon et al., 2000) and are in agreement with patterns from southern Sweden (Björkman and Bradshaw, 1996; Bradshaw and Lindblad, 2005). The considerable human impact on the forest in this upper zone is supported by *Plantago lanceolata* attaining its highest values throughout the core, *Rumex acetosella* and other herb types also being abundant, and the cultivated species having their main abundance (Figure 4; Table 2).

Discussion

The coherence of the sedimentary record

Owing to the very early records for thermophilous trees, including *Fagus*, the lower sediment and its dating should be carefully evaluated, and the possibility of pollen downwash needs to be considered. There is a change in sediment type, from wood peat to fen peat, at 100–99 cm. There may be a hiatus at this depth, although the age–depth relationship and the pollen record indicate that this was of short duration. The sediment change and possible hiatus could be caused by drier site conditions and consequent sediment desiccation, decomposition and cracking. This could have allowed some fine material to leach down through the sediment, particularly through the coarse, underlying wood peat layers down to 195 cm. On rewetting the sediment there would be little sign of this dry period except for any possible re-worked pollen.

The main arguments in support of this ‘re-working’ theory are the very early records for *Fagus*, *Fraxinus*, *Quercus*, *Tilia* and *Ulmus* and the unusual records for certain herbaceous types e.g. *Plantago lanceolata*. The arguments against the re-working theory are (1) the fairly typical age–depth relationship for the site with dates distributed throughout the Holocene (Figure 2), (2) a plant macrofossil stratigraphy that is consistent with other comparable sites e.g. Kåremose in southern Sweden (Hannon et al., 2008) and (3) a pollen stratigraphy younger than c. 6500 cal. BP that is also consistent with other Danish small hollow records (Andersen, 1984, 1985, 1989; Hannon et al., 2000).

Down-core transportation due to tree-trunks and larger branches falling into the hollow or wallowing by large mammals bringing younger sediment down the core would have been even more likely to disrupt the coherent age–depth relationship. In

Table 3. Sediment description of the Gribskov-Ostrup hollow.

Depth (cm)	Troels-Smith formulae	Sediment description
0–10	Th2 Tb1 DhI	Humus
10–99	Dg3 DhI	Fen fibres; lots of vegetative detritus, little identifiable
99–100		Transition wood peat to fen fibres ^a
100–120	Tl3 DhI	Wood peat
120–195	Tl3 DhI	Mainly wood but with some macrofossils
195–225	Ld3 DhI	Lacustrine sediments with leaves and some wood
225–240	Ld4	Lacustrine sediments

^aA short-lived hiatus may be located in this interval.

addition, we find it unlikely that the deeper parts of the core were contaminated during sampling. We used a Russian corer and took appropriate care when sampling the core. Prior to subsampling for pollen analysis the core was scraped cautiously at each sampling point to remove any potential surface contamination.

The *Fagus* record is particularly intriguing. The most likely source of the ‘early pollen’ is from recent material dating from the last millennium, which is the only period with high *Fagus* pollen percentages and PAR at the site. This suggests a far greater mobility of pollen than outlined above and the consistent nature of the late-Holocene record argues against this. Potential contamination of the lower parts of the core must have originated from sediments just above the possible hiatus (100–99 cm) and the outlying dates at 105 and 116–118 cm, respectively, dating the contamination to have arisen from c. 6000–6500 cal. BP (92–98 cm), which is c. 2000 years earlier than any other evidence of beech from Denmark (Odgaard, 2010). A north German small hollow also contains an early-Holocene *Fagus* record c. 8500 cal. BP (Bradley, 2010).

One pollen grain of *Secale cereale* is found at c. 4500 cal. BP (70 cm) and one grain at c. 5900 cal. BP (90 cm). In Denmark it usually occurs in pollen diagrams c. 2000–2100 BP (Odgaard, 1994) and Rasmussen (2005) found scattered *Secale cereale* pollen from c. 2500 cal. BP in a study from a Danish lake. This could indicate downwash of small proportions, but the finding of *Secale cereale* is on the other hand contemporary with the general spread of agriculture in Denmark (Odgaard, 2006), though this has been attributed to cultivation of species of *Hordeum* and *Triticum*. Behre (1992) reported on single grains of *Secale cereale* from different sites in central Europe since the early Neolithic period, e.g. a Neolithic find close to Göttingen in Northern Germany. The finds were very rare and did not reflect cultivation of *Secale cereale* – it was a weed among other cereals (Behre, 1992). At Gribskov, large wild grass (*Hordeum* type) is found at the same time in somewhat larger proportions (four pollen from c. 5600–5900 cal. BP). In general, this type is interpreted as being *Glyceria* in accordance with the findings of Andersen (1979, 1984, 1985), but some of the more recent finds of this type are likely to have been *Hordeum* owing to the cultivation in the immediate vicinity of the hollow at least during the last c. 1500 years. Maybe the early single grains of *Secale cereale* appeared as a rare weed in early *Hordeum*-cultivated fields, though it would be the first find as far north as Denmark for this period. Small forest hollows are more sensitive to such rare pollen than larger sites (Bradshaw, 2007).

Subsequent sections of this discussion rest on the assumption that the entire core can be interpreted with some confidence as we judge the downwash scenario to be rather unlikely and hence support the hypothesis of early-Holocene occurrence of thermophilous trees in Denmark.

The possible evidence for early-Holocene presence of thermophilous broadleaved tree species

There are few full Holocene pollen diagrams from small forest hollows in Denmark and from Zealand only two from the southern

part; Countess Hollow and *Glyceria* Hollow in Næsbyholm forest (Andersen, 1985, 1989). The present site is located in an area of Denmark where relatively little is known of the early-Holocene development – even from regional sites. This study has revealed evidence for an extremely early record of *Fagus sylvatica* together with very early records of thermophilous tree species such as *Alnus*, *Corylus*, *Fraxinus*, *Quercus*, *Tilia* and *Ulmus*. This finding is of great significance in order to understand the way in which species spread into northern Europe after the last glacial.

The *Fagus* record pre-dates former Danish records of the species by approximately 5000 years (Aaby, 1986; Odgaard, 2006; Rasmussen, 2005). Nevertheless, it adds to an increasing amount of evidence that *Fagus* in the early Holocene spread in a different manner than is presently understood and was possibly able to establish as far north as northern Germany, southern England and Denmark following long-distance founding events (Bialozyt et al. 2012; Giesecke et al., 2007; Grant, 2005; Magri et al., 2006). As discussed by Rasmussen (2005) the precise timing of *Fagus* immigration in a region is difficult to identify based on conventional pollen analysis alone. This is likely true for most tree species first establishing in an area as single trees or small populations (Bennett, 1986).

While the overall pattern of tree species succession at the Gribskov-Ostrup hollow follows the previously established pattern for Denmark, the record suggests early-Holocene small founding populations of thermophilous tree species earlier than previously documented. The continuous tails of low pollen values of thermophilous broadleaved tree species at the site could partly represent long-distance transportation of pollen, but owing to the high spatial resolution of small hollows (Bradshaw, 2007; Overballe-Petersen and Bradshaw, 2011) it is highly possible that these tails actually reflect local occurrence of small populations or scattered single trees. Accepting this interpretation calls for a re-interpretation of early-Holocene tails of thermophilous broadleaved trees species in southern Scandinavian regional pollen diagrams. Tails of *Alnus*, *Corylus*, *Quercus* and *Ulmus* expand back c. 11,000 years and *Fraxinus* and *Tilia* expand back c. 9000–9500 years in regional pollen analyses from Denmark (Odgaard, 1994, 1999) and southern Sweden (Berglund et al., 2008), whereas *Fagus* has discontinuous tails from c. 6000 to 7000 yr cal. BP in the same diagrams. Andersen (1989) found continuous, discontinuous and trace values of all the thermophilous broadleaved tree species in question extending back to c. 9400 (*Alnus* and *Fraxinus*) – 11,700 (*Corylus*) cal. BP in a small forest hollow analysis from southern Zealand. He also found trace values of *Fagus* c. 9500 cal. BP, but no values between this and the start of the continuous tail c. 5400 cal. BP.

Väliranta et al. (2011) found scattered occurrences of tree populations consisting of *Picea abies*, *Betula*, *Larix sibirica* and *Abies sibirica* together with *Alnus* in the Lateglacial and early Holocene in northeastern European Russia. These populations started spreading and increasing their density at the beginning of the Holocene warming supporting the emerging view that early-Holocene population expansions at high latitudes did not originate from southern

refugia, but rather from these small outlying populations (Väliranta et al., 2011). The thermophilous broadleaved tree species record from the Gribskov-Ostrup hollow might reflect such a spread from outlying populations just south of Denmark close to the ice margin during the last glacial period. Another possibility is that the early thermophilous populations in Gribskov established as a result of a long-distance founding event from more southern refugia as e.g. revealed by Magri et al. (2006). Alsos et al. (2007) have shown that long-distance dispersal from Russia and Norway to Svalbard has occurred for many species during the early Holocene and is assumed to occur regularly also at present. Similar long-distance founding events might have occurred in northern Europe during the Lateglacial and early Holocene, when the landscapes were presumably rather open and accessible for establishment of newly arrived tree species. Dispersal agents could be wind, running water or animals, such as migrating birds.

The early-Holocene part of the Gribskov-Ostrup record shows a highly disturbed forest ecosystem with frequent burning. The main tree species *Betula* and *Populus* had created a forest cover by c. 11,200 cal. BP as evidenced by the rich macrofossil records of those species. This early established forest microclimate together with the undulating topography of the Gribskov area might have provided a favourable, relatively protected habitat enabling the thermophilous broadleaved tree species to establish small populations. The frequent disturbances might have created seed beds for establishment as well as keeping the population densities of the thermophilous tree species low, since the succession would be kept in early stages with dominance of pioneer tree species such as *Betula* and *Populus*. The present-day soils of Gribskov are mixed sandy and loamy till alternating with peat soils and hollows offering a wide range of site conditions. All of the thermophilous tree species in question grow well on richer soils with good water supply (Larsen et al., 2005; Peters, 1997), though *Alnus* and *Ulmus* mainly grow on wet ground, which is also abundant in Gribskov.

Despite the ideal spatial scale of small forest hollow pollen analysis for establishing the first arrival of tree species in an area, most of these types of records in Denmark and southern Sweden only cover the last 2000–6000 years (Overballe-Petersen and Bradshaw, 2011). Therefore it is difficult to conclude whether or not the present record from the Gribskov-Ostrup hollow is unique or reflects a more general pattern. The disadvantage of small forest hollow analysis is that the relevant pollen source area is so small that single trees or small populations only have to migrate relatively short distances before the distance to the hollow greatly reduces the probability of the species being recorded. Hence, a network of small forest hollows in a larger area is desirable when trying to establish species arrival times.

A scanning of six samples from the bottom of a new core from the site did not yet record *Fagus* pollen, but *Alnus*, *Corylus*, *Quercus*, *Tilia* and *Ulmus* pollen were observed. Analysis of ancient DNA could clarify the questions of early-Holocene establishment of thermophilous broadleaved tree species in Gribskov.

Conclusion

The pollen data from the small forest hollow is consistent with the initial hypothesis that thermophilous tree species, including *Alnus*, *Fagus*, *Fraxinus*, *Quercus*, *Tilia* and *Ulmus*, were able to track closely their suitable climate and habitats by long-distance founding events from currently known glacial refugia (Magri et al., 2006; Petit et al., 2003; Tzedakis et al., 2002) and establish small founding populations in a scattered pattern over northern Europe ahead of their main spreading fronts, if the soils and microclimate of the site were favourable for supporting the specific species. This has important implications for the understanding of how trees spread into northern Europe during the early Holocene.

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