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ORIGINAL ARTICLE

The *Fagus sylvatica* forests in the Larvik region, south-eastern Norway: their origin and history

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Abstract The origin and developmental history of *Fagus sylvatica* forests in south-eastern Norway have been studied through pollen analysis and AMS radiocarbon-dating of peat from two small forest hollows. In this area *F. sylvatica* appears to have a long history, from the first occurrence of *F. sylvatica* pollen at ca. 9100 cal. B.P. to its local expansion ca. 1300–1200 cal. B.P. At this time a shift from a diverse landscape mosaic with many plant taxa present, including broad-leaved trees, to a less diverse landscape mosaic with *Picea abies* and *F. sylvatica* trees is interpreted from the pollen data. The long history of *F. sylvatica* suggests that the existing forests are not recent plantations, but implies that these forests are native. The presence of pollen indicative of anthropogenic activity combined with charcoal before the expansion of *F. sylvatica*, as well as comparison with data from nearby sites, suggest that the forest development was likely to be a result of human activity and climatic changes, particularly changes in moisture conditions.

Keywords Beech · Forest hollow · Norway · Pollen analysis · *Picea* · Vegetation history

Introduction

Fagus sylvatica is a widespread and ecologically important forest tree in much of central and western Europe. It just reaches western and south-eastern Norway where it grows in its northernmost known presumed native localities in Europe. The distribution of *F. sylvatica* in Norway is restricted to two distinct areas—a small population at Seim, north of Bergen in western Norway, and its main area in south-eastern Norway (Jalas and Souminen 1976). Botanists have long been interested in the origin and age of the Seim forest as a remarkable botanical outlying stand. Fægri (1954) published results of pollen analyses of a core from a small hollow in the Seim forest, but was not able to draw any clear conclusions about the origin of the forest. However, he suggested that the forest may have been planted, most likely between ca. 1450 and 950 cal. B.P.. (A.D. 500 and 1000). As the area had been occupied by the Norwegian kings during the Viking Age it has been hypothesised that beech was introduced by early settlers. However, its origin remains uncertain. Both Lid and Lid (2005) and Gjærevoll (1992) propose that *F. sylvatica* is native to Norway and that *F. sylvatica* migrated there via southern Sweden. Another hypothesis is that the establishment of *F. sylvatica* was a result of anthropogenic activity such as agriculture and trading connections with Denmark. On the basis of modern molecular analyses,

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Myking et al. (2011) argue that *F. sylvatica* in eastern Norway originates from Denmark and was most likely brought to Norway before and during the Viking Age.

Since the late 18th century, botanists have also carried out ecological (e.g. Økland 1988; Semb 1983; Diekmann et al. 1999) and palaeoecological research on the beech forests in south-eastern Norway. Høegh (1924) carried out the first palaeoecological study. He suggested that beech was a late arrival, probably before the Viking Age. Henningsmoen (1988) has made several palaeoecological studies of the beech forests in the Vestfold area of south-east Norway. In her 1988 study of a core from a small hollow within the beech forest in Larvik (Fig. 1), she dated the increase of *F. sylvatica* pollen to ca. 930 cal. B.P. (1020 ± 70 yr B.P.). In a study from a bog in Stokke (Fig. 1), Henningsmoen (1988) dated the increase in *F. sylvatica* pollen to ca. 1150 cal. B.P. (1230 ± 60 yr B.P.). In a study from the Kaupang area (Fig. 1), the rise in *F. sylvatica* pollen occurs at ca. 1400 cal. B.P. (Sørensen et al. 2007). This area lies close to the coast, and was therefore deglaciated earlier than the other sites mentioned above. In a study of a small hollow at Kapteinstjern north-west of Larvik (Fig. 1), Molinari et al. (2005) dated the establishment of *F. sylvatica* to 1150 cal. B.P. (A.D. 850). In another study from the same area at Årum (Fig. 1) *F. sylvatica* pollen has very low values (Bjune et al. 2009). In a detailed study from the Østfold area, Danielsen (1970) concluded that *F. sylvatica* probably did not grow spontaneously in Østfold. Many of these studies suffer from very few or noradiocarbon dates, and limited taxonomic resolution in the pollen analyses. The study presented here was designed to build on these earlier studies by providing more detailed pollen stratigraphies with robust chronologies.

Fagus sylvatica is a monoecious tree with a rather low pollen production, but produces easily recognisable pollen. It has a lifespan of about 300 years and can grow to more than 40 m high. Its shallow root system makes it very vulnerable to drought and wind throw, and its thin bark provides little protection from forest fires (Ellenberg 1988; Giesecke et al. 2007). It starts flowering at an age of about 40–60 years. The seedlings are also very vulnerable to drought and late frost in the spring. Because of their high shade tolerance, seedlings are able to regenerate under the dense canopy of a mature *F. sylvatica* forest and thus few,

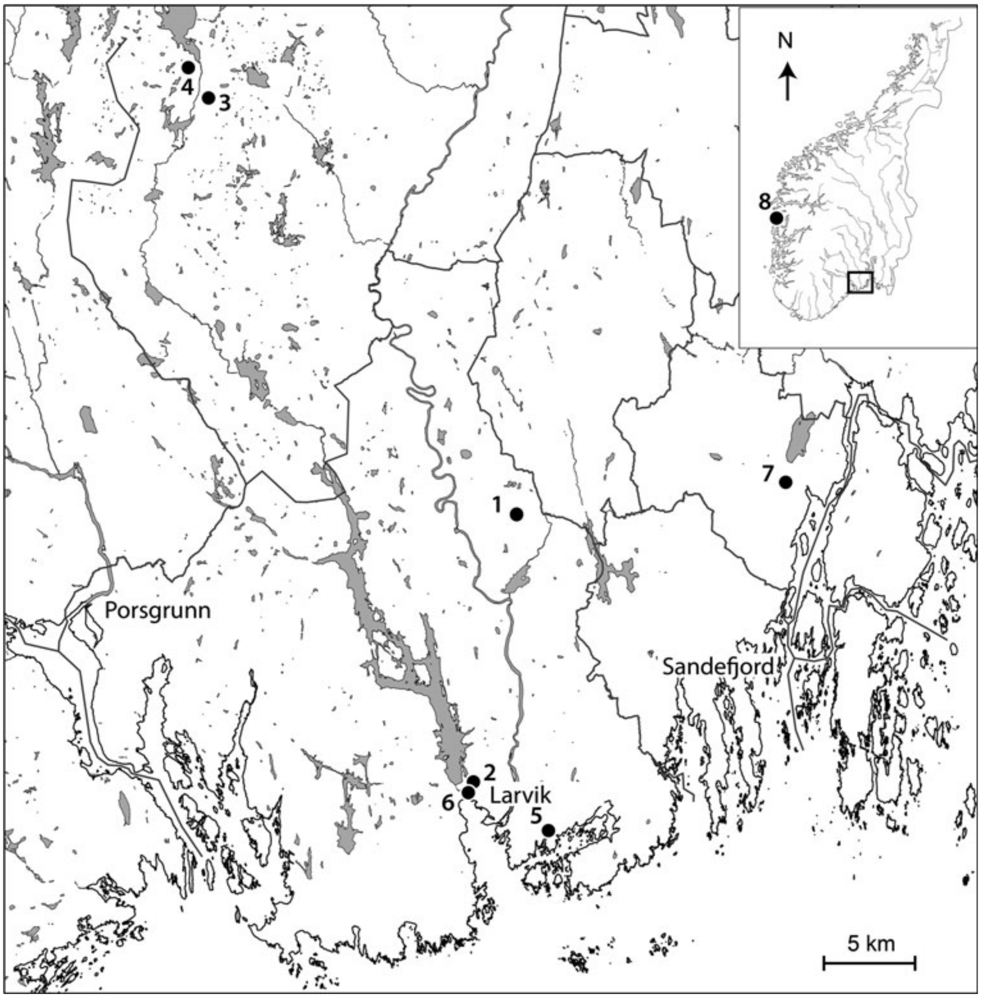


Fig. 1 Map showing the study sites Brånakollane (*1*) and Bøkeskogen (*2*) in relation to other sites mentioned in the text: (*3*) Årum, Bjune et al. (2009), (*4*) Kapteinstjern, Molinari et al. (2005), (*5*) Kaupang, Sørensen et al. (2007), (*6*) Bøkeskogen Larvik, Henningsmoen (1988), (*7*) Bøkeskogen Stokke, Henningsmoen (1988), and (*8*) Bøkeskogen Seim, Holmboe (1908) and Fægri (1954)

if any, other tree species can out-compete *F. sylvatica* (Ellenberg 1988; Bolte et al. 2007). According to Bolte et al. (2007) the climatic requirements of *F. sylvatica* are:

- Precipitation of 500 mm per year, or ca. 250 mm between May and September
- A July mean temperature of <19 °C
- <141 frost days with a daily minimum temperature below 0 °C
- A January mean temperature above −3 °C
- More than 217 days with a daily mean temperature of 7 °C or more.

F. sylvatica can thus occur under a wide range of climatological conditions.

The use of small hollows as study sites for pollen analysis is a suitable method for investigating the history and development of vegetation at a local scale (e.g. Björkman and Bradshaw 1996; Overballe-Petersen and Bradshaw 2011). Many studies have shown that it is possible to detect patterns in local pollen records from small hollows that are obscured in regional pollen records from lake sediments (e.g. Bradshaw1988; Lynch 1998; Björkman 1999; Lindbladh et al. 2000). This local spatial resolution makes it possible to study succession and replacement processes within a forest, to reveal local ecological patterns, and thus to suggest conditions prior to the establishment of, for example, *F. sylvatica* (Bradshaw 1988). From the results from a simulation model, Poska and Pidek (2010) found that *F. sylvatica* pollen loading is significantly reduced at a distance of 300 m from the nearest stand, and that dispersal of *F. sylvatica* pollen did not exceed 1,800 m from the nearest stand. It is thus an ideal tree for local scale pollen analysis.

The aim of this study is to study the local history of the *F. sylvatica* forests in south-east Norway using detailed pollen analysis and AMS radiocarbon dates of peat from two small forest hollows. The primary research questions are:

(i) Are the *F. sylvatica* forests in south-eastern Norway recent plantations or are they native?
(ii) If they are native, under what conditions did they form?
(iii) What factors were important in their origin and subsequent development—human activity, climate change, soil changes, or a combination of these factors?

Study area

The study area belongs to the Oslo Rift geological area. The bedrock consists of syenite, granite and monzonite (Solli and Nordgulen 2007). The first site, Brånakollane, lies in an area of bare rock partly covered with thin surficial deposits and weathering materials. The second site, Bøkeskogen, lies at the top of thick moraine deposits deposited during the Younger Dryas. Mean annual precipitation is 1,000 mm, mean February temperature is −3.3 °C, and mean July temperature is 15.8 °C (www.met.no).

Brånakollane (59.19740, 10.05593 (DD)) lies north of the town of Larvik (Fig. 1), in the eastern part of Norway. The area is a nature reserve with a very well developed and almost undisturbed *F. sylvatica* forest covering ca 19 ha. It was protected by law in 1980 and there has been no significant forestry at Brånakollane since charcoal-burning ceased with the closure of the Hagenes Ironworks in 1837. The area is hilly with large rocks and outcrops. The border of the reserve is very clear, with *F. sylvatica* on one side and *P. abies* on the other side. The dense *F. sylvatica* forest is surrounded by *P. abies* forest which is still logged. The small hollow where the core was sampled lies at 184 m a.s.l. and is situated in a dense *F. sylvatica* stand. The surrounding *F. sylvatica* trees are about 20–30 m high, with a few young *P. abies* trees and many young *F. sylvatica* trees. The ground is covered by a thick layer of old fallen leaves and the soil cover is thin. There are a few old *F. sylvatica* logs. The field layer is very sparse and consists of *Oxalis acetosella*, *Anemone nemorosa*, *Poa* sp. and ferns. *P. abies* logs on the ground are partly degraded. The distance to the surrounding *P. abies* forest is about 30 m.

The second site, Bøkeskogen (59.05761, 10.02251 (DD)), is a *F. sylvatica* forest in a protected landscape resembling a park inside Larvik (Fig. 1). The forest covers an area of 30 ha. Inside this forest there is one of the largest collections of burial mounds in Vestfold, the oldest one dating from Younger Iron Age/Viking Age 1100–1000 cal. B.P. (A.D. 800–950) (Bjørvik 2007). The sampling point lies in a small hollow at 64 m a.s.l. close to a ditch and with very wet soil. In addition to *F. sylvatica*, the main species near the sampling point are *Populus tremula*, *Prunus padus*, *Sorbus aucuparia* and *P. abies*, as well as *Vaccinium myrtillus* and *A. nemorosa*. At the other side of the ditch there is a small *P. abies* forest with one *Betula* tree. The *F. sylvatica* trees are rather tall and large, 25 m high and 1 m in diameter, with dense canopies and much under-storey vegetation of young saplings and small bushes of *F. sylvatica*. *P. tremula* grows where old *F. sylvatica* trees have fallen down and created clearings. The ground is covered with dead leaves of *F. sylvatica*.

Materials and methods

Field work

Overlapping cores were taken with a 50 cm long Russian peat-sampler and were stored in a cold room at 4 °C prior to sampling. The core from Brånakollane is 130 cm long and was obtained in September 2007. The core from Bøkeskogen is 124 cm long and because of the very wet and soft surface it was impossible to drive the corer down to the base. This core was collected in May 2009. The sediment layers were described according to Troels-Smith (1955) (see also Helvik 2010; Figs. 4, 5).

Laboratory work

Subsamples of 0.5 cm^3 were extracted from the two cores. The samples were prepared according to standard methods (acetolysis and HF, Fægri and Iversen 1989). To permit estimation of pollen and spore concentrations, a known number of *Lycopodium* spore tablets were added to each sample prior to preparation (Stockmarr 1971). About 500 terrestrial pollen grains and spores were identified to the lowest taxonomic level using keys (Punt et al. 1976–95; Fægri and Iversen 1989; Beug 2004) and the modern pollen reference collection at the Department of Biology, University of Bergen. At levels 104 and 100 cm at Brånakollane. only 170 and 217 terrestrial pollen grains and spores, respectively, were counted because of low concentrations.

Charcoal fragments were identified and divided into two size classes, <60 and >60 µm. Identification was restricted to black, completely opaque and angular fragments (Clark 1988).

The pollen diagrams were drawn using TILIA (Grimm 1990) and TGView 2.0.2 (Grimm 2004). The percentages were calculated based on the sum of terrestrial pollen and spore types. The pollen diagram was zoned by optimal partitioning using the sum of-squares criterion in the program ZONE (Birks and Gordon 1985). The number of statistically significant zones was determined by comparison with the broken-stick model (Bennett 1996; Birks 1998), using the program BSTICK (Birks and Line unpublished). Plant nomenclature follows Lid and Lid (2005).

Loss-on-ignition (LOI)

Subsamples were extracted from the cores for LOI analysis at the same depths as the pollen samples. Dry weights of the samples were determined after drying overnight at 105 °C. The samples were ignited at 550 °C for six hours and then placed in a desiccator for cooling to room temperature prior to weighing (Bengtsson and Enell 1986; Heiri et al. 2001). LOI was calculated as percentages of dry weight.

Chronology

Fourteen samples of terrestrial plant macrofossils were prepared for AMS radiocarbon-dating, nine from Brånakollane and five from Bøkeskogen (Tables 1, 2). Samples of 1 cm thickness were extracted from the cores and washed through a 250 µm mesh sieve (Birks 2001). Terrestrial plant macrofossils, mainly twigs and woody fragments, were picked out from the residues, identified, and counted at 12× magnification under a stereo-microscope. The samples were analyzed by Laboratoriet for Radiologisk Datering, NTNU, Trondheim.

Calibration of the radiocarbon dates (Tables 1, 2) and age-depth modelling were done using R (R Development Core Team 2011) and routine Clam (Blaauw 2010). Calibration is based on the IntCal09 calibration curve (Reimer et al. 2009). All ages in the text have been rounded to the nearest 10 years, but it should be borne in mind that their probability ranges are larger than this (Figs. 2, 3). For Brånakollane the age-depth model was constructed using linear interpolation (Fig. 2). As the dates show that there is a clear hiatus between 101 and 104 cm at Brånakollane this was taken into account when making the age-depth model for this site (Fig. 2). The age-depth model for Bøkeskogen (Fig. 3) was constructed using a smooth spline run through randomly sampled point estimates from calibrated dates and iterating this process a thousand times. The smooth

Table 1 Radiocarbon-dates of plant macrofossils for Brånakollane; calibration is based on the IntCal09 calibration curve (Reimer et al. 2009)

Lab. ref	Depth (cm)	^{14}C-age (yr B.P.)	Calibrated age, 2σ-range (cal. B.P.)
TRa-2237	15–16	255 ± 25	300 ± 20
TRa-84	25–26	200 ± 25	180 ± 35
TRa-2238	40–41	1105 ± 30	1045 ± 55
TRa-85	59–60	1850 ± 25	1775 ± 60
TRa-2239	75–76	2335 ± 30	2345 ± 30
TRa-2240	91–92	2335 ± 30	2345 ± 30
TRa-2241	100–101	2435 ± 35	2450 ± 95
TRa-2242	106–107	8040 ± 55	8870 ± 170
TRa-86	117–118	9320 ± 45	10530 ± 140

Table 2 Radiocarbon-dates of plant macrofossils from Bøkeskogen; calibration is based on the IntCal09 calibration curve (Reimer et al. 2009)

Lab. ref	Depth (cm)	^{14}C-age (yr B.P.)	Calibrated age, 2σ-range (cal. B.P.)
TRa-2234	15–16	Modern	–
TRa-82	40–41	935 ± 25	860 ± 65
TRa-2235	59–60	965 ± 30	845 ± 45
TRa-2236	89–90	1165 ± 30	1115 ± 65
TRa-83	120–121	1680 ± 25	1580 ± 50

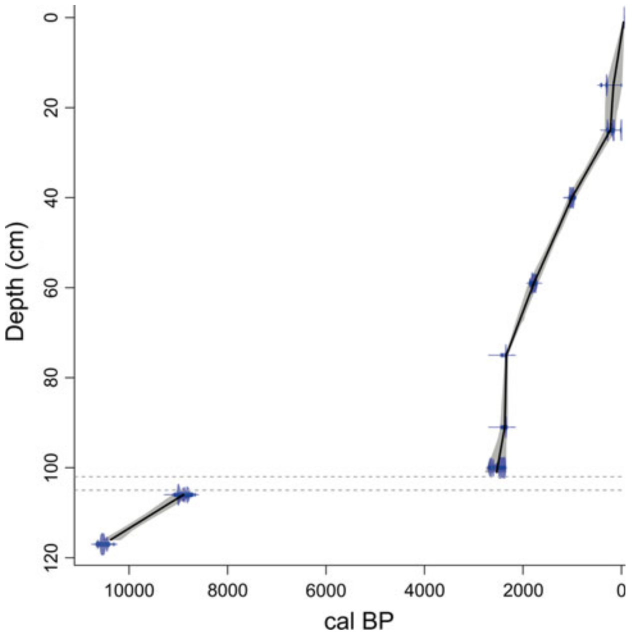


Fig. 2 Age-depth model for Brånakollane constructed using linear interpolation. At each date the *solid line* indicates the calibrated age ranges and the *grey field* around it represents the probability distribution. The top 10 cm is missing. The hiatus at 101–106 cm is taken into account when fitting the model. Theradiocarbon dates are given in Table 1

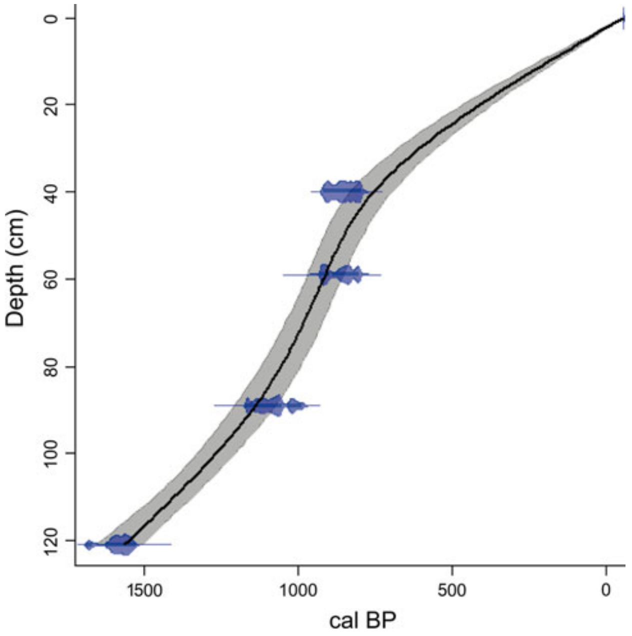


Fig. 3 Age-depth model for Bøkeskogen based on a smooth spline. At each date the *solid line* indicates the calibrated ranges and the *grey field* around it represents the probability distribution. The radiocarbon dates are given in Table 2

spline was weighted by the probabilities of the sampled calibrated years (Blaauw 2010). Any of the 1,000 models with age reversals were rejected in the final model.

Chronology is presented as calibrated years before present (cal. B.P.), where B.P. is A.D. 1950 (Tables 1, 2; Figs. 4, 5, 6, 7, 8).

Palynological richness

To estimate palynological richness, rarefaction analyses using the program RAREPOL 1.0 (Birks and Line 1992) were carried out using the raw counts of all terrestrial pollen and spores. Estimates of the number of expected taxa, [$E(Tn)$] were based on a standardized count of 170 at Brånakollane and 482 at Bøkeskogen.

Principal components analysis

To detect the hidden latent structure or major directions of variation in multivariate pollen data-sets under the assumption of linear responses of the variables to the hidden latent variable (ter Braak and Prentice 1988) principal components analysis (PCA) (Birks and Gordon 1985) was used. Preliminary detrended correspondence analysis of the two data-sets showed that both have gradient lengths of compositional turnover of <2 standard deviations, indicating that linear-based PCA is the appropriate technique to use (ter Braak and Prentice 1988). The percentage data were square-root transformed to stabilise their variances, the PCA was based on a covariance matrix between variables, and the sample scores were scaled for a Euclidian distance biplot. Computations were done using CANOCO version 4.52 (ter Braak and Šmilauer 2002).

Sample scores on PCA axes I and II were plotted stratigraphically along with the palynological richness estimates, selected pollen taxa and pollen groups, and charcoal in Figs. 6 and 7. Both PCA axes are statistically significant when compared with the broken-stick model (Legendre and Legendre 1998).

Results and reconstruction of the general vegetation development

The results are presented as stratigraphical pollen diagrams in Figs. 4 and 6 and are summarised in Figs. 5 and 7.

Brånakollane

The results from Brånakollane are described according to the local or site pollen-assemblage zones (LPAZ) suggested by optimal partitioning (Fig. 4). The two first zones BRÅ-1 and BRÅ-2 are described together as they are very short and are represented by only two samples. BRÅ-3 is divided into subzones BRÅ-3a and BRÅ-3b on the basis of

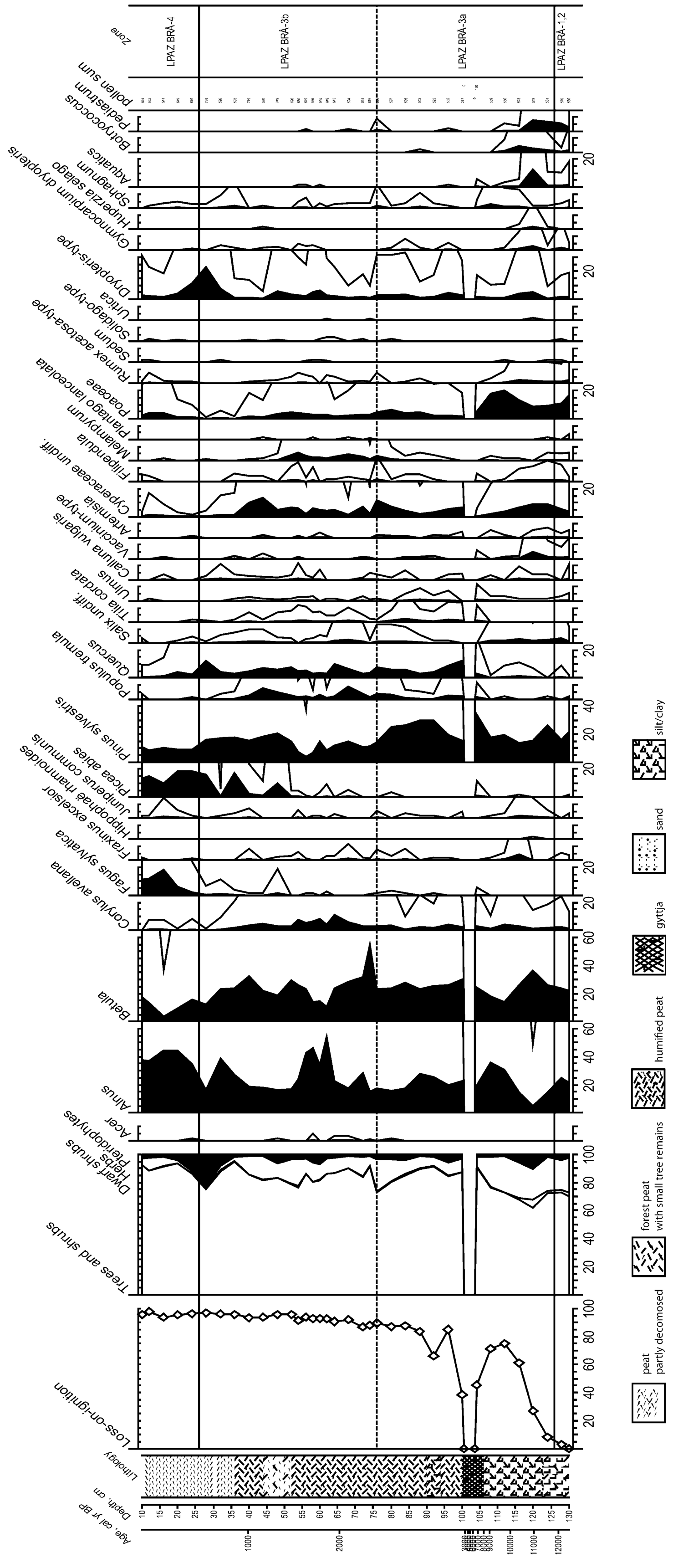


Fig. 4 Percentage pollen diagram showing selected pollen and spore taxa from the forest hollow at Brånakollane. The data are presented on a depth basis along with a calibrated age-scale. The group Aquatics consists of *Isoetes lacustris*, *Myriophyllum alterniflorum*, *Nymphaea*, *Potamogeton* (sect. Eupotamogeton), *Sparganium*-type and *Typha latifolia* pollen combined. The percentages are based on the sum of terrestrial pollen and spore types. The *white silhouettes* denote a 10× exaggeration of the percentage values. The local pollen-assemblage zones (LPAZ) are shown in the right-hand column

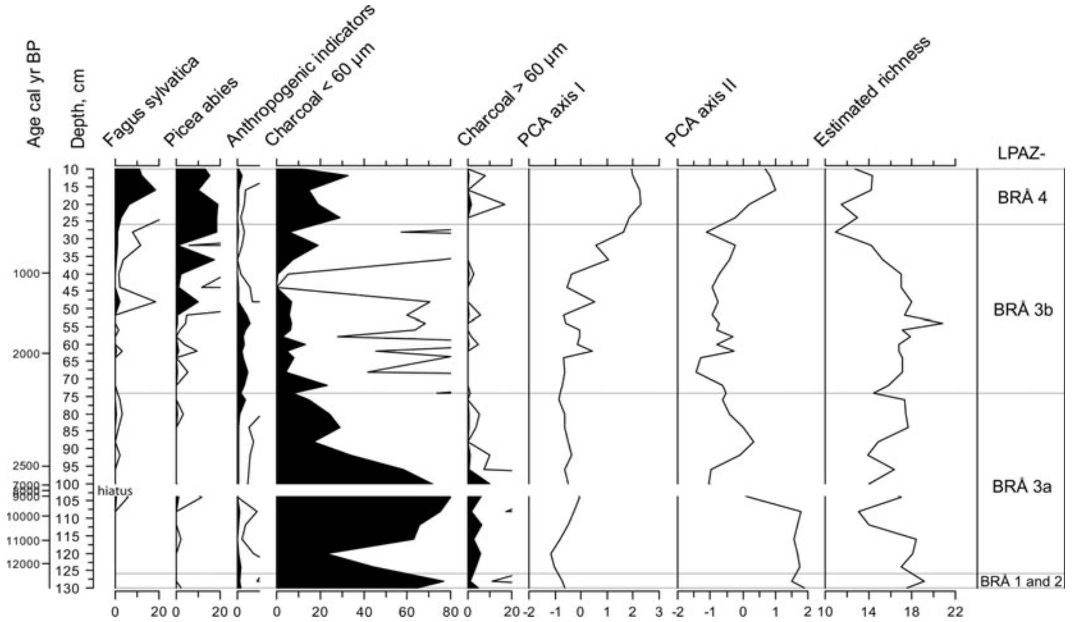


Fig. 5 Summary diagram from Brånakollane showing the %values of *Fagus sylvatica* and *Picea abies* pollen and a sum of selected anthropogenic indicators, charcoal, sample scores on PCA axis I (36.7 % of the total variance) and II (16.7 % of the total variance),and estimated palynological richness. These are plotted on a depth scale, along with a calibrated age-scale

visual inspection. Full details of the pollen data are given in Helvik (2010). A summary of the major changes found at Brånakollane is given in Fig. 6.

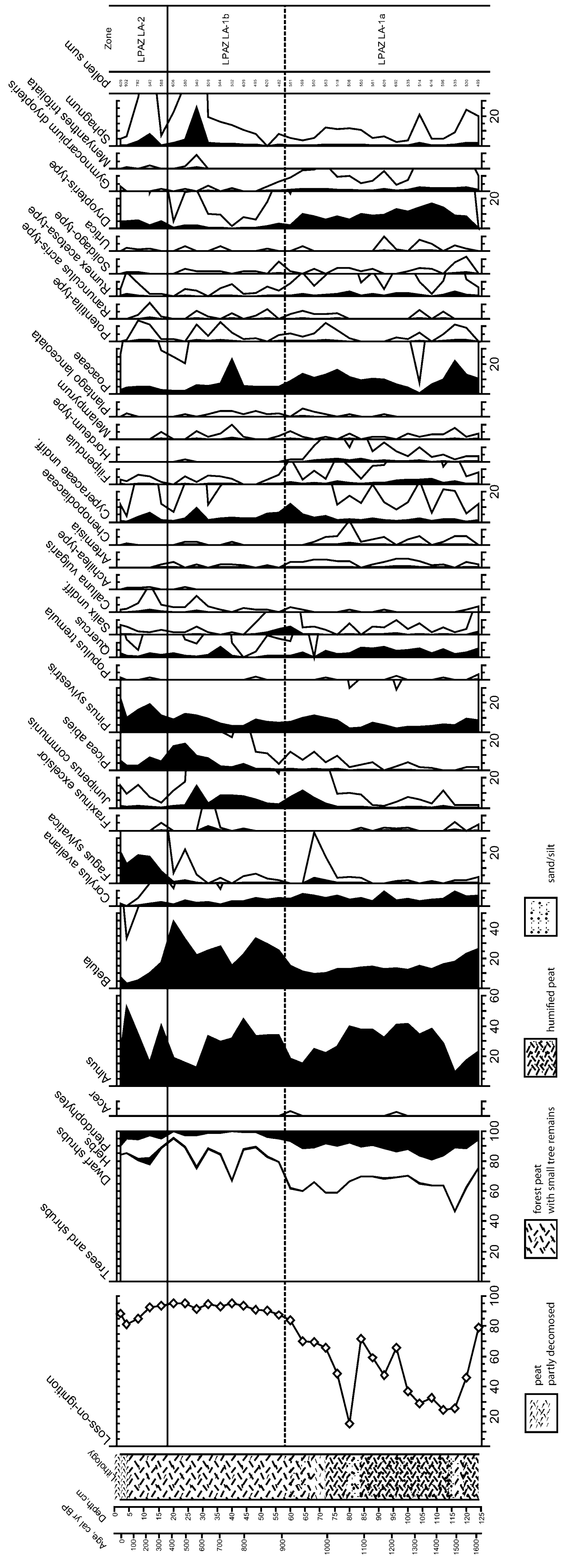
LPAZ BRÅ-1 and 2 (12500–11750 cal. yr B.P.) pioneer phase

In these zones (Fig. 4) the LOI-curve increases from 0% to 6 %. Characteristic of this initial phase are occasional pollen of many different taxa, some of them typical pioneer taxa. *Alnus*, *Betula* and *Pinus sylvestris* are the dominant tree types, probably a result of long-distance pollen transport or pollen from local forest stands outside the moraine. The amount of dwarf-shrub pollen is almost constant, dominated by *Calluna vulgaris* and *Vaccinium*-type. The major herb pollen types are Poaceae and Cyperaceae. However, pollen from taxa such as *Artemisia*, *Filipendula*, *Melampyrum*, *Plantago lanceolata*, *Rumex acetosa*-type and *Sedum* are also important. Although the site is today situated at 184 m a.s.l, finds of *P. lanceolata* may reflect the site once being close to sea level, as land-uplift has been about 160 m in this area. *P. lanceolata* can occur in presumed natural coastal vegetation (Birks 1973). Ferns are dominated by *Dryopteris*-type and *Gymnocarpium dryopteris. Potamogeton* (sect. Eupotamogeton), *Nymphaea* and *Typha latifolia* pollen and *Botryococcus* and *Pediastrum* algae are present, indicating shallow open-water at the site.

LPAZ BRÅ-3a (11750–2300 cal. B.P.) Betula-Pinus sylvestris forest

In this zone (Fig. 4) there is a clear hiatus representing the period from 2550–6750 cal. B.P. (at 101–105 cm). Therefore, description of this zone is divided in two; the period before (11750–6750 cal. B.P.) and the period after (6750–2300 cal. B.P.) the hiatus.

The lower part is characterized by large fluctuations in the LOI-curve (Fig. 4). It rises from less than 10–75 % at 9800 cal. B.P., and shows a minimum value of 40 % at 6800 cal. B.P. The occurrence of *Hippophaë rhamnoides* pollen suggests that the landscape may still have been open. The dominant tree pollen throughout is *Alnus*, *Betula* and *P. sylvestris*, most likely long-distance transported pollen or pollen from stands outside the immediate area. Other tree pollen present in the lower part of BRÅ-3a is *Corylus avellana*, *Fraxinus excelsior*, *Populus tremula*, *Quercus* and *Salix* sp., all relatively light-demanding taxa suggesting a mixed forest, but a rather open landscape as suggested by total herb pollen percentages of more than 20 %. Regular occurrences of *Artemisia*, *Filipendula* and *R. acetosa*-type support this reconstruction (Greisman and Gaillard 2009). From ca. 9500 cal. B.P., herbs such as *Artemisia*, *Filipendula*, *Melampyrum* and *R. acetosa*-type all show discontinuous pollen curves, suggesting less light-availability and thus a denser forest. However, *Filipendula* and *Melampyrum* pollen increases towards the top. Pteridophyte spores increase simultaneously with a decline in



◀ **Fig. 6** Percentage pollen diagram showing selected pollen and spore taxa from the forest hollow at Bøkeskogen. The data are presented on a depth basis along with a calibrated age-scale. The percentages are based on the sum of terrestrial pollen and spore types. The *white silhouettes* denote a 10× exaggeration of the percentage values. The local pollen-assemblage zones (LPAZ) are shown in the right-hand column

tree pollen percentages between 11000–9600 cal. B.P. as *Dryopteris*-type, *Gymnocarpium dryopteris* and *Huperzia selago* all increase.

At ca. 6800 cal. B.P. when the hiatus is observed, there is an abrupt drop in the LOI-curve simultaneously with a peak in charcoal particles of both size classes. The sediment consists of gyttja at this level. The most likely explanation for the hiatus is drying out of the site, leading to the total decomposition of organic material. Just before the hiatus, pollen or spores from aquatic plants appear, such as *Isoetes lacustris*, *Potamogeton* (sect. Eupotamogeton) and *Sparganium*-type, which along with the algae *Botryococcus* and *Pediastrum* suggest the presence of open water at the site, but these rapidly disappear. At the same time, the first pollen of *F. sylvatica* occurs with values higher than 0.5 %. Scattered pollen of *P. abies* also occurs in the previous zone.

The pollen composition after the hiatus is quite similar to the pollen spectra before the hiatus; LOI fluctuates, but is high. From 2400 cal. B.P. *F. sylvatica* shows an almost continuous pollen curve, varying between 0.2 and 0.3 %. Towards the end of this period ca. 2350 cal. B.P., there are palynological indications of clearings and openings in the forest and the total tree pollen decreases while *F. excelsior*, *J. communis*, *P. tremula*, *Quercus* and *Salix* sp. pollen all show small increases. An increase is seen in Cyperaceae, *Filipendula*, *Melampyrum* and *R. acetosa*-type pollen. The last two may indicate grazing by cattle (Hjelle 1999). Increases in *Filipendula* pollen and *Sphagnum* spores suggest wetter conditions locally.

LPAZ BRÅ-3b (2300–300 cal. B.P.) broad-leaved deciduous forest and the establishment of *F. sylvatica* and *P. abies*

Throughout this zone (Fig. 4), the LOI-curve is stable around 95 %. Although the individual tree pollen types indicate large fluctuations, the total tree pollen shows small variations around its 75 % values. The total herb pollen curve fluctuates between 10 and 20 % until ca. 350 cal. B.P. when it decreases to <5 % for the rest of the zone. The dominant tree taxa are *Alnus*, *Betula* and *P. sylvestris*. The onset of this period is marked by a large peak in *Betula* pollen, probably the effect of local pollen deposition. Large fluctuations in the various tree pollen curves may indicate continuous disturbances that created gaps and openings,

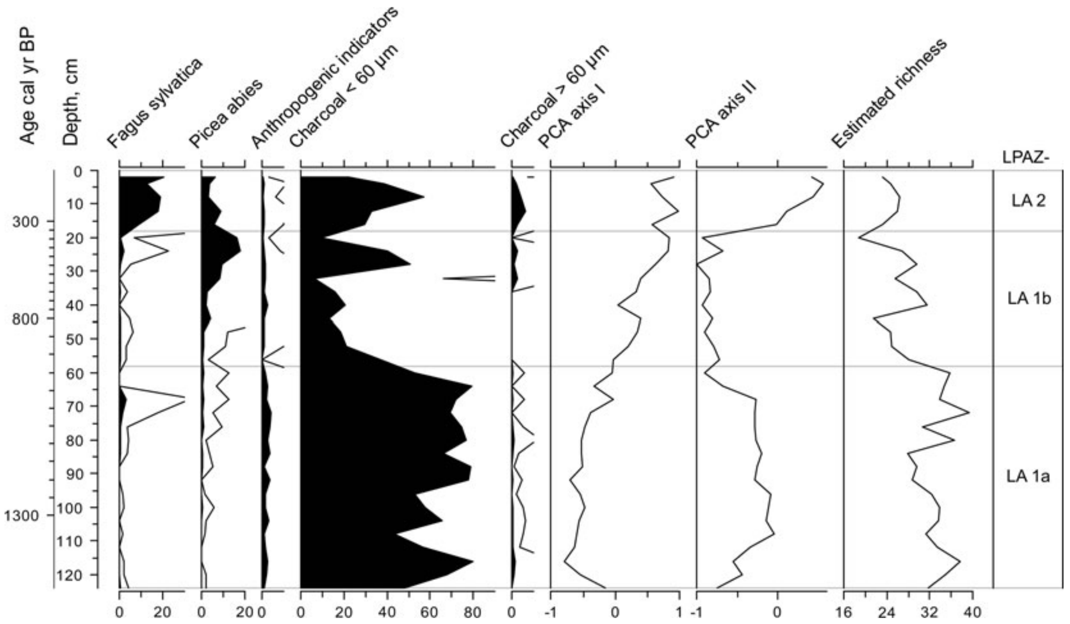


Fig. 7 Summary diagram from Bøkeskogen showing the %values of *Fagus sylvatica* and *Picea abies* and a sum of selected anthropogenic indicators, charcoal, sample scores on PCA axis I (30.0 % of the total variance) and II (17.9 % of the total variance), and estimated palynological richness. These are plotted on a depth scale, along with a calibrated age-scale

resulting in changes in the composition of the vegetation. Except for *Ulmus* and *F. excelsior* which decline and disappear towards the top, pollen types of other broad-leaved deciduous trees show more or less continuous pollen curves throughout the zone. The presence of *Melampyrum*, *Plantago lanceolata*, *R. acetosa*-type and *Urtica* pollen suggests some anthropogenic activity, most likely fire and grazing by cattle (Behre 1981; Hjelle 1999). *Alnus* pollen shows a very distinct increase in the period from 1950 to 1500 cal. B.P., simultaneous with increases in pollen and spores from several moisture-demanding taxa such as Cyperaceae, *Filipendula* and *Dryopteris*-type. Increases in pollen from light-demanding taxa such as *C. avellana*, *J. communis* and *Artemisia*, and in charcoal suggest clearance of the forest, as a result of natural or man-made fire or other human activity. From ca. 2200 cal. B.P. the *P. abies* pollen curve becomes continuous, and from ca. 1450 cal. B.P. it expands with two distinct peaks between 1350 and 800 cal. B.P. Single finds of *F. sylvatica* pollen occur at the same time. The *F. sylvatica* pollen shows a small peak at 1330 cal. B.P. and becomes continuous. This value may suggest that *F. sylvatica* became locally established at the site (Huntley and Birks 1983; Lindbladh et al. 2008). Just before this, there are some scattered finds of *Carpinus betulus* and *Frangula alnus* pollen (not shown on Fig. 4). These types have been connected to the establishment of *F. sylvatica* in southern Sweden (Greisman and Gaillard 2009). The Cyperaceae pollen curve shows some fluctuations before it peaks ca. 1000 cal. B.P.

From ca. 800 cal. B.P., there is a change in the forest composition. Light-demanding taxa such as *Acer*, *C. avellana*, *F. excelsior*, *Populus tremula*, *Salix*, *Tilia cordata* and *Ulmus* are shaded out and the main components of the forest are now *Alnus*, *Betula*, *F. sylvatica*, *P. abies* and *Pinus sylvestris*. From ca. 600 cal. B.P., there is a steep decline in the total amount of herb pollen. Herbs such as *Artemisia*, *Filipendula*, *Melampyrum*, *Plantago lanceolata* and *R. acetosa*-type soon disappear, suggesting a denser forest and cessation of locally anthropogenic activity. Meanwhile, increases in fern and *Sphagnum* spores suggest wetter conditions.

LPAZ BRÅ-4 (300 cal. B.P.—present) *F. sylvatica*: *P. abies* forest

The LOI-curve (Fig. 4) has similar values in this zone as in the previous zone. Pollen of *F. sylvatica* and *P. abies* reaches values of 20 %. This period is characterised by a new type of forest, dominated by *F. sylvatica* and *P. abies* together with *Alnus*. The high percentages of *F. sylvatica* pollen suggest a dense local *F. sylvatica* stand with a closed canopy, similar to the forest in the reserve today. Pollen from broad-leaved deciduous trees such as *F. excelsior*, *P. tremula*, *Tilia cordata* and *Ulmus* soon disappears and the pollen of *Betula*, *C. avellana*, *P. sylvestris* and *Quercus* decreases during this period. Small but distinct peaks in Cyperaceae, Poaceae, *Rumex acetosa*-type and *Solidago*-type may reflect anthropogenic activity close to the sampling site, most likely involving cattle-grazing.

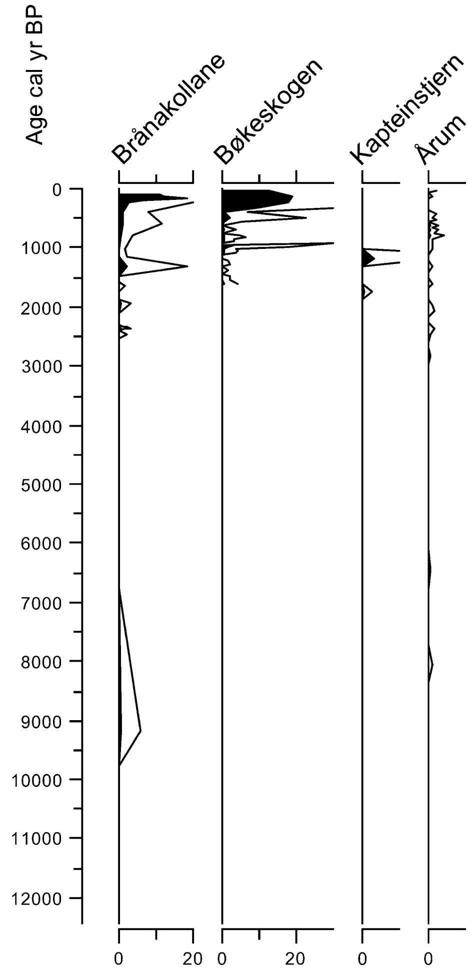


Fig. 8 A comparison of *Fagus sylvatica* pollen percentages at four different sites in the region: Brånakollane (this study), Bøkeskogen (this study), Kapteinstjern (Molinari et al. 2005) and Årum (Bjune et al. 2009), plotted on a common calibrated age-scale. Percentages are based on the sum of terrestrial pollen and spore types

Summary of Brånakollane

In Fig. 5 the *F. sylvatica* and *P. abies* pollen curves are discontinuous in zone BRÅ 3a, the first PCA axis (36.7 % of the total variance) shows a rather consistent trend, and the estimated palynological richness shows fluctuating high values. The charcoal curves indicate a sharp decrease in fire activity. The anthropogenic indicator taxa rise at the top of the zone. In BRÅ-3b the *P. abies* pollen curve becomes continuous, the *F. sylvatica* pollen curve is discontinuous at the start but becomes continuous when the anthropogenic indicator pollen curve ceases. In this zone sample scores on the first PCA axis show an increasing trend and by the end of the zone the estimated species richness shows a decrease. In the uppermost zone, when *F. sylvatica* and *P. abies* are well established, the PCA scores level off and estimated species richness shows a small increase. Taking all the data into account, the largest changes in the local forest vegetation occurred ca. 1350 cal. B.P. *F. sylvatica* and *P. abies* show continuous pollen curves, the anthropogenic indicator pollen types decrease, the PCA axis I scores increase, and the estimated palynological richness starts to decrease, suggesting a decrease in the local mosaic structure of the landscape. The first PCA axis thus reflects the shift from a diverse landscape with broad-leaved trees to a less diverse landscape with *P. abies* and *F. sylvatica* trees. PCA axis II (16.7 % of the total variance) appears to reflect more local changes, associated with changes in soil and site moisture.

Bøkeskogen

The results from Bøkeskogen are described according to the three local or site pollen-assemblage zones (LPAZ) and are shown in Fig. 6. LA1 is divided into two subzones based on visual inspection. Full details of the pollen data are given in Helvik (2010). A summary of changes at this site is given in Fig. 8.

LPAZ LA-1a (1600–900 cal. B.P.) deciduous forest and anthropogenic activity

The LOI-curve (Fig. 6) varies throughout the zone. The main tree pollen curves, both *Alnus* and *Betula*, decrease simultaneously with the LOI-curve. At the same time there is a peak in large and small charcoal particles, suggesting clearances caused by fires, either natural or man-made. The pollen curves of deciduous trees such as *Quercus* and *Corylus avellana* show high values. Scattered pollen of *Acer*, *Fraxinus excelsior* and *Populus tremula* also indicates some disturbance of the forest, as these tree species respond quickly and sprout in openings and gaps in the forest. They are subsequently out-competed by more competitive taxa to form a mixed deciduous forest. From the onset of this period, a typical *F. sylvatica* pollen curve is present with a long tail of scattered grains with low percentages (Van der Knaap et al. 2005). *F. sylvatica* pollen values of 0.4 % from ca. 1090 cal. B.P. and > 1.5 % at 1000 cal. B.P. suggest that the tree was locally present (Huntley and Birks 1983; Lindbladh et al. 2008). Studies from Denmark suggest that human impact may be the underlying reason for the lack of, or restricted, expansion of *F. sylvatica* in some areas (Odgaard 1994). The juvenile seedlings and saplings of *F. sylvatica* are susceptible to browsing (Boulanger et al. 2009) and this may have prevented their further expansion at this time. The *P. abies* pollen curve shows scattered finds at the start but becomes continuous throughout the zone. The herb pollen present suggests that the field layer was rich in species, several of which are strong indicators of anthropogenic activity. The main herb pollen type is Poaceae which has its peak simultaneously with the decrease in the tree pollen curve and the peak in charcoal particles, indicating open vegetation. The continuous presence of *Hordeum*-type pollen is the strongest evidence for the role of human activity in keeping the vegetation open (Lindbladh et al. 2007). Pollen from herbs such as *Artemisia*, Chenopodiaceae, *Filipendula* and *Urtica* are all known indicators of human activity. *Ranunculus acris*-type and *Rumex acetosa*-type are indicators of grazing by cattle (Behre 1981; Hjelle 1999). Small but significant peaks in cultural grazing indicators such as *Melampyrum* and *R. acetosa*-type are strongly suggestive of local anthropogenic impact on the forest (Molinari et al. 2005). Several herb species suggest that fire may have been an important factor in disturbing the vegetation. The charcoal curves are continuous throughout, suggesting high fire activity. *Melampyrum* is thought to be one of the most reliable pollen signals of burning, correlating closely with charcoal at many scales of resolution (Innes and Simmons 2000; Tinner and Lotter 2006). *Melampyrum* pollen percentages are low but present throughout the period. Small fires do not have a great impact on forest composition, but *Potentilla*-type pollen comes from several taxa, many of which can respond quickly to fire that can cause forest disturbance and an increase in available light (Delarze et al. 1992; Tinner et al. 2000; Tinner and Lotter 2006). The *Salix* and Cyperaceae pollen curves are rather constant and low until there is a slight rise at the top of the zone ca. 950 cal. B.P. This may be a result of the clearance of the local *Alnus* stand at this time. The fern curve is rather constant throughout the period, although there is a slow rise simultaneous with a rise in *Alnus* and *Filipendula* pollen that may suggest wetter conditions locally.

LPAZ LA-1b (900–400 cal. B.P.) abandonment and reforestation

The LOI-curve (Fig. 6) is rather smooth throughout this zone. *Alnus*, *Betula* and *P. sylvestris* pollen fluctuate, perhaps indicating disturbance and change. The transition to this period starts with steep increases in the *Alnus* and *Betula* pollen curves, which suggest that reforestation was taking place. The forest changes from a mixed deciduous forest to a mixed *Betula*-*Pinus sylvestris* forest with the establishment and expansion of *P. abies*, which reaches its maximum pollen value of 17 % ca. 600 cal. B.P. An increase in *Betula* pollen may be indicative of a post-disturbance succession (Bradshaw and Lindbladh 2005). The *F. sylvatica* pollen curve starts very low at 900 cal. B.P. and remains low until a small peak >2 % at ca. 500 cal. B.P.; it then starts to increase, suggesting the local expansion of *F. sylvatica*. *Hordeum*-type pollen shows only one occurrence in this zone and cultural indicators such as *Artemisia*, *Filipendula*, *Melampyrum*, *Plantago lanceolata*, *Potentilla*-type, *Ranunculus acris*-type, *Rumex acetosa*-type, *Solidago*-type and *Urtica* (Behre 1981; Hjelle 1999) are present but in lower amounts than in the previous zone, probably reflecting reduced anthropogenic activity. High values of *Juniperus communis* pollen suggest some grazing. A decrease in fern spores and pollen from *Filipendula* suggests drier conditions until ca. 750 cal. B.P. when conditions again became wetter. From then on, Cyperaceae pollen increases and *Sphagnum* shows a steep rise, simultaneous with an increase in terrestrial spores and finds of *Menyanthes trifoliata* pollen. About 750 cal. B.P., there is a peak in Poaceae pollen, indicative of forest clearance since total tree pollen decrease. Simultaneously, there is a peak in charcoal particles, suggesting that fire may be the reason for the clearance, and after this disturbance, light-demanding species such as *F. excelsior* and *Quercus* show increases in the pollen curves, possibly reflecting a post-disturbance succession. From ca. 700 cal. B.P., the total tree pollen percentages start to increase and the total herb pollen percentages decrease, indicating a denser forest (Broström et al. 2005; Lindbladh et al. 2007). The forest is now dominated by *Pinus sylvestris*, *Picea abies*, *Betula* and *F. sylvatica*.

LPAZ LA-2 (400 cal. B.P.—present) Fagus: Pinus forest

The LOI-curve (Fig. 6) starts at 95 % and drops to 80 % ca. 30 cal. B.P. This period is characterised by high values of *Alnus*, *F. sylvatica* and *Pinus sylvestris* pollen. A distinct decrease in *Alnus* pollen, simultaneous with a peak in large charcoal particles, may suggest forest clearances ca. 230 cal. B.P. caused by fire. *F. sylvatica* pollen increases from 5 to 25 %, suggesting that *F. sylvatica* was becoming well established and even became the dominant tree locally. The *P. abies* pollen curve decreases throughout the period. During the fifteenth and sixteenth centuries, two ironworks were established in the area, which required a considerable supply of charcoal. The preferred tree was *P. abies* and this may be the reason for the decreased pollen values of *P. abies* (Molinari et al. 2005). Increases in *J. communis* and dwarf-shrub pollen may indicate a reduction in browsing intensity (Molinari et al. 2005). Increases in Cyperaceae and Poaceae pollen suggest more open vegetation. Small but distinct increases in *Achillea*-type, *Filipendula*, *Potentilla*-type, *Ranunculus acris*-type, *R. acetosa*-type and *Urtica* pollen indicate that there was still some anthropogenic activity locally. Wetter conditions may be reflected by increases in the *Sphagnum* spore curve and the occurrence of *Menyanthes trifoliata* pollen.

Summary of Bøkeskogen

Compared with the record from Brånakollane, this record (Fig. 8) only reflects a limited time from ca. 1600 cal. B.P. to the present-day, although the same trends can be observed. The *F. sylvatica* and *P. abies* pollen curves are present discontinuously from the start of the sequence. Anthropogenic indicator pollen is present throughout the record, but decreases simultaneously with the charcoal curves. The charcoal curves indicate high fire activity in the first zone, LA-1a, but show an abrupt fall at the end of the zone. Scores on PCA axis I (30.0 % of total variance) show an increasing trend throughout the record and the estimated palynological richness curve, despite short-term fluctuations, shows a decreasing trend through the record. The interpretations of the PCA axis I scores and the estimated palynological richness are similar to those at Brånakollane, namely a shift towards oligocratic trees in LA-1b and LA-2 and a decrease in the local mosaic structure of the landscape as *P. abies* and *F. sylvatica* expanded in LA-2.

Discussion

The Holocene spread of *F. sylvatica*, as the last of the major European trees, started about 9,000 years ago. The spread is not simultaneous through different part of Europe and does not show a continuous “moving wave” pattern, as there are long delays in different regions at different times (Küster 1997; Magri et al. 2006). Much research has been carried out to establish the major driving forces for the migration of *F. sylvatica* (e.g. Bradshaw et al. 2010). Climate, natural disturbance, and/or disturbance caused by human activity have all been suggested as possible forcing factors.

Several studies of small hollows have been used to study the immigration and local establishment of *F. sylvatica* in Denmark and southern Sweden (Lindbladh and Bradshaw 1998; Björkman 1999; Bradshaw and Lindbladh 2005). *F. sylvatica* arrived in an already forested landscape, but managed to become an important tree in the woodlands of northern Europe where it mainly replaced *Quercus* (Küster 1997). It spread from central Europe into the southern part of Scandinavia and reached its maximum distribution at about 930 cal. B.P. (1000 B.P.). In Denmark the spread of *F. sylvatica* shows a clear pattern, beginning about 3200 cal. B.P. (3000 B.P.) in the east, then extending to the west and north where it reached its maximum distribution at about 500 B.P. (Bradshaw and Holmquist 1999; Fritzbøger and Odgaard 2010). The spread of *F. sylvatica* is probably linked to anthropogenic activity and disturbance by fire. Site conditions such as water availability, soil texture, nutrient availability, microclimate and disturbance can also be important rate-limiting factors and may explain the patchy spreading dynamics of *F. sylvatica* (Bradshaw and Lindbladh 2005). Studies of palaeo-records show that *F. sylvatica* values are low at levels where there is evidence for local fire. Mean charcoal concentrations are higher before the establishment of *F. sylvatica* than after (Bradshaw and Lindbladh 2005). This may suggest that *F. sylvatica* was able to establish after fire had created disturbance and gaps. Since *F. sylvatica* is vulnerable to fire, this may also indicate a lower fire frequency after the establishment of *F. sylvatica.*

The first occurrences of *F. sylvatica* pollen at Brånakollane are recorded at ca. 9100 cal. B.P. with a percentage of only 0.6 % (Fig. 8). From this time the pollen curve remains discontinuous, and is most likely a result of long-distance pollen transport, but Björkman (1999) suggests that pollen percentages >0.5 % may indicate small stands in the region. The *F. sylvatica* pollen curve is discontinuous until ca. 1350 cal. B.P. when it reaches a pollen value of 1.9 % suggesting local establishment (Huntley and Birks 1983; Lindbladh et al. 2008). This is in accordance with results from other studies in the area (Henningsmoen 1988; Molinari et al. 2005; Sørensen et al. 2007; Bjune et al. 2009) and suggests that the establishment of *F. sylvatica* was broadly synchronous within south-east Norway (Fig. 8). *P. abies* was also established at the site at this time. Variation in the pollen values for *Alnus*, *Corylus avellana* and *Pinus sylvestris* and occasional *Acer* pollen can be observed in the period before *F. sylvatica* pollen increases. These may suggest clearances and local successions of trees at or near the site. Simultaneously an increase in *Filipendula* and Cyperaceae pollen and fern spores and the presence of scattered aquatic-plant pollen types may suggest wetter conditions. Increases in large and small charcoal particles may indicate local fires (Innes and Simmons 2000). Such fires may have resulted in an increase of *Corylus avellana*, *Pinus sylvestris*, *Calluna vulgaris*, *Melampyrum* and *Potentilla*-type, all of which are regarded as positive pyrophytes or, at least, as being competitively favoured by fire (Innes and Simmons 2000). Due to the wet climatic conditions at this time (Seppä et al. 2009) the fires were most likely man-made. Pollen from anthropogenic indicator species decreases, suggesting less human activity in the immediate surroundings of the site (Fig. 8).

At the Bøkeskogen site in Larvik (Fig. 7), *F. sylvatica* pollen is present from ca. 1600 cal. B.P. (0.4 %). Similar to Brånakollane, the low and discontinuous pollen percentages suggest the presence of scattered trees in the area or may be the result of long-distance pollen transport (Fig. 8). This is in accordance with Henningsmoen (1988) where the *F. sylvatica* pollen curve is present but discontinuous from the bottom of the core at 190 cm depth. At ca. 950 cal. B.P. *F. sylvatica* reaches pollen percentages that are high enough to indicate local establishment at this site (Huntley and Birks 1983; Lindbladh et al. 2008). The values of the charcoal particle curves suggest more or less continuous fire activity until ca. 900 cal. B.P. (Fig. 7). Simultaneously continuous curves of pollen from anthropogenic indicators such as *Hordeum*-type are observed, suggesting human activity in the area. In the period preceding ca. 1000 cal. B.P. several small peaks in large charcoal particles occur simultaneously with fluctuations in the LOI-curve, indicating fire as a disturbance factor, making conditions suitable for *F. sylvatica* to establish. Clearance of *Alnus* may have facilitated this. During the next 600 years the conditions at the site became drier, the forest denser, and human activity had changed, perhaps with a stronger pressure from grazing cattle. All this may have contributed to the failure of *F. sylvatica* to expand. The charcoal curve suggests reduced fire activity. Competition from *P. abies* may also be a critical factor. This may have been exacerbated by a drier climate during the Medieval Warm Period or by grazing by cattle, or, more likely, by a combination of both (Odgaard 1994; Bolte et al. 2007). At 500 cal. B.P. it is likely that the clearance of *Alnus* and a wetter climate made it possible for *F. sylvatica* to expand and become the dominant tree at this site (Fig. 7).

Based on the data from these two forest hollows it is most likely that the establishment of *F. sylvatica* is a result of succession after disturbance by fire and human activities at the two localities studied. At Brånakollane small changes in moisture can be inferred from the pollen diagram simultaneous with the establishment and expansion of *F. sylvatica*, as reflected by an increase in fern spores and *Sphagnum* spores in the pollen diagram. In contrast to the establishment of beech in Denmark and southern Sweden, the establishment in Norway coincides with the establishment of *P. abies*. Competition between *F. sylvatica* and *P. abies* may thus have occurred. *F. sylvatica* is more vulnerable to drought than *P. abies* (Bolte et al. 2007). This may be a reason why *F. sylvatica* established after *P. abies* at Brånakollane. The location of the forest on top of a hill may have benefited *P. abies* in competition with *F. sylvatica*. Because of drier climatic conditions *F. sylvatica* failed to expand in competition with *P. abies* which expanded simultaneously. Even though *F. sylvatica* is known to be a strong competitor in forests, it did not manage to be the dominant tree in the forests in south-eastern Norway, as it did in Denmark (Bradshaw and Holmquist 1999) and southern Sweden (Lindbladh et al. 2000). Competition from *P. abies* may be the reason for this. In this region *F. sylvatica* is close to its northernmost limits of its natural distribution. This may cause climatic stress which can intensify competition with *P. abies*. Severe frost during winter and late frost in spring may be critical factors in the regeneration of *F. sylvatica* (Bolte et al. 2007). In Denmark it was *F. sylvatica* that out-competed the broad-leaved deciduous forest ca. 3200–2600 cal. B.P. (3000–2500 B.P.) (Bradshaw and Holmquist 1999) and in southern Sweden ca. 1400–900 cal. yr B.P. (1500–1000 B.P.) (Björse and Bradshaw 1998), but in Norway it was *F. sylvatica* and *P. abies* that caused this change.

At Bøkeskogen it is possible that *F. sylvatica* was present in the surroundings from the beginning of the record but it did not become established until the amount of anthropogenic indicator pollen decreased. Seedlings of *F. sylvatica* are vulnerable to grazing (Odgaard 1994) and pressure from cattle-grazing may have hindered the establishment and expansion of *F. sylvatica* in Bøkeskogen. The moisture conditions at the site seem to be stable in this period and may therefore not have influenced the establishment of *F. sylvatica* here. Björkman (1999) suggests that to evaluate whether climatic or anthropogenic causes are the driving forces in establishment of *F. sylvatica* in a region, it is necessary to see if there is coherence in the time of establishment at the different sites. His study from southern Sweden showed large variations in the time of establishment of *F. sylvatica* and he proposed therefore that climatic change had not been the limiting factor. As shown in Fig. 8 the establishment of *F. sylvatica* in south-eastern Norway can be dated to ca. 1300 cal. B.P. In addition the study of Sørensen et al. (2007) dates the establishment of *F. sylvatica* to ca. 1400 cal. B.P. This suggests that the time period for *F. sylvatica* establishment was ca. 100–200 years. This narrow interval suggests that climatic conditions may have been an important factor, or at least a contributory factor together with human activity, for the establishment of *F. sylvatica* in the Larvik region of south-eastern Norway. This contrasts with results from many studies in southern Sweden (e.g. Björse and Bradshaw 1998; Björkman 1999; Lindbladh et al. 2000, 2007) that emphasize anthropogenic activities as the main driving force for the establishment and expansion of *F. sylvatica*.

Conclusions

Studies of the two localities, Brånakollane and Bøkeskogen, show that *F. sylvatica* has a long history in this region of south-eastern Norway, from the first occurrence of *F. sylvatica* pollen ca. 9100 cal. B.P. to its local expansion ca. 1300–1200 cal. B.P. Such a long history strongly suggests that these *F. sylvatica* forests are not recent plantations. To decide if they are “natural” forests requires further detailed ecological and demographic investigations. Our pollen-analytical data suggest that the forests are native, and thus that *F. sylvatica* can be considered a native tree in Norway, at least in south-eastern Norway. The results from these two localities suggest that the *F. sylvatica* establishment was likely to have been a result of human activity and climatic changes, particularly changes in moisture conditions. This is in contrast to studies in southern Sweden where climatic factors appear to have been unimportant or to have played a minor role in the establishment of beech.

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