Exploring the requirement for anthropogenic disturbance to assist the stand-scale expansion of *Fagus sylvatica* L. outside southern Scandinavia

The Holocene
23(4) 579–586
© The Author(s) 2013
Reprints and permission:
sagepub.co.uk/journalsPermissions.nav
DOI: 10.1177/0959683612465447
hol.sagepub.com

Lee R Bradley,¹ Thomas Giesecke,² Karen Halsall¹ and Richard HW Bradshaw¹

Abstract

This paper presents a pollen and charcoal record from a forest hollow located in northern Germany. The initial stand-scale colonization and subsequent expansion of the species *Fagus sylvatica* (European Beech) is examined and compared with examples from southern Scandinavia. In the early Holocene, a diverse forest stand is present. The recording of *Fagus sylvatica* in nine contiguous samples over the time period 8600–7950 cal. yr BP, constrained by three AMS dates, suggests its presence close to the hollow. This early occurrence is critiqued against the current paradigm of mid- to late-Holocene *Fagus sylvatica* spread in northern Central Europe. Between 6200 and 2900 cal. yr BP, *Fagus sylvatica* was a minor constituent of the forest community but did not expand despite periods of favorable conditions including relatively open forest landscape, wetter-cooler climatic conditions and a suitable fire regime. The eventual expansion of *Fagus sylvatica*, around 2900 cal. yr BP, is initiated by significant anthropogenic disturbance around the hollow. After the initial phase of expansion, its growing importance in the forest was potentially aided by a period of wetter-cooler conditions and a switch in the fire regime from one of regular episodes, to one of sporadic occurrence. Two fire events and an increase in anthropogenic activity occur at the same time as the decline in the relative abundance of *Fagus sylvatica* at 1200 cal. yr BP. This site highlights the strong anthropogenic influence on the species dynamics throughout the late Holocene.

Keywords

charcoal, *Fagus sylvatica*, Germany, pollen, small forest hollow, stand-scale palynology

Received 20 April 2012; revised manuscript accepted 10 September 2012

Introduction

Fagus sylvatica (European Beech), at present, is a dominant constituent in many forests in northern Central Europe and southern Scandinavia (Jalas and Suominen, 1972–1999). The species became established in these areas relatively late in the Holocene (Magri et al., 2006) compared with other deciduous species, with the exception of *Carpinus betulus* (Huntley and Birks, 1983). The factors that have led to the current abundance of the tree in many of these areas are still debated (Bradshaw et al., 2010a; Gardner and Willis, 1999; Giesecke et al., 2007; Küster, 1997; Tinner and Lotter, 2006), with Holocene climate change and altering land-use practices receiving most attention. A number of studies have suggested a combination of these factors is required to aid expansion. In southern Central Europe, Valsecchi et al. (2008) indicated the likely need for wet-cold phases of climate, human impact and a decrease in fire to occur for the species population to expand in size. Whilst in northern Central Europe, Ralska-Jasiewiczowa et al. (2003) argued that shifts to wetter-cooler periods of climate, alongside anthropogenic activities, are responsible for the species expansion.

In northern Central Europe, fossil pollen data often show that anthropogenic activity occurred immediately prior to the expansion phase of *Fagus sylvatica* populations (Küster, 1997). This activity, in the form of felling of rival species and the opening up of the landscape, provided space for colonization on abandoned fields (Behre, 1988). The need for a clearance in the forest ecosystem and opening up of the landscape to allow *Fagus sylvatica* to expand in

the gap created is one potential explanation for the species' late expansion but is contradictory to the observation of the species' ability to regenerate under dense shade (Ellenberg, 1996). The relationship between disturbance and expansion is not universally explicit. In northern Germany, pollen diagrams with regional pollen source areas highlight situations where the continuous or rising *Fagus sylvatica* curve is preceded or followed by anthropogenic pollen indicators (Brandt, 2003; Jahns, 2000, 2001, 2007; Wolters, 1999). One explanation is that of Gardner and Willis (1999) who argued that the interplay between *Fagus sylvatica* and transition to agriculture is merely coincident with the rate of migration from refugia rather than any requirement for anthropogenic disturbance.

In southern Scandinavia the link between expansion and anthropogenic disturbance has been studied extensively (Bradshaw and Lindbladh, 2005; Bradshaw et al., 2010a). These studies have shown that the rise in *Fagus sylvatica* pollen occurred immediately after a disturbance event in the forest ecosystem.

¹University of Liverpool, UK

²University of Göttingen, Germany

Corresponding author:

Lee R Bradley, University of Liverpool, School of Environmental Science, Roxby Building, Liverpool L69 7ZT, UK.
Email: L.R.Bradley@liverpool.ac.uk

Figure 1. Location and details of the study area. (a) Continental Europe: dark shading indicated the location of potentially dominating *Fagus sylvatica* forests (Bohn et al., 2000); star: Carlshof small forest hollow. (b) Overview of land use in study area (star: Carlshof small forest hollow; dark grey: forest; light grey: open ground; striped areas: settlements; white: water; solid lines: roads; dashed lines: railway). (c) Photograph of the site taken at the time of sampling, September 2007.

Björkman (1996) suggests that at the local scale the expansion was associated with a phase of woodland clearance. Southern Scandinavia represents the current northern distribution of the species. In this region *Fagus sylvatica* loses its dominance and may be near its physiological limits (Björkman, 1996). This is one potential reason for the need for assistance in expansion. Many of the studies in southern Scandinavia have used small forest hollows (Björkman, 1999; Bradshaw and Lindblad, 2005; Lindblad et al., 2000, 2008). These types of sites with their small pollen source area (sensu Sugita, 1994) permit more spatially precise reconstruction and allow assessment of composition change of individual forest stands (Bradshaw, 2007).

Testing the impact of localized anthropogenic activities at the initial time of expansion, outside of southern Scandinavia, is hampered by a lack of stand-scale records. A recent search by Spangenberg (2008) highlighted that only a few stand-scale sites have been studied in the north German states of Mecklenburg and Brandenburg. Furthermore, studying the linkage between alterations to fire regimes and *Fagus sylvatica* expansion is hampered by a lack of charcoal records in northern central Europe (Robin et al., 2012). The presence of *Fagus sylvatica* and numerous hollows with sediment in the forests of Mecklenburg and Brandenburg make these areas ideally suited for testing ideas relating to the influence of disturbance and the role of fire on the species expansion outside southern Scandinavia.

This paper presents a fossil pollen and charcoal record from a stand-scale site. The data are used to examine the initial colonisation and subsequent expansion of the species *Fagus sylvatica* in northern Central Europe (Figure 1a). The relationship between

competing tree species, anthropogenic indicators, climate, fire and the events in the *Fagus sylvatica* pollen curve are examined. We test the hypothesis that immediately prior to the stand-scale expansion of *Fagus sylvatica*, pollen grains indicating anthropogenic disturbance will be present.

Study area and site

Peutscher forest (Figure 1b) is situated north of the town of Neustrelitz in Mecklenburg-Vorpommern. The forest lies among areas of cultivated land and small villages. The area is within Muritz National Park, where over half the landscape at present is covered by forest, predominantly *Fagus sylvatica* and *Pinus silvestris*. Carlshof small forest hollow (53°25'N 13°04'E, 60 m a.s.l.) (Figure 1c) is surrounded by forest dominated by regenerating *Fagus sylvatica* with some *Quercus*, coexisting next to managed stands of *Picea abies*. One of these *Picea abies* stands is located approximately 300 m from the site, on the slopes that descend towards the basin. The climatic averages for the period 1961 to 1990 (www.dwd.de), show an annual mean temperature of 8°C. Lowest monthly mean temperatures are recorded at -1.1°C in January; highest monthly mean temperature is 16.9°C in July. Mean annual precipitation is ~584 mm.

Material and methods

Sampling and sediment analyses

Sediment from Carlshof small forest hollow was collected using a 100 cm Russian corer (Jowsey, 1966) in September 2007. The

Table 1. Radiocarbon dates from Carlshof small forest hollow.

Depth (cm from the surface)	Lab number	Material dated	Reported ^{14}C age BP	Cal. yr BP min	Cal. yr BP max
115–116	SUERC-28851	Sediment	1026±37	904	1006
167–168	SUERC-28850	Sediment	1215±37	1058	1190
188–189	BETA-261653	Sediment	3690±40	3910	4100
313–314	SUERC-28849	Sediment	2219±37	2150	2332
364–365	LUS-8458	<i>Corylus</i> Nut	2735±50	2756	2929
383–384	SUERC-28848	Sediment	3135±37	3319	3444
450–451	SUERC-28847	Sediment	4044±38	4421	4623
517–518	SUERC-28846	Sediment	5398±36	6176	6289
537–538	BETA-261654	Sediment	5890±40	6635	6797
623–624	SUERC-28845	Sediment	7222±39	7964	8159
671–672	SUERC-28842	Sediment	7566±37	8333	8421
745–746	SUERC-28841	Sediment	7676±40	8403	8544
768–769	SUERC-28840	Sediment	9024±43	10,152	10,252

cores were cleaned to remove any surface contamination caused by a result of the extraction from the sedimentary basin. The cores were then sliced into 1 cm thick segments and stored at 6°C. The section 0–100 cm was damaged in storage and therefore it has no charcoal or loss-on-ignition (LOI) data. The sediment composition was described and samples were taken for pollen analysis before the damage occurred. LOI was carried out on all samples below 100 cm to assess the organic content of the sediment. Each sample was oven dried at 105°C for 12 h to assess moisture content before being heated at 450°C for 4 h to determine the organic matter content.

Preparation of the 66 samples for pollen analyses followed standard methods (Berglund and Ralska-Jasiewiczowa, 1986; Moore et al., 1991) and counts were made at $\times 400$ magnification with some finds checked at $\times 1000$ magnification. The identification key in Moore et al. (1991) and the photographic book Reille (1992) guided the analysis. Differentiation of the Poaceae family into natural and cultivated species follows Andersen (1979). Pollen percentages were expressed as the sum of terrestrial pollen and spores excluding *Sphagnum* and aquatics, although these were counted. Although the pollen grain of the *Fagus sylvatica* is identical to that of *Fagus orientalis*, the present ranges of the two species only overlap in the southern Balkans, therefore *Fagus* pollen found in this study are attributed to *Fagus sylvatica*.

Quantitative charcoal analysis (Mooney and Radford, 2001) was performed on 646 samples below the core depth of 100 cm. Approximately 2 cm³ of sample measured by volumetric displacement was analysed from every sample. The samples were sieved at 250 μm and the retained residue bleached in sodium hypochlorite overnight. The sample was then photographed and the total area of charcoal present (mm²) was analysed using Scion Image (Scion Corporation). Samples containing abundant amounts of charcoal were checked under a binocular microscope using magnification $\times 10$. Charcoal was defined as black objects with angular sides with large pieces appearing crystalline.

Sediment age determination

Thirteen levels from the core were submitted for radiocarbon age determination by accelerator mass spectrometry (AMS). Twelve of the samples were thin sediment samples and one sample was a *Corylus avellana* nut (Table 1). The samples analysed at the SUERC and Beta laboratories were all thin sediment slices. The pre-treatment included hot acid and hot alkali washings to remove humic material and mineral acid. The samples from Beta followed an acid/alkali/acid treatment to remove

carbonate and humic acid. The *Corylus avellana* nut was dated at Lund. All radiocarbon age calibrations and the construction of the age–depth model were carried out using the R code Clam (Blaauw, 2010; R Development core team, 2011) with the IntCal09 calibration curve (Reimer et al., 2009). Smoothing splines were fitted to the calibrated age probabilities by drawing random numbers from the distributions, yielding a best fit and upper and lower probabilities for all sample ages. Ages are given as calendar years before present (cal. yr BP), where present is defined as AD 1950.

Numerical analyses

The pollen diagram was constructed in PSIMPOLL v4.26 (Bennett, 2007) and divided visually into zones corresponding to major changes in the pollen assemblages. To assist in the interpretation of the multidimensional pollen diagram three indices were extracted summarizing different aspects of the data set (Figure 4): The first axis of a principal component analysis (PCA), carried out on the percentage data containing all upland pollen, indicates the major shifts in vegetation composition. A compositional difference was calculated as the squared cord distance between the youngest sample representing the most recent conditions and down-core samples. This measure highlights which periods in the past that were most different from the present and indicates times where the vegetation composition was similar to the present. The rarefaction technique was used to compare palynological richness between samples (Birks and Line, 1992). Palynological richness is influenced by the floristic diversity as well as the equability or evenness in the abundance of different species (Odgaard, 2001) and in particular the number of different pollen types encountered in a low count is indicative of evenness (Giesecke et al., 2012; Odgaard, 2008). Here rarefaction was calculated to a base of 30 counted grains. The charcoal concentration per sample was added up over 100 year periods based on the assignment of ages to the samples. This makes the results of the charcoal analysis visually comparable with the pollen analysis, as it yields the amount of charcoal over 100 year periods. The effect of individual severe fires may thus be masked and the original data plotted beside the pollen diagram (Figure 3) should be consulted here.

Results

Sediment analysis and chronology

The sediment sequence retrieved was 787 cm in length. Pollen analysis combined with radiocarbon dating revealed a complex stratigraphy over the lower 37 cm. Sudden shifts in sediment accumulation and the potential mixing of sediment meant that the timing of vegetation change could not be reconstructed with confidence and the section below the dated level at 746 cm was omitted from further analysis. The AMS determinations (Table 1) are internally consistent except for one reversal at a depth of 188–189 cm (Beta-261653). The age–depth relationship (Figure 2a) indicates a relatively high sedimentation rate. Three phases of differing sediment accumulation rates can be distinguished (Figure 2a). The basin appears to fill quickly prior to 8000 cal. yr BP (620 cm) before filling at a slower rate until ~ 2200 cal. yr BP (310 cm). The youngest section appears to have higher rates of accumulation, similar to the oldest section. The LOI data (Figure 2c) show that the majority of the sediments are mainly organic with values above 90%. Three notable exceptions are recorded. A reduction in LOI values occurs in the period 3200–3100 cal. yr BP (375 cm), associated with high mineral particle content within the sediment matrix. A sharp, but brief, drop also occurs at approximately 2500 cal. yr BP (328–333 cm), associated with a 5 cm thick band of clay (Figure 2b). Finally, at 1600 cal. yr BP (240 cm) another drop in LOI is associated with a switch in sediment type (Figure 2b)

Figure 2. (a) Age–depth model based on the AMS dates (Table 1). (b) Sediment description (1: Woody peat; 2: *Sphagnum* peat; 3: *Substantia humosa* and plant remains; 4: clay with mineral particles; 5: *Substantia humosa* with mineral particles; 6: decomposed *Sphagnum* peat; 7: *Substantia humosa*). (c) LOI data, no samples analysed between 900 cal. yr BP and present.

from *Sphagnum*-dominated peat to more fibrous, woody peat but is not correlated with any palaeoecological events. Between 900 cal. yr BP (100 cm) and present there are no LOI measurements. However there is consistent stratigraphy from ~1800 cal. yr BP to core top. This uniform stratigraphy and consistent pollen concentrations support the age-model throughout. The small peak in *P. abies* pollen during the most recent 100 years of the pollen diagram (Figure 3a) supports the conclusion that the surface sediment is modern.

Vegetation and fire history with interpretation

The pollen diagram from Carlshof small forest hollow (Figure 3a) provides an uninterrupted stand-scale record of vegetation changes between 8600 cal. yr BP and present. The taxa with the most pronounced representation in the pollen sum throughout the sequence are *Pinus*, *Betula*, *Alnus* and *Quercus*. These taxa must have grown close to the hollow during the entire recorded sequence. *Corylus*, *Tilia*, *Carpinus* and *Fagus sylvatica* also have pronounced percentages but only in certain sections of the sequence. The shifting proportions of *Pinus* and *Fagus sylvatica* explain the major variance in the pollen data set as captured by the first PCA axis (Figure 4b). The composition of the pollen diagram from Carlshof suggests that a forest stand with a mixture of species was present throughout the Holocene. Although this site is lacking in macrofossils, its pollen composition, with the exception of *Carpinus*, is comparable with Suserup forest hollow, eastern Denmark (Hannon et al., 2000). The pollen diagram from Suserup is supported by abundant macrofossil finds and combined with Carlshof suggests that diverse forest stands where *Pinus* mixed with a number of deciduous species existed throughout the Holocene.

The charcoal record from this site (Figures 3b and 4a) is high resolution and a number of differing phases of fire regime are shown to exist during the Holocene (Figure 4a). The highest charcoal values are recorded between 5000 and 7000 years ago, but the values are low compared with those reported in Scandinavian hollows, suggesting low-intensity fires (Bradshaw et al., 2010b). In the late Holocene, peaks in charcoal are more sporadic. During

the phase in which *Fagus sylvatica* expands, very little charcoal is recorded.

PAZ C-1 (8600–6400 cal. yr BP). Pollen assemblages in the oldest part of this zone are dominated by *Betula*. A spike in charcoal ~8500 cal. yr BP is recorded before a switch to *Pinus*-dominated pollen assemblages. The high percentages of *Pinus* correlate with a period of relatively little charcoal. This is interrupted at ~7300–7200 cal. yr BP when a peak in charcoal is followed by another small rise in *Pinus* pollen and a small, but sustained, increase in *Tilia* percentages. Throughout this zone, *Alnus*, *Ulmus*, *Quercus*, *Tilia* and *Corylus* exhibit consistent percentages, suggesting relatively stable population sizes. Rarefaction analysis indicates the lowest evenness over the entire sequence, which is a consequence of the dominance of *Pinus* pollen. These assemblages suggest that around the hollow the forest was probably dense, with a closed canopy. Pollen grains of *Fagus sylvatica* are recorded in the lower and upper part of this pollen zone. Low percentages of *Fagus sylvatica* are present in contiguous samples dated to 8600–7900 cal. yr BP. The pollen type is then absent from younger samples in this zone except for a few grains in the uppermost samples.

PAZ C-2 (6400–4700 cal. yr BP). The forest composition is a diverse mixture of *Pinus* and *Betula* forest, mixed with *Alnus*, *Quercus*, *Tilia* and *Ulmus*. The youngest part of this zone is characterized by a large spike in the relative abundance of *Betula* occurring at ~6200 cal. yr BP. This event was brief and occurred during a charcoal minimum. Sediments are consistent and there is no change in LOI values suggesting the slopes around the hollow to be stable despite this vegetation change. *Fagus sylvatica* pollen grains are sporadically recorded also at the beginning of this zone. The major forest type is similar to that of the previous zone (PAZ C-1). *Pinus* dominates but with more fluctuations in its percentage curve, with peaks correlated with periods of high charcoal values. *Corylus* percentages rise slowly throughout, suggesting a more open forest confirmed by an increase in pollen diversity with the recording of more herbs. Low amounts (<1%) of *Plantago lanceolata* are present from 4800 cal. yr BP. This combination of increased *Corylus* and the recording of *Plantago lanceolata* is similar to the findings of Robin et al. (2012) from a site in Schleswig-Holstein, northern Germany, who suggested this signal represented the first moderate human impact on the forest.

PAZ C-3 (4700–3350 cal. yr BP). Compositional analysis (Figure 4c) suggests this zone is the most different from present-day conditions, with the area around the hollow being less forested. The light-demanding *Corylus* dominates and the recording of numerous NAP pollen types suggest an open forest landscape. Similar high *Corylus* percentages found in Denmark have been associated with early coppicing activities (Andersen, 1996). *Fagus sylvatica* becomes continuous in small percentages (<5%) in this zone and *Carpinus* is recorded discontinuously. A peak in charcoal values occurs prior to the maximum abundance of *Corylus* at 3400 cal. yr BP. However overall charcoal values are lower than in older zones coinciding with relatively low *Pinus* percentages.

PAZ C-4 (3350–1300 cal. yr BP). *Tilia* expands in this zone reaching a maximum at 3300 cal. yr BP. A series of short-lived events are recorded (Figure 5). A distinct drop in LOI values coupled with the recording of mineral particles in sediment occur ~3150 cal. yr BP suggesting erosion on the slopes of the hollow, potentially caused by deforestation. This is followed by a sharp peak in *Betula* (~50%) at 3100 cal. yr BP. No charcoal is found in this short period. Although present in small abundances, *Fagus sylvatica* does not expand in the open forest conditions prior to or

Fagus sylvatica pollen percentages rise from ~2% to 50%. A small drop in *Fagus sylvatica* percentages coincides with a charcoal peak. The relatively open landscape of the previous zone changes to a more closed forest in which *Fagus sylvatica* dominates. The composition of the forest moves towards a stand similar to present between 3000 and 2500 cal. yr BP. During this phase there are relatively high percentages of *Pinus* and *Betula*. *Carpinus* becomes continuous whereas *Tilia* percentages, NAP percentages and pollen diversity fall in value. A significant drop in LOI and switch to clay and mineral sediment (2500–2400 cal. yr BP) dates to a period of wetter climate identified by Van Geel et al. (1996), but does not appear to affect pollen assemblages. However, such a wet shift could have benefitted the continued expansion of *Fagus sylvatica*. The youngest part of the zone is characterized by the dominance of *Fagus sylvatica* (~50%) which

occurs after a prolonged period where charcoal is not recorded in the sediment.

PAZ C-5 (1300 cal. yr BP–present). Between 1200 cal. yr BP and present the *Fagus sylvatica* pollen curve declines from its maximum percentages (~50%), but is still a dominant component of the pollen assemblage and therefore the forest around the site. The decline coincides with a phase of high charcoal values. This decline also coincides with an increase in NAP and notable anthropogenic indicators. The presence of *Avena/Triticum*, *Centaurea*, *Hordeum* and *Humulus*-type suggests that cereals were being grown close to the site. However, the major change is an increase in *Betula* and *Pinus*, suggesting the other tree species (most notably *Tilia*) were being removed from the area. Preceding a large peak in *Betula* at 700 cal. yr BP, *Quercus* values rise for a sustained, 450 year period. *Quercus* is useful in shipbuilding and may have been selectively grown in the forest. Around 150 cal. yr BP there is a sharp rise in the percentages of *Fagus sylvatica*. Today it is a co-dominant in the forest around Carlshof small forest hollow.

Discussion

Stand-scale expansion of *Fagus sylvatica*

Fagus sylvatica began its expansion in the forest stand, close to the basin, around 2900 cal. yr BP (Figure 5), corresponding to the Bronze Age. This is comparable with a *Fagus sylvatica* mass expansion occurring ~2750 cal. yr BP, at Löddigsee, a regional site, ~80 km west of Carlshof (Jahns, 2007). The data set from Carlshof suggests that anthropogenic disturbance is required for the species to expand. Immediately prior to expansion, a series of short-lived events that indicate significant levels of disturbance in the area immediately around the basin are recorded (Figure 5). A distinct drop in LOI values coupled with the recording of mineral particles in sediment occur ~3150 cal. yr BP suggesting pronounced anthropogenic activity that triggered erosion on the slopes of the hollow. Contemporaneous with the erosion is a shift in vegetation composition, characterized by the decline in *Corylus*, *Ulmus* and *Tilia* and marked by the peak in *Betula*. The NAP percentages only rise to a peak in the next sample, which also shows a first rise in *Fagus sylvatica* pollen. Declining NAP percentages together with the decline of taxa indicating human land

Figure 4. (a) Charcoal averages collated in 100 year periods, *Fagus* and *Pinus* percentage pollen curves; (b) principal component analysis axis one; (c) composition difference and (d) rarefaction analysis of 30 pollen grains.

Figure 5. Time series of major events in Carlshof small forest hollow record: (a) PAZ zones; (b) LOI record; (c) NAP percentage curve; and (d–e) key pollen percentage curves for key taxa.

use (e.g. *Chenopodiaceae*, *Apiaceae* and *Plantago lanceolata*) suggest that the strength of anthropogenic activity declined. During this period of reduced land use *Fagus sylvatica* pollen percentages continually rise from ~2% to 50% potentially preventing the regeneration of *Tilia* during the woodland recovery phase (Behre, 1988). In Denmark, the colonization of abandoned field systems by *Fagus sylvatica* is also highlighted by Odgaard (1994). The data from Carlshof also suggest that a threshold needs to be crossed in the amount of disturbance before populations of *Fagus sylvatica* start to expand. It is however also conceivable that co-occurring climate conditions have to be adequate. In this context it is important to note that the *Fagus sylvatica* population did not expand earlier, for example around 4800 cal. yr BP, when the occurrence of *Plantago lanceolata* demonstrates human activity, or during subsequent peaks of *Betula* or *Corylus* indicating open forest conditions, that were likely caused by human management.

At the subcontinental scale, Ralska-Jasiewiczowa et al. (2003) highlight climatic change to wetter-cooler conditions to be an important factor in the expansion of *Fagus sylvatica* in northern central Europe, coupled with anthropogenic activities. The data from Carlshof suggest that the continued expansion, after colonization of abandoned land around the hollow, could have been catalysed by a switch to wetter/cooler conditions ~2650 cal. yr BP (Van Geel et al., 1996). This climatic event is recorded at the hollow with a dramatic rise in the number of *Sphagnum* spores and *Potamogeton* pollen grains and a brief switch to clay sedimentation, indicating standing water, which ends around 2400 cal. yr BP. Also, the expansion phase coincides with lower amounts of charcoal being present in the sediment (Figure 4a), indicating a less severe fire regime. *Fagus sylvatica* is considered to be disadvantaged by fire (Tinner et al., 1999), although pollen/charcoal records from southern Scandinavia suggest initial local establishment is assisted by fire (Björkman and Bradshaw, 1996; Bradshaw and Lindbladh, 2005). The record from Carlshof indicates that the presence of a more conducive, less severe, fire regime may aid expansion.

The initial hypothesis that the stand-scale expansion of *Fagus sylvatica* is facilitated by anthropogenic disturbance is accepted. However, the record from Carlshof small forest hollow cannot disprove that other factors, notably a switch to wetter-cooler climate conditions and a suitable fire regime potentially helped catalyse the species expansion in Peutscher forest. However, this study suggests that these two factors are unlikely to be the primary controls on the expansion as wetter-cooler conditions and low charcoal values are also present in the period 3700–3400 cal. yr BP and *Fagus sylvatica* does not expand despite being present in the region (Jahns, 2007) and close to the hollow, albeit in small numbers (Figure 3). During this period the forest stand is dominated by *Corylus* shrubbery indicating a relative open forest in which *Fagus sylvatica* should be able to colonize easily (Ralska-Jasiewiczowa et al., 2003). Instead, *Tilia* appears to take advantage of the more open forest and expands reaching a maximum at 3300 cal. yr BP (Figure 5).

Corroboration using other hollows in the region would allow testing of the findings from this study and test if the species needs specific climate conditions, after initial expansion begins, or expands in a more sporadic way, similar to southern Scandinavia (Bialozyt et al., 2012; Bradshaw and Lindbladh 2005).

Early outpost of *Fagus sylvatica*?

Between 9000 and 7950 cal. yr BP, nine contiguous samples record *Fagus sylvatica* pollen grains (Figure 3a). The chronology of these samples is constrained by three AMS dates of thin sediment slices. The presence of *Fagus sylvatica* is contrary to data from regional pollen diagrams which suggest that *Fagus sylvatica* was not present in northern central Europe in the early Holocene

(Küster, 1997). Jahns (2007) noted one find of *Fagus sylvatica* at ~9150 cal. yr BP and other sporadic finds at ~7800 cal. yr BP at Löddigsee, to the west of Carlshof. Recorded percentages are low (0.2–2%) and the data presented from Carlshof could be interpreted either as pollen from a small outpost population close to the hollow, pollen of long-distance origin or contamination of pollen grains of a younger age caused by the Russian corer carrying younger sediments downwards. The site type is stand-scale and therefore receives the majority of its pollen grains from trees surrounding the hollow (Sugita, 1994), making these types of sites less susceptible to pollen of non-local origin (Bradshaw, 2007). The observation that the *Fagus sylvatica* pollen curve is continuous in this period argues against this being chance long-distance pollen. Contamination, via the introduction of younger sediment, in the coring process is theoretically possible, although these samples are spread across two separate cores and *Fagus sylvatica* is not recorded in other sections of these two cores which would be expected with contamination. During preparation the core edges were removed and sampling took place from the middle of the remaining sediment.

The hollow is situated close to non-wetland habitats favoured by *Fagus sylvatica*, meaning any trees present could be very close to or overhang this hollow. This scenario would mean only a very few *Fagus sylvatica* trees would need to be present to be detected at this small site and these would not be detected at the regional scale. Bennett (1988) and Woods and Davis (1989) discussed the possibility of small populations existing on a landscape, long before larger pollen sites can detect them and McLachlan et al. (2005) provided evidence for this scenario using a genetic marker study. In respect of *Fagus sylvatica*, two other recent sites also show early populations, long before regional pollen data suggested the main population migrated into the area. Bradshaw et al. (2010a) cited the finding of a 9000 year old Danish population whilst Grant (2005) discussed the discovery of an 8500 year old English population. Conclusive proof using replicate cores and other palaeoecological proxies is required for this early population hypothesis to be accepted or rejected at this site. If this record is corroborated, this finding, combined with the results of Grant (2005) and Bradshaw et al. (2010a), would mean assumed migration rates and pattern of spread for the species would need revision.

Conclusion

Fagus sylvatica expands its population size in the forest stand around 2900 cal. yr BP, after a ~3300 year period of low abundance in the forest. This expansion is facilitated by a clearance event, which opened up the area around the hollow and reduced the amount of *Tilia* in the forest. This disturbance is significant enough to cause erosion of slopes around the hollow. In older sections of this site, other periods of relatively open forested conditions are present but *Fagus sylvatica*, despite being present, did not expand. This suggests that a threshold of disturbance is required for the species to take advantage of the conditions and expand its population size. The charcoal record suggests that fires were much less frequent after ~2500 cal. yr BP. This also appears to benefit the expansion of *Fagus sylvatica*. In historical times, *Fagus sylvatica* appears disadvantaged by anthropogenic activities, mainly farming and clearance, in the area. The decline of *Fagus sylvatica* coincides with a period of fire activity. These findings suggest that there is strong anthropogenic control on the species dynamics, at least at the stand-scale in northern Central Europe. The site also provides tentative evidence that a small population of *Fagus sylvatica* existed around the hollow, long before regional pollen data suggest it should be present. If corroborated, this finding adds to the growing volume of evidence that the species had a number of outlying populations away from the main migrating front and has important consequences for the

interpretation of how the species spread across the continent of Europe in the Holocene.

Acknowledgements

Sandra Mather is thanked for cartographic assistance. We are grateful for the constructive criticism of two anonymous reviewers.

Funding

Financial support from the EU Network of Excellence EVOL-TREE and NERC is gratefully acknowledged.

References

- Andersen ST (1979) Identification of wild grass and cereal pollen. *Danmarks Geologiske Undersøgelse*, pp. 69–92.
- Andersen ST (1996) Pollen analyses from early Bronze Age Barrowa in Thy. *Journal of Danish Archaeology* 13: 7–17.
- Behre KE (1988) The role of man in European vegetation history. In: Huntley B and Webb T III (eds) *Vegetation History*. Kluwer Academic Publishers, pp. 633–672.
- Bennett KD (1988) Holocene geographic spread and population expansion of *Fagus grandifolia* in Ontario, Canada. *Journal of Ecology* 76: 547–557.
- Bennett KD (2007) Psimpoll 4.26: C program for plotting pollen diagrams and analysing pollen data. <http://www.chrono.qub.ac.uk/psimpoll/psimpoll.html>.
- Berglund BE and Ralska-Jasiewiczowa M (1986) Pollen analysis and pollen diagrams. In: Berglund BE (ed.) *Handbook of Holocene Palaeoecology and Palaeohydrology*. Chichester: John Wiley, pp. 455–484.
- Bialozyt R, Bradley LR and Bradshaw RHW (2012) Modelling the spread of *Fagus sylvatica* and *Picea abies* in southern Scandinavia during the late Holocene. *Journal of Biogeography* 39: 665–675.
- Birks HJB and Line JM (1992) The use of rarefaction analysis for estimating palynological richness from Quaternary pollen-analytical data. *The Holocene* 2: 1–10.
- Björkman L (1996) Long-term population dynamics of *Fagus sylvatica* at the northern limits of its distribution in southern Sweden: A palaeoecological study. *The Holocene* 6: 225–234.
- Björkman L (1999) The establishment of *Fagus sylvatica* at the stand-scale in southern Sweden. *The Holocene* 9: 237–245.
- Björkman L and Bradshaw R (1996) The immigration of *Fagus sylvatica* L. and *Picea abies* (L.) Karst. into a natural forest stand in southern Sweden during the last 2000 years. *Journal of Biogeography* 23: 235–244.
- Blaauw M (2010) Methods and code for 'classical' age-modelling of radiocarbon sequences. *Quaternary Geochronology* DOI 10.1016/j.quageo.2010.01.002.
- Bohn U, Gollub G and Hettwer C (2000) *Karte der natürlichen Vegetation Europas*. Bonn: Bundesamt für Naturschutz.
- Bradshaw RHW (2007) Stand-scale palynology. In: Elias SA (ed.) *Encyclopaedia of Quaternary Science*. Amsterdam: Elsevier.
- Bradshaw RHW and Lindbladh M (2005) Regional spread and stand-scale establishment of *Fagus sylvatica* and *Picea abies* in Scandinavia. *Ecology* 86: 1679–1686.
- Bradshaw RHW, Kito N and Giesecke T (2010a) Factors influencing the Holocene history of *Fagus*. *Forest Ecology and Management* 259: 2204–2212.
- Bradshaw RHW, Lindbladh M and Hannon G (2010b) The role of fire in southern Scandinavian forests during the late Holocene. *International Journal of Wildland Fire* 19: 1040–1049.
- Brande A (2003) Late Pleistocene and Holocene pollen stratigraphy of Lake Stechlin. *Advances in Limnology* 58: 281–311.
- Ellenberg H (1996) *Vegetation Mitteleuropas mit den Alpen*. Stuttgart: Ulmer.
- Gardner AR and Willis KJ (1999) Prehistoric farming and the postglacial expansion of beech and hornbeam: A comment on Küster. *The Holocene* 9: 119–122.
- Giesecke T, Hickler T, Kunkel T et al. (2007) Towards an understanding of the Holocene distribution of *Fagus sylvatica* L. *Journal of Biogeography* 34: 118–131.
- Giesecke T, Wolters S, Jahns S et al. (2012) Exploring Holocene changes in palynological richness in northern Europe – Did postglacial immigration matter? *PLoS ONE* 7(12): e51624. doi: 10.1371/journal.pone.0051624.
- Grant MJ (2005) *The palaeoecology of human impact in the New Forest*. University of Southampton: Unpublished Ph.D dissertation.
- Hannon GE, Bradshaw R and Emborg J (2000) 6000 years of forest dynamics in Suserup Skov, a seminatural Danish woodland. *Global Ecology and Biogeography* 9: 101–114.
- Huntley B and Birks HJB (1983) *An Atlas of Past and Present Pollen Maps for Europe 0–13,000 Years Ago*. Cambridge: Cambridge University Press.
- Jahns S (2000) Late-glacial and Holocene woodland dynamics and land-use history of the Lower Oder valley, north-eastern Germany, based on two, AMS ¹⁴C-dated, pollen profiles. *Vegetation History and Archaeobotany* 9: 111–123.
- Jahns S (2001) On the Late Pleistocene and Holocene history of vegetation and human impact in the Ücker valley, north-eastern Germany. *Vegetation History and Archaeobotany* 10: 97–104.
- Jahns S (2007) Palynological investigations into the Late Pleistocene and Holocene history of vegetation and settlement at the Löddigsee, Mecklenburg, Germany. *Vegetation History and Archaeobotany* 16: 157–169.
- Jalas J and Suominen J (1972–1999) *Atlas Florae Europaeae: Distribution of Vascular Plants in Europe*. Helsinki: The Committee for Mapping Europe and Societas biologica Fennica Vanamo.
- Jowsey PC (1966) An improved peat sampler. *New Phytologist* 65: 245–248.
- Küster H (1997) The role of farming in the postglacial expansion of beech and hornbeam in the oak woodlands of central Europe. *The Holocene* 7: 239–242.
- Lindbladh M, Bradshaw R and Holmqvist BH (2000) Pattern and process in south Swedish forests during the last 3000 years, sensed at stand and regional scales. *Journal of Ecology* 88: 113–128.
- Lindbladh M, Niklasson M, Karlsson M et al. (2008) Close anthropogenic control of *Fagus sylvatica* establishment and expansion in a Swedish protected landscape – Implications for forest history and conservation. *Journal of Biogeography* 35: 682–697.
- Magri D, Vendramin GG, Comps B et al. (2006) A new scenario for the Quaternary history of European beech populations: Palaeobotanical evidence and genetic consequences. *New Phytologist* 171: 199–221.
- McLachlan JS, Clark JS and Manos PS (2005) Molecular indicators of tree migration capacity under rapid climate change. *Ecology* 86: 2088–2098.
- Mooney SD and Radford K (2001) A simple and fast method for the quantification of macroscopic charcoal from sediments. *Quaternary Australasia* 19: 43–46.
- Moore PD, Webb JA and Collinson ME (1991) *Pollen Analysis*. London: Blackwell Science.
- Odgaard BV (1994) The Holocene vegetation history of northern West Jutland, Denmark. *Opera Botanica* 123: 1–171.
- Odgaard BV (2001) Palaeoecological perspectives on pattern and process in plant diversity and distribution adjustments: A comment on recent developments. *Diversity and Distributions* 7: 197–201.
- Odgaard BV (2008) Does pollen type diversity reflect vegetation diversity? *IPC-XII / IOPC – VIII Abstract Volume, Terra Nostra* 2: 209.
- R Development Core Team (2011) *R: A Language and Environment for Statistical Computing*. Vienna.
- Ralska-Jasiewiczowa M, Nalepka D and Goslar T (2003) Some problems of forest transformation at the transition to the oligocentric/*Homo sapiens* phase of the Holocene interglacial in northern lowlands of central Europe. *Vegetation History Archaeobotany* 12: 233–247.
- Reille M (1992) *Pollen et spores d'Europe et d'Afrique du Nord*. Marseille.
- Reimer PJ, Baillie MGL, Bard E et al. (2009) IntCal09 and Marine09 radiocarbon age calibration curves, 0–50,000 years cal BP. *Radiocarbon* 51: 1111–1150.
- Robin V, Rickert BH, Nadeau MJ et al. (2012) Assessing Holocene vegetation and fire history by a multiproxy approach: The case of Strothagen Forest (northern Germany). *The Holocene* 22: 337–346.
- Spangenberg A (2008) *2000 Jahre Waldentwicklung auf nährstoff- und basenreichen Standorten im mitteleuropäischen Jungpleistozän – Fallstudie Naturschutzgebiet Eldena (Vorpommern, Deutschland)*. Ph.D dissertation, University of Greifswald.
- Sugita S (1994) Pollen representation of vegetation in Quaternary sediments: Theory and method in patchy vegetation. *Journal of Ecology* 82: 881–897.
- Tinner W and Lotter AF (2006) Holocene expansions of *Fagus sylvatica* and *Abies alba* in Central Europe: Where are we after eight decades of debate? *Quaternary Science Reviews* 25: 526–549.
- Tinner W, Hubschmid P, Wehrli M et al. (1999) Long-term forest fire ecology and dynamics in southern Switzerland. *Journal of Ecology* 87: 273–289.
- Valsecchi V, Finsinger W, Tinner W et al. (2008) Testing the influence of climate, human impact and fire on the Holocene population expansion of *Fagus sylvatica* in the southern Prealps (Italy). *The Holocene* 18: 603–614.
- van Geel B, Buurmann J and Waterbolk HT (1996) Archaeological and palaeoecological indications of an abrupt climate change in The Netherlands and evidence for climatological teleconnections around 2650 BP. *Journal of Quaternary Science* 11: 451–460.
- Wolters S (1999) Spät- und postglaziale Vegetationsentwicklung im Bereich der Fercher Berge südwestlich von Potsdam. *Gleditschia* 27: 25–44.
- Woods KD and Davis MB (1989) Paleocology of range limits: Beech in the upper peninsula of Michigan. *Ecology* 70: 681–696.