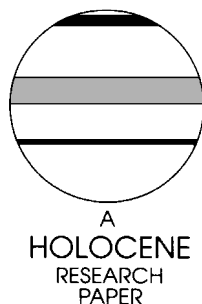


Pinus and *Prostomis*: a dendro-chronological and palaeoentomological study of a mid-Holocene woodland in eastern England

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Abstract: Tree-ring analysis of subfossil *Pinus sylvestris* L. and *Quercus* sp. and their associated subfossil insect assemblages from tree rot-holes have been used to study a prehistoric forest buried in the basal peats at Tyrham Hall Quarry, Hatfield Moors SSSI, in the Humberhead Levels, eastern England. The site provided a rare opportunity to examine the date, composition, age structure and entomological biodiversity of a mid-Holocene *Pinus*-dominated forest. The combined approaches of dendrochronology and palaeoentomology have enabled a detailed picture of the forest to be reconstructed, within a precise time-frame. The *Pinus* chronology has been precisely dated to 2921–2445 BC against the English *Quercus* master curve and represents the first English *Pinus* chronology to be dendrochronologically dated. A suite of important xylophilous (wood-loving) beetles that are today very rare and four species that no longer live within the British Isles were also recovered, their disappearance associated with the decline in woodland habitats as well as possible climatic change. The subfossil insects indicate that the characteristic species of the site's modern-day fauna were already in place 4000 years ago. These findings have important implications in terms of maintaining long-term invertebrate biodiversity of forest and mire sites.

Key words: Dendrochronology, palaeoentomology, *Pinus*, *Quercus*, subfossil insects, Holocene, Humberhead Peatlands, Hatfield Moors, eastern England.

Introduction

The abundance of *Quercus petraea* L./*Quercus robur* L. (sessile oak/pendunculate oak, collectively *Quercus*) and *Pinus sylvestris* L. (Scots pine, hereafter referred to as *Pinus*) macrofossils, preserved in lowland raised mires in Great Britain and Ireland, indicate that both species, but particularly *Pinus*, were formerly significant components of raised-mire habitats (Pilcher, 1990; Pilcher *et al.*, 1995). Across much of Europe, Scandinavia and Eurasia, *Pinus* is a common tree species, occupying a wide range of different habitats, from dry, well-drained soils, to wet, acidic mires (Rodwell and Cooper, 1995). In Great Britain, the current natural range of *Pinus* is largely restricted to the Scottish Highlands, although isolated patches occur in some areas of lowland heath. *Pinus* was abundant during the early Holocene, being present widely but locally in southern England 9000 years ago, spreading northwards between 9000 and 8500 years ago (Birks, 1989) and

reaching its most extensive distribution between 7500 and 4400 years ago (Bennett, 1995). However, around 4400 cal. BP, *Pinus* appears to have undergone a sudden and widespread decline (Bennett, 1984; 1995; Bridge *et al.*, 1990; Gear and Huntley, 1991). The most widespread view is that the decline was caused by a shift to cooler and wetter climatic conditions, promoting the expansion of peat to the detriment of *Pinus* (Bennett, 1984; Gear and Huntley, 1991; Anderson *et al.*, 1998; Lageard *et al.*, 1999). Trees growing in marginal locations may have been particularly vulnerable to short-term acidification, or increased soil moisture, particularly if they were already stressed by a longer-term climatic change (Blackford *et al.*, 1992; but see Hall *et al.*, 1994). Bradshaw (1993) notes that a decreased occurrence of wildfire, in response to possible climatic change, may have been a contributory factor in the decline of populations.

Quercus is also found widely in Europe and Great Britain. By 5000 years ago, *Quercus* woodland extended into the far north of Scotland and was widely distributed elsewhere (Bennett, 1989; Pilcher, 1990), retaining a significant presence to the present day.

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Quercus woodland grows predominantly on poor, infertile and acidic soils (Bennett, 1989). The recovery of numerous subfossil remains from fen-peat in England and Ireland indicates that this species was a component of fen woodlands, sometimes preceding or overlapping with the development of raised mire, and colonization of acidic peat by *Pinus* (Godwin and Deacon, 1974; Pilcher, 1990; Lageard and Chambers, 1993).

In this paper we present the combined results of a palaeontological and dendrochronological investigation of a recently exposed subfossil forest from Hatfield Moors, in the Humberhead Levels, eastern England. The forest consisted predominantly of *Pinus*, interspersed with *Betula* and isolated *Quercus* remains. The main focus of the investigation concentrated on the numerous *Pinus* remains and their associated insect faunas, as *Quercus* remains formed only a very minor component of the fossil forest, with just one tree providing material suitable for dendrochronological dating and fossil insect analysis. Dendrochronology was applied to date precisely the span of the *Pinus* woodland, in addition to providing information on its history and dynamics (Boswijk, 1998). The suitability of this species for tree-ring analysis has been demonstrated by the construction of long *Pinus* chronologies in Europe (Zetterberg *et al.*, 1996) and robust site chronologies from raised bogs in Great Britain (Chambers *et al.*, 1997; Boswijk, 1998; 2002; Lageard *et al.*, 1999) and Ireland (McNally and Doyle, 1984; Pilcher *et al.*, 1995). The primary aim of the subfossil insect study was to characterize the faunal biodiversity of undisturbed *Pinus* woodland, and to examine the site's development from a palaeontological perspective and its wider implications (Whitehouse, 1998).

These two palaeoenvironmental studies, when combined, characterized the biodiversity of undisturbed primary woodland within a defined period. Other palaeoenvironmental evidence from Hatfield Moors (cf. pollen and plant macrofossil studies carried out by Smith, 1985) was also considered in the investigation. Abundant charcoal was recovered from the peat samples, and surface-charred trees were observed, but consideration of the role of fire in the early mire landscape has been addressed elsewhere (Whitehouse, 2000). The project formed part of a wider palaeoenvironmental investigation of Thorne and Hatfield Moors Sites of Special Scientific Interest (SSSI) (Boswijk, 1998; Whitehouse, 1998) and their surrounding floodplains (Whitehouse, 1998).

The Humberhead Peatlands

Thorne and Hatfield Moors are two adjacent, but distinct, raised mires within the Humberhead Levels, an extensive area of former wetlands in south Yorkshire and Lincolnshire (Figure 1), where peat extraction during the mid-1990s uncovered substantial areas of subfossil *Quercus* and *Pinus*. The Moors have formed important foci for palaeoenvironmental research, with much previous work largely concentrating on Thorne Moors (cf. Erdtman, 1928; Smith, 1958; Buckland and Kenward, 1973; Buckland, 1979; Smith, 1985; 2002; Roper, 1993; 1996; Whitehouse, 1993; 1997a; Dinnin, 1997; Boswijk, 1998; 2002). Here, recent dendrochronological analyses of *Pinus* showed that the spatial and temporal pattern of *Pinus* colonization correlated with the expansion and contraction of the mire (Boswijk, 1998; 2002).

Subfossil insect analysis of material from the basal deposits of Thorne Moors has identified 20 beetles (Coleoptera) that are now extinct in Great Britain (Buckland and Kenward, 1973; Buckland, 1979; Roper, 1996; Whitehouse, 1997a; 1977b; 1998). Less research has, however, been carried out on Hatfield Moors (Figure 2). On this site, south of Thorne Moors, peat had formed directly over gently undulating windblown sands (Smith, 1985; 2002). These were initially deposited during the Younger Dryas, although some reworking may have occurred during the Holocene

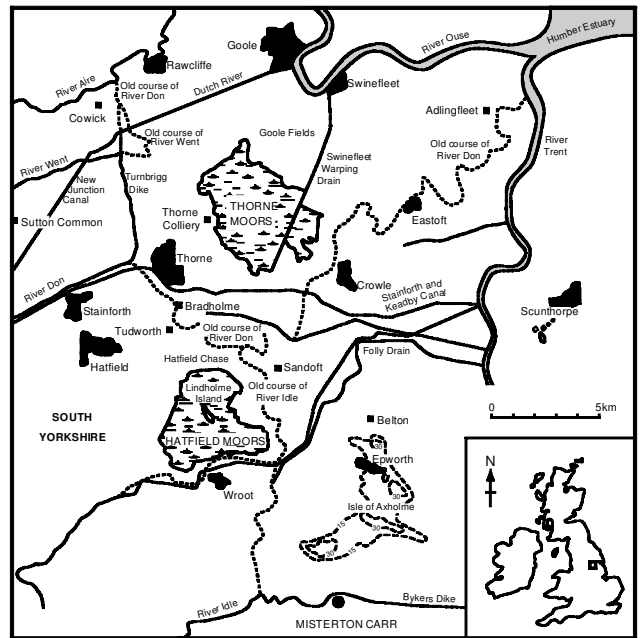


Figure 1 Location map of Hatfield Moors and the Humberhead Levels, eastern England (after an original by P.I. Buckland, ©Thorne and Hatfield Moors Conservation Forum). Hatfield Moors: NGR: SE 700060, lat. 53° 44'N, long. -0° 57'W. Thorne Moors: NGR: SE 730160, lat. 53° 32'N, long. -0° 57'W.

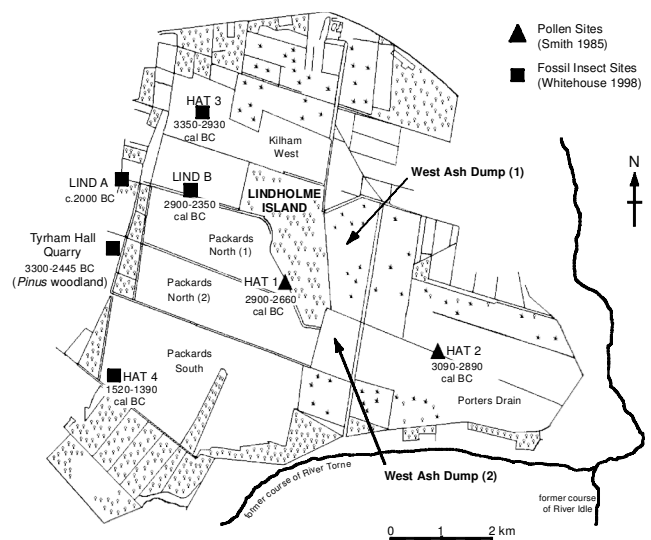


Figure 2 Map of Hatfield Moor, with study sites and basal peat initiation dates (reprinted from Whitehouse *et al.*, 2001, Figure 58).

(Gaunt, 1994; Bateman, 1995; Bateman *et al.*, 2000). The sands overlie the late Devensian lacustrine clay-silts of proglacial Lake Humber (Gaunt, 1994). In places, sand dunes protrude through the milled peat. A late-Devensian end-moraine outcrops in the centre of the site, on Lindholme Island (Gaunt, 1994). The Moor is bounded on the north, east and south by alluvium associated with the former courses of the Rivers Don, Idle and Torne.

On Hatfield Moor, where peat depth is greater than at Thorne Moors, *Pinus* trees were observed on parts of the milled bog, their stunted size and shape suggestive of growth on wet mire. However, Tyrham Hall Quarry, on the western edges of the moor, was different. Here, an area of basal peats had been exposed prior to sand and gravel extraction, revealing numerous *Pinus* stumps and trunks of a size indicative of mature woodland (*Urwald*). The trees were no longer *in situ*, making determination of the phases of woodland development impossible on stratigraphic grounds alone.

Many of the trees were rooted into the underlying sands, indicating that they represented either a pre-peat forest or one that belonged to the very early stages of mire development. In addition, it was unclear whether the trees represented a single phase of *Pinus* growth, or several successive episodes of growth and decline, similar to the pattern observed at Thorne Moors (Boswijk, 1998; 2002). Peat formation began at about the same time on both mires (around 3000 cal. BC), but a detailed palaeoenvironmental study by Smith (1985; 2002) and more recently by Whitehouse (1998) suggested that the developmental history of the sites was different.

Dendrochronology

Methodology

Cross-sections were taken from the lower trunks of 25 *Pinus* and a single *Quercus* (THQ01-26) that were in a 100 × 100 m area of the quarry that was being cleared of peat. The samples were air-dried and then sanded using progressively finer sandpaper to reveal the ring sequence clearly. All the samples had over 50 rings, which is the minimum number of rings required to determine whether a ring sequence is unique (Baillie, 1982).

Baillie (1982) describes the principles and methodology of dendrochronology. The ring sequences were measured to an accuracy of 0.01 mm using a binocular microscope and a travelling stage. An input program, part of the Dendro for Windows suite (Tyers, 1999), recorded ring-widths. *Quercus* has a consistent growth pattern and the measurement of a single radius is considered representative of the ring sequence (Baillie, 1982). For *Pinus*, a minimum of three radii per cross-section were measured, allowing potential problems, such as locally absent rings, to be identified and a reliable mean ring sequence to be produced for each *Pinus* sample (Pilcher *et al.*, 1995; Zetterberg *et al.*, 1996). The CROS programs (Baillie and Pilcher, 1973; Munro, 1984) were used to aid cross-matching. The CROS programs measure the correlation coefficient between samples at every position of overlap, which are expressed statistically as a Student's *t*-value. For *Quercus*, a *t*-value of 3.5 and over is usually indicative that one sample matches another, providing the visual match is acceptable (Baillie, 1982). For *Pinus*, statistical testing of *Pinus* data by Pilcher *et al.* (1995) indicates that *t*-values of 4 or greater may be significant. At all stages, the suggested matches were visually checked using plotted graphs of the ring sequences. Table 1 lists details of the *Quercus* and *Pinus* samples.

Results

The *Quercus* sample cross-matched with *Quercus* from Thorne Moors and was dated to 3618–3418 BC by comparison with English prehistoric *Quercus* chronologies (Whitehouse *et al.*, 1997; Boswijk, 1998). The outer surface of the tree, as well as the pith, had rotted and the absence of bark edge means that the actual death-date is unknown, but the addition of the minimum number of sapwood rings expected to be present (Hillam *et al.*, 1987) provides a *terminus post quem* of 3408 BC. The contemporary *Quercus* woodland at Thorne Moors continued growing until 3017 BC, but little is known about the extent of *Quercus* woodland at Hatfield Moor, or its spatial and temporal relationship with the *Pinus* woodland.

A 21-tree *Pinus* chronology (PISY/Hatfield) was established (Tables 1 and 2). Four samples could not be cross-matched due to unresolvable problems within the ring sequences caused by very narrow bands of rings or multiple missing rings. The undated samples included a tree from which a rot-hole sample (K) for insect remains was collected.

The chronology cross-matched with a floating *Pinus* chronology from Thorne Moors (PISY/Thorne; Boswijk, 1998; 2002),

but the absolute dating of PISY/Hatfield was dependent on inter-species cross-matching against the English prehistoric *Quercus* master curve (Hillam *et al.*, 1990; Brown and Baillie, 1992). The dating of *Pinus* against *Quercus* chronologies has been shown to be successful in Ireland (Pilcher *et al.*, 1995) and proved to be equally successful in England, as the chronology was dated precisely to 2921–2445 BC (Table 3). PISY/Hatfield was also found to be contemporary with a phase of *Pinus* from Garry Bog, Co. Antrim, Ireland (Pilcher *et al.*, 1995), and White Moss, Cheshire, England (Chambers *et al.*, 1997; Lageard *et al.*, 1999). During tree-ring analysis, consideration was given to the possibility that the *Pinus* could contain a strong site-specific growth pattern that may have overridden the common climate signal on which cross-dating is dependent (Baillie, 1982), inhibiting cross-matching between the *Quercus* and *Pinus* chronologies. Radiocarbon dates were obtained from two *Pinus* samples, THQ21 (4125 ± 45 BP, SRR-5829) and THQ23 (4105 ± 45 BP, SRR-5834). These trees were included in PISY/Hatfield and were dated absolutely by dendrochronological cross-matching.

The chronology PISY/Hatfield spans 477 years (Figure 3). Between 2921 and 2610 BC three cohorts of *Pinus* were established. Almost half the trees, however, have start dates within a 35-year period between 2921 and 2887 BC, indicating that conditions were optimal at this time to support the germination and growth of new recruits. The length of ring sequences ranged from 73 years to over 336 years. While the steady rate of die-back over 400 years is probably indicative of natural woodland mortality, the pattern of end and start dates suggests that stress events may also have contributed to the death of some trees, creating suitable gaps in which seedlings could be established.

Stress events can be indicated by narrow ring phases, which occur when growth is restricted, perhaps as a result of changes in the local or immediate environments, or by events specific to individual trees. The years 2857–5 BC stand out as indicating a significant event which appears to have affected the growth of several trees (Figure 4). The sampled trees show a rapid decline in ring-width at this time, with some *Pinus* producing locally absent rings for these years. While most recover, the growth of at least two trees was irrevocably altered. Sample THQ07 died within a decade, while the ring sequence for THQ11 (unmeasurable after 2865 BC) became extremely narrow, although the tree continued to grow until at least 2812 BC. This sample displayed lobate growth, the initiation of which coincides with an earlier narrow band at 2905 BC, suggesting that the tree had slumped and was growing at an angle. The combination of narrow rings on many of the samples and the occurrence of lobate growth on some trees suggests that, temporarily at least, the area was very wet and the underlying substrate unstable.

Subfossil insect fauna

Methodology

Six contexts were bulk-sampled for subfossil insect analysis. Five samples were collected from *Pinus* rot-holes and one from a *Quercus* rot-hole. The extraction of subfossil Coleoptera followed the paraffin flotation technique devised by Coope and Osborne (1968). Identification of insect subfossil material was carried out through the use of standard British and other European entomological keys and by direct comparison with modern material. Only Coleoptera (beetles) were identified.

Much of the rot-hole material was in exceptional condition, with many of the subfossil insects still articulated, suggesting a largely *in situ* death population, particularly those invertebrates associated with wood. However, there was also an allochthonous element to the faunas, such as the water beetles, which presumably became incorporated into the rot-holes when the dead trees

Table 1 Details of the dated oak and pine samples from Tyrham Hall Quarry

Sample	Dimensions (mm)	No. of rings	Pith	Bark	AGR	Date span (BC)	End dates (BC)	Comments
<i>Quercus</i>								
25	577 × 350	201	–	–	1.49	3618–3418	3408+	pith and outer rotted
<i>Pinus</i>								
01	300 × 235	181	+C	–	0.95	2901–2721		
02	197 × 170	55	+C	–	1.72	–		
03	177 × 155	58	+C	–	1.52	–		
04	440 × 305	177	+C	+B	1.58	2916–2740		
05	265 × 252	95	+C	+B	1.45	2901–2807		lobate
06	360 × 275	129	+C	+B	1.29	2610–2482		
07	269 × 234	73	+C	+B	2.36	2921–2849		
08	369 × 306	192	+C	+B	1.14	2889–2708		
09	292 × 285	120 +93h	+C	+B	1.28	2907–2788	2715	lobate
10	353 × 285	144 +54h	+C	–	1.02	2787–2644	2590+	
11	245 × 205	53 +53h	+C	–	1.77	2917–2865	2812+	lobate
12	226 × 195	195	+C	–	0.57	–		insect rot-hole
13	242 × 215	150	+G	–	1.11	2852–2703		
14	232 × 210	118	+G	+B	1.10	2908–2791		
15	170 × 165	115	+C	+B	0.72	–		
16	288 × 252	94 +21h	+C	+B	1.38	2899–2806	2785	
17	190 × 170	38h+ 70	+C	–	0.95	2846–2777		lobate
18	260 × 217	94	+F	–	1.05	2915–2822		
19	207 × 176	142	+C	–	1.09	2784–2643		
20	411 × 340	265	+C	–	0.79	2793–2529		
21	525 × 442	261 +75h	+C	–	0.84	2902–2642	2567+*	
22	392 × 350	179	+C	+B	1.08	2678–2501		
23	374 × 255	182	+F	–	1.32	2627–2446		
24	360 × 300	207	+C	+B	1.01	2651–2445		
26	330 × 300	252	+C	+B	0.64	2814–2563		

*THQ21 has an unresolved problem after 261 with several missing rings.

No. rings – n = measured rings; $n+/\pm n$ = inner/outer unmeasured rings.

Pith – C = pith present; F = 5–10 rings to pith; G = >10 rings to pith; + n = unmeasured rings.

Bark – B = bark edge present.

AGR – Average growth rate.

Date span – measured sequence only.

End dates – with sapwood estimate for *Quercus*; $n+$ denotes tpq ; includes unmeasured rings for *Pinus*; $n+$ denotes tpq .

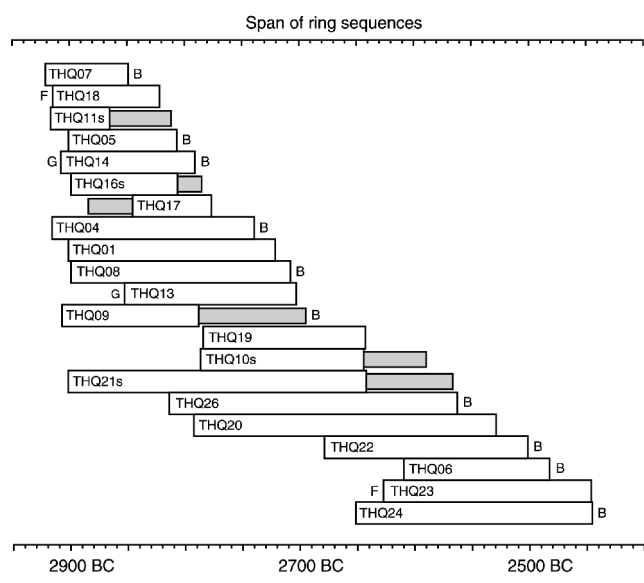
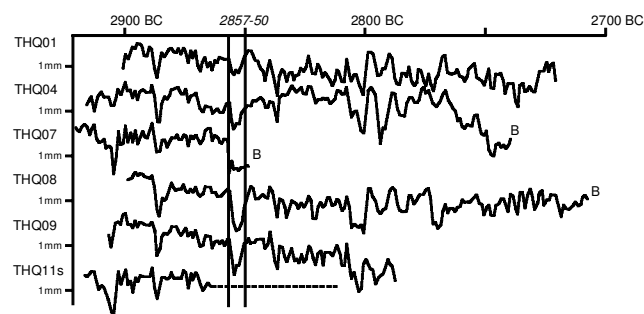
Table 2 t -value matrix for PISY/Hatfield

	04	05	06	07	08	09	10	11	13	14	16	17	18	19	20	21	22	23	24	26
01	8.96	10.91	\	3.40	14.29	8.14	5.55	4.85	11.37	10.05	10.31	7.02	9.08	–	6.88	13.24	\	\	\	3.95
04		11.85	\	4.02	12.59	7.27	–	5.37	8.02	7.87	9.78	5.12	9.12	–	–	11.74	\	\	\	–
05			\	5.05	11.50	11.34	\	6.74	8.09	11.59	9.66	9.71	7.70	\	\	10.39	\	\	\	\
06				\	\	\	\	\	\	\	\	\	\	\	5.41	\	9.66	7.60	7.83	3.95
07					3.54	3.11	\	11.27	\	3.78	–	\	5.69	\	\	3.87	\	\	\	\
08						8.22	5.08	5.85	15.69	9.69	11.73	9.98	9.34	–	7.35	19.16	\	\	\	4.60
09							\	5.18	5.55	15.10	12.32	6.77	11.43	\	\	8.22	\	\	\	–
10								\	5.44	\	\	\	\	4.88	10.78	11.03	–	\	\	10.64
11									\	6.17	5.26	\	10.60	\	\	5.07	\	\	\	\
13										9.08	11.09	9.53	9.83	3.91	8.67	16.49	\	\	\	6.06
14											14.09	7.72	14.67	\	\	11.18	\	\	\	–
16												9.67	13.15	\	\	10.76	\	\	\	\
17													8.98	\	–	8.13	\	\	\	–
18														\	\	9.62	\	\	\	\
19															7.39	5.01	–	\	\	6.34
20																10.29	9.56	11.36	8.84	19.07
21																	–	\	\	8.10
22																		12.32	9.96	9.03
23																			24.25	9.51
24																				7.41

\ = overlap <15 years; – = t -values less than 3.00.

Table 3 *t*-value table for PISY/Hatfield against the English *Quercus* master chronology and independent site chronologies

Oak chronologies	<i>t</i> -value
English prehistoric <i>Quercus</i> chronology (Hillam <i>et al.</i> , 1990; Brown and Baillie, 1992)	7.59
Independent site oak chronologies	
Croston Moss, Lancashire (Brown and Baillie, 1992)	5.30
Wicken Sedge Fen (Brown <i>et al.</i> , 1986)	5.97
Holme Fen (Brown <i>et al.</i> , 1986)	5.17
Feltwell Fen (Brown <i>et al.</i> , 1986)	4.26
Hereford and Worcester Palaeochannel (Hillam, 1997)	4.18

**Figure 3** Bar chart showing the dated positions of the *Pinus* samples included in PISY/Hatfield. Note: except where otherwise indicated, the tree-ring sequences begin at the pith. Pith/bark codes as Table 1. Wide bars = measured sequence. Narrow bars = unmeasured rings.**Figure 4** Ring-width sequences from selected samples. Trees 07 and 11 have narrow ring bands that relate to a stress event at 2857–5 BC, from which 07 appears not to have recovered. Other samples show narrow rings in 2856/55, but by 2850 growth had improved. The vertical scale is semi-logarithmic.

became immersed into the mire. Many of the wood-dependent beetles belong to the terminal stages of the woodland as they feed off rotting wood rather than live wood. These species would have continued feeding and breeding within the rot-holes as long as the habitat remained suitable. Some of the aquatic and woodland insects probably postdate the main phase of the *Pinus* chronology, but it is likely that both elements were deposited at more or less

the same time. This is suggested by the excellent state of the wood, which indicates a very rapid submersion; its associated insect fauna thus probably represents a more or less co-existing population.

The subfossil insect data were analysed by reference to a habitat classification system devised for the wider palaeontomological study of the Humberhead Levels (Whitehouse, 1998). The categories utilized are summarized in Table 4, but are not discussed here. Detailed ecological information was obtained from the Coleopteran habitat data base BUGS (Sadler *et al.*, 1992). The categories are presented graphically as they provide a useful representation of the sample's proportions for interpretational purposes, although it should be emphasized that they have little meaning in terms of proportions of habitat represented (Figure 5). Insect nomenclature follows Lucht (1987), while plant nomenclature follows Stace (1991).

Results

The rot-holes supported abundant very rare and non-British species, particularly from the wood-loving genera of the weevil and cucujid families. Table 4 displays the full species list, together with habitat categories assigned to each species. The list includes four non-British species, four RDB1 species, four RDB2 species, one RDB3 species and 11 Notable B species. (The Nature Conservancy Council published *British Red Data Books: 2. Insects* (Shirt, 1987), referred to as RDB. This is a comprehensive statement of the most threatened insects in Great Britain. The *Book* contains three major categories based upon degree of threat (RDB1 endangered; RDB2 vulnerable; RDB3 rare). These categories were added to in the various reviews, including Notable A and B species (Hyman, 1992, 1994).) These are either aquatics or saproxylics (species which are dependent for some part of their life cycle on wood) and their present status reflects the decline of their associated habitats. The list today would have no match within forest habitats in Great Britain or Ireland since it contains species that no longer live in the British Isles. Within subfossil insect contexts, it is comparable in importance to mid-Holocene material recovered from Thorne Moors (Buckland and Kenward, 1973; Buckland, 1979; Whitehouse, 1997a) and Stileway, in the Somerset Levels (Girling, 1985).

Quercus assemblage, c. 3618–3418 BC

The *Quercus* assemblage provides an insight into the nature of the pre-peat and early peat landscape. The most important categories represented by the beetles in this sample include: woodland; damp woodland; non-acid wetland; aquatic; and hygrophilous communities (Figure 5A). There is a marked absence of species associated with *Calluna* heath and acid peatland conditions. Some species are clearly associated with the *Quercus* itself, such as the leaf miner *Rhynchaenus quercus*. The weevil *Rhyncolus ater* is usually associated with *Pinus* in Britain (Alexander, 1994), but in mainland Europe it is as common in both deciduous and coniferous wood (Palm, 1951; 1959). Its presence in a *Quercus* rot-hole indicates that it was associated with deciduous rather than coniferous wood, and suggests that this species may have been less fussy about its host in Britain during the mid-Holocene. Several of the insect species are typical of fen and *Alnus glutinosa* carrs (e.g., *Pterostichus nigrita*, *P. diligens*, *Plateumaris sericea*), while the detritus of *Phragmites*, *Carex*, *Juncus* and other vegetation are indicated by several species (e.g., *Olophrum fuscum*). Permanent pools with rich littoral vegetation were almost certainly present in the immediate vicinity, as suggested by some of the larger Dytiscidae, such as *Ilybius guttiger* and *Agabus unguicularis*. Both beetles are often associated with mesotrophic conditions (Nilsson and Holmen, 1995).

Table 4 Coleoptera list from Tyrham Hall Quarry, Hatfield Moors (* denotes non-British species), including assigned habitat categories

Coleoptera	1	2A	2B	3	K	Oak	Classif.
Carabidae							
<i>Dyschirius globosus</i> (Hbst.)	9	1		1	2		21
<i>Trechus obtusus</i> Er.	1			1			9
<i>T. rubens</i> (F.)		1					22
<i>Bembidion quadrimaculatum</i> (L.)				1			10
<i>lquadripustulatum</i> F.							
<i>Bembidion</i> sp.		1			1		21
<i>Bradycellus ruficollis</i> (Steph.)	1						10
<i>B. verbasci</i> (Duft.)	1						21
<i>B. harpalinus</i> (Serv.)	1						10
<i>Bradycellus</i> sp.	1						10
<i>Pterostichus strenuus</i> (Panz.)	1						9
<i>P. diligens</i> (Strm.)	8	3	1	4	4	2	14
<i>P. nigrita</i> (Payk.) / <i>rhaeticus</i> Heer	1			1	1		14
<i>P. ? nigrita</i> (Payk.) / <i>rhaeticus</i> Heer					1	3	14
<i>P. minor</i> (Gyll.)	4	3			2		14
<i>P. ? minor</i> (Gyll.)	2						14
<i>Pterostichus</i> spp.	2		1		1		21
<i>Agonum fuliginosum</i> (Panz.)	2	1					14
<i>A. obscurum</i> (Hbst.)	2				2		9
<i>Agonum</i> sp.	1						21
<i>Dromius quadrinotatus</i> Zenk.	1						1 & 38
Carabidae gen. et sp. indet.	1	3					UN
Dytiscidae							
<i>Hygrotus decoratus</i> (Gyll.)	1						27
<i>Hydroporus scalesianus</i> Steph.		5					27
<i>H. gyllenhalii</i> Schdte.	3						28
<i>H. ? umbrosus</i> (Gyll.)	1						29
<i>H. tristis</i> (Payk.)	83						28
<i>H. pubescens</i> (Gyll.)	13						27
<i>H. melanarius</i> (Duft.)	52						28
<i>Hydroporus</i> spp.	59	52	9	9	23	20	27
<i>Agabus chalconatus</i> (Panz.)	4						27
<i>A. ? guttatus</i> (Payk.)	8			1			32
<i>A. melanarius</i> Aube	1						32
<i>A. bipustulatus</i> (L.)	2	1	1			1	26
<i>A. ? unguicularis</i> Thoms.		2				2	29
<i>Agabus</i> spp.	4	2	1	2	2		26
<i>Ilybius aenescens</i> Thom.	2	3					28
<i>I. guttiger</i> (Gyll.)						1	27
<i>Agabus</i> / <i>Ilybius</i> sp.					1		26
<i>Graphoderus ? bilineatus</i> (Deg.)	1						29
Hydrophilidae							
<i>Ochthebius ? minimus</i> (F.)	2			2	1		30
<i>Ochthebius</i> spp.		3					26
<i>Limnebius aluta</i> Bed.			1				29
<i>Cercyon ? convexiusculus</i> Steph.			1				16
<i>Cercyon</i> sp.		1			3		35
<i>Megasternum obscurum</i> (Marsh.)				2			22
cf. <i>Paracymus scutellaris</i> (Rosen.)				1	3		28
<i>Hydrobius fuscipes</i> (L.)		1		1			26
<i>Anacaena globulus</i> (Payk.)	3	6				1	30
<i>Anacaena</i> sp.					2		26
<i>Laccobius</i> sp.		1					26
<i>Helochaers/Ermochrus</i> sp.			1				26
<i>Ermochrus</i> sp.	1						26
Hydrophilidae gen. et sp. indet.		1					26
Silphidae							
<i>Silpha ? tristis</i> Ill.		1					35

Table 4 Continued

Coleoptera	1	2A	2B	3	K	Oak	Classif.
<i>Silpha</i> sp.			1				UN
Scydmaenidae							
<i>Neuraphes ? elongatulus</i> (Mull.)	2						09
Scydmaenidae gen. et sp. indet.		1					UN
Clambidae							
<i>Clambus</i> sp.			1	1			22
Ptiliidae							
<i>Acrotichis</i> sp.	1						35
Staphylinidae							
<i>Megathrus/Proteinus</i> sp.	1					1	35
<i>Olophrum piceum</i> (Gyll.)	2	2	2			1	16
<i>O. fuscum</i> (Grav.)						1	2
<i>Eucnecosum brachypterum</i> (Grav.)	2						20
<i>Acidota crenata</i> (F.)			2				20
<i>Lesteva punctata</i> Er.					1		24
<i>L. ? punctata</i> Er.				1			24
<i>Bledius</i> sp.	2				1		24
<i>Carpelimus</i> sp.	1	1					21
<i>Anotylus</i> sp.	1						35
<i>Stenus comma</i> LeC.	1						22
<i>Stenus</i> spp.	7	5	2	1	4	2	22
<i>Scopaeus sulcicollis</i> (Steph.)	1						21
<i>/gracilis</i> (Sperk.)							
<i>Lathrobium rufipenne</i> Gyll.	5				1	2	20
<i>L. terminatum</i> Grav.				1	1		20
<i>L. fulvipenne</i> (Grav.)				1		2	22
<i>L. brunripes</i> (F.)	1	3					22
<i>Lathrobium</i> spp.	5	8	1	1	1	3	21
<i>Xantholinus linearis</i> (Ol.)						1	10
<i>X. longiventris</i> Heer	1					2	35
<i>Philonthus</i> spp.		2					UN
<i>Gabrius</i> sp.		1					UN
<i>Staphylinus brunripes</i> F.						1	22
<i>Staphylinus</i> sp.	1						UN
<i>Quedius</i> sp.	3						UN
<i>Mycetoporus</i> sp.						1	1
Aleocharinae gen. et sp. indet.	2	1	1	1		2	35
Staphylinidae gen. et sp. indet.		2					UN
Pselaphidae							
<i>Bryaxis bulbifer</i> (Reich.)	2				1	1	20
<i>B. curtisi</i> (Leach)		8	1				09
<i>Bryaxis</i> sp.	2						22
<i>Brachygluta fossulata</i> (Reich.)		1				1	22
<i>Pselaphus heisei</i> (Hbst.)		1					20
Pselaphidae gen. et sp. indet.	1						UN
Elateridae							
<i>Ampedus ? rufipennis</i> Steph.	1						05
<i>Ampedus</i> sp.						1	03
<i>Agriotes sputator</i> (L.)	1						13
<i>Hypnoides riparius</i> (F.)	1						21
Elateridae gen. et sp. indet.	2						UN
Scirtidae							
<i>Microcara testacea</i> (L.)	2						09
<i>Cypon padi</i> (L.)	8						30
<i>Cyphon</i> spp.	16	20	3	1	1	3	21

Table 4 Continued

	1	2A	2B	3	K	Oak	Classif.
Byrridae							
? <i>Curimopsis nigrita</i> (Palm.)	1						18
Ostomidae							
<i>Ostoma ferrugineum</i> (L.)	1						04
Rhizophagidae							
<i>Rhizophagus ferrugineus</i> (Payk.)					1		06
Cucujidae							
* <i>Prostomis mandibularis</i> (F.)		1					05
Lathriididae							
<i>Lathridius minutus</i> (L.) / <i>pseudominutus</i> Strand.							36
<i>L. ? anthracinus</i> Mann.	2						36
<i>Corticaria gibbosa</i> (Hbst.)	1		1				36
<i>Corticarina</i> sp.	1						36
Corticariinae indet.	1		1				36
Lathriididae gen. et sp. indet.			1		1		36
Colydiidae							
<i>Bitoma crenata</i> (F.)						1	05 & 38
<i>Cerylon histerooides</i> (F.)				1			06
Colydiidae ? gen. et sp. indet.		1					06
Anobidae							
<i>Grynobius planus</i> (F.)	1						06
Ptinidae							
<i>Ptinus ? clavipes</i> Panz.	1						37
Scarabaeidae							
<i>Aphodius sphacelatus</i> (Panz.)	1						35
Chrysomelidae							
<i>Plateumaris sericea</i> (L.)				2			14
<i>Plateumaris ? sericea</i> (L.)						1	14
<i>P. discolor</i> (Panz.)	5						19
<i>P. discolor</i> (Panz.) / <i>sericea</i> (L.)	4	5		5	2		14
Donacinae indet.	1	1					14
<i>Chaetocnema concinna</i> (Marsh.)						1	13
<i>C. hortensis</i> (Fourc.)						1	13
Chrysomelidae Gen. et Sp. indet.				1			UN
Scolytidae							
<i>Leperisinus varius</i> (F.)					1		02
<i>Dryocoetinus villosus</i> (F.)		2					05 & 38
<i>Pityophthorus lichtensteini</i> (Rantz.)		1					04
<i>Pityophthorus/Pityogenes</i> sp.	1						03
<i>Xyleborus saxeseni</i> (Ratz.)	1	1					03
Ipinidae gen. et sp. indet.	1						03
Scolytidae gen. et sp. indet.	2				1		03
Curculionidae							
<i>Apion</i> spp.	1	4					13
<i>Phyllobius</i> sp.		1					UN
<i>Sitona</i> sp.			1				13
<i>Dryophthorus corticalis</i> (Payk.)	21				2		06
* <i>Rhyncolus elongatus</i> (Gyll.)	31				1		04
<i>R. ater</i> (L.)	10					1	04
<i>R. cf. ater</i> (L.)						1	04
* <i>R. punctulatus</i> Bohe.	1						06
* <i>R. sculpturatus</i> Walt.	29						04
<i>Phloeophagus lignarius</i> (Marsh.)	1						05
Cossinine gen. et sp. indet.	1						05

Table 4 Continued

	1	2A	2B	3	K	Oak	Classif.
Coleoptera							
<i>Acalles roboris</i> Curt.		1					02
<i>A. ptinooides</i> (Marsh.)	1						11
<i>Micrelus ericae</i> (Gyll.)	6			1	4		10
<i>Ceutorhynchus</i> sp.	1						13
<i>Ceutorhynchus pallidactylus</i> Marsh.					1		13
<i>Anthonomus ? rubi</i> (Hbst.)					1		07
<i>Rhynchaenus quercus</i> (L.)		1				1	02
<i>R. ? rusci</i> (Hbst.)		1					11
<i>Rhynchaenus</i> spp.		3				1	03
Curculionidae gen. et sp. indet.		1				1	UN
Coleoptera gen. et sp. indet.						1	UN
Total Coleoptera individuals	482	174	38	44	85	54	
Total Coleoptera species	102	64	26	28	44	27	

Classification: Habitat categories (after Whitehouse, 1998)

Woodland/trees: (1) pinewoods/heaths; (2) deciduous woodland; (3) woodlands (all types); (4) dead and decaying tree habitats (coniferous); (5) dead and decaying tree habitats (deciduous); (6) dead and decaying tree habitats (all types); (7) woodland/flowers/herbs; (8) woodland/fungi and mouldy plant debris. **Damp woodland:** (9) damp woodland (e.g., *Alnus* carr). **Heath and grassland:** (10) sandy heath/*Calluna* (11) **Heath/woodlands:** (12) xerophilous; (13) grassland, herbs and flowers. **Non-acid wetlands:** (14) non-acidic bogs/wetlands; (15) fens/reeds and sedges; (16) non-acid/plant debris; (17) reeds/brackish water. **Acid wetlands:** (18) acid bogs; (19) acid bogs/*Eriophorum* and *Sphagnum*; (20) bogs/plant debris. **Hygrophilous (wet-loving):** (21) hygrophilous; (22) hygrophilous/plant debris; (23) water margins/riverbanks; (24) water margins/plants and mud; (25) wet locations/herbs and marsh plants. **Aquatics:** (26) aquatic/generalists; (27) aquatics/bogs; (28) aquatic/acid bog; (29) aquatic/non-acidic bog; (30) aquatic/vegetation and detritus-rich; (31) aquatic/stagnant and sometimes brackish water; (32) aquatic/slow-moving water; (33) aquatic/running water. **Decaying debris:** (34) exclusively dung; (35) decaying animal and plant debris; (36) fungi/plant debris; (37) fungi/wood/plant debris. **Others:** (38) fire indicators; (UN) unclassified.

Pinus assemblages, 2921–2445 BC

The *Pinus* samples consist of two major faunal components: taxa related to wood habitats and aquatics. Figure 5B provides an overview of the habitats represented.

The range of wood-loving taxa recorded from the site is representative of mixed woodland in varying states of decay. In addition to *Pinus*, the insects indicate that *Betula*, *Quercus*, *Fraxinus* and possibly *Fagus* grew locally. The continued presence of *Quercus* is suggested by its leaf miner *Rhynchaenus quercus*. The non-British ancient woodland relic species (*Urwaldrelikt*) *Prostomis mandibularis* is often found in decayed red rotted *Quercus*, typically in areas of primary woodland (Horion, 1960), although, singly, it can be found in decaying *Pinus* (Koch, 1992), which was presumably its habitat in this case. The non-British '*Urwaldrelikt*' *Rhyncolus punctulatus* is found in hollow deciduous trees, often in *Quercus*, as well as in conifers (Reitter, 1916; Palm, 1959). It is often associated in dry wood with the weevil *Phloeophagus lignarius* (Palm, 1959), which was recovered from the same sample. *Fraxinus excelsior* is the host of the bark beetle *Leperisinus varius*, indicating the presence of this tree within the vicinity. The rare RDB2 elaterid *Ampedus rufipennis* is commonly found in mouldy, deciduous wood, predominantly on *Fagus* (Horion, 1953; Palm, 1959), although it can also live on *Betula*, a tree that was certainly represented within the woodland, as its leaf miner *Rhynchaenus rusci* and its macrofossils suggest.

Dryophthorus corticalis, an ancient woodland inhabitant, was feeding on the *Pinus* in large numbers. The quantities recovered

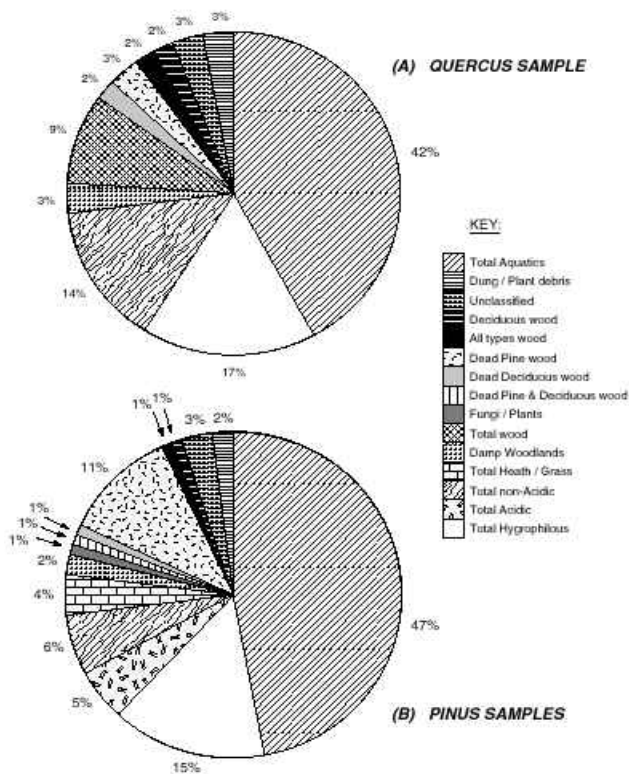


Figure 5 Proportions of wood and other habitat Coleoptera indicator categories. (A) Tyrham Hall Quarry, *Quercus* sample. (B) Tyrham Hall Quarry, *Pinus* samples.

from one of the rot-holes and their intact state of preservation suggests they were feeding and breeding within the rot-hole. In England, this endangered species is usually only associated with *Quercus* (Donisthorpe, 1939; Hyman, 1992), although it is frequently recorded in coniferous wood on the Continent, often in high numbers, in both modern and subfossil contexts (Palm, 1959; Koponen and Nuorteva, 1973). Again, the recovery of this species within a *Pinus* context would suggest a change in its preferred host in Britain more recently. As a subfossil, this species is closely associated with the genus *Rhyncolus* (Whitehouse, 1997a), a connection noted within the European literature (Palm, 1959). This association is nowhere clearer than at Tyrham, where other members of this genus, including the non-British *R. elongatus* and *R. sculpturatus*, as well as the British *R. ater*, were present, appearing to have been attracted to the rotting *Pinus* in great numbers. Most of the species described above are those that attack wood during the early stages of decomposition and there is no evidence of infestation by insect pests among the wood-associate beetles that could have played a role in the decline of the woodland.

A small group of species indicates damp woodland conditions, such as *Agonum obscurum* and *Trechus obtusus*, while *Pterostichus strenuus* is found in the drier parts of *Alnus* swamps and fen woodland (Lindroth, 1945). There are also several species commonly found in *Calluna* and heathland, including significant numbers of the heather feeder, *Micrelus ericae*, and other typical beetles (e.g., *Bradycellus ruficollis*, *B. harpalinus*, *Xantholinus linearis*). As the woodland declined, aquatic and peatland assemblages of beetles became incorporated within the rot-holes, presumably as the trees became buried within the mire and its pools. Species identified are those predominantly associated with wet, mesotrophic and ombrotrophic conditions – members of the genus *Pterostichus* (*P. nigrita/raeticus*, *P. minor*, *P. diligens*), in addition to *Agonum fuliginosum*, are typical of mesotrophic peatlands. The recovery of one of the Humberhead Peatlands' endangered (RDB1) species, the byrrhid *Curimopsis nigrita*, a lowland

peatland specialist, is notable as it illustrates that the particular character of these lowland raised mires formed about 4000 years ago. This mixture of eutrophic and ombrotrophic conditions is also evident among aquatic vegetation associates, with the presence of species such as *Plateumaris sericea* and *P. discolor* – the former is typical of eutrophic fens, and the latter of ombrotrophic conditions, living on *Eriophorum*, *Sphagnum* and *Carex* species (Bullock, 1993). The aquatic beetles also indicate a varied range of habitats; the RDB3 fen-loving hydrophilid *Limnebius aluta* and RDB1 *Graphoderus bilineatus* can be found in deep ponds and lakes, generally with dense marginal vegetation (Shirt, 1987). *Hydroporus scalesianus*, *H. pubescens* and *Agabus chalconatus* all indicate vegetation-rich standing fen pools with *Sphagnum* (Shirt, 1987; Koch, 1989). There are, however, also many acid-loving aquatics, although most originate from one sample (1), including *Hydroporus tristis*, *H. melanarius* and *H. gyllenhalii*. The presence of larger water beetles indicates pools of some size, including several species often associated with slowly moving water, such as *Agabus guttatus* and *A. melanarius* (Friday, 1988; Koch, 1989).

Discussion

The dendrochronological and subfossil insect evidence is indicative of an early, *Quercus*-fen woodland community, with a date of 3618–3418 BC for the single, incomplete, *Quercus*. The remains of other, undated, *Quercus* elsewhere on Hatfield suggests that there may have been contemporary trees. The tree overlapped temporally with the *Quercus* woodland on Thorne Moors (3777–3017 BC), probably the relic of widespread forest growing across the Humberhead Levels (Boswijk, 1998; 2002). Eutrophic and mesotrophic fen conditions are indicated by the insect fauna which was probably living contemporaneously with the *Quercus* or soon after its demise. The aquatic beetles indicate that the *Quercus* was submerged into a permanent, deep pool, perhaps an indication of a rising water table.

Between 2921 and 2445 BC, sandy *Pinus*-heath woodland grew on the western edge of Hatfield Moor. By this time, black, well-humified peat had started developing elsewhere: on the northern side of Hatfield well-humified peat had begun to accumulate c 3350–3030 cal. BC at HAT 3 (4480 ± 45 BP, SRR-6119) (Whitehouse, 1998) and on the eastern side c 3090–2890 cal. BC (HAT 2; 4335 ± 75 BP, CAR-254) and 2900–2620 cal. BC (HAT 1; 4180 ± 70 BP, CAR-168) (Smith, 1985; Figure 2). The range and variety of insect species recovered suggest that the woodland comprised a mix of tree species in addition to *Pinus*, including *Quercus*, *Betula* and *Alnus*, with *Fraxinus* and *Fagus* further afield. This mix of trees is also indicated by the palynological data from the centre of the Moor (HAT 1: Smith, 1985). The mixed age structure of the Tyrham *Pinus* woodland, with ongoing die-back and periodic regeneration of new trees over 400 years, suggests that the woodland was probably reasonably open, enabling seedlings to become established in clearings caused by dead standing trees or fallen trees. The understorey supported insect species typical of *Calluna* heathland, such as those associated with moss, raw humus and *Calluna*, interspersed with deep and shallow pools, and slow-moving water. The dominant *Calluna* understorey would have been suitable for seedling establishment. McVean (1963) found that regeneration of *Pinus* in Scotland was successful in woodland classed as *Pinetum-Vaccinium-Callunetum*, where there was a thick moss and raw humus layer into which the seedlings could strike and develop the essential mycorrhizal fungal associations. The presence of beetle feeders on fungi indicates that there was a supply of rotting wood to support such a community. Thus, the woodland would have included decaying and dead wood as well as mature trees and new growth.

The tree-ring evidence indicates that the woodland declined slowly as trophic conditions in the area gradually changed. There is an increasing representation of a mesotrophic invertebrate community, although significant events accelerating the transition from eutrophic to mesotrophic conditions may also have occurred. Some aquatic subfossil beetle indicate moving-water and deeper-water environments and may explain a period of severe stress experienced by some *Pinus* in 2857–5 BC, perhaps representing an episode of groundwater flooding, created by a rising water table. It is relevant to note that Smith (1985), in his analysis of plant macrofossils from the eastern side of Hatfield Moors, identified an initial episode of flooding, sometime around 2900–2620 cal. BC (4180 ± 70 BP, CAR-168) and 3090–2890 cal. BC (4335 ± 75 BP, CAR-254). This is indicated by the presence of *Sphagnum cuspidatum* within profiles at HAT 1 and 2 (Figure 2).

Over time, as ground conditions become increasingly waterlogged, and the nature of understorey vegetation altered, the growth of *Pinus* seedlings would have been inhibited. In addition, standing trees may have become unstable. In mature form *Pinus* has a tall, branchless trunk, spreading crown and predominantly shallow root system (Humphries *et al.*, 1992). They may be prone to becoming top-heavy, and narrow ring episodes, coinciding with the onset of lobate growth, suggest that many trees slumped but continued growing at an angle. It is possible that these trees grew near or alongside a pool or watercourse, as the good preservation of the *Pinus*, as well as the abundant water beetles, suggests that when they fell they were either submerged or rapidly buried in anaerobic deposits. Many of the trees, although without branches, were intact between the trunk and root. This contrasts with other peatland sites from which *Pinus* have been recovered, where only the root system and small amount of trunk often have remained. The slow growth of blanket peat in Rannoch Moor, Scotland, resulted in many of the trees rotting *in situ* (Bridge *et al.*, 1990), while at Lindow Bog and White Moss, Cheshire, few trunks were recovered though the root system and a small area of lower trunk were well preserved in the peat (Lageard, 1992).

The woodland at Tyrham contrasts with the contemporaneous *Pinus* woodland growing on Thorne Moors (2916–2475 BC; Boswijk, 1998; 2002). At the time when the PISY/Hatfield chronology begins, a few dispersed pioneer trees became established predominantly on the western side of Thorne Moors. Tree density increased dramatically from 2744 BC onwards as an even-aged stand grew between the pioneers. The Thorne *Pinus* tended to display rapid growth, particularly in the early years, suggesting that the seedlings were established in an open environment. By 2570 BC the cohort had largely died back, most probably in response to the development of wetter conditions (Boswijk, 1998; 2002). There was only limited regeneration after this date. The decline of the Thorne woodland was swifter than at Tyrham as PISY/Hatfield extends for a further 100 years after the demise of the Thorne *Pinus*. This suggests that the Tyrham trees did not respond as quickly to changing conditions as those on Thorne Moors, although it is important to note that the woodland was already in decline at this time. It is likely that local edaphic conditions played a part in delaying the reponse of trees. Eventually, a much wetter environment, as indicated by the high proportion of aquatic beetle species recovered, replaced the Tyrham woodland.

The structure of PISY/Hatfield is similar to the contemporary woodland growing on White Moss, Cheshire (Lageard *et al.*, 1999), as well as the floating *Pinus* chronology from Glashburn, Ireland, dated to 2500–2000 cal. BC (McNally and Doyle, 1984). The Tyrham trees were visibly rooted into the sandy substrate (i.e., an example of pre- and early-mire landscape), whereas the Irish and Cheshire *Pinus* were examples of mire-*Pinus* woodlands, growing on peat. The Glashburn trees were separated from the underlying lake marl deposit by approximately 1.75 m of peat (McNally and Doyle, 1984). At White Moss, the dendrochronol-

ogically dated *Pinus* were growing on peat that was, on average, 1.39 m thick over the sandy substrate (Lageard *et al.*, 1999). Thus, the growth environment of these trees, and their westerly locations, may have made them sensitive to shifts towards wetter conditions in their host bogs. Lageard *et al.* (1999) suggested that the decline of the White Moss trees supports the premise of a staged retreat in response to a climatic shift to wetter conditions at about 2500 BC, which had significant effect on the survival of mire *Pinus* populations across the British Isles. The end dates of 2569 BC for Garry Bog *Pinus* (Pilcher *et al.*, 1995) and 2559 BC for White Moss (Lageard *et al.*, 1999) as well as the decline of PISY/Thorne by 2475 BC (Boswijk, 1998; 2002) and PISY/Hatfield in 2445 BC, may also be indicative of such a change in climate. On Thorne Moors, however, within 200 years, *Pinus* recolonized the mire, and was present episodically for almost 1000 years, until at least 1489 BC (Boswijk, 1998; 2002), suggesting that, in eastern England at least, periods unfavourable to *Pinus* growth were short-lived. The subfossil invertebrate record from other sites on Hatfield Moors would corroborate this idea (Whitehouse, 1998) and Hatfield still supports an important modern pine fauna (Skidmore, 2001).

Buckland (1979), Buckland and Sadler (1985), Dinnin (1997) and more recently Buckland and Smith (2002) and Whitehouse *et al.* (2001) have discussed the probable factors influencing peat development of the wetlands in the Humberhead Levels. Rather than seeing a shift to wetter climate as the primary cause of bog genesis and development, and the consequent decline of the *Quercus* and *Pinus* woodlands, the models stress the influence of a rising water table associated with an increase in runoff caused by forest clearance activities in the upriver catchments, leading to widespread paludification. In addition, the general trend in sea-level rise around this time (Gaunt and Tooley, 1974; Dinnin and Lillie, 1995; Long *et al.*, 1998) could have caused a backing-up of freshwater runoff from rivers which run into the Humber estuary, causing regional freshwater flooding, as well as affecting the levels of the underlying water table. During these periods of marine transgression, marine conditions penetrated far into the Humber estuary and its tributary valleys (Long *et al.*, 1998). However, there is no palaeoecological or stratigraphic evidence for the presence of any saline influences indicating marine or estuarine conditions as far inland as the Humberhead Levels (Buckland, 1979; Buckland and Sadler, 1985; Smith, 1985; Whitehouse, 1998). This is despite the base of the peat deposits at Thorne Moors now lying over 4 m below high water at Goole.

The importance of these pre- and early-mire woodlands in establishing the faunal communities of the subsequent raised mire is clearly demonstrated by the analyses of subfossil insects from the basal forest deposits of Tyrham Hall Quarry, as well as elsewhere on Thorne and Hatfield Moors. There are many faunal elements from the Tyrham assemblage, and other sites on Hatfield Moors, that still appear on the modern Coleopteran list, such as the rare peatland specialist *C. nigrita*. However, among the extinct species recovered, many are today restricted to isolated enclaves within mature forests of mainland Europe. The larvae or pupae of many saproxylic invertebrates typically have long periods of development, sometimes over several years, hidden within decaying wood of suitable quality and age. Many often have short imaginal (adult) lifespans, often inhabiting only a proportion of potentially suitable trees, representing a fraction of the total tree population of most forests (Warren and Key, 1991; McLean and Speight, 1993). The destruction of undisturbed forest and in particular the disappearance and lack of continuity of dead wood habitats, decline in *Pinus* and associated fire frequency, and possibly the subtle interplay of climatic change have all contributed to the near or total loss of these species (e.g., Buckland, 1979; Buckland and Dinnin 1997; Whitehouse, 1997b; 2000; Whitehouse *et al.*, 1997; Dinnin and Sadler, 1999). The recovery of these species in

the Tyrham, and Hatfield, deposits is therefore highly significant, as they suggest a former abundance of these extinct species, highlight the importance of woodland and dead wood habitats, and indicate that only a portion of the former faunal community remains to recolonize restored mires.

Conclusion

Dendrochronological and palaeontomological analyses of subfossil *Quercus* and *Pinus* have provided new data concerning a mid-Holocene woodland. A single *Quercus* was dated to 3618–3418 BC, and a 477-year *Pinus* chronology was established and absolutely dated to 2921–2445 BC, by reference to the English *Quercus* master curve. The subfossil entomological fauna indicate mixed woodland growing in the area, although *Pinus* became the dominant taxon, with an understorey characterized by *Calluna* and sedges. Over the period of the *Pinus* chronology, the woodland began to die back, in response to rising groundwater and changing trophic levels. It is clear that, at Tyrham at least, mire development on this site caused tree death, rather than mire spreading as a result of the death of trees; the insect samples from the *Quercus* rot-hole indicate the onset of fen development during this early stage. A rise in aquatic insect species and the good preservation of the trees would suggest that the area became increasingly wet and ombrotrophic. Some *Pinus* may have fallen into pools, but peat also appears to have developed relatively quickly, preserving the woodland at the base of the bog. The decline in the woodland appears to be part of a significant demise of bog *Pinus* also recorded in sites from western England and Ireland, at about 2500 BC. However, the presence of *Pinus* on Thorne Moors until at least 1489 BC suggests that, in eastern England at least, periods unfavourable to *Pinus* growth were short-lived. Moreover, ongoing populations of *Pinus* and its associated invertebrates continued to thrive in remote locations such as the raised mires of the Humberhead Levels, potentially into the post-mediaeval period.

The fossil insect evidence clearly shows that the faunal origins of the ombrotrophic mire can be traced back to events which occurred c. 4000 years ago, in a mixed *Pinus*-mire environment. Effectively, time and history of a site appear to have a considerable influence on the faunal characteristics of our mires today. This suggests that recreating raised mire with the 'correct' (climax) vegetation, the goal of present management practices, may not allow the longer-term restoration of faunal communities, since the faunal characteristics of these sites were generated 4000 years ago – something which cannot be restored or regenerated over a short timespan. The end result of any restoration work on these sites may be a visually satisfying, but a faunally depleted, landscape.

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