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Vegetation dynamics from a coastal peatland: insights from combined plant macrofossil and pollen data

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Abstract

This paper reports the results of plant-macrofossil investigations from a peat layer buried within coastal alluvium at the Caburn, a site adjacent to the English chalkland. The data collected are compared against a previously published mid-Holocene pollen sequence with the macrofossil record providing greater taxonomic resolution and establishing a local presence for many taxa. *Alnus glutinosa* pollen is abundant and *Alnus* macrofossils are recorded continuously over a c. 3000 cal year period. Fluctuations in the number of *Alnus* propagules and the presence of seeds of light-demanding herbaceous plants suggest that regeneration occurred at a local-scale, a process which is likely to have been promoted by a rising water-table and sediment consolidation. *Taxus baccata* macrofossils were also recovered indicating that the high pollen values previously reported may be the result of yew being present within the wetland area. The *Tilia* macrofossils establish the presence nearby of *T. cordata*, *T. x europaea* and *T. platyphyllos*. High pollen values for *Quercus*, *Tilia* and *Alnus* coincide with the occurrence of their anthers. Deposition within inflorescences is therefore likely to have been an important mode of pollen delivery. The usefulness of both techniques in studies that utilize peats derived from fen carr vegetation are discussed.

KEYWORDS: chalkland vegetation history; *Alnus glutinosa*; *Tilia*; *Taxus baccata*; mid-Holocene;

Introduction

Poor taxonomic resolution is a well recognised limitation of pollen-based studies of vegetation history. Particular problems arise where the sediment utilised derives from eutrophic fen environments, as many of the herbaceous pollen types (e.g. *Rumex*, Apiaceae, Poaceae) could originate from either the local peat forming vegetation or vegetation growing on areas of dry land. With wood remains common in such deposits, the wetland/dry land origin of pollen derived from tree taxa tolerant to waterlogging (e.g. *Quercus* and *Fraxinus excelsior*) can also be unclear. In south-east England these problems are acute as, due both to the absence of natural lakes and scarcity of oligotrophic peats, most of the data on Holocene vegetation history originate from eutrophic peats buried within areas of coastal and riverine alluvium (e.g. Godwin 1962; Waller 1993, 1994a; Waller and Schofield 2007; Branch *et al.* 2012).

One such study examined the mid-Holocene vegetation history of the chalkland through a pollen sequence constructed from a peat deposit buried in alluvium at the foot of the steep scarp slope of the Caburn, part of South Downs in East Sussex (Waller and Hamilton 2000). Here, as at other valley sites within the chalkland area of southern England (Waton 1982) the problems associated with taxonomic precision were exacerbated by poor pollen preservation. As a consequence of these difficulties a number of issues were left unresolved. Notably, with *Tilia* pollen abundant, these included which species of lime were present. In England *Tilia cordata* occurs on a range of soil types, while *T. platyphyllos* is regarded as native on calcareous soils (Preston *et al.* 2002) and extant populations occur on the South Downs in West Sussex (Abraham and Rose 2000). High *Taxus baccata* values were found after *c.* 5400 cal a BP. As *Taxus* forms pure woodland stands on the chalk today this pollen was assumed by Waller and Hamilton (2000) to be derived from the dry land. However, a number of subsequent studies (Deforce and Bastiaens 2007; Branch *et al.* 2012) have demonstrated that yew was present on peat in alluvial environments around the southern North Sea during the mid-Holocene and this may also have been the case at the Caburn. Increases in herbaceous pollen were used to infer phases of woodland disturbance on the slopes of the Caburn from as early as *c.* 6350 cal a BP. The origin of much of this pollen is nevertheless ambiguous and in some cases the increases are accompanied by high values for aquatics suggesting they may be indicative of changes in the wetland environment.

Problems relating to the poor taxonomic precision and the uncertain (regional or local) origin of pollen grains can be addressed by combining pollen and plant macrofossil investigations from sites (Birks and Birks 2000). The macrofossils recovered from the pollen washings in the original study indicated that plant macrofossils were abundant and suggested that analysis of the original cores (which remained in good condition) would enable the issues outlined above to be addressed. This paper reports the results of this analysis which, with the macrofossil investigation undertaken at a high resolution, can be compared directly against the results of the original pollen study.

The site and the previous investigations

Above the Chalk bedrock, the alluvial sequence of the Glynde valley at the base of the Caburn (Fig. 1) consists of a thin layer of organic silt overlain by a woody detrital peat (at least 2.88 m thick) and grey silty clays and sandy silts. The site for palaeoecological investigation was selected so as to maximise the pollen derived from the adjacent dry land while including the deeper layers of the peat. The minimum distance between this site and the edge of dry land will have increased through time though will not have exceeded 20 m during peat formation. A summary of the lithology of the sediments used in this investigation is provided (Table 1).

Radiocarbon dating indicated (Waller and Hamilton 2000) that, at the cored site, peat accumulation commenced *c.* 7100 cal a BP and ceased *c.* 3750 cal a BP (see Fig. 2). The sediment accumulation rate declines up the sequence. The 5 cm slices used for the macrofossil analysis accumulated over *c.* 42.5 cal years at the base, rising to *c.* 73 cal years below the upper contact of the peat.

Waller and Hamilton (2000) defined a series of local pollen assemblage zones, which are used here as the basis for comparing the pollen and macrofossil sequences. *Alnus glutinosa* values are very high (up to 65% Total Land Pollen - TLP) and consequently *Alnus* was removed from the pollen sum. After an initial zone (LPAZ-1a) in which high Cyperaceae and

Quercus values are recorded, tree and shrub pollen dominates until c. 6300 cal a BP. The main taxa are *Alnus glutinosa*, *Quercus*, *Tilia* and *Corylus avellana*-type. *Ulmus* and *Fraxinus excelsior* also attain values >5% TLP-*Alnus*. LPAZ-2 is characterised by high herbaceous pollen values notably Poaceae, Cyperaceae and the Asteraceae. A number of shrub taxa associated with the Chalk today are also regularly recorded including *Taxus baccata*, *Juniperus communis* and *Cornus sanguinea*. This zone was divided into three subzones as a consequence of a phase (LPAZ-2b) with unusually high *Tilia* values. The dominant taxa in LPAZ-3 (from c. 5400 cal a BP) are *Alnus glutinosa*, *Quercus*, *Corylus avellana*-type and *Taxus baccata*. Increases in Cyperaceae and Poaceae pollen occur in the upper part of the sequence.

Ordination of the pollen data offers little extra information, as although the local pollen assemblage zones are reasonably distinct, the herbaceous taxa are not well grouped. Microscopic charcoal was sparse and not counted.

Methods

The material used for the macrofossil analysis was collected using a Russian corer in 1998 and subsequently stored in the dark at 3-4°C. The cores were divided into 5 cm slices which, when intact, had a volume of 40 cm³, though this material had previously been sampled for pollen analysis and loss-on-ignition (2 cm³) and material had been extracted for four AMS radiocarbon dates (4-6 cm³). Samples were left to disperse in water, though many also required a period of gentle heating after the addition of 5% KOH, before being passed through sieves of respectively 2 mm, 1 mm, 0.5 mm and 0.2 mm mesh size.

The residues were examined under a stereomicroscope and the plant propagule and vegetative remains extracted. The latter included wood (only fragments >0.5 mm in diameter were identified), buds/bud scales, catkin fragments, leaf fragments, glumes and rhizomes. Molluscan remains were also recovered from the base of the peat and foraminifera from the clayey silt immediately overlying the peat. For the quantification of the propagules; where seeds were present within fruits (e.g. for *Alisma plantago-aquatica*, *Carex*) only the fruits were counted. Where broken remains were recovered the counts are based on the minimum number of individuals present. As it was only possible to examine a proportion of the 0.2 mm fraction from each sample (c. 5 cm³) the remains extracted (*Juncus* spp., *Typha*, *Salix* and *Epilobium* seeds, anthers, and the foraminifera) should be regarded as minimum values. Vegetative remains, where the number of individuals recovered cannot be consistently counted, are problematic to quantify (Birks 2014). In this study, the wood and bud remains disintegrated during processing and therefore the vegetative remains are recorded only as present/absent. Mosses (the leaves of which were also present in the finest fraction) are presented using an ordinal abundance scale (Dickson 1986).

Plant remains were identified primarily using reference material held at the Department of Geography and Geology at Kingston University complemented by reference texts notably Cappers *et al.* (2006) for propagules, Schweingruber (1978) for wood, Tomlinson (1985) for buds/bud scales and Smith (2004) for mosses. The diagrams of fossil remains were constructed using the program TILIA*GRAPH (Grimm 2011).

Nomenclature for the propagules follows Cappers *et al.* (2006), plant taxonomic nomenclature follows Stace (2010) and Smith (2004), and nomenclature for mollusca and foraminifera follow Anderson (2005) and Murray (1979) respectively.

Results

Macrofossils: general considerations

Waller and Hamilton (2000) reported on the poor state of pollen preservation in the Caburn sequence. In contrast, macrofossil preservation was generally good even from the outer sections of core material. The variation in preservation which was observed is therefore likely to be related to taphonomic processes operating within the depositional (fen carr) environment; some macrofossils are likely to have fallen directly into depressions/pools (see the Discussion), while others were washed into such areas after a delay or accumulated in drier areas. As a result some bias towards both the easier to identify and more robust remains, such as the fruits of *Eupatorium cannabinum*, is inevitable.

The variable but considerable presence of wood remains (in this case ranging up to 3 cm in diameter) imposes a severe, though largely unacknowledged, constraint on plant macrofossil analyses from coastal/floodplain peat deposits. They result in a high degree of heterogeneity between the content of samples. In such circumstances the number of propagule remains recovered is not made comparable by standardising either by the initial sample size or by the period over which they accumulated. This is demonstrated in the macrofossil summary diagram from the Caburn (Fig. 2) where the samples with low abundance show a close correspondence to the presence of large fragments of wood, irrespective of such data manipulation. Significantly, this lack of comparability limits numerical data-analysis.

The results of the macrofossil investigations (with propagule numbers standardized to a volume of 40 cm³) are presented in Fig. 3 with the palynological data alongside, where equivalent taxa were recorded. Table 2 details the molluscan and foraminiferal remains. With emphasis here on the comparison between the pollen and macrofossil records in terms of representation and taxonomic precision and the local or regional origin of individual taxa, the results are detailed under life-form/ecological groupings.

Trees (Fig. 3a)

Both the pollen and fruits of *Betula* were recovered in small quantities from all three zones (Fig. 3a). *Betula* fruits are wind dispersed and with birch likely to be over-represented in both records it appears not to have been common in either the dry or wetland vegetation around the site during peat formation. *Ulmus* and *Fraxinus excelsior* are also recorded both as pollen and macrofossils. For *Fraxinus*, pollen representation and the presence of bud/budscales suggest it occurred in greater abundance/closer to the site during LPAZ-1 and 2. Although associated with calcareous soils and represented in the pollen record, neither *Acer campestre* (which unusually is consistently recorded) or *Fagus sylvatica*, were recorded as macrofossils.

Quercus is well represented in both records with the macrofossil remains (bud/budscales, wood, fruits, involucre and anthers) indicating oak was present nearby throughout peat formation. Of the budscales recovered most belonged to *Quercus*, with a maximum of 80 recorded from 680-675 cm. This can be attributed to the number of *Quercus* budscales produced per bud, more than 20 compared with 2-4 for *Alnus glutinosa* (Tomlinson 1985). More significantly, the very high pollen values (73% TLP-*Alnus*) at the top of LPAZ-1a coincide with the presence of oak anthers.

A variety of *Tilia* remains (bud/budscales, wood, fruits, seeds, flowers and anthers) were also recovered, the occurrences of which correspond well with the high *Tilia* pollen values in LPAZ-1 and particularly LPAZ-2. Again, very high *Tilia* pollen values (maximum 43% TLP-*Alnus*), along with the presence of clusters of pollen grains (Fig. 3a), coincide with the presence of anthers and flowers with anthers. A total of 220 *Tilia* fruits were recovered. *T. cordata* and *T. platyphyllos* along with the hybrid *T. x europaea* appear to be represented, which together with the presence of immature fruits/infertile fruits and shrinkage (the fossil fruits are smaller than modern material), has resulted in an assemblage difficult to classify. The fruits of *T. cordata* (106) were distinguished on the basis of their thin-walls, relatively small size and shape, while the *T. platyphyllos* (21) fruits are relatively large and ribbed (see Supporting Information). The *T. x europaea* (38) fruits are intermediate in character. The immature and/or infertile fruits have been designated ‘*Tilia*’ fruits (55). Pigott (1991) indicates that most fruits of *T. cordata* (the smallest of the fruits) fall within 100 m of the parent tree. This, along with the abundance and variety of remains, demonstrates that at least during LPAZ-2 *Tilia* grew very close to the site and therefore the wetland edge.

Given the abundance of *Alnus glutinosa* pollen in the Caburn sequence it is not surprising that *Alnus* remains also dominate the macrofossil record. The fruits are particularly abundant with three samples containing over 150. *Alnus* anthers and catkin fragments, many of which contained anthers (see Supporting information) are also common, lending weight to previous suggestions that the very high frequencies of *Alnus* pollen often encountered in fen carr deposits (e.g. > 60% TLP) result in part from the deposition of pollen in inflorescences (Waller 1993). With the fruits and cones deposited almost continuously, it appears that *Alnus*, after the initial stages of peat formation, grew at or close to the site for some 3000 cal years.

Small trees/shrubs and the Rosaceae

Three *Taxus baccata* seeds and one fragment of wood were recorded from the pollen zone with high yew pollen values (LPAZ-3). *Taxus* pollen is said to be poorly dispersed (Deforce and Bastiaens 2007), while the potential for yew macrofossils to be missed, even when present within the wetland, is highlighted by the study of Branch *et al.* (2012); none were recovered despite high pollen values, large samples being taken and yew remains being recorded from an earlier test pit. The combined pollen-macrofossil evidence from the Caburn then demonstrates a presence nearby, and while it is not conclusive evidence for, it seems plausible that *Taxus* grew on the peat surface.

Unusually for the mid-Holocene in south-east England *Juniperus communis* pollen was recorded in the upper part of LPAZ-1 and during LPAZ-2 (Fig. 3b). Macrofossil remains closely resembling the rather indistinct *Juniperus* stones and their associated resinous growths were also recovered from LPAZ-2. *Juniperus* is suggestive of the expansion of scrub after woodland clearance, with such activity potentially focussed on the gentler slopes immediately above the site (Waller and Hamilton 2000).

In contrast to the pollen, which was only sparsely recorded from the upper part of the sequence, *Ilex aquifolium* macrofossils (wood and endocarps) were recovered from all three pollen zones. Although it is often considered intolerant of both base-rich and waterlogged soils, holly has been recorded on carboniferous limestone and in the drier parts of fen carr (Peterken and Lloyd 1967), with *Ilex* pollen recorded in some abundance from a few fen carr sites (see Deforce *et al.* 2014). At the Caburn, the regular occurrence of macrofossils including wood, strongly suggests a presence within the wetland area.

For *Rhamnus cathartica* and *Corylus avellana* macrofossil occurrence does not correspond with the highest pollen values (in LPAZ-1b). This can be attributed to abundance of large wood fragments in this zone. Both taxa are tolerant of waterlogging and their presence at the wetland edge is unsurprising. *Corylus* appears to have occurred close to the site throughout peat deposition, though is notably less well-represented in the macrofossil record (with in addition to fruits, only one budscale and one wood fragment recorded) than the other taxa which dominate the pollen record (*Quercus*, *Alnus glutinosa* and *Tilia*).

Salix was recorded in most of the pollen samples from the Caburn, though at very low frequencies (generally < 1% TLP-*Alnus*). The macrofossil remains give a rather different impression of *Salix* abundance with buds/budscales, wood, fruits, seeds and leaf fragments recorded throughout LPAZ-2 and 3. The latter demonstrate an on-site presence and confirm the potential for *Salix* to be heavily under-represented in pollen diagrams from fen carr deposits (e.g. Bush 1993; Waller 1994b).

The large endocarps of *Cornus sanguinea* were regularly recorded during LPAZ-1 and 2. *C. sanguinea* is therefore likely to have occurred adjacent to the site for an extended period, though on the drier soils (Preston *et al.* 2002). While *C. sanguinea* macrofossils are absent during LPAZ-3, the pollen continues to be regularly recorded suggesting a continued dry land presence.

The poor state of pollen preservation prevented the separation of much of the Rosaceae pollen recorded in the Caburn sequence. Such pollen occurs throughout the sequence with values of 5% TLP-*Alnus* in LPAZ-2 suggesting a local presence. Given their occurrence in modern *Alnus* woodland (Rodwell 1991); the macrofossil record suggests that much of this pollen derives from the shrubs *Crataegus* and *Prunus spinosa* in LPAZ-1, while in LPAZ-3 *Rubus* seems the most likely candidate. All three taxa are recorded as macrofossils in LPAZ-2.

Both the pollen and seeds of *Sambucus nigra* were recovered from LPAZ-2. *S. nigra* is a constituent of modern fen woodland and macrofossils are frequently recorded in investigations from floodplain sites (e.g. Branch *et al.* 2012; Deforce *et al.* 2014). The presence of *Viburnum opulus* seeds suggests that the poorly preserved *Viburnum* pollen recorded largely derives from this wetland species rather than the chalkland shrub *Viburnum lantana*.

A single pollen grain of *Buxus sempervirens* was recorded from the Caburn sequence. While this is insufficient to demonstrate box occurred in southern England in the mid-Holocene, with *Buxus* pollen also recorded from northern France at this time (Domenico *et al.* 2012), such a presence is plausible. No *Buxus* macrofossil remains were recovered.

Herbaceous taxa

A number of herbaceous taxa are only represented in the pollen record. Most are recorded sporadically and/or at low frequencies, though they include wetland taxa such as *Thalictrum*, *Lysimachia vulgaris*, *Chrysosplenium*, *Filipendula*, *Lotus*, *Lythrum portula*, *Gentianella campestris*-type and *Stachys*-type. As all are likely to have been growing nearby, their macrofossil absence probably in part reflects the small sample size. Others (*Limonium*, *Armeria maritima*, *Glaux maritima*, *Plantago maritima* and *Artemisia*-type) are associated

with brackish conditions and occur at the transition to and in the upper silty clays (in LPAZ-3d). A few, notably *Cynoglossum*, *Sanguisorba minor*, *Plantago media*, *Papaver rhoeas*, are likely to have been derived from open and disturbed dry habitats on the adjacent Chalk. The only unambiguously dry land herbaceous taxa regularly recorded in the pollen record (and not as a macrofossil) was *Plantago lanceolata* and pollen frequencies for this taxon only exceed 1% TLP-*Alnus* in LPAZ-2c and 3c/d.

Conversely a few herbaceous taxa are recorded as macrofossils while their palynological equivalent is absent (Fig. 3c). These include *Persicaria*, 27 fruits of which were recovered in LPAZ-2c, and rare *Viola*, and *Epilobium* seeds. With the *Persicaria*, low pollen production and limited dispersal, *P. hydropiper* is for example sometimes cleistogamous (Timson 1966), provide likely explanations. *P. hydropiper* is found in the margins of water and occurs along woodland rides. *P. maculosa* and *P. lapathifolia* are usually associated with disturbed land but also grow on exposed mud with Simmonds (1945) noting the presence of *P. lapathifolia* in fens and salt-marshes in North Germany. Also included in this category are taxa the pollen of which is not normally preserved (*Juncus* and *Luzula*). *Juncus articulatus* and *J. effusus* seeds occur immediately prior to the end of peat formation (Fig. 3d). Both are tolerant of brackish conditions (Preston *et al.* 2002), while the seeds of the saltmarsh taxon *J. gerardi* are abundant in the upper silty-clays. *J. inflexus*, which is recorded in LPAZ-2, is associated with base-rich soils and occurs in both herbaceous fens and open woodland. *Luzula sylvatica*, recorded from LPAZ-3, is likely to have grown in shaded habitats in drier areas (Rodwell 1991).

The small sample size used in the macrofossil investigations probably explains the mismatch between the common pollen and comparative rare macrofossil occurrence of the Brassicaceae, *Lythrum salicaria*, Scrophulariaceae and Rubiaceae all of which are likely to have been growing in the wetland. *Mercurialis perennis* pollen is regularly recorded and, as it is also present as macrofossil, is likely to have occurred in drier shaded areas close to the site alongside *L. sylvatica*. *Urtica*, *Rumex*, Caryophyllaceae, *Potentilla* and *Solanum dulcamara* are well-represented in both records, though as would be expected their macrofossil occurrence is more erratic. Where greater taxonomic precision is available (e.g. *Urtica dioica*, *Rumex cf. crispus*, *Lychnis flos-cuculi*) the macrofossil record is useful in showing that most of the pollen is likely to have been derived from taxa growing within the wetland.

Three herbaceous taxa (*Mentha/Origanum*, *Eupatorium cannabinum* and *Sium latifolium*) are particularly well represented as macrofossils. *Mentha*-type pollen is only occasionally recorded while the fruits of *Lycopus europeus* and *Mentha* are comparatively common. The former is associated with a variety of wet habitats and the latter almost certainly derive from the common fen taxa *Mentha aquatica*, though the fruits cannot easily be separated from other *Mentha* species or the chalkland herb *Origanum*. Most of the *Solidago virgaurea*-type pollen seems to have been derived from *Eupatorium cannabinum*, the seeds of which are abundant in LPAZ-2a. This species is found in a range of base-rich moist habitats including wet woodland (Preston *et al.* 2002) though seed production is likely to be associated with areas where the canopy is relatively open. Apiaceae pollen and the fruits of *Sium latifolium* occur throughout LPAZ-2 and 3. *Sium* is associated with alkaline conditions and occurs in a variety of tall-herb rich fen habitats often growing as an emergent. Unlike many of the other herbaceous taxa recorded it is intolerant of shade (Hill *et al.* 2004).

The macrofossil occurrence of *Carex* closely corresponds to the Cyperaceae pollen record suggesting that the pollen largely derives from wetland taxa. Both tussock (e.g. *Carex*

paniculata) and mat forming (e.g. *Carex acutiformis*) sedges commonly occur in modern *Alnus* dominated fen carr. The only other member of the Cyperaceae it was possible to resolve further taxonomically in the macrofossil record, *Scirpus sylvaticus*, is associated with wet woodland (Preston *et al.* 2002). In contrast, while Poaceae macrofossils were regularly recorded their occurrence does not match well with Poaceae pollen abundance. This does not just apply to the seeds, glumes were recorded during a period (LPAZ-3b/c) when Poaceae pollen frequencies are consistently < 5% TLP-*Alnus*. The source area for the Poaceae pollen may therefore be comparatively large, though whether it mostly derives from wet or dry habitats is still unclear.

Aquatics

Aside from *Sparganium emersum*-type, the pollen of aquatics is scarce if well distributed throughout the Caburn sequence. In contrast the macrofossils are generally unevenly distributed but often occur in some abundance (Fig. 3d). With *Ranunculus* wet or dry taxa may have contributed to the pollen record, though given that all are insect pollinated under-representation is likely. *R. flammula* macrofossils were recorded from the upper contact of the peat, while subgenus *Batrachium* fruits occur in some abundance in LPAZ-2. The latter suggest the presence of standing water, though some taxa (e.g. *R. hederaceus*) occur on the edges of shallow and/or impermanent waterbodies, a habitat that might also contain *Hydrocotyle vulgaris*, *Callitriche* and *Alisma plantago-aquatica*. All of these taxa are also shade tolerant (Grime *et al.* 2007). *A. plantago-aquatica*, which produces flowers on long stalks well above water-level, is exceptional in that the pollen and macrofossil records closely coincide suggesting that pollen occurrence indicates a local presence. *A. plantago-aquatica* is characteristic of sites with a fluctuating water-table (Grime *et al.* 2007). The presence of *Typha* fruits along with the high *Sparganium emersum*-type (which includes *Typha angustifolia*) pollen values in LPAZ-2 may indicate an expansion nearby in emergent vegetation. However, the coincidental abundance of *Artemisia*-type pollen, which is most likely to have been derived from the salt marsh taxon *Seriphidium maritimum*, suggests the presence of material inwashed as a result of inundation. Deforce *et al.* (2014) recovered the remains of such brackish indicators well above usual the tidal node, which was attributed to deposition during spring-tides or storm surges.

Mosses

Fifteen moss species were identified (Fig. 3d). Many have previously been recorded from Holocene coastal peats (Dickson 1973). Four species are regularly recorded in LPAZ-1 (*Brachythecium rutabulum*, *Homalothecium sericeum*, *Neckera complanata* and *Hypnum cupressiforme*). All are associated with woodland and, as is consistent with the abundant wood remains, occur as epiphytes. *B. rutabulum* and *N. complanata* are shade tolerant, while *H. sericeum* and *H. cupressiforme* prefer lightly shaded conditions (Blockeel *et al.* 2014). Of the minor taxa, *Bryum pseudotriquetum* and *Campyliadelphus elodes*, are associated with light shade/open conditions, including fens. In contrast, *Thamnobryum alopecurum* is shade tolerant and grows in abundance in woodland over Chalk (Blockeel *et al.* 2014) and is of particular interest as it was recorded at the very base of the sequence.

The abundance and diversity of mosses is greatest in LPAZ-2. Again the main species (which now include *Amblystegium serpens*) are associated with wet woodland. Most are likely to have been growing on wood, with *Ulota crispa* commonly occurring on *Salix* and *Mnium hornum* associated with dead wood on calcareous soils (Blockeel *et al.* 2014). *Calliergonella cuspidata*

has a wide ecological amplitude while *Oxyrrhynchium hians* occurs on the ground in woodland over Chalk (Blockeel *et al.* 2014). Mosses were least abundant in LPAZ-3, though taxa indicative of wet woodland (*A. serpens* and *B. rutabulum*) continue to be regularly recorded and *H. cupressiforme* (which will occur on dead wood) is common immediately prior to the end of peat formation.

Mollusca and Foraminifera

Nine terrestrial gastropod taxa were recovered from the basal sample (Table 2). All are tolerant of shaded environments and consistent with presence of woodland/scrub. The remains of *Carychium* are most abundant. *Carychium tridentatum* is frequent in deciduous woods and well-shaded places (Preece and Bridgland 1998). *Discus rotundatus*, *Clausilia bidentata*, *Aegopinella nitidula*, *A. pura* are associated with moist locations, while *Vitrea crystalline*, *Trochulus hispidus* and *Cochlicopa* sp. occur in wetter environments including fens (Kerney and Cameron 1979). *Pomatias elegans* occurs in shade, but is associated with loose friable calcareous soils (Kerney and Cameron 1979). A single specimen of *Discus rotundatus* was recovered from the overlying sample.

Foraminifera were recovered from the clayey silts which overlie the peat (Table 2). *Trochammmina inflata* and *Elphidium williamsoni* are indicative of hyposaline and inter-tidal sand flat environments respectively (Horton and Edwards 2006) and along with the remains of *Juncus gerardi* confirm a marine/brackish origin for this deposit. The continued occurrence of macrofossils of freshwater plants (e.g. *Alnus glutinosa* and *Salix*) in this deposit is therefore likely to indicate the presence of reworked material.

Discussion

The mid-Holocene vegetation of the Chalk

Reconstructing the vegetation history of the Chalk was the primary aim of the original investigations at the Caburn, with the pollen site selected so as to maximise the extra-local pollen component (*sensu* Jacobson and Bradshaw 1981). Waller and Hamilton (2000) concluded that the slopes above the site remained well-wooded throughout the mid-Holocene, with communities analogous to modern *Fraxinus excelsior*-*Acer campestre*-*Mercurialis* woodland (Rodwell 1991) present. Such woodland is typically found on calcareous mull soils.

The macrofossil investigations provide some extra detail as to the likely composition of this woodland. *T. platyphyllos* usually grows on freely draining soils and occurs on Chalk slopes. It is therefore one of the few taxa, along with *Cornus sanguinea*, recorded as a macrofossil in the Caburn sequence which is more certainly associated with dry woodland.

Rodwell (1991) notes that transitions between fen carr and dry deciduous woodlands are often gradual, masking discontinuities in substrate composition. *Quercus* is likely to have been favoured by moister and heavier soils and therefore to have occurred in such a wet-dry ecotone along with other taxa tolerant of waterlogging (e.g. *Ilex aquifolium*, *Crataegus*, *Mercurialis perennis*, *Rubus* and *Luzula sylvatica*). *Tilia cordata* rarely occurs on soils directly over Chalk (Pigott 1991, 2012). The nearest outcrop of an alternative solid stratum, the Gault (clay), lies *c.* 1 km to the south. It is therefore likely to have grown either on clay-

rich superficial deposits at the base of the slope or at the wetland edge. Interestingly, Pigott (1991) notes the occurrence of *T. cordata* in riverine woodland on the continent.

Tilia cordata and *T. platyphyllos* have been recorded in close association from modern situations (e.g. Pigott 1969, 1991) and previously from macrofossil investigations of alluvial deposits (e.g. Kelly and Osborne 1965; Deforce *et al.* 2014). Hybridisation between these taxa appears to have a long history, as demonstrated by the presence of *T. x europaea* fruits in the Caburn record and suggested from pollen morphology in previous studies (Godwin 1975; Pigott 1991, 2012). An effective isolating mechanism must therefore exist. *T. platyphyllos* flowers *c.* 15 days earlier than *T. cordata* and Pigott (1991, 2012) indicates that the hybrids flower simultaneously or at an intermediate time.

The fossil representation of a number of the taxa recorded in the Caburn sequence declines up the sequence. This in itself is likely to indicate a preference for the drier parts of the ecotone or the Chalk and to reflect the retreat of such areas away from the site as the wetland area expanded through time (see Waller 1994c; Deforce *et al.* 2014). In the pollen record this phenomenon is evident for *Ulmus*, *Fraxinus excelsior*, *Tilia*, *Corylus avellana*, *Rhamnus catharticus* and *Hedera helix*, while in the macrofossils it is most apparent for *Tilia* spp., *Cornus sanguinea* and *Prunus spinosa*.

While indicating that the pollen source area remained well-wooded, Waller and Hamilton (2000) detail evidence for a number of woodland disturbance phases. High frequencies of herbaceous pollen in LPAZ-2a, 2c and 3c were attributed to clearance, fluctuating tree pollen values in LPAZ-2 to woodland management and high *Taxus baccata* pollen frequencies in LPAZ-3a and 3b to the establishment of secondary woodland. The macrofossil evidence offers little support for such interpretations. The increases in herbaceous pollen occur in types with an ambiguous environment of origin, but which now can be shown to coincide with the local presence of wetland taxa notably *Eupatorium cannabinum*, *Rumex crispus*, *Sium latifolium* and *Carex*. In addition, *Taxus baccata* may have been growing locally. That most of the tree and herbaceous types well-represented in the pollen record occur as macrofossils confirms, as would be expected for a wooded site, that the pollen source area for the Caburn sequence is small. Modern pollen studies of *Alnus* dominated fen carr (Bunting *et al.* 2005) indicate a relevant source area (*sensu* Sugita 1994) in the order of 50-150 m. Therefore while the occurrence of *Juniperus communis* and the pollen of herbs such as *Sanguisorba minor* hint at the occurrence of open habitats on the Chalk, their presence and changes in extent are masked by the surrounding woodland.

Wetland vegetation dynamics

The Caburn macrofossils primarily provide information on the nature and dynamics of the wetland environment. The mid-Holocene sediments at the base of the Caburn are the product of a high water-table (the minerotrophic peat) or are waterborne (the clastic component). The accumulation of 3 m of such sediment requires the creation of accommodation space, which ultimately in such coastal locations is provided by sea-level rise, though sediment consolidation and compaction can also be important (e.g. Horton and Shennan 2009). The sea-level curves produced for the southern North Sea indicate peat formation at the Caburn commenced at the end of a long period of rapid sea-level rise, with a notable decline in the rate of rise occurring around 6000 cal a BP (see for example Vink *et al.* 2007; Waller and Long 2010). The latter is probably reflected in the up-sequence decline in the rate of peat

accumulation, though this is also likely to have been influenced by differential compaction of the upper layers following the deposition of the overlying clayey silts.

With the basal organic sediment highly humified, paludification appears to have commenced prior to the site becoming permanently waterlogged. LPAZ-1a, the plant macrofossils and molluscs all suggest the development of woodland in which taxa tolerant of waterlogging predominated (with *Quercus* and shrubs including *Corylus avellana*, *Crataegus* and *Prunus spinosa*). Herbaceous taxa indicative of wet conditions (e.g. *Mentha*, *Carex*) are also present in the macrofossil record and along with the mollusc *Trochulus hispidus* are probably an indication of gaps left as species less tolerant of such conditions were eliminated. As the water-table continued to rise *Alnus glutinosa* dominated woodland became established.

From the beginning of LPAZ-1b until the deposition of the clayey silts (LPAZ-3d) *Alnus glutinosa* macrofossils are continuously, if variably, recorded. Other taxa associated with modern *Alnus* dominated communities (the *Alnus glutinosa*-*Carex paniculata* and *Alnus glutinosa*-*Urtica dioica* woodlands of Rodwell 1991) notably *Salix*, *Urtica dioica* and *Carex* also occur regularly as macrofossils. With fen carr a component of the wetland vegetation over an extended period, this community must have undergone internal regeneration. Under stable conditions, as a result of producing large quantities of organic material, *Alnus* dominated vegetation might be expected to outgrow the water-table, leading to the establishment of species with a preference for drier conditions (e.g. Walker 1970). In coastal situations such as the Caburn the long-term maintenance of fen carr is, however, likely to be linked to the continued creation of accommodation space and therefore allogenicly driven. During the earlier stages of peat formation at the Caburn (LPAZ-1), the combination of rising water-levels and rapid sediment accumulation will have resulted in trees becoming moribund, without surfaces becoming sufficiently dry to enable the establishment of successor communities (Rodwell 1991). The collapse of trees would then have promoted a further phase of development. As the depth of peat increased (LPAZ-2 and 3) consolidation is likely to have become increasingly important in initiating regeneration. As described by Lambert (1951), the weight of trees over unconsolidated surfaces produces subsidence leading to the development of pools and eventually tree death. The up-sequence decline in the quantity of wood remains, despite the continued abundance of *Alnus* fruits and cones, may reflect a decline in the size of trees (related to their longevity and weight) as consolidation became increasingly influential, with the increasing peat depth also giving shallower rooted species a competitive advantage (see below).

The ability to identify such regeneration phases in palaeoecological records is dependent upon the temporal and spatial scales over which they occur. With local variations in the stability of the surface (influenced by factors such as the depth to bedrock and the composition of the peat), neither the simultaneous dieback of trees over large areas or regular cycles would be expected. This probably explains why in coastal/floodplain situations, where fen carr vegetation is likely to have been extensive, regeneration phases are difficult to discern in pollen records which show the long-term persistence of *Alnus glutinosa* (e.g. Waller 1993, 1994a). Pollen data may not be sensing the vegetation at an appropriate spatial scale, particularly as local openings are likely to be accompanied by an increase in the pollen source area. At the Caburn, the substantial fluctuations in the number of *Alnus glutinosa* propagules provide support for phases of decline and regeneration (e.g. low numbers at the LPAZ3a/b boundary and increase in LPAZ-3b). In addition, with high light intensities required for the survival of *Alnus* seedlings (McVean 1956), increases in herbaceous taxa would be expected following the creation of gaps. Although the number of macrofossils

recorded is often small and patterns in abundance are not always evident, light demanding taxa (e.g. *Sium latifolium*, *Persicaria* and the moss *Campyliadelphus elodes*) occur throughout the sequence. The macrofossil data is then consistent with gap creation and regeneration occurring on a small-scale. However, due to the limitations of the technique, the lack of comparability between samples and taphonomic issues, notably the high dispersal capacity of *Alnus* propagules (Greatrex 1983), it is not possible, unequivocally, to resolve individual phases.

The increases in the macrofossils of aquatics (e.g. *Ranunculus* subgenus *Batrachium*, *Alisma plantago-aquatica*) and semi-aquatic herbs (e.g. *Sium latifolium*, *Lycopus europaeus*) in LPAZ-2 and LPAZ-3 appear inconsistent with the drier conditions which might be expected to accompany the slower rate of water-table rise, as indicated by the up-sequence decline in the sediment accumulation rate. This apparent contradiction may be explained by the creation of pools through consolidation, the presence of which is compatible with the occurrence of large numbers of well-preserved macrofossil remains (notably in LPAZ-2). Alternatively, changes in the distribution of watercourses on the floodplain as a result of channel avulsion may periodically have brought open water transitions closer to the site. In addition, the slow-down in the sediment accumulation and/or sediment consolidation is likely to have been responsible for the overall increase in the inorganic content of the sediment, evident in the loss-on-ignition data from the start of LPAZ-3 (Fig. 2). With the height of sediment surface rising more slowly, the floodplain would have been increasingly vulnerable to inundation. This appears to be reflected in the fossil record through the presence of taxa associated with sites flooded with mineral enriched water in LPAZ-3 (e.g. *Scirpus sylvaticus*, Rodwell 1991). As a consequence, the inwash of pollen and macrofossils from aquatic environments may also have increased (as suspected for LPAZ-2c).

The combined pollen-macrofossil record suggests that *Taxus baccata* may have occurred within the wetland area during LPAZ-3 (c. 5400 to 4000 cal a BP). If so, then the Caburn adds to the number of sites in the lowland areas adjacent to the southern North Sea where yew was a component of fen carr vegetation (e.g. Godwin 1968; Deforce and Bastiaens 2007; Branch *et al.* 2012). Dated sequences with high (> 5% TLP) *Taxus* pollen values fall into a relative narrow time-window; c. 4900 to 3900 cal a BP for Hornchurch marshes (Branch *et al.* 2012) and from c. 5600 to 3600 cal a BP for the sites in Belgium and the southern Netherlands (Deforce and Bastiaens 2007). This suggests regional factors underlie both the development and disappearance of the conditions which enabled *Taxus* to grow in such environments. As discussed by Branch *et al.* (2012), *Taxus* is likely to have been favoured by relatively dry and stable conditions. At the Caburn, local establishment in LPAZ-3 ties in with the up-sequence decline in the rate of peat accumulation. Regionally, this was an extended period of peat formation and the shallow rooting habit of yew (Thomas and Polwart 2003) may, for the reasons noted earlier, be the critical factor which enabled *Taxus* to grow on peat, though as indicated at the Caburn, it seems that trees growing in such situations would still have been subject to regular inundation. The proximity of seed sources is an additional consideration in terms of colonisation. *Taxus* pollen is recorded at the Caburn consistently, if at low values, from c. 7000 cal a BP and the presence of yew nearby on the Chalk is likely to have enabled colonisation earlier than at many of the other sites and may also explain the apparent absence of yew from similar deposits found adjacent to acid lithologies along the south coast of England (e.g. the Romney Marsh depositional complex). The disappearance of *Taxus* from such environments can locally be attributed to a number of factors; inundation with marine/brackish water (Hornchurch Marshes, the Caburn) or in the case of some of the continental sites the development of raised bog. Such proximate causes

can also ultimately be linked to regional environmental changes (see Waller and Grant 2012, Deforce and Bastiaens 2007).

Conclusions

With a large number of plant macrofossils recovered for the quantity of sediment examined, the investigations described in this paper complement the earlier pollen study and together they provide a detailed picture of the vegetation of the wetland and at the wet-dry ecotone prior to extensive human modification. The occurrence of *Tilia platyphyllos* fruits shows that the association of this taxon with calcareous soils extends back into the mid-Holocene, as does hybridization between *T. platyphyllos* and *T. cordata*. *Taxus baccata* appears to have occurred in, or at least at the very edge of, the wetland.

The combined investigations from Caburn serve to illustrate the constraints that must be borne in mind when palaeoecological reconstructions are made from peats deposited within coastal/floodplain alluvium. With plant macrofossils analysis, they include a lack of homogeneity in the sediment matrix as a result of the presence of wood remains which compromises the comparability of the samples. In this respect the calculation of wood volume may be more useful than the number of fragments present. In addition, in the southern North Sea region, such studies are likely to be temporally biased towards the mid-Holocene with later sediments deposited at higher altitudes and invariably highly humified as a result of recent land drainage.

Many of the short-comings of pollen analysis have already been noted. Most importantly, this combined pollen-macrofossil study supports previous work both in terms of the small size of the pollen source area indicated for fen carr sites and the likely wetland origin for many of the herbaceous pollen types generally regarded as indicators of anthropogenic activity. Both must be borne in mind when attempting to reconstruct the vegetation of adjacent dry land areas. The use of pollen data from such situations in land-cover reconstructions is likely, for example, to produce anomalous results if openness is equated with the clearance of dry land areas (see Trondman *et al.* 2014). The Caburn macrofossil analysis also suggests that deposition via inflorescences is likely to be an important mode of pollen delivery from plant to sediment. Caution is therefore required when interpreting fluctuations in pollen values and using data derived from such deposits in pollen models (e.g. Sugita 2007) that assume aerial transport is the dominant mode.

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Figures and Tables

Figure 1 Location maps and stratigraphy. (A) The Chalk outcrop in England. (B) The Lower Glynde-Ouse valleys and Mount Caburn. (C) Lithostratigraphy of the Glynde valley adjacent to the Caburn.

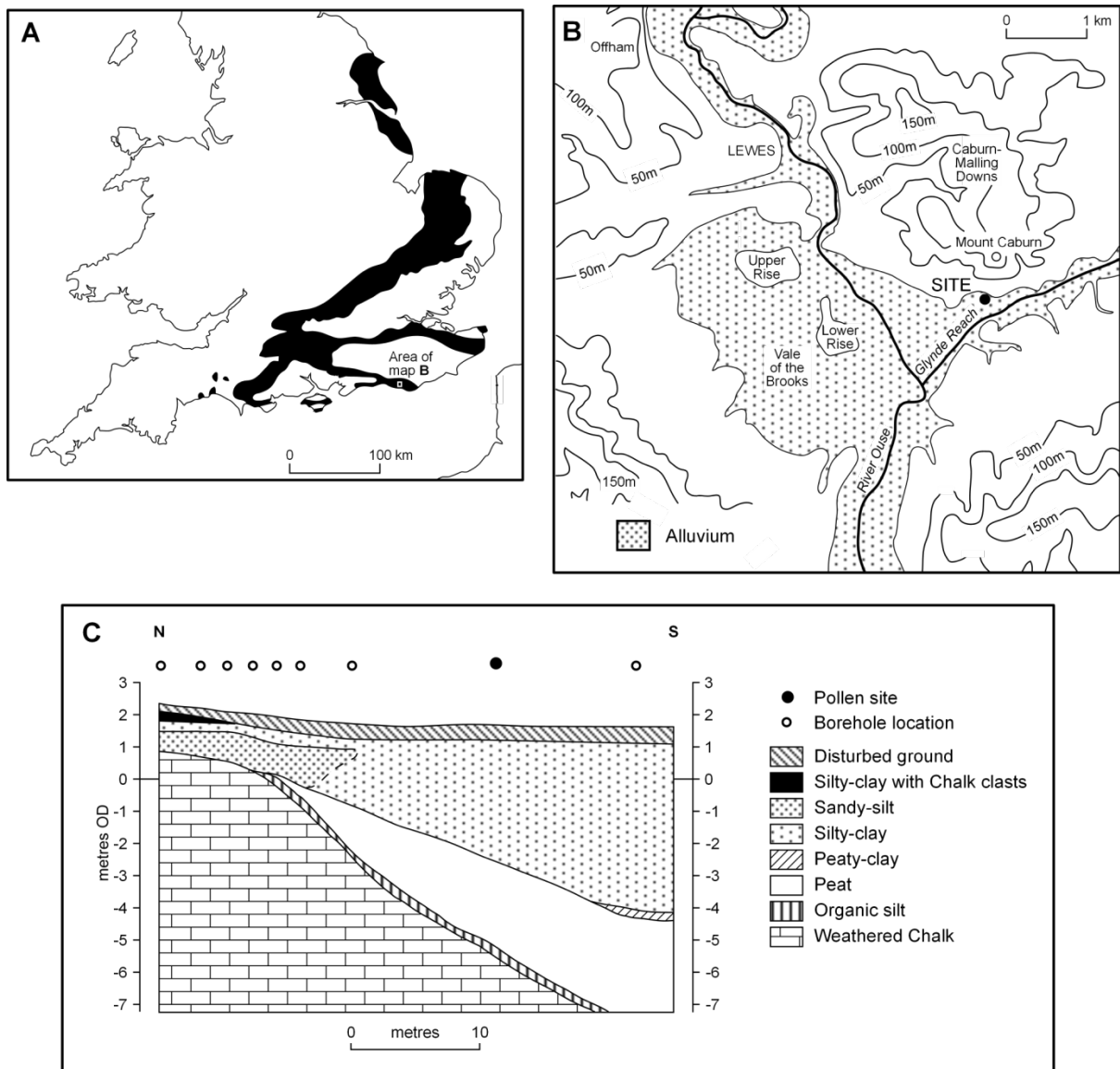


Figure 2 Macrofossil summary diagram: propagule numbers recovered, propagule numbers to a standardized volume (40 cm^3), propagule accumulation rate, numbers of species present, moss abundance and loss-on-ignition values. Lithology follows Troels-Smith 1955.

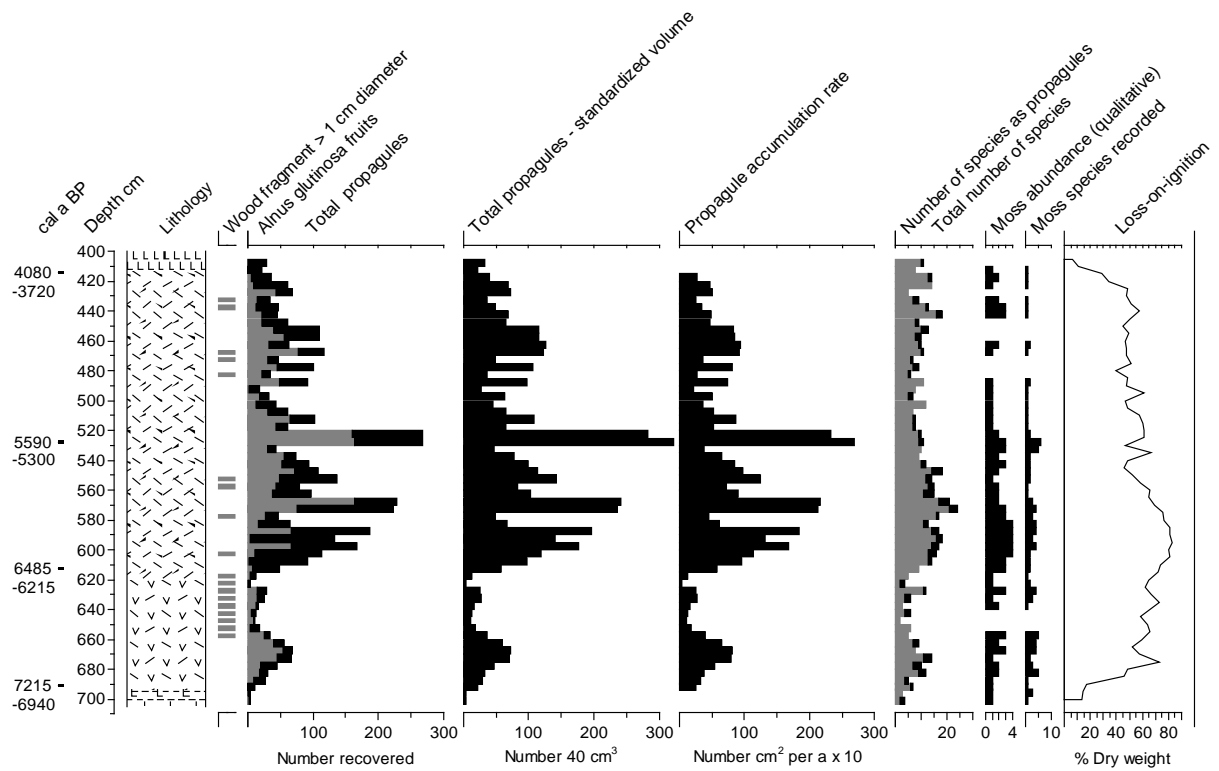
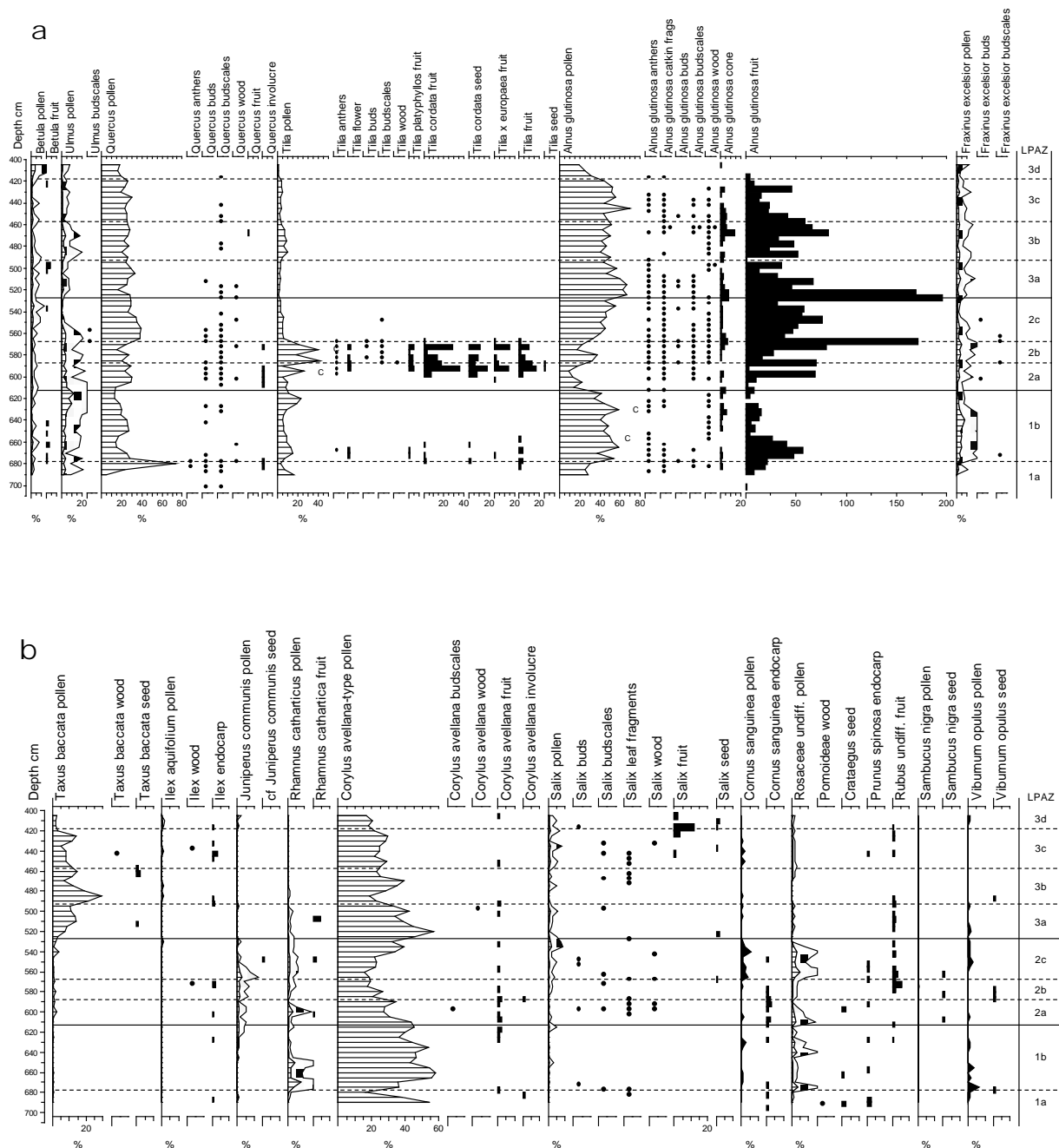
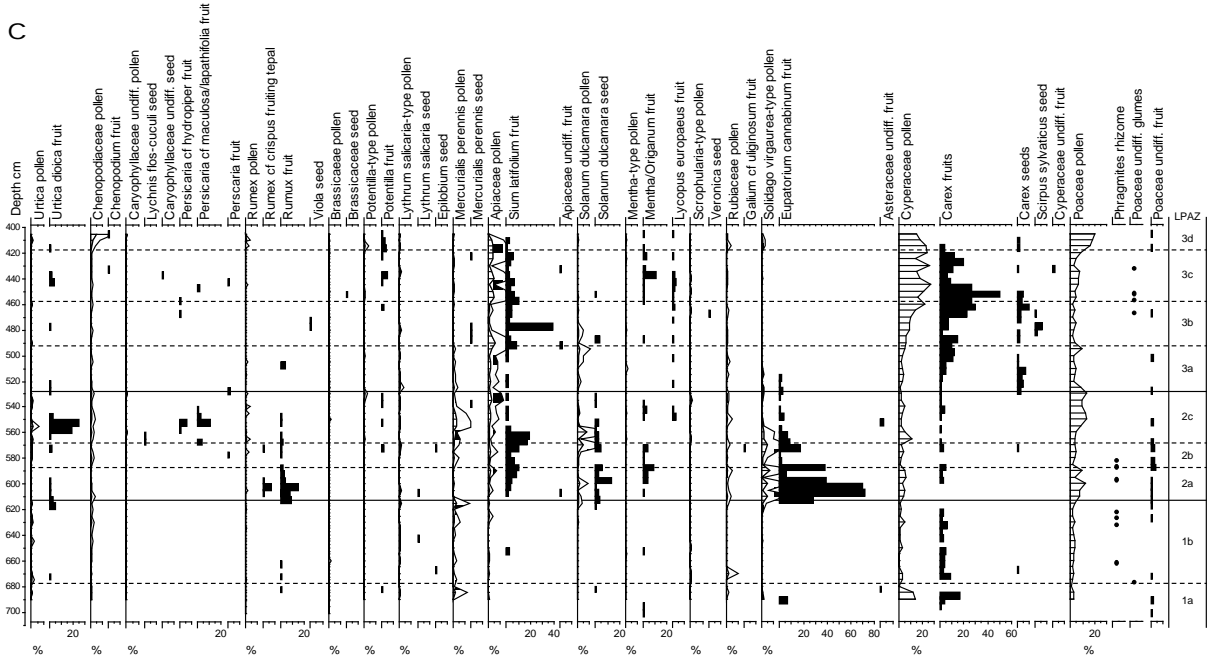


Figure 3 Comparison of the pollen and macrofossil data from the Caburn. (a) trees (b) small trees/shrubs and the Rosaceae (c) herbs, Cyperaceae and Poaceae (d) Juncaceae, aquatics and mosses. For the pollen data, with exception of *Alnus* (% TLP), the % TLP-*Alnus* values are shown as a continuous curve (with x 5 exaggeration where necessary), the vegetative remains as a presence (closed circles) and the reproductive remains as numbers to a standardize volume (40 cm³). C = pollen clusters. As indicated, ordinal values are used to show moss representation. The zonation follows Waller and Hamilton (2000).



C



d

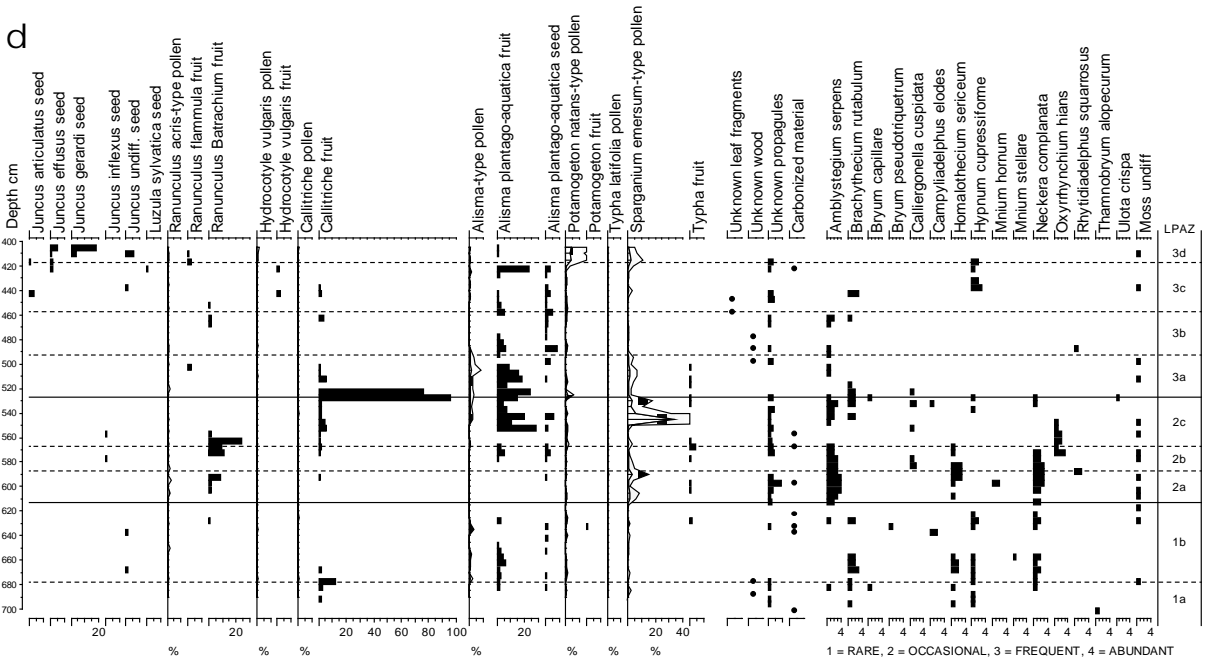


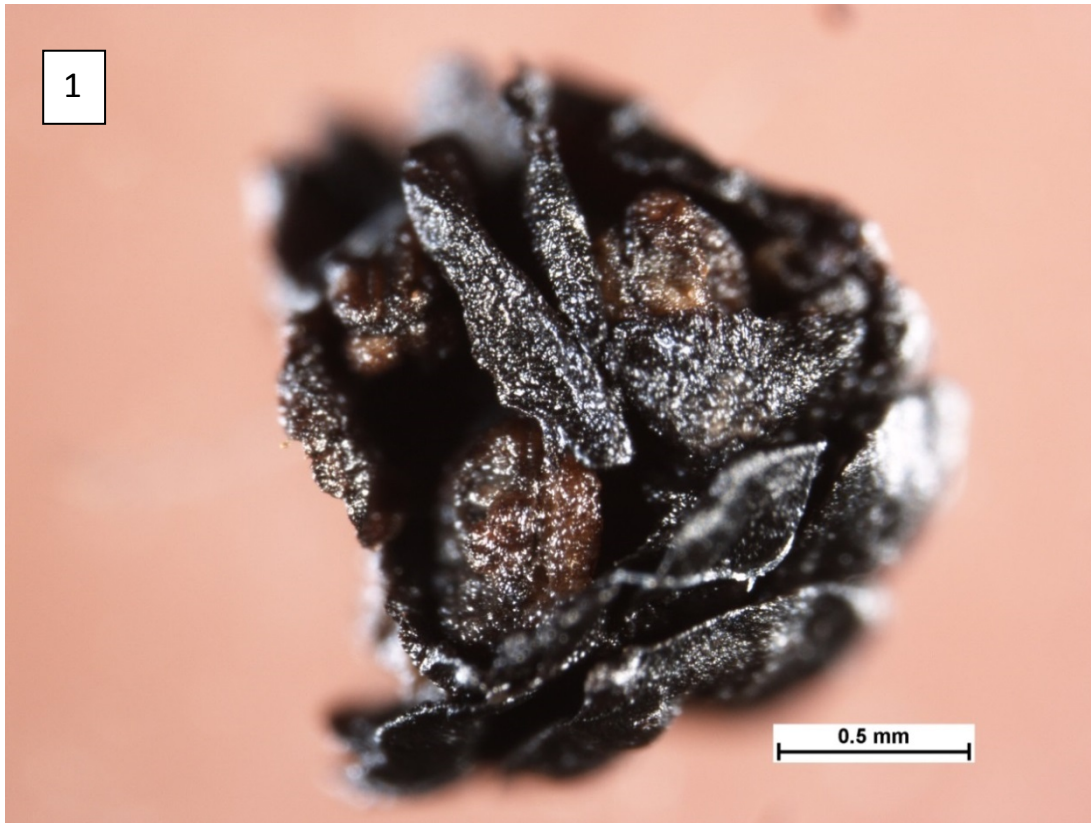
Table 1 Lithology of the core used for the pollen and macrofossil analyses. Notation follows Troels-Smith (1955).

Depth	Lithology
above 413 cm (-2.54 m OD)	Bluish grey clayey silt Nig. 2, Strf. 0, Elas. 0, Sicc. 2. Ag3, As1, Ga+, Dg+, Th ²⁺ , Tm+
413-551 cm (-2.54 to -3.92 m OD)	Brown slightly silty detrital peat Nig. 3, Strf. 0, Elas. 0, Sicc. 2, Lim sup. 0. Dg3, Dh1, Dl+, Th ²⁺ , Tb+, Ag+
551 - 620 cm (-3.92 to -4.61 m OD)	Brown detrital peat Nig. 3, Strf. 0, Elas. 0, Sicc. 2, Lim sup. 0. Dg3, Dh1, Dl+, Tb+, Th ²⁺ , Ag+
620 - 693 cm (-4.61 to -5.34 m OD)	Brown detrital peat with wood Nig. 3, Strf. 0, Elas. 0, Sicc. 2, Lim sup. 0. Dg2, Dh1, Dl1, Th ²⁺ , Ag+
693 - 704 cm (-5.34 to -5.45 m OD)	Transitional brownish grey organic silt Nig. 2, Strf. 1, Elas. 0, Sicc. 2, Lim sup. 0. Sh2 Ag2, Dg+, Th ²⁺ , Gg+
below 704 cm (-5.45 m OD)	Greyish white silt with Chalk fragments Nig. 1, Strf. 0, Elas. 0, Sicc. 1, Lim sup. 0. Ag3, Gg1

Table 2 The mollusca and foraminifera recovered respectively from the base and top of the Caburn sequence.

Species	403-408 cm	408-413 cm	413-418 cm	693-698 cm	698-704 cm
Mollusca					
<i>Discus rotundatus</i>				1	4
<i>Clausilia bidentata</i>					5
<i>Pomatias elegans</i>					1
<i>Cochlicopa</i> sp.					1
<i>Vitrea</i> sp.					2
<i>Carychium tridentatum</i>					7
<i>Carychium</i> sp.					4
<i>Aegopinella nitidula</i>					4
<i>Aegopinella pura</i>					2
<i>Trochulus hispidus</i>					1
Foraminifera					
<i>Trochammina inflata</i>	10	7	1		
<i>Elphidium williamsoni</i>	126	10			

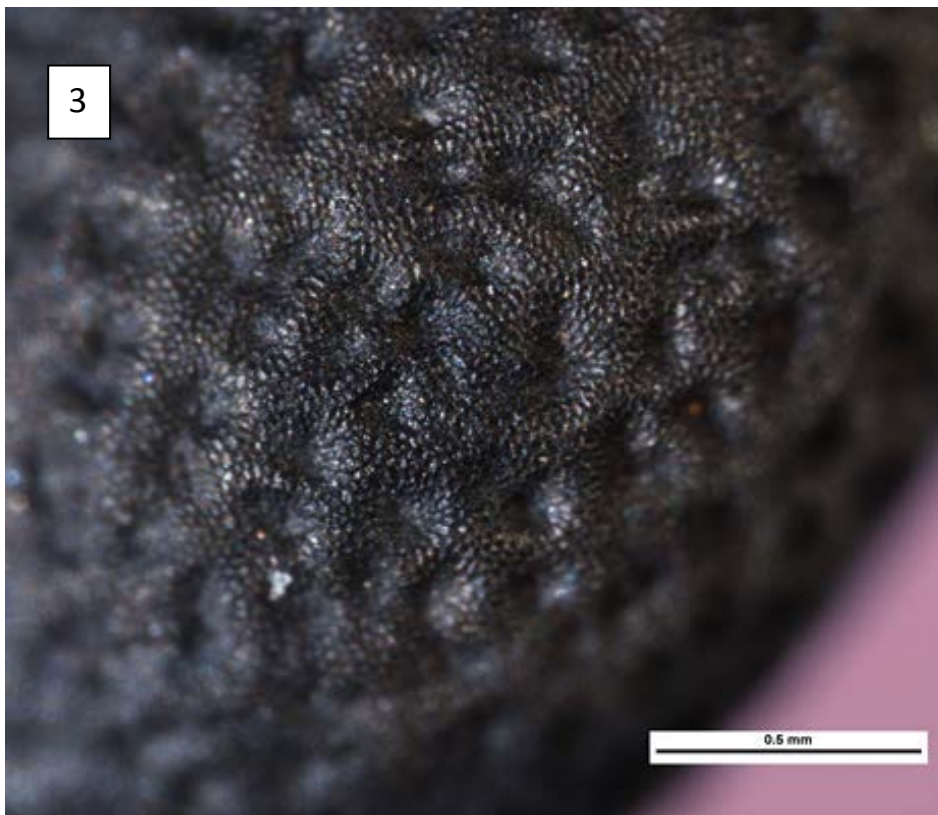
Supporting Information: Photographs of select plant macrofossil remains from the Caburn



1. *Alnus glutinosa* catkin fragment showing *in situ* anthers



2. *Alnus glutinosa* anthers



3. *Mercurialis perennis* seed: detail of sculpturing pattern (not shown in most seed illustration guides)



4. *Sium latifolium* fruit



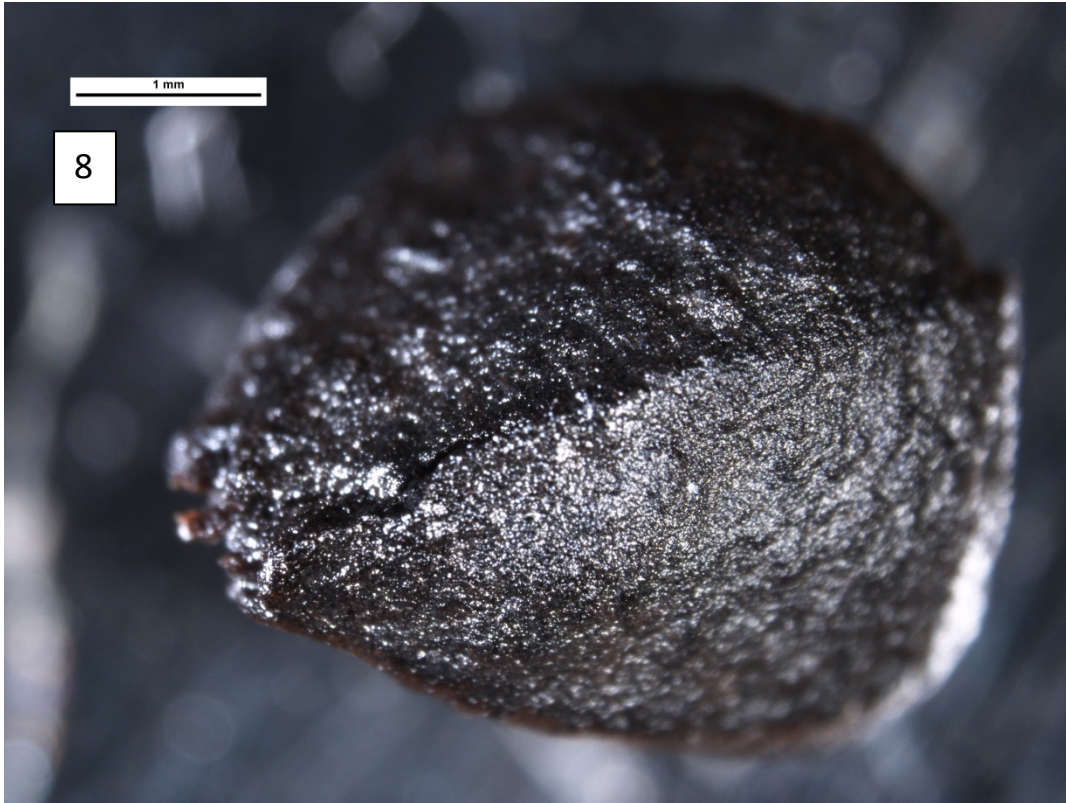
5. *Tilia* 'flower'. The anthers and the edge of the ovary and style are visible



6. *Tilia* stamens



7. *Tilia cordata* fruit



8. *Tilia platyphyllos* fruit showing rib