Disentangling the pollen signal from fen systems: modern and Holocene studies from southern and eastern England.

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Abstract

Thick deposits of peat derived from fen environments accumulated in the coastal lowland areas adjacent to the North Sea during the middle and late Holocene. These sediments are frequently used in pollen-based reconstructions of *in situ* and more distant vegetation. However, discriminating between wetland and dry land originating pollen signals, and between the potential fen communities present in the wetland, is complex. In this study, a suite of analytical approaches are used to explore the pollen signal of modern fen communities and compare them against Holocene pollen assemblages. At two sites in eastern England, Woodwalton Fen and Upton Broad, vegetation composition was recorded around a series of moss polster sampling points. The communities investigated included herbaceous fen communities under different cutting regimes, a grazed area, glades, and woodland with canopies dominated by *Alnus glutinosa* and *Betula*. Cluster analysis is used to provide an overview of, and compare the structure within, the datasets consisting of the vegetation, the vegetation converted to palynological equivalents, and the pollen data. It is demonstrated that any loss of taxonomic precision in pollen identifications does not pose particular problems when attempting to identify fen communities, including tall-herbaceous vegetation, in the pollen record. Indices of Association imply pollen presence can be interpreted as indicating the local presence for some taxa, though few of these are confined to a particular community. Herbaceous fen vegetation subject to different management regimes are, however, shown to produce distinctive pollen signatures. Middle and late Holocene pollen assemblages from eastern (Fenland) and southern (Romney Marsh) England, interpreted as derived from fen vegetation, are compared against the modern pollen dataset using ordination. Most of the fossil samples plot out within or adjacent to the groupings produced by the modern samples in the ordinations. While these investigations demonstrate that modern pollen work can help improve the interpretation of Holocene assemblages they also call attention to a number of limitations including the restricted range of communities from which modern samples are currently available and the potential for non-analogous modern vegetation. The paper concludes with ideas to aid the interpretation of pollen data collected from fen peats and suggestions for future work.

Keywords: fen vegetation, pollen-vegetation relationships, Holocene palaeoecology, coastal lowland, modern pollen deposition, peat

1. Introduction

The palynological properties of fens, base-rich mires which include both herbaceous and wooded vegetation (Wheeler and Proctor, 2000), have received little attention in comparison to lakes and raised bogs (though see Janssen, 1967, 1973, 1984; Waller et al., 2005; Bunting et al., 2005; Barthelmes et al., 2006; Prager et al., 2006, 2012). This, in part, reflects the representation of fen communities in the stratigraphic record of north-west Europe which is often limited to a transitional phase in hydroseral successions. In such successions, the accumulation of material in the productive reedswamp, semi-terrestrial herbaceous fen and fen woodland stages can rapidly bring the sediment surface above the groundwater level and, when climatic conditions are conducive, lead to the formation of raised bog (Walker, 1970; Hughes and Barber, 2003). The presence of swamp and fen vegetation over extended periods of time seems to require sediment accumulation to be matched by rising groundwater-levels. Such conditions do however seem to have prevailed during the Holocene in some lowland riverine and coastal settings in Britain and the North Sea region, leaving thick deposits of fen peat (Godwin, 1943, 1945).

Such deposits generally accumulated under woody fen communities, dominated notably by *Alnus glutinosa*. Fens like this occupied some coastal lowland sites for several thousand years (e.g. Waller, 1993, 1994a; Deforce, 2011; Branch et al., 2012; Deforce et al., 2014; Waller and Early, 2015) in the middle Holocene, defined as *c*. 8200-4200 cal. yrs BP (following Walker et al., 2012). Ground water conditions remained suitable as a result of rising relative sea-level (e.g. Kiden et al., 2002, Shennan et al., 2006; Bradley et al., 2011) with regeneration probably occurring continuously, at a small-scale in a mosaic pattern (Waller and Early, 2015). Areas of swamp and herbaceous fen also appear capable of persisting over long periods. Waller (1994b), Long and Innes (1995), Waller et al. (1999) and Jennings et al. (2003) report late Holocene (*c*. 4200-0 cal. yrs BP) pollen assemblages dominated by Poaceae, Cyperaceae and other herbs, interpreted as representing open fen vegetation, at sites in the East Anglian Fenland and around the south coast of England, which span periods >1000 years. However, discriminating between the different potential swamp and fen vegetation types present is hampered by a number of factors, including the lack of taxonomic precision in pollen identifications, notably in the Poaceae and Cyperaceae. In many sedimentary records from coastal lowland regions plant macrofossils are not preserved, probably as a result of extensive drainage of the wetlands in historical times. Modern studies of the pollen signal from herbaceous fen vegetation are therefore required to understand the nature of these inferred communities and the conditions required for their persistence.

Fen peats make up a significant proportion of the resource available for palaeoecological investigation in the regions which border the southern North Sea (see Grant and Waller, In Press), and thus are potentially useful sources of information on the past vegetation communities of, and changes in land-cover on, adjacent dry land areas. Such reconstructions presuppose that the pollen signals from the dry and wet communities can be effectively separated. Determining the source of pollen types is made more challenging by the lack of taxonomic precision; for example plants in the pollen types Apiaceae, Brassicaceae and *Rumex* occur in fen as well as dry land communities. This is especially true in the late Holocene, when the proportion of herbaceous pollen in sequences rises and both wet and dry land are likely to have been subject to anthropogenic activity. Particularly problematic are assumptions that low frequencies of herbaceous pollen in records dominated by fen woodland taxa such as *Alnus* derive from dry land areas and that major increases in Poaceae pollen result from the clearance of dry land areas. In addition, large Poaceae grains should not be habitually attributed to ‘cereal’ categories given the occurrence of wetland grasses which have overlapping pollen size characteristics (Waller and Grant, 2012).

This paper presents vegetation and modern pollen data from sites where a range of both woody and herbaceous fen/swamp communities are present and looks at the potential for using both the indicator species and modern analogue (comparative) approaches in the interpretation of Holocene pollen data believed to be derived from fen communities. The specific research questions addressed are:

1) What influence does the loss of taxonomic precision in pollen identification have on the differentiation of fen plant communities?

2) What pollen signal do small open areas in fen woodland produce and could herbaceous pollen in assemblages dominated by fen carr taxa be derived from regeneration gaps rather than from dry land?

3) Do herbaceous fen communities that are subject to different management regimes (variations in cutting/mowing and grazing) have distinct pollen signatures?

4) How comparable are Holocene pollen assemblages from fen peats to the pollen signals produced by modern fen communities?

2. Description of Study Sites

2.1 Characteristics of fen vegetation communities

As with other mire communities, fen vegetation is complex and difficult to classify. Here we follow Wheeler and Proctor (2000) who argue that three gradients account for most of the ecological and floristic variation in north-west European mires. In addition to water level these are pH and fertility (mainly levels of N and P), with fen vegetation associated with neutral and base-rich conditions and a wide range of nutrient levels (Fig. 1).

Swamps are species poor communities dominated by tall monocotyledons that occur at transitions to open water, where the sediment surface is seasonally or permanently submerged (Rodwell, 1995). The species commonly associated with such areas in north-west Europe is *Phragmites australis*, though other grasses with similar growth forms can also dominate (e.g. *Phalaris arundinacea*, *Glyceria maxima*). Fens occupy the seasonally or periodically flooded habitat zone between swamps and dry land communities and include both herbaceous fens and wet woodlands. Herbaceous fens are both floristically and ecologically varied. Sedges are often, though not always, dominant, with other monocotyledons including rushes (e.g. *Juncus subnodulosus*) and grasses (e.g. *Calamagrostis canescens*) frequently abundant (Wheeler, 1980a). The sedges present include both tussock forming species (*Carex paniculata*) and species with stout shoots which form dense clumps (e.g. *Cladium mariscus*). Sedge dominated communities occupy a continuum between eutrophic and oligotrophic conditions with species such as *Carex rostrata* characteristic in nutrient poor environments (Wheeler and Proctor, 2000). Historically, in eastern England, such communities were exploited by cutting and/or grazing (Darby, 1983; Coles and Hall, 1994; Rippon, 2000). Today such management, which is likely to be required to prevent rapid (< 50 years) encroachment by scrub (Weigers, 1992), is generally undertaken to maintain their characteristic biodiversity and conservation value.

The term carr can be used to describe a number of woodland and shrub communities associated with freshwater wetlands, which are generally regarded as representing a relatively dry environment, where the sediment surface is close to the average water level (Weigers, 1992). On nutrient-rich substrata, *Alnus glutinosa* frequently forms the canopy layer in what is often a diverse community (Wheeler, 1980b; Rodwell, 1991a). Typically, a shrub layer is present, often with *Salix cinerea*, though many other species are possible. At ground level conditions vary from the presence of tall herbs (those associated with herbaceous fens) and climbing-trailing plants, to a carpet of small herbs (e.g. *Chrysosplenium oppositifolium*) and grasses, or to 'hummock' areas (moss covered trunk bases and sedge tussocks), interspersed between pools of water. Carr dominated by *Salix* can form separate communities or transitional zones between herbaceous fen and *Alnus* carr, while *Betula* dominated communities (often again with *Salix*) occur in meso- and oligotrophic situations (Rodwell, 1991a).

2.2 Fen study sites

Two sites in Eastern England (Fig. 2) containing fen systems that include both herbaceous and woody vegetation were selected for investigation.

On the south-western edge of the Fenland basin in Huntingdonshire (Fig. 2c), Woodwalton Fen (52°26'N 0°11'W) comprises a 205 ha block of relict peatland (Fig. 2a). A nature reserve since 1919, Woodwalton forms a core part of the 'Great Fen' restoration project, though when sampled in 2014/5 was mostly surrounded by root crops. A range of wetland plant communities are present including woodland and both acidophilous herb-dominated vegetation (*Molinia caerulea* dominated heath/mire) and herbaceous fen. The areas sampled in 2014/5 (see Table 1 and Fig. 2) comprise woodland dominated by *Alnus glutinosa* and *Betula*, glades (areas of herbaceous fen surrounded by woodland, some unmanaged and some mown annually), sedge fen (with *Carex viridula*, *Carex panicea* and *Molinia*) mown annually, and a *Juncus* and sedge dominated grazed area. In the mown areas the cuttings are gathered and removed. The *Juncus* pasture (sampled in 2015) was subject to light grazing with cattle in the autumn of 2014. A fifth habitat, referred to here as *Phragmites* fen, is classified as reedswamp (S26; Rodwell, 1995), and listed as having been subject to a 4 year cutting rotation in the management plan. However, while apparently remaining uncut for *c*. 20 years (Bowley pers. comm.), it has been subject to renovation via scrub clearance (1983/4) and local lowering of the ground surface (1997-2003). That the area now more closely resembles S24 tall-herb fen rather than S26 (following Rodwell, 1995) is likely to reflect the lack of recent management.

Upton Broad (52°40'N 1°31'E) in Norfolk (Fig. 2b) is a 105 ha site in which tall-herbaceous fen and fen woodland communities surround an area of open water. The communities sampled in 2013 (Table 1) consist of two wooded areas, one with *Alnus glutinosa* and *Fraxinus excelsior* the main canopy-forming species, and one consisting of predominantly *Betula, Quercus robur* and *Salix*. The open habitats comprise reedswamp with *Phragmites australis* and *Carex riparia* and tall-herbaceous fens in which *Calamagrostis canescens* is abundant alongside *Cladium mariscus* or *Juncus subnodulosus*. The herbaceous communities are mown, with the cuttings collected and removed, on a 7-8 year rotation. The surrounding land consists of both pasture and arable.

3. Methods

Each distinct fen community at Woodwalton and Upton (Table 1) was sampled at least at ten points, located along transects to ease relocation. The points were a minimum distance of six metres apart. The vegetation within a 2 m radius circular sampling area at each location was recorded using a point quadrat method (Waller et al., 2005). The circle was divided into five rings of equal area with each ring sampled at 45° intervals around the circle. The central point was also sampled (giving a total of 41 locations). The canopy (recorded using a mirror) and the flora < 1 m high was recorded on a first hit basis for each species. Any ground flora or canopy species not hit, but occurring within 2 m of the centre of the circle, were also noted. To record the spring ephemerals and perennials present (Farrell et al., 2016), the woodlands were sampled earlier (April/May) than the open communities (July/September). Taxa recorded in the vegetation were reclassified into their palynological equivalents (see Table 2) using the scheme of Bennett (1995-2007), and both the original plant lists (V) and palynological equivalent vegetation lists (PEv) were used in the analyses.

A 2 m radius survey area was chosen both to limit vegetation disturbance and effort-cost, but also since we believe that the effective pollen source area for much of the local vegetation in these systems is on the order of a few metres, especially for the shorter components. Our research questions focus on palynological identification of ecologically different fen communities and the detectability of the pollen signal of the wider landscape, therefore survey distance around individual samples is less important than ensuring that as many communities as possible were sampled with multiple sampling points in each community. Evidence for a strongly local component in the pollen signal comes from multiple investigations of modern pollen representation in wetland and grassland communities (e.g. Janssen, 1984; Hjelle, 1997; Bunting et al., 1998; Waller et al., 2005; Bunting et al., 2016) and from the fine scale heterogeneous mosaic nature of the vegetation deriving from the small size of individual plants and micro-scale variations in habitat (e.g. Bunting, 2003).

Pollen samples (2 cm^3) were collected from the green parts of mosses (largely *Kindbergia praelonga*, *Brachythecium rutabulum*, *Calliergonella cuspidata* and *Rhytidiadelphus squarrosus*) from locations close to the central point of the sampled areas at the end of the flowering season (September/October). Mosses were scarce in the reedswamp at Upton, and therefore samples of surface litter were used instead. Standard palynological preparation methods, including acetolysis, were employed (Moore et al., 1991), with the residues suspended in silicon oil. Identifications were made using reference material held at the Department of Geography and Geology at Kingston University. The pollen counts exceeded a minimum of 500 land pollen grains (excluding obligate aquatics and spores). The pollen type definitions follow Bennett (1995-2007), with large Poaceae grains (those with a long axis >33µm) further separated using the criteria of Küster (1988). The majority of the latter fell within the Küster groupings which include *Glyceria* species (*Glyceria*-type and *Bromus hordeaceus*-type) and are subsequently referred to here as *Glyceria/Bromus*. Only two large Poaceae grains were actually categorised as Cerealia-type (following Küster, 1988). The pollen diagrams were constructed using TILIA v2.0.41 (Grimm, 1993) with rarefaction analysis (Birks and Line, 1992) performed using PSIMPOLL v4.27 (Bennett, 2014). Fungal spores were very scarce, even from the grazed area, and the data obtained are not presented here.

Cluster analysis, carried out using TWINSPAN v2.3 (performed in WINTwins; Hill and Šmilauer, 2005), was used to provide an initial and separate overview of the structure within the vegetation, palynological equivalent vegetation and modern pollen datasets (see Table 2). Plant taxa/palynological equivalents were included if present at more than four sample points, or if hit more than four times at one sample point. Pollen taxa were included if the plant equivalent was recorded in the vegetation survey and if they occurred at > 2% of total land pollen (TLP), or if the pollen was recorded at four or more sample points.

The relationship between pollen and vegetation occurrence was examined using Indices of Association (e.g. Davis, 1984; Hjelle, 1997; Bunting, 2003; Schofield et al., 2007). This approach is suitable where the pollen representation of ecologically diagnostic taxa is low and in situations where the source area is likely to be small (Bunting et al., 2016). Indices were calculated for taxa with at least four occurrences in both the pollen and vegetation records (excluding tree taxa and two taxa, Poaceae and Cyperaceae, which occur ubiquitously in the pollen and vegetation records) using the following formulae:

$$A = B_0/(P_0 + P_1 + B_0)^{-1}$$

$$O = P_0/(P_0 + B_0)^{-1}$$

$$U = P_1/(P_1 + B_0)^{-1}$$

where A = Association, the co-occurrence of plant and pollen in a sample, O = Over-representation, where a type is present in the pollen assemblage but not the local vegetation, U = Under-representation, where a plant is present without being recorded in the pollen sample, B_0 = number of samples where pollen type and associated plant taxon are both present within the defined distance, P_0 = number of samples where the pollen type is present in the surface sample, but the plant taxon is absent in the vegetation within the defined area and P_1 = number of samples where the pollen type is absent in the surface sample but the plant taxon is present in the vegetation within the defined area.

The structure underlying the pollen assemblages produced by fen vegetation was explored using ordination. Firstly, Principal Component Analysis (PCA) was undertaken on the modern dataset (taxa were included if the plant equivalent was recorded in the vegetation survey and if they occurred at > 2% TLP, or if the pollen was recorded at four or more sample points; see Table 2) after initial Detrended Correspondence Analysis suggested linear rather than unimodal methods should be applied (Lepš and Šmilauer, 2003). Fossil pollen assemblages (with the pollen sum comprising the same taxa as in the modern dataset) interpreted as being derived from fen communities were then placed passively into this ordination and scatterplots produced to enable comparison between the modern and fossil samples in the same geometric space (see section 4.3.2, Table 5). All ordinations were performed using the program CANOCO v4.52 (ter Braak and Šmilauer, 2003) with the data subject to log transformation.

Plant taxonomic nomenclature follows Stace (2010) and Smith (2004).

4. Results

4.1 The modern vegetation and pollen datasets

The pollen data are presented in Fig. 3 and species present in the vegetation are listed in Table 2. In this section both datasets are explored using the results of the cluster analysis. It was not possible to achieve the minimum pollen sum from two sample points (104 and 106) which have therefore been omitted from the analysis of the pollen data.

4.11 Diversity

Table 3 summarises the diversity measures for each dataset. Rarefaction confirms the species poor status of the reedswamp at Upton (where the number of samples was small) and also indicates, as would be expected (Vermeer and Berendse, 1983; Grime, 2002), that the most intensely managed communities (the sedge fen and *Juncus* pasture at Woodwalton) are relatively species rich. The latter areas are dominated by members of Cyperaceae, Poaceae and *Juncus*, and consequently only slightly over half the taxa recorded in the vegetation are palynologically distinguishable (PEv/V around 0.5). The ratio of recorded pollen/spore types that could be derived from the local vegetation against those that might potentially be present (Lp/PEv) is consistent at 0.7-0.8, with the exception of the *Cladium* fen. The overall palynological richness of the samples also remains relatively constant, presumably reflecting the small size of the areas investigated and the consistency of the species pool across both sites. That the open areas are more palynologically diverse is likely to result from the greater palynological influence of the woodland on the open communities than the reverse, as a result of the higher production and greater dispersal of tree pollen (Meltsov et al., 2011; Birks et al., 2016). There is a negative relationship between pollen richness and floristic richness when rarefaction values are compared. This is, however, a consequence of leverage by samples from the reedswamp at Upton, which form a notable outlier. This anomaly is likely to reflect these samples being derived from sediment rather than mosses. Sediment presents a different preserving environment, and it is possible that the pollen content sampled has accumulated over a longer time period than the samples from mosses. Mosses are generally assumed to preserve and average several years of pollen rain (e.g. Andersen, 1970; Mulder and Janssen, 1999; Lisitsyna and Hicks 2014), although some studies indicate that they represent little more than a single growing season (Räsänen *et al*., 2004; Pardoe et al., 2010; Farrell et al., 2016), whereas sediment surface samples may represent ≥10 years of accumulation, although current understanding of the temporal properties of natural pollen traps is based on limited data.

4.12 Cluster analysis: the modern vegetation

The cluster analysis of the modern vegetation data produces groupings which match the areas sampled closely (Fig. 4a), with the herbaceous (0) and woodland (1) samples separated first. The Upton woodlands (10) are then separated from the *Alnus-Betula* woodland at Woodwalton (11), reflecting differences in the ground flora as well as canopy. The relatively open woodlands at Upton notably support *Lonicera periclymenum*, *Carex acutiformis* and *Dryopteris dilatata* while the denser canopy at Woodwalton is coupled with an understorey containing *Crataegus monogyna*, with *Glechoma hederacea*, *Poa trivalis* and *Urtica dioica* abundant in the ground-flora. Clusters 100 and 101 then divide the two Upton woodlands. In the *Betula-Quercus* woodland (100) *Salix cinerea* and the grasses *Calamagrostis canescens* and *Phragmites* are common. In the *Alnus-Fraxinus* woodland (101) the shrub *Prunus padus* occurs.

For the herbaceous vegetation, locations with tall herbs (01), notably *Calamagrostis* and *Phragmites*, are separated first from the areas subject to high intensity management at Woodwalton (00), the *Juncus* pasture and the sedge fen (with *Carex viridula* and *Hydrocotyle vulgaris* in both areas). The latter sites are subsequently separated between the pasture (000: with *Ranunculus flammula*, *Juncus articulatus*, *J. effusus, Glyceria fluitans*) and sedge fen (001) with *Molinia* and *Cladium*. The clusters containing the tall herbaceous elements are less well related to location. The 011 cluster comprises the reedswamp at Upton and some of the glade (all samples from the unmanaged glades) samples along with four *Phragmites* fen samples from Woodwalton. At these locations *Phragmites* is abundant, and *Calystegia sepium* and *Urtica dioica* consistently recorded. The reedswamp at Upton subsequently forms a distinct cluster (0111) in which *Carex riparia* is co-dominant with *Phragmites*. The 010 samples are all characterised by the presence of *Juncus subnodulosus*, *Lysimachia vulgaris* and *Eupatorium cannabinum*. The *Phragmites* fen and managed glade locations at Woodwalton (0101) are distinguished from the Upton samples (0100) by the presence of *Symphytum officinale* and *Thelypteris palustris* respectively. The Upton samples are then split by location, with *Cladium*, *Salix repens* and *Myrica gale* exclusive to the *Cladium* fen (01000).

4.13 Cluster analysis: modern vegetation reclassified into palynological equivalent taxa.

As one approach for investigating the impact that the taxonomic limitations of pollen identification has on our ability to reconstruct fen communities, the vegetation data were subjected to a second cluster analysis after being reclassified into palynological equivalents (PEv). The major changes between the datasets arise as a result of combining the Poaceae (though *Glyceria/Bromus* has been kept separate), Cyperaceae (with *Cladium* remaining separate) and Pteropsida monolete spores (the diagnostic outer coat of which is usually lost during fossilization) groups, and omitting the Juncaceae (the pollen of which is rarely preserved). Nevertheless, the clusters that TWINSPAN identifies in the PEv dataset (Fig. 4b) retain their close relationship to location, and terminal clusters are similar to those previously outlined. The herbaceous (0) and woodland (1) locations again separate first. However, an abundance of Poaceae undiff. links the *Alnus* woodland at Woodwalton with the *Betula-Quercus* woodland at Upton (10) and results in the *Alnus-Fraxinus* woodland at Upton splitting off first (11).

For the herbaceous fen locations, the first division splits the samples in which the Poaceae undiff. and Cyperaceae undiff. are abundant (01), namely those from the reedswamp at Upton and the sedge fen and *Juncus* pasture locations at Woodwalton, from the areas in which tall herbs (*Lysimachia vulgaris*-type, *Solidago virgaurea*-type) are consistently recorded (00). The 01 cluster is then split into branches consisting mostly of the reedswamp locations at Upton (010) and the intensively managed areas (011) at Woodwalton. The latter remain distinctive with *Glyceria/Bromus* and *Ranunculus acris*-type notably present in the *Juncus* pasture (0111). The 00 cluster separates into the Upton samples (000), where Pteropsida monolete spores are common, and the *Phragmites* fen and glade locations at Woodwalton (001) with *Symphytum*.

4.14: The pollen data

In the cluster analysis of the pollen data, identified Pteropsida spores were again combined into one taxon, Pteropsida monolete. While the terminal groups retain a strong link to location, the pollen data (Fig. 4c) initially fail to divide between the woodland and herbaceous areas, though the presence of some of the unmanaged glades sample points at Woodwalton (with high *Betula* pollen values) in the 1 cluster with the woodland areas is unsurprising as they formed part of a contiguous transect with the *Alnus-Betula* woodland locations (Fig 1a) and fall within the 'edge effect' zone (Binney et al., 2005). The 1 cluster samples are characterised by high values of Pteropsida monolete spores and arboreal pollen. The 10/11 division splits off the woodland locations from the *Cladium* and *Juncus* communities at Upton (11) which have notably lower arboreal and higher Poaceae values. The *Cladium* community at Upton (110) is characterised by high *Myrica* values (maximum 26% TLP) rather than *Cladium* (which was only recorded at one location, at <1 % TLP). The 10 division (high *Alnus* and *Urtica*) splits the samples with high (100) and low (101) *Betula* values. The latter consist almost exclusively of the *Alnus* woodland locations at Upton where *Fraxinus* and *Hedera helix* are well represented. The 100 cluster is sub-divided by the abundance of the canopy components co-dominant with *Betula*; *Quercus* in the mixed woodland at Upton and in some of the unmanaged glade areas at Woodwalton (1001) and *Alnus* at Woodwalton (1000).

The 0 samples divide first into samples from the locations (00) experiencing high intensity management (the sedge fen, pasture and managed glades areas) at Woodwalton and those from the reedswamp and *Phragmites* fen communities (01). The 00 cluster areas are distinguished by high Cyperaceae undiff. and *Ranunculus acris*-type pollen values (the latter exceeding 20% TLP in the pasture and glades). The pasture (000) and sedge fen/managed glade samples (001) are then separated in the subsequent sub-division; in the former Cyperaceae values are high while in the latter *Hydrocotyle* is recorded in some abundance (maximum 23% TLP). The 01 cluster communities are characterised by high Poaceae values (consistently >40% TLP). In the species poor reedswamp community at Upton (010), Cyperaceae (*c*. 20% TLP) is the only other taxon with consistently high pollen values. In contrast, in the *Phragmites* fen and a number of unmanaged glade locations at Woodwalton (011), the pollen of other herbaceous types (including *Lysimachia vulgaris*-type and *Symphytum*) is well represented.

High *Quercus* pollen values (*c*. 20% TLP) also occur in samples in the 001 cluster, with values declining away from the woodland edge at Upton suggesting a high extra-local input (sensu Jacobson and Bradshaw, 1988). In contrast, *Alnus* pollen values are generally low except from the communities in which alder is a major canopy component (see Fig. 3). *Salix* pollen values are low at all the woodland locations, despite being consistently present, with values of < 5% TLP recorded even where *Salix* is common as an understorey component (in the mixed woodland at Upton). Higher values do, however, occur in the *Cladium* fen, particularly in the samples from which *Salix repens* was recorded, and samples from locations where *Salix cinerea* bushes occur outside woodland (the glades and *Phragmites* fen at Woodwalton). The pollen diagrams (Fig. 3) show that Cyperaceae values of > 5% TLP are limited to, but not recorded from all, the open areas sampled and that while Poaceae values are also higher at the open locations, grass pollen values in the woodland communities remain generally > 10% TLP.

4.2 Indices of Association

The samples were divided into four groups for the calculation of Indices of Association (Table 4) on the basis of broad habitat type (woodland or open communities) and site (Upton or Woodwalton), to investigate the consistency or otherwise of the results. The pollen source area for taxa occurring within the woodland is likely to be smaller and associations within 2 m may therefore be stronger for some taxa, while in other cases flowering may be reduced beneath a woodland canopy.

The shrubs *Salix*, *Sorbus*-type, *Viburnum opulus* and *Myrica* are all 'Weakly Associated' with vegetation presence within 2m. Four herbaceous taxa, *Hydrocotyle vulgaris*, *Ranunculus-acris* type, *Urtica* and *Rubus* and *Dryopteris dilatata/*Pteropsida monolete spores, are 'Strongly Associated' in at least one group. Of these only *Hydrocotyle* has a limited vegetation distribution, with presence at the frequently managed locations (SW, PW) consistent with a preference for disturbed and, for flowering, open sites (Grime et al., 2007). In addition, *Lysimachia vulgaris*, *Lythrum salicara* and *Solidago virgaurea*-type are 'Associated' in the open communities at both sites. Of the taxa for which it was possible to calculate an index in both open and woody communities; *Lonicera periclymenum*, Brassicaceae and *Urtica* are only 'Associated' with vegetation presence in woodland. However, Rubiaceae, *Symphytum* and *Thelypteris palustris* are more 'Strongly Associated' in the open communities. 'Over-Representation' of the tall herbaceous types Apiaceae, *Filipendula* and *Cirsium*-type in the woodland group might suggest pollen input from neighbouring open communities, though it is also possible that this is due to the early timing of the vegetation survey.

4.3 Ordination

4.3.1 Modern pollen samples

PCA results are shown in Figure 5. Eigenvalues for the first two axes of 0.377 and 0.215 respectively indicate only moderate separation of the modern pollen assemblages. In part, this reflects the high overlap of the likely overall pollen source area of the sample locations within each site (e.g. Schofield et al., 2007), and the similarity in habitats between the sites. Differences between samples in terms of the major taxa are a matter of quantity rather than presence or absence, partly as a result of the lack of taxonomic resolution in some important components. However, groupings can be delineated which contain most of the sample points within the different communities investigated (Fig. 5a). Areas with high axis 1 scores comprise the wooded locations, along with the *Juncus* and *Cladium* communities at the relatively well-wooded Upton site and the unmanaged glade locations at Woodwalton. The heavily managed areas (with high Cyperaceae) and the *Phragmites* dominated communities have low axis 1 scores. On axis 2, the *Juncus* fen (S24) and reedswamp (S26) are at opposite limits to the mixed woodland at Upton (W2) and the *Alnus* woodland at Woodwalton (W6). Axis 2 therefore probably reflects the degree of wetness (rather than pH or fertility, compare Fig. 5b with Fig. 1).

4.3.2 Comparison with Holocene samples

The relationship between fossil pollen assemblages that have previously been interpreted as being derived from eutrophic and mesotrophic fen (rather than acidophilous) vegetation and the modern communities sampled at Upton and Woodwalton has been explored through the PCA. It is recognised that such comparison is limited by a number of factors, including the number and variety of modern communities sampled (and therefore the range of taxa included and their potential pollen values), equifinality (that similar pollen assemblages can be produced by different vegetation/landscape types), and by differences in regional pollen input (minimised by the selection of middle and late Holocene assemblages). However, the analysis allows investigation of two questions: whether the suppositions that have been made in previous interpretations of these assemblages are consistent with the modern data, and whether dissimilarities from the modern pollen assemblages can help to identify other potential vegetation types which should be sampled in future studies.

The Holocene assemblages selected (Table 5, with the pollen diagrams provided as Supplementary data) are from large sedimentary systems, the Romney Marsh area (Waller et al., 1999) and Fenland (Waller, 1994b), and were deposited during periods of widespread peat formation (Fig. 6). Sample locations were distant (> 1 km) from contemporary dry land, and therefore pollen assemblages are likely to be dominated by the pollen of fen and other mire types. Most of the peats are intercalated between marine-brackish sediments and transitional assemblages indicative of brackish conditions (with high Chenopodiaceae pollen values) or marginal aquatic vegetation (with high *Sparganium emersum*-type), situated at the base and top of these deposits, have been omitted from consideration. Plant macrofossils, which can provide high taxonomic resolution and are generally locally deposited (Birks and Birks, 2000; Waller and Early, 2015), were rarely preserved at these sites; any occurrences have been noted in the following paragraphs.

The three Romney Marsh sites (Table 5, Fig. 6A) originate from the same single laterally extensive peat layer which extended from the upland edge out across a back barrier environment from *c*. 5000 cal. yrs BP onwards (Long et al., 2007). In these sequences, initial phases suggestive of open vegetation are generally short-lived, though at the site closest to the dry land (The Dowells) this phase (DOW-4) is more extended and has been placed within the ordination. There followed an extended period when tree pollen was abundant at all three sites (DOW-5 and 6, HF3-4 and BR-2). The assemblages in the upper half of the peat are more variable, but generally dominated by herbaceous pollen. At the site furthest from the upland, Brookland, non-arboreal pollen (notably Cyperaceae and *Myrica*) is prominent throughout the last 2000 years of peat formation (BR-3).

Five Fenland sites have been selected (Table 5, Figs 6b and c). At Welney Washes a basal peat and 3 intercalated peat layers were recorded in a sequence over 9 m deep within which 16 pollen zones were defined by Waller (1994b). The upper two peats (3rd and 4th) have been placed within the ordination. Peat formation at Redmere is initially accompanied by high *Salix* pollen values (RM-2), whose local presence is demonstrated by leaves found within adjacent boreholes. At Redmere and the 3rd Welney Washes peat, high tree/shrub pollen values are followed by assemblages dominated by herbaceous pollen. This situation is reversed at Murrow. At Meadowgate Lane, *Alnus* wood fragments were found throughout peat formation, though Poaceae and Cyperaceae values of *c*. 10% TLP were consistently recorded. The Swineshead and 4th Welney Washes peats are from the most recent stage of peat formation in Fenland (Fig. 6c) and likely to have been deposited close to rivers (the Witham and Great Ouse respectively). The pollen assemblages from both of these sites are dominated by herbaceous taxa with the presence of horizontally bedded *Phragmites* remains at Swineshead strongly suggestive of *in situ* reedswamp.

The fossil assemblages are shown within the ordination space created by the modern samples in Fig. 7, with the results summarised in Table 5 and discussed in Section 5.5.

5. Discussion

5.1 General considerations

The differences between the modern pollen assemblages from the woody and open communities are marked (Fig. 3) and confirm that major shifts in the abundance of arboreal and herbaceous pollen, of the type recorded in late Holocene sequences (see Grant et al., 2011; Waller and Grant, 2012), can be produced by changes occurring within the wetland environment alone, without any change in the surrounding dry landscape.

Local pollen (*sensu* Jacobson and Bradshaw, 1981) clearly makes a major contribution to these assemblages, though the representation of both tree and herbaceous pollen in samples collected from the plant communities in which they grow is generally highly variable (e.g. *Betula* in the mixed carr at Upton and Poaceae and *Solidago virgaurea*-type in the *Juncus* fen at Upton). As Janssen (1973, 1984) reported, this is likely to reflect an *in situ* effect, with the maximum values for taxa found where they occur at the source itself. This variable representation, which was also reported from *Alnus* carr by Waller et al. (2005), is often mirrored in Holocene sequences, with major fluctuations occurring between adjacent samples.

An extra-local component, defined as the enhanced but diminishing pollen input from adjacent communities (Janssen, 1984), is also evident at some locations. It is most notable in the high tree pollen values found in the glade and sedge fen areas at Woodwalton, and is also present in areas adjacent to *Alnus* dominated vegetation. Binney et al. (2005) report that dry land tree pollen values decline to background levels within the first *c*. 80 m into the fen carr from the dry land wood edge. The Upton and Woodwalton results (e.g. low arboreal pollen values in the *Juncus* pasture and *Phragmites* fen) indicate that the influence of extra-local input of pollen from fen carr into herbaceous communities is on a similar scale.

The contribution of regional pollen (*sensu* Jacobson and Bradshaw 1981) appears to be minor with few taxa which were not recorded, or likely occur, in the wetland vegetation well-represented in the modern pollen assemblages. Only *Pinus*, *Corylus avellana*-type, *Plantago lanceolata* and *Pteridium aquilinum* occur above 2% TLP, and then inconsistently. *Betula* and *Quercus* frequencies at sites away from any local or extra-local influences are also low (< 10% TLP). In contrast, Poaceae pollen values remain persistently above 10% TLP even in the woody communities. This is consistent with other modern pollen studies from woodland communities in eastern England (e.g. Waller et al., 2005; 2012), but not with the frequencies generally recorded in middle Holocene sequences, suggesting that a relatively high proportion of modern Poaceae pollen is probably regionally derived.

Given the high pollen values for most of the canopy forming taxa (*Alnus*, *Betula*, *Quercus* and *Fraxinus*) in the vegetation in which they occur, identifying the presence of, and distinguishing between, the major woody types associated with fen environments would appear relatively straightforward. However, the pollen representation of *Salix* is erratic. Very high values are recorded at some sites (e.g. >50 % TLP at Hope Farm and Redmere), while both modern pollen (Waller et al., 2005) and plant macrofossil studies (Waller and Early, 2015) have demonstrated that this genus can be present in the local vegetation while producing little or no pollen. *Salix* is insect pollinated and dioecious, with female biased ratios reported in some populations of *Salix cinerea* (Faliński, 1980), so in part this inconsistency is likely to reflect poor pollen dispersal and the distribution of male plants. However, this study (see section 4.14) and the results from Wheatfen (Waller et al., 2005) also suggest that flowering is inhibited under a canopy. High frequencies are therefore likely to reflect the presence of *Salix* in the canopy, with the low frequencies recorded in diagrams from many fen carr deposits misleading as to its former abundance as *Salix* spp. occur as understorey components in all modern carr communities (Rodwell, 1991a).

Distinguishing the ground level vegetation and conditions in fen woodland from the presence of particular herbaceous types is more problematic. As would be expected low growing, entomophilous, pollen grains of shade tolerant taxa occur infrequently (e.g. *Circaea lutetiana*, *Glechoma hederacea*) or are 'Under-Represented' (*Geranium robertianum*) in the moss samples. Others, *Rubus* undiff., Brassicaceae (presumably derived from spring-flower *Cardamine* sp.), *Urtica dioica* and *Dryopteris dilatata* occur at higher frequencies and are 'Associated' with, though not confined to, woodland vegetation. Of the taxa which occur in both woodland and open fen, *Carex acutiformis* (which is often abundant in fen carr) seems under shade to consistently produce little pollen (see also Waller et al., 2005). The origin of the pollen of tall herbaceous plants in the woodland samples is more ambiguous. Their 'Over-Representation' suggests that extra-local input is possibly occurring, though the high values recorded for some taxa (notably *Solidago virgaurea*-type) indicates that some flowering occurs within the woodland as well.

High Poaceae and Cyperaceae pollen values distinguish the open vegetation types. The sampled areas remain relatively distinct in both the cluster and PCA analysis of the modern pollen data and some taxa are associated with particular communities (e.g. *Hydrocotyle*, *Myrica*, *Lysimachia vulgaris*, *Lythrum salicaria*-type and *Mentha*-type). This suggests that it is possible to use variations in the presence and representation of herbaceous types to palynologically discriminate between at least some herbaceous community types (see section 5.4).

5.2 What influence does the loss of taxonomic precision in pollen identification have on the differentiation of fen plant communities?

When comparing the number of potentially identifiable pollen types to the number of plant taxa recorded in the vegetation, the reduction in taxonomic resolution in the palynological data is greatest in the most highly managed communities (Table 3). Overall, however, when these figures are compared to those compiled by Birks et al. (2016), they suggest that the loss of precision in assemblages derived from fen communities is equal to or less than that from a range of other wooded and herbaceous vegetation types.

Comparison of the structure within the vegetation and palynological-equivalent vegetation datasets, using cluster analysis, shows differences in the division of both the open and woodland communities. Initial splits in the vegetation data are made using species level distinctions in the Poaceae (notably *Phragmites*) and Cyperaceae in the open communities, while in the palynological equivalents dataset, for the woodland communities, combining the Poaceae creates a different structure (linking the mixed woodland at Upton and the *Alnus* woodland at Woodwalton rather than the *Alnus* and mixed woodlands at Upton). However, the taxonomic detail remains sufficient in the palynological equivalents dataset for the areas sampled to be effectively separated. Comparison with clusters produced from the modern pollen dataset suggests that factors other than loss of taxonomic detail are likely to have a much stronger influence on the ability to reconstruct *in situ* communities from pollen assemblages, notably a) pollen input from neighbouring communities, with relatively high arboreal frequencies resulting in the *Juncus* and *Cladium* fen areas at Upton being placed in the initial woodland cluster, and b) visibility of significant palynological taxa in the record (e.g. the absence of *Glechoma* pollen in the woodland and the vagaries of *Salix* representation).

Taxonomic precision is likely to be much more important when attempting to establish whether herbaceous pollen derives from wet or dry land communities. In general terms, the ‘Associations’ between many of the herbaceous taxa regarded as anthropogenic indicators (e.g., Apiaceae, *Solidago virgaurea*-type, *Cirsium*-type) and *in situ* plant presence in the open fen communities confirms the dangers of assuming that herbaceous pollen types in fen peat sequences originate from dry land environments as has often been inferred in palaeoecological investigations (see Waller, 1993; Waller, et al., 1999; Waller and Grant, 2012; Perez et al., 2015). In particular, the presence of ‘cereal’ pollen has been widely used as evidence to support an interpretation of dry land clearance for agriculture. This presupposes the effective separation of wild grasses from cereal pollen. Many authors use the work of Andersen (1979) to split large, potentially cereal, Poaceae grains into a *Hordeum* Group, which includes a number of wild grass genera, and an *Avena-Triticum* Group. Following Waller and Grant (2012), at Woodwalton and Upton the work of Küster (1988) was used to separate grains with the characteristics of wild grasses commonly found in fens from cereals. While the pollen allocated to *Glyceria/Bromus* (comprising almost all the ‘potential’ cereal grains) is weakly associated with pasture at Woodwalton, it occurs consistently at values *c*. 1% TLP and above, even at locations where species included in this type are not present in the vegetation (Fig. 3), suggesting that it is relatively well-dispersed. Such frequencies are comparable with those reported as belonging to Andersen's *Hordeum* Group in late Holocene pollen sequences, lending weight to suggestions that such grains are much more likely to be derived from *Glyceria* and other wild grasses than from cleistogamous cereals.

5.3 What pollen signal do small open areas in fen woodland produce and could herbaceous pollen in assemblages dominated by fen carr taxa be derived from regeneration gaps rather than from dry land?

The representation of herbaceous taxa in fen woodland is of interest as the persistence *in situ* of *Alnus*-dominated carr over long time periods requires that the community undergoes internal regeneration. Studies from both enclosed basins and floodplain sites in central Europe show cyclic development, with *Alnus* dieback leading to the development of a sedge fen phase lasting several hundred years (Barthelmes et al., 2010; Pokorný et al., 2000) before recolonization by *Alnus* carr. The absence of fluctuations in *Alnus* and herbaceous pollen frequencies similar in magnitude and time-span in coastal records from the UK led Waller and Early (2015) to suggest that regeneration in these areas occurred at a smaller scale as a consequence of subsidence, the weight of trees as they age over deep and rapidly accumulating peat resulting in water-logging and dieback (see also Lambert, 1951). Such a process would create small-scale openings diachronously rather than larger spatial scale synchronous changes.

The dominance of herbaceous pollen in extensive areas of modern open fen confirms that large-scale regeneration phases should be visible, at least in the Holocene sequences that are temporally well-resolved, and therefore probably did not occur. In contrast, the assemblage from the unmanaged glades suggests that small-scale openings (< 20 m in diameter) are likely to be difficult to detect in pollen records; the unmanaged glade pollen samples were split between TWINSPAN clusters (grouped with both the mixed woodland and *Phragmites* fen areas) and situated close to the woodland groups in the PCA. The changes in composition (shifts in arboreal pollen and increases in herb pollen) indicated between the *Alnus* woodland at Woodwalton and the adjacent glade areas are slight enough to not be detected in Holocene pollen records if occurring over a short time interval. In part this appears to be the result of the "glade effect", increased light levels and hence flowering activity in the crown area of trees and shrubs (including *Salix*), which can result in increases in both arboreal and herbaceous pollen production (Feeser and Dörfler, 2014). This suggests that natural processes causing small, temporary openings in wet woodland canopy, such as internal regeneration following the death of individual trees, could be represented by and contribute to the 'background' level of herb pollen that is invariably recorded in pollen sequences from fen carr environments (see for example Waller, 1994a; Waller and Hamilton, 2000). Clearly, however, such pollen may also derive regionally, extra-locally from more persistent openings (with taxa such as *Filipendula* potentially over-represented), or from *in situ* plants flowering under the shade of the canopy.

5.4 Do herbaceous fen communities that are subject to different management regimes (variations in cutting/mowing and grazing) have distinct pollen signatures?

Of the herbaceous communities investigated, the TWINSPAN and PCA analyses suggest the reedswamp community at Upton is relatively palynologically distinct, though the number of samples collected was small. Low plant species diversity is typical of *Phragmites* dominated swamps (Rodwell, 1995) and at Upton this is reflected in the pollen data. Although a number of the herbs associated with other tall herb communities are recorded, frequencies are consistently low, as would be expected for externally-derived pollen.

For the remaining open areas, division between locations subject to relatively low and high intensity management regimes seems possible. The tall-herb communities associated with the longer cutting rotations (the *Cladium*, *Juncus* and *Phragmites* fens) give rise to pollen assemblages with high Poaceae and relatively low Cyperaceae values. In addition, a number of the taxa 'Associated'/'Weakly Associated' in open vegetation such as *Lysimachia vulgaris, Hypericum perforatum*-type, *Lythrum salicaria*, *Mentha*-type and *Solidago virgaurea*-type not only occur consistently in the pollen records from these areas, but are sporadically recorded at high values. The presence of a number of these taxa, with some values >2% TLP, along with high Poaceae and relatively low Cyperaceae values, would therefore seem to be indicative of communities that are broadly analogous to the tall-herbaceous fens (S24 and variants) of Rodwell (1995). Pteropsida monolete/*Thelypteris* spores are also likely to derive from such vegetation if accompanied by low arboreal pollen frequencies. In addition, some taxa associated with these communities can be identified to species level in the pollen record, with *Myrica* and *Cladium* said to be indicators of more specific conditions. In fen systems, *Myrica* is reported as being associated with slightly acidic and more elevated surfaces (Wheeler, 1980a) while *Cladium* has a preference for shallow water at sites high in calcium (Rodwell, 1995) though, as at Upton, these two species can occur in close proximity (the S2 community of Rodwell, 1995).

The most intensely managed communities (*Juncus* pasture, sedge fen) are characterised by assemblages with high Cyperaceae pollen values. The species abundant in both of these areas include *Carex viridula*, which is of low stature and therefore able to flower under such conditions. In addition, pollen frequencies for types characteristic of disturbed areas (*Hydrocoyle vulgaris*, *Ranunculus*-acris type) are high and their presence is 'Strongly Associated' with vegetation presence in the intensely managed areas. Much of the *Ranunculus acris*-type pollen is likely to be derived from *Ranunulus flammula*, which was particularly abundant at the grazed locations and is known to be toxic to stock (Grime et al., 2007). As appears likely in the pasture at Woodwalton, grazing has been shown to reduce grass pollen production in other studies (e.g., Groenman-van Wateringe, 1993). However, it is clearly difficult to generalise with this limited dataset, particularly given the number of potential grazing (in terms of both animal density and frequency) and cutting regimes (with the timing of cutting in relation to flowering important) fen vegetation may potentially be subject to.

Glyceria/*Bromus* pollen is 'Weakly Associated' with local vegetation in the grazed area at Woodwalton (where *Glyceria fruitans* is common), and *Glyceria maxima*, another common component of tall-herbaceous fens, is known to be favoured by both cutting (Gryseels et al., 1989a) and grazing (Ausden et al., 2005). The increased representation of the *Hordeum* Group in late Holocene pollen sequences from the Thames estuary (see Waller and Grant, 2012), as well as the Fenland and Romney Marsh sites, could thus reflect the human use of wetland, though the types defined by Küster (1988), as with the Andersen (1979) group, include taxa which are associated with a range of open habitats.

5.5 How comparable are Holocene pollen assemblages from fen peats to the pollen signals produced by modern fen communities?

Most of the fossil samples plot out within or adjacent to the groupings produced by the modern samples. This suggests that a comparative approach to the interpretation of fossil pollen data is broadly applicable where fen communities are suspected. In many cases the position of a fossil sample in the PCA is consistent with previous interpretations (Waller, 1994a; Waller et al., 1999) and, where available, macrofossil evidence. However, as exemplified below, issues of pollen representation, differences in the extra-local components, communities from which modern samples are not available and non-analogous vegetation all imposed limitations on this approach.

The samples with high arboreal pollen percentages from Romney Marsh mostly plot within the MU and AW woodland clusters. This reflects the abundance of *Alnus* and *Betula* in the Holocene samples. Few fossil samples plot within the AU group (*Alnus-Fraxinus* woodland). In fen carr, *Fraxinus excelsior* is often associated with drier areas (Thomas, 2016) and margins (Waller et al., 2005) and it is therefore unlikely to have been abundant at the sites investigated on Romney Marsh or Fenland during phases of widespread peat formation. In Fenland, some Holocene samples with high arboreal pollen frequencies (notably from Redmere, the Welney 3rd peat and Meadowgate Lane) plot away from the woodland groups. These samples are linked by high *Salix* pollen frequencies and their position in the PCA is due to higher *Salix* percentages occurring in the open communities at the modern sites.

The presence and abundance of pollen types associated with the tall-herbaceous communities at Woodwalton and Upton in the Fenland and Romney Marsh samples suggests the presence and persistence of similar vegetation types during the late Holocene. Many of the Holocene samples (particularly from Fenland) plot within or close to the PCA herbaceous groups, mostly TW and RU. For the assemblages with high Pteropsida monolete spores at the Dowells, Redmere and the Welney peats, their position in the PCA seems largely to reflect differences in the input of arboreal pollen between the modern and fossil samples and they are likely (particularly the DOW-4 and HF-3 samples where *Thelypteris* has been identified) to be broadly analogous to the S24 communities (Rodwell, 1995) investigated at Upton. The samples with high Cyperaceae and *Myrica* values at Brookland (BR-3) plot between CU and TW, reflecting the scarcity of Cyperaceae in the CU pollen samples (though not vegetation) where *Myrica* occurs. The vegetation which produced assemblages with high *Myrica* pollen values (but with bog indicators such as *Sphagnum* and *Calluna* scarce) in the Romney Marsh sites and from the Rye area (Waller and Schofield, 2007) in the late Holocene is probably analogous to Rodwell's (1995) S2 (*Cladium* swamp) community. However, particularly as the representation of *Cladium* seems erratic ('Over-Represented' at Woodwalton while virtually absent at Upton, possibly due to identification difficulties arising from imperfectly preserved grains), further modern samples are needed. The Swineshead site shows that pollen assemblages similar to those of modern reedswamp communities were present in the past. However, other swamp communities occur adjacent to the wettest parts of fen systems (Wheeler, 1980b; Rodwell, 1995) which have not been included in this study, and the fossil samples which fall into or close to the RU group at

Murrow and the Welney peats and contain high *Sparganium emersum*-type pollen values are likely to indicate the presence and longevity of alternative semi-aquatic communities.

Few late Holocene samples plot close to the intensely managed areas at Woodwalton in the PCA. This is perhaps not surprising as, although today and historically herbaceous fens were maintained by cutting/grazing, these processes remove biomass and are therefore likely to be under-represented (due to low accumulation rates) in the stratigraphic record. The continued accumulation of thick peat layers and the longevity of a number of open fen community types, demonstrated in the late Holocene sites from Fenland and Romney Marsh, require other explanations. As sea-level in these regions appears to have been rising only very slowly over most of this period (e.g. Shennan et al., 2006; Bradley et al., 2011), persistence is likely to have been due either to their occurrence in locations on the outer margins of the freshwater zone too exposed for tree colonisation (e.g. Swineshead, see Waller, 1994a) or to consolidation, with the sediment (10-20m of soft material accumulated during the Holocene in Fenland and Romney Marsh area) unable to support the weight of large trees (Waller and Early, 2015).

Notable differences between these fossil samples and the modern pollen assemblages include the abundance of *Urtica* in the latter. *Urtica* frequencies >10% TLP were also recorded from Wheatfen (Waller et al., 2005) and it is a diagnostic element in Rodwell's (1991a) classification of fen woodland. However, pollen values from the Fenland and Romney Marsh sequences never exceed 1% TLP. Given its high requirement for mineral nutrients it seems probable that the modern abundance of *Urtica dioica* in fen carr is a result of anthropogenic eutrophication. *Symphytum officinale*, which has similar preferences (Hill et al., 2004), occurs in both herbaceous and woody communities, and is well represented in the modern pollen samples from the open areas at Woodwalton. However, presumably also because of relatively low nutrient levels, it is poorly represented in Holocene fen pollen sequences, being only recorded from Wingham on the Chalkland (Godwin, 1962). Conversely, *Osmunda regalis* is a common constituent of a number of the Romney Marsh assemblages, while absent from the sites investigated in this study. Although present in modern fen systems, populations were severely reduced as a result of being heavily collected in the Victorian period (Preston et al., 2002). Although rare, *O. regalis* was recorded in fen carr vegetation at Calthorpe Broad (Waller et al., 2005) where spores were recovered from only one site (at < 1% TLP+Pter.), suggesting its representation in the Romney Marsh records is likely to reflect its vegetation abundance rather than being over-represented.

6. Conclusions and recommendations

The dominance of local pollen in the surface samples from Woodwalton and Upton suggests that it is not only possible to infer the presence of woody communities but also herbaceous fen vegetation from pollen data; namely reedswamp, tall-herb fen (and some variants) and sedge fen. Variations in the proportions of Poaceae, Cyperaceae, the presence of herbs associated with particular habitats, and pollen richness are all useful indicators. Given the continuous floristic variation found across such vegetation types and their likely proximity to each other, the high values connected with local vegetation presence are of particular diagnostic value.

Variable pollen representation is significant as it affects the taxa that dominate fen pollen assemblages (also see Waller et al., 2005), both woody and herbaceous. In percentage pollen diagrams, variations in the deposition of local and extra-local pollen of one taxon will result in reciprocal changes in the representation of all taxa in the pollen sum. Sequences must therefore be sufficiently well-temporally resolved for interpretation of the dominants to be based on trends rather than, as is often the case, representation in a small number of, or even single, samples.

It is clearly advantageous to take pollen identifications to the highest taxonomic resolution possible. For the Poaceae it would be beneficial if the Küster (1988) types were more widely adopted. Distinguishing both *Myrica* (from *Corylus avellana*) and *Cladium* (from Cyperaceae) also enhances the interpretation of pollen data derived from fen environments. However, it is not always possible to distinguish *Myrica* pollen from that of *Corylus avellana*, hence the use of *Corylus avellana*-type to capture grains of uncertain origin (Bennett, 1995-2007), and the difficulties in distinguishing *Cladium* where preservation is imperfect are such that little can be read into its absence or scarcity in pollen records.

Further studies to validate the findings presented here are required. The number of modern samples available to characterise the pollen signal of herbaceous eutrophic and mesotrophic fens and semi-aquatic vegetation remains small, particularly given their complexity and the variety of potential management regimes. In addition, modern studies could usefully be undertaken to establish the pollen signal from *Salix* dominated carr (after establishing sex ratios) to determine the circumstances under which such vegetation produces the high *Salix* pollen values seen in some Holocene sequences.

Fen and swamp vegetation provide challenges that are not so readily encountered in other modern pollen studies. The difficulties in undertaking such work that should be noted include: sampling without causing major disturbance in tall-herbaceous vegetation, the likely scarcity of bryophytes and therefore availability of moss polsters in some habitats and difficulties in finding sites with appropriate or even consistent management regimes, given the constraints under which much conservation management work is undertaken. Identifying suitable analogues is also an issue given the modern abundance of nitrogen-loving plants (e.g. *Urtica*) and relatively dry conditions. Many fens have experienced drainage, with the widespread reintroduction of re-wetting management schemes a relatively recent phenomenon. Dry conditions are likely, for example, to have heavily influenced the occurrence of *Calamagrostis canescens,* which appears to have greatly increased at sites in the Netherlands over recent years (Gryseels, 1989b).

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Figures and Tables

Table 1. The vegetation communities (prefix code) sampled at Upton Broad (postfix code: U) and Woodwalton Fen (postfix code: W). Initial selection of these locations was based on descriptions provided by the site managers. NVC (National Vegetation Classification) follows Rodwell (1991a, 1991b, 1995).

Table 2. Palynological equivalents table. A hyphen indicates absence. If a taxon was recorded in the vegetation then the pollen type is the 'palynological equivalent'(Pe). The taxonomic precision to which identification of the pollen was possible varied (with preservation) and, where indicated by brackets, some of the grains likely to have been derived that species may also have been included in a Pe with a lower level of taxonomic resolution. ^{1}Taxa recorded at < 4 locations or < 4 hits in the vegetation survey, *pollen taxa included in the PCA (Figure 5). U = Upton Broad and W= Woodwalton Fen. Order (trees, shrubs, climbers, herbs then pteridophytes) follows Figure 3.

Table 3. Summary of the number of taxa/types recorded by community. ^{1}Vegetation samples, ^{2}pollen samples, ^{3}subject to rarefaction by area, ^{4}found within the vegetation of the area, ^{5}subject to rarefaction by pollen count, ^{6}reflects the summation of counts from the different sample points in each community. For the community codes see Table 1.

Table 4. Table of Association by site and vegetation structure (following Bunting et al. 2016; A >0.75: Strongly associated; A >0.5: Associated; A >0.25: Weakly associated; A < 0.25, U >O: Under-represented; A < 0.25, O >U: Over-represented; A <0.1, O > 0.75, U > 0.75: Unassociated). For the community codes see Table 1. Order follows shrubs, climbers, herbs then pteridophytes. Taxa that occur ubiquitously in the pollen and vegetation records were excluded (see section 3).

Table 5. Details of Holocene pollen sites and pollen assemblages placed within the PCA and their relationship to the PCA groups.

Figure 1 Wetland vegetation in Britain in relation to pH and fertility (modified after Wheeler and Proctor 2000). A. The main phytosociological alliances of mires. B. Schematic arrangement of the main categories of mire vegetation assumed to be self-sustaining (ombr. = ombrotrophic) with the position of the wooded communities (following the National Vegetation Classification - NVC) investigated in this study shown. C The position of the NVC herbaceous mires investigated in this study.

Figure 2. The vegetation communities sampled at (A) Woodwalton Fen and (B) Upton Broad. Site codes and numbers follow Table 1. (C) Location of sites and the Romney area and Fenland basin in England.

Figure 3. Modern pollen data from a) Upton Broad and b) Woodwalton Fen. All taxa occurring at >2% TLP plus the palynological equivalents of taxa recorded in the vegetation surveys.

Figure 4. The results of the cluster analysis using TWINSPAN. a) Modern vegetation. b) Vegetation as palynological equivalents. c) Modern pollen. The indicator taxa are derived from WINTwins, the numbers underlined are sites which do not fall within the same clusters as the majority of areas from the same location. For the community codes see Table 1.

Figure 5. PCA of modern fen data A) sample points and communities and B) fen taxa.

Figure 6. Location of fossil pollen sites. Palaeogeographic reconstructions of Romney Marsh at *c*. 3000 cal. yr BP (A) and Fenland at *c*. 2800 cal. yr BP (B) and *c*. 1200 cal. yr BP (C) follow Long et al. (2007) and Waller (1994b).

Figure 7. PCA of the modern fen locations derived from pollen data, with Holocene pollen data from the Romney Marsh area and Fenland sites placed passively into this ordination.

Table 1. The vegetation communities (prefix code) sampled at Upton Broad (postfix code: U) and Woodwalton Fen (postfix code: W). Initial selection of these locations was based on descriptions provided by the site managers. NVC (National Vegetation Classification) follows Rodwell (1991a, 1991b, 1995).

Code	Vegetation-name	Main species	NVC	Management	Sample numbers
RU	Reedswamp	*Phragmites, Carex riparia, Calystegia sepium*	S26	Cut on 7-8 year rotation; last cut 2006	1-10
CU	*Cladium* fen	*Cladium mariscus, Calamagrostis canescens, Salix repens*, *Myrica gale*	S2/ S24	Cut on 7-8 year rotation; last cut 2006	11-22
JU	*Juncus subnodulosus* fen	*Juncus subnodulosus, Calamagrostis canescens, Thelypteris palustris*	S24	Cut 7-8 year rotation; last cut May 2011	23-34
AU	Alder carr Upton	*Alnus*, *Fraxinus, Carex acutiformis*	W5	None	35-51
MU	Mixed woodland	*Betula, Quercus robur, Salix cinerea*	W2	None	52-68
AW	Alder carr Woodwalton	*Alnus*, *Betula, Glechoma hederacea*	W6	None	69-85
GNW	Glade (< 20 m wide)	*Phragmites*, *Calamagrostis canescens Symphytum officinale*	S24	None	86-93
GMW	Glade (< 30 m across)	*Phragmites*, *Calamagrostis canescens*, *Carex acutiformis*	S24	Cut annually August	94-102
TW	*Phragmites* fen	*Phragmites, Calamagrostis canescens, Lysimachia vulgaris*	S24	Uncut for *c*. 20 years	103-119
SW	Sedge fen	*Carex panicea*, *Carex viridula* and *Molinia caerulea*	M22	Cut annually August	120-136
PW	*Juncus* pasture	*Carex* spp., *Juncus* spp., *Ranunculus flammula*	M23	Grazed (autumn)	137-157

Table 2. Palynological equivalents table. A hyphen indicates absence. If a taxon was recorded in the vegetation then the pollen type is the 'palynological equivalent'(Pe). The taxonomic precision to which identification of the pollen was possible varied (with preservation) and, where indicated by brackets, some of the grains likely to have been derived that species may also have been included in a Pe with a lower level of taxonomic resolution. [1]Taxa recorded at < 4 locations or < 4 hits in the vegetation survey, *pollen taxa included in the PCA (Figure 5). U = Upton Broad and W= Woodwalton Fen. Order (trees, shrubs, climbers, herbs then pteridophytes) follows Figure 3.

Species recorded in the vegetation	Site	Pollen type	Site
-	-	*Abies*	U
-	-	*Picea*	U W
-	-	*Pinus*	U, W
-	-	*Ulmus*	U, W
-	-	*Fagus sylvatica*	U, W
-	-	*Castanea sativa*	U
Quercus robur	U, W	*Quercus**	U, W
Betula	U, W	*Betula**	U, W
Alnus glutinosa	U, W	*Alnus glutinosa**	U, W
-		*Carpinus betulus*	U, W
-		*Tilia*	U, W
-		*Taxus baccata*	U, W
Ilex aquifolium	U	*Ilex aquifolium*	U
Acer pseudoplatanus	U	*Acer*	U, W
Fraxinus excelsior	U	*Fraxinus excelsior**	U, W
-		*Corylus avellana*	U, W
Salix cinerea	U, W	*Salix**	U, W
Salix fragilis[1]	U	*Salix*	U, W
Salix repens	U	*Salix*	U, W
Crataegus monogyna	U, W	*Sorbus*-type*	U, W
Prunus padus	U	*Sorbus*-type	U, W
Sorbus aucuparia	U	*Sorbus*-type	U, W
-		*Cornus sanguinea*	U
Frangula alnus[1]	U	*Frangula alnus*	U, W
Rhamnus cathartica[1]	W	*Rhamnus cathartica**	U, W
-		*Ligustrum vulgare*	U, W
-		*Sambucus nigra*	U, W
Viburnum opulus	U	*Viburnum opulus**	U, W
Myica gale	U	*Myrica gale*	U, W
Lonicera periclymenum	U	*Lonicera periclymenum**	U, W
Hedera helix	U	*Hedera helix**	U, W
Calystegia sepium	U, W	*Calystegia*	U, W
-		*Convolvulus*	W
Humulus lupulus	U	*Humulus lupulus**	U, W
-		*Bryonia dioica*	U
Tamus communis[1]	U	-	
-		*Caltha palustris*-type	U, W
Ranunculus acris	W	*Ranunculus acris*-type*	U, W
Ranunculus ficaria[1]	U	*Ranunculus acris*-type	U, W

Ranunculus flammula	W	*Ranunculus acris*-type	U, W
Ranunculus repens	U, W	*Ranunculus acris*-type	U, W
Thalictrum flavum	W	*Thalictrum*	U
Ceratocapnos claviculata[1]	U	-	
Urtica dioica	U, W	*Urtica**	U, W
-		Chenopodiaceae	U, W
Cerastium fontanum[1]	U	Caryophyllaceae undiff.*	U, W
Moehringia trinervia	W	Caryophyllaceae undiff.	U, W
Stellaria media	U, W	Caryophyllaceae undiff.	U, W
Stellaria palustris	W	Caryophyllaceae undiff.	U, W
Stellaria uliginosa[1]	W	Caryophyllaceae undiff.	U, W
Lychnis flos-cuculi	U	Caryophyllaceae undiff.	U, W
Silene dioica[1]	W	Caryophyllaceae undiff.	U, W
-	U	*Persicaria maculosa*-type	U, W
-		*Polygonum*	U, W
-		*Rumex acetosa*	U, W
Rumex crispus[1]		*Rumex obtusifolius*-type*	U, W
Rumex sanguineus	W	*Rumex sanguineus*-type*	U, W
Hypericum tetrapterum	W	*Hypericum perforatum*-type*	U, W
Viola sp.[1]	U	*Viola palustris*-type*	U, W
Cardamine flexuosa	W	Brassicaceae*	U, W
Cardamine pratensis	U	Brassicaceae	U, W
Ribes nigrum	W	*Ribes*	U, W
Ribes rubrum	U	*Ribes*	U, W
-	U, W	*Calluna vulgaris*	U, W
Lysimachia vulgaris		*Lysimachia vulgaris*-type*	U, W
-	U, W	*Chrysosplenium*	U
Filipendula ulmaria		*Filipendula**	U, W
Rubus fruticosus agg.	U, W	*Rubus* undiff.* (Rosaceae undiff.*)	U, W
Potentilla anserina	U, W	*Potentilla*-type*	U, W
Potentilla erecta	W	*Potentilla*-type	U, W
Potentilla palustris[1]	W	*Potentilla*-type	U, W
Geum urbanum[1]	U	-	
Rosa sp.	U	*Rosa** (Rosaceae undiff.*)	U, W
Lotus pedunculatus	U, W	*Lotus**	U, W
Vicia cracca	U, W	*Vicia cracca** (Fabaceae undiff.)	W
-	W	*Vicia sylvatica*-type (Fabaceae undiff.)	U, W
-		*Lathyrus* (Fabaceae undiff.)	U, W
Trifolium repens[1]		*Trifolium*-type (Fabaceae undiff.)	W
Lythrum salicaria	W	*Lythrum salicaria**	U, W
Circaea lutetiana	U, W	*Circaea*	W
Epilobium hirsutum	U, W	-	
Epilobium montanum	U, W	-	
Epilobium palustre	W	-	
-	U, W	*Mercurialis perennis*	W
-		*Euphorbia*	U
Geranium robertianum		*Geranium**	U, W
Impatiens sp.[1]	U, W	-	
Hydrocotyle vulgaris	W	*Hydrocotyle vulgaris**	U, W
Angelica sylvestris	W	Apiaceae undiff.*	U, W
Apium nodiflorum[1]	U, W	Apiaceae undiff.	U, W

Sium latifolium	U, W	Apiaceae undiff.	U, W
Peucedanum palustre	U	Apiaceae undiff.	U, W
Solanum dulcamara	U	*Solanum dulcamara**	U, W
-	U, W	*Echium vulgare*	U
Symphytum officinale		*Symphytum**	U, W
Myosotis scorpioides	W	*Myosotis arvensis*-type*	U, W
Stachys palustris	W	Lamiaceae undiff.*	U, W
Stachys sylvatica	W	Lamiaceae undiff.	U, W
Lamium purpurea[1]	W	Lamiaceae undiff.	U, W
Scutellaria galericulata	W	-	
Glechoma hederacea	U, W	-	
Prunella vulgaris	U, W	-	
Lycopus europaeus	W	*Mentha*-type*	U, W
Mentha aquatica	W	*Mentha*-type	U, W
-	U, W	*Plantago major*	U, W
-		*Plantago lanceolata*	U, W
-		*Scrophularia-type*	U, W
Veronica anagallis-aquatica[1]		*Veronica*	U, W
Veronica scutellata[1]	U	*Veronica*	U, W
Odontites vernus[1]	W	-	
Galium aparine	W	Rubiaceae*	U, W
Galium palustre	U, W	Rubiaceae	U, W
Galium uliginosum	W	Rubiaceae	U, W
Valeriana officinalis	U, W	*Valeriana officinalis*	U, W
Cirsium arvense	U	*Cirsium*-type*	U, W
Cirsium palustre	W	*Cirsium*-type	U, W
Cirsium vulgare[1]	U, W	*Cirsium*-type	U, W
Centaurea nigra[1]	W	*Centaurea nigra*	U, W
Lapsana communis[1]	W	Lactuceae	U, W
Taraxacum sp.[1]	W	Lactuceae	U, W
Sonchus sp.[1]	W	Lactuceae	U, W
Eupatorium cannabinum	W	Solidago virgaurea-type*	U, W
Senecio sp.[1]	U, W	Solidago virgaurea-type	U, W
-	W	*Artemisia*-type	U, W
Achillea millefolium		*Achillea*-type*	U, W
Juncus articulatus	W	-	U, W
Juncus bufonius[1]	W	-	U, W
Juncus conglomeratus	W	-	
Juncus effusus	W	-	
Juncus inflexus[1]	W	-	
Juncus subnodulosus	W	-	
Luzula multiflora	U, W	-	
Cladium mariscus	W	*Cladium mariscus** (Cyperaceae und.)	U, W
Carex acutiformis	U, W	Cyperaceae undiff.*	U, W
Carex diandra[1]	U, W	Cyperaceae undiff.	U, W
Carex elata	U	Cyperaceae undiff.	U, W
Carex nigra[1]	W	Cyperaceae undiff.	U, W
Carex otrubae	W	Cyperaceae undiff.	U, W
Carex panicea	W	Cyperaceae undiff.	U, W
Carex riparia	U, W	Cyperaceae undiff.	U, W
Carex rostrata	U	Cyperaceae undiff.	U, W

Carex viridula	W	Cyperaceae undiff.	U, W
Eleocharis palustris	W	Cyperaceae undiff.	U, W
Agrostis capillaris	W	Poaceae undiff.*	U, W
Agrostis stolonifera	W	Poaceae undiff.	U, W
Anthoxanthum odoratum	U, W	Poaceae undiff.	U, W
Brachypodium sylvaticum[1]	W	Poaceae undiff.	U, W
Calamagrostis canescens	W	Poaceae undiff.	U, W
Calamagrostis epigejos	U, W	Poaceae undiff.	U, W
Elytrigia repens	W	Poaceae undiff.	U, W
Festuca rubra	W	Poaceae undiff.	U, W
Holcus lanatus	W	Poaceae undiff.	U, W
Holcus mollis	W	Poaceae undiff.	U, W
Molinia caerulea	U	Poaceae undiff.	U, W
Poa trivialis	W	Poaceae undiff.	U, W
Poa pratensis[1]	U, W	Poaceae undiff.	U, W
Phalaris arundinacea	W	Poaceae undiff.	U, W
Phragmites australis	W	Poaceae undiff.	U, W
Glyceria fluitans	U, W	*Glyceria/Bromus**	U, W
-	W	Cerealia-type	U, W
Dactylorhiza sp.[1]		-	U, W
-	W	*Myriophyllum spicatum*	U
-		*Callitriche*	U
-		*Alisma*-type	W
-		*Potamogeton natans*-type	W
-		*Sparganium emersum*-type	U, W
Typha latifolia[1]		*Typha latifolia*	U, W
Iris pseudacorus	U	*Iris*	U, W
Equisetum palustre	U, W	*Equisetum**	U
-	U	*Osmunda regalis*	U, W
-		*Polypodium*	W
-		*Pteridium aquilinum*	W
Thelypteris palustris		*Thelypteris palustris* (Pteropsida	U, W
	U	(monolete) indet.*)	U
Athyrium filix-femina[1]	U	*Athyrium filix-femina* (Pteropsida (monolete) indet).	U
Dryopteris filix-mas[1]	U	*Dryopteris filix-mas* (Pteropsida (monolete) indet).	U, W
Dryopteris dilatata	U, W	*Dryopteris dilatata* (Pteropsida (monolete) indet.)	U, W

Table 3 Summary of the number of taxa/types recorded by community. [1]Vegetation samples, [2]pollen samples, [3]subject to rarefaction by area, [4]found within the vegetation of the area, [5]subject to rarefaction by pollen count, [6]reflects the summation of counts from the different sample points in each community. For the community codes see Table 1.

	RU	CU	JU	AU	MU	AW	TW	GNW/ GMW	SW	PW
No. samples	10	12	12	17	17	17	17[1] 15[2]	17	17	21
No. of taxa recorded in vegetation (*V*)	10	30	32	42	33	36	47	42	51	52
Relative vegetation richness[3] E(T 31.4m^2)	10	28.2	30.2	34.2	28	31.5	40.1	34.9	42.3	39.7
No. of potentially identifiable pollen/ spores types in vegetation (*PEv*)	9	23	26	31	27	28	30	24	27	29
PEv/*V*	0.9	0.8	0.8	0.7	0.8	0.8	0.6	0.6	0.5	0.6
No. of local[4] pollen/ spores types found (*Lp*)	7	23	19	24	18	21	20	19	19	22
Lp/*PEv*	0.8	1	0.7	0.8	0.7	0.8	0.7	0.8	0.7	0.8
Relative palynological richness[5] E(T 1000[6]) mean	45.4	43.5	35.9	38.5	37.8	35	39.8	42.4	41	40.3

Table 4. Table of Association by site and vegetation structure (following Bunting et al. 2016; A >0.75: Strongly associated; A >0.5: Associated; A >0.25: Weakly associated; A < 0.25, U >O: Under-represented; A < 0.25, O >U: Over-represented; A <0.1, O > 0.75, U > 0.75: Unassociated). For the community codes see Table 1. Order follows shrubs, climbers, herbs then pteridophytes. Taxa that occur ubiquitously in the pollen and vegetation records were excluded (see section 3).

Pollen type	Upton Open	Upton Woodland	WW Open	WW Woodland	Vegetation community presence
Myrica gale	Weakly Ass.	-	-	-	CU
Salix	Weakly Associated		-	-	TW, CU, AU, MU
Sorbus-type	-	Weakly Ass.	-	Weakly Ass.	AU, AW, MU
Viburnum opulus	Weakly Ass.	-	-	-	CU, JU, AU
Hedera helix		Over-Rep.	-	-	AU, MU
Lonicera periclymenum	Under-Rep.	Weakly Ass.	-	-	CU, JU, *A*U, MU
Apiaceae undiff.	Weakly Ass.	-	Over-Represented		PW, CU, JU, SW, GNW, AU
Brassicaceae	-	Weakly Ass.	Over-Rep.	-	PW, GNW, AU, AW, MU
Caryophyllaceae undiff.	-	-	Under-Rep.	-	PW, SW, GNW, GMW, AU, AW, MU
Cirsium-type	Associated	Over-Rep.	Under-Rep.	Weakly Ass.	PW, TW, CU, JU, SW, GNW, AU, AW, MU
Cladium mariscus	-	-	Over-Rep.	-	SW
Filipendula	Over-Represented			Unassociated	PW,TW, CU, SW, JU, GNW, GMW, AU, AW
Geranium	-	Under-Rep.	-	-	AU, MU
Glyceria/Bromus	-	-	Weakly Ass.	-	PW
Hydrocotyle vulgaris	-	-	Strongly Ass.	-	PW, SW
Hypericum perforatum-type	Weakly Ass.	-	-	-	CU, JU
Lactuceae	-	-	Over-Rep.	-	PW, SW, AW
Lamiaceae	-	-	Weakly Ass.	-	TW, GNW, AW
Lotus	-	-	Weakly Ass.	-	PW, TW, SW, GNW, GMW
Lysimachia vulgaris	Associated	-	Weakly Ass.	-	TW, CU, SW, JU
Lythrum salicaria	Weakly Ass.	-	Weakly Ass.	-	TW, CU, JU, SW; GNW, GMW
Mentha-type	Weakly Ass.	-	Under-Rep.	-	PW, TW, JU, CU, SW, GNW, GMW
Potentilla-type	-	-	Under-Rep.	-	PW, SW
Ranunculus acris-type	-	Over-Rep.	Strongly Ass.	-	PW, SW, GMW, AU, AW, MU
Rubiaceae	Associated	Under-Rep.	Associated.	Weakly Ass.	All communities

Rubus undiff.	Weakly Ass.	Strongly Ass.	-	Weakly Ass.	CU, JU, AU, AW, MU
Solidago virgaurea-type	Associated	-	Weakly Ass.	-	PW, RU, TW, CU, JU, GNW, MU
Solanum dulcamara	-	Unassociated	-	-	RU, AU, AW, MU
Symphytum	-	-	Associated	Weakly Ass.	TW, SW, GNW, GMW, AW
Urtica	Over-Rep.	Weakly Ass.	Over-Rep.	Strongly Ass.	RU, TW, GNW, GMW, AW, MU
Vicia cracca-type	-	-	Under-Rep.	-	TW, SF, GNW, GMW
Equisetum	Unassociated	-	-	-	CU, JU
Dryopteris dilatata		Strongly Ass.	-	-	CU, AU, MU
Thelypteris palustris	Associated	Weakly Ass.	-	-	CU, JU, AU
Pteropsida	Associated	Strongly Ass.	-	-	CU, JU, AU, MU

Table 5 Details of Holocene pollen sites and pollen assemblages placed within the PCA and their relationship to the PCA groups.

Site and site details/ pollen assemblage	Main taxa in pollen assemblage [1]Pteropsida (monolete) indet. [ ] fen/swamp taxa not in PCA	Location in ordination space
Romney Marsh (Long and Innes 1995, Waller et al. 1999)		
The Dowells: 51°02'N 0°49'E, 26 samples, age range *c*. 5700-2400 cal. yrs BP		
DOW-4	*Alnus,* Cyperaceae, Pteropsida[1] (*Thelypteris palustris* also recorded)	1 in JU. 3 close to CU. 1 between TW and CU.
DOW-5	*Alnus*, *Betula*, *Salix*	5 in AW. 1 in MU.
DOW-6	*Alnus*, Betula, *Salix*, *Filipendula*, [*Osmunda regalis*]	5 in AW. 8 in MU. 2 close to CU.
Hope Farm: 51°01'N 0°50'E, 27 samples, age range *c*. 5100-1750 cal.yrs BP		
HF-3	*Alnus*, Cyperaceae, Pteropsida[1] (*Thelypteris palustris* also recorded)	5 in or close to MW. 2 in or close to CU. 3 in JU.
HF-4	*Alnus*, *Betula*, *Quercus*, *Salix,* [*Osmunda regalis*]	5 in AW. 3 in MU. 1 close to MU.
HF-5	Cyperaceae, Poaceae, Pteropsida[1]	1 in RU. 1 between RU and JU.
HF-6	*Salix*, *Betula*	2 close to MU. 1 close to GNW.
HF-7	*Myrica gale*, *Betula,* Cyperaceae*,* Poaceae	1 in RU. 1 in MU. 1 between TW and CU.
Brookland: 50°59'N 0°50'E, 24 samples, age range *c*. 4900-1750 cal. yrs BP		
BR-2	*Alnus*, *Betula*,*Salix*, Pteropsida[1]	6 in or close to MU. 3 in or close to AU. 3 in or close to CU. 2 in or close to JU.
BR-3	Cyperaceae, Poaceae*, Myrica gale*, Pteropsida[1], [*Osmunda regalis*]	5 in or close to TW, 3 between TW and CU/MU. 1 close to RU. 1 between RTU and JU.
Fenland (Waller 1994)		
Redmere: 52°26'N 0°26'E, 32 samples, age range *c*. 4250-1800 cal. yrs BP		
RM-2	*Salix*, *Alnus*, Brassicaceae, Cyperaceae, Poaceae	5 in or close to TW. 4 higher axis 1 scores than TW. 1 close to PW. 2 in RU.
RM-3	Cyperaceae, Poaceae, Rubiaceae, Brassicaceae, Pteropsida[1]	6 in or close to RU. 2 higher axis 1 scores than RU. 1 close to PW. 1 close to TW.
RM-4a	Poaceae, Cyperaceae, Brassicaceae, [Lactuceae], *Glyceria*/*Bromus*, Pteropsida[1]	6 lower axis 1 scores than JU. 4 higher axis 2 scores than RU.
Welney Washes 3rd peat: 52°30'N 0°15'E, 27 samples, age range *c*. 4200-2200 cal. yrs BP		
WW-10	*Alnus*, *Quercus*, *Salix,* Poaceae	2 in MU. 1 in TW. 4 close to TW. 2 between CU and TW.

WW-11	Cyperaceae, Brassicaceae, *Salix*, Poaceae, Pteropsida[1]	6 in or close to RU. 6 lower axis 1 scores than JU.
WW-12	Poaceae, Cyperaceae, Apiaceae, Pteropsida[1] , [*Sparganium emersum*-type]	2 close to RU. 4 lower axis 1 scores than JU.
Murrow 2nd peat: 52°38’N 0°01’E, 11 samples, age range *c*. 2800-2100 cal. yrs BP		
MU-5	Cyperaceae, Poaceae, Rubiaceae,[*Sparganium emersum*-type]	3 in RU. 1 in PW. 1 close PW.
MU-6	Cyperaceae, Poaceae, *Salix*, *Betula*, *Alnus*,Pteropsida[1]	1 close to JU. 4 between JU and TW. 1 lower axis 1 scores than JU.
Meadowgate Lane: 52°38’N 0°11’E, 12 samples, age range *c*. 2800-2100 cal. yrs BP		
MGL-2	*Alnus*, *Salix*, Poaceae, Cyperaceae, Pteropsida[1]	3 within CU. 9 between CU and TW
Swineshead: 52°56’N 0°09’W, 6 samples, age range *c*. 1550 cal. yrs BP		
SH-2	Poaceae, Cyperaceae, [Lactuceae]	4 within RU. 1 within TW. 1 close to PW/SW
Welney Washes 4th peat: 52°30’N 0°15’E, 14 samples, age range *c*. 1650-700 cal. yrs BP.		
WW-14	Poaceae, Cyperaceae, [*Sparganium emersum*-type]	7 in or close to RU. 2 close to PW
WW-15	Poaceae, Cyperaceae, *Glyceria* /*Bromus*, Pteropsida[1]	All 5 higher axis 2 scores than RU.

Figure 1 Wetland vegetation in Britain in relation to pH and fertility (modified after Wheeler and Proctor 2000). A. The main phytosociological alliances of mires. B. Schematic arrangement of the main categories of mire vegetation assumed to be self-sustaining (ombr. = ombrotrophic) with the position of the wooded communities (following the National Vegetation Classification - NVC) investigated in this study shown. C The position of the NVC herbaceous mires investigated in this study.

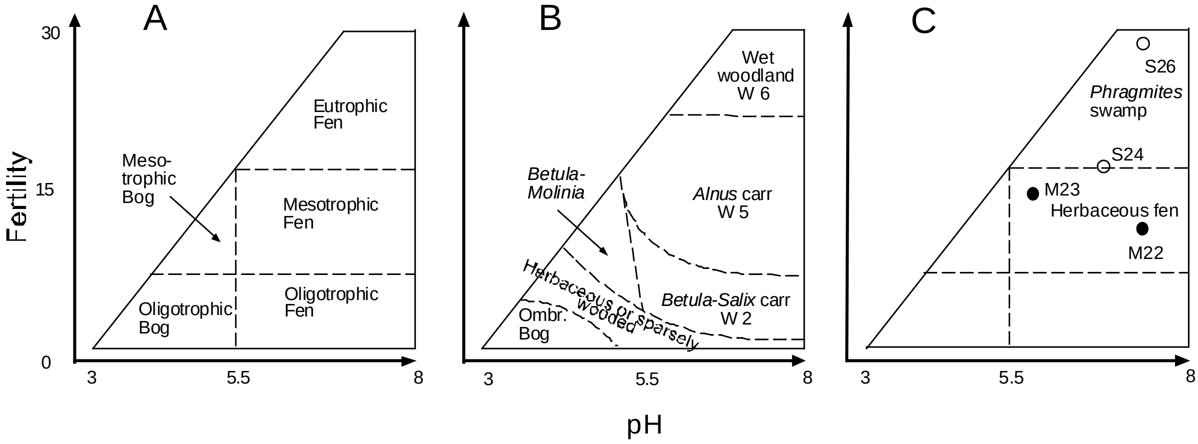


Figure 2. The vegetation communities sampled at (A) Woodwalton Fen and (B) Upton Broad. Site codes and numbers follow Table 1. (C) Location of sites and the Romney area and Fenland basin in England.

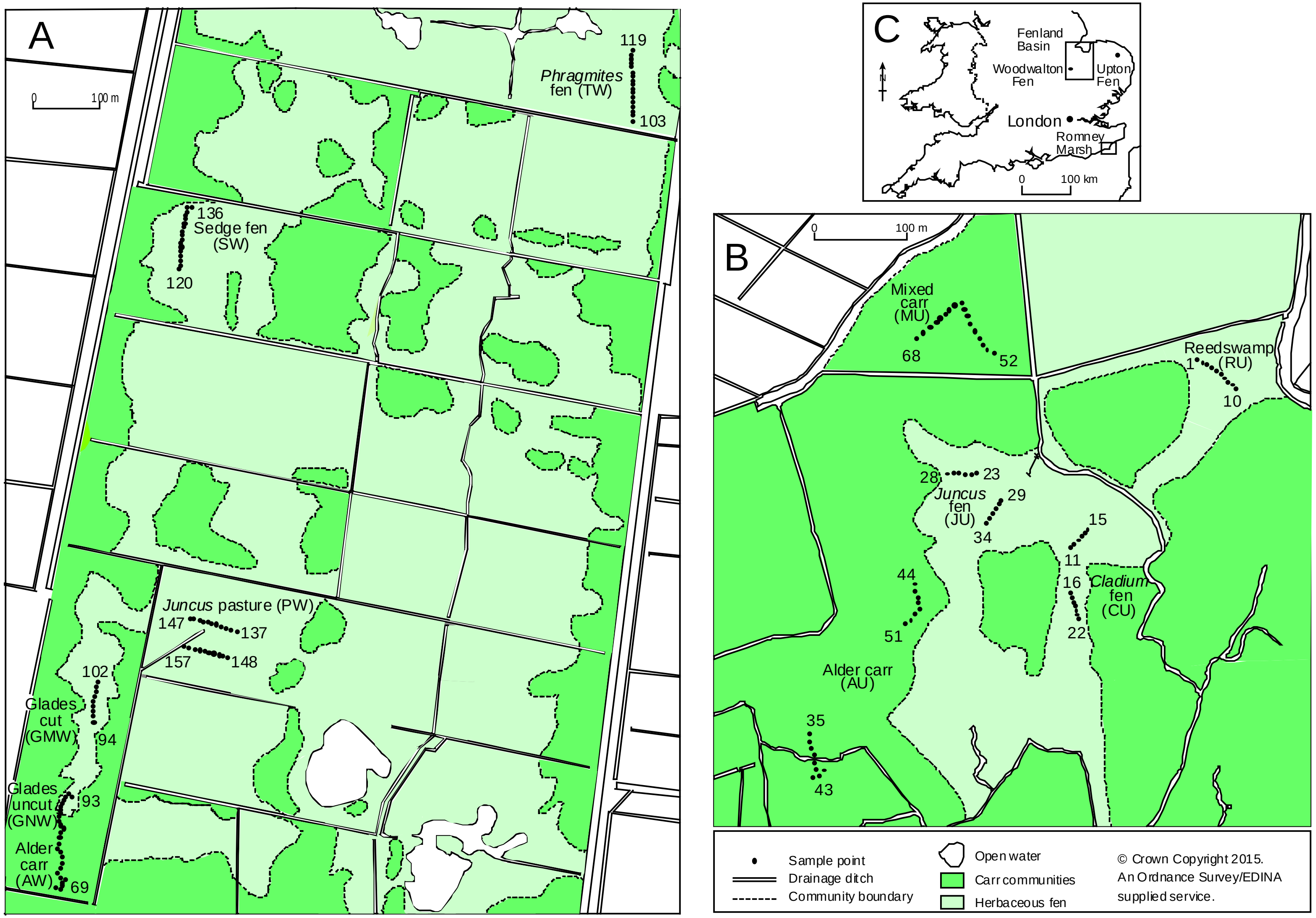


Figure 3a Modern pollen data from Upton Broad. All taxa occurring at >2% TLP plus the palynological equivalents of taxa recorded in the vegetation surveys.

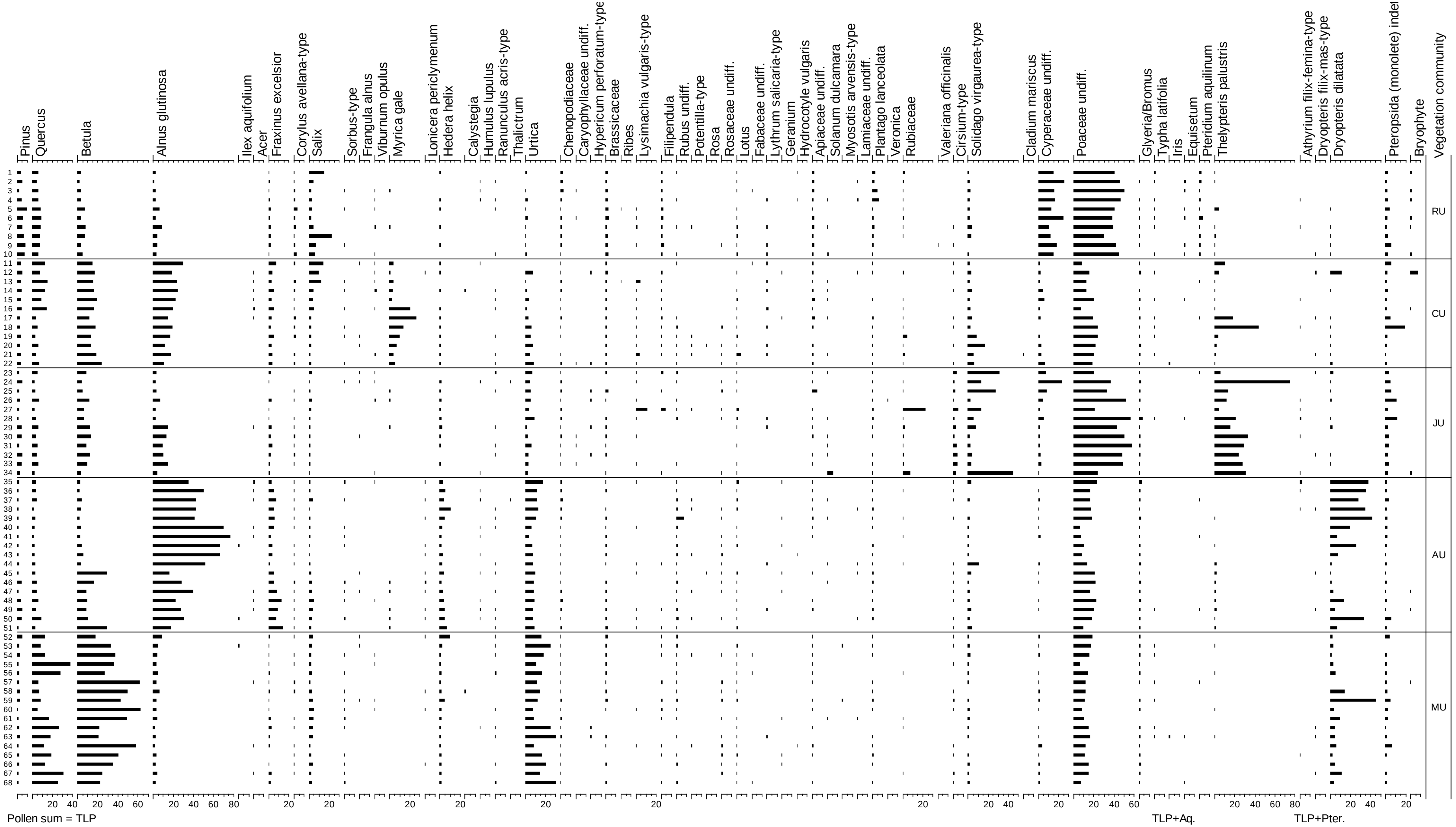


Figure 3b Modern pollen data from Woodwalton Fen. All taxa occurring at >2% TLP plus the palynological equivalents of taxa recorded in the vegetation surveys.

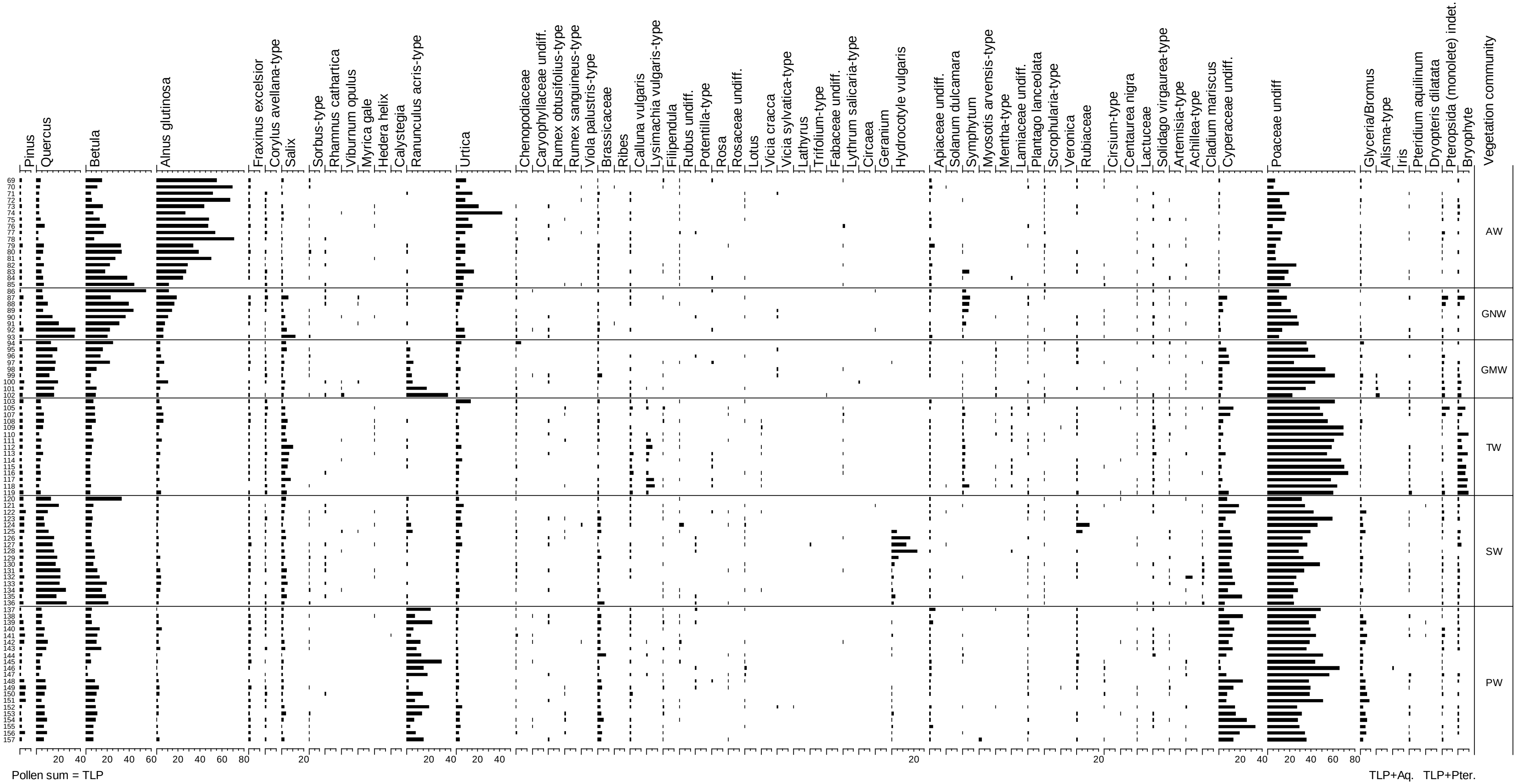
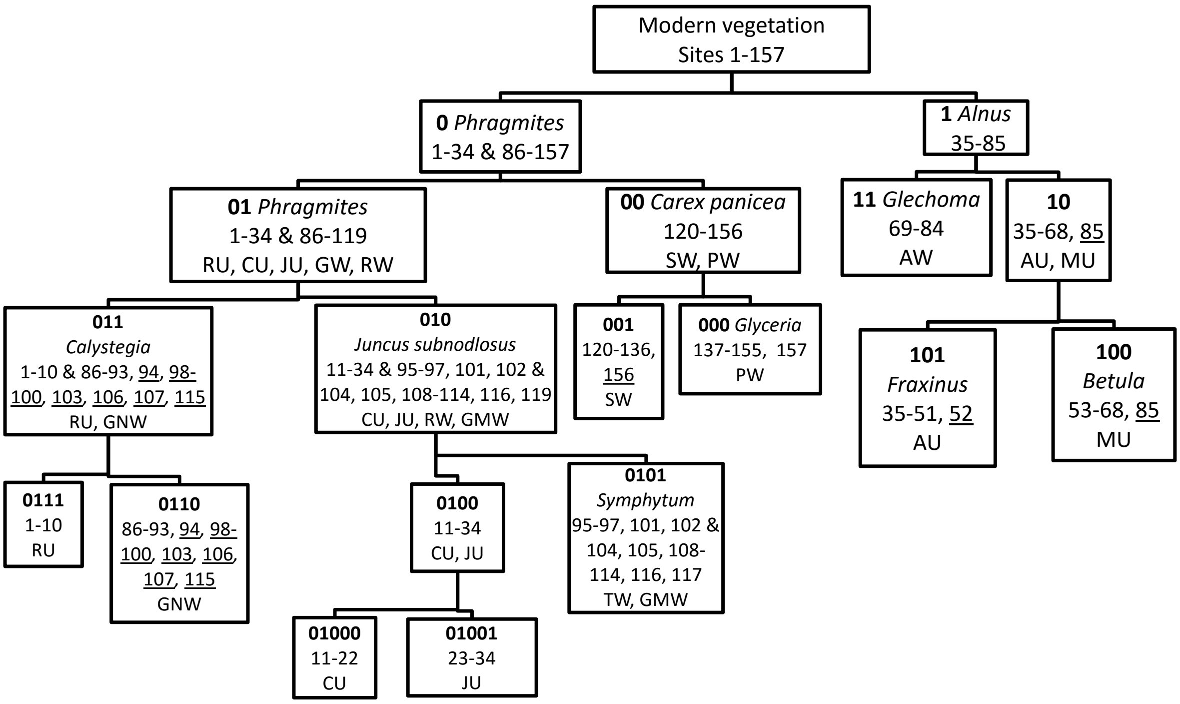
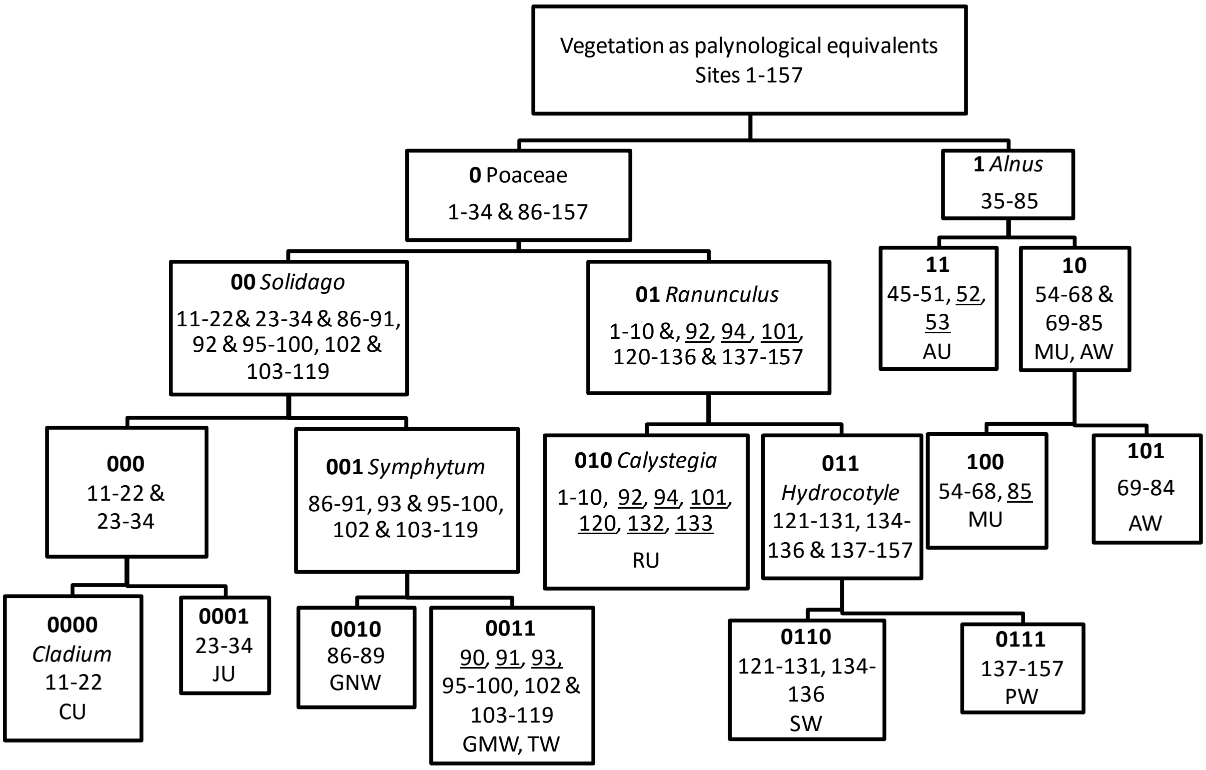


Figure 4. The results of the cluster analysis using TWINSPAN. a) Modern vegetation. b) Vegetation as palynological equivalents. c) Modern pollen. The indicator taxa are derived from WINTwins, the numbers underlined are sites which do not fall within the same clusters as the majority of areas from the same location. For the community codes see Table 1.

a) Modern vegetation



b) Vegetation as palynological equivalents



c) Modern pollen

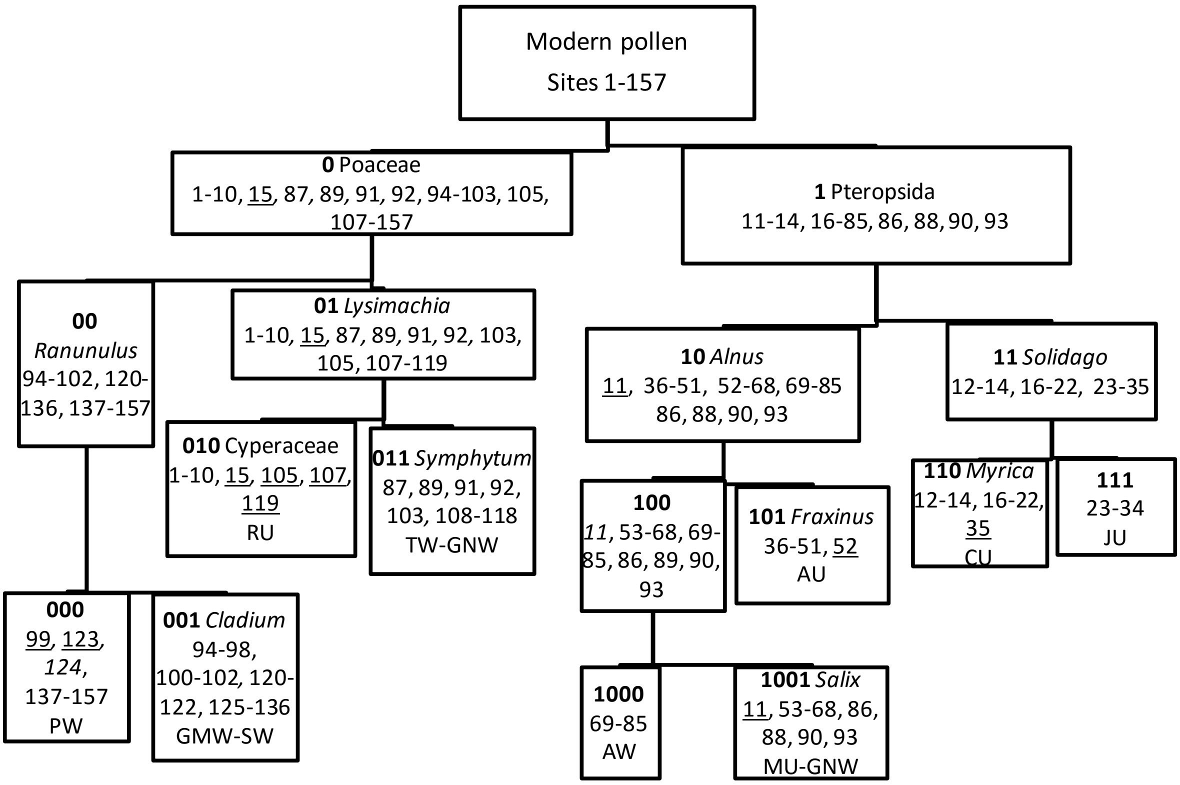


Figure 5 PCA of modern fen data: A) sample points and communities and B) fen taxa

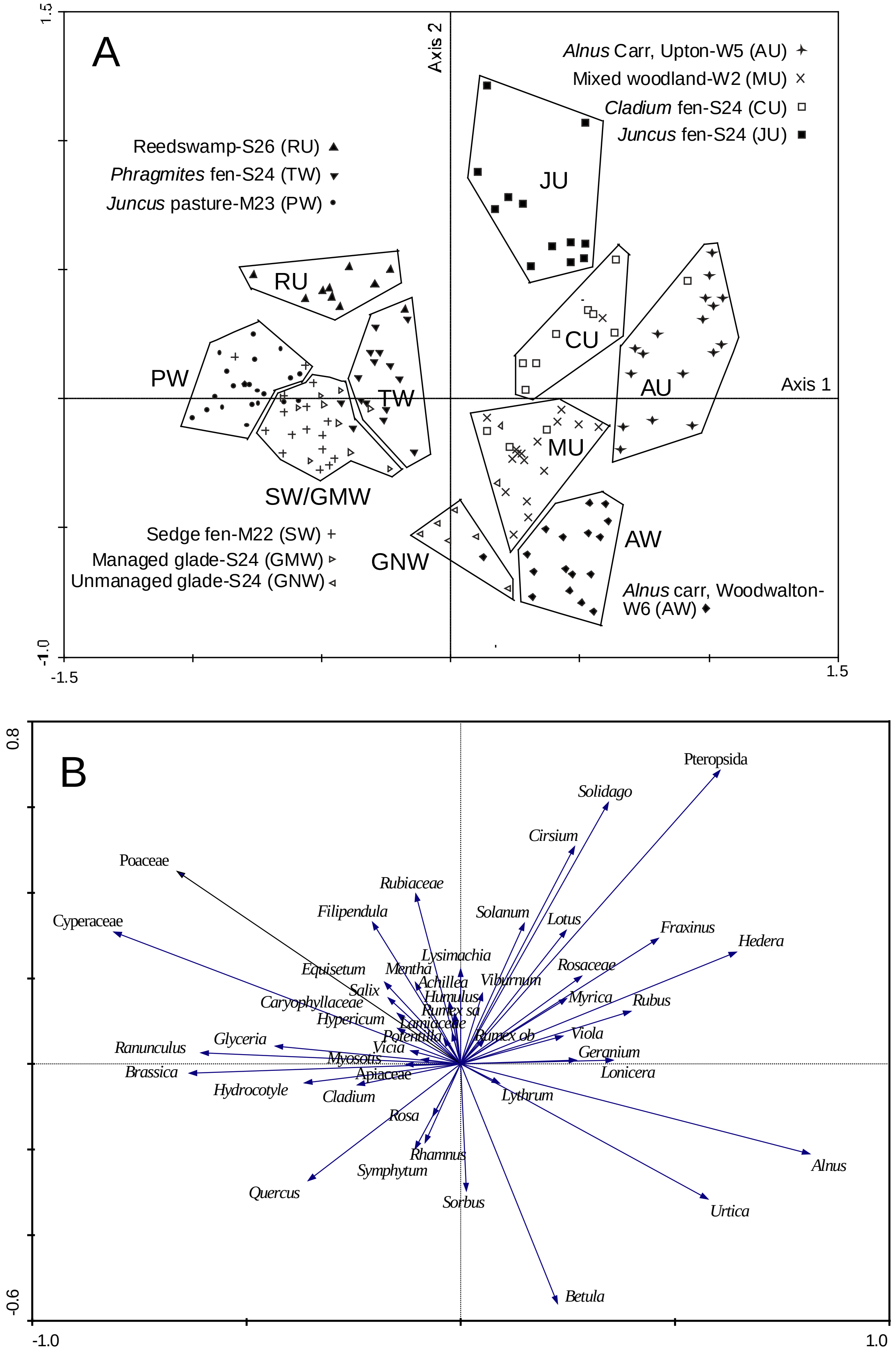
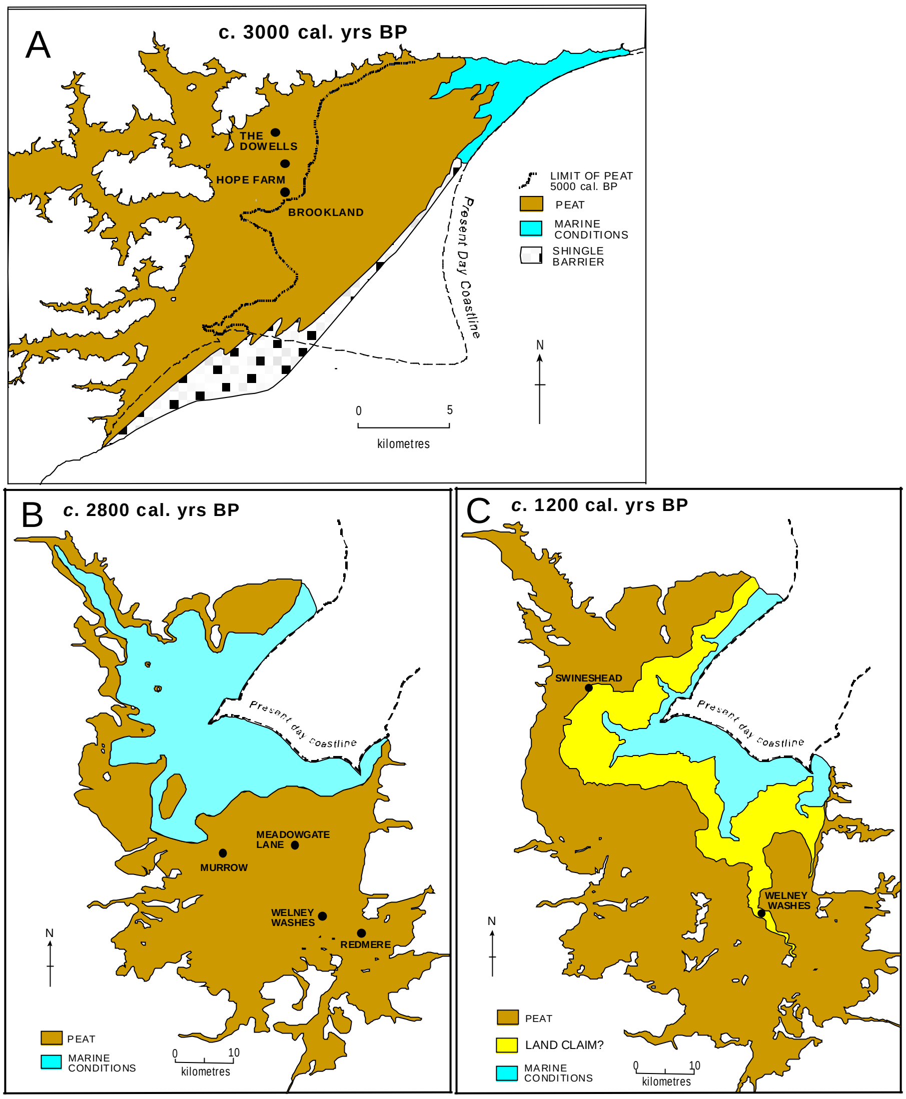


Figure 6. Location of fossil pollen sites. Palaeogeographic reconstructions of Romney Marsh at *c*. 3000 cal. yr BP (A) and Fenland at *c*. 2800 cal. yr BP (B) and *c*. 1200 cal. yr BP (C) follow Long et al. (2007) and Waller (1994b).



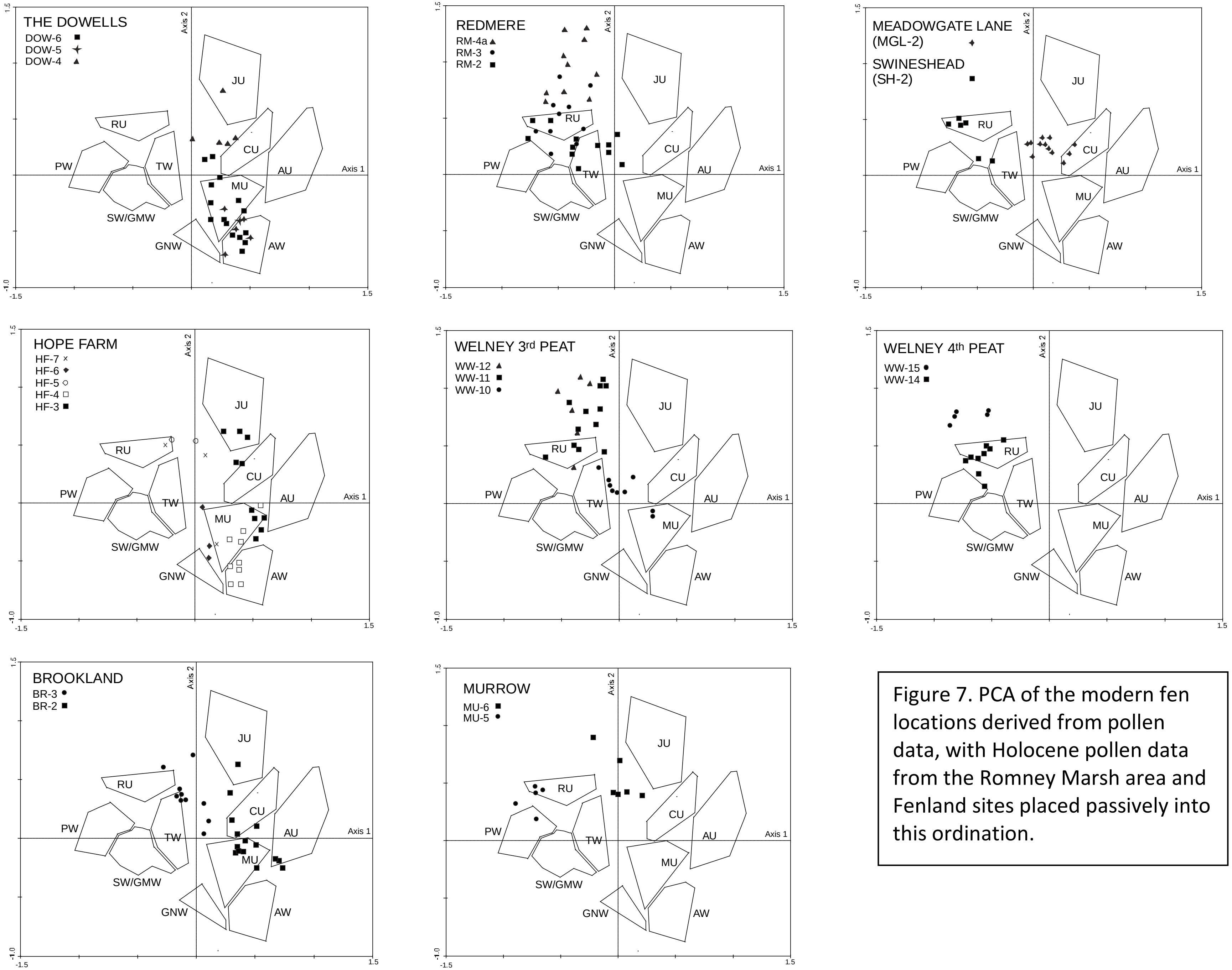


Figure 7. PCA of the modern fen locations derived from pollen data, with Holocene pollen data from the Romney Marsh area and Fenland sites placed passively into this ordination.