A STUDY OF THE DEPOSITION OF, AND TAPHONOMIC PROCESSES AFFECTING, PLANT MACROFOSSIL RECORDS FOR AN ISLAND IN PALAEOLAKE FLIXTON, NORTH YORKSHIRE

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1. INTRODUCTION

Plant macrofossil analysis is used in the study of developing environments and is especially applied to the study of the formation of a hydrosere, due to the excellent preservation conditions usually found in the peat associated with the lakes infilling. Modern studies of the flora present in an area and the correlation to the associated macrofossils give proxies for the study of a Palaeolake, such as Lake Flixton in the Vale of Pickering, North Yorkshire. While the proxy studies broadly concur in the approach to be taken, the deposition and taphonomy of specific plant species and the value of any results, there are elements not considered in them, one being that here are no extant studies of the dispersal of macro-remains and the associated taphonomic processes that are particular to islands within a lake. This dissertation aims to correct this by studying No Name Hill, a former island within Palaeolake Flixton. Cores for examination were collected from the island during excavations in 2018 and the resultant data compared with previous studies from other sites around the lake. While the hydroseral succession was demonstrated consistently across the lake environment, the cores from the island highlighted differential processes of deposition and taphonomy affecting the macrofossil record. It is probable that the shoreline cores give a more generic picture of the environment of the lake and surroundings, while cores taken from an island produce results which are more reflective of the localised flora.

2. USE OF MACROFOSSILS

Definitions

Macrofossils are the remains of plants, often seeds, that survive in anaerobic conditions such as those found in peat deposits, although they are also found outside of these conditions if, for example, they have been subject to burning or charring (Manquoy and Van Geel, 2007, 2316). The remains are usually of magnitude 0.5-2mm, visible to the naked eye but a microscope is required for identification to species level (Birks, 2007, 2266). The term macrofossil also encompasses diaspores, algae, mosses and fungi, as well as the more visible components of the plant, such as wood, bark, leaves and stems and it should be noted that it also represents non-plant derived remains such as molluscs and fish scales, however, for the purposes of this dissertation only plant remains will be discussed (Birks, 2014, 311; Mannion, 1986, 194). Macro-remains are used to determine the species of plants that were growing at a location and point in time and because plants tend to thrive in particular, limited conditions, can be used to determine the environment and climate prevailing. This applies to all classes of flora, including aquatic, bog and fen species, which can then be used to ascertain the development of a hydrosere (Manquoy and Van Geel, 2007, 2316). As peat becomes more humified when dry and macrofossil preservation is then compromised, the wet environments typically found in lakes and bogs lend themselves better to the study of macrofossils (Castro, Souto, Garcia-Rodeja, Pontevedra-Pombal and Fraga, 2014, 82). The study of modern plant ecology in various lacustrine, bog and fen conditions is necessary to provide accurate information which can then be used to construct paleoenvironmental conditions (Manquoy and Van Geel, 2007, 2333). The major corpus of these studies will be reviewed below following a brief discussion of the historic development of macrofossil studies.

Figure 1: Reed bed fringing open water, Brown Moss Nature Reserve, Whitchurch, Shropshire. *Typha latifolia* (Bulrush) is seen on right hand side of the picture, and *Juncus* sp. is growing across the foreground. (Photograph authors own)

History of macrofossil studies

Flora macrofossil analysis and its companion study, pollen analysis, have been used as techniques in the study of the Quaternary period for over one hundred and fifty years, when Swedish palaeobotanist Nathorst first analysed plant remains found below Holocene peats in Sweden, although Mannion suggests that their use predated even this (Mannion, 1986, 194). In Britain, Godwin undertook the first detailed synthesis of plant macrofossils in the 1950’s and in the 1960’s, Watts, working in Minnesota, USA, proposed plotting macrofossil profiles as stratigraphic diagrams, allowing the possibility of their use in dating events within the contexts (Birks, 2014, 310). This link to stratigraphic analysis was to later facilitate use of the macro-remains in archaeology (Birks, 2001, 50). The technique was not universally adapted, and criticisms came from such people as Iversen, who felt that macrofossil studies were limited to relatively narrow environments such as local aquatic flora, not for example upland vegetation (Birks, 2014, 310). Through the mid twentieth century, the use of macrofossils was superseded by pollen analysis, macrofossils being used only to confirm the data from these studies (Birks and Birks, 2001, para. 1). However, subsequent research has attempted to redefine the place of macrofossil analysis in support of archaeological studies, amongst other fields of research.

Modern macrofossil studies have a number of different applications in the reconstruction of past environmental conditions. Perhaps the most important is the reconstruction of the vegetation which prevailed during a particular time period. Gałka and Apolinarska (2014), for example, used plant macrofossils in a study of Lake Purwin, north east Poland. They sampled a core from a peat bog which had previously been part of the lake and analysed this, identifying of three stages of vegetation history within the lake, based on the arboreal species which had dominated at the time, over the period 8600 cal BP to 59 cal BP. The influence of the fluctuating environment on the growth of these differing types of trees was also an influence on the lake levels, which varied throughout the period studied as shown by the macrofossil record from the lake (Gałka and Apolinarska, 2014, 218-221). This has implications for settlement, both in terms of physical availability of dry land, but also in terms of resource types present at the time. Closely linked to this type of study is the ability to determine climactic conditions prevailing in the period under review. This is perhaps especially pertinent in the present day, as we approach a possible climate catastrophe (McKie, 2018, para. 2), as understanding past conditions can offer indicators which can be applied to analysis of modern climactic change. It was previously the case that the basic rate of accumulation of peat was used an indicator for historic climatic conditions, building up a succession of chronological periods known as the Blytt-Sernander periods (Mannion, 1986, 194). Birks however demonstrated that this accumulation often depended on more localised conditions, and the development of radiocarbon dating invalidated its use as a proxy for Holocene period dating (Evans, 1978, 23). Castro, Souto, Garcia-Rodeja, Pontevedra-Pombal and Fraga (2014) studied an area of ombrotrophic peatland (where moisture content is controlled only by precipitation, and not, for example, by river inflow) in south-west Europe during the Holocene period, using plant macrofossil analysis. They identified the main indicator species for the measure of the prevailing environment, in this case *Eriophorum angustifolium*, a plant which grows only under specific, limited conditions. Although ubiquitous, it has a narrow range of tolerance, needing to grow in a wet, but not deep, situation, which characteristic makes it a good indicator of the environment (Grime, Hodgson and Hunt, 2007, 290-1). It could therefore be used today to determine the condition of modern areas of swamp, bog and so on. Following the fluctuations in growth of such species allowed the development of a model for hydrological change in the bog studied (Castro, et al., 2014, 82). The use of such indicator species gives vital information about water level changes.

As already discussed, one of the most useful applications of macrofossil analysis is in determining environmental changes within the lakes and other bodies of water. Barnekow (2000) studied a number of lakes in the Torneträsk area of northern Sweden. From study of plant pollen in addition to macrofossils, she was able to demonstrate accurately a fall in the level of one lake of 1-1.5m at c. 6350 cal BP, and subsequent rise at 4500 cal BP, and attribute these changes to climate fluctuations by analysing not only the arboreal species which grew in the area at different periods but also how the shore- and tree-lines had fluctuated during this time (Barnekow, 2000, 399).

Environmental reconstructions based on macrofossil analysis can also be used to establish the landscape contexts of episodes of past human activity and the depositional contexts of archaeological material. This can best be illustrated with an example from the early Mesolithic site of Star Carr, North Yorkshire. When Graham Clark first excavated at Star Carr during 1949-51, he found an incredible range of artefacts, which he considered had been deposited in the reed beds at the edge of the lake; thus, he concluded that they had been discarded *in situ*, in an area of habitation (Clark, 1954, 9). This model of deposition has been contested over the years since, and it has been important to the resolution of the issue that the level of the lake waters at the time of deposition were accurately established. Work carried out at the site between 2004 and 2015 included sampling for macro-remains in trenches originally opened by Clark (Taylor, Elliot, Conneller, Milner, Baylis, et al., 2017, 24). This analysis led to the important conclusion that the artefacts found by Clark, and others since, had been deposited in shallow water and so it appears that there was an indeed an element of ritual in the disposal of these items (Taylor, et al., 2017, 37, 39).

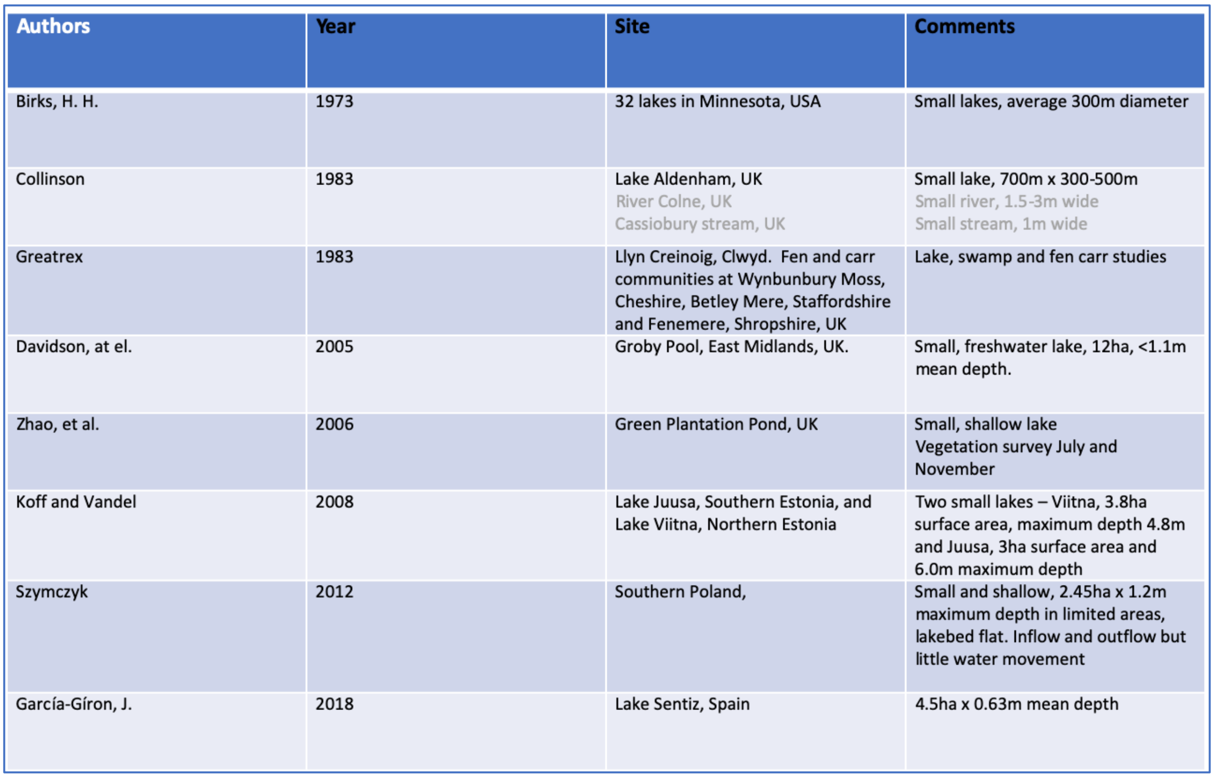
In addition, plant macrofossil analysis can be used in consideration of domestication or cultivation of plants, or their use as foodstuffs by examination particularly of carbonised remains found at sites. Bishop, Church and Rowley-Conwy (2013) analysed charred remains from a number of Mesolithic sites in Scotland and from this established the wide variety of plant foodstuffs, not only fruits but roots and tubers, which had been utilised by Mesolithic peoples at the sites.

Macrofossils are not the only plant remains that can be used to determine past climactic conditions, reconstruct vegetation profiles, lake levels and hydroseral succession with the resultant implications for human activity. Pollen, as discussed, can also be used but it can be seen that macrofossils have a number of advantages over pollen. Firstly, researchers such as Birks (2007, 2267) demonstrated that macrofossils were generally less dispersed from their source plant than anemophilous pollen, and therefore provided a better record of the local environment. In some areas incoming pollen might confuse local signals (see for example Mannion, 1986 for a discussion on production of *Juncus* seed). Secondly, macro-remains are also often available when pollen is not, such as in the case of certain taxa which produce little pollen. Finally, pollen can usually only be identified to genus level, whereas it is often possible to identify the species that a macrofossil is from, offering a more nuanced analysis of the vegetation and environment (Birks, 2001, 55; Mannion, 1986, 197). Indeed, Birks and Birks (2001) urge that pollen analysis must always be supported by the use of macrofossils, and cited examples of misinterpretations that were corrected by subsequent analysis of macrofossils: For example an area currently under the Bering Sea that had been thought to be one of steppe grassland previously was reinterpreted as a landscape of shrubs and boggy pools, obviously a significant change with resultant implications for human activity in the area (Birks and Birks, 2001, Conclusions). Birks was later to develop standard methodologies for the use of plant macrofossils in palaeoecological research (Birks, 2014, 310). As seen above, this standardisation included the use of macrofossil diagrams which present the results of the analysis in a stratigraphic manner, therefore facilitating the comparison of results both within and between sites and to support the interpretation of an area. This standardisation has been supplemented with studies aiming to determine the different dispersal and taphonomic processes which may affect various plant species or groups. They are based on analysis of plants and other flora growing in contemporary lakes and the veracity of their representation in the macrofossil record; the most influential studies will be reviewed below.

Contemporary studies of dispersal and taphonomy

One of the issues with interpretation of macrofossil studies is to understand how representative they are of the contemporary flora. A number of researchers have studied the relationship between plant macro-remains and the extant plant communities in modern environments, providing important information on the ways in which plant macrofossils are dispersed in lakes and wetlands, and the degree to which they then represent the past plant communities. These are summarised in Table 1, below.

Table 1: Summary of modern proxy studies of macrofossil deposition and taphonomy



Authors	Year	Site	Comments
Birks, H. H.	1973	32 lakes in Minnesota, USA	Small lakes, average 300m diameter
Collinson	1983	Lake Aldenham, UK River Colne, UK Cassiobury stream, UK	Small lake, 700m x 300-500m Small river, 1.5-3m wide Small stream, 1m wide
Greatrex	1983	Llyn Creinoig, Clwyd. Fen and carr communities at Wynbunbury Moss, Cheshire, Betley Mere, Staffordshire and Fenemere, Shropshire, UK	Lake, swamp and fen carr studies
Davidson, at el.	2005	Groby Pool, East Midlands, UK.	Small, freshwater lake, 12ha, <1.1m mean depth.
Zhao, et al.	2006	Green Plantation Pond, UK	Small, shallow lake Vegetation survey July and November
Koff and Vandel	2008	Lake Juusa, Southern Estonia, and Lake Viitna, Northern Estonia	Two small lakes – Viitna, 3.8ha surface area, maximum depth 4.8m and Juusa, 3ha surface area and 6.0m maximum depth
Szymczyk	2012	Southern Poland,	Small and shallow, 2.45ha x 1.2m maximum depth in limited areas, lakebed flat. Inflow and outflow but little water movement
García-Gíron, J.	2018	Lake Sentiz, Spain	4.5ha x 0.63m mean depth

The studies

The first of these was carried out by Hilary H. Birks (1973) who looked at the relationship between plant macrofossils and the local plant communities of 32 small lakes (average diameter 300m) in Minnesota, USA. The availability in a relatively small area of many lakes of similar dimensions afforded a comprehensive analysis while maintaining a consistent set of parameters across the range of different habitats which the lakes inhabited (Birks, 1973, 174). The floating or emergent vegetation present in and around the lakes was recorded, and samples taken of the peat or sediments in transects across the lake from shore to deep water, the macrofossils recorded as number present per 100cm^3 of sediment (Birks, 1973, 173-4). Collinson (1983) studied three different aquatic environments, only one of which will be considered here; Lake Aldenham in the UK, a small lake approximately 700m x 500m. A fall in depth of the lake in 1975 allowed the development of a population of emergent aquatic plants for study (Collinson, 1983, 584-5). Sampling was designed to evaluate the congruence or otherwise apparent in the macrofossil record between differing micro-depositional environments within in a lake (Collinson, 1983, 583). Another study published in 1983 was carried out by Greatrex, who sampled four different environments in England, encompassing lacustrine, swamp, fen and carr communities, in an attempt to broaden the discussion through the wider hydroseral process (Greatrex, 1983, 773). Davidson, Sayer, Bennion, David, Rose and Wade (2005) studied the deposition of predominantly aquatic macrofossils and pollen in a lake and compared this with written records of the species growing at the site that had been maintained since the early eighteenth century, in order to measure the correlation between the recorded historical populations and the macrofossil record. Groby Pool in the east Midlands of England, selected for the study, was approximately 12ha in surface area but shallow, with a mean depth of 1.1m (Davidson, et al., 2005, 1672). Another small, shallow lake in Norfolk, England, was analysed by Zhao, Sayer, Birks, Hughes and Peglar (2006). Green Plantation Pond was 1.6ha in area with a maximum depth of 300cm and was selected for the clear zoning of a variety of species which allowed for a more defined interpretation (Zhao, et al., 2006, 336). The aquatic plant population, the focus of the study, was surveyed during the month of July 2000, these observations were also supplemented by plant records from surveys carried out in previous years. The sediment was sampled in November of the same year (Zhao, et al., 2006, 338, 340). A similar study was undertaken by Koff and Vandel (2008) of two small lakes in south and north Estonia. Lake Juusa was 3ha in area (250m maximum length), and a maximum of 6m depth, while Lake Viitna had a larger area at 3.8ha but was shallower, at 4.8m maximum (Koff and Vandel, 2006, 6). The sampling was similar to that employed by Birks, in that the all of the species present in the littoral zones were recorded, and macro-remains were taken from samples of sediment following the bathymetric profile of the lake basin from the shore to the deepest areas (Koff and Vandel, 2006, 7, 9). Szymczyk (2012) studied a reservoir located in southern Poland, of 2.45ha area and a maximum depth of 1.2m, although this maximum occurred at only a few places within the basin. There was limited movement of water through the reservoir, and the effect of wind on distribution of seed and other remains was diminished by the shelter afforded by the hills and tree cover found around the lake (Szymczyk, 2012, 504). The forty sediment samples collected were again aligned along bathymetric intervals, from littoral locations into the deepest water (Szymczyk, 2012, 505). García-Gíron, Fernández-Aláez, Nistal-García and Fernández-Aláez (2018) studied a small lake in Mediterranean Spain, partly because of the lack of studies of temperate lakes but also with the aim of determining the optimum location for taking core samples. They documented the species present in the lake and took sediment samples at corresponding points for macrofossil analysis (García-Gíron et al., 2018, 498).

The overall conclusion from all of the studies was that modern plant macrofossil distribution could form a sound proxy for past environmental reconstruction, with the codicil that both plants and macrofossils could be differentially represented, so other factors had to be considered in analysis of any results (Birks, 1973, 188). The correlation of the plants found in the lake versus those present in the macrofossil record was tested in all of the studies with the following outcomes. Firstly, there was a variance between the plant population and the macrofossil record. Certain species were found to be either under- or over-represented in, or even absent from, the macrofossil record. Birks initially considered that this may have been a function of the sampling process, but the method of plant reproduction was subsequently found to be a factor in the distribution and quantity of macro-remains (Birks, 1973, 178-9). A perennial species, which relies on vegetative means of reproduction such as rhizome growth, may appear to be sparse in the area based solely on the number of seeds present, even though it may actually be well represented in the environment. Conversely an annual could be over-represented due to the large quantities of seeds it produces. (Birks, 1973, 179). Greatrex (1983, 789) in her study also demonstrated this in the small amount of seed observed for *Iris pseudacorus,* which reproduces vegetatively, while Koff and Vandel (2008, 15) found only a single seed from this species in their study, immediately adjacent to the modern plant. Koff and Vandel (2008, 16) noted too that vegetative parts of the plant are fleshy and potentially do not survive as well as seeds, another way in which a perennial could be further under-represented in the macrofossil record. These factors are pivotal to understanding distribution and deposition and therefore the interpretation of plant macro-remains.

Another conclusion from the studies is around the differential deposition of macro-remains. Firstly, the number of macrofossils found in the samples tends to increase as cover increases (Birks, 1973, 179; Davidson, et al., 2005, 167). In addition, they are more plentiful both in number and diversity around lake margins than in the deeper waters further from the shore (Koff and Vandel, 2008, 16). In Szymczyk's (2012, 510) study the samples from littoral zones also showed most diversity, which he attributed to the mechanisms that many seeds have for floating, limited only by the shape of the lake and the tendency for emergent vegetation to trap the seeds. The exceptions are those plants whose remains are not well transported, such as *Potamogeton natans*, which in Szymczyk's study were hindered in their distribution by the emergent shoots of *Hippuris vulgaris* (Szymczyk, 2012, 510). While plant communities, including aquatics and surrounding terrestrial species, were reflected accurately in the macrofossil record from the lake margins, several researchers found that this was not the case in the deeper parts of the lake basin; the remains found in these areas were likely to have originated from species with seeds that are abundant and readily transported such as *Characeae*, or from the species of aquatic taxa which produce seed only in low numbers, which then sink rapidly, such as *Myriophyllum spicatum* (Birks, 1973, 179; Collinson, 1983, 589; Davidson, et al., 2005, 1682-3). Furthermore, littoral zone samples were only valuable and accurate when the area selected was not affected by any inflow to the lake, which might have contaminated the local record with plant remains brought in from another catchment zone (Collinson, 1983, 583). Collinson concurs with Birks too in concluding that while the plant species growing in the lake are well represented by macrofossils, the abundance of such plants cannot be inferred straightforwardly, and other factors, for example biodegradation, have to be considered (Collinson, 1983, 589). Generally, macrofossils were seen to under-represent diversity, for example Davidson, et al. (2005, 1671) found only three out of a recorded eight species of *Potamogeton* present as macrofossil traces. This agrees with other studies, such as that by Zhao, et al. (2005, 340) who observed that *P. natans* was not represented at all in their study; they ascertained its presence instead by observing the presence of the plant's leaves. *Potamogeton* species which were represented in the macrofossil record where found, again by study of leaf remains, to have seeds which fell in close proximity to the parent plant, in contrast to Birks (Zhao, et al., 2006, 341). Davidson, et al, (2005, 1671) in their study concluded that, of the 42 aquatic species present, only 40% of those taxa were reliably represented in the macrofossil record, while the pollen record also highlighted some taxa which are not found as macrofossils. Zhao, et al. (2005, 347) cautioned that although most plant macrofossils were to be found at 20-30m from the source plant and while littoral locations were still the most species rich areas, observations here were 'temporally smoothed' and any interpretation needed to consider the resultant lack of subtly in the record.

Plant dominance too is an important factor. This is seen with *Typha*, when large numbers of macrofossils are found when the plant is dominant, however when it is more sporadic in growth, seed numbers are disproportionally low; alternatively, *Carex* numbers were always found to be low in Birks study (1973, 179). However, Greatrex showed that while *Carex* was found to be under-represented in the macrofossil record at Llyn Creinog (a lake) in spite of it being the dominant species there, in a fen environment, where macro-remains are not moved away from the parent plant by water, its presence could be over-represented (Greatrex, 1983, 775, 778). Part of the reason for this was that localised 'hot-spots' were generated, for example in the case of one large *Carex* tussock which skewed the seed record for that sample, while over a larger area it was not widely found (Greatrex, 1983, 779). Generally, *C. paniculata* grows extremely well when it is not in competition so one large plant may produce many seed heads which then leading to a false conclusion of its dominance (Greatrex, 1983, 779). As stated above, the anomaly was also a function of water transport, or lack of it, as a lake infills *Carex* (and other species) seeds will be moved less, this is discussed further below. Localised concentrations can represent other specific conditions, for example as already discussed the seeds of *Potamogeton natans* and *Menyanthes trifoliata* were found only in areas where they could disperse free of the roots of other plants (Szymczyk, 2011, 510).

Birks considered the transport and distribution mechanisms of those seeds to be a major factor for the appearance of seeds in the plant macrofossil record (Birks, 1973, 178-9). She demonstrated that *Betula*, an arboreal species growing around or near a lake, produces abundant seed which is wind dispersed and is therefore often present in large numbers in the macrofossil record and further, is often the only seed found in the centre of large lakes (Birks, 1973, 180). Greatrex (1983, 775) however, made a distinction between the winged fruits of *Betula* and its catkin scales, concluding that the latter were a better indication of the presence of *Betula* in the local environment due to their comparatively restricted distribution. *Typha*, a wetland marginal plant, also produces seed designed to be wind dispersed, and again can be found at considerable distances from its source, a point confirmed in Birk's study and in both of the lakes studied by Koff and Vandel (Birks, 1973, 181; Koff and Vandel, 2008, 15). Other wetland species can produce seeds with adaptations for floating as a means of dispersal, thus for example *Ranunculus* seeds can be found at some distance from the shore but generally not in as large numbers as wind dispersed seed species are (Birks, 1973, 180). In contrast to *Ranunculus, Viola*, another wetland plant, produces seeds with no dispersal adaptations and thus the number found falls off rapidly at any distance from the source plant (Birks, 1973, 181). Another particular case is that of *Phragmites australis*. Although found to be growing in many of the studies by the presence of its leaves and stems, its seed remains were rare. Szymczyk (2012, 512) confirmed this as did Koff and Vandel (2008, 11), who observed *Phragmites* growing in both lakes, but seeds were present only in Lake Viitna. *Phragmites* do not ripen seed in cold summers so not only is seed production is very variable annually, but the seed itself is very fragile, and it may not survive well in older or humified deposits, this can again lead to the species being under-represented (Greatrex, 1983, 785; Koff and Vandel, 2008, 15; Szymczyk, 2012, 512).

Obligate aquatics in contrast mainly reproduce vegetatively and therefore have correspondingly low seed production (Birks, 1973, 178). Generally, few macrofossils from aquatics were found at any distance from the plant, any seeds often being designed to sink near to the source in order to facilitate rapid germination (Birks, 1973, 182). There are exceptions, as discussed, some *Potamogeton* species have seeds that are adapted to float and can therefore be found at littoral zones, in contrast to other species of the family which produce seeds that sink almost immediately (Birks, 1973, 182). Zhao, et el. (2006, 346) confirmed this, their analysis of *P. pusillus* seeds found that freshly shed seed tended to float to the shore, either on their own or in a raft of other plant material, in some case still attached to their inflorescence, which then created artificially high concentrations of seeds away from their source. However, their measure of nearness was between 20 and 30m from the source - in some of the lakes examined this could represent a distance of halfway across the body of water (Zhao, et al., 2005, 346). Contrast this for example with Greatrex (1983) who studied distribution in some environments at distances of only 1m and 5m from the parent plant.

Other exceptions in Birk's study were *Najas*, discussed below, *Nitella flexilis* and other *Chara* spp., all of which were found at distance from the source (Birks, 1973, 182). *Characeae* is confirmed in a number of the studies as having high concentrations over wide areas from its source. Szymczyk (2012, 510) though tempered this observation on *Characeae,* which he found to occur in large quantities only near to the parent vegetation; however, this can represent large areas of a lake and it could therefore be considered to be a widely occurring species as opposed to widely distributed. Further, Zhao, et al. (2006, 338, 341) confirmed that *Characeae* could not only be more localised than previously considered, but that the growth of *Chara spp*. could be very variable; in their 1998 and 1999 plant surveys *Chara* was recorded as abundant but it was not present in the survey taken in the following year. Finally, Koff and Vandel (2008, 14) found *Chara* macrofossils where there were no contemporary plants and it seems that oospores can survive in a dormant state. Seeds of *Najas flexilis,* an annual obligate aquatic and another *Characeae* species, were found in concentration around the area of plant growth but they can also be found away from the source as they are readily transported; further oospores were also found when there were no plants present, which may be explained by factors such as the survival of seeds when the plant has ceased to grow (as above), and the sampling bias already discussed (Birks, 1973, 179). In addition, seeds of many species tend to wash up near to the shore to in order to obtain the best conditions for germination (Birks, 1973, 180).

In contrast, plants whose main mechanism for dispersal was by animal action (such as the ingestion of seeds through the consumption of their fruits) were often under-represented, for example Greatrex (1983, 789) observed that *Solanum dulcamara* seeds were not only underrepresented in the macrofossil records but tended to be sporadic in distribution, while one sample yielded six seeds another taken only 60cm away from the first contained none; overall their presence was only due 'to chance' (Greatrex, 1983, 778). Even the movement of fish may be responsible for the transportation of lighter seeds to the deeper areas (Szymczyk, 2012, 510, 514). Zhao, et al. (2006, 344) considered that *Chara* was widely distributed as a result of the large numbers of oospores produced, their light weight, which facilitates movement in water, and their use as a foodstuff for waterfowl which results in their redistribution as a result of defecation. This is in addition to the reasons already discussed for the widespread population of *Characeae* in a lake.

Some of the studies underlined the importance of the conditions in which the macro remains had been deposited as contributing to their survival. In Collinson's (1983, 585) study of Lake Aldenham, samples were taken from three random areas. In sample A, a moisture rich area, 11 out of 12 growing aquatic or emergent species were present and macro-remains, in B, a drier zone, only 3 from 12 were represented and in C, no longer submerged, only the most robust samples survived. The low count in sample C was attributed either to a lack of taxa in the first place or the degradation by abrasion of samples, but was concluded to be most probably a result of oxidisation, as the area was not consistently waterlogged; seeds with thinner walls or smaller seeds are less likely to survive oxidisation (Collinson, 1973, 586). This was echoed in Greatrex's (1983, 777) study of Betley fen carr where species representation was found to be low in aerobic conditions.

Greatrex's study (1983, 774-5) utilised the same counting methods for each differing wetland environment sampled, noting the plants growing within 1m and 5m of the sample site in order to provide a measure of seed dispersal in the seventeen sediment samples taken from the sites. She concluded that between 50-100% of modern vegetation was represented by the macro-remains record, although this was not evenly distributed across habitats (Greatrex, 1983, 773). In environments with less water available as a means of dispersal, Wynbunbury Moss and Fenemere, carr and swamp respectively, high percentages of seeds (up to 98%) could be found within 1m of their source plant. However, in an even drier environment such as found at Betley Mere only 50-56% of species were represented by macro-remains thereby demonstrating that water is not only a medium for transport, but is also an important factor in preservation. Further, tree canopy cover increases in fen, reducing the diversity of flowering species growing under it (Greatrex, 1983, 777-9). Finally, flooding of the environment may introduce traces of species from outside of the immediate area that would not usually be represented (Greatrex, 1983, 779). Distribution of macrofossils was therefore considered to be a function of these various conditions in her study.

In their study of Lake Sentiz in north-west Spain, García-Gíron et al. (2018, 499) first developed a simulation model which was then used to ascertain the representativeness of the results obtained from their cores. Again, the conclusion was that the species are represented differentially, so *Potamogeton* spp. were under- and *Characeae* over-represented. However, their conclusion on proximity of plants to their macrofossil deposits differed from other studies in that they observed that seeds from submerged and helophyte species were generally to be found near to their source, and in deeper parts of the lake, whereas floating leaved species were better represented in samples taken from closer to the shore (García-Gíron, et al., 2018, 495). All samples from deeper areas of the lake correlated to the modelled populations, but samples from a slope within the lake did not, and nor did samples from near to the shore, although the number of macrofossils present here was overall greater than in the deeper parts of the lake (García-Gíron, et al., 2018, 502) Additionally, they advocated that cores taken from the deeper areas would better represent the original lake plant population, while a transect of cores across the lake was required to establish growth and development of the hydrosere (García-Gíron, et al., 2011, 495) This is in contrast to, for example, Collinson (1983, 509) who concluded that sample cores from the centre of the lake were not at all useful in determining plant population. Greatrex (1983, 790) too concluded that hydroseral succession cannot be inferred from surface samples, a stratigraphic investigation was found to be critical in this.

Conclusions

Overall these studies have demonstrated that plant macrofossils provide a reasonable reflection of the contemporary vegetation within a wetland environment, although there are factors affecting the representation of particular species. There are some issues too with the studies. Firstly, they are all are based around relatively small bodies of water. The largest lake area covered 12ha., but this was only 1m deep and although many of the studies considered the effect of depth and distance from shore, this was of lakes of a minimal depth, with the exception of those in Koff and Vandel's (2008) study. Secondly, to date, no-one has tested these findings against a palaeoecological record, all have tested modern environments, so there is no current confirmation of the principle of uniformitarianism.

A specific weakness in Davison, et als. study arises from the timespan of the recording; over 250 years there had inevitably been a variety of people compiling the historical records, as the diversity of sources used shows, possibly with different understanding of plant identification, although the team did try to take account of these possible errors, for example in the identification of *Callitriche,* which they acknowledged had been problematic over the period (Davidson, et al., 2005, 1674). The first record used in the study dates from 1747, which pre-dates the publication that pioneered the modern binomial system of plant classification, perhaps creating further anomalies (Ingram, Vince-Prue and Gregory, 2008, 51). These difficulties were highlighted by the presence of plant macrofossils for which there were no recorded observations (Davidson et al., 2005, 1676).

Most studies considered the reproductive characteristics of the plant and its resultant macrofossil record. Annual plants, for example, generally produce far more seed than perennials, and thus may be over-represented (Koff and Vandel, 2008, 15); further, many aquatic plants are perennial, reproducing by vegetative means (Birks, 1973, 179). Seasonal variation too is important, in a short, relatively cold season some perennial plants may not have the opportunity to produce seed (Koff and Vandel, 2008, 15). *Typha latifolia* (in a year with favourable conditions) produces many small, wind borne seeds, so in spite of it being a plant that grows in shallow water it is possible to find the seeds in the deepest areas (Allaby, 2006, 41; Koff and Vandel, 2008, 15). *Carex* spp., in contrast, can produce few seeds that are then not apparent in the macrofossil record (Birks, 1973, 179). Zhao, et al. (2006, 346) make an interesting point about sample bias in that some seeds may float as complete inflorescences containing many seeds, and if counted at the point that it has come to rest, the species would be over-represented.

The number of present-day species that were represented in the macrofossil record varied, from 40% (Davidson, et al., 2005), or 50% (Koff and Vandel, 2008, 17), to 100% in some environments (Greatrex, 1983, 789). That sufficient fossils to allow good representation of species are found only in anaerobic, waterlogged environments is agreed by all; Greatrex (1983, 789) in particular highlighted this in her comparison of macrofossil survival in drier environments. The distribution of the macrofossils across a lake is discussed by most researchers. Again, there is general agreement that macrofossils are found in greater quantities and with greater diversity at the lake margins, either as a result of the conditions required for reproduction (Birks, 1973, 180), or as a natural consequence of movement within the lake, or as a result of being held in floating rafts of debris that are in turn held by the plants growing in the marginal areas (Zhao, et al., 2006, 346). Overall the accuracy of macrofossil records is dependent on the conditions for preservation as shown in the drier fen-carr area versus the samples taken from a swamp environment, the survival of seeds in older deposits, the reproductive strategy of the plant and the cover-abundance/seed representation relationship such as that of *Carex,* on which interpretation may be pivotal

(Greatrex, 1983, 789). Further, the degree to which the macrofossil profile of a lake represents the plant population in that lake depends upon lake size, depth, morphology of the lake bottom and plant spacing. (Koff and Vandel, 2008, 5; Zhao et al., 2006, 347). Koff and Vandel specifically addressed the bathymetric characteristics of the lake being studied and concluded that slopes with a gradient above 14% should not be sampled, nor should areas in the path of prevailing winds, as post depositional processes would have a stronger effect in these areas, thereby lessening the accuracy of local studies for the species (Koff and Vandel, 2008, 17). Szymczyk (2011, 504) took into account the possible effect of wind in the selection of the reservoir for his study, as it was sheltered by the surrounding hills and trees.

García-Gíron, et al. (2018, 495) considered the type of plant and its growth strategy. Those hydrophytes and helophytes with submerged leaves tended to have a more accurate macrofossil record in close proximity to the source, including in deep water conditions, while those with floating leaves deposited macrofossils which were to be found on the shoreline.

Overall, while macrofossils provide a good proxy for past environments, transects of cores will produce a more even picture of the distribution in a lake, while samples taken from the shoreline, while providing a good record of the presence of species may over-represent them numerically. The sampling strategy of each study varied; many did not follow Digerfeldt's recommendations for sampling a transect which allows the development of stratigraphic data (Greatrex, 1983, 790; Mannion, 1986, 198). The local conditions, profile of the lake bottom, and the reproductive strategies of the plants all need to be taken into consideration for an accurate picture.

The deposition of macrofossils and the taphonomic processes that affect their presence has largely been defined in terms of the characteristics of the plant and its reproductive strategy. Some mention is made of the effect of aquatic animals which may affect the dispersal of macrofossils, and of some other, limited circumstances, such as the direction of the prevailing wind. Further the majority of these studies have been carried out on small bodies of water, and none have considered the differential deposition which may take place, for example on an island in the main body of water. However, to date there is no analysis of the possibility of differential deposition and taphonomy around such a large lake, as the modern proxy studies discussed above are all from much smaller lake areas. Furthermore, the presence of an island, and the possible effect on deposition of such a feature, has not been explored. This dissertation will consider data from macrofossil studies already carried at Palaeolake Flixton, coupled with two new profiles developed from excavations in 2018, in an attempt to analyse differential deposition and taphonomy at various site types around a large lake.

Figure 2: Lake edge, Cholmondeley Mere, Cheshire. Showing *Betula* growing at the edge of standing water. *Mentha aquatica* is also growing into the water.

(Photograph: Authors own)

3. AIMS, OBJECTIVES AND METHODS

The aim of this project is to identity the effect on the macrofossil record of any differential deposition and taphonomic processes apparent at sites of different characteristics; specifically, on an island shore within a large lake. Any differences identified may give rise to new understanding of the effect of different locations and characteristics of micro-environments within a larger system for the study of macrofossils as a proxy for palaeoecological conditions and change.

The project will be focussed on Palaeolake Flixton, North Yorkshire, UK, an area that has been the subject of a number of detailed palaeoecological studies, including plant macrofossil studies, since the mid-20th Century. See Figure 3 below.

This will be achieved through the successful completion of the following objectives:

- Discussion of modern macrofossil studies and their value as proxies for the study of paleoenvironmental change
- Analysis of macrofossil assemblages from two samples taken from No Name Hill during the excavation carried out in 2018
- Comparison of these with a previous profile for No Name Hill
- Comparison with macrofossil profiles obtained for two other areas within the landscape of Palaeolake Pickering, that is Star Carr and Flixton School House Farm
- Interpretation of these profiles, considering the possible influences in dispersal and taphonomy of plant remains on an island within a large lake

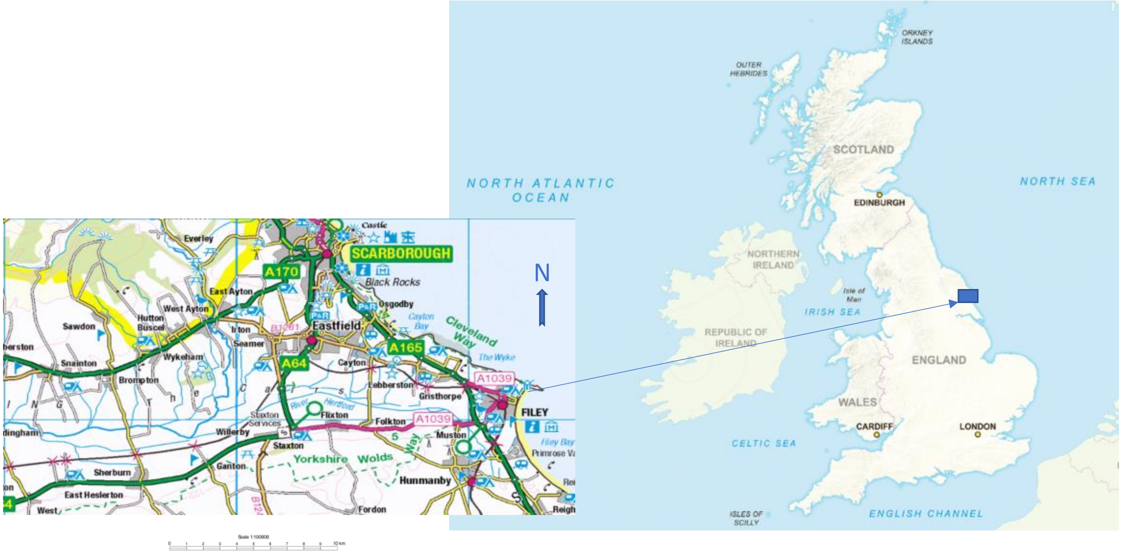


Figure 3: Approximate location within the United Kingdom of the Vale of Pickering and a detail of the area with the River Hertford shown (Credit: Digimap)

Paleolake Flixton

The lake had first been identified by John Moore in the 1940’s and Godwin was to develop an initial paleoenvironmental analysis of the Star Carr area using pollen records obtained from the site of Moore’s excavations in 1948 (Clarke, 1954, xviii). As part of Clark’s later excavations from 1949 to 1951, Godwin and Walker made a series of auger transects across the area of the lake in order to establish the profile of the basin, and also carried out pollen and macrofossil analysis from across the area (Clark, 1954, 25-69): Thus, the first comprehensive environmental history of the lake and its environs was established. In the mid-1970’s an application was made by North Yorkshire County Council to build a waste site at Seamer Carr, only 1.3km to the north of Star Carr. This site was then excavated, during which time

Cloutman carried out detailed auger surveys in the area, which lies on the north-west edge of the lake, later extending this work further around the western shore (Mellars, 1998, 12). Pollen profiles taken during this survey where used to refine the dating for the environmental changes that Godwin and Walker had identified (Taylor, et al., 2018, 44). Smith and Cloutman then surveyed the Star Carr area and combined the results of their pollen analysis with radiocarbon dating, allowing the development of a definitive chronology for the evolution of the hydrosere (Taylor, et al., 2018, 44). The Vale of Pickering Research Trust (VPRT) then initiated other palaeoecological surveys around the lake; Dark was to establish a detailed chronology for the early development of the lake during the late glacial/early Holocene transition, and of the later wetlands at Star Carr (Taylor, et al., 2018, 44). Star Carr was again the focus for a later study by Dark, using pollen and macrofossil analysis alongside study of any charcoal deposits present to determine the extent of human impact in the area (Dark, 1998, 115-6). Taylor and Allison (2018, 123) used plant and insect records to confirm the environmental context in which artefacts had been deposited at Star Carr. Taylor (2011, 69) carried out macrofossil analysis at No Name Hill and Flixton School House Farm, using these results to supplement and confirm information from Star Carr as well as identifying the characteristics of the other sites. Taylor also carried out macrofossil analysis at Flixton School House Farm (2019), placing cores further out into the lake than had previously been done, up to 150m from the shore, in order to build up a more comprehensive picture of the palaeoenvironment.

All of this work has provided a detailed understanding of the development of Palaeolake Flixton and the environment in which it sits and has also facilitated accurate dating of events in this development. The lake was formed as ice retreated from the area at the end of the last glacial maximum at approximately 14,600 cal BP, a moraine deposit blocking drainage to the sea in the east of the site (Taylor, et al., 2018, 45). At its maximum extent the lake covered an area of approximately 4.5km west to east, and 2.0km north to south (Mellars and Dark, 1998, 19). Further temperature fluctuations occurred over the intervening period, but by the start of the early Mesolithic (11,300 cal BP) the lake was its maximum level at 23.5m OD (Taylor, et al, 2018, 45). As the climate warmed the lake became populated with aquatic and emergent species of flora, and the surrounding area with grasslands, pioneer species of arboreal taxa and terrestrial herbaceous plants; the development of a *Cladium* reed swamp at the edge of the lake had already been initiated by 10,450-10,165 cal BP and the shoreline plants had been supplemented with fen taxa (Taylor, et al 2018, 47). The development of the hydrosere could be accurately traced; for example an area 50m out from the shore at Flixton School House Farm was outside of the reach of standing water by approximately 9,200 cal BP and the lake was fully terrestrialised by around 7,750 cal BP (Taylor, 2011, 70; Taylor, et al., 2018, 43). In spite of some small but significant fluctuations in climate conditions and water level, which would have affected the environment and resultant flora for relatively short periods, overall the development of the hydrosere was linear (Taylor, 2019, 572).

The land surrounding the lake was populated from the early Mesolithic and, while Star Carr is currently the most researched site, twenty further sites of Mesolithic period human activity have been identified around the lake (Taylor, 2019, 559). Star Carr (herein SC) is located on the north shore of an embayment on the west side of the lake; Flixton School House Farm (FSHF) on a broad shoreline on the south side of the lake; and No Name Hill (NNH) is a former island in one of the deepest parts of the lake which survives today as a raised mound; these are three of the occupied sites, and macrofossil analysis from each these will be utilised in completing the aims of this study. See Figure 4 below.

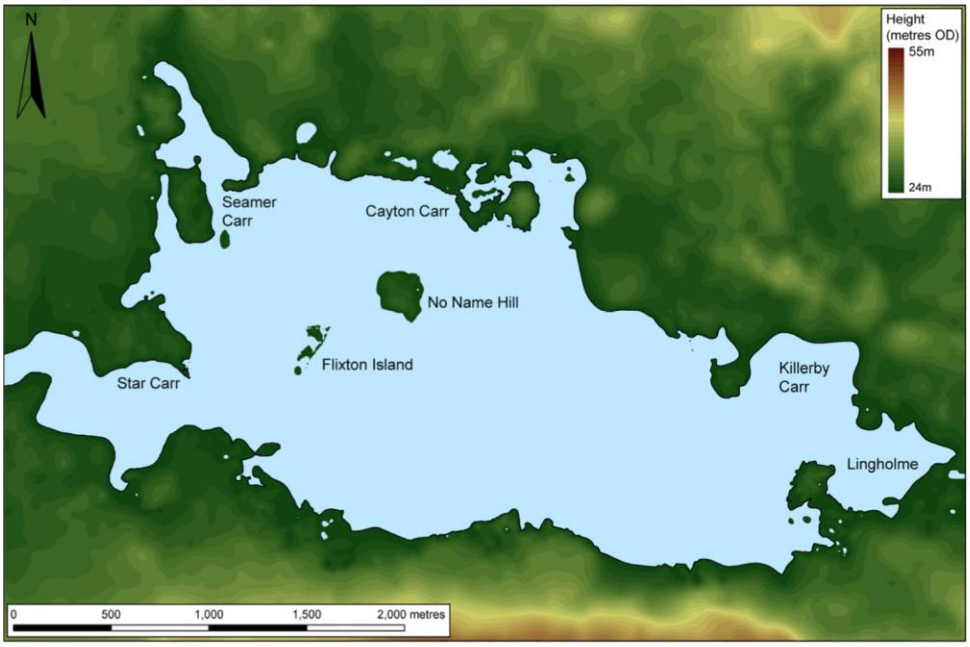


Figure 4: Palaeolake Flixton at its maximum extent, showing key areas studied

(after Taylor, Blockley, Candy, Langdon, Matthews et al, 2018, 49, image Copyright Barry Taylor).

Methodology

For this study, two new cores from the north west side of NNH have been analysed by the author, cores 68 and 78. The information from these will be supplemented by a previous core taken from the north of the island prepared by Taylor (2011), three cores from SC (Taylor and Allison, 2018) and three cores from the area of FSHF (Taylor, 2019). The new cores from NNH were obtained during an excavation which took place during July and August 2018, by University of Chester students under the supervision of excavation directors Doctors Barry Taylor, Nick Overton and Amy Gray Jones. Twelve test pits were excavated on the west side of the island, on or below the 23.5m OD contour at which the early Mesolithic shoreline lay (Taylor, et al., 2018, 45). The samples evaluated by the author came from test pits B (core 78) and C (core 68); C is further away from the early Mesolithic shoreline into the lake, than B. A contiguous sequence of samples, between 2.5-5cm thick, were taken from a line below the modern humified peat to the natural base of the palaeolake. These were bagged in plastic to prevent drying, with the test pit number, sample indicator and depth below datum noted, and subsequently stored in a refrigerator (Mannion, 1986, 199). In the laboratory, these were subsampled at 50ml volume (by water displacement) and disaggregated by boiling in a 10% solution of sodium hydroxide. The resultant material was then sieved through 1mm, 500μm, 250μm and 125μm mesh sieves and collected as four further subsamples. Each subsample was examined through a stereo microscope, at x10 to x40 magnification, the macrofossils being counted on a tally chart, or, in the case of fern sporangia and fronds, *Nymphaea alba* fragments and charcoal, allocated a scale of abundance from 0 = absent to 3 = abundant (see Taylor and Allison, 2018, 126). The samples from the larger three sieve sizes were 100% counted, only a sample from the smallest sieve size was examined. Identification of the macrofossils was carried out using various plant reference samples such as the online source the Digital Seed Atlas of the Netherlands or print sources such as that of Manquoy and Geel (2007, 2315-2336) or Cappers and Bekker (2013). These results were then processed using C2 software to produce the macrofossil profile charts. While there are no radiocarbon dates for the excavation at NNH, these can be understood to be analogous with previous studies. All radiocarbon dates used have been calibrated using OxCal 4.2 and the IntCal 13 calibration curve, and are expressed at two standard deviations, or 95.4% certainly, and rounded to the nearest ten years (Taylor, 2019, 561).

The results from the two new cores from NNH will be compared to data from previous plant macrofossil studies of NNH, SC and FSHF, in order to assess the depositional and taphonomic processes which may be in effect at different points around the lake. The previous macrofossil analysis for NNH, core NAZ, was carried out by Taylor (2011, 73). The three cores for SC (VP85A/2010, CII/2010 and P3178) were obtained during excavations carried out between 2010 and 2015, and represent the sequence of detrital muds and peats that are found at the edge of the lake, thereby allowing a complete understanding of the local environment in that area (Taylor and Allison, 2018, 125). The cores at FSHF and were obtained during excavations carried out between 2008 and 2012 by Taylor and Gray-Jones (Taylor, 2019, 561): Trench F is located on the shoreline at 23.5 OD, Core A 50m into the lake and Core B 150m out from the shoreline. These nine cores will form the basis of the analysis in this dissertation. The sequences at FHSF extend into a much later period than those from NNH and SC and so only the first part of these cores, which date to the early Mesolithic period, will be discussed.

Figure 5: Initial measurement at No Name Hill, July 2018. The slight rise to the foreground is the island, and the person nearest in the picture is standing approximately on the shoreline. Star Carr is sited in the distance to the left of the picture and the Seamer Carr area is visible as a spoil heap on the right-hand side of the image. (Credit: Photograph authors own).

4. Results

No Name Hill, cores 68 and 78

Considering first core 68, from test pit C, which is located on the north western shoreline of the island. The plant macrofossil chart divides into three major zones (see Figure 6).

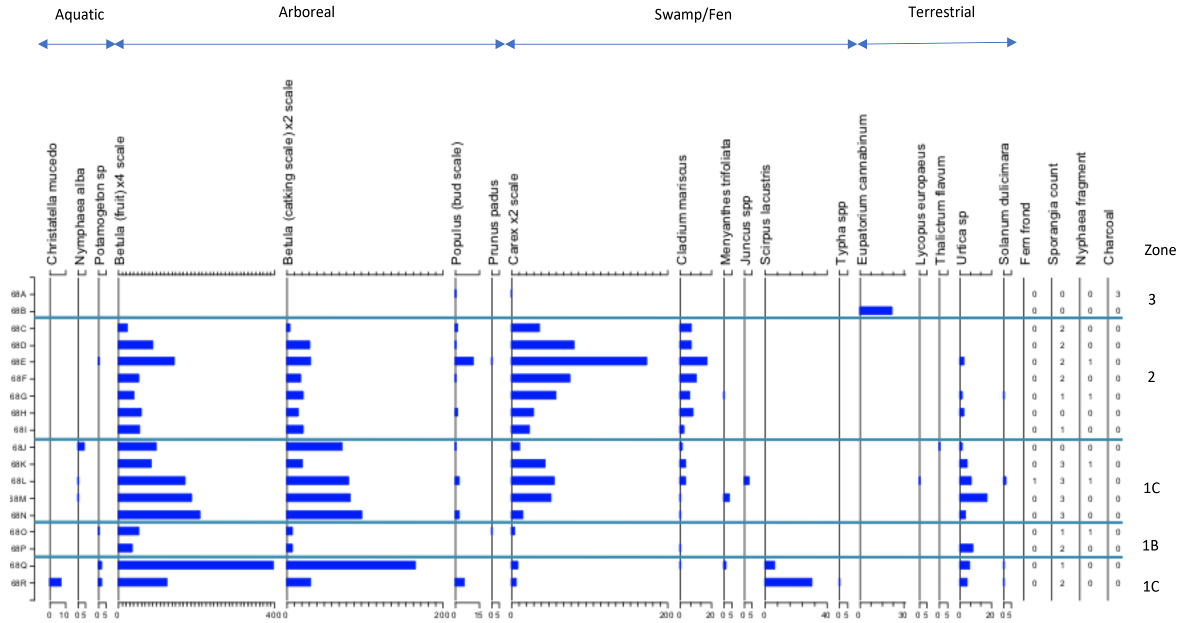


Figure 6: Plant macrofossil profile core 68, No Name Hill 2018

Zone 1 is characterised by high taxonomic diversity and the presence of aquatic material; it has been further divided into three sub-zones on the basis of fluctuating quantities of aquatic material.

Zone 1A. The remains of obligate aquatic, swamp and fen and terrestrial plants are all well represented in this zone. Aquatic material (*Christatella mucedo* and *Potamogeton* seeds) occurs consistently, albeit in low numbers. Terrestrial taxa are dominated by *Betula* (fruit and catkin scales), which occur in very high numbers, while *Urtica* sp. (seeds), *Populus* (budscales) and *Solanum dulcimara* (seeds) are present, although in lower quantities. A range of wetland taxa are represented, notably the emergent species *Scirpus lacustris* (fruits) and *Carex* (nutlets), while *Cladium mariscus* (seeds), *Menyanthes trifoliata* (seeds) and species of *Typha* are also present. Fern sporangia are also seen in the sample.

Zone 1B. This zone is characterised by a near absence of aquatic species, and *Betula* numbers, both fruit and catkin scales, also decline considerably. The aquatic plants are represented by a single *Potamogeton* seed and low occurrence of *Nymphaea alba* seed fragments. *Betula* (fruits and catkin scales) decline to very low levels and a single *Prunus padus* (seed) completes the arboreal representation. The diversity of wetland/emergent plants declines with only two species, *Carex* and *Cladium*, present. The non-arboreal terrestrial species are limited to *Urtica* and fern sporangia.

Zone 1C. Diversity increases, aquatic specie *Nymphaea alba* seed and fragments appear and *Betula* remains increase in number. *Carex* and *Cladium* numbers increase, and *Menyanthes* and *Juncus* wetland taxa are also present. The terrestrial plants are again dominated by *Betula*, although *Populus* budscales are also present. *Urtica* and fern sporangia both increase in number from zone 1B, *Solanum dulcimara* is represented by a single sample.

Zone 2. Aquatic plants decline in this zone, represented by a single *Potamogeton* seed and sporadic *Nymphaea alba* fragments. *Betula* (fruit and catkin scale) decline although they are still present in significant numbers, *Populus* budscales increase, although numbers remain low. Overall diversity of wetland species falls; *Carex* dominates while *Cladium* numbers also increase, *Menyanthes trifoliata* is present as a single sample. *Urtica, S. dulcimara* and fern sporangia are present but in lower numbers than Zone 1.

Zone 3. This zone is characterised by a sharp fall in both the quantity and range of macrofossils. The aquatic species and *Betula* are absent and the zone is dominated by the terrestrial plant *Eupatorium cannabinum* (seed). *Carex* occurs in small quantities and *Populus* is the only arboreal taxa represented. (Note: Charcoal is present in this horizon, but the discussion of charcoal is beyond the scope of this dissertation, and it is noted only).

Core 78, from test pit B, further from the shoreline into the lake, has different zonation but follows a similar sequence, see Figure 7.

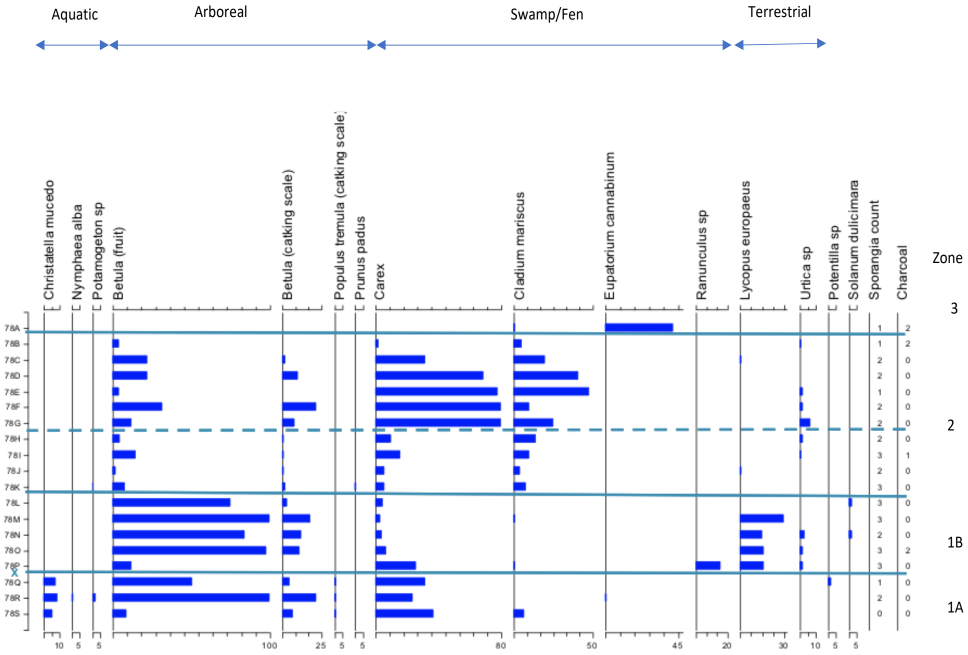


Figure 7: Plant macrofossil profile core 78, No Name Hill 2018

Zone 1 is characterised by high taxonomic diversity and the presence of aquatic material and has been further divided into two sub-zones.

Zone 1A. The remains of aquatic, swamp, fen (emergent) and terrestrial plants are all well represented in this zone. Aquatic material *Christatella mucedo* (statoblasts), *Nymphaea alba* (seed) and *Potamogeton* (seed) occur consistently, albeit in low numbers. Terrestrial taxa is dominated by *Betula* (fruit and catkin scales), which occur in very high numbers, with *Populus* (catkin scales), some *Potentilla* (seed) and *Eupatorium* (seed) present. Wetland taxa are represented by species of *Carex*, and low levels of *C. mariscus,* limited to a single sample. Fern sporangia are present.

Zone 1B. Aquatic species are absent. *Betula* numbers decline at the bottom of this zone, and catkin scales are absent, before increasing again but not to the levels seen in Zone 1A. Species diversity is still high. Emergent plants *Carex* and *Cladium* (seeds) are still present, terrestrial plants are represented by seeds of *Lycopus europaeus* (which occur throughout the zone), and lower levels of *Ranunculus* sp., *Urtica* sp. and *S. dulcimara*.

Zone 2. *Betula* (fruit and catkin scales) decline in numbers from Zone 1 but persist through Zone 2. A sub division for this zone could be proposed due to the significant increase in the presence of *Carex,* and a corresponding, but not as steep, increase in *Cladium* approximately half way through. Species diversity declines, non-arboreal terrestrial plants are represented only by low levels of *Urtica* sp*.,* a single seed of *Lycopus europaeus* and fern sporangia.

Zone 3. This zone is characterised only by the presence of high numbers of *Eupatorium cannabinum*.

Interpretation

The two cores compare well in terms of the quantities of the macrofossils and the species represented, though species diversity is greater in core 68 than 78, mainly in the swamp and fen, and the terrestrial taxa. The arboreal species, *Betula* and *Populus* are well represented in both samples, although overall numbers are higher in core 68. A significant decline in these occurs at the same point in both profiles, in samples 68P-N and 78P-O. The same aquatic species are present in both profiles in low quantities, although they persist for longer in core 68. Both profiles show corresponding patterns of increase, decline and increase again of both *Cladium* and *Carex*, albeit that there are greater numbers of both species' macrofossils in core 78. *Eupatorium* is the single terrestrial plant represented in zone 3 in both profiles. Some species are found in one profile but not the other, for example *Ranunculus* sp. appears in core 78 but not 68, and the reverse is true for *Typha*, although it is represented only in very low numbers.

Given their broad similarities, the results from the two cores will be interpreted together. Zone 1 is populated by a range of species from different environments, including obligate aquatic, swamp and fen, and terrestrial plants. In zone 1B in core 68, and the start of zone 1B in core 78, *Betula* declines, along with species diversity in core 68 although diversity conversely increases in core 78; later in core 78 zone 1B and in core 68 zone 1C both macrofossil numbers and species diversity increase. Aquatic taxa become more sporadic through zone 1C core 68 but are absent from the start of 1B in core 78. Zone 2 is notable for the presence of *Carex*, a wetland species (Dieffenbacher-Krall and Halteman, 2000, 221) and *Cladium,* which grows optimally at a depth of 0.4m and is therefore a reliable indicator of shallower water forming (Rodwell, 1995, 128). This can be seen as part of the infilling of Palaeolake Flixton, as the area that previously formed the shore of the lake is now one of swamp or fen. Finally, in zone 3 the area has terrestrialised, no aquatic or emergent/fen/swamp species are represented.

Zone 1A:

This zone represents a swamp environment forming in standing water at the edge of the island. The presence of macrofossils of obligate aquatic plants show that the sediments were forming in standing water. A range of aquatic and emergent plants are present in the samples, notably *Carex, Scirpus lacustris* and *Urtica*, but also *Nymphaea alba*, *Cladium mariscus, Menyanthes trifoliata, Christatella mucedo, Typha, Solanum dulcimara* and *Potamogeton.* However, as some of these can be transported over considerable distances by lake water the plants themselves may not have been growing close to the site (Birks, 1973, 182). The high levels of *Betula* fruits and catkin scales suggest that trees were growing on the island, close enough to the shore for the macrofossils to be transported onto the sampling point. *Urtica* and species of fern were also growing on the island, again close enough to the shore for their macrofossils to reach the sampling point.

Zone 1B:

In this zone, the aquatic species decline sharply, and are represented by only a single *Potamogeton* seed in core 68 and rare *Nymphaea* fragments. Zone 1B in core 78 contains no aquatics. This zone then represents a possible fall in the level of lake. *Betula* fruits and catkin scales also decline considerably in number, and this could also be a result of a fall in the lake level restricting transportation of the seeds, rather than a reduction in the number of trees on the island. The decline in species diversity of fen and swamp species could also be attributed to a fall in water level, *Urtica* and fern sporangia however are still present. Although the change is not as pronounced in core 78 there is still a matched decline in *Betula* and *Cladium mariscus* appears in both cores for the first time, confirming a possible fall in water level.

Zone 1C (1B in 78):

If the water level did fall in Zone 1B, in Zone 1C in core 68 this seems to reverse, as aquatics are again present. In addition, the count of *Betula* seed and catkin scales increases considerably over Zone 1B, although not to the levels of the lowest zone, perhaps indicating that the water levels do not rise to the previous highest level but recover enough for transportation of these to restart. This is supported by the appearance of *Juncus* sp. This same pattern is seen in core 78 zone 1B, but without the presence of *Juncus.*

Zone 2:

Zone 2 in both cores contain examples of the same species and follow similar patterns of numerical expansion and decline such as that seen with *Betula* fruit and catkin scales. This can be characterised as a seasonally flooded environment, as overall less macrofossils are reaching the area, and aquatic species decline, represented by a single *Potamogeton* in each core. Further, the peak in the quantities of *Cladium* macro-remains in both cores' indicates the development of a shallower environment.

Zone 3:

The zone represents the formation of a terrestrial fen environment at the sampling point. The complete absence of aquatic material in both of the profiles suggest that the lake water is no longer reaching the sediments. As such the profile is now only registering macrofossils from plants growing in the immediate vicinity. The fen plant *Eupatorium cannabinum* is well represented in both profiles and was probably growing in the immediate area. The lack of *Betula* may be partly due to the absence of water (which can transport its fruits). However, given that these can also be transported by wind their absence may also suggest that trees were no longer present in the vicinity of the sampling point.

No Name Hill, core NAZ

As noted above, previous work had been carried out at NNH between 1986 and 1996, during which time a monolith sample was obtained from trench NAZ, which was located on the shoreline on the north side of the island; samples from this monolith tin were processed and analysed in 2009, the resultant macrofossil profile is shown in Figure 8 (Taylor, 2011, 73-4).

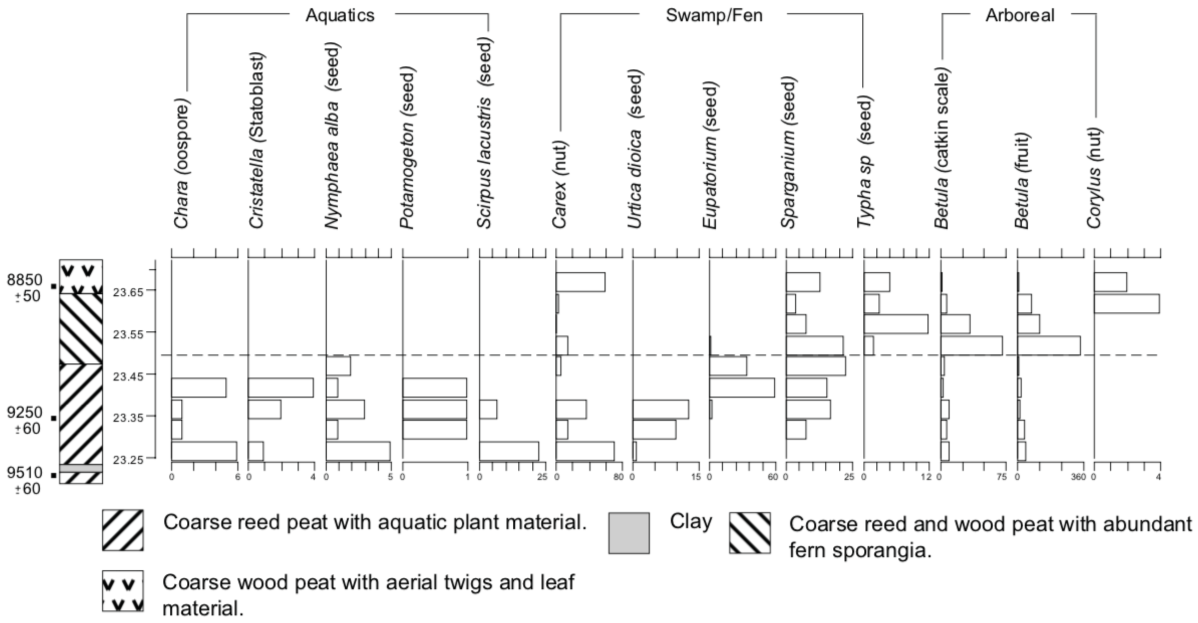


Figure 8: Macrofossil profile for trench NAZ, No Name Hill.

(Credit: Taylor, 2011, 74)

The species and quantities represented in this profile correlate broadly with the 2018 cores. In the lower half of the profile for NAZ, aquatic, swamp and fen and arboreal species are found. As in cores 68 and 78 zone 1 the overall number of aquatic plant macrofossils is low but here the diversity is higher, with *Chara*, *Nymphaea, Christatella*, *Scirpus lacustris* and *Potamogeton* all present. Fen and swamp species are also found in this area, *Carex* and *Urtica* as in the profiles from cores 68 and 78, but in NAZ there is also *Sparganium*, a species of rush in the Typhaceae family. The presence of *Typha* sp. in more abundance in this profile is possibly attributable to there being a localised plant in the area of trench NAZ; as seen above, *Typha* seeds are found in large numbers when the plant is dominant (Birks, 1973, 179). *Eupatorium* remains increase in number towards the top of this zone, but unlike profiles 68 and 78 this is at the same time as the aquatic species are still being deposited. The other difference is in the low count of *Betula* fruit and budscales. That the sampling point in the lower half of the profile NAZ is in water is indicated by the presence of so many other macrofossils, it may be that *Betula* does not grow on this side of NNH island until terrestrialisation is further advanced, when the number of *Betula* macrofossils increases significantly in upper half of the NAZ profile. This is supported by the presence of *Eupatorium* and *Urtica* (Taylor, 2011, 74). In the upper zone aquatic taxa are absent and a fen environment develops representing a period where the lake is infilling, signalled by the increase in arboreal macrofossils, and the presence of fern sporangia, while the swamp species *Carex* and *Sparganium* persist (Taylor, 2011, 74). By the top of the profile arboreal species, in particular *Corylus*, dominate, along with *Carex*, signalling the establishment of a wooded carr (Taylor, 2011, 74).

In summary, this profile from the north shore of the island is comparable to cores 68 and 78 in terms of presence and number of obligate aquatics, and reasonable correlation in swamp and fen species. However, *Betula* remains do not occur here until later in the profile than the cores from the north west shore, suggesting that *Betula* did not grow on the north side of the island initially.

No Name Hill profiles, summary

The macrofossil profiles from the north side of the island, and the 2018 cores taken from the north west side show some differences. The distance separating these is approximately 15m around the shore. *Chara* does not occur in cores 68 and 78. This is in spite of it being considered to be widely distributed (Birks, 1973, 182); but in this case the absence from the 2018 profiles would support the assertion by Szymczyk (2012, 510) that it is more local to the source. The other difference is in the distribution of *Betula.* Although all of the profiles indicate high numbers of seed, which is wind distributed and therefore found over wide areas, as seen in analysis of Core B, below, the catkin scales, which are a better indication of local population, are found in much lower numbers in the open water area of the NAZ profile as opposed to 68 and 78 (Greatrex, 1983, 775). This probably indicates that few trees grew on the north shore. *Sparganium* and *Scirpus* both appear in the NAZ profile, with *Scirpus* also present in core 68. The presence of both of these on the north shore may indicate that the gradient of the shore is gentler here as they tend to be found in shallower water (Dieffenbacher-Krall and Halteman, 2000, 217).

Analysis and discussion of macrofossil results from other areas of Palaeolake Flixton

As indicated above, the macrofossil profiles for the island of No Name Hill can be compared with those from other areas of the lake. First it is necessary to briefly review the macrofossil profiles from Flixton School House Farm and Star Carr. Detailed interpretation of these profiles is contained in Taylor (2011 and 2019) and will not be reproduced here; instead a summary of the macrofossils only will be discussed. Then the profiles from the differing area will be compared in order to highlight any differential factors affecting the deposition and taphonomy of macro fossils.

Flixton School House Farm, Trench F, see Figure 9.

Zone F1 represents the period when the lake was at its maximum. A broad spectrum of aquatic and emergent plants are present here, with high numbers of macrofossils of *Christatella* and *Carex,* and of the arboreal species *Betula*, in particular the fruit, and *Populus*. Although some species are categorised as rare, there is high species diversity overall (Taylor, 2019, 565).

Zone F2 shows a decline in species variation and volume of macrofossils and this can be tentatively attributed to a change to a seasonally flooded environment (Taylor, 2019, 565). *Nymphaea* are the only obligate aquatics and are present only in low numbers. *Cladium* and *Typha* seeds appear in the record, indicting shallower water, and *Corylus, Salix* and *Viburnum* arboreal species are also found, probably growing in the near environment.

Zone F3. Here aquatic taxa are absent (and are not found again in the profile), and diversity declines overall, indicating a drier environment as the lakeshore is now beyond the sampling point (Taylor, 2019, 565). Emergent and terrestrial taxa are present in the area and including *Corylus, Cornus*, and *Sparganium*.

Zone F4 is characterised by swamp, fen/carr and arboreal species in near terrestrial conditions, still however wet enough to support *Menyanthes* (Taylor, 2019, 566-7). In zone 4a a layer of humified peat indicates a drop in the water table, leading to decreased numbers of macrofossils as conditions for preservation are poor. This fall is reversed in Zone 4b as the number and diversity of emergent and terrestrial macrofossils increase.

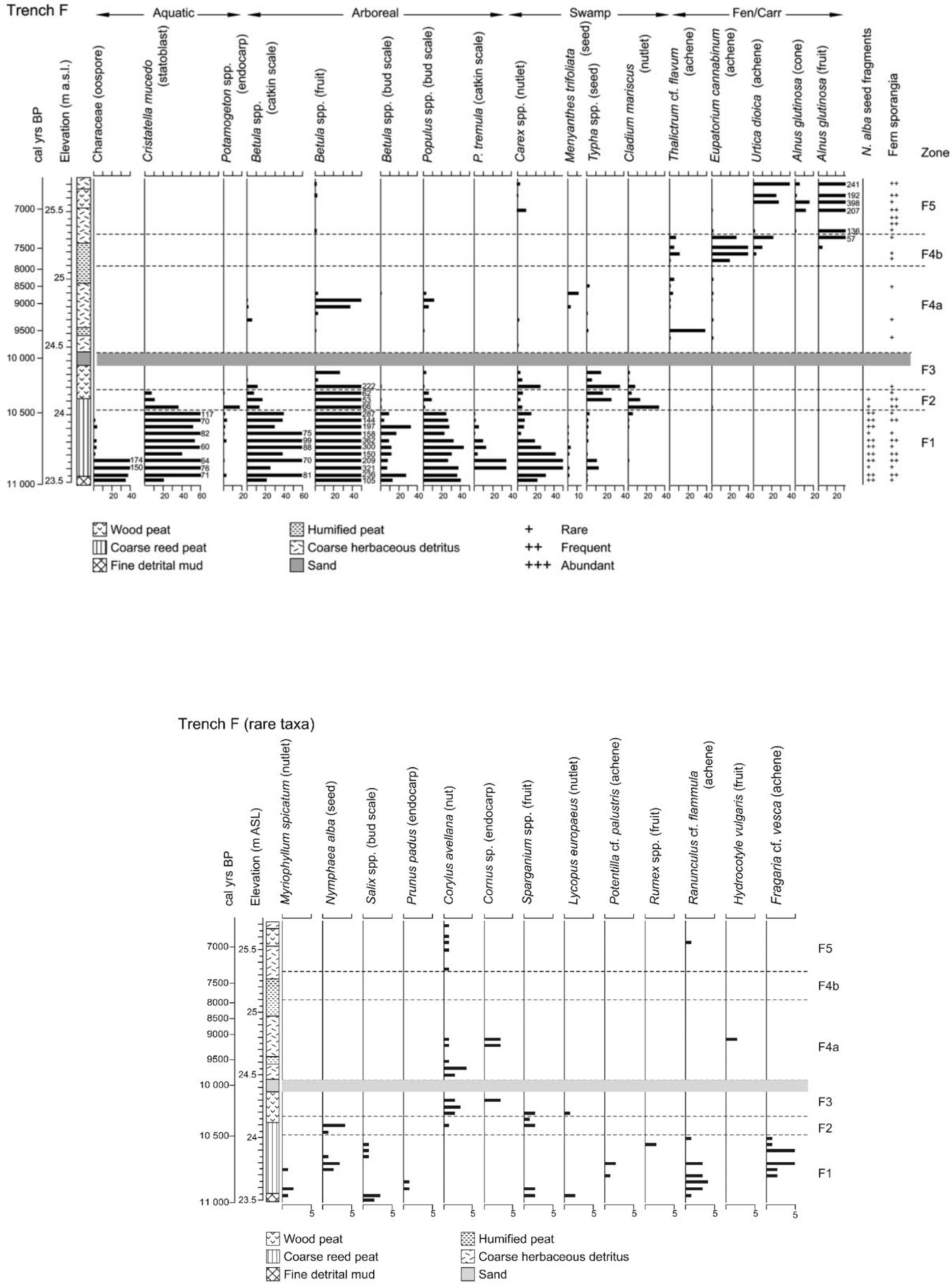


Figure 9: Macrofossil profiles for FSHF, Trench F, common and rare taxa, original shoreline 23.5m OD

(Credit: Taylor, 2019, 564)

Zone F5 sees the presence of mainly arboreal and terrestrial species, although *Carex* is still present in low numbers. *Corylus* and *Alnus* are both present (Taylor, 2019, 567).

Flixton School House Farm, Core A, see Figure 10

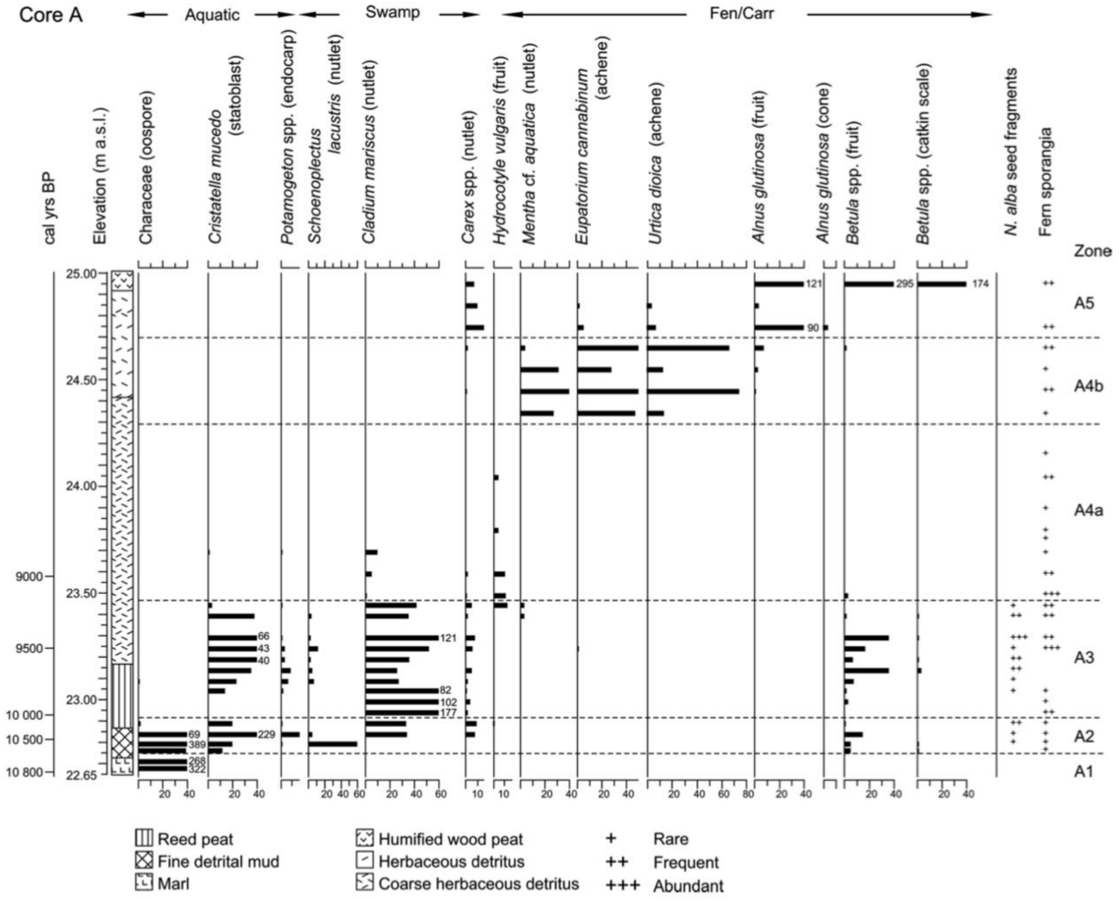


Figure 10: Macrofossil profile FSHF, Core A, 50m from the original shoreline, all taxa

(Credit: Taylor, 2019, 565)

Zone A1 shows the presence of high numbers only of the aquatic *Characeae* oospores, A1 thus represents an area of open water.

Zone A2 shows an increase in diversity of aquatic species, with *Christatella*, *Nymphaea* and *Potamogeton* present. Emergent swamp and fen/carr species such as *Schoenoplectus lacustris* and *Cladium* are also found, indicating a fall in water level at the sampling point. Arboreal *Betula* fruit appears for the first time and the presence of fern sporangia also indicates a decrease in water level.

Zone A3 sees a fall in the number and diversity of aquatics present, *Christatella, Potamogeton* and *Schoenoplectus* are all present but in lower quantities, while diversity of the fen/carr and swamp species seen in A2 increases with *Hydrocotyle vulgaris* and *Mentha* present. Both factors suggest a further fall in the water level. *Betula* count increases.

Zone A4 onwards sees an absence of aquatic macrofossils, and fluctuations in water level as shown by the carrying degrees of preservation. The area is largely terrestrial at this point, with predominantly fen/carr species seen, diversity of the macrofossils is high and includes *Alnus* and *Hydrocotyle vulgaris* (Taylor 2019, 567).

The zones above A4 are outside the time period represented in the NNH cores and will not be discussed.

Flixton School House Farm, Core B, see Figure 11

In this profile the same pattern of increase in swamp and fen/carr plants occurs. Because the profile is in open water for longer though, what is notable is that the species diversity persists from the lowest point and throughout the profile, albeit the quantities of macrofossils change. Zone B1 is dominated by large numbers of *Characeae*, however there are small numbers of seeds from *Christatella* and *Myriophyllum*. *Betula* fruits are present in low numbers, unsurprising given the ability of these to be distributed over a wide area.

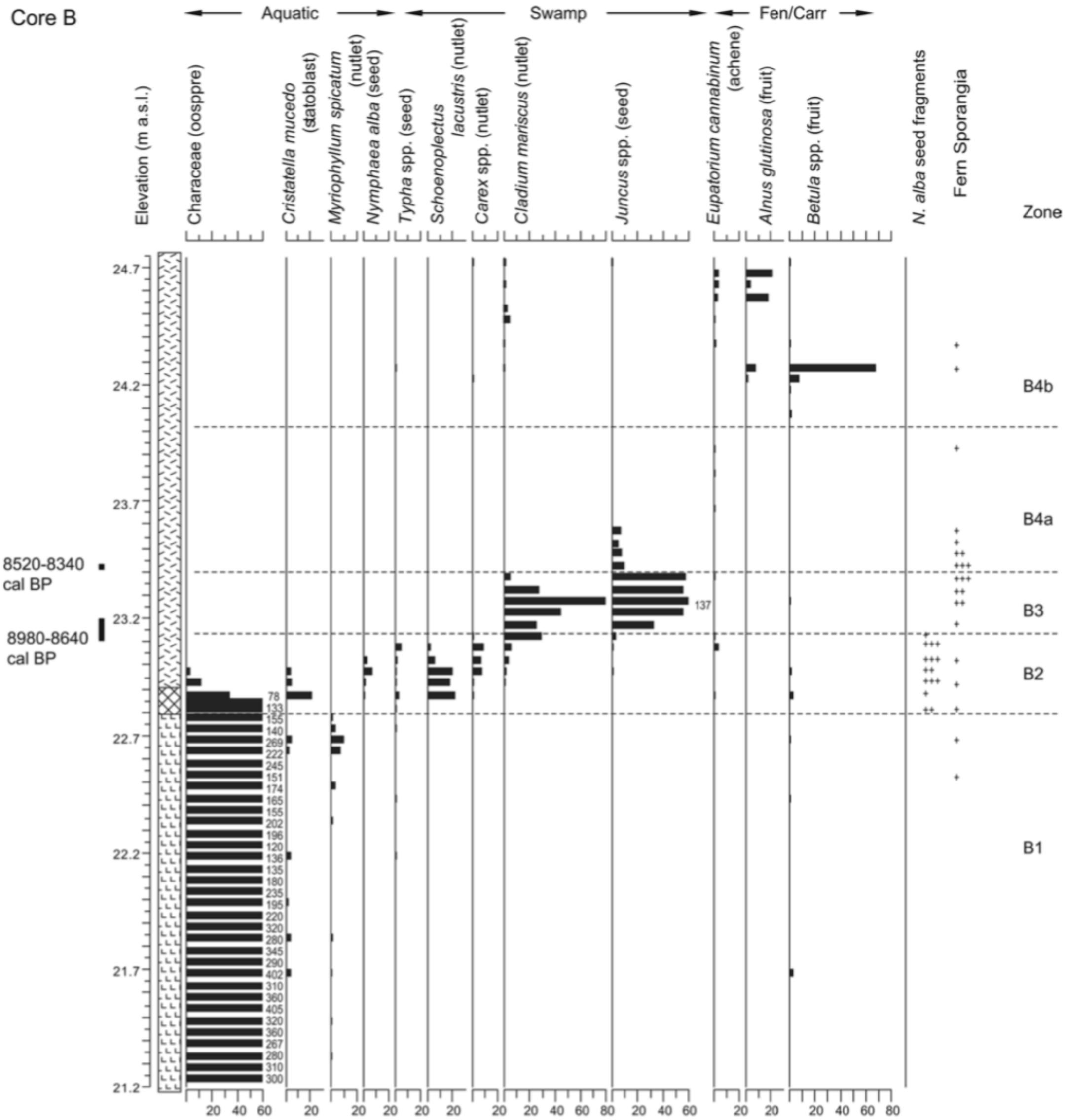


Figure 11: Macrofossil profile for FSHF, Core B, 100m from the original shoreline, all taxa

(Credit: Taylor, 2019, 566)

In zone B2 *Nymphaea* is found and swamp and fen/carr species also increase in diversity and number. The presence of *Cladium i*n particular would indicate shallowing water, as does *Eupatorium,* which occur in very low numbers.

Cladium continues to increase through Zone B3, from which aquatics are absent. *Juncus* is dominant indicating the presence of a significant population of plants. *Juncus* persists into the first part of Zone B4a but then disappears from the record. In this zone only *Eupatorium* and fern sporangia are present but in very small quantities.

Zone 4b is fully terrestrialised with *Alnus, Betula* and *Eupatorium* present (Taylor, 2019, 567).

Star Carr, cores VP85A/2010, CII/2010 and P3178.

Core VP85A/2010 is adjacent to the profile sampled by Dark as M1 and also to the brushwood platform excavated by Clark (Taylor and Allison, 2018, 125; Clark, 2009, 17); CII/2010 was taken in Clark's cutting II and the final core was taken from trench 34, which was excavated in 2014 (Taylor and Allison, 2018, 125). These cores were all taken at the original shoreline, OD23.5m. In their 2018 publication, Taylor and Allison discuss the three shoreline profiles from their Star Carr investigations as one, owing to their similarity (2018, 126-130), see Figures 12 to 14.

Zone 1 has a wide range of taxa from all of the categories in all three profiles. In profiles VP85A/2010 and CII/2010 there are some very high counts, notably of *Betula, Carex* and *Typha*; *Characeae* is also present in high numbers in VP85A/2010. P3178 exhibits least diversity, although macrofossils are again present from arboreal, swamp and fen/carr communities. This diversity is a feature of Zone 2 as well, although absolute numbers decline, again reflecting the shift to a shallower environment as has been seen in the FSHF samples, above. Most notable is the near-total decline in Characeae in each profile. Zone 3 here too is devoid of aquatics and is therefore an area represented by swamp and fen/carr.

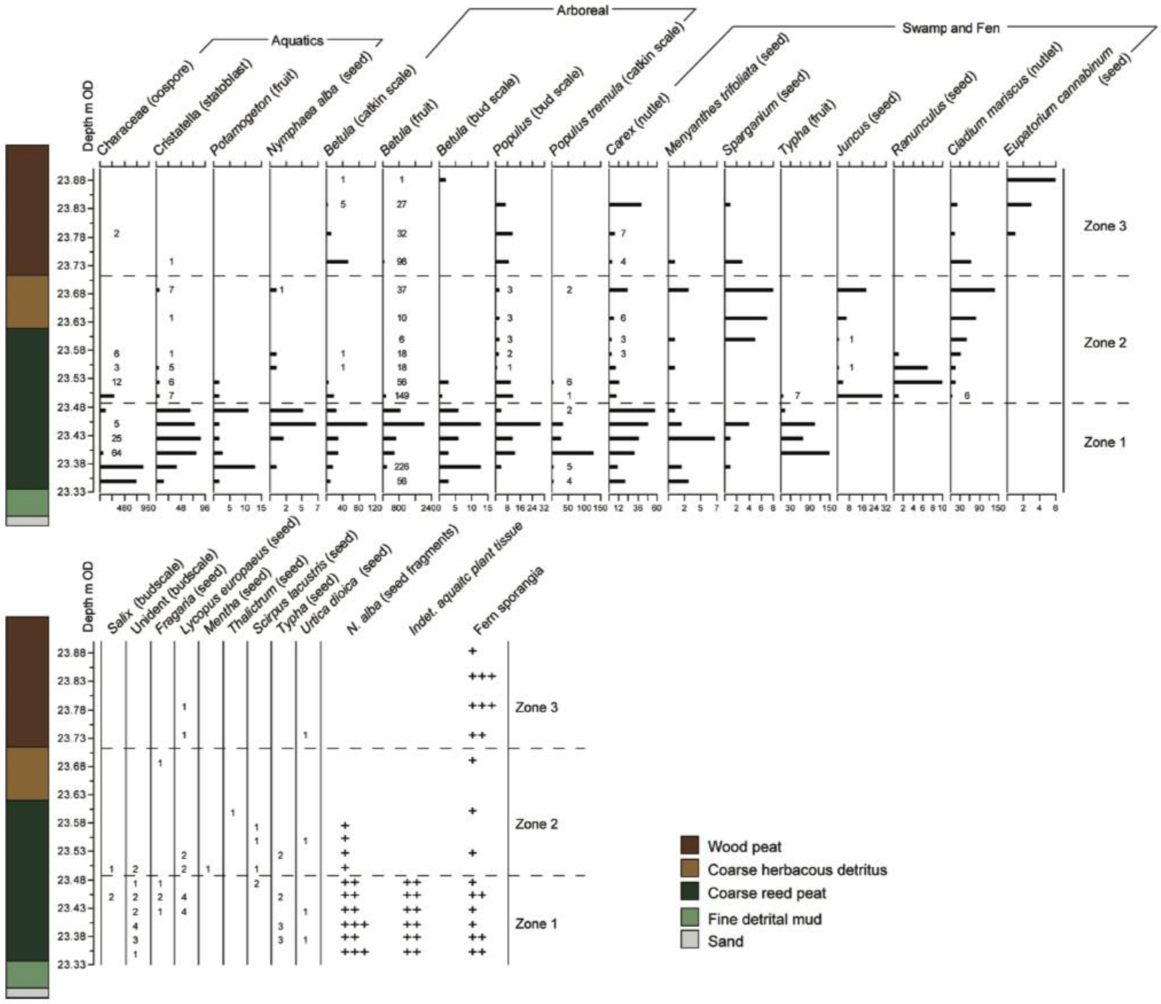


Figure 12: Macrofossil profile SC core VP85A/2010, original shoreline 23.5m OD, all taxa

(Credit: Taylor and Allison, 2018, 127)

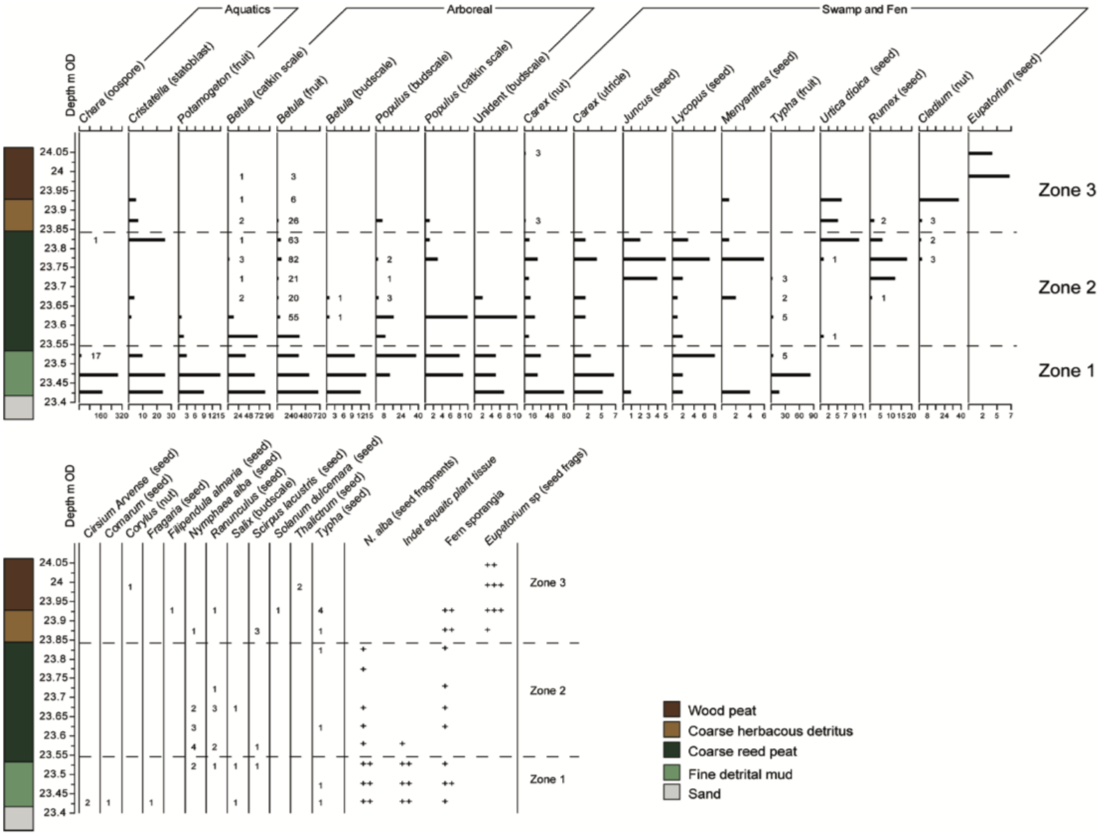


Figure 13: Macrofossil profile SC core CII/2010, original shoreline 23.5OD, all taxa

(Credit: Taylor and Allison, 2018, 128)

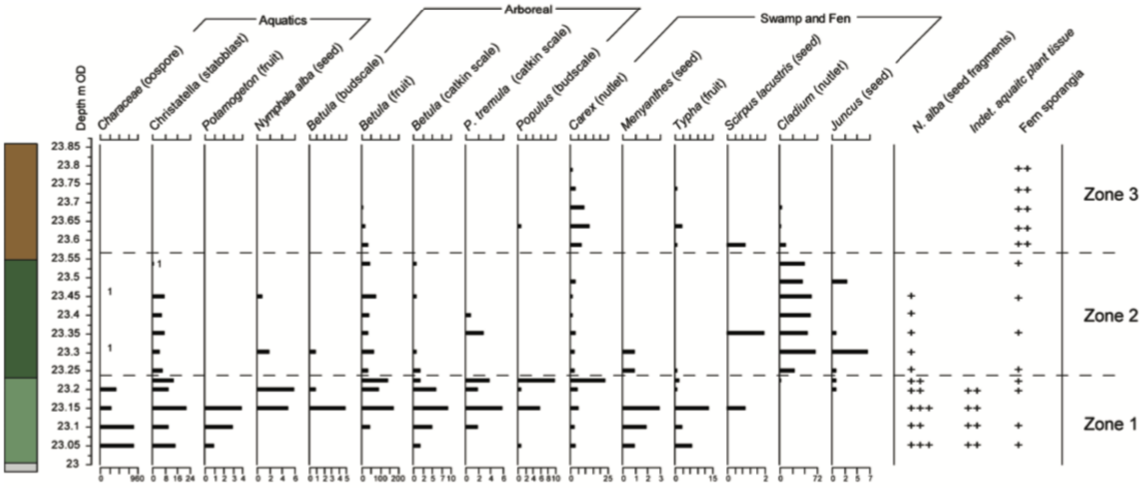


Figure 14: Macrofossil profile for Star Carr core P3178, original shoreline 23.5OD, all taxa

(Credit: Taylor and Allison, 2018, 129)

Zone 2 shows a decline in taxa and in numbers of macrofossils present. Aquatic species decline significantly in all three profiles with the exception of an isolated increase in *Christatella* towards the top of the zone in CII. *Betula* fruits continue to appear but in lower numbers, and *Populus* initially persists but also declines as the zone develops. *Cladium* increases in number and other swamp and fen species are found, often unique or at least in majority in a given profile, for example *Ranunculus* in VP85A, *Rumex* in CII and *Scirpus* in P3178.

Zone 3. Numbers of remains and diversity declines sharply in all profiles in this zone. Small numbers of aquatic species persist in two of the cores but are completely absent from P3178. All of the cores show a decline in arboreal species, *Betula* and *Populus* persist to the top of the zone in core VP85A but become absent from the others. The diversity of swamp and fen plants declines, *Eupatorium* becomes evident in VP85A/2010 and CII/2010 but is not noted in P3178.

Comparison of the lake edge profiles

Star Carr, VP85A/2010, C11/2010 and P3178 and Flixton School House Field Trench F

Overall, the profiles from both shoreline locations are very similar. First, the environmental sequence is the same for all of the profiles in that they demonstrate the three phases of succession; that is, an initial submerged swamp environment (Zone F1 at FSHF and Zone 1 in the SC profiles), then transition to a shallower and perhaps seasonally flooded swamp (Zone F2 and 2), and finally a terrestrial environment as deposits form above the level of the lake (Zones F3 and 3). This is visible in the macrofossil record as initially high levels of aquatic materials along with high species diversity, followed by a decline in aquatics, which coincides with a fall in *Betula*. At the same time, species which are adapted to drier conditions (notably

Cladium) show an increase in number. Finally, aquatics become completely absent from the profile, species diversity falls while numbers of non-arboreal terrestrial taxa, such as *Eupatorium*, increase.

Second, there are significant similarities in the taxa represented at each location. In Zone 1 all profiles contain the same species of aquatic plants, *Chara, Christatella*, *Potamogeton* and *Nymphaea alba* – the latter represented by seed in three profiles and fragments in all. The numbers present do vary though, for example *Characeae* is present in numbers up to 960 in profiles VP85A and P3178, but much lower, only to a maximum of 320 in the remaining samples. Some swamp and fen/carr taxa are found in all profiles, such as *Menyanthes* and *Typha* while some cores contain species not seen in others, such as S*parganium* in VP85A. CII/2010has the greatest diversity of fen and carr taxa. The quantities present do vary, so *Typha* is not found in large numbers in Trench F and P3178 as for example in VP85A/2010. The arboreal species across the four samples show less variability; all contain *Betula* fruits and catkin scales, and *Populus* remains and most sites also have low numbers of *Salix*. The counts of *Betula* remains vary considerably though, ranging from 200 fruits in P3178 to 2400 in VP85A/2010. Non arboreal terrestrial species are usually found in low numbers. They are broadly common across profiles with some small variation, for example *Potentilla* is only found in Trench F in zone 1.

In zone 2 the number of aquatics falls in all profiles, *Characeae* almost absent from all but two profiles and the numbers occurring are very much lower than in zone 1. While other aquatics persist, such as *Potamogeton* or *Christatella*, they are in much lower numbers than zone 1. Diversity of fen/swamp species increases and *Cladium* now features in all profiles except CII and generally the species found are widespread. Numbers of arboreal species fall across the sites and the numbers present are more consistent between sites, unlike zone 1.

Non-arboreal taxa generally increase in diversity but vary at each site, for example *Rumex* and *Urtica* are found in CII/2010, *Ranunculus* and *Eupatorium* in VP85A/2010

Zone 3 sees a reduction in species diversity in all of the profiles, and an absence of aquatic material, barring small numbers of *Christatella* in CII/2010. Cladium is still present in the three profiles that it has featured in previously, albeit in reduced numbers. Diversity of all classes of plant is lower in zone 3 and varies a little between sites, for example *Eupatorium* is only found in VP85A/2010 and CII/2010, *Urtica* in CII/2010 only.

Comparison of the lake edge profiles to those for No Name Hill

The new profiles for NNH, cores 68 and 78, show the same environmental transition as the other lakeshore profiles. That is, zone 1 represents a period of standing water, with the core being sampled taken from an area of swamp forming at the edge of this water, zone 2 represents a change to shallower water and a seasonally flooded environment as signalled partly by the presence of *Cladium*, while zone 3 is the transition to a fen/carr environment. However, overall species diversity and number of macrofossils on the island is lower than at the lake edge and the detail of the cores varies too.

In Zone 1 the aquatic species are lower both in diversity and number. *Characeae* does not occur at all in the NNH profiles, *Christatella* is found but in significantly lower numbers than at the lake edge, as is the case for *Potamogeton* in all but the profile from Trench F. There are a similar number of fen/carr species present, but macrofossils again occur in lower numbers than found around the shore. Unique to NNH are the comparatively large numbers of *Urtica* remains in the profiles; if found at all in the other profiles they are categorised a rare, as at VP85A/2010. Arboreal species are limited to *Betula,* which occur in high concentrations, in 1A but this declines at the start of 1B before recovering somewhat in cores

68 and 78; this is not seen in any of the lakeshore profiles. Small amounts of *Populus* remains are found in all areas. No *Salix* is present, although this is also uncommon around the lake edge.

Zone 2 sees the same decline of aquatic species as the lake edge profiles although it is possibly more definitive on NNH. The taxonomic diversity is lower on the island profiles than on the shore, being limited to only a few species, in the main *Carex, Cladium* and *Urtica*.

Zone 3 in both profiles on NNH is striking for the presence of *Eupatorium* only, even *Urtica*, which has been persistent to this point, is absent. In contrast zone 3 of the lake shore profiles exhibits a broader range of species, both arboreal and fen, including *Alnus, Typha* and *Cladium*.

Comparison of the profiles from the deeper part of the lake to those from the shore

Cores A and B

As core A was taken at 50m from the original shoreline of Palaeolake Flixton, and B at 150m from it (Taylor, 2019, 561), it is expected, from the modern studies reviewed above, that these profiles will be different to those at the shore, here this difference will be quantified for each core.

In Core A, zones A1 and A2 are broadly contemporary with the zone 1 in Trench F and with zone 1 in the SC profiles (Taylor, 2019, 564-7; Taylor and Allison, 2018, 79). Overall species diversity is much lower. Initially, the only obligate aquatic present in zone A1 is *Characeae,* zone A2 is more diverse as *Christatella* and *Potamogeton* are found here, in approximately comparable numbers to those at the shore. *Betula* is the only arboreal species represented, in very low numbers compared to all of the other profiles – fruit, for example being counted at a maximum of 40 in A2, while in Trench F the maximum was in excess of

350, but also with less consistency than in other profiles. Swamp species in A2 are represented by *Carex*, which also appears in this zone in the shoreline profiles, *Schoenoplectus* and *Cladium*, which appears earlier in the deeper water.

There is no equivalent to F2 in Core A, as its duration was too brief to have been demonstrated here; Core A zone 3 is however comparable with Trench F zone 3 in terms of time period (Taylor, 2019, 564-7). *Characeae* has gone from the Core A profile but *Christatella* and *Potamogeton* persist, unlike in F3 which contains no obligate aquatics. These aquatics and emergent *Cladium* dominate A3; *Cladium* is only found in F3 in low numbers. *Carex* is more significant in F3 than A3, along with *Typha* which does not appear in A3. *Betula* appears in large numbers in F3, with some *Populus*. *Betula* is present in F3 but in smaller quantities, and sporadically.

Core B is not dated in the lower part of the profile, but zone B2 ends c.7000 cal BC; the early part of zone B1 is contemporary with the shoreline zones 1-3 (Taylor, 2019, 567; Taylor, et al., 2018, 79). Zone B1 is comprised mainly of aquatic species, *Chara* in the main but *Christatella, Myriophyllum spicata* and *Nymphaea alba* seeds are also present. *Chara* persists in large numbers, over a greater period and with more regularity than the shoreline zones. There are small numbers of *Typha* in B1, and terrestrial species are represented by small numbers of *Betula* which occur inconsistently. In B2 diversity increases. Low in the zone *Chara* still occurs but this disappears from the profile, as *Christatella* and *Schoenoplectus (Scirpus) lacustris* increase although neither are to be found in large numbers. At the top of the zone *Cladium* starts to appear in number.

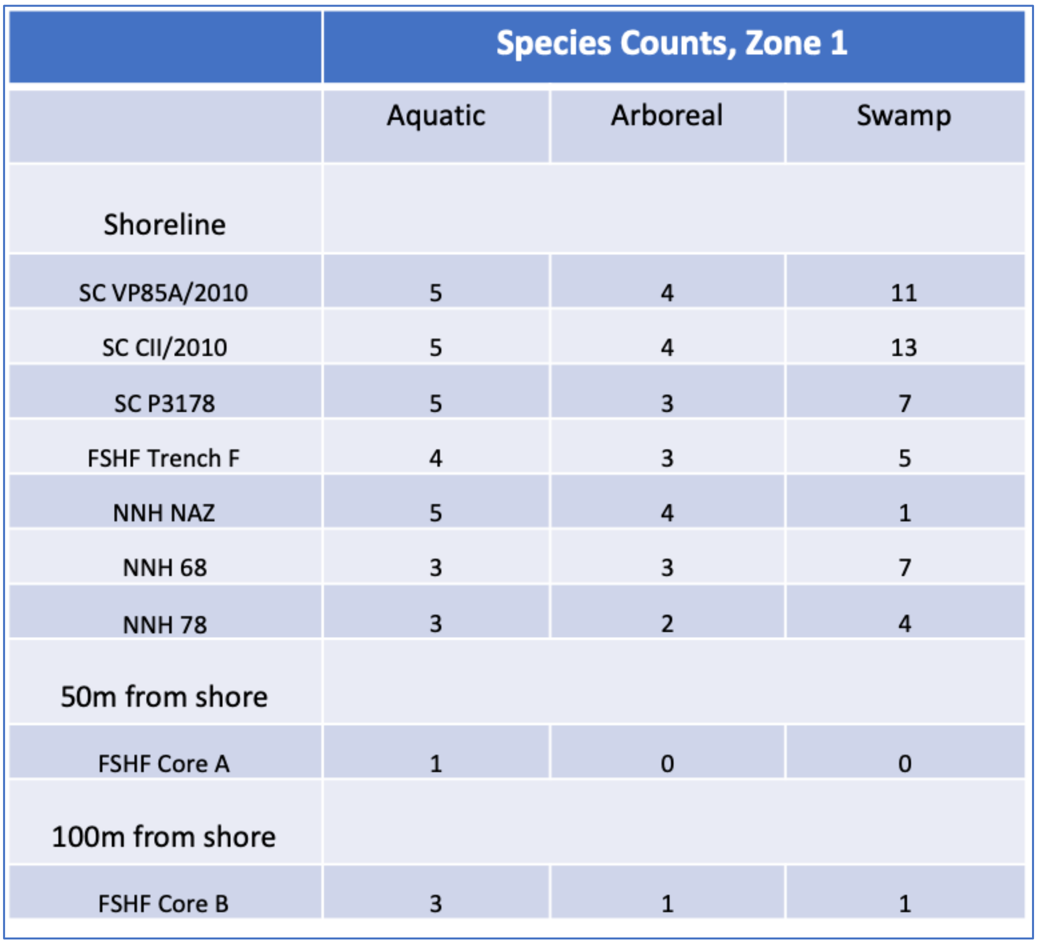
5. INTERPRETATION

The profiles from the lakeshore at SC and FSHF, and those from the island of NNH all demonstrate a similar pattern of environmental change and wetland succession, in three phases. The first, seen in zone 1, is of swamp area at the edge of a lake, demonstrated by the presence of aquatic, swamp, fen and arboreal species. The next phase, in zone 2, is of a shallowing environment, with emergent species becoming more apparent, and declining quantities of aquatics due to reduced transportation as well as perhaps the onset of only seasonal flooding. The final phase, in zone 3, is one of increasing terrestrialisation in the sample areas with the presence of mainly fen and carr species of plant. Overall the sequence has a relatively uniform macrofossil signature; that is high numbers of aquatic and arboreal species and greater species diversity, followed by declining aquatics with an increase in plants tolerant of drier conditions, followed by absence of aquatics, low diversity and the presence of terrestrial species. This is in part an environmental response, as plants which require drier conditions become more abundant as the lake infills and peat formation is initialised. However, there is also a taphonomic response apparent. As already established from the modern proxy studies, where there is standing water the number of macro-remains is higher; as the number of aquatics decline (indicating that there is less water reaching the sample site), the presence and number of arboreal and other species also decline as there is no mechanism for transport. When the area is fully terrestrialised there is then more material which tends to reflect the local source area more than the plant population of the remaining lake environment or surrounding area (see e.g. Greatrex, 1983).

However, while the hydroseral sequence is broadly similar at all points, there are important differences in the macrofossil profiles from around the lake. Firstly, in the period where the lake is at or near its maximum, zone 1, there is greater species diversity generally in the lakeshore cores as opposed to those from NNH, see Table 2, below. This accords with the modern macrofossil studies discussed above which concluded that up to 94% of species present in the lake and up to 76% of the total macrofossil numbers could be represented in the material found at the lakeshore (Birks, 1973, 180). This is the result of a number of factors; firstly, the dense and diverse vegetation that is found at the edge of the lake would naturally give rise to higher numbers of macrofossils, in contrast to the centre of the lake which generally is less well populated (Birks, 1973, 180). Also, the macrofossil studies demonstrate that material is being transported to the edge of the lake, perhaps in rafts of detritus, and being held there (e.g. Szymczyk, 2012, 510). In addition, the proximity of the terrestrial species found adjacent to the shore would also be found in the macrofossil record of that area (Greatrex, 1983, 773). This diversity is of course lower again in the deep-water cores, in keeping with this pattern (e.g. Collinson, 1983, 589).

That species diversity is also not as high in the profiles for P3178 and Trench F as in the first two SC cores might also suggest differential deposition across these areas. Considering specifically the aquatic species, which are in the main common to all cores but with small differences. The numbers of aquatic macrofossils present in the new NNH profiles are lower than at any other site, including the deep-water cores, which would suggest differential deposition is occurring on the island. Further, the aquatic species in Trench F shows lower diversity and lower numbers than are found in the other shoreline cores.

Table 2: Approximate species counts for all cores



	Species Counts, Zone 1		
	Aquatic	Arboreal	Swamp
Shoreline			
SC VP85A/2010	5	4	11
SC CII/2010	5	4	13
SC P3178	5	3	7
FSHF Trench F	4	3	5
NNH NAZ	5	4	1
NNH 68	3	3	7
NNH 78	3	2	4
50m from shore			
FSHF Core A	1	0	0
100m from shore			
FSHF Core B	3	1	1

It is possible that there is a uniform pattern of aquatic vegetation within the lake which accounts for the occurrence of these species in most of the cores, but it is more likely that the profiles are reflecting a broad, 'averaged' pattern of vegetation within the lake. The differences in occurrence of the aquatic species in some cores as opposed to others does however suggests differential deposition. Swamp species diversity is also lower at these sites and it is possible that the material to 'trap' the aquatic remains is not there is such proliferation. This is surprising at Trench F though, as Taylor, (2011, 75) found that this was located on a shallow shore on which a swamp environment developed quickly. Also, on NNH, *Phragmites australis* (pers. observation) was present in all of the shoreline test pits, and it might have been expected that this would also hold material, even though the island is known to have been located in a deep part of the basin (Taylor, 2011, 75) and therefore aquatic species local to the island may have shown lower diversity. *Chara* acts differently too and is not found in cores 68 and 78 from NNH, although it is present in very low numbers in profile NAZ. *Chara* is discussed further below.

Thirdly, the emergent and arboreal species in these cores seem to reflect more localised populations. While *Cladium*, the species which indicates shallowing water, appears consistently in zone 2 in all of the shoreline cores, the other species present vary considerably in this zone (Rodwell, 1997, 128). For example, in zone 2, *Ranunculus* appears in significant numbers only in VP85A/2010, *Rumex* only in CII/2010, while Trench F contains only swamp species *Typha* in addition to *Cladium*. *Typha* only appears in large numbers only at Trench F and P3178, it is found in quantity only when dominant and there appears to be localised hot spots around the lake (Birks, 1973, 179). Typha latifolia is an anemophilous plant with very small seeds (Cappers and Bekker, 2006) and these should be found in the deeper part of lakes as it was the case in L. Juusa (Koff and Vandel, 2006, 15); that they are not in the deep-water profiles of Paleolake Flixton would suggest that the plant is not dominant enough here, or the climate was not conducive to its seed production (Koff and Vandel, 2008, 15). Taylor, et al. (2018, 48) noted for example that *Sparganium* was more relevant in profile NAZ on the north side of NNH, due in part at least to localised changes in water depth through the hydrosere; this was also demonstrated at Seamer Carr, where water depth was shallower than at Killerby, which had less plant material as a result. At Killerby too the shoreline was steep, resultanting in only a narrow band of vegetation at the shore, potentially trapping less material; this may be the case on the shores of NNH, which is surrounded by deep water (Taylor, et al., 2018, 48).

This would indicate that differential distribution and/or taphonomic processes were in action at the shore of the island, and perhaps also at some points at the shore of the lake. It has already been identified that material moves to the edges of the lake. The area of FSHF that the cores were obtained from is an of long, open shoreline, and SC is located in a large embayment, in which currents may act to trap material. In contrast the length of shoreline at NNH which faces into the open water at any point is relatively short and there is the possibility that this then fails to 'capture' seeds and other debris floating in the water because of its smaller catchment area.

The lower diversity at NNH may also be due to the paucity of vegetation in the surrounding area, as the island is located in deep water towards the centre of the lake consequently with fewer species growing - Cores A and B also exhibit this low diversity in species (Taylor, 2019, 565-6). The lower diversity in zones A1 and 2, and B1 support the idea that macrofossils move to the lake edge; the increase in diversity in macrofossils in A2 only occurs when vegetation starts to colonise the area and cover increases (Taylor, 2019, 567). This is perhaps supported by the presence of *Urtica* in the NNH cores throughout the profiles, which, if present at all is not found until much later in the development of the hydrosere in the shore cores. Overall it may be suggested that a profile obtained from an island is representative of a more local plant population than one from a shoreline.

There are some specific species worth considering. *Chara* oospores, while being present in all of the shoreline profiles in zone 1 are not found in cores 68 and 78, appearing only in core NAZ and even then, in very low numbers. While most of the modern studies found that *Chara*, being light and plentiful, was distributed over a wide area, Szymczyk (2012, 510) considered that they were a more localised species than previously thought and their apparent wide distribution was actually a function of the presence large *Chara* beds. This would be confirmed by their absence on NNH in spite of wide occurrence at the shorelines if the *Chara* beds were not local to the island. Further caution is given by Zhao, et al. (2006, 346) who noted that *Chara* could be found even when the charophytes were absent, and they seemed to survive long after the plant had died, acting as a 'seedbank'.

Betula macro-remains are also differentially distributed on NNH, this can be seen from Table 3 below.

Table 3: Approximate counts for *Betula* macrofossil types for all cores.

	***Betula*, approximate maximum count, Zone 1**		
	Fruit	Catkin scale	Bud scale
Shoreline			
SC VP85A/2010	2000	100	13
SC CII/2010	700	80	14
SC P3178	170	8	5
FSHF Trench F	362	99	35
NNH NAZ	40*	12*	0
NNH 68	400	170	0
NNH 78	140	23	0
50m from shore			
FSHF Core A	37	2	0
100m from shore			
FSHF Core B	2	0	0

* NAZ figures taken from the section of profile which represents a shoreline environment.

Note – numbers are read approximately from the macrofossil profiles above (with the exception of Trench F) and are used only as a comparison rather than absolute measure.

Betula counts are lower in all three NNH cores than at the shorelines, with the exception of P3178. However, there is another change in the *Betula* profile at NNH, the decline in numbers through zone 1B of core 68 and at the start of 1B in 78 and at the top of the earliest zone in NAZ profile. This decline is not seen in any of the other profiles. *Betula* seed occurs in the profiles from the cores taken in the deeper parts of Paleolake Flixton, in accordance with their wide anemophilous distribution pattern (Birks, 1973, 178-9). These should then be well represented in Core 78, just off the main shore of the island but the numbers of seed are low. Greatrex (1983, 775) considered *Betula* catkins to be more representative of the local population than the seed as they are not so well distributed by wind. If this is indeed the case, then for a period of time the *Betula* population declined on NNH and this is reflected in all of the cores from the island. As *Betula* seeds but not catkins are found in this study up to 150m from the shoreline in Core B in open water, this would further indicate that catkin scales are a more indicative measure of local population. In addition, from zone 2 onwards *Betula* numbers, both of seed and catkin scale, fall in number in all profiles. If wind was indeed the major factor in distribution of seeds this is not supported by the macrofossil records – numbers fall as areas of standing water start to infill so it may be the case that water distribution of seed is a more important mechanism than previously considered. This is counter to Greatrex, who found large numbers of *Betula* macrofossils present in a sample from a fen environment even though no trees were present (Greatrex, 1983, 784). Alternatively, *Betula* could have declined in the landscape but it is difficult to envisage a scenario where this occurs over a large area around the lake.

Nymphaea alba is considered to be widely distributed within a lake, either as whole seeds or in fragments and Koff and Vandel (2008, 11) found a clear correlation between the presence of two *Nymphaea* species and their macro-remains. Seeds and fragments of *N. alba* were found in the deepest part of the lakes that they studied, at 5.5m depth (Koff and Vandel, 2008, 13). While seeds and fragments of *N. alba* occur at all of the shoreline sampling points for Lake Flixton, they are virtually absent any in the NNH profiles zones 1, or in the deeper parts of the lake at the period of maximum extent of the standing water. It is possible that *Nymphaea* are found in areas where *Chara* is dominant as a strong link exists in the environment conditions required for each species to grow (Hannon and Gaillard, 1997, 17); at NNH both species are absent.

Finally, as already noted *Phragmites australis* leaves were plentiful at the bases of the two test pits sampled on NNH in 2018, however there were no seeds recorded in the macrofossil profiles. This is echoed in the same absence of *Phragmites* seeds that Greatrex (1983, 785), Koff and Vandel (2008, 11) and Szymczyk (2015, 512) found in their sampling, and is an illustration that understanding seed dispersal and taphonomy is crucial in use of macrofossil studies to build up a complete picture of the environment.

6. CONCLUSION

The examination of the macrofossil profiles from sites around Palaeolake Flixton has fulfilled the aim of this dissertation in studying deposition and taphonomy in these contrasting areas, revealing differential deposition patterns in the No Name Hill/island profiles, against the shoreline cores. These shoreline cores exhibit the pattern predicted by the modern proxy studies – high species diversity and macrofossil counts. The deep-water cores too are typical – low species diversity, lower numbers of seeds in general, and the only non-aquatic taxa present in the deepest part of the lake are of species with anemophilous seed. The No Name Hill cores however contain low numbers of macrofossils, and lower diversity than majority of the shoreline cores display. This low diversity may be a function of a less varied plant population on the island, but the lower quantities of macrofossils found overall is a feature of differential deposition. This pattern is also seen, albeit not to as great an extent, in cores P3178 and Trench F. Overall it would appear that deposition is indeed different on an island from the shoreline, however further comparisons are required to verify this. There is another set of islands in the Paleolake, known as Flixton Island but these are significantly smaller than No Name Hill and may be subject to a further pattern of deposition. There are two roughly circular areas of land which extend into the lake near Killerby and Lingholme, which may act as island, therefore they might be suitable sites for further analysis, in particular Killerby, which is in a deep embayment, echoing the location of No Name Hill in the deepest art of the lake (Taylor, 2012, 456).

Dieffenbacher-Krall (2007, 687) summarized the main reasons for discrepancies between macrofossil remains being a function of plant reproduction, dispersal and loss of seeds, within-lake sample location (shore versus deep water) and basin characteristics. As already seen above, macrofossil availability is confirmed as dependent in the first place on the reproductive strategies of plant species, and how the seeds are dispersed, or not in the case of some species where seeds fall near to the parent plant. In Paleolake Flixton broadly the same species are seen around the lake, particularly the aquatic and arboreal plants, with some small local variations in swamp and fen taxa. The difference between shoreline and deep-water cores in their representation of macro-remains was also discussed, with deep water cores showing little diversity and consisting in the main of aquatic species only, and this has been borne out in the studies of Paleolake Flixton. What had not been examined in any detail in the modern studies is basin characteristics. The only contributions to these factors are found in Koff and Vandel (2008, 17), who advised against sampling on a slope of greater than 14 degrees, and they and Szymczyk (2011, 504) also advocated not sampling at a site which was in the path of a prevailing wind. It is not known if either of these conditions applied across Paleolake Flixton, although No Name Hill is located in some of the deepest water in the lake and it is therefore possible that its shores fall off steeply, perhaps accounting for the lack of material found (Taylor, 2011, 75). This however does not apply at Flixton School House Farm, which is a shallow area into which the reed swamp expanded rapidly (Taylor, 2011, 75). Therefore, the potential to trap material should be high but this is not necessarily reflected in the profile for Trench F. There is another factor which may be affecting the macrofossil record for Trench F which is not apparent and would warrant further study.

With regard to particular species. This study confirms that Chara remains are probably only found where the algae had actually been growing and is not as widely dispersed as some research would suggest (Birks, 1973, 182). Nymphaea too is eccentric in its deposition; in spite of being considered to be widely distributed its occurrence in the profiles reviewed for

Paleolake Flixton is sparse (Koff and Vandel, 2008, 11). *Betula* catkins, as Greatrex (1983, 775) proposed, would appear to be a better proxy for the local presence of trees as shown by their fluctuation on No Name Hill, than the seeds, which are dispersed over many metres, being found up to 150m into Paleolake Flixton.

The main gap in knowledge of macrofossil deposition and taphonomy comes from the size of Paleolake Flixton. No extant studies have been carried out on an area even approaching that of this lake, the largest studied is 12ha in area, at its maximum extent Paleolake Flixton was approaching 900ha. Poor transportation and limited mixing of remains will mean that samples may vary even from the same lake, this is seen in the differential fen and swamp species represented at points around Paleolake Flixton, and there is no study of the transport of remains over such significant distances as seen here (Mannion, 1986, 197). In addition, the pattern of deposition on an island is little understood. The data above suggests that the macrofossils sampled on an island are a very good representation of local conditions, given firstly, the restricted species diversity, and secondly, the sensitivity to the decline in *Betula*. The restricted species diversity is shown in the absence of *Chara*, while ubiquitous elsewhere, which indicates also that the 'temporal smoothing' seen on a lakeshore by Zhao, et al. (2005, 347) is mitigated on an island. This may mean that samples from the shore of a large body of water are very general to the surrounding environment, while those on an island represent the immediate flora.

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