

Lateglacial and Early Holocene palaeoenvironmental change and human activity at Killerby Quarry, North Yorkshire, UK

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ABSTRACT: The hunter-gatherers that entered the British peninsula after ice-retreat were exploiting a dynamic, rapidly changing environment. Records of vegetation change and human occupation during the Lateglacial to Early Holocene in northern Britain are more commonly found at upland and cave sites. However, recent research highlights many areas of the Swale–Ure Washlands that preserve extensive environmental sequences in low-lying ice-wastage basins, channels and depressions. The Lateglacial–Early Holocene environment of Killerby Quarry, North Yorkshire, is investigated here using a multi-proxy approach of sedimentary ancient DNA (*sedaDNA*), pollen, sedimentological (geochemistry and portable optically stimulated luminescence), and rare and well-preserved archaeology (Lavvu structures and lithics). Results show that the wetland basins and kettleholes were small lakes or ponds in the Lateglacial surrounded by sedge-fen and birch woodland. A gradual (centennial scale) succession to reed-swamp and then marsh is seen by the Early Holocene. This environment formed the resource-scape for hunter-gatherer transitory settlement in both the Lateglacial (Late Upper Palaeolithic) and Holocene (Early Mesolithic), attracted by the rich communities of pond-related flora and fauna as well as easy strategic landscape access by way of the River Swale, an arterial route through the landscape connecting the North Sea Basin with the Pennine uplands via the palaeolakes around Killerby. © 2022 The Authors *Journal of Quaternary Science* Published by John Wiley & Sons Ltd.

KEYWORDS: Lateglacial; Late Upper Palaeolithic; Mesolithic; *sedaDNA*; hunter-gatherers

Introduction

The Lateglacial period, marking the transition from the Pleistocene to the Early Holocene, is characterized by climatic instability and abrupt environmental change in North-Western Europe (Walker *et al.* 1993; 1994; Birks and Birks 2014; Rasmussen *et al.* 2014; Candy *et al.* 2016). The climatic shifts of the Lateglacial (Windermere) Interstadial, Younger Dryas (Loch Lomond Stadial) and Holocene transition are well reflected in a series of successional vegetation changes in geomorphological and palaeoecological records, along with a number of briefer climatic oscillations, although the exact timing of phase-transitions can vary regionally (Innes *et al.* 2009; Walker *et al.* 2012; Walker and Lowe 2019; Simmonds *et al.* 2021).

In Britain, well-dated palaeoenvironmental sequences covering the entire Lateglacial period are scarce, particularly in lowland areas where extensive peat deposits are less common, and questions remain regarding the speed and trajectories of vegetation development in Lateglacial Britain in response to climate change. The existence of micro-climates where thermophilous woodland taxa survived in cryptic refugia has been postulated (Young *et al.* 2021; Kelly *et al.* 2010; but see Scourse, 2010), as opposed to a gradual, regional expansion of these species northward from lower

latitudes with climatic amelioration (Gieseke *et al.* 2017). Previous palaeoenvironmental studies have also indicated brief climatic downturns during the Lateglacial Interstadial, correlating with GRIP events GI1-d (older Dryas) and GI1b (intra-Allerød cold period). However, further studies are needed to identify and therefore better define these oscillations at local levels and to assess their implications for the early colonization of the British Isles (Gearey 2008; Innes *et al.* 2009; Whittington *et al.* 2015).

To understand the complex nature and variation of vegetation during the Lateglacial, multi-proxy analyses of environmental sequences are often applied (Jones *et al.* 2002; Whittington *et al.* 2003; 2015; Walker *et al.* 2012; Bos *et al.* 2017). Recently, sedimentary ancient DNA (*sedaDNA*) has been added to the toolbox of palaeoecological techniques and is becoming an increasingly powerful proxy for the study of paleoenvironments, particularly when applied complementarily with palynological analyses (Clarke *et al.* 2020; Edwards, 2020; Rijal *et al.* 2021; Brown *et al.* 2022). The predominantly open-ground conditions of the Lateglacial can lead to pollen signals being swamped by grass and sedge taxa (Walker *et al.* 1994; Birks and Birks 2000). Therefore, the use of *sedaDNA*, which has been shown to better reflect localized vegetational change than pollen evidence alone, particularly of aquatic and shrub species, should lead to both local wetland and regional dryland species being well represented (Sjögren *et al.* 2017; Alsos *et al.* 2018).

Here we present the results of a multi-proxy examination of a Lateglacial–Early Holocene environmental record from

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Killerby Quarry, in the Swale Valley, Vale of Mowbray, North Yorkshire, based on *sedaDNA*, pollen and sedimentological data. The environmental sequence is supported by a radiocarbon chronological framework. The Vale of Mowbray lies within the limits of glacial advance during the Last Glacial Maximum of the Vale of York Lobe (Davies *et al.* 2019). As part of an innovative programme of archaeological investigation in advance of gravel quarrying, Killerby provided an ideal opportunity to investigate environmental changes after deglaciation and climatic amelioration within the edge-zone of the British–Irish Ice Sheet (BIIS). Study of the Lateglacial environmental sequences in the Swale–Ure Valleys (Bridgland *et al.* 2011; Young *et al.* 2021; Innes *et al.* 2009; 2021) is providing a picture of Lateglacial–Early Holocene environmental changes, and the sequences from Killerby add to this growing body of research. The region was also occupied by humans prior to the Holocene in the Windermere Interstadial around 12 500 BC (Jacobi *et al.*, 2011; Lord 2013) and Killerby provided an opportunity to assess evidence of local Lateglacial human activity, as well as activity in the early Holocene.

The site

Killerby Quarry is situated to the south-east of Catterick (Fig. 1), in the Leeming Moraine complex of the Swale Valley, North Yorkshire, immediately south and west of the River Swale (1°35' 39.95"W, 54°21'38.74"N). The site is used for gravel quarrying and agriculture and is topographically characterized by pronounced undulations which vary between 38 and 55 m above ordnance datum as a result of glacial and post-glacial formation processes (Parker *et al.* 2019). The solid geology of the area comprises Carboniferous Millstone Grit and Permian Magnesian Limestone, which is overlain by thick glacial tills, glaciofluvial sands/gravels and marls, alongside in-filled ice-wastage features such as wetland basins and distinctive kettle-type depressions formed from delayed melt-out of isolated ice blocks and masses (Bridgland *et al.* 2011). The north-eastern portion of the site comprising the Holocene floodplain displays a complex sequence of intercutting fluvial palaeochannels which reflect former watercourses of the River Swale. The southern portion of the site is located at the northern part of the Leeming Moraine, a glacial landform c. 38–50 m in elevation which extends for 7 km south of Catterick along the route of the A1 road (Bridgland *et al.* 2011). Organic-rich sediments are extensively preserved in the wetland basins and kettleholes across the site. The sedimentary record presented here originates from a Test Pit within Wetland Basin 1b (W1b) (Fig. 1) and is presented alongside *sedaDNA* data directly sampled from sediment within an Early Mesolithic 'tepee' or 'Lavvu' type-structure just 25 m north within W1b (Waddington *et al.* 2020).

Archaeological investigations

The wetland basins, kettleholes and poorly drained depressions provide ideal locations for the accumulation of organic-rich sediments and peats, within which many of the archaeological remains are preserved. Wetland Basin 1 (Fig. 1C, D), in the south-western section of the site, was shown to preserve exceptional archaeological remains dating to the Early Mesolithic (Waddington *et al.* 2020). The carefully designed geoarchaeological evaluation and excavation works (Waddington and Passmore, in press) have revealed rare and well-preserved sedimentary and archaeological records across the development site, including the timber poles for Early Mesolithic tepees, or 'Lavvu'-type structures, extensive lithic scatters in the topsoil around the relict wetlands, together

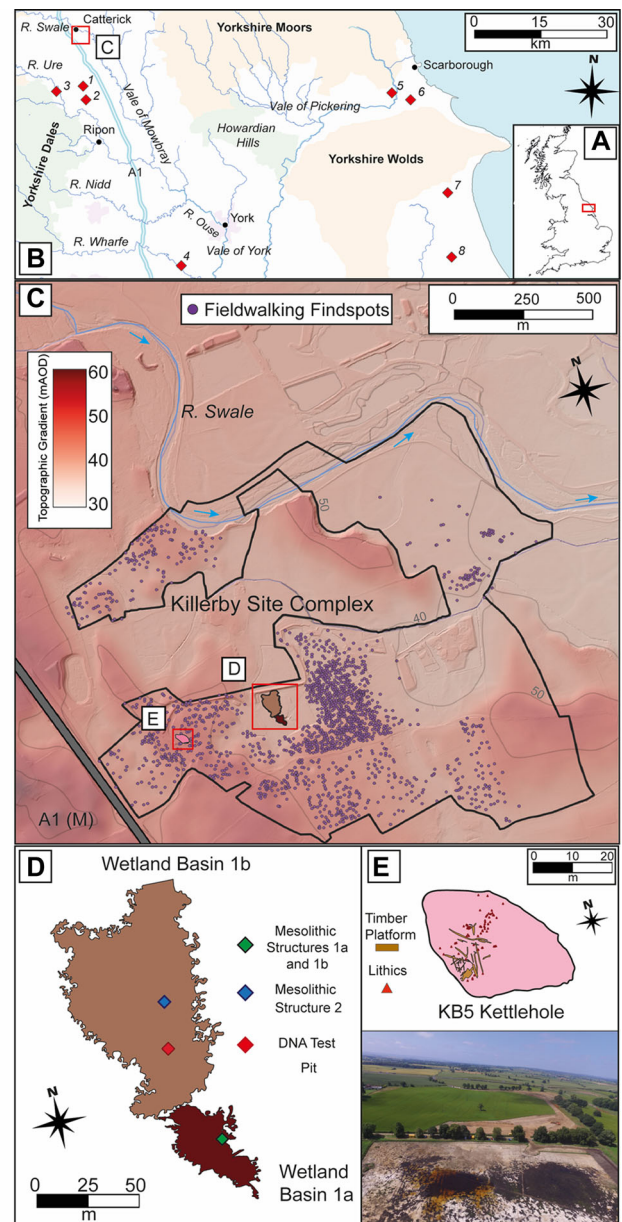


Figure 1. (A) Map showing site location in the UK. (B) Lateglacial sites in the Yorkshire region, with Killerby indicated in the red square. Other sites are as follows: 1 – Snape Mires (Innes *et al.* 2009), 2 – Nosterfield (Innes *et al.* 2009), 3 – Marfield (Innes *et al.* 2021), 4 – Tadcaster (Bartley 1962), 5 – Wykeham Quarry (Lincoln *et al.* 2017), 6 – Vale of Pickering (Day 1996), 7 – Gransmoor Quarry (Walker *et al.* 1993), 8 – Routh Quarry (Gearey 2008). (C) LiDAR-derived local relief model of the Killerby Quarry site complex with Wetland Basin 1 highlighted. Fieldwalking findspots are derived from Waddington *et al.* (2009) and LiDAR data from UK Environmental Agency open source digital terrain models. (D) Wetland Basin 1a and 1b with locations of the DNA Test Pit and Mesolithic Structure. Photo: Wetland Basin 1 looking west with A1 motorway visible in the distance. [Color figure can be viewed at wileyonlinelibrary.com]

with a Late Mesolithic timber platform extending out into a pond (Waddington *et al.* 2009; Hunter and Waddington 2018; Waddington *et al.* 2020) amongst other later remains.

The most fully preserved of the tepees was timber structure 2 located in WB1b which had long poles surviving, mostly of alder, including one nestled in the fork of another where the latter had been used to hold the other long timbers at the apex of a conical-shaped structure. The poles appeared to be felled young alder trees, and not coppiced material, which had evidence for modification with off-shoots and small branches removed by hand (Bamforth in Cockcroft and Waddington



Figure 2. The Early Mesolithic tepee timber structure 2, and hearth during excavation of Wetland Basin 1b with sample holes for the *sedDNA* visible below one of the long poles. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.com)]

2021). This type of tent structure with light poles is of very different constructional form to the Mesolithic ‘houses’ with substantial postholes and postpads found at Howick, East Barns, Echline and Mount Sandal which are 1000 or so years later in time. The Killerby structures date to earlier in the Holocene at a time of colder climate, and reflect a different residential mode altogether than the later more substantial houses referred to above. A fireplace, or hearth, survived inside the structure, overlain by some of the long timbers which had fallen over it, and had part-burnt logs extending out from it and masses of charcoal at its centre (Fig. 2). Radiocarbon determinations from both the hearth and the long timbers were virtually identical, dating this structure to 11 080–10 710 cal a BP (all dates to 95.4%). Another of the tepees, timber structure 1a, provided a similar date of 10 750–10 570 cal a BP, whilst the third tepee, timber structure 1b, produced a date of 11 080–10 690 cal a BP. These timber structures are contemporary with the earliest phases of the well-known Early Mesolithic site at Star Carr (Milner *et al.* 2018), and slightly earlier than the Early Mesolithic flint scatters, possible structures, and hearth at Money Howe on the North York Moors, which is dated to 9430 ± 390 cal a BP (Q-1560; Jacobi 1978). The sediments immediately below the hearth in timber structure 2 in WB1b were chosen for the additional *sedDNA* analysis reported here.

Microcharcoal concentrations were remarkably high in both the Lateglacial and Early Holocene Killerby sediment units, comparable to those seen at other sites in North Yorkshire such as Snape Mires, Nosterfield (Innes *et al.* 2009; 2021) and Star Carr (Day 1996). Microcharcoal pieces are often found in large numbers at Lateglacial sites (Edwards *et al.* 2000) and it is possible that this is the result of natural fires in a period known for its aridity (Walker *et al.* 1994). However, the presence of humans is attested to across the site from the Late Upper Palaeolithic to Early Holocene by the flint assemblage that includes a tanged point of Ahrensburgian affinity from Wetland Basin 2 (Waddington *et al.* 2020), and from the distribution of the chipped lithics recovered by high-resolution fieldwalking (Waddington *et al.* 2009) (Figs 3 and 4), as well as at other sites in the region (Sheldrick *et al.* 1997; Jacobi *et al.*, 2011), and the microcharcoal can be seen more probably as evidence for human activity in sediments that otherwise contained no archaeological remains.

Elsewhere on the site excavation of Kettlehole KB5, located on a plateau c. 350 m to the south-west, uncovered a complex



Figure 3. Assorted Early (top row obliquely truncated broad microliths) and probably Later Mesolithic (rows 2, 3 and 4) microliths from the Killerby fieldwalking including pieces made from the locally available chert. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.com)]



Figure 4. A tanged point-type piece of Ahrensburgian affinities (Waddington *et al.* 2020) found in Wetland Basin 2, of Lateglacial (i.e. Upper Palaeolithic to Early Holocene) date, with retouch either side of the small tang at the base of which is a triangular-sectioned blade. The tip does not form a sharp point, though there is retouch, and there is edge trimming along both long sides. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.com)]

sequence of lacustrine-fluvial sediment and peat deposits (Fig. 1; Supporting Information Fig. S2) spanning from the Late Devensian to the present day – one of the most complete for the entire Swale–Ure region (Hunter and Waddington 2018). Within this kettlehole a Late Mesolithic timber structure in the form of a substantial oak platform of roughly worked wood (Fig. 5) was discovered. Timber from the platform’s base dated to 7560–7360 cal a BP (Table S1), whilst small roundwood hazel packing for a vertical oak post set into the



Figure 5. Late Mesolithic timber platform emerging during excavation in the fill of kettlehole KB5 under light snow conditions with the area of Wetland Basin 1 situated immediately behind the first treeline in the middle distance. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/jqs.3488)]

platform produced a date of 6750–6630 cal a BP (Hunter and Waddington 2018).

Stratigraphy and chronology of Wetland Basin 1

Previous research at the site has revealed the major stratigraphic units (Supporting Information Fig. S6) and radiocarbon framework of Wetland Basin 1b (Table 1 and Fig. 6), which can be correlated to the *sedaDNA* test pit (Fig. 7) (Parker *et al.* 2019). The lowermost sedimentary units comprise a series of laminated silts and clays which extend to an indeterminate depth below 3 m where excavation ceased due to groundwater ingress. These are Glacial and Lateglacial fluvial–lacustrine laminated silts/clays within which Wetland Basin 1 was formed. Overlying these clays are irregularly interspaced marl deposits, which have been dated to 12 750–12 680 cal a BP. The marl is overlain with a green-brown peat deposit dated to 12 760–12 720 cal a BP (Younger Dryas). It is not thought that either of these dates are in error as, although the upper date appears marginally later than the date of the sediment immediately beneath, because they overlap this still allows that lower date to be older, and this being the case would indicate that the transition from marl to peat occurred rapidly during the tightly dated 30-year span between 12 750 and 12 720 cal a BP.

The green-brown peat was overlain by a series of organic-rich peat layers. Radiocarbon dates from these layers gave determinations of 10 490–10 240 cal a BP at the base of the peat, and 10 210–9910 and 9700–9540 cal a BP in the overlying peats, suggesting approximately a 1000-year timespan. The sequence included a number of disregarded dates which are explained further in Supporting Information Text S1.

Methods

Sampling

In July 2019 a 1-m² × 3-m² test pit, known as ‘Kil19 PSA DNA Pit 1’ inside Wetland Basin 1b (WB1b; 1°35′58.31″W, 54°21′19.29″N; Figs 1 and 7) was excavated as part of the wider archaeological excavation. This test pit was sampled for *sedaDNA* and pollen using 17 50-ml Falcon tubes. An additional 100-cm half-pipe ‘core’ was also taken between depths of 25 and 125 cm for sedimentological and geochemical

analyses. The core contained 87 cm of sediment after being removed from the face of the section. Before sampling, the sediment face was cleaned with a trowel sterilised with bleach. Samples for DNA analyses were taken by pressing sterilised Falcon tubes horizontally into the cleaned surface, starting from the bottom to prevent cross-contamination from falling sediment. After recording depths, the 50-ml tubes were removed and immediately stored at 4°C, along with the sampled core. In October 2019 further sampling took place inside Wetland Basin 1b, placing six 50-ml tubes (K1–6) underneath the hearth of the Early Mesolithic tepee structure 2 (Fig. 7E, F). Methodology was as for the Test Pit sampling. The six 50-ml tubes sampled from beneath the Mesolithic structure were all placed at a depth of 7 cm below the structure with the exception of K6 which was placed 12 cm beneath.

Sedimentology: loss-on-ignition, geochemistry, magnetic susceptibility, pOSL, and pollen

LOI, pXRF and magnetic susceptibility

Loss-on-ignition (LOI) followed standard methodology (Heiri *et al.* 2001) and consisted of 87 samples of 2 mg of sediment, one run of 64 and a second of 23, with the core being subsampled at 1-cm resolution. Samples were placed in an oven for 12 h at 50 °C to estimate moisture content, burned at 550 °C for 2 h to estimate organic content and finally burned at 950 °C for 4 h to estimate carbonate content. Magnetic susceptibility analysis was performed manually using a Bartington MS2 meter at 1-cm resolution on the entire core using both the MS2B Dual Frequency Sensor for HF and LF, and the MS2K downcore Surface Sensor. To support the sedimentology, portable X-ray fluorescence (pXRF) was performed using a NITON XL3 analyser at 5-cm resolution on the core. Both the geochemical and soil settings were used to obtain a final suite of 44 elements. A total of 18 were freeze-dried and analysed within 15-ml plastic sample pots covered with 160-µm Ultralene film within the mounted test stand. Readings were taken twice using the ‘Soils’ and ‘Geochemistry’ modes with a dwell time of 60 s composed of 15 s ‘main’ filter (0–100 keV), 15 s ‘low’ filter (0–40keV), 10 s ‘high’ filter (40–100 keV) and 20 s ‘light’ filter (0–10 keV). Each setting was run at its factory set length to ensure quick scans. Results presented in this study are from the ‘Geochemistry’ setting and use pre-existing factory calibration settings.

Portable optically stimulated luminescence

To develop the variation in sediment texture and mineralogy of the Killerby sequence, portable optically stimulated luminescence (pOSL) analysis was conducted using the equipment and process pioneered by SUERC (Sanderson and Murphy 2010). pOSL has been used to determine variations in feldspar and quartz mineralogy (Aitken 1994), and used in hydrological environments to detail depositional conditions, sediment provenance and flooding events (Muñoz-Salinas *et al.*, 2011, 2016; Ghilardi *et al.* 2015; Portenga and Bishop 2016; Gray *et al.* 2019; Pears *et al.* 2020). Luminescence analysis was conducted on 25-g bulk ‘dark’ sediment samples extracted at 2- to 3-cm resolution from the centre of the sediment core. Each of the 65 samples was stimulated for 60 s using the protocol [dark 60 s, infrared (IRSL 880 nm) 60 s, dark 60 s, blue light (OSL 470 nm) 60 s, dark 60 s]. Data quality was maintained by conducting four sets of independent replicates across sections of the sediment sequence that demonstrated particularly large shifts in results determined in the initial data

Table 1. The radiocarbon dates from Wetland Basin 1, including those from the three Mesolithic structures and from an additional Test Pit within WB1b–KB6 (see Supporting Information Fig. S6). Dates excluded from analysis are in grey. Dates were calibrated in OxCal v4.4.2 using the IntCal 2020 calibration curve (Reimer *et al.* 2020).

Lab. ID	Context [Location]	Context description	Material dated	$\delta^{13}\text{C}$ (‰)	C^{14} age (BP)	Calibrated date BC (68%)	Calibrated date BC (95%)	Calibrated date BP (95%)
Wetland Basin 1 (WB1)								
Lateglacial Period (Younger Dryas) to Late Upper Palaeolithic								
SUERC-94950	(1919) [WB1], (1558) in test pit	Wetland Basin 1 organic sediment	Bulk peat: humic acid	-24.1	10 769 ± 25	10 800–10 770	10 810–10 770	12 760–12 720
SUERC-79316	(6003) [KB6] (1559) in test pit.	Pale yellow silty sand marl	Bulk peat: humic acid	-21.7	10 713 ± 32	10 790–10 750	10 800–10 730	12 750–12 680
Early Holocene to Early Mesolithic Timber Structures								
SUERC-92018	(2437) [WB1]	Lower charcoal deposit from hearth within Structure 2	Charcoal: Willow (<i>Salix</i> sp.) roundwood	-28.1	9551 ± 27	9120–8800	9130–8760	11 080–10 710
SUERC-94931	(2408) [WB1]	Structure 2 timber	Waterlogged alder (<i>Alnus</i>)	-31.5	9541 ± 23	9120–8790	9130–8760	11 080–10 710
SUERC-92016	(2411) [WB1]	Structure 2 timber	Waterlogged alder bark	-31.5	9531 ± 27	9120–8770	9130–8750	11 080–10 720
SUERC-94932	(1897) [WB1]	Structure 1a timber	Waterlogged pine (<i>Pinus</i>)	-27.5	9521 ± 25	9120–8760	9130–8740	11 080–10 690
SUERC-92017	(1873) [WB1]	Structure 1b Y-shaped timber	Waterlogged alder bark	-27.5	9435 ± 27	8760–8640	8800–8620	10 750–10 570
Early Holocene to Middle Mesolithic								
SUERC-94949	(1921) [WB1]	Wetland Basin 1 organic sediment	Bulk sediment: humic acid	-25.8	9450 ± 25	8780–8640	8810–8630	10 760–10 580
SUERC-79317	(6004) [KB6]	Dark brown/black peat	Bulk sediment: humic acid	-25.1	9257 ± 32	8560–8350	8620–8330	10 570–10 280
SUERC-94951	(1918) [WB1] (1556) in test pit	WB1 Organic sediment	Bulk peat: humic acid	-28.0	9190 ± 24	8430–8300	8540–8290	10 490–10 240
SUERC-94933	(1895) [WB1]	Tree stump	Field maple (<i>Acer campestre</i>)	-24.9	9070 ± 25	8300–8260	8300–8240	10 250–10 190
SUERC-95144	(1916) [WB1] (1555) in test pit	WB1 Organic Sediment	Bulk sediment: humic acid	-27.9	8943 ± 24	8250–8010	8260–7960	10 210–9910
SUERC-94952	(1917) [WB1]	WB1 organic sediment	Bulk peat: humic acid	-28.2	8802 ± 23	7950–7810	8170–7740	10 120–9690
SUERC-98267	(1915) [WB1] (1553) in test pit	WB1 organic sediment	Bulk sediment: humic acid	-27.3	8678 ± 31	7720–7600	7750–7590	9700–9540
SUERC-79315	(6002) [KB6] (1555) in test pit	Dark brown organic-rich clay	Bulk sediment: humic acid	-28.4	8519 ± 32	7590–7540	7600–7530	9550–9480
SUERC-79314	(6001) [KB6] (1553) in test pit	Dark brown/black peat	Bulk sediment: humic acid	-27.1	8029 ± 32	7060–6830	7070–6820	9020–8770
Late Holocene								
SUERC-98263	(1895) [WB1]	(1895) Tree stump overlying WB1	Wood: Field maple (<i>Acer campestre</i>)	-24.5	1898 ± 24	cal AD 120–210	cal AD 70–220	1880–1730

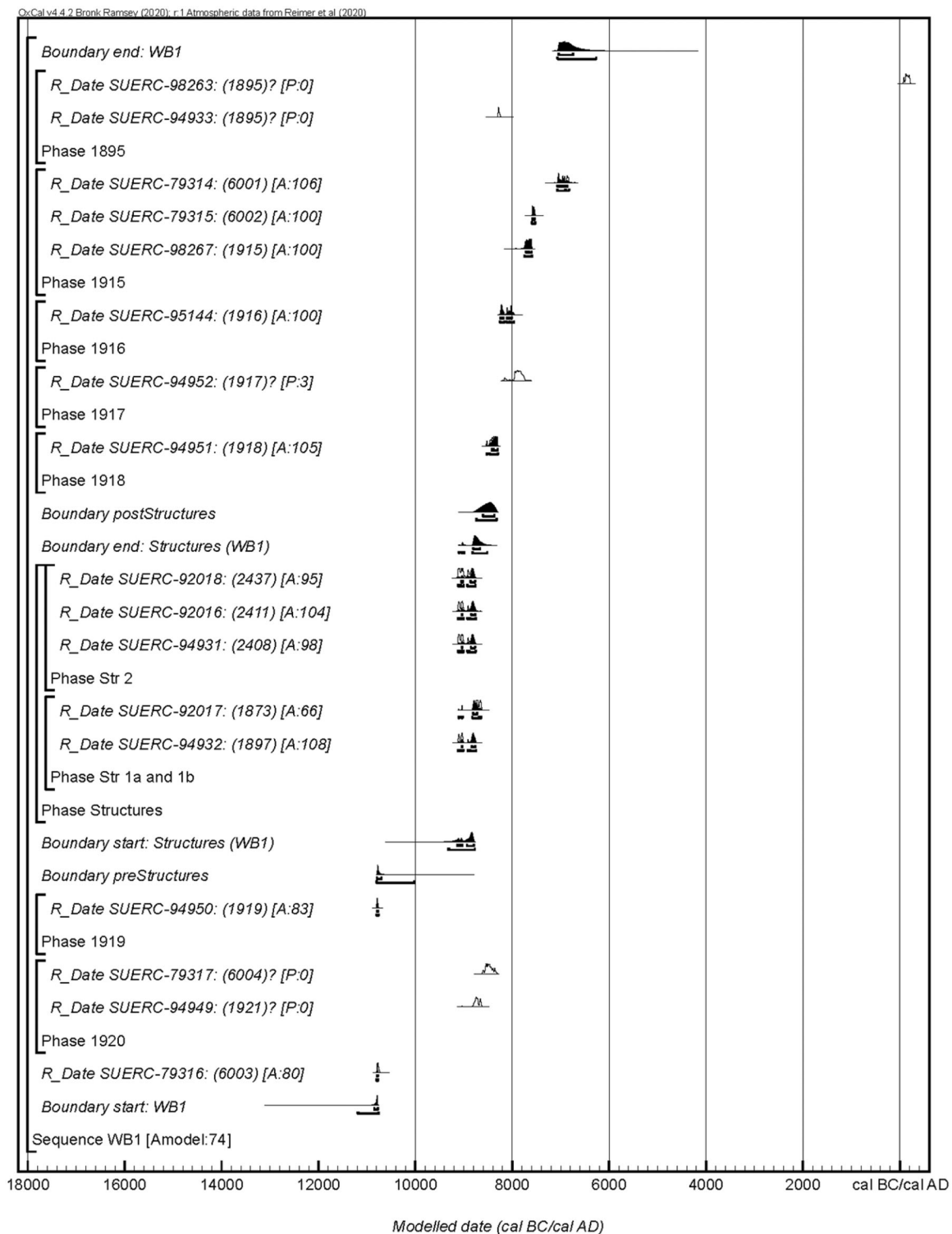


Figure 6. Chronological model for the radiocarbon dates from Killerby Wetland Basin 1 (WB1), modelled in OxCal v4.4.2 using the IntCal 2020 calibration curve (Reimer *et al.* 2020). Each distribution represents the relative probability that an event occurred at some particular time. For each of the radiocarbon measurements, two distributions have been plotted, one in outline, which is the result of simple radiocarbon calibration, and a solid one, which is based on the chronological model. The large square 'brackets' along with the OxCal keywords define the overall model exactly.

run. The resultant analysis enabled the determination of Net pIRSL as well as the Net pOSL and the calculation of IRSL:OSL.

Particle size analysis

To further analyse the variability of the clastic-dominated lower section of the core between 64 and 111 cm, particle size analysis was conducted at 1-cm resolution using a Malvern 3000 Digisizer, following methodologies determined by Konert and Vandenberghe (1997) and Blott *et al.* (2004). Prior to

analysis 5 g of wet sediment was combusted at 550°C for 2 h to remove organic material and the remaining residue sieved through a 2-mm sieve and then mixed with Calgon and deionized water to disaggregate the sediment for 24 h. Each sample was then placed into a centrifuge for 10 min and the resultant centrate carefully dispensed. At the time of analysis, a subsample of sediment was added to a Petrie dish with more Calgon and gently agitated with a rubber pestle before being added to the analyser until an optimum obscuration of 10–15% had been achieved. Background and sample measurement time

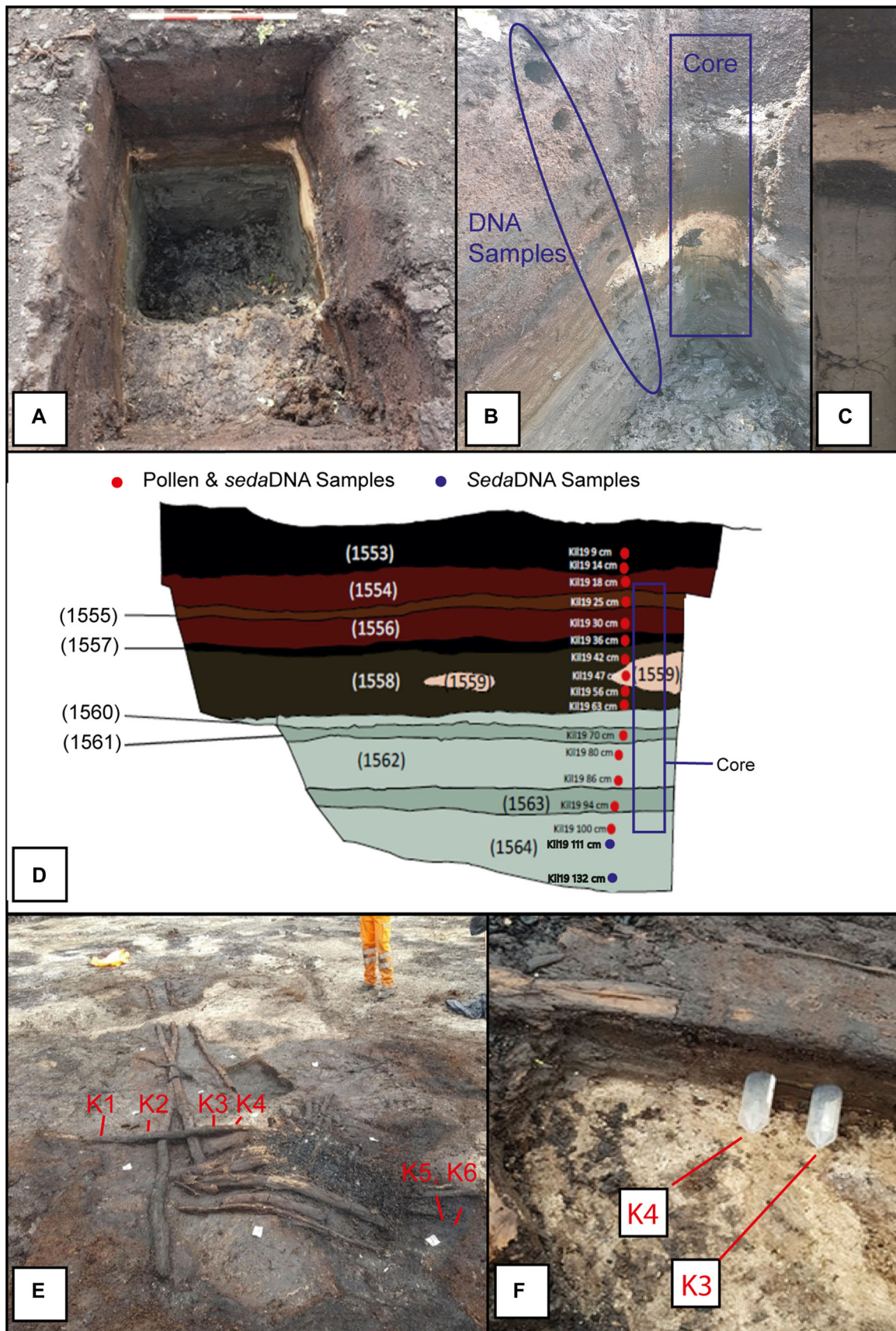


Figure 7. Details of the Killerby site sampling. (A) Kil19 DNA Pit1. (B) DNA Pit sample locations. (C) DNA Pit core sample. (D) DNA Pit stratigraphy. (E) Mesolithic timber structure 2 in WB1 during excavation with long poles surviving over underlying hearth; K1–6 indicate DNA sample locations beneath the structure. (F) Structure DNA samples inserted into sediment. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.com)]

was set to 90 s and each sample was analysed five times in order to get a good statistical dataset as determined by the international standard ISO-13320-1. All samples analysed had a standard deviation lower than 2% for the fine-grained percentile

(<Dx10), less than 3% for the median percentile (<Dx50) and less than 5% for the coarsest percentile (<Dx90). Classification of the resultant particle size data then followed the descriptive determination of Wentworth (1922).

Pollen

Pollen analysis was performed after *sedDNA* analysis on the same homogenized material in order to minimize contamination and maximize comparability. The majority of the slides conveyed grains of good/moderate preservation. A total of 15 slides were prepared for WB1 and 11 for KB5. The counts of every slide for WB1 reached a sum of ≥ 500 total land pollen. The concentration of pollen grains on the KB5 slides was poorer. A total land pollen sum of ≥ 300 was reached at 80, 86, 91, 69, 101, 160, 167 and, 187 cm. The slides for KB5 were mounted with small coverslips and the whole slide was counted in order to reach the count figure. There was a high concentration of pollen grains on slides 86, 91, 96 and 101 cm but there was a significant amount of debris on the slides that may have impeded the identifications. Poor concentration of pollen grains was found on slides 120 cm = 223 total terrestrial pollen (TTP), 135 cm = 294 TTP, 177 cm = 276.5 TTP and 234 cm = 246 TTP. Preparation of the samples followed that indicated in Moore *et al.* (1991). Pollen sums were calculated including grasses and sedges in herbaceous pollen. The percentages are presented as percentages of the terrestrial pollen sum. Taxonomy follows that of Stace (1991) and pollen diagrams were constructed in Tilia v2.6.1 (Grimm 2015).

Sedimentary ancient DNA

Extraction of *sedDNA* followed protocols documented by Hudson *et al.* (2022) using the Qiagen DNeasy Powersoil Kit and was performed in a dedicated ancient DNA laboratory at the University of Southampton. Polymerase chain reaction (PCR) amplification used primers of the P6 loop of the *trnL* UAA intro of the plant chloroplast genome (Taberlet *et al.* 2007) and the exact PCR procedure followed Alsos *et al.* (2021). Four negative extraction controls, two PCR-negative controls and one positive control were carried out. Eight individually tagged PCR repeats were made for each sample to increase the chance of detecting taxa represented by low quantities of DNA, as well as to increase confidence in the taxa identified. We pooled PCR products and then cleaned the resulting pool following Rijal *et al.* (2021). Each amplicon pool was then converted into a DNA library at Tromsø using the Illumina TruSeq DNA PCR-Free protocol (Illumina Inc., CA, USA) with unique dual indexes, the only modification being that the magnetic bead clean-up steps were altered to retain short amplicons. Each library was sequenced on $\sim 10\%$ of 2×150 -cycle mid-output flow cells on the Illumina NextSeq platform at the Genomics Support Centre Tromsø (GSCT) at The Arctic University of Norway in Tromsø.

All next-generation sequence data were aligned, filtered and trimmed using the OBITools software package (Boyer *et al.* 2016) using the same criteria as in Rijal *et al.* (2021). Resulting barcodes were assigned to taxa using the *ecotag* program and four independent reference datasets. One reference contained arctic (Sønstebo *et al.* 2010) and boreal (Willerslev *et al.* 2014) vascular plants as well as bryophytes from the circumpolar region (Soininen *et al.* 2015) (ArcBor-Bryo, $n = 2280$ sequences of which 1053 are unique), one the NCBI nucleotide database (January 2021 release), and finally the PhyloNorway p6loop database (Alsos *et al.* 2022). The resulting identifications were merged and filtered, retaining barcode sequences if they were identified to $>98\%$ in at least two reference sets and had at least 10 reads across the entire dataset. Where a reference dataset was unable to assign to specific species due to sequence sharing, we have listed all species that share the sequence.

False positives relating to common PCR errors and food contaminants were removed based on 'blacklists' built up from previous research at The Arctic University Museum of Norway (Rijal *et al.* 2021). We also removed sequences that could only be identified above the family level. For the last step of filtering, the frequency of PCR repeats in samples compared to negative controls was examined. Sequences were retained if they had an overall frequency of PCR repeats in samples at least twice as high as that in negative controls. Quantification of *sedDNA* data may not be straightforward as some taxa may be overrepresented in terms of sequence reads whereas using PCR repeats may underestimate abundance of the most abundant taxa (Alsos *et al.* 2022). Thus, we present the data both as the proportions of PCR repeats and proportion of total identified reads.

Results

Sedimentology and geochemistry

Windermere Interstadial

At the base of the sequence the dark grey lake sediments were characterized by a distinctive coarsening up-profile with clear micro-horizonation from fine silts to sandy silts and silty sands reflected by the particle size, magnetic susceptibility, LOI and pOSL analysis (Fig. 8). Together these illustrate a clear increase in depositional energy from a moderately deep lake body of water to a shallower lacustrine ecosystem with greater terrestrial input possibly because of brief fluvial activity within the lake catchment. An increase in the frequency and magnitude of high-energy events may have also resulted in the cutting off or infilling of wetland basin channels, thereby leading to further shallowing and the onset of peat development through terrestrialization. Up-profile shallowing in the lacustrine deposits is also demonstrated by the elemental evidence (Supporting Information Fig. S7) with increases in coarse-grained clastic indicators (Zr, Ti), stable levels of fine-grained indicators (K, Al, Rb), the mobility and transfer of Fe, Mn representing greater alteration between oxic and anoxic conditions, and the decreases in carbonate levels (Ca and LOI). Within the continually shallowing lacustrine conditions, development of the gyttja horizon appears to have occurred quickly given the sharp boundary and no clastic lake sediment transfer into the gyttja. From the pOSL analysis, the major shift in luminescence clearly shows a major change in depositional process and also probably a major hiatus or unconformity in time, with minimal clastic material in the upper sequence greatly affected by bleaching as opposed to the rapidly buried lake sediments.

Younger Dryas–Early Holocene

Around the end of the Interstadial, very shallow carbonate lake conditions resulted in the deposition of the distinctive whitish yellow, carbonate-rich marl. The sample sequence suggests a single phase of very shallow lake conditions, although across the site as a whole up to two or three phases of rhythmic marl–peat/gyttja formation appears to have occurred, suggesting a prolonged period of alternate depositional conditions reflecting the variable climatic conditions of the period. Critically, the high-resolution lithostratigraphic analysis of the gyttja and peat deposits demonstrates little to no clastic input at any stage and suggests that there was a prolonged phase of stable conditions with no clastic input from fluvial or lacustrine sources.

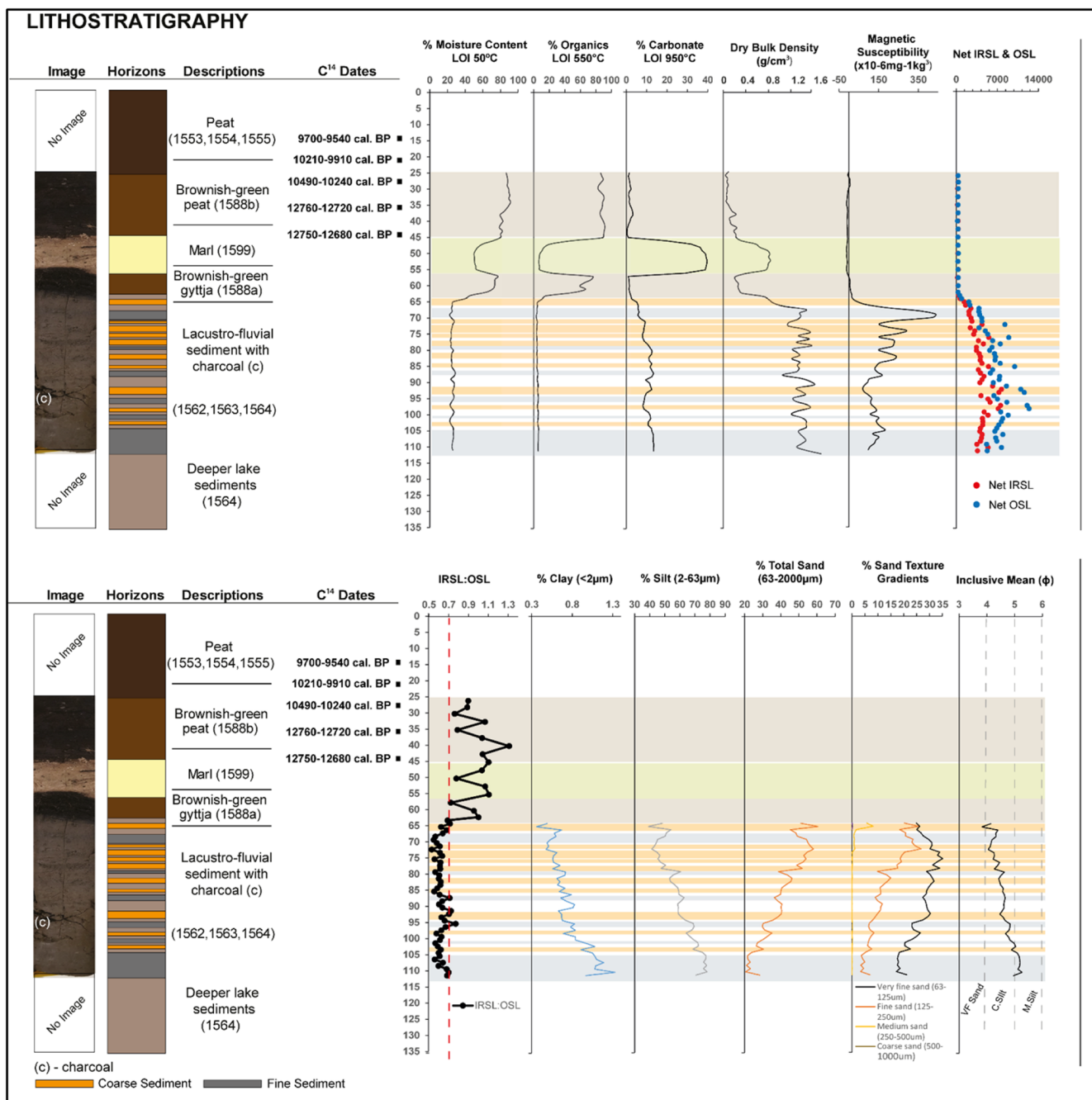


Figure 8. Combined sedimentological analysis of the half-pipe core taken from the DNA test pit immediately adjacent to the DNA and pollen samples from the DNA test pit. From left to right are loss-on-ignition (LOI), magnetic susceptibility, portable optically stimulated luminescence (pOSL) and particle size measurements. Additional portable X-ray fluorescence (pXRF) measurements are given in Supporting Information Fig. S7. In the pOSL graph, all results to the right illustrate a greater infrared SL (IRSL) (feldspar) signature, i.e. finer sediment and those to the left a greater OSL (blue) (quartz) signature, i.e. more clastic and typically defining the laminated deposition. The combined evidence suggests shallowing of the water body, followed by a stage of terrestrialization, a subsequent return to marl and shallow lake conditions, topped by a final phase of terrestrialization. [Color figure can be viewed at wileyonlinelibrary.com]

Plant sedaDNA

The samples from the Test Pit produced 4 463 037 raw reads. After pre- and post-identification filtering this was trimmed to 2 564 456 reads, with 34 accepted taxa, eight to species level, 18 to genus, and eight to family, sub-family or tribe level (Figs 9–11; Supporting Information Dataset S1). Four samples (14, 25, 47 and 51 cm) returned no identified taxa after filtering and DNA preservation was generally poor. The six Falcon tubes from below the Mesolithic hearth inside the tepee (timber structure 2) returned 1 534 144 raw reads. After pre- and post-identification filtering this was trimmed to 824 632, with 13 accepted taxa, five to species level, five to genus level and three to family level. As all six originated from the same

archaeological context, their results were combined, and the maximum number of PCR replicates for each taxon was taken as representative. An average of ~45% of reads was retained across both sampling locations.

Killerby Test Pit sedaDNA and pollen, spores and microcharcoal

Basal Lateglacial silt/clay 132 cm–Windemere Interstadial

The basal *sedaDNA* sample contained a lower signal of trees than the higher lacustrine depths. The *Betulaceae* and *Salix* seen probably indicate some form of shrub woodland around the wetland basin. The identification of *Betulaceae* almost

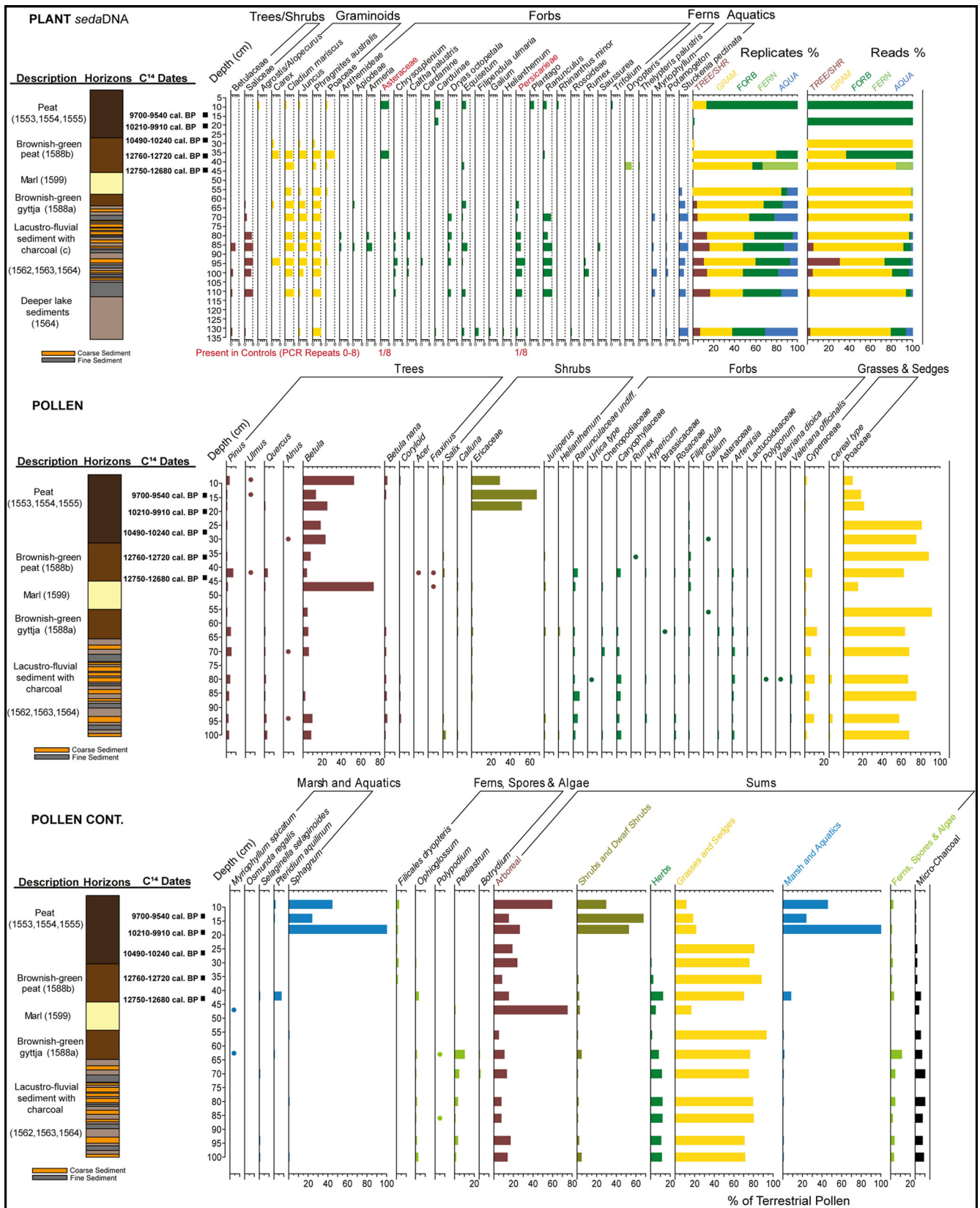


Figure 9. Combined *sedaDNA* and pollen analysis from the samples within the test pit. DNA is displayed as PCR replicates 1–8 and total read and replicate percentages per sample. Sequences appearing in negative controls are highlighted in red in the DNA. Note that pollen samples only cover 0–100 cm depth. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

certainly reflects the presence of *Betula*, but *Betula* was not identified to 100% in the reference databases, so this classification remains at the family level. There remains the possibility of early appearances of *Corylus* or *Alnus*, for which there is some evidence in the region (Tallantire 2002; Young

et al. 2021). Notably, the sample contained DNA from a number of more thermophilous tundra-herb species not seen in any other samples such as *Helianthemum*, *Filipendula ulmaria*, *Galium* and *Rosoideae*. These may indicate a warmer period within the Interstadial at the beginning of the sequence.

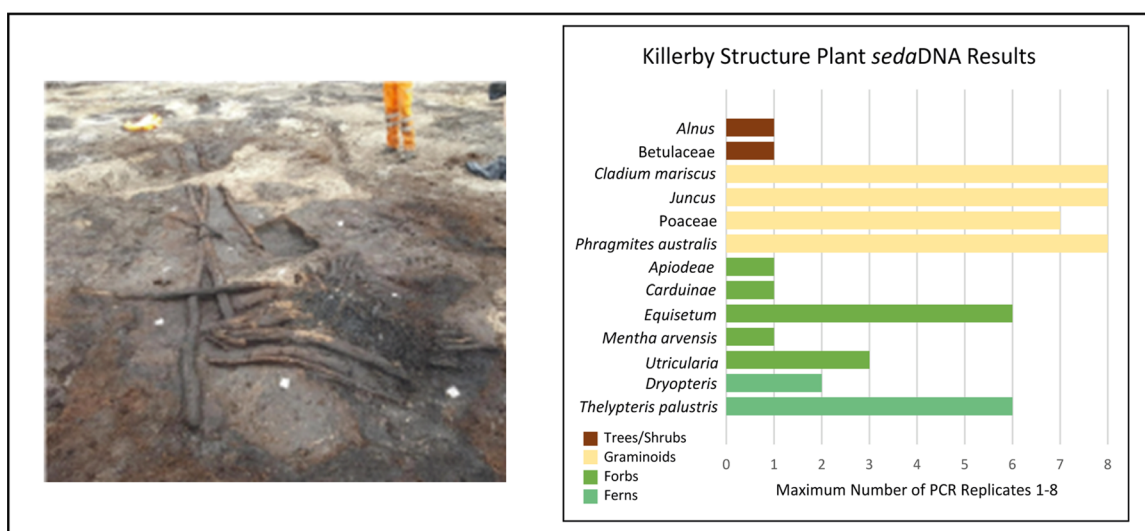


Figure 10. The *seda*DNA results from beneath the Mesolithic timber structure (structure 2). [Color figure can be viewed at wileyonlinelibrary.com]

The presence of standing or slow-moving water that was relatively warm is indicated by the presence of *Myriophyllum*, the pondweeds *Potamogeton* and *Stuckenia pectinata*, and the wetland taxa *Equisetum* and Persicariae. Since aquatic plants have relatively well-known climatic tolerances, we can assign a probable climatic July temperature to this assemblage – which using the data for Fennoscandia would be a minimum mean July temperature of approximately 13.6°C for *Potamogeton* (Väliranta *et al.* 2005), >10°C for *Myriophyllum* (*M. spicatum*, CABI), to 19°C for *Stuckenia pectinata* (Sebilian 2017), suggesting a thermal regime similar to the Northern Boreal zone today.

Lateglacial silts/clays 111–64 cm–Windermere Interstadial

In the upper lacustrine sediment, both pollen and *seda*DNA assemblages are dominated by graminoids. *Phragmites australis* dominates total read percentages between these depths along with other open-fen species such as *Cladium mariscus*, *Juncus* and *Carex*, with Poaceae and Cyperaceae also dominating the pollen data. Trees and shrubs were low in both assemblages, being predominantly limited to low quantities of *Betula*, *Pinus*, *Salix* and *Juniperus* (10–20 pollen grains) in the pollen, and with the exception of the sample at 94 cm, around 5% of total reads for *Salix* and Betulaceae in the *seda*DNA (Fig. 9). Very small quantities of deciduous tree-type pollen in the form of *Quercus* (one to 10 counts) and *Alnus* (one or two counts) are also present. Both the *Quercus* and *Pinus* pollen seen at these depths almost certainly derive from long-distance transport as these species were not present locally during the Lateglacial (Walker *et al.* 1993) or in the *seda*DNA. The small counts of Coryloid pollen present may represent bog myrtle (*Myrica gale*).

A small group of open-ground forbs were encountered in the combined datasets from the Lateglacial clays, including *Rumex*, *Plantago*, *Caltha palustris*, *Polygonum/Persicaria*, *Ranunculus*, Caryophyllaceae and typical Lateglacial taxa: *Dryas*, *Valeriana officinalis*, *Filipendula ulmaria*, *Chrysosplenium*, *Armeria*, *Artemisia* and *Saussurea*. Aquatic and marsh species were represented by numerous counts of sedges in the pollen (~10–60 counts) as well as counts of the green freshwater algae *Pediastrum*, with lesser amounts of the fern *Osmunda regalis*, *Myriophyllum* and pondweeds, with *Stuckenia pectinata* appearing in every *seda*DNA sample

between these depths. Microcharcoal concentrations were very high (7–10/10) throughout.

Marl deposits, gyttja (1558a) and greenish-brown peat (1558b) 63–25 cm–Younger Dryas–Early Holocene

Grasses and sedges remain well represented in both assemblages, but dryland forb species diminish, resulting in an overall reduction of identified taxa. The dryland/seasonally wet forbs that remain are horsetail *Equisetum*, Persicariae and very small amounts of Apiodeae in the *seda*DNA. In the pollen, herbs are also somewhat reduced, with smaller amounts of Caryophyllaceae, buttercups *Ranunculus* and *Artemisia* seen. Shrubs such as *Juniperus*, *Calluna vulgaris* and the heather family (Ericaceae) increase in pollen counts alongside *Pteridium aquilinum*. Aquatic species also diminish in the *seda*DNA and only four grains of *Myriophyllum* are seen in the pollen. Together, the decrease in aquatic taxa and increase in heathland species reflects the increasingly shallow water conditions suggested by the sedimentological analyses. Trees are almost completely absent from the *seda*DNA in this period, but *Pinus*, *Salix*, *Quercus* and *Betula* are a continued presence in the pollen, with a particularly high number of *Betula* pollen grains (310) within the marl at 47 cm. At 36 cm, an increase of graminoid taxa is seen, particularly Poaceae, which is identified in high numbers of PCR replicates (6–8), reads (c. 15%) and 369 pollen grains (88% of TTP). The two datasets indicate a localized domination of sedges and wetland within the basin and growth of woodland in the surrounding area, but not draining into the small lake which was receiving input of bicarbonates.

Overlying peat deposits (1553, 1554 and 1555) 25–0 cm–Early Holocene

The upper samples show a continually high presence of birch (pollen grains), at the expense of grasses which begin to decrease from the sample at 25 cm. Significantly, a large rise in both Ericaceae and *Sphagnum* from 0 to around 100% of the total land pollen is also seen in these upper samples. Deciduous trees and shrubs such as *Corylus*, *Ulmus*, *Alnus* and *Quercus* appear in limited quantities in the pollen, reflecting more varied woodland growth near the wetland basin. Forb taxa such as *Ranunculus* and *Equisetum* reappear

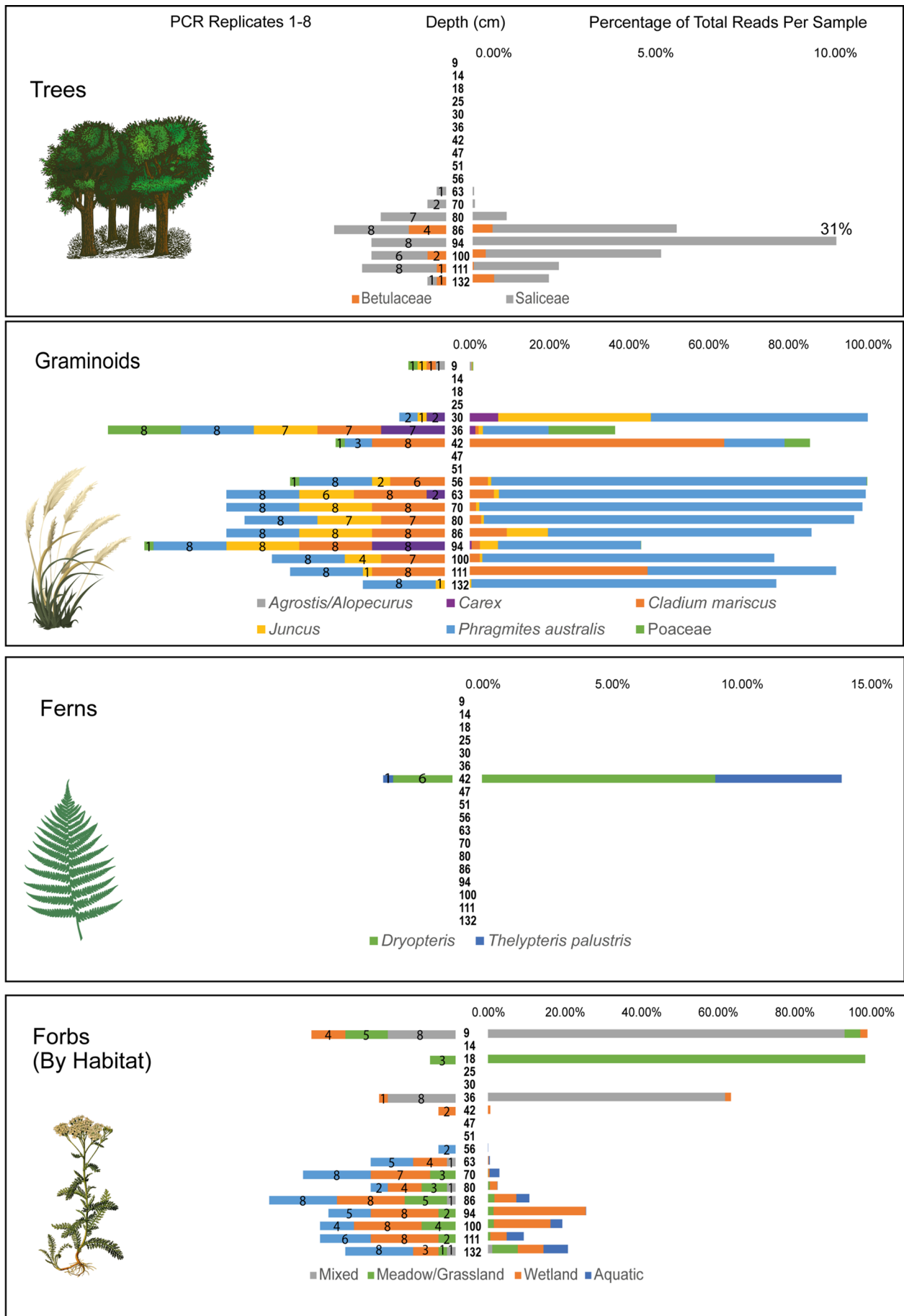


Figure 11. The plant *seda*DNA data from the test pit displayed through both number of PCR replicates 1–8 and percentage of total reads per sample. The classification of forbs to habitat are as follows. Mixed: taxa identified to family or genus level that contain various species adapted to different habitats. Meadow/Grassland: taxa that are commonly identified in open ground conditions with Ellenberg light values >5. Wetland: taxa with Ellenberg moisture values between 7 and 9. Aquatic: taxa with Ellenberg moisture values between 10 and 12. [Color figure can be viewed at wileyonlinelibrary.com]

alongside *Rhianthus minor*, Asteraceae, *Trifolium*, Carduinae and *Plantago*. The significant increase of heathland and marsh taxa could be indicative of human management of the area surrounding the lake through the clearance or modification of woodland, perhaps by, or for, grazing animals. Microcharcoal concentrations are very low for these depths (1–2/10), suggesting burning is unlikely, but the presence of the Early Mesolithic tepees shows some use of nearby woodland for timber. Together with the general reduction in grasses, a movement away from reed beds towards marsh meadow within the wetland basin and a reduction of open grassland in the surrounding area in favour of wetland and mixed deciduous woodland is indicated.

Killerby timber structure

The Mesolithic timber structure 2 (11 080–10 720 cal a BP, 95.4%) immediately overlies a peat layer that returned a plant *sedaDNA* assemblage (Fig. 10) dominated by the open-fen taxa, with *Cladium mariscus*, *Juncus*, *Equisetum* and the marsh-fern *Thelypteris palustris* well represented. The presence of the aquatic *Utricularia* indicates standing or slow-moving water in the vicinity of the structure. *Alnus* and Betulaceae were the only woodland taxa present, supporting the identification of *Alnus* as one of main timber poles used to construct the nearby tepee structure 2 (Cockroft and Waddington 2019). Further woodland was probably present nearby on the surrounding higher and drier ground, as suggested by the strong presence of the fern *Dryopteris*. Overall, a marsh or swamp environment dominated by grasses and sedges is suggested within this low-lying enclosed basin, with some *Alnus* carr-woodland present around its fringe, aligning with samples of similar age from the wetland basin and KB5 kettlehole (see below).

Kettlehole KB5 pollen

Palynological analysis from the KB5 sequence is included (Supporting Information Fig. S2), alongside its radiocarbon dates (Table S1), for comparison with the nearby Wetland Basin 1 (WB1b) Test Pit sequence. Summarized briefly, its basal units dated to the Windermere Interstadial show open woodland consisting of *Betula*, *Juniperus* and *Salix* with high counts of grasses and a small community of open-ground herbs very similar to that seen in the test pit. The succeeding Younger Dryas sediments show reduced arboreal pollen and an increase in grasses and sedges. Very high counts of microcharcoal are seen throughout both these Lateglacial contexts. The radiocarbon dating of the Lateglacial sediment unit (1022) produced a date of 15 280–15 010 cal a BP (SUERC-79306), whilst the immediately overlying lower boundary of the Windermere Interstadial sediment unit (1026) is dated to 13 310–13 210 cal a BP (SUERC-79305), the upper boundary to 12 970–12 750 cal a BP (SUERC-79304), and the overlying fibrous peat (1025) that completed the Windermere interstadial units is dated to 12 820–12 720 cal a BP (SUERC-79300). The beginning of the Holocene is marked by an appearance of small components of *Corylus*, *Pinus* and *Quercus*, though *Betula* remains the dominant woodland taxon, along with a continuing small community of herbs. Aquatic taxa are limited to small counts of *Myriophyllum* (<5%) and similar levels of *Pediastrum*, reflecting the presence of a small pond in the kettlehole at this time. In the upper sediment layers, dated to the Mid- to Late Holocene, mixed deciduous woodland expands to include *Tilia*, *Fraxinus* and *Ulmus*, and a large component of *Alnus* by 7560–7360 cal a BP. Ferns also increase, but grasses and aquatics decrease

dramatically in the uppermost samples, suggesting the increasing expansion of woodland in the local area and an almost complete terrestrialization of the kettlehole by the late Holocene at 3690–3480 cal BP (Bronze Age). The small amounts of cereal-type pollen seen in the upper layers all measured >40 µm and is not likely to be wild grass as the annulus diameter to grain diameter is around 1:3 (Joly *et al.* 2007). The Late Mesolithic through Neolithic timber platform built out into the pond was constructed mainly from *Quercus* at 7560–7360 cal a BP (SUERC-80722) with the latest timber of the platform, also made from *Quercus*, dated to 4420–4250 cal a BP (SUERC-80721). A substantial *Quercus* post was set within the Late Mesolithic platform cut down into a post socket within the underlying clay (1010) packed with small *Corylus* sticks around its edge to give it stability, with one of the short-lived *Corylus* packing sticks dated to 6750–6630 cal a BP (SUERC-80723).

Discussion

Environmental interpretation and wider context

Together with nearby Swale–Ure Lateglacial and Early Holocene records (Fig. 1B) from Snape Mires, Nosterfield (Innes *et al.* 2009; 2021) and Marfield (Bridgland *et al.* 2011), and other North Yorkshire sites such as Tadcaster (Bartley 1962) and Wykeham Quarry (Lincoln *et al.* 2017), the sequence from Killerby (Fig. 12) adds to a growing understanding of deglaciated environmental change in the region. The poorly drained basins and kettleholes seen at Killerby are present in many areas of the Leeming Moraine complex and probably formed during the early stages of deglaciation (Bridgland *et al.* 2011; Innes *et al.* 2009; 2021). The infilling of these ice-wastage features with water and the formation of ponds, palaeochannels and lakes during the Lateglacial is visible in the pollen and plant macrofossil data from Snape Mires (Bridgland *et al.* 2011), but is reflected particularly well at Killerby.

Windermere Interstadial

The lacustro-fluvial silts/clays at the base of the sequence are the upper horizons of a Glacial–Lateglacial water body that extended at least 3 m below the excavated sections of the test pit, as shown by coring, connected to other water bodies at the site through outflow channels (Parker *et al.* 2019). The analysed horizons of these clays probably date to the Windermere Interstadial due to their increased diversity of tree/shrub, forb, graminoid and aquatic taxa, a period dating from 13 310–13 210 to 12 820–12 720 cal a BP at the adjacent kettlehole KB5 (Supporting Information Table S1). The *Betula* and *Juniperus* identified in the pollen at these depths probably occupied nearby relatively drier areas such as the moraine ridges to the immediate east, west and south that encompass this small palaeolake, whereas *Salix* may have formed wetland in the wetland basin itself. The wide variety of forbs seen at these depths show many taxa typical of scrub tundra, such as *Dryas*, *Chrysosplenium* and *Armeria*. These were joined by classic open ground tall-herbs such as *Artemisia*, *Filipendula* and *Helianthemum* which are also seen at Nosterfield and Marfield (Innes *et al.* 2009), along with a variety of lakeside grasses and sedges, and wetland plants.

The local wetland and aquatic vegetation of the basin during this period, in particular taxa such as *Equisetum*, *Utricularia*, *Persicariae* and *Chrysosplenium*, which are not well represented in pollen assemblages in this region, have been found

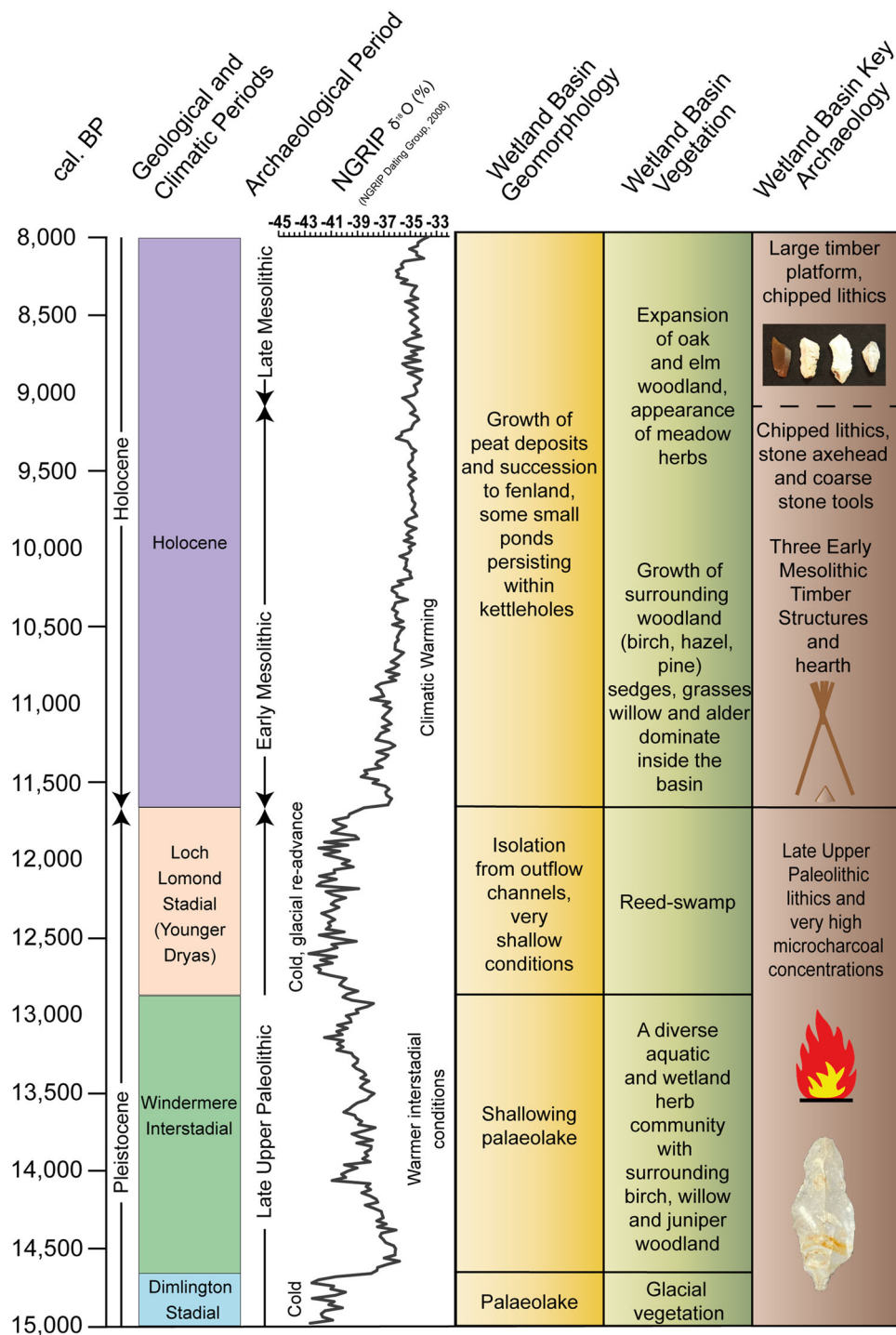


Figure 12. A timeline of climatic periods, NGRIP oxygen isotope $\delta^{18}\text{O}$ (‰), and the development of geomorphology, vegetation and archaeology in the Wetland Basin. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

to be present. Interestingly, very few aquatic taxa are seen in the pollen at these depths. It is possible that this disparity is due to *sedaDNA* more effectively identifying aquatic vegetation, such as *Stuckenia* and *Potamogeton* (Alsos *et al.* 2018; Kuzmina *et al.* 2018). It is also possible that the small size and/or shallow depth of the water body led to the low-pollen-producing aquatic species being swamped by a more regional pollen assemblage. All aquatic species identified could be found growing in standing or slow-moving water, with a minimum depth of 1 m suggested from the presence of the pondweeds and *Myriophyllum*. Above the clays, the samples from the marl and underlying gyttja show a similar assemblage to the lacustrine depths but with decreased forb diversity and a

large rise in *Betula* pollen. Together with a decrease in the aquatic and wetland plants seen in the *sedaDNA*, these levels represent shallowing of the lake and the succession to reed-swamp towards the end of the Interstadial.

Loch Lomond Stadial (Younger Dryas)

The peat overlying the marl is placed within the early stages of the Younger Dryas (generally dated to 12 900–11 700 cal a BP) from its date of 12 760–12 720 cal a BP, and a decrease of woodland, herbs and aquatic taxa is seen in both assemblages. However, there are particularly high numbers of pollen from Poaceae, and the DNA from the brownish-green peat shows a

greater representation of graminoids than any other depth, whilst trees and shrubs disappear almost entirely from the pollen and Poaceae reach their peak. This suggests continuing shallowing of the water body in Wetland Basin 1b and the final phases of terrestrialization. The overall dominance of grasses and sedges at Killerby is seen at all Lateglacial sites in the region (Bartley 1962; Walker *et al.* 1993; Bridgland *et al.* 2011; Lincoln *et al.* 2017; Innes *et al.* 2009, 2021; Young *et al.* 2021).

Early Holocene

In the overlying peats, which also overlie the Mesolithic tepees, the samples dated to the Early Holocene [between 10 490 and 10 240 cal a BP from peat layer WB1 (1918) and the test pit (1556)] initially show particularly high numbers of pollen from Poaceae. This aligns well with the DNA signal from the nearby tepee (timber structure 2, Fig. 10), which has a slightly older date of 11 080–10 720 cal a BP and is also dominated by grasses and sedges. However, a subsequent decrease in grasses and sedges then occurs alongside the development of mixed deciduous woodland and the expansion of marsh and shrub taxa, along with some ruderal herbs, reflecting a final succession to wetland and mire inside the wetland basin, and woodland on drier ground.

The limited Holocene pollen assemblage shows the clear dominance of *Betula* as the dominant component of woodland, with stands of *Ulmus*, *Pinus*, *Quercus* and *Corylus* by the final phases of the sequence around 9000 BP. All of these tree species are present in the timbers associated with the Early Mesolithic tepees and hearth. A similar hydroseral succession and development of woodland can be seen in North Yorkshire in the Early Holocene at Lake Flixton, which enters its final phases slightly later around 8000 cal a BP (Taylor 2019). The observed woodland composition is also similar to those from Snape Mires (Bridgland *et al.* 2011), Nosterfield and Star Carr (Day 1996; Innes *et al.* 2021), though the *sedDNA* shows that the immediate area of the Wetland Basin continued to be relatively open and instead dominated by *Salix*, grasses, sedges and wetland herbs, together with *Alnus*, as indicated by the timbers used for the tepees—which combined suggest a mosaic of vegetation on the valley floor with wetland species around the pond/lake fringe.

Summary

Overall, the combined plant assemblages show the development of rich pondside vegetational communities around the wetland basins and kettleholes in the Windermere Interstadial period of the Lateglacial. Marl formation occurred during the Younger Dryas (probably due to high calcium bicarbonate from weathering before buffering by soil formation) and the wetland basins at Killerby became isolated from wider fluvial activity and drainage by the beginning of the Holocene. In the early Holocene, Wetland Basin 1b underwent succession to reed-beds and sedge-fenland, with deciduous woodland nearby. A final transition to mire and heathland from reed-swamp may be indicated by decreases in graminoids and aquatics and increases in wetland mosses and heaths in the uppermost samples. *Alnus* was locally present by the Early Holocene, as evidenced by the timbers and DNA from the tepee structures and very small amounts in the pollen, supporting previous evidence for the early appearance of the species in the region (Young *et al.* 2021). However, given the limited amounts of non-*Betula* tree pollen, it is likely that the test pit sequence ceases before the mid-Holocene, where

a more varied deciduous woodland is seen from the pollen of KB5.

Using *sedDNA* to reveal the Lateglacial environment

The climatic fluctuations of the Lateglacial and their effects on vegetation have conventionally been explored using palynological analysis in this region (Bridgland *et al.* 2011; Innes *et al.* 2009; 2021). However, in the largely treeless environment of the Lateglacial, some authors have suggested that other environmental proxies are needed to create a more complete picture of sub-regional vegetation change (Birks and Birks 2000). This is because Lateglacial pollen assemblages can be dominated by well-dispersed, high-pollen-producing indicator taxa such as *Betula* and *Artemisia* and have no comparable modern analogues (Birks 2003). As has been found on north Norway sites, we see *Artemisia* (type) in the pollen but not in the *sedDNA* (Clarke *et al.* 2019). Also, modern pollen samples from northern Fennoscandia and Svalbard show *Artemisia*, although it does not grow in the region, suggesting long-distance dispersal of this pollen taxon (Hättestrand *et al.* 2008). The addition of *sedDNA* provides greater detail of the locally growing flora and the numerous (predominantly herbaceous) species that are not high pollen producers, including easier distinction between separate sedge and grass species, with the five taxa identified at Killerby only able to be described to the family level in the pollen assemblage. Moreover, the *sedDNA* reveals more of the localized aquatic taxa that thrived in the short-lived Lateglacial lakes and ponds within the wetland basins and ice-wastage features of the site.

There were some interesting contrasts between the two environmental proxies, the most notable being that trees and shrubs were not high in the *sedDNA*, but more widely represented within the pollen. The differences between the pollen and DNA assemblages may largely be explained by the sources of plant material that are analysed for each method. Sedimentary DNA has been shown to represent a very localized catchment-based picture of plant diversity in lacustrine contexts (Sjögren *et al.* 2017; Parducci *et al.* 2017; Alsos *et al.* 2018), suggesting *sedDNA* is deposited locally, similar to the deposition and taphonomy of macrofossils. Pollen, which has been shown not to contribute much to *sedDNA* records due to its low biomass and tough sporopollenin coating, requires a different extraction method (Alsos *et al.* 2018). In terrestrial contexts, such as the soils and peats seen in the upper half of the Killerby Test Pit sequence and at timber structure 2, the localized nature of *sedDNA* may be more pronounced (Edwards *et al.* 2018), as there is no wider catchment of plant material as occurs in lacustrine sequences. Therefore, if there is limited influx of outside DNA sources, then contexts such as peat may be swamped by locally growing plants. This may explain the lack of woodland species above the fluvio-lacustrine contexts (with the exception of the data from the timber structure) in the *sedDNA* assemblage. Pollen will represent a greater extra-local to regional diversity from any given sample, due to long-distance transport from many pollen-producing taxa, so the two environmental proxies complement each other well, with pollen representing some species not in the immediate area of the Wetland Basin and *sedDNA* providing a highly localized signal.

Hunter-gatherer exploitation

Archaeological excavations at Killerby Quarry have been on a significant scale and so far c.14 ha has been stripped of topsoil

and investigated, although further works will continue through the life of this 200-ha quarry. In the Lateglacial, the high microcharcoal concentrations in both the KB5 and DNA Test Pit sequence from relatively small source areas suggest human activity, as was concluded at Star Carr (Day 1996) and Snape Mires (Bridgland *et al.* 2011), though natural fires cannot be ruled out. For KB5, this was interpreted as humans undertaking burning activity around the edge of the kettlehole (Hunter and Waddington 2018) where Lateglacial–Early Holocene flint tools have been found immediately around it during fieldwalking (Waddington *et al.* 2009). A similar scenario is equally likely for Wetland Basin 1b where a later Mesolithic microlith was even found in the higher level of middle Mesolithic peat within the *seada*DNA test pit. It is certainly known that Late Upper Palaeolithic communities were present in North Yorkshire (Laurie 2003) and the Yorkshire Dales (Jacobi *et al.*, 2011; Lord 2013) at this time. The lithics recovered from Wetland Basin 2 include a slightly unusual, tanged piece (Fig. 4) with Ahrensburgian affinities, a class of artefact associated with the Lateglacial (Late Upper Palaeolithic) period. Given that Britain was connected to Continental Europe at this time, the presence of an Ahrensburgian-related tanged point (Fig. 4) complements similar assemblages identified to the south on the Humber margins at Risby Warren, at Tayfen Road, Suffolk, and Doniford Cliff, Somerset (Barton 2009), but also from sites to the north at Low Hauxley (Waddington and Bonsall 2016) and in Scotland at Shieldaig (Ballin and Saville 2003), Howburn Farm (Ballin *et al.* 2010) and Rubha Port (Mithen *et al.* 2015), as well as from the main cluster of sites across the north European Plain from Belgium to western Poland and north into southern Denmark (Cziesla 1992; Baales 1996; Weber 2011). The evidence from Killerby adds to the growing evidence for human occupation at least towards the end of the Younger Dryas, if not possibly during it, although the latter remains uncertain until more securely stratified deposits are dated. Within the chipped stone fieldwalking, assemblage pieces that could be ascribed to the Lateglacial–Early Holocene (ie. Late Upper Palaeolithic–Early Mesolithic), but not at any greater chronological resolution, were found on the ridges immediately surrounding Wetland Basin 1 to the south, east and west, as well as around nearby kettlehole KB5.

The combination of settlement sites adjacent to kettleholes, as well as the Lateglacial–Early Holocene landscape setting, is directly analogous to the southern Jutland site at Slotseng where multiphase Lateglacial sediments containing human-modified reindeer bones, together with an adjacent settlement, have been investigated (e.g. Holm 1993; Mortensen *et al.* 2011). At both Killerby and Slotseng the benefit of targeting deglaciation features such as wetland basins, kettleholes and the immediately surrounding higher morainic ridges, for geoarchaeological, palaeoenvironmental and archaeological investigation has been demonstrated and underlines the possibilities furthering understanding of Lateglacial landscapes and early human settlement.

The evidence of timber-framed tepee, or Lavvu, structures and flint scatters in and around both Wetland Basin 1 and KB5 indicates that Early Mesolithic communities were occupying the marshland, as well as the ridges, and the abandoned fire inside the tepee of timber structure 2 included the use of *Alnus*, *Betula*, *Pinus* and *Salix* as fuel. The environmental data indicate large elements of heath and marsh during these periods, suggesting that this anthropogenic activity may have led to the creation of more open areas around the wetland basins. Timber structure 2 dates to the same period as the earliest phase of lakeside settlement at Star Carr (Milner *et al.* 2018) and is further evidence of Early Mesolithic adaptation to,

and exploitation of, marsh/pondside areas, as is seen from its *seada*DNA assemblage of mostly wetland sedges, grasses, shrubs and ferns. During the Interstadial the kettleholes and wetland basins would have been exploited for their rich pondside vegetation community, which supported many sedges and wetland herbs suitable for consumption, burning or construction. For example, all parts of *Phragmites australis* are edible, and the stems can be used for basket-making or roofing. Many others contain edible parts (*Armeria*, *Cardamine*, *Polygonum*) valuable to local hunter-gatherer communities (Zvelebil 1994). A range of animals (e.g. deer, wild boar) and birds (water-fowl including migratory species) may have also come for water at the many smaller ponds and channels, which were more accessible than the nearby River Swale.

Interestingly, a notched sandstone cobble with sooting on its notched surface was retrieved from the Mesolithic palaeosol at Wetland Basin 2, c. 150 m east of Wetland Basin 1, which is thought could be the remnants of a bow-drill cordage (fire-starting) kit (Cockcroft and Waddington 2021). The short-stay Lavvu tented settlements for groups of up to around six people (their estimated basal diameter is around 6 m; Cockcroft and Waddington 2021) indicates small mobile groups visiting this riparian landscape, probably during the late spring to early summer, given the earlywood harvested to make these camps (see Bamforth in Cockcroft and Waddington 2021).

The substantial Late Mesolithic timber platform in KB5 provides a very rare example of a platform extending out into a pond which had structural features, including upright timber posts, associated with it. From the presence of cattle/aurochs teeth, together with a variety of flint processing tools and a coarse stone tool probably used as a skin softener, within the lower layers of the platform, the most likely use of this small water-filled kettlehole is considered to be as a tanning pit with the associated platform for drying, stretching and softening of leather (Hunter and Waddington 2018).

The geographical location of this site is also of note in understanding why the human exploitation of this landscape took place here, and at this time. During the Lateglacial and Early Holocene the palaeogeography of the British Isles was very different to that of today with Britain forming a peninsula off north-west Europe connected via East Anglia to the Low Countries (Shennan *et al.* 2000; Bradley *et al.* 2011; Sturt *et al.* 2013). Travelling south along the River Swale, the early hunter-gatherer communities would have been able to access Glacial Lake Humber rapidly and directly, which flowed further south and east before debouching into the North Sea basin at the Outer Silver pit estuary flanked by what is now East Yorkshire to the west, and Doggerland to its east. South of Killerby a short overland journey from the Swale would give access to Glacial Lake Pickering and its vestige in the Holocene, palaeolake Flixton, on the immediate southern flank of the North York Moors, which in turn gave access to the North Sea Basin coastal margin around Filey where the palaeolakes were blocked by the Flamborough Head Moraine (Evans *et al.* 2017). At the same time, there is good access north through the Vale of Mowbray to the Tees valley and west to the Pennine massif where seasonally migrating animals such as deer could be easily tracked and hunted, and east along the Tees to the rich estuarine location of what is today Teeside. The area of Killerby lies at a constriction in the Vale of Mowbray, between the uplands of the North York Moors to the east and the Pennines to the west, and therefore lies on the convergence of key arterial communication routes. These routes would have been of even greater significance than today given the different palaeogeography, which enabled direct access north–south through the lowland along the

course of the Swale and Lake Humber, as well as the east–west Tees valley to the north and proglacial Lakes Pickering and Flixton to the south.

Conclusions

In a region characterized by complex glacial and periglacial climatic conditions, we have demonstrated vegetation change using the first application of *sedaDNA* to a Lateglacial to Early Holocene site in the UK. The combined environmental and sedimentological analyses of Killerby Quarry Wetland Basin 1 have provided detailed insight into deglaciated vegetation changes in the Swale–Ure region. In particular, the Kettlehole and Wetland Basin ice-wastage features show succession from Lateglacial lakes and ponds into sedge-fen reed beds and wetlands by the Early Holocene. This succession is represented particularly well by the *sedaDNA*, which gives a more localized picture of the aquatic and wetland vegetation in the wetland basin and its change over time. When combined with pollen data, which can represent regional taxa not present in the wetland basin, and the identifiable and dated timbers from the Lavvu structures, the three methods can complement each other in a period where other forms of environmental evidence are sparse. The environmental data help explain why there were prolonged periods of archaeological activity on site, as the small ponds/lakes at Killerby provided water bodies where wildfowl and other animals and plants could be taken. Together with other recent *sedaDNA*-based research (Brown *et al.* 2021; 2022; Hudson *et al.* 2022), this study shows that *sedaDNA* can be applied effectively to wetland archaeological sites to create a more complete and reliable picture of the vegetation sequence and the use of the wetlands by human groups, at a time when very little is known about these early human groups in Britain, and especially in the north and on ‘open’ sites away from the caves of the limestone areas. This study shows *sedaDNA* to be a powerful and informative technique that can complement and extend other analyses, particularly pollen analysis and plant macrofossil analysis, and is potentially applicable to a wide range of Quaternary studies.

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Competing interests—The authors have declared that no competing interests exist.

Data availability statement

The data that supports the findings of this study are available in the supplementary material of this article

Author contributions—**Samuel M Hudson:** Writing - original draft; Writing - review & editing; Visualization; Formal analysis; Investigation; Project administration; Validation. **Clive Waddington:** Investigation; Writing - review & editing; Conceptualization; Resources; Funding acquisition. **Ben Pears:** Investigation; Visualization; Writing - review & editing; Methodology; Formal analysis. **Natalie Ellis:** Investigation; Formal analysis. **Luke Parker:** Investigation; Formal analysis. **Derek Hamilton:** Investigation; Visualization; Formal analysis. **Inger Greve Alsos:** Supervision; Writing - review & editing; Investigation; Resources; Software; Data curation; Funding acquisition; Methodology; Validation. **Paul Hughes:** Writing - review & editing; Supervision. **Antony Brown:** Conceptualization; Resources; Supervision; Methodology; Project administration; Data curation; Investigation; Funding acquisition; Writing - review & editing.

Supporting information

Additional supporting information can be found in the online version of this article.

Dataset S1. Metabarcoding sequences identified in the *sedaDNA* data and controls in reads and PCR replicates.

Dataset S2. The full pollen assemblage from Wetland Basin 1b and from the KB5 kettlehole.

Dataset S3. The full sedimentological datasets, including LOI, pXRF, magnetic susceptibility and pOSL data.

Figure S1. KB5 kettlehole stratigraphy.

Figure S2. KB5 pollen assemblage.

Figure S3. An Early Mesolithic patinated flaked flint axehead found in the Mesolithic palaeosol in Wetland Basin 2.

Figure S4. An Early Mesolithic broad blade microlith found on the edge of Wetland Basin 2.

Figure S5. Two quartz hammerstones found in Wetland Basin 2 Mesolithic palaeosol.

Figure S6. Wetland Basin 1b section plan and KB6 test pit sequence with radiocarbon date locations (those in red disregarded).

Figure S7. All pXRF data (ppm) from the half pipe core graphed together with corresponding stratigraphy and radiocarbon dates.

Abbreviations. *sedaDNA*, sedimentary ancient DNA; CABI, Centre for Agriculture and Bioscience International; pOSL, portable optically stimulated luminescence; pXRF, portable X-ray fluorescence.

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