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Holocene floristic diversity and richness in northeast Norway revealed by sedimentary ancient DNA (*sed*aDNA) and pollen

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We present a Holocene record of floristic diversity and environmental change for the central Varanger Peninsula, Finnmark, based on ancient DNA extracted from the sediments of a small lake (*sed*aDNA). The record covers the period *c*. 10 700 to 3300 cal. a BP and is complemented by pollen data. Measures of species richness, sample evenness and beta diversity were calculated based on *sed*aDNA sampling intervals and 1000-year time windows. We identified 101 vascular plant and 17 bryophyte taxa, a high proportion (86%) of which are still growing within the region today. The high species richness (>60 taxa) observed in the Early Holocene, including representatives from all important plant functional groups, shows that modern shrub-tundra communities, and much of their species complement, were in place as early as *c*. 10 700 cal. a BP. We infer that postglacial colonization of the area occurred prior to the full Holocene, during the Pleistocene-Holocene transition, Younger Dryas stadial or earlier. Abundant DNA of the extra-limital aquatic plant *Callitriche hermaphroditica* suggests it expanded its range northward between *c*. 10 200 and 9600 cal. a BP, when summers were warmer than present. High values of *Pinus* DNA occur throughout the record, but we cannot say with certainty if they represent prior local presence; however, pollen influx values >500 grains cm^{-2} a^{-1} between *c*. 8000 and 7300 cal. a BP strongly suggest the presence of pine woodland during this period. As the site lies beyond the modern tree limit of pine, it is likely that this expansion also reflects a response to warmer Early Holocene summers.

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In the mid- to high-latitudes, the repeated waxing and waning of continental ice sheets throughout the Quaternary has regulated habitat availability for plants (Hultén 1937; Abbott & Brochmann 2003). By around 13 000–11 000 a BP, the Fennoscandian Ice Sheet had retreated from the northeasternmost peninsulas of Finnmark, Norway (Sollid *et al.* 1973; Stokes *et al.* 2014; Hughes *et al.* 2016; Stroeven *et al.* 2016), and newly deglaciated land became accessible for plant colonization and vegetation development (Prentice 1981, 1982). Today, these peninsulas harbour the ecotone from boreal forest to tundra. At and near their northern limit, tree species are particularly sensitive to climate changes; climate variation may cause shifts in tree species ranges that may in turn generate changes in vegetation structure and habitat (Hyvärinen 1976; Barnekow 1999; Bjune *et al.* 2004; Jensen & Vorren 2008). The deglacial history and proximity to the tree-line suggest that records from the region can potentially address key ecological questions: how floristic richness and/or composition is affected by tree-line dynamics and/or Holocene climate variation; whether taxa show discernible migration lags (and thus locally variable postglacial successional sequences); and how today's dominant plant communities assembled over the Holocene.

The understanding of tree-line fluctuations has inspired palynological studies of vegetation history for many years (Hyvärinen 1975; Seppä 1996; Allen *et al.* 2007). Pollen percentage and influx values have been used to track tree-line fluctuations across northeast Finnmark in response to Holocene climate changes (Hyvärinen 1975; Hicks 1994; Seppä 1996; Hicks & Hyvärinen 1999; Høeg 2000; Huntley *et al.* 2013). During the regional Holocene Thermal Maximum (HTM; 8000–6000 cal. a BP; Seppä *et al.* 2009; Huntley *et al.* 2013), the ecotonal boundaries between *Pinus* and *Betula* forests and *Betula* forest with low shrub-tundra had more northerly positions (Høeg 2000). In contrast to tree-line dynamics, less is known about the development and composition of the shrub and herb communities of northern Fennoscandia and their response to Holocene climate changes. Tundra pollen records are often interpreted in terms of broad-scale community dynamics rather than local compositional changes, due to features such as low accumulation rates and the over-representation of woody anemophilous taxa that mute the signal of entomophilous forbs in many records (Lamb & Edwards 1998; Gajewski 2015).

The Lateglacial and Holocene vegetation history of Finnmark has been documented in several pollen and plant

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macrofossil records since the 1970s (e.g. Hyvärinen 1975; Prentice 1981, 1982; Høeg 2000; Allen *et al.* 2007; Birks *et al.* 2012; Sjögren & Damm in press), reflecting interest in understanding events linked to the early deglaciation of the region (Sollid *et al.* 1973; Stokes *et al.* 2014; Hughes *et al.* 2016; Stroeven *et al.* 2016). The initial postglacial landscape supported sparse, open, herbaceous vegetation with some shrubs (Hyvärinen 1975; Prentice 1981, 1982; Seppä 1996). The oldest pollen record in northeast Finnmark is that of Østervatnet, southern Varanger Peninsula, which records the Older Dryas (*c.* 13 900–13 600 cal. a BP) and Younger Dryas (*c.* 13 500–11 500 cal. a BP) climate oscillations, with *Artemisia* replacing *Salix* and Poaceae in the cold stages (Prentice 1981). The end of the Younger Dryas chronozone is distinguished by a rise in *Oxyria*/*Rumex*, *Salix*, Poaceae and Cyperaceae with species-rich meadows colonized by a succession of shrub and tree species in the Holocene (e.g. *Betula*, *Pinus*). More information on the rate of community assemblage and local variation in community development through time will help inform our understanding of the resilience and longevity of the current dominant communities in this area.

Pollen data have been used to reconstruct past changes in floristic diversity and richness, including studies in Scandinavia (Odgaard 1999; Berglund *et al.* 2008a, b; Fredh *et al.* 2012; Reitlau *et al.* 2015). Records from Scandinavia indicate a rapid increase in species richness from the Lateglacial to the Early Holocene (*c.* 12 000–8000 cal. a BP), while spatially and temporally inconsistent trends characterize the Middle to Late Holocene (*c.* 8200 cal. a BP – present; Seppä 1998; Berglund *et al.* 2008a, b; Birks & Birks 2008; Felde *et al.* 2017). These later Holocene trends have been attributed to climate fluctuations, the first appearance of trees at a locality, and/or human impact. A significant ($p < 0.001$) negative relationship was identified between *Pinus* pollen influx and species richness at the boreal site Lake Rautuselkä, northern Finland, reflecting the importance of vegetation density on floristic richness (Seppä 1998). A significant ($p < 0.05$) negative correlation between *Pinus* and *Betula* pollen influx and species richness was also identified at the tundra site Lake Hopseidet on the Nordkinn Peninsula, northeast Norway, which was not reached by northward expansion of the *Pinus* tree-line during the Holocene. High influx of wind-pollinated taxa in the tundra site probably reduced the statistical probability of other, less frequent insect-pollinated herbaceous types being counted (Birks & Line 1992; Seppä 1998). Records from central Scandinavia show that species richness has remained rather stable, with no long-term trends observed over the Holocene (Giesecke *et al.* 2012). Nevertheless, biases resulting from non-linear relationships between pollen and vegetation representation may confound richness estimates derived from pollen (Prentice 1985; Sugita 1994; Odgaard 2001). Furthermore, the relationship between species richness derived from pollen data (palynological richness) and the observed floristic richness in the landscape remains poorly understood (Meltsov *et al.* 2011; Goring *et al.* 2013).

Analysis of sedimentary ancient DNA (*sed*aDNA) has recently emerged as a promising proxy for reconstructing past floral diversity, augmenting information gained from pollen and macrofossil analyses (Jørgensen *et al.* 2012; Epp *et al.* 2015; Alsos *et al.* 2016; Pedersen *et al.* 2016; Parducci *et al.* 2017; Zimmerman *et al.* 2017). When rigorously applied, the analysis of *sed*aDNA from lake sediments can detect more species per sample than other palaeoecological methods (Alsos *et al.* 2016). It also permits the detection of some key plant taxa that are poorly resolved taxonomically by pollen or plant macrofossil analysis alone (Parducci *et al.* 2013; Sjögren *et al.* 2017; Edwards *et al.* in press). Recent investigation of the representation of contemporary vegetation in the DNA signal of superficial sediments in small lakes with limited inflowing streams from northern Norway revealed that 73 and 12% of the taxa detected in the DNA were recorded in vegetation surveys within 2 and 50 m of the lake shore, respectively (Alsos *et al.* 2018). Thus, analysis of plant *sed*aDNA from small lakes with limited inflowing streams may give a more local signal of vegetation change and floristic richness than records derived from pollen, as wind-dispersed grains tend to be dispersed over long distances, particularly at the northern limit of trees (Rousseau *et al.* 2006).

This study represents the first palaeoecological exploration of Arctic vegetation dynamics in Finnmark using a *sed*aDNA record, in this case from sediments of a small lake on the Varanger Peninsula, northeast Finnmark. We use metabarcoding techniques (Taberlet *et al.* 2012) to develop the *sed*aDNA record, together with X-ray fluorescence (XRF) to determine geochemical element concentrations over time, sedimentological data and pollen analysis. We then compare the results with published pollen records. Finally, we use the *sed*aDNA data to reconstruct Holocene trends in species richness using rarefaction and measures of beta diversity and evenness for all samples and for 1000-year windows.

Study site

The lake (latitude 70°19′6.85348″ N, longitude 30°1′43.83653″ E; Fig. 1) is unnamed on the 1:50 000 Norwegian Topographic Map (Norgeskart; https://www.norgeskart.no). We refer to it here informally as 'Uhca Rohči', or UR, the Sami name for an adjacent river feature. UR is a small lake (<1 ha) in a depression situated at 138 m above sea level (a.s.l.) within the river valley of Komagdalen on the Varanger Peninsula, northeast Finnmark, Norway. The peninsula is a plateau lying between 200 and 600 m a.s.l. with low relief: ridges are formed of Cambrian quartzites and sandstones, while valleys are eroded into shales and mudstones (Siedlecka & Roberts 1992). After Pliocene uplift, the area was affected by sea-level change and subject

to glacial erosion (Fjellanger & Sørbel 2007). UR Lake lies in the middle section of the glaciated southeast-draining Komagdalen valley. As shown in Fig. 1D, the lake vicinity is associated with probable subglacial scour features on the former valley floor, which is now ~3 m above the present river. The valley lies between the Gaissattrinnet and Hovedtrinnet (Younger Dryas) moraines to the southwest and the older Ytre Porsangertrinnet and Korsnestrinnet moraines to the north and east (ice advance to NE, retreat to SW; Sollid *et al.* 1973). A reconstruction of the lower section of the Komagdalen valley by Olsen *et al.* (1996) suggests that the middle valley lies just north (outside) of an ice margin dated to 17 000 cal. a BP as well as a more southerly ice margin associated with the Vardø moraine stage (13 500 a BP) as mapped by Tolgensbakk & Sollid (1981). Cosmogenic dating at the head of Varangerfjorden and Tanafjorden suggests a local retreat age of *c.* 15 400–14 200 cal. a BP, and it is certain that the peninsula was free of glacial ice by 13 000–12 000 cal. a BP (Stokes *et al.* 2014; Stroeven *et al.* 2016). UR Lake lies approximately 60 m above the main (Younger Dryas) postglacial shoreline (75–85 m a.s.l.), which is reflected by a markedly steeper valley floor reach at approximately 13 km downstream (Fig. 1E; Fletcher *et al.* 1993). It is likely that the site received fluvial input from all of the upstream Komagdalen catchment, at least prior to downcutting associated with postglacial isostatic uplift in the later Holocene, and this is important in the interpretation of the *sed*aDNA data.

The present-day climate of the Varanger Peninsula is characterized as sub-Arctic (<10 °C arctic isotherm in July), with annual precipitation between 500 and 800 mm. It is situated within the meeting zone of the westerlies and the sub-polar low pressure system (with polar easterlies) and thus has highly variable weather (Hanssen-Bauer & Tveito 2014). Large local heterogeneity exists due largely to the topography, and summer temperature may vary from 6–12 °C, with corresponding differences in local vegetation (Karlsen *et al.* 2005). Present-day tundra vegetation of the Varanger Peninsula is classified as erect shrub tundra (Virtanen *et al.* 1999; Walker *et al.* 2005), and is dominated by dwarf shrubs, such as *Empetrum nigrum* subsp. *hermaphroditum* and *Betula nana.* Species-rich meadows occur along the wide riparian plains of the Komagelva River where tall shrubs such as *Salix lanata*, *S. hastata* and *S. glauca* form a spatially and temporally diverse vegetation mosaic with mesic forbs such as *Bistorta vivipara*, *Thalictrum alpinum* and *Viola biflora*, and graminoids such as *Avenella flexuosa*, *Deschampsia cespitosa* and *Eriophorum angustifolium* (Ravolainen *et al.* 2013; Bråthen *et al.* 2017). The headwaters of the Komagelva River originate from the north to northwest of the main Komagelva channel, which flows eastwards to Varangerfjord (Fig. 1B). The entire watershed lies outside of the present-day *Pinus* limit (Fig. 1B). UR Lake is one of several small lakes surrounded by the species-rich riparian meadows of the Komagdalen valley, which is one of the principal sites for the Climate Ecological Observatory for Arctic Tundra (Henden *et al.* 2011; Ravolainen *et al.* 2011, 2013; COAT 2018).

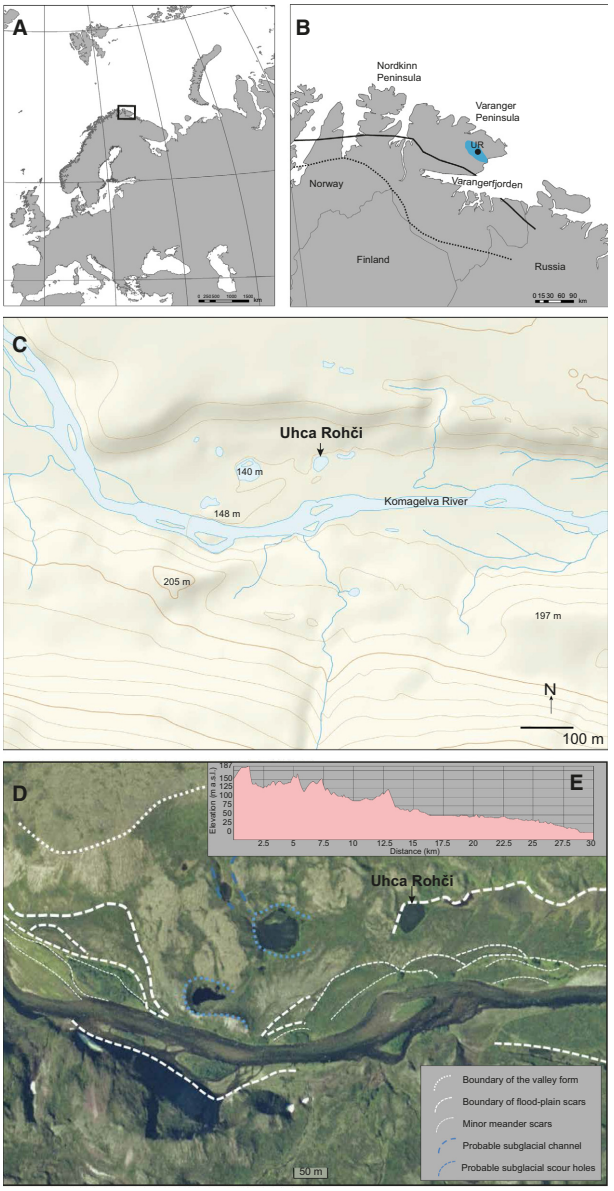

Fig. 1. Location of Uhca Rohči Lake (unofficial name) on the Varanger Peninsula, northeast Finnmark, Norway. A. Map highlighting the location of Finnmark in northeastern-most Norway. B. Varanger Peninsula with watershed of Komagelva River indicated in green. Dashed line indicates the *Pinus* forest limit according to Heikkinen (2005) and the solid black line indicates the tree limit of *Pinus* according to Hustich (1983). Location of Uhca Rohči Lake is indicated by a black circle. C. Map detailing the position of Uhca Rohči Lake within the Komagelva River (Komagdalen) valley (norgeskart.no). D. Geomorphological map created from aerial photography and inset E. valley floor height profile downstream of Uhca Rohči Lake created using Google Earth 2017.

Early Holocene climate in northern Fennoscandia was affected by summer insolation that was higher than present (Berger 1978; Berger & Loutre 1991). Quantitative summer temperature estimates based on aquatic plant macrofossils

suggest an early onset of the HTM, with temperatures ~2 °C warmer than pollen-based estimates between 11 700–7500 cal. a BP (Väliranta *et al.* 2015). However, pollen-based summer temperature reconstructions indicate July temperatures of +1.5±0.5 °C above modern (1961–1990) values in northern Fennoscandia during the regional HTM identified at *c.* 8000–6000 cal. a BP (Møller & Holmeslet 2002; Jensen & Vorren 2008; Seppä *et al.* 2009; Sejrup *et al.* 2016). Northeast Finnmark was characterized by warmer summer temperatures and higher precipitation (Allen *et al.* 2007). Warm conditions were interrupted by a short cold spell at *c.* 8200 cal. a BP (Seppä *et al.* 2009).

Material and methods

Core retrieval and subsampling

A 10-cm-diameter and 2.5-m-long lake sediment core (UR-1) was retrieved in February 2016 from the winter ice surface using a modified Nesje piston-corer (Nesje 1992) with a 4-m-long continuous section of acrylonitrile-butadiene-styrene (ABS) pipe. Total lake depth including winter ice thickness was 2 m, as measured by a single-beam echo-sounder (Echotest II Plastimo) and tape measure. Coring and retrieval of sediments started at 2 m, with the assumption, based on the echo-sounder data, that the top of the core sequence would include surface or near-surface sediments. After retrieval of the sediments, the pipe was cut into 1-m sections and sealed immediately to minimize the risk of contamination by airborne or other modern environmental DNA. The core sections were stored in a shed (2–6 °C) to prevent freezing before transport and stored at 4 °C in the cold room at the Tromsø University Museum (TMU), Norway. Core sections were opened by longitudinal splitting. One half was used for subsampling, and the other half kept for archival purposes. Core UR-1 was subsampled at 1-cm resolution within a dedicated ancient DNA clean-room facility at TMU using sterile tools, a full bodysuit, facemask, and gloves. Following the protocol described by Parducci *et al.* (2017), the outer 10 mm of sediment was avoided or discarded and an ~20-g subsample was retrieved from inside the freshly exposed centre only.

An additional short 50-cm-long and 7-cm-diameter core (UR-2), which included a clear sediment-water interface, was retrieved using a UWITEC gravity corer (UWITEC Corp., Austria) lowered from the surface of the lake ice. Subsampling of core UR-2 was not performed in the clean-room at TMU, as this core was only used for pollen analysis and age-depth model determination (described below).

Lithological and elemental analyses

Subsamples (2 cm^3) were taken for bulk density and loss-on-ignition (LOI) analyses at 3-cm intervals using a volumetric sampler. Samples were weighed in crucibles and dried overnight at 100 °C before dry weight and bulk density were determined (Chambers *et al.* 2011). Samples were then ignited at 550 °C for 2 h, placed in a desiccator to cool to room temperature and reweighed. Total LOI was calculated as the percentage loss of dry weight after ignition (Heiri *et al.* 2001). Magnetic susceptibility and XRF analyses were performed on the archival core halves at the Department of Geosciences, UiT - Arctic University of Norway. Magnetic susceptibility was measured at 1-cm intervals using a Bartington point sensor on the Geotek Ltd. Multi-Sensor Core Logger using a 10-s exposure time. Quantitative element geochemical measurements were performed with an Avaatech XRF core scanner. XRF scanning was performed at 1-cm resolution with the following settings: 10 kV, 1000 μA, 10 s exposure time and no filter. To minimize closed sum effects, we normalized the raw peak area data against Ti, as this element is considered a reliable indicator of allochthonous catchment inputs (Croudace & Rothwell 2015).

Radiocarbon dating and age-depth model construction

Seven samples of terrestrial plant macrofossils from Nesje core UR-1 and an additional two samples from UWITEC core UR-2 were radiocarbon (^{14}C) dated with accelerator mass spectrometry (AMS) at the Poznań Radiocarbon Laboratory (Goslar *et al.* 2004). All radiocarbon ages were calibrated according to the terrestrial IntCal13 curve (Reimer *et al.* 2013), and an age-depth relationship was established using the Bayesian framework calibration software 'Bacon' (v. 2.2; Blaauw & Christen 2011), which was implemented in R v. 3.2.4 (R Core Team 2017).

Pollen analysis

In total, 16 pollen samples were analysed from core UR-1 and an additional two samples from UR-2. Subsamples of 1.5 cm^3 were prepared using standard methods (acid-base-acid-acetolysis; Fægri & Iversen 1989) and were mounted in glycerol. Two *Lycopodium* spore tablets (Batch no. 3862; n = 9666) were added to each sample to calibrate pollen concentration estimation. At least 300 pollen grains of terrestrial taxa were identified per sample using taxonomic keys (Fægri & Iversen 1989) and type material held in the Palaeoecology Laboratory at the University of Southampton. Results are presented as pollen percentages, with trees, shrubs, herbs and graminoids based on the sum of total terrestrial pollen ($\sum P$), and percentages for spores and aquatics based on $\sum P + \sum$spores and $\sum P + \sum$aquatics, respectively.

DNA extraction, amplification, library preparation, and sequencing

DNA extraction, PCR amplification, PCR product pooling and purification, and sequencing follow the protocols of Alsos *et al.* (2016) unless otherwise stated. Within the TMU clean-room facility, DNA was extracted from 80

sediment subsamples and nine negative extraction controls, which consisted of no sediment and were used to monitor for contamination. Aliquots of DNA extracts were then shipped to the Laboratoire d'ÉCologie Alpine (LECA, University Grenoble Alpes, France) for metabarcoding. Each DNA extract and negative extraction control was independently amplified using uniquely tagged generic primers that amplify the *trn*L P6 loop of the plant chloroplast genome (Taberlet *et al.* 2007), a widely applied marker for the identification of vascular plants in environmental samples. Each sample and negative control underwent eight PCR replicates to increase confidence in the results and improve the chance of detecting taxa with small quantities of template in the DNA extracts. We also ran 13 negative PCR controls, consisting of no DNA template. Pooled and cleaned PCR products were then converted to two Illumina-compatible amplicon libraries using the single-indexed, PCR-free MetaFast method (FASTERIS SA, Switzerland). These libraries were then sequenced on the Illumina HiSeq-2500 platform for 2× 125 cycles at FASTERIS.

Sequence analysis and taxonomic assignments

Next-generation sequence data were filtered using the OBITools software package (Boyer *et al.* 2016; http://metabarcoding.org/obitools/doc/index.html) following the protocol and criteria defined by Alsos *et al.* (2016). Taxonomic assignments were performed using the *ecotag* program (Boyer *et al.* 2016) by matching sequences against a local taxonomic reference library comprised of 815 arctic and 835 boreal vascular plant taxa, and 455 bryophytes (Sønstebo *et al.* 2010; Willerslev *et al.* 2014; Soininen *et al.* 2015). In order to minimize any erroneous taxonomic assignments, only taxa with a 100% match to a reference sequence were retained. We further considered a taxon to be undetected in a PCR replicate if it was represented by fewer than 10 reads. Moreover, sequences that displayed higher average reads in negative extraction or PCR controls than lake sediment samples were also removed. Identified taxa were compared with the local flora from Komagdalen (Ravolainen *et al.* 2013), Species Map Service 1.6 (https://artskart1.artsdatabanken.no/Default.aspx), the Norwegian Flora (Elven 2005) and the circumpolar flora (Hultén & Fries 1986). Sequences assigned to taxa not present in northern Scandinavia today were checked against the NCBI BLAST database for multiple or alternative taxonomic assignments (http://www.ncbi.nlm.nih.gov/blast/).

Indices of richness, diversity and evenness

Species diversity was measured by three parameters – beta diversity (β-diversity), richness, and evenness (Magurran 2004; Soininen *et al.* 2012) – and analysed for both the DNA sampling intervals (3-cm resolution) and 1000-year time windows. On average, each 1000-year time window encompassed nine *sed*aDNA samples, whereas time windows of 500 years or less contained too few samples (>4), on average, for estimating long-term changes in diversity. Following Koleff *et al.* (2003), β-diversity was measured using Whittaker's (b_w) index computed using the PAST v. 3.19 software package (Hammer *et al.* 2001). A comparison of richness between samples with different count sizes can be biased, as the chance of detecting rare taxa increases simultaneously with count size (Birks & Line 1992; Brown 1999). We, therefore, rarefied the *sed*aDNA data to estimate the number of vascular plant taxa that would have been detected if the DNA read count had been standardized amongst samples. Rarefaction analysis was performed using the minimum count size in the Vegan (Oksanen *et al.* 2017) package for R (R Core Team 2017). We chose the Simpson evenness index ($E_{1/D}$) to measure DNA sample evenness across the 1000-year time windows, following Meltsov *et al.* (2011). This index of evenness is independent of the number of taxa detected.

Results

Chronology and lithostratigraphy

In total, seven AMS radiocarbon dates were obtained from the UR-1 core (Nesje). Ages span 3330±30 to 9480±50 ^{14}C a, which corresponds to a calibrated weighted-mean range of 3606–10 705 cal. a BP (Table 1). The resulting age-depth model (Fig. 2) suggests a fairly linear sedimentation rate, with the exception of a period of faster accumulation of sediment between 125 and 150 cm depth (as measured from the top of core UR-1; *c.* 7600–8100 cal. a BP). We consider these radiocarbon ages to be reliable for age-depth modelling as they are in the correct stratigraphical sequence, have small errors and are all derived from terrestrial plant macrofossils. It can, therefore, be assumed that the uppermost sediments that correspond to the last *c.* 3000 years are missing from core UR-1. This was most likely caused by a lake-depth measurement error, potentially from the ice layer affecting the echo-sounder, which resulted in the non-retrieval of upper sediments. To test this assumption, two additional AMS radiocarbon dates were obtained from the surface core UR-2 (UWITEC), which displayed a clear sediment–water interface. Radiocarbon ages from these two additional samples (275±30 and 1485±30 ^{14}C a; a calibrated weighted-mean range of 15 and 1433 cal. a BP) confirm that UR-1 is missing the uppermost sediment.

LOI values vary around 20% in the lower part of the core and reach a maximum of 47% in the upper part, indicating a generally increasing organic component with time (Fig. 3). Core UR-1 is divided into three main lithostratigraphical units, labelled A–C from the core base (Figs 2, 3):

Unit UR-1A (234–204 cm; c. 10 700–9900 cal. a BP). Silty-clay with traces of fine sand characterize this unit. Coarse (~2–3-cm thick bands) greenish-brown banding is

Table 1. Radiocarbon ages of plant macrofossil remains from Uhca Rohči Lake shown with their 1σ error, calibrated weighted mean, calibrated median and calibrated 95% confidence age ranges. All radiocarbon ages were calibrated using the IntCal13 curve (Reimer *et al.* 2013).

Core no.	Lab. ID	Depth below sediment surface (cm)	Age±1σ (^{14}C a BP)	Cal. weighted mean age (cal. a BP)	Cal. median age (cal. a BP)	Cal age, 2σ (cal. a BP)	Material
UR-2	Poz-98146	1–2	275±30	15	6	−2 to 150	*Salix* leaves
UR-2	Poz-98147	42–43	1485±30	1433	1417	1305–1598	*Salix* leaves
UR-1	Poz-93338	9–10	3330±30	3606	3592	3479–3819	*Salix* leaves
UR-1	Poz-87278	22–23	3850±40	4246	4244	4059–4408	*Salix* leaves
UR-1	Poz-87277	74–75	5490±50	6280	6287	6040–6432	Charcoal
UR-1	Poz-87276	120–121	6890±50	7715	7717	7572–7842	*Empetrum* wood
UR-1	Poz-93339	140–141	7150±40	8038	8024	7920–8195	*Empetrum* wood
UR-1	Poz-87275	178–179	8240±35	9208	9205	9027–9402	Charcoal
UR-1	Poz-87274	231–232	9480±50	10 706	10 702	10 417–11 030	*Salix* leaves

evident. LOI values range from 15 to 22% (mean 18%) and mean bulk density is 0.4 g cm^{-3}. The unit is characterized by high Ti, K and Fe, suggesting that sedimentation is driven by input of terrigenous minerogenic sediment.

Unit UR-1B (204–15 cm; c. 9900–3800 cal. a BP). A sharp transition into more organic-rich silty clay with small monocot rootlets and wood fragments occurs at 204 cm, marking the base of Unit B. Thin (1–3 mm) laminae of medium-coarse sand alternating with olive-brown organic silty clay comprise this second unit, with silt content decreasing upwards. Higher mean LOI values of 27% and fluctuations in Ti, K and Si characterize Unit B, with peaks in Ca probably related to the presence of inclusions, such as shells, within this unit. Bulk density values range from 0.2 to 0.4 g cm^{-3} and display a general decline through this unit, with the exception of a short-lived interval of higher values between 165 and 138 cm, which may result from sediment compaction after cutting the core sections.

Unit UR-1C (15–0 cm; c. 3800–3300 cal. a BP). This unit comprises mid- to dark-brown silty-clay gyttja with some detritus, including abundant monocot rootlets. A small decline in LOI values from 37 to 33% in this unit suggests a slight rise in terrigenous minerogenic input. The lithology of this unit is similar to that of core UR-2.

DNA analysis

In total, we obtained around 72 000 000 raw reads for the two UR libraries (Table S1). Following post-identification filtering, 118 taxa remained, of which 41% were identified to species level, 47% to the genus and 12% to the family (Figs S1–S3). Of the taxa detected in the *sed*aDNA, 44% are found growing in the Komagdalen valley today and a large proportion (86%) within Finnmark and the Kola Peninsula today (Table S2). Salicaceae and *Pinus* were present in nearly all samples but display variation in the number of PCR replicates (out of eight) in which they were detected; this was unrelated to sample depth/age. The steep drop in *Pinus sed*aDNA in the uppermost three samples (*c.* 3600–3300 cal. a BP) appears to be an artefact of the rapid increase in *Salix sed*aDNA during this time.

Although not present in the study region today, stands of *Pinus* forest occur ~50 km south of the Komagdalen valley (Elven 2005) and scattered trees are observed at the nearby site Østervatnet on the southern Varanger Peninsula (Prentice 1981). In addition, the *sed*aDNA results indicate that Holocene vegetation was dominated by woody taxa such as *Betula*, *Empetrum*, *Vaccinium* spp. and the *Rhododendron tomentosum* complex, the latter of which is also not found in the catchment today. The most common terrestrial forb was *Bistorta vivipara* followed by *Cakile* and Apiaceae, all common in the area today, although *Cakile* occurs mainly at the coast. The most dominant aquatic taxon, *Limosella aquatica*, is restricted to four inner fjord sites in Finnmark today (Alta, Lakselv, Neiden and Pasvik) whereas the second most common aquatic taxon, *Callitriche hermaphroditica*, has a slightly wider distribution in the inner fjord zone and along the main valleys. However, it does not occur within Varangerhalvøya National Park today (Table S2).

Trees and tall shrubs (e.g. *Pinus*, *Betula*, *Empetrum*, Salicaceae) dominate the *sed*aDNA record, accounting for 50% of total DNA reads on average (Fig. 4), followed by total terrestrial forbs (23%) and graminoids (12%; Fig. 5). The percentage dominance of functional groups remains relatively constant across samples, except for a distinct peak in the *sed*aDNA of aquatics between 10 200–9600 cal. a BP. This short period is described by the appearance of *Callitriche hermaphroditica*, *C. palustris*, and *Potamogeton* (Fig. 5). *Callitriche hermaphroditica* is a northern species (<53°N) typically found in shallow lakes and slow-moving rivers; it is on the IUCN Red List (http://www.iucnredlist.org/details/167828/0), and based on current distribution in Finland, it is inferred to indicate a minimum July temperature of 13–14 °C (Väliranta *et al.* 2015). *Callitriche palustris* and *Potamogeton* (not identified to species level) are more common and found in a wide range of aquatic habitats.

Pollen analysis

Pollen analysis detected 39 taxa across the 16 samples analysed from UR Lake, with *Betula* dominating the pollen

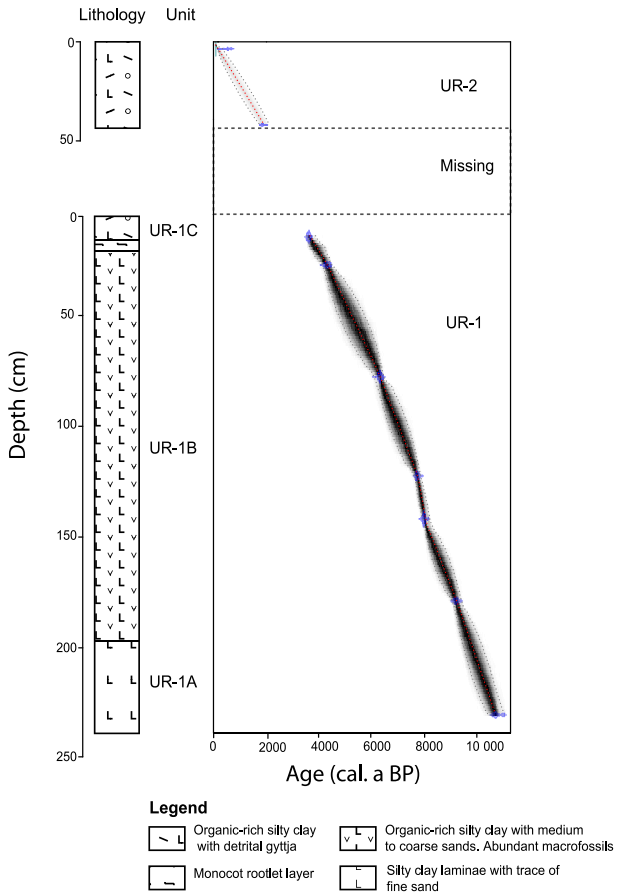

Fig. 2. The age-depth relationship and lithostratigraphical units (labelled UR-1A to C) for Uhca Rohči Lake, Varanger Peninsula. Age-depth relationships for core UR-1 (Nesje) and UR-2 (UWITEC) were analysed independently due to the hiatus remaining unknown. Radiocarbon ages were calibrated following IntCal13 (Reimer *et al.* 2013) and the age-depth model produced using the software Bacon (Blaauw & Christen 2011). Note that only UR-1 was analysed further in this study.

percentages and accounting for 65% of total land pollen (TLP) and influx of 2263 grains cm^{-2} a^{-1}, on average (Fig. 4). Of the 39 taxa, 72% could be identified to genus level, 21% to family level and 7% to species level. Four taxa (Ericales, *Myrica gale*, *Picea* and *Ulmus*) are assumed to be long-distance dispersed based on their current native ranges and their absence in the *sed*aDNA signal (Table S2). Three distinct zones are identified based on the pollen (Fig. 6), numbered from the base as follows:

Ur-Ia (234–190 cm; c. 10 700–9500 cal. a BP) – Betula-Empetrum-Salix zone. This basal pollen assemblage is characterized by high and rising percentages of *Betula* (up to 70%) and *Empetrum* (up to 20%) with high *Salix* (5–15%). Poaceae percentages are up to 17% at the beginning of the zone, decreasing to around 5% near the end of the zone boundary. *Pinus* values remain low at around 5% and influx of 70 grains cm^{-2} a^{-1}. *Filipendula* and Cyperaceae are present at percentages of 5 and 3%, respectively.

Ur-Ib (190–155 cm; c. 9500–8400 cal. a BP) – Betula-Salix-Empetrum zone. This is a short-lived subzone characterized by the rapid decline in values for *Empetrum* (up to 7%) from the previous (Ur-Ia) subzone. *Pinus* values remain consistently low at around 5% and influx of 50 grains cm^{-2} a^{-1}. The Ur-I/Ur/II boundary is defined by a decrease in Empetrum and Salix to low values.

Ur-II (155–80 cm; c. 8400–6400 cal. a BP) – Betula-Pinus-Empetrum zone. Rising *Pinus* values from 5 to 10% (110–860 grains cm^{-2} a^{-1}) accompany an increase in *Betula* values up to a peak of 80% (~1600–8300 grains cm^{-2} a^{-1}) in this zone. *Salix* values are low or zero whilst *Empetrum* values gradually increase.

Ur-III (80–0 cm; c. 6400–3300 cal. a BP) – Betula-Pinus-Empetrum-Poaceae zone. The Ur-II/Ur-III boundary is defined by rising values of Poaceae and *Pinus* and a decline in *Betula*. *Pinus* reaches maximum values in this zone, increasing from around 10% at the start of the zone up to a peak of 18% (200 grains cm^{-2} a^{-1}). *Empetrum* continues to rise through the transition between Ur-II and Ur-III zones coincident with increasing percentages of herbaceous taxa such as Chenopodiaceae and *Rumex*. Poaceae and *Salix* rise slightly. *Isoetes* reaches a maximum value of 10% before declining towards the end of the zone.

Comparison between pollen and aDNA

The combined approach of *sed*aDNA and pollen analysis resulted in 137 taxa of 64 families identified to varying taxonomic levels (Table S2). In total, 20 families were shared between pollen and *sed*aDNA, with poor taxonomic resolution seen for families such as Poaceae, Cyperaceae and Caryophyllaceae based on pollen whilst identification to genus or even species level was possible with *sed*aDNA. Of the 39 taxa detected by pollen analysis, 12 were also identified in the *sed*aDNA to the same taxonomic level. Selected taxa found as pollen are presented in Figs 4, 5 as a percentage of total terrestrial pollen and compared with the results of *sed*aDNA analysis. No algal taxa were detected in the *sed*aDNA record based on the vascular plant *trn*L P6 loop marker, whilst a high abundance of *Pediastrum* was identified throughout the pollen record at UR Lake (Table S2). Both the pollen and *sed*aDNA record are dominated by trees and shrubs, but they differ in terms of the percentage dominance of key taxa. For example, *Betula* accounts for 65% of total terrestrial pollen on average, followed by *Pinus* (8%) and *Empetrum* (7%) whilst *Pinus* and Salicaceae are found to be dominant in the *sed*aDNA, accounting for 21 and 20% of total DNA reads, respectively. The greater dominance of *Empetrum* in the Early Holocene (*c.* 10 700–9500 cal. a BP) revealed by *sed*aDNA is mirrored in the pollen record (Fig. 4). Moreover, the absence of *sed*aDNA belonging to the family Poaceae between *c.* 5500 and 4500 cal. a BP is simultaneous with a rapid and short-lived decline in

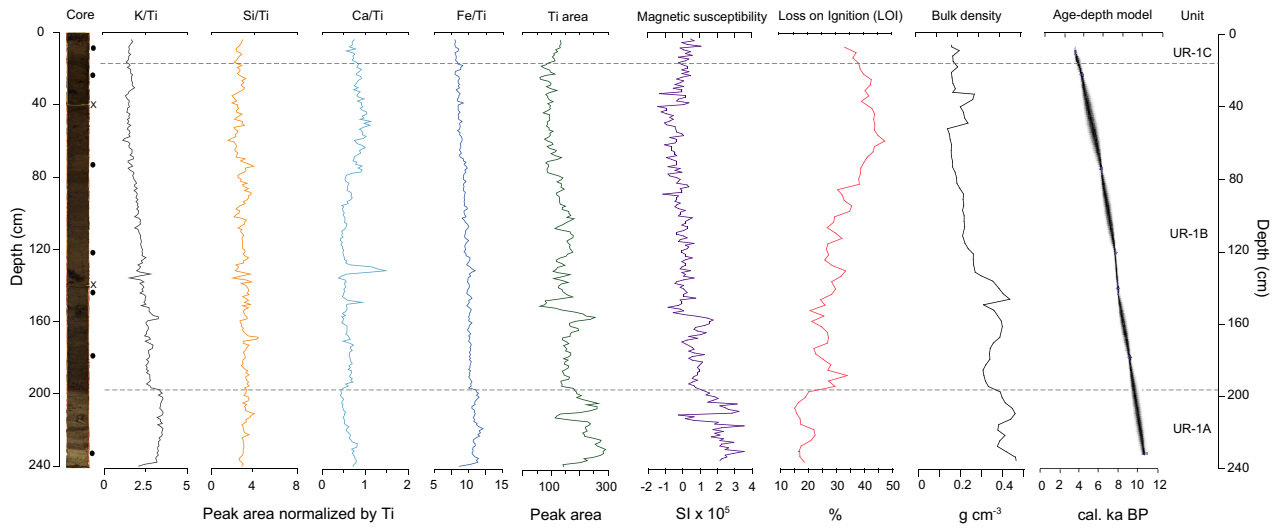

Fig. 3. Sediment properties and element profiles for Uhca Rohči Lake, Varanger Peninsula. Lithostratigraphical units (UR-1A to C) described in the text are indicated. Black circles indicate the depth of ^{14}C samples analysed and black crosses indicate the position of core breaks after splitting the continuous Nesje core (UR-1) sequence. Selected elements measured by XRF are given as a ratio to Ti (see Material and methods). Loss-on-ignition (LOI) is given as a percentage of dry sediment weight.

Poaceae pollen (Fig. 5). Furthermore, two pollen grains of *Callitriche* sp. were found within samples at 198 and 162 cm depth, coincident with the interval of high *sed*aDNA values for *Callitriche hermaphroditica* and *C. palustris* (Fig. 5).

Floristic richness and diversity results

No long-term trends in floristic richness were observed over the time period investigated (Fig. 7) although species richness reconstructed from individual samples shows high-frequency variation. *sed*aDNA detected an anomalously high number of taxa (48 taxa pre-rarefaction) within a single sample at *c.* 6020 cal. a BP (68 cm depth; 39 taxa remaining following rarefaction). Differences in the composition of this sample compared to adjacent samples largely result from the presence of many forb taxa such as *Viola biflora*, *Stellaria borealis*, *Rumex*, *Oxyria digyna*, *Geranium* and *Dryas.* Some bryophyte (e.g. *Andreaea rupestris*, *Dicranum*, *Sphagnum russowii*) and woody taxa (e.g. *Alnus*, *Kalmia procumbens*, *Vaccinium* spp.) are also present but are not found in adjacent samples. There is no clear explanation from the lithological (Fig. 2) or geochemical (Fig. 3) data for the anomalously high floristic richness observed in this sample.

β-diversity calculated based on individual samples displayed variation (SD = 0.09), despite species richness remaining fairly constant amongst samples (Fig. 7A). Whilst the number of taxa detected by *sed*aDNA remains similar amongst samples, the taxonomic composition differed between adjacent samples. Typically, the woody taxa remain a common component of adjacent samples but the herb (forb and graminoid) taxa show sporadic occurrences throughout the record. Merging samples into 1000-year time windows largely removes the effect of these sporadic occurrences, with β-diversity displaying little variation between time windows (Fig. 7B). The number of taxa identified as common between adjacent 1000-year time windows remained consistently high throughout the record, accounting for, on average, 70% of all taxa detected. Six taxa belonging to trees and shrubs (Salicaceae, *Pinus*, *Empetrum*, *Betula*, *Rhododendron tomentosum*, *Vaccinium uligonosum*) seven to forbs (Anthemideae, Asteraceae, Apiaceae, *Bistorta vivipara*, *Comarum palustre*, *Dryas*, *Limosella aquatica*) and three to graminoids (Agrostidinae, *Festuca*, Poaceae) were consistently detected across all time windows. The small variation observed in β-diversity (SD = 0.04) and sample evenness (SD = 0.06) across 1000-year time windows therefore results from the typically sporadic occurrences of the remaining 30% of taxa detected (Fig. 7B).

Floristic diversity and tree-line changes

Rarefied species richness based on pollen (palynological richness) from UR Lake varies between 10 and 24 taxa. Compilation of palynological richness patterns from Lake Rautuselkä and Hopseidet (Seppä 1998) with estimates obtained at UR Lake indicates long-term trends in richness reconstructed from pollen data (Fig. 8). A sharp decline in species richness from 24 to 10 taxa is observed in UR Lake between *c.* 8000–7300 cal. a BP, coincident with maximum values for *Pinus* pollen influx (~110 to 860 grains cm^{-2} a^{-1}), which occur in zone UR-II (Figs 4, 6). No significant relationship (r^2 = 0.08, p > 0.01) between *Pinus* pollen influx and palynological richness was identified at UR Lake, however. Floristic richness reconstructed from *sed*aDNA from UR Lake displays no long-term trends (Fig. 8), indicating richness remains relatively stable with

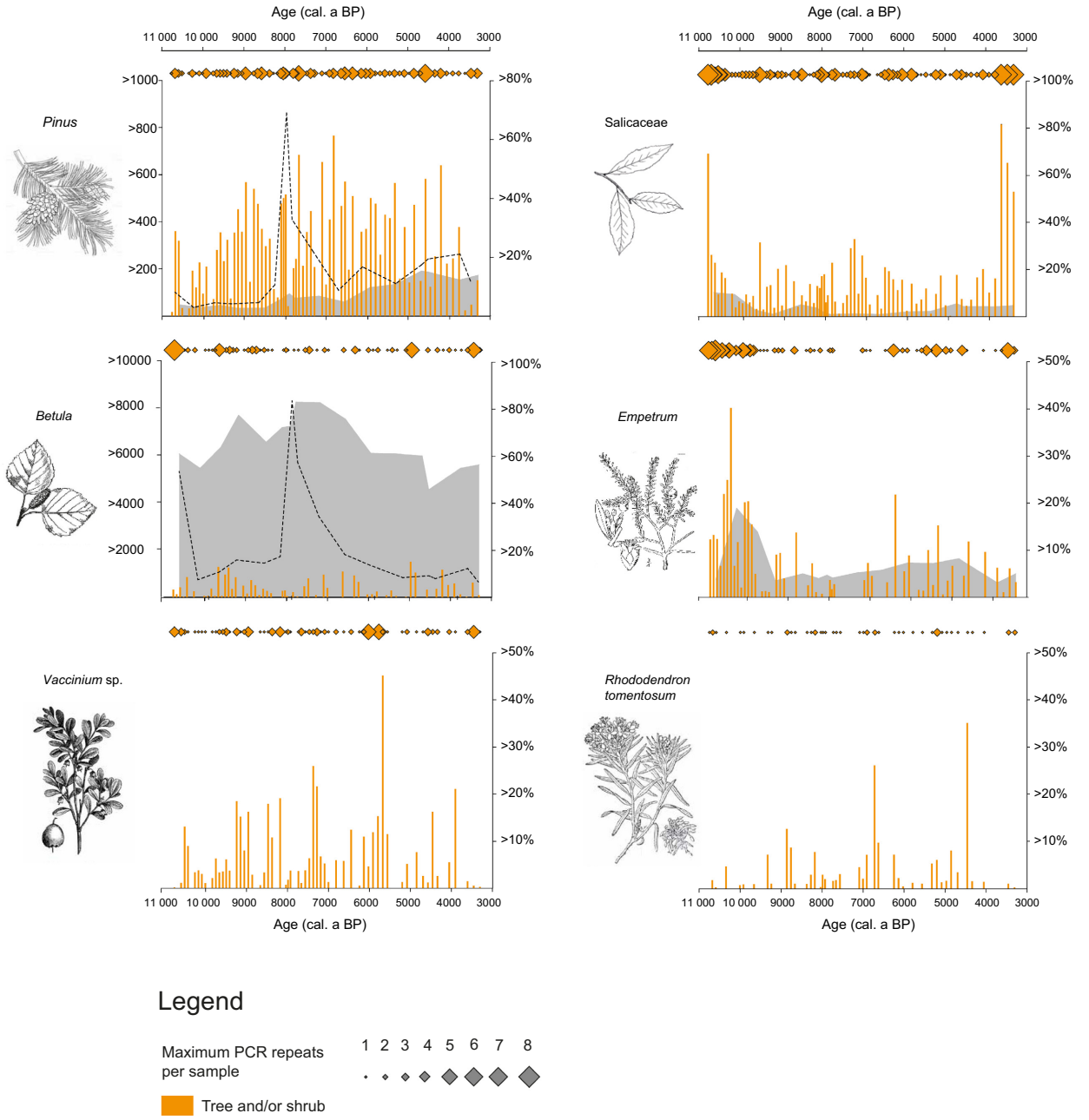

Fig. 4. Selected woody taxa as a percentage of total DNA reads per sample (histogram; right-hand *y*-axis) and maximum number of PCR replicates (diamond symbols) for the Uhca Rohči Lake record. Grey shaded area depicts pollen percentages based on sum of total terrestrial pollen (∑P; right-hand *y*-axis) with pollen influx for *Pinus* and *Betula* indicated by a dashed line (left-hand *y*-axis). Note that the height of the *y*-axis varies amongst panels.

the exception of the anomalously high richness observed at 68 cm depth (*c*. 6000 cal. a BP).

Discussion

Holocene development of Uhca Rohči Lake and the surrounding landscape

The lithostratigraphical record (Figs 2, 3) indicates a continuous input of fine sediment into UR Lake throughout the Holocene. Our results suggest an increase in lake production at *c*. 9900 cal. a BP, with a gradual transition from minerogenic sediments, composed of silty-clay laminae with low LOI and high Ti and magnetic susceptibility, to silty-clay gyttja with gradually increasing values for LOI (Fig. 3). Following this transition, lithostratigraphical properties remain relatively stable for the remainder of the record with only small fluctuations observed in LOI, magnetic susceptibility, and geochemical elements in the uppermost zone. The position of the lake on the Early to

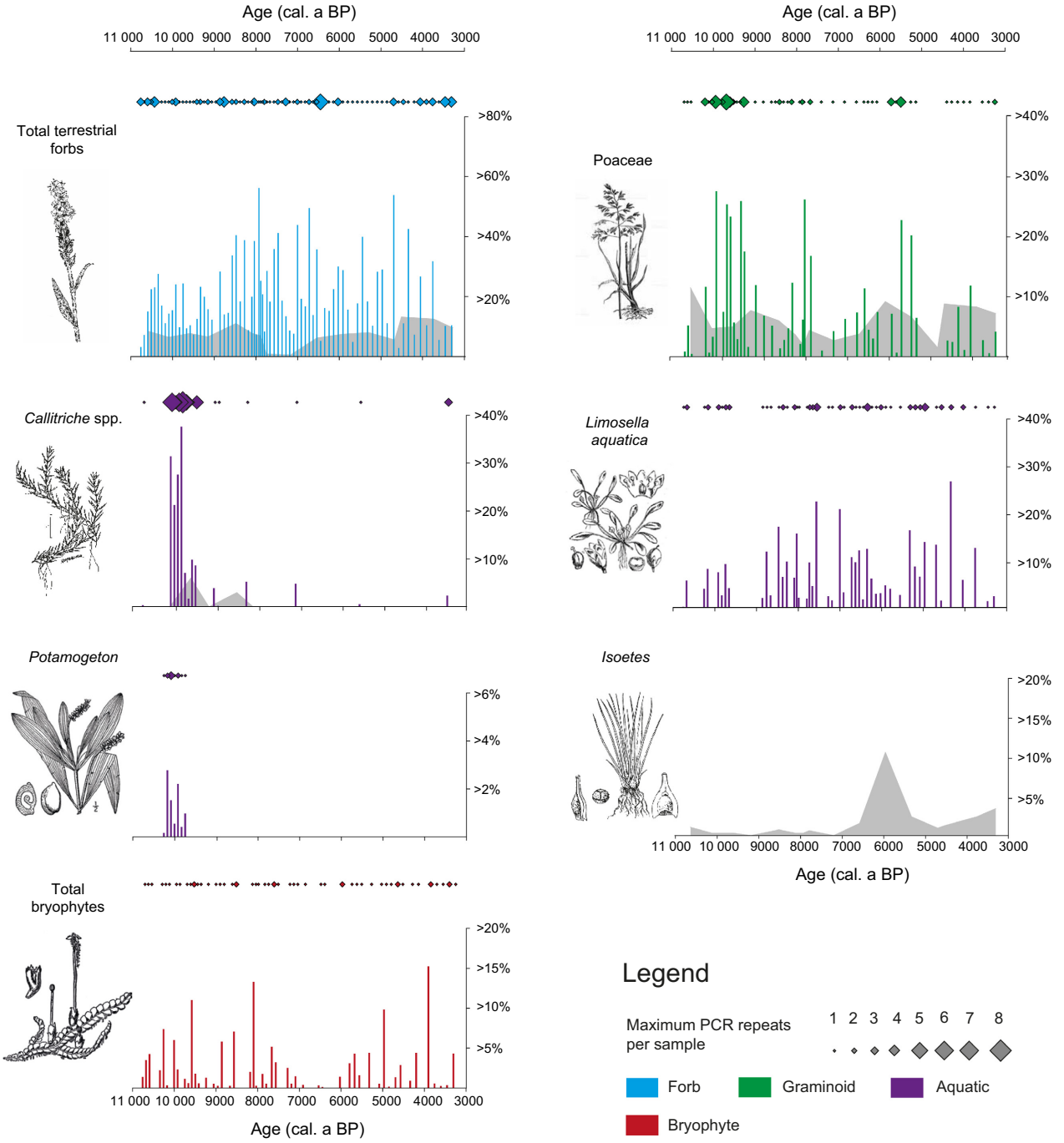

Fig. 5. Selected herbaceous taxa as a percentage of total DNA reads per sample (histogram) and maximum number of PCR replicates (diamond symbols) for the Uhca Rohči Lake record. Grey shaded area depicts pollen percentages based on sum of total terrestrial pollen ($\sum$P). Proportion of aquatics and spores are calculated based on the sum of total terrestrial pollen plus aquatics ($\sum$P + $\sum$aquatics) or spores ($\sum$P + $\sum$spores). Pollen percentages for *Callitriche* spp. are presented with a 10× exaggeration. Note that the height of the right-hand *y*-axis varies amongst panels.

Middle Holocene flood-plain (Fig. 1) and laminated nature of the minerogenic sediments in lithostratigraphical unit A and to a lesser extent, unit B (Fig. 3), probably reflect periodic flood events of the Komagelva River prior to river incision forced by continued isostatic uplift (Fletcher *et al.* 1993; Fjellanger & Sørbel 2007). Very local slope wash may also have played a role at this time. Furthermore, the high sand content of these laminae suggests the influence of a relatively high-energy system in these early lithostratigraphical units. Our results suggest UR Lake was isolated from riverine influence at *c.* 3800 cal. a BP, at the transition from silty-clay with thin laminae (unit B) to silty-clay gyttja with detritus (unit C), when the Komagelva River subsequently downcut to an elevation below the lake. Thus, the

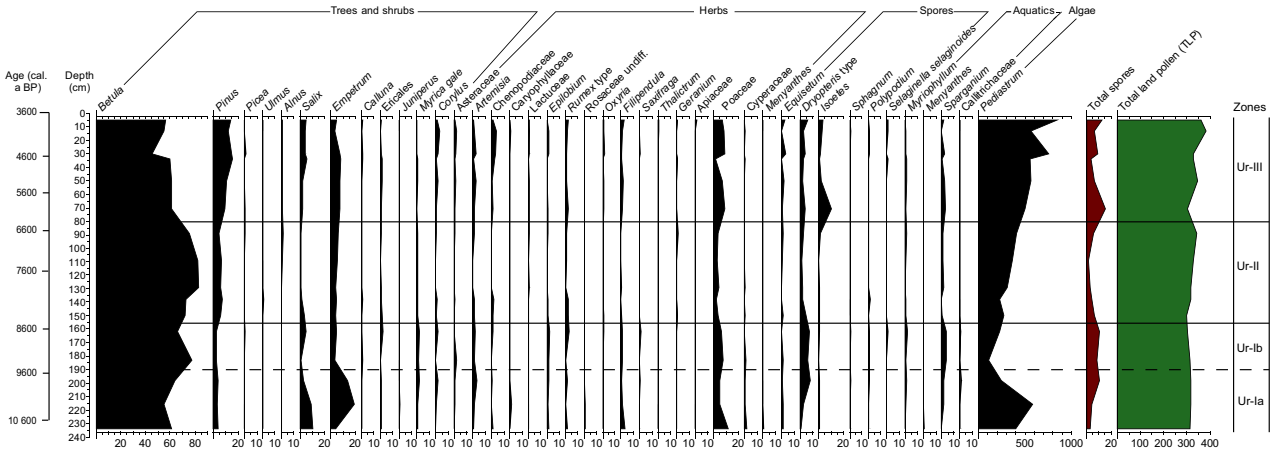

Fig. 6. Percentage pollen diagram for Uhca Rohči Lake with local pollen assemblage zones (LPAZs) Ur-I to Ur-III indicated. Pollen percentages are based on the sum of total terrestrial pollen (∑P). Proportion of aquatics and spores are calculated based on the sum of total terrestrial pollen plus aquatics (∑P + ∑aquatics) or spores (∑P + ∑spores).

source of the *sed*aDNA has probably changed over time, with the Komagelva River delivering some of the DNA to the lake from a larger source area of the upstream catchment during periodic flood events prior to downcutting in the later Holocene. Nevertheless, no distinct change in the taxonomic composition of *sed*aDNA samples is observed between units A, B and C, nor was any clear pattern observed between the presence of banding and/or laminae and the taxonomic composition of samples.

The prominence of aquatic taxa such as *Callitriche hermaphroditica*, *C. palustris* and *Potamogeton* in the *sed*aDNA between *c*. 10 200–9600 cal. a BP (Fig. 5) may reflect particularly good growing conditions in the lake, for example clear water conditions, warmer temperatures and/or more nutrients. In addition, aquatic plants are efficiently dispersed by birds and are therefore likely to show a rapid geographical response to climate change (Birks 2000; Väliranta *et al.* 2015). *Callitriche hermaphroditica*, which is not found in Varangerhalvøya National Park today, occurs in more continental sites in Finnmark and appears to require a minimum July temperature of 13–14 °C (Väliranta *et al.* 2015). The pattern of occurrence of the aquatic taxa suggests a response to warmer-than-present Early Holocene summers.

A handful of other taxa (*Rhododendron tomentosum*, *Limosella aquatica*) that are dominant in the *sed*aDNA signal (Figs 4, 5) do not occur in the region today, with current native ranges more than 50 km south or southeast of the Varanger Peninsula (see above). Thus, the continued presence and dominance of these taxa in the *sed*aDNA signal suggest a warmer climate between, at least, *c*. 10 000–4000 cal. a BP. This is in accordance with the general interpretation from pollen-based temperature reconstructions in northern Fennoscandia, which indicate July temperatures of +1.5±0.5 °C during the HTM (e.g. Møller & Holmeslet 2002; Jensen & Vorren 2008; Seppä *et al.* 2009; Sejrup *et al.* 2016).

Interpreting the major vegetation patterns

Little change is observed in the relative dominance of functional groups between *c*. 10 700 and 3300 cal. a BP, with trees and tall shrubs such as *Pinus*, Salicaceae, *Betula* and *Empetrum* accounting for a high percentage of the terrestrial pollen (mean 87%) and total DNA records (mean 50%; Fig. 4). Wind-pollinated woody taxa (e.g. *Betula*, *Pinus*) are generally over-represented in pollen studies (Prentice 1985; Sugita 1994). Likewise, we note that the abundance of these plant growth forms may be over-represented in our *sed*aDNA, dataset due to polymerase-related biases that generally occur during metabarcoding PCR (Alsos *et al.* 2018; Nichols *et al.* 2018), although calibration against modern vegetation suggests a bias in the opposite direction (Yoccoz *et al.* 2012).

Whilst a large majority (>85%) of the taxa detected in the *sed*aDNA are also found growing in Finnmark and the Kola Peninsula region today, the occurrence of *Pinus* in the *sed*aDNA signal from UR Lake raises questions. *Pinus* is found in nearly every sample, usually in high abundance, yet it is not a major component of the present-day flora of the Varanger Peninsula. The nearest forest stands occur around 50 km south of Varangerfjorden, although some scattered trees are present in the southern Varanger Peninsula (see above; Fig. 1B). The watershed of the Komagelva River, a likely source of *sed*aDNA to UR Lake during the time represented by lithostratigraphical units UR-1A and 1B, is situated outside of the present-day *Pinus* limit (Fig. 1B). The sustained high abundance of *Pinus* throughout the record, including lithostratigraphical unit UR-1C when the lake is presumed to have been isolated from riverine influence, suggests a source of *Pinus sed*aDNA to UR Lake other than the Komagelva River.

It is possible that *Pinus sed*aDNA in UR Lake originates from pollen and thus may indicate long-distance dispersal rather than local growth. Unlike angiosperms, pollen

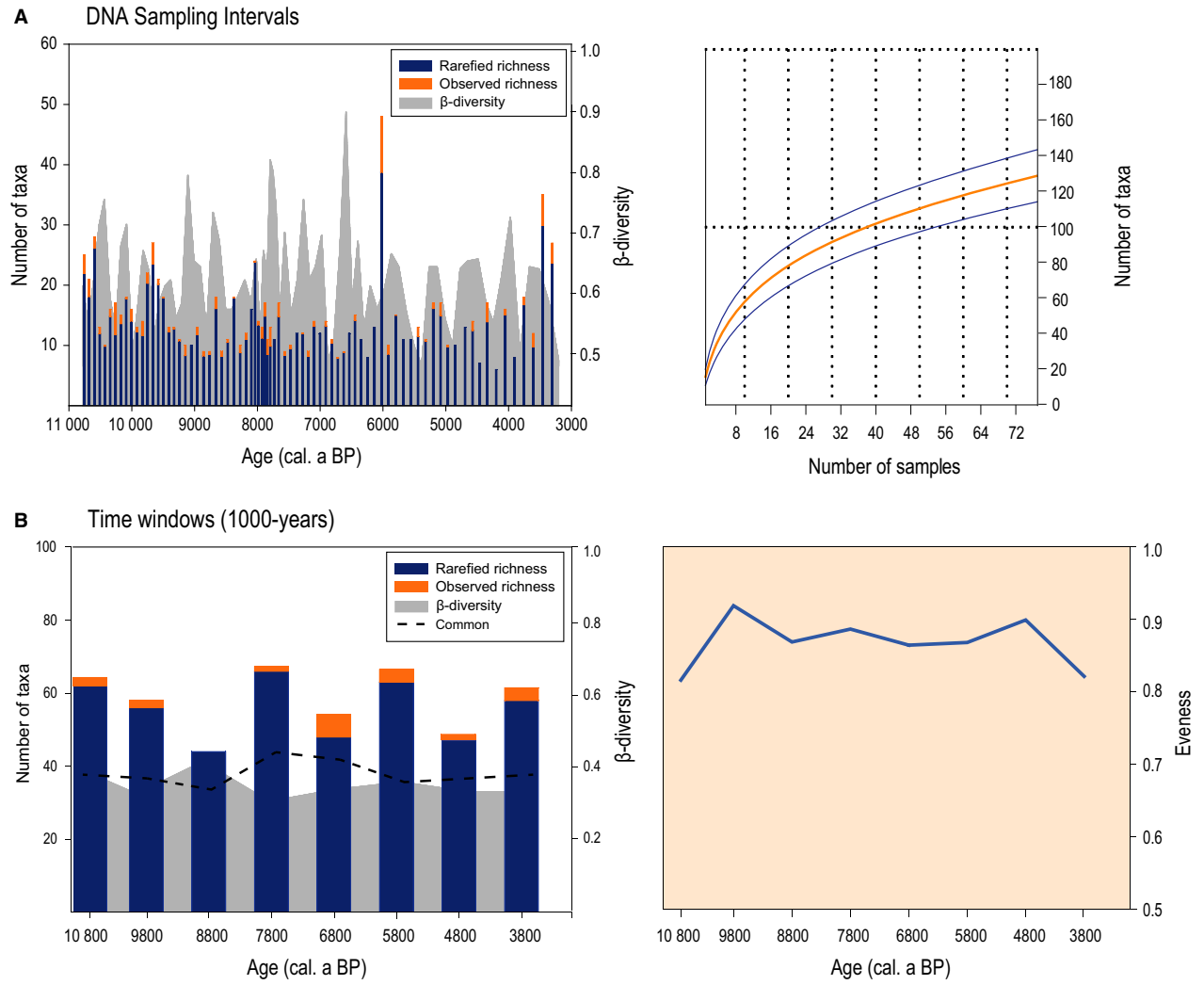

Fig. 7. Measures of species richness, beta diversity and sample evenness for (A) DNA sampling intervals (3-cm resolution) with a sample rarefaction curve presented in the right-hand graph outlining the relationship between sample size and the number of taxa identified (orange line) with 95% confidence intervals (blue lines) and (B) the same data amalgamated into 1000-year time windows for the Uhca Rohči Lake *sed*aDNA record. Dashed line indicates the number of taxa common between 1000-year time windows.

grains derived from gymnosperms contain some chloroplast DNA (cpDNA) within their reproductive cells (Suyama *et al.* 1996; Parducci *et al.* 2005) that, theoretically, could be introduced into the sediment matrix, either naturally or during DNA extraction. However, current thinking from *sed*aDNA studies suggests that DNA extracted from sediments does not derive from pollen grains (Jørgensen *et al.* 2012; Pedersen *et al.* 2016; Sjögren *et al.* 2017; Wang *et al.* 2017), but instead from other components embedded in the sediment matrix (Parducci *et al.* 2017). This is probably due to the generally lower biomass of pollen compared to stems, roots and leaves, and to the resilience of their sporopollenin coats, which requires a separate lysis step in the extraction of DNA (Kraaijeveld *et al.* 2015). The extraction of cpDNA from fossil pollen grains has proven difficult (Parducci *et al.* 2005; Bennett & Parducci 2006), which suggests that consistent detection of pollen-derived cpDNA from the sediment matrix itself is unlikely. Another possibility is contamination. *Pinus* passed the filtering stage, but there was a high number of *Pinus* reads in the negative controls (Table S2). Therefore, our *Pinus* record may support the inference of local presence, but there is enough doubt that other proxy data are required to establish whether pine was locally present during the Holocene.

Pinus was found in all of the pollen samples analysed from UR Lake (Fig. 6; mean 8% TLP; mean concentration 6100 grains g^{-1}). Maximum *Pinus* pollen influx rates (~200–870 grains cm^{-2} a^{-1}) are observed between *c.* 8000–7300 cal. a BP (Table S4). These are comparable to influx values reported from nearby Østervatnet (400–650 grains

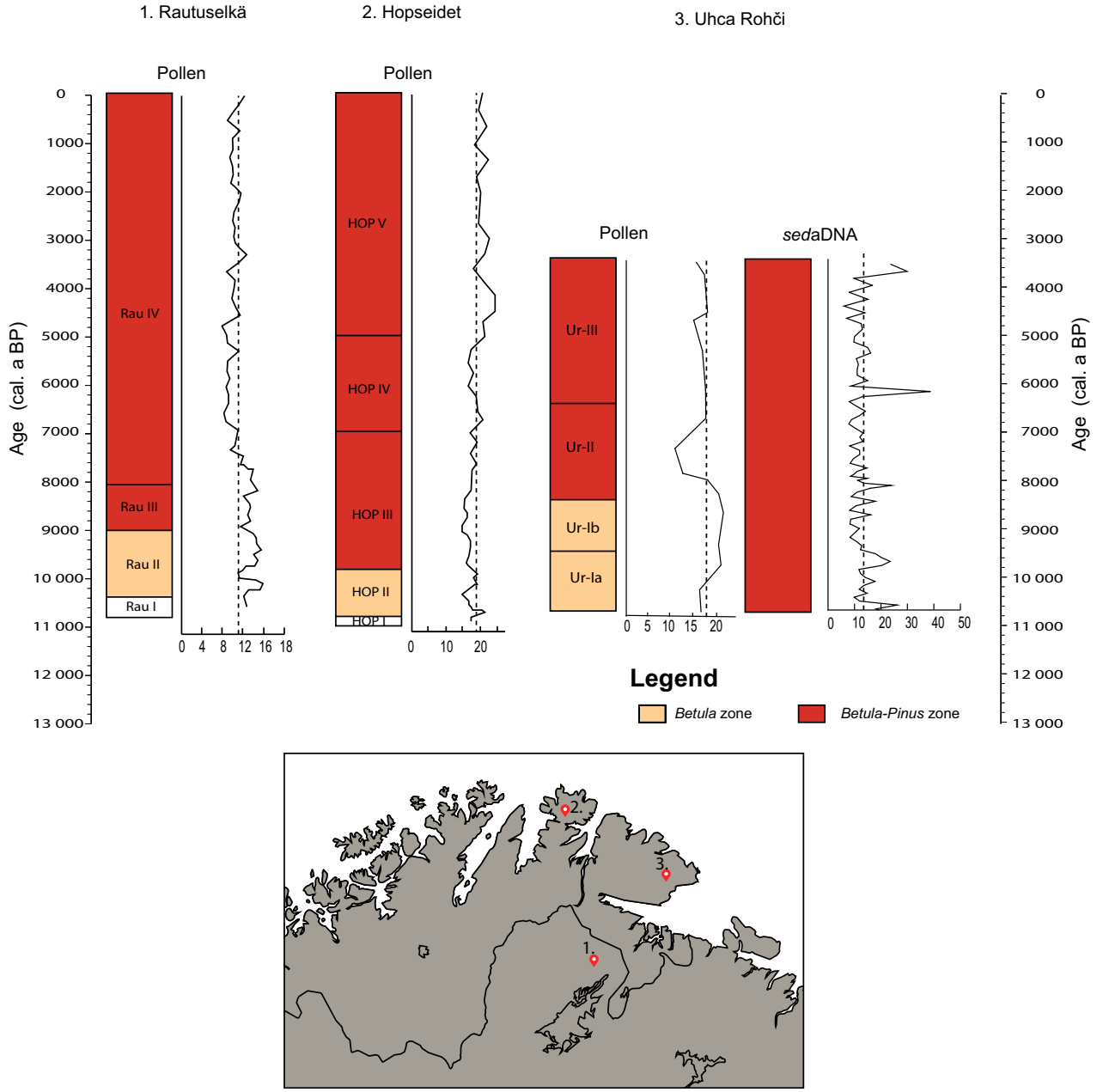

Fig. 8. Compilation of palynological richness for two published records (Rautuselkä and Hopseidet; Seppä 1998) and the Uhca Rohči pollen record (this paper). Floristic richness derived from *sed*aDNA record from Uhca Rohči Lake also indicated (this paper). Dashed line indicates mean species richness. *Betula* and *Betula-Pinus* pollen zones are indicated. Map (inset) details location of sites with 1 = Lake Rautuselkä; 2 = Lake Hopseidet and 3 = Uhca Rohči Lake.

cm^{-2} a^{-1}) *c.* 8000 cal. a BP (Table S3) and Mortensnes (2000 grains cm^{-2} a^{-1}), which is only 46 km to the SW (Høeg 2000). A threshold value of 500 grains cm^{-2} a^{-1} given by Hyvärinen (1985) and Hicks (1994) for indicating pine presence means that from our pollen data, *Pinus* may have been present at the site *c.* 8000–7300 cal. a BP (Table S3). This accords with the northward range expansion across northern Fennoscandia beginning *c.* 8500 cal. a BP (Hyvärinen 1975; Seppä 1996; Huntley *et al.* 2013) that probably reflected Early and Middle Holocene summer warmth, but demonstrates a probable lag in response, compared to aquatic taxa. Maximum *Betula* influx rates (~1300–8300 grains cm^{-2} a^{-1}; Table S4) are also observed during this interval *c.* 8000–7300 cal. a BP (Fig. 4), suggesting a mixed birch-pine forest.

Continuity and stability in Holocene flora

The record obtained from UR Lake reveals stability in the Holocene flora, with over 85% of the total taxa

detected by *sed*aDNA still growing within the catchment and/or in the broader region today (Table S2). Our *sed*aDNA results indicate that the erect shrub-tundra and the riparian grassland communities became established early: dominant taxa of the shrub communities (e.g. Salicaceae, *Betula*, *Empetrum*, *Vaccinium uligonosum*) and riparian meadows (*Bistorta vivipara*, *Caltha*, *Viola biflora*, *Rumex*, *Stellaria longifolia* and *S. borealis*) had appeared by *c*. 10 700 cal. a BP (Figs 4, 5), in accordance with pollen records from nearby Østervatnet and Bergebyvatnet showing a *Salix*-Poaceae assembly from *c*. 12 500 cal. a BP (Prentice 1981, 1982). Presence of these taxa continued to *c*. 3300 cal. a BP and they are common in the catchment today.

Overall, *sed*aDNA permitted identifications at a higher taxonomic resolution than was possible with pollen; the main exception is Salicaceae, which, based on the *trn*L marker, can only be identified to family level due to hybridization and similarity in cpDNA sequences amongst individuals. The *sed*aDNA signal detected taxa from a range of different ecological habitats including shrub tundra, riparian meadows and/or open grassland rich with herbs and bryophytes. It also reveals the dynamics of aquatic taxa. In contrast, the pollen record from UR Lake is largely confined to northern boreal and low arctic taxa (e.g. *Betula*, *Pinus*, *Salix*, *Empetrum*), with a minor signal deriving from herbaceous (e.g. Asteraceae, Chenopodiaceae, *Rumex*, Poaceae) and aquatic taxa (e.g. *Sparganium*, Callitrichaceae). In contrast to the *sed*aDNA record, entomophilous forbs typical of low tundra settings, such as *Bistorta vivipara*, are largely absent or in low percentages in the pollen record from UR Lake (Fig. 6, Table S2). The limited number of pollen samples and dominance of taxa such as *Betula* and *Pinus* probably restrict or mask the presence of low pollen-producing entomophilous taxa in the pollen record from UR Lake.

Direct comparison of the number of taxa contributed by each proxy to overall species richness is not appropriate due to disparity in sampling effort. Although previous comparisons between pollen and *sed*aDNA have shown only partial overlap of taxa (Pedersen *et al.* 2013; Parducci *et al.* 2015), our data demonstrate high similarity in the records for taxa such as *Empetrum*, *Callitriche* and Poaceae, as well as a dominance of *Betula* and *Pinus* (Figs 4, 5). Thus, in contrast to lakes that only receive inflow from catchments/small streams (Alsos *et al.* 2018), the DNA signal in UR Lake, which may have been affected by sediment inputs from the large, upstream catchment, more closely resembles the regional vegetation signal typical of many pollen records (Jacobson & Bradshaw 1981; Rousseau *et al.* 2006).

Postglacial patterns in floristic richness and diversity

Floristic richness reconstructed from *sed*aDNA displays only minor variations over the Holocene interval investigated, particularly when the effect of sporadic occurrences of herb taxa is minimized by merging samples into 1000-year time windows (Fig. 7). High floristic richness (61 taxa) characterizes the earliest time window between 10 700–9800 cal. a BP, and richness remains consistently high throughout the record; small fluctuations may be due to flood-related inputs from the extensive, up-river catchment. No long-term trends in floristic richness are evident, based on either individual samples or 1000-year time windows (Fig. 7). High sample evenness across time windows indicates the persistence of dominant taxa over the Holocene, with a large percentage (>70%) of taxa detected as common amongst 1000-year time windows (Fig. 7B). Our findings derived from *sed*aDNA support the conclusions of Normand *et al.* (2011) and Giesecke *et al.* (2012), which are derived from pollen, that the current distribution of plants in previously glaciated regions established quickly after the onset of the Holocene. For the Holocene at least, there is no evidence for increased floristic richness over time that might be due to the delayed immigration of species, but it should be noted that as the area was deglaciated prior to the end of the Younger Dryas (see above), the earliest part of the record is missing.

Palynological richness from UR Lake and two published records from Lake Rautuselkä and Hopseidet (Seppä 1998) show more variation than floristic richness reconstructed from *sed*aDNA (Fig. 8). Palynological richness displays long-term trends in response to variation in the pollen abundance of anemophilous woody taxa (e.g. *Pinus* and *Betula*). Dominance of taxa producing high amounts of pollen (e.g. *Pinus*, *Picea* and *Betula*) occurs at the expense of entomophilous forbs and leads to a likely underestimation of floristic richness. On the other hand, where low palynological richness coincides with high *Pinus* pollen influx, this may reflect an ecological effect whereby dense forest reduces niche availability for herbaceous taxa (Seppä 1998). Our *sed*aDNA data do not show such patterns, whereas the UR pollen data do, albeit at a coarse sampling resolution. The limitations on the effectiveness of pollen spectra for estimating species richness (Meltsov *et al.* 2011; Goring *et al.* 2013) mean that *sed*aDNA can provide improved estimates; less sensitive to 'swamping' by dominant taxa, as total numbers are not limited by counting time, and all valid reads contribute to the floristic list.

Conclusions

The pollen and *sed*aDNA records from this site on the Varanger Peninsula show a largely consistent pattern. Erect shrub-tundra vegetation was established early in the Holocene. This was soon followed by the establishment of *Betula* forest probably mixed with *Pinus* as indicated by high pollen influx rates of both taxa. This, together with the persistence of *Limosella aquatica* and *Rhododendron tomentosum* through the *sed*aDNA record, indicates a climate warmer than present throughout most of the Early and Middle Holocene.

As species richness reconstructed from pollen data is limited by differential pollen productivity, dispersal and often low taxonomic resolution, alignment with contemporary data often proves difficult if not impossible. Reconstructions of past changes in floristic diversity and richness can be improved by using *sed*aDNA, as it better reflects local floristic composition and diversity. The *sed*aDNA data on floristic richness between *c*. 10 700 and 3300 cal. a BP show that high diversity, richness and sample evenness prevailed across the record, despite known climatic variations in the Holocene. Nevertheless, when considering past and future responses to climate change, important questions remain as to how the crossing of critical climatic thresholds may interact with sub-regional heterogeneity and drivers of vegetation composition and change, including herbivory. Here, as this paper shows, s*ed*aDNA studies can make an important contribution.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at http://www.boreas.dk.

Fig. S1. Woody and graminoid taxa detected by *sed*aDNA in Uhca Rohči Lake.

Fig. S2. Forb taxa detected by *sed*aDNA in Uhca Rohči Lake.

Fig. S3. Ferns, bryophytes, clubmoss and aquatic taxa detected by *sed*aDNA in Uhca Rohči Lake.

Table S1. Total DNA read numbers remaining after each filtering step described in the Material and methods section.

Table S2. All taxa detected from *sed*aDNA (orange) and pollen (blue) analyses, sorted according to family within groups: vascular plants, bryophytes and clubmosses, aquatics and algae.

Table S3. Published *Pinus* pollen influx values from Finnmark, northern Norway, (administrative region in brackets) and adjacent sites in Finland.

Table S4. Pinus and *Betula* pollen influx values for Uhca Rohči Lake for cores UR-1 and UR-2.