



A 24,000-year ancient DNA and pollen record from the Polar Urals reveals temporal dynamics of arctic and boreal plant communities

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ABSTRACT

A 24,000-year record of plant community dynamics, based on pollen and ancient DNA from the sediments (*sedaDNA*) of Lake Bolshoye Shchuchye in the Polar Ural Mountains, provides detailed information on the flora of the Last Glacial Maximum (LGM) and also changes in plant community composition and dominance. It greatly improves on incomplete records from short and fragmented stratigraphic sequences found in exposed sedimentary sections in the western Russian Arctic. In total, 162 plant taxa were detected by *sedaDNA* and 115 by pollen analysis. Several shifts in dominance between and within plant functional groups occurred over the studied period, but most taxa appear to have survived *in situ*. A diverse arctic-alpine herb flora characterised the interval ca. 24,000–17,000 cal years BP and persisted into the Holocene. Around 17,000 cal years BP, sedges (e.g. *Carex*) and bryophytes (e.g. *Bryum*, *Aula-comnium*) increased. The establishment of shrub-tundra communities of *Dryas* and *Vaccinium* sp., with potentially some *Betula pubescens* trees (influx ~290 grains cm² year⁻¹), followed at ca. 15,000 cal years BP. Forest taxa such as *Picea* and ferns (e.g. *Dryopteris fragrans*, *Gymnocarpium dryopteris*) established near the lake from ca. 10,000 cal years BP, followed by the establishment of *Larix* trees from ca. 9000 cal years BP. *Picea* began to decline from ca. 7000 cal years BP. A complete withdrawal of forest tree taxa occurred by ca. 4000 cal years BP, presumably due to decreasing growing-season temperatures, allowing the expansion of dwarf-shrub tundra and a diverse herb community similar to the present-day vegetation mosaic. Contrary to some earlier comparative studies, *sedaDNA* and pollen from Lake Bolshoye Shchuchye showed high similarity in the timing of compositional changes and the occurrence of key plant taxa. The *sedaDNA* record revealed several features that the pollen stratigraphy and earlier palaeorecords in the region failed to detect; a sustained, long-term increase in floristic richness since the LGM until the early Holocene, turnover in grass and forb genera over the Pleistocene-Holocene transition, persistence of a diverse arctic-alpine flora over the late Quaternary, and a variable bryophyte flora through time. As pollen records are often limited by taxonomic resolution, differential productivity and dispersal, *sedaDNA* can provide improved estimates of floristic richness and is better able to distinguish between different plant assemblages. However, pollen remains superior at providing quantitative estimates of plant abundance changes and detecting several diverse groups (e.g. Poaceae, Cyperaceae, Asteraceae) which may be underreported in the *sedaDNA*. Joint use of the two proxies provided unprecedented floristic detail of past plant communities and helped to distinguish between long-distance transport of pollen and local presence, particularly for woody plant taxa.

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1. Introduction

While palaeoecological records based on pollen and plant macrofossils have identified a broad array of vegetation responses to past climate changes (Jackson and Overpeck, 2000; Nolan et al., 2018), interpretations of long-term vegetation dynamics are often constrained by various features, such as the degree of productivity and preservation potential. For pollen especially, taxonomic resolution is a problem (~23% taxonomic resolution to species-level; Giesecke et al., 2012), and the specific nature of the site may constrain the data retrieved (Prentice, 1985; Sugita, 1994; Gajewski, 2015). Ancient DNA from sediments (*sedDNA*) can provide considerable detail on floristic composition and plant community responses to climate change, augmenting information gained from pollen and macrofossil analyses (e.g. Jørgensen et al., 2012; Parducci et al., 2015). The *trnL* intron (P6 loop) of the plant chloroplast genome (Taberlet et al., 2007) is the most commonly used DNA marker for vascular plants to date. In arctic-alpine settings, this marker has a typical taxonomic resolution to species-level of between 77 and 93% when applied to small lake catchments (Alsos et al., 2018) and around 33% on the circumpolar scale (Sønstebo et al., 2010).

Low pollen accumulation rates and long-distance transport of pollen from woody, wind-pollinated taxa in arctic-alpine areas often constrain interpretations of local compositional changes and mute the signal from insect-pollinated taxa (Fall 1992; Hicks, 1994; Gajewski et al., 1995; Paus, 2000). However, due to the long history of palynological research and substantial efforts to calibrate relationships between pollen and vegetation representation, detailed and informative records of floristic richness in arctic-alpine regions have been developed based on pollen (e.g. Birks et al., 2016; Felde et al., 2017). When rigorously applied, the analysis of *sedDNA* often detects more species per sample than other palaeoecological methods and it better reflects local plant community composition than pollen (Alsos et al., 2016; Sjögren et al., 2017; Zimmermann et al., 2017a,b; Clarke et al., 2019a; Parducci et al., 2019). However, *sedDNA* analyses may underreport some taxa such as Asteraceae, Cyperaceae and Poaceae (Alsos et al., 2018; Nichols et al., 2018), which are generally well-represented in pollen analyses though they are unable to be distinguished below family level which limits their usage (Sugita, 1994; Pisaric et al., 2001; Oswald et al., 2003). Biases in representation and taxonomic resolution in both *sedDNA* and pollen analyses likely confound richness estimates. In contrast to *sedDNA*, biases in pollen/spore production and/or dispersal rates are well understood thanks to extensive calibration efforts undertaken across diverse regions of the world, and it can therefore provide a more robust, quantitative estimate of plant abundance changes compared to *sedDNA* (Prentice, 1985; Sugita, 1994; Oswald et al., 2003; Marquer et al., 2014). Thus, a combined approach using both proxies may give a more complete reconstruction of past plant communities.

Here we combine a pollen and *sedDNA* record of plant community composition over the last 24,000 years from a sediment core retrieved from the largest and deepest lake in the Polar Ural Mountains (Russian Arctic)—Lake Bolshoye Shchuchye. The chronology and sediment characteristics of the sediment core are described elsewhere (Hafliðason et al., 2019a, b; Regnéll et al., 2019; Svendsen et al., 2019). The core is exceptionally well-dated, with the chronology being based on 27 ¹⁴C AMS dates of plant remains and a sequence of annual laminations (Svendsen et al., 2019). The 24-m long sediment sequence is unique for western Eurasia as it has a high resolution, spanning ca. 24,000 years without any breaks or disturbances. It provides a taxonomically rich plant *sedDNA* record (Clarke et al., 2019b) and thus an excellent opportunity to assess whether the *sedDNA* and pollen records show

similar changes in plant community composition and floristic richness over the past 24,000 years. This study is by far the most detailed comparison to date of the taxonomic overlap and resolution of these two proxies in the reconstruction of past vegetation changes. Further, the combined records provide unprecedented floristic detail that can be used to understand the nature of past plant communities and satisfactorily address issues such as the nature and extent of plant community compositional changes across the Pleistocene-Holocene transition, the responses of different functional groups to Quaternary environmental changes, and temporal trajectories of species richness.

1.1. The Polar Urals—environmental history

The Polar Urals form the northernmost part of the Ural Mountain chain (Fig. 1). The last Eurasian ice sheet complex (British-Irish, Scandinavian, and Svalbard-Barents-Kara Seas ice sheets) attained its maximum extent and volume at ca. 21,000 cal years BP (Hughes et al., 2016), when mean annual temperatures over some parts of the Arctic were as much as 20 °C lower than at present (Dahl-Jensen et al., 1998; Elias et al., 1996; Miller et al., 2010), but relatively warm summer growing season temperatures could support vegetation in ice-free regions (Berger and Loutre, 1991). At their Last Glacial Maximum (LGM) maxima, the ice-sheet complexes covered vast areas of the British Isles, Scandinavia and the Barents-Kara Sea and adjacent regions, yet most of the northern coast of Russia remained ice-free during this glaciation (Svendsen et al., 2004; Hughes et al., 2016). Large parts of the Polar Urals appear to have been ice-free for at least the last 60,000 cal years BP, but there is evidence to suggest that cirque glaciers and probably even larger mountain glaciers existed during the LGM (Mangerud et al., 2008; Svendsen et al., 2019).

Increasing summer insolation due to orbital forcing from ca. 20,000 cal years BP, and later, rising greenhouse gas concentrations, initiated the recession of the Eurasian ice sheet complex, with a noticeable increase in the rate of recession seen by ca. 16,000 cal years BP (Clark et al., 2009; Miller et al., 2010; Hughes et al., 2016). During the early Bølling period, there seems to have been a rapid deglaciation of the ice sheet in the Barents Sea (Brendryen et al., 2020), and by the onset of the Holocene, ca. 11,700 cal years BP, the last ice-sheet remnants were restricted to Scandinavia and Svalbard (Hughes et al., 2016). From ca. 10,000 cal years BP, and lasting until ca. 4000 cal years BP, pollen-based estimates from northern Russia suggest mean July temperatures were at least 1–3 °C higher than present (Andreev and Klimanov, 2000; Salonen et al., 2011). Pollen and plant macrofossil-based evidence suggest that forest trees such as *Picea*, *Pinus*, *Larix*, *Betula* and *Alnus* reached their northernmost extent early in the Holocene (Panova et al., 2003; Paus et al., 2003; Andreev et al., 2005; Jankovska et al., 2006; Salonen et al., 2011; Svendsen et al., 2014). Finds of shallow marine molluscs indicate that summer temperatures were as warm as today in the areas around the Svalbard archipelago as early as ca. 11,000 cal years BP, and that peak summer warmth occurred between ca. 10,200–9200 cal years BP, when July temperatures were 6 °C higher than today (Mangerud and Svendsen, 2018).

1.2. Ecological and biogeographic importance of the Polar Urals

The Polar Urals contain important structural and biogeographic boundaries. They encompass the current forest-tundra ecotone (MacDonald et al., 2008; Shiyatov and Mazepa, 2011), and the present treeline (250–400 m a.s.l.), primarily formed by Siberian larch (*Larix sibirica*), lies nearby Lake Bolshoye Shchuchye (altitude 187 m a.s.l.). Thus, the study site should be sensitive to Holocene

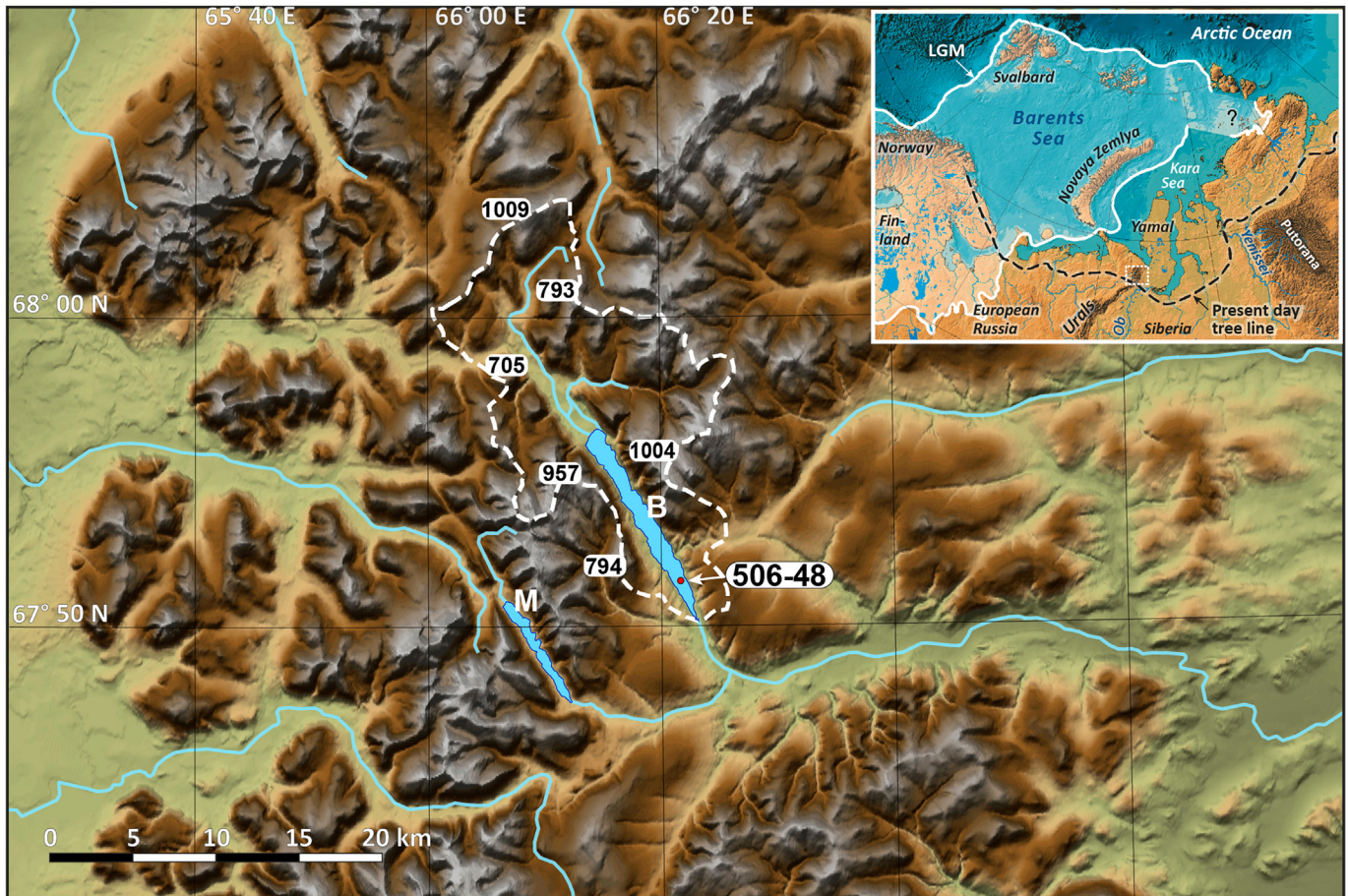


Fig. 1. Location of Lake Bolshoye Shchuchye (B) and its hydrological catchment (dashed white line), alongside its smaller sister lake Maloye Shchuchye (M), in the Polar Urals Mountains of Arctic Russia. Red dot indicates the location where the sediment core (506–48) analysed for *sedaDNA* and pollen was taken. Remaining text indicates the altitude of the highest mountain peaks within the lake's catchment. Map inset shows the ice sheet limit during the Last Glacial Maximum (bold white line) from Svendsen et al. (2004) and the present-day boreal tree line (black dashed line).

climate changes affecting the treeline and its species composition. The Polar Urals also mark the boundary between the floras of the western Siberian and the east European lowlands (Rebristaya, 1977; Morozova et al., 2006; Elven et al., 2011; Eidesen et al., 2013). The latter carries the imprint of post-glacial expansion and recolonization by taxa from ice-free areas, whereas the former has had longer to accumulate species and is far more species-rich (e.g. Brochmann et al., 2013; Stewart et al., 2016). The flora of the Polar Urals is intermediate in richness (Hultén and Fries, 1986; Elven et al., 2011; Clarke et al., 2019b). Given the mountainous terrain, climate conditions vary across small spatial scales, and would have done so in the past. Thus, the area may have played an important role both as a source of populations for westward recolonization of deglaciated terrain and as a refugium for a variety of species, not only during the LGM, but also as conditions changed with deglaciation and the onset of the Holocene interglaciation (see Clarke et al., 2019b).

The full-glacial ecosystem of unglaciated northern Eurasia hosted a rich herbivore fauna (Astakhov, 2004; Hubberten et al., 2004; Sher et al., 2005) and an early human population (Pavlov et al., 2001; Svendsen et al., 2010; Slimak et al., 2011; Pitulko et al., 2017; Hufthammer et al., 2019). A predominantly treeless ecosystem known as 'tundra-steppe' (e.g. Kozhevnikov and Ukraintseva, 1999; Yurtsev, 2001; Zimov et al., 2009), or 'mammoth steppe' (e.g. Guthrie, 1982, 1990; Zimov et al., 2012), extended across the region (e.g. Kaplan et al., 2003; Sher et al.,

2005; Bezrukova et al., 2010; Kuzmina, 2015; Chytrý et al., 2019). With many of the faunal elements now extinct, and widespread vegetation analogues lacking, the structure of the full-glacial vegetation and its relation to the megafauna for which it was forage is still not clearly understood. It remains debated whether the prevailing flora comprised a dry, productive grassland (e.g. Guthrie, 1982, 2001; Zimov et al., 2012), sparsely vegetated Arctic herb communities (e.g. Cwynar, 1982), or a range of communities dominated by forbs and graminoids, with rare dwarf shrubs (e.g. Kienast et al., 2001, 2005; Bigelow et al., 2003; Anderson et al., 2004; Zazula et al., 2007; Chytrý et al., 2019). Small-scale analogues of this full-glacial ecosystem have been proposed from steep, south-facing slopes, rock or fellfield habitats, and dry and/or disturbed sites in Alaska, Yukon and eastern Siberia (Cwynar and Ritchie, 1980; Edwards and Armbruster, 1989; Chytrý et al., 2019). Pollen records from northern Eurasia typically suggest a predominance of graminoids (e.g. Guthrie, 2001; Yurtsev, 2001; Zimov et al., 2012), whereas a large-scale *sedaDNA* survey of 242 sediment samples from 21 sites across the Arctic by Willerslev et al. (2014) questioned the predominance of graminoids, suggesting instead that the importance of forbs in the full-glacial flora has been underestimated. The samples analysed by Willerslev et al. (2014) originated from a range of depositional settings and individually represent only short snapshots in time. Whether similar patterns in plant community composition over the late Quaternary period occur in a single landscape represented by a single site remains to

be tested.

A lack of well-dated, continuous records currently constrains knowledge of the long-term environmental history of the region. Most palaeorecords in the region come from exposures of coastal and riverbank sediment which cover short time windows (e.g. Andreev et al., 1998, 2003; Jankovska et al., 2006). This study aims to provide new, detailed floristic records derived from *sedaDNA* and pollen which can contribute information on the functional and bioclimatic features of the vegetation of the Polar Urals over the late Quaternary interval. The 24-m long sediment sequence from Lake Bolshoye Shchuchye will address several key ecological research questions: what was the composition of the full-glacial flora; was there a difference in the response of different plant functional groups and/or communities to late Quaternary climate variations; and to what extent do *sedaDNA* and pollen show similar changes in plant community composition and temporal trajectories of floristic richness over the past 24,000 years.

1.3. Regional setting

Lake Bolshoye Shchuchye (latitude 67°53'24"N, longitude 66°18'36"E) is located at 187 m a.s.l. in the central part of the Polar Urals mountain chain, ~105 km north-east of the mining town of Vorkuta (Fig. 1). The lake has a catchment area of 215 km², with a deltaic inlet at its northern shore of the River Pyriatanyu and the outlet along its southern shore named the Bolshoye Shchuchya River, a tributary of the Ob River. Steep-sided valley slopes and bedrock faces surround the lake, with mountain peaks reaching 700–1100 m a.s.l. at its north-western shore (Figs. 1 and 2). Compared with smaller lakes, often used for reconstruction of past vegetation communities (e.g. Jacobson and Bradshaw, 1981; Sugita, 2007; Alsos et al., 2016; Voldstad et al., 2020), Lake Bolshoye Shchuchye may capture a signal from a larger area and an elevational range of 187–1100 m a.s.l. When using a lapse rate of 0.7 °C (100 m)⁻¹ (Rolland, 2003), this represents a gradient of 6.4 °C in July air temperature.

Lake Bolshoye Shchuchye was formed by glacial erosion during repeated past glaciations, following weaknesses along ancient NW-SE striking faults. The last major ice cap that covered the lake appears to have deglaciated ca. 50,000–60,000 cal years BP (Svendsen et al., 2019). Present-day climate conditions at Lake Bolshoye Shchuchye are characterised as cold and continental, with a mean summer (June-July-August) temperature of 7 °C (Solomina et al.,

2010). The present-day vegetation mosaic in the catchment of Lake Bolshoye Shchuchye has not been studied in the field and knowledge of the latitudinal and elevational gradients in vegetation composition of the region is poor. The vegetation in the lake's surrounding is for the most part thin and patchy tundra, comprising grasses, dwarf shrubs, sedges, mosses and lichens. Thickets of green alder (*Alnus viridis*) grow on south-facing slopes up to an elevation of around 300 m a.s.l. (Fig. 2). There are no other trees growing within the catchment today, but the lake is situated just north of the regional treeline (Fig. 1 inset) with isolated trees of larch (*Larix sibirica*) observed growing a few kilometres to the southeast of the lake (Svendsen et al., 2019). At the higher elevations in the catchment, the vegetation is discontinuous with alpine herb communities growing on exposed rocky surfaces.

2. Material and methods

2.1. Sediment retrieval and sampling

The 24-m long sediment core that has been analysed (core number 506–48; see Fig. 1) was retrieved in 2009 at a water depth of 105 m from the southern end of the lake (67°51'22.20"N, 66°21'30.07"E). The core was retrieved with a UWITEC piston corer using a combination of 2-m long by 10-cm diameter PVC sample tubes for most sections and 2-m long by 9-cm diameter steel tubes for the deepest sections. Since collection in July 2009, the core sections remained sealed within a cold storage facility until they were opened and longitudinally split in the winter of 2014, when subsamples were taken to be sieved and plant macrofossil remains to be picked for radiocarbon dating. Fig. 3 presents the lithostratigraphy and chronology of the analysed core. The preservation of plant macrofossil remains in the sediment core is very poor, with the plant remains picked for radiocarbon dating being too small for identification (most had a diameter of only 1 mm) and thus had to be combined to meet the minimum sample weight for AMS radiocarbon dating. The core sections were sealed and placed back into cold storage until the winter of 2015 when subsamples for *sedaDNA* and pollen were taken. The sediment core was subsampled for *sedaDNA* at ~15-cm resolution and for pollen at ~24-cm resolution in a laminar flow cabinet in a clean laboratory at the Centre for Geobiology and Microbiology, Department of Earth Sciences, University of Bergen, Norway, using sterile tools, a full bodysuit, facemask, and gloves. Where possible, pollen samples were taken from the same levels or immediately adjacent to the subsamples taken for *sedaDNA*. Subsampling took place in the presence of subsampling controls (open water samples) in order to detect potential laboratory contamination (Clarke et al., 2019b). Following the protocol described by Parducci et al. (2017), the outer 10 mm of sediment was avoided and a ~20 g subsample was retrieved from inside the freshly exposed core centre only.

2.2. Sedimentary ancient DNA (*sedaDNA*) analysis

Full details of the extraction, PCR amplification, sequencing and taxonomic assignment of *sedaDNA* is presented by Clarke et al. (2019b). DNA was extracted from 153 sediment subsamples taken from the 24-m long sediment core. In addition, a total of 35 negative controls were analysed which contained no sediment and were used to monitor for contamination at each step of the process: nine negative controls taken during sediment subsampling (open tubes containing DNA-free water left in fume hood during subsampling), 17 negative DNA extraction controls (all stages of DNA extraction were performed, but no sediment was added) and nine negative PCR controls (DNA-free water was added in replacement of DNA template during PCR amplification). Each DNA extract and negative



Fig. 2. Photograph of Lake Bolshoye Shchuchye in the Polar Ural Mountains taken in July 2009 from the southern end of the lake, where sediment core number 506–48 (analysed in this study) was taken. The dark green bushes growing in the lower elevations of the valley are green alder (*Alnus viridis*). Photo: J.I. Svendsen.

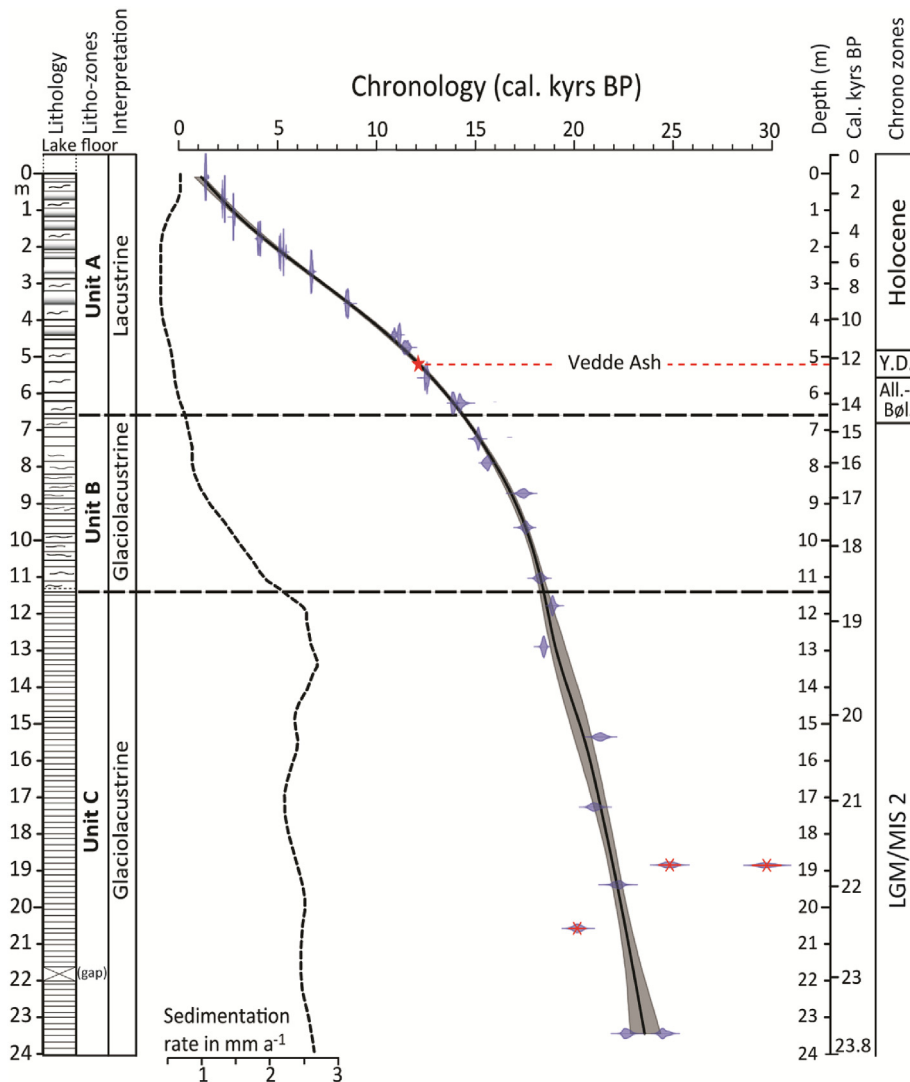


Fig. 3. Lithostratigraphy and chronology of core 506–48 from Lake Bolshoye Shchuchye, which was analysed for *sedaDNA* and pollen (adapted from Regnéll et al. (2019) and Svendsen et al. (2019)). The sedimentation rate (dashed line) and the age model (solid line) are based on 27 AMS ^{14}C ages on plant macrofossils (Svendsen et al., 2019), the occurrence of the Vedde Ash (dashed red line; Hafliðason et al., 2019a), and in lithostratigraphic Unit C, counting of varves (Regnéll et al., 2019). The calibrated radiocarbon dates are plotted with 95% confidence intervals. Three radiocarbon ages (indicated by a red cross) are more than two standard deviations outside the curve for the age–depth model and are therefore considered outliers. Lithological Unit C comprises finely laminated sediments or rhythmites which are interpreted as annual varves. The rhythmites are occasionally interrupted by turbidites (5–20 mm). Unit B is a transitional unit that comprises both distinct rhythmic laminations similar to those in Unit C, with more diffusely laminated sections interrupted by turbidites (5–20 mm). Unit A is a diffusely layered and partly massive unit. It contains somewhat thicker turbidites (10–30 mm) than the two lower units.

extraction control was independently amplified in eight PCR repeats (replicates) using uniquely tagged generic primers that amplify the *trnL* P6 loop of the plant chloroplast genome (Taberlet et al., 2007). The eight PCR repeats per *sedaDNA* sample were given equal weight for all of the statistical analyses presented in this paper. The number of DNA sequence reads across the eight PCR repeats were summed to give total DNA reads per *sedaDNA* sample. The dataset of DNA sequence reads was also converted to presence-absence data to calculate the number of PCR repeats (out of eight) a taxon was detected within per *sedaDNA* sample.

In order to minimise any erroneous taxonomic assignments, only taxa with a 98% match, or greater, to a reference sequence were retained. As the taxonomic coverage of plant taxa in the reference library for the Polar Urals region is incomplete, we used a cut-off of 98% match, instead of 100%, to allow identification to at least genus level for species currently lacking in the reference library. We further removed sequences (sequences belonging to

Pinus, *Juniperus*, *Acer*, *Allium*, *Artemisia*, *Cucurbitaceae*, *Capsicum*, *Quercus*, *Persea*, *Taxus baccata* and *Viola biflora*) that displayed higher average reads in the negative extraction or PCR controls than in the lake sediment samples they were present.

2.3. Pollen/microfossil analysis

In total, 105 pollen samples were analysed from core number 506–48. Subsamples of 1 cm³ were prepared using standard methods (acid–base–acid–acetolysis; HF; Fægri and Iversen, 1989) and were mounted in glycerol. Four *Lycopodium* spore tablets ($n \approx 18,584$ per tablet) were added to each sample to calibrate pollen concentration estimation. Where possible, at least 300 pollen grains of terrestrial taxa were identified per sample using taxonomic keys (Fægri and Iversen, 1989) and an extensive reference collection at the Department of Biological Sciences, University of Bergen. The combination of a thin and patchy vegetation cover, a

rapid sedimentation rate, and an absence of trees producing large amounts of pollen for much of the record make it incredibly challenging to reach a higher pollen count at this site, particularly during the full-glacial part of the record. Six samples (860 cm, 1420 cm, 1630 cm, 1920 cm, 1980 cm and 2020 cm) had low pollen concentrations and sums were therefore lower (<100 grains). The pollen sum ($\sum P$) includes all terrestrial pollen and spore taxa (including Cyperaceae) and excludes aquatic taxa. The identification of *Picea* sp. stomata followed the taxonomic key of Sweeney (2004).

2.4. Floristic richness

A comparison of richness (i.e. number of taxa) between samples with different count sizes can be biased, as the chance of detecting rare taxa increases with count size (Birks and Line, 1992). We therefore rarefied the *sedadna* and pollen data to estimate the number of terrestrial plant taxa that would have been detected if the count had been standardised among samples. Rarefaction analysis was performed using the minimum count size in the Vegan (Oksanen et al., 2017) package for R (R Core Team, 2017) using the function *rarefy*. Rarefaction curves were produced using the function *rarecurve* in the Vegan package. Due to very low counts (<100 grains), the six pollen samples mentioned above (Section 3.3) were removed from the rarefaction analysis. The minimum count size used for rarefaction was 19,115 DNA reads and the eight PCR repeats per *sedadna* sample were included with equal weight, with total DNA reads across the repeats summed to give a total DNA read count per sample. For pollen, the minimum count size used for rarefaction was 108 grains. It is important to note that the low total pollen counts compared to other palynological studies likely lead to an underrepresentation of total floristic richness estimates but as stated earlier in Section 3.3., a higher pollen sum approaching 1000 grains (as suggested by Odgaard, 2001) is impossible at this site due to the low pollen accumulation rates. We thus focus on the general temporal trajectories in floristic richness instead of absolute numbers.

2.5. Statistical analyses

To compare the timing of key plant community compositional changes between the two records, a stratigraphically constrained sum of squares (CONISS) cluster analysis (Grimm, 1987) was performed in the Tilia v. 2.6.1 software (Grimm, 2011) on all plant taxa identified by *sedadna* and pollen. Quantitative data measures of the number of PCR repeats per *sedadna* sample and pollen percentage data were used for the cluster analysis. An ordination was then performed on the full *sedadna* and pollen records separately using a non-metric multidimensional scaling (NMDS) analysis using the same quantitative data (i.e. number of PCR repeats per *sedadna* sample and pollen percentage data) in the PAST v. 3.19 software package (Hammer et al., 2001).

3. Results

3.1. *SedaDNA* and pollen record

We obtained around 75 million paired-end raw DNA sequences for the 153 *sedadna* samples analysed from Lake Bolshoye Shchuchye. Following the post-identification filtering steps (removing sequencing artefacts, sequences with <98% match to reference library and sequences which displayed higher average frequency in negative controls than in lake sediment samples, described in Clarke et al. (2019b)), we retained around 19 million reads, representing 134 vascular plant and 28 bryophyte taxa. Of

these, 40% were identified to species level, 45% to genus, and 15% to a higher taxonomical level (e.g. subtribe, tribe, family; Supplementary Table S1). Inferences to species level in the *sedadna* record were made for *Dryas octopetala* and *Empetrum nigrum* based on the present-day native distributions of species within these genera.

Microfossil analysis detected 114 vascular plant taxa, plus *Sphagnum*, across the 105 samples analysed from Lake Bolshoye Shchuchye. Where possible, pollen grains were identified to species level based on their morphological characteristics, such as the distinction of *Lycopodium annotinum* and *Juniperus communis* from other species within their genus. In other cases, inferences to species level were made for some taxa, including *Picea abies*, *Dryas octopetala* and *Empetrum nigrum*, based on known native and past distributions of species within these genera (Supplementary Table S1). In general, most of the *Betula* pollen grains encountered are considered to represent the tree *Betula pubescens* rather than shrub forms of this taxon due to the overall size of the grains. We also noted two different types of *Alnus* pollen throughout the record which are thought to be *A. incana*-type and *A. viridis*-type. A more detailed investigation of the diameter-pore depth ratio and proportion of the different categories of *Betula* and *Alnus* is underway and will be presented in a later paper. Of the total 115 taxa, 29% were identified and/or inferred to species level, 30% to the genus, 10% to the family and 31% to a pollen type above family level.

A combined approach of *sedadna* and pollen analysis resulted in an additive total of 239 taxa of 89 families identified to varying taxonomic levels (Supplementary Table S1). In total, 31 families were shared between *sedadna* and pollen. Of the 119 vascular plant taxa, plus *Sphagnum*, detected by pollen analysis, 18 were also identified by *sedadna* to the same taxonomic level. In this section, we summarise the key changes observed in the combined 24,000-year *sedadna* and pollen record before comparing, in detail, the taxa identified by each of the proxies and their pattern of occurrences (Section 4.2), along with the dominance (Section 4.3) and diversity (Section 4.4) of different functional groups based on *sedadna* and pollen.

A stratigraphically constrained cluster (CONISS) analysis revealed five distinct zones in the pollen data from Lake Bolshoye Shchuchye, which shows high similarity to those identified in the *sedadna* data (Supplementary Fig. S1). One main exception is that an additional zone was identified in the *sedadna* data between 13,000 and 11,700 cal years BP which is not as visible in the pollen data, although we note a complex pattern in clustering around this interval in the pollen results (zone BS3; Supplementary Fig. S1). We impose six distinct zones (named BS1 to BS6) identified based on *sedadna* to the pollen record from Lake Bolshoye Shchuchye to investigate the similarities and differences between the two records in terms of plant community compositional changes over the past 24,000 years. A description of the main characteristics of the *sedadna* and pollen record for each of the six zones is provided in Supplementary Table S2.

Reworked microfossils, including Dinophyceae cysts and pre-Quaternary trilete spores are present in the earliest part of the record from ca. 24,000–17,000 cal years BP accounting for between 0 and 0.04% of the total pollen sum, with a few sporadic occurrences lasting until ca. 12,000 cal years BP (range = 0–0.02% of total pollen sum; Supplementary Table S1). Mass movement and sedimentation of older material limits an interpretation of the local vegetation composition during this period, and this will be discussed later in Section 4.2.2.

The full-glacial period in our dataset from Lake Bolshoye Shchuchye (24,000–17,000 cal years BP) is characterized by an abundance of herbaceous tundra taxa in both the pollen (Fig. 4) and the *sedadna* (Figs. 5–7; also see Clarke et al., 2019b) records. A high

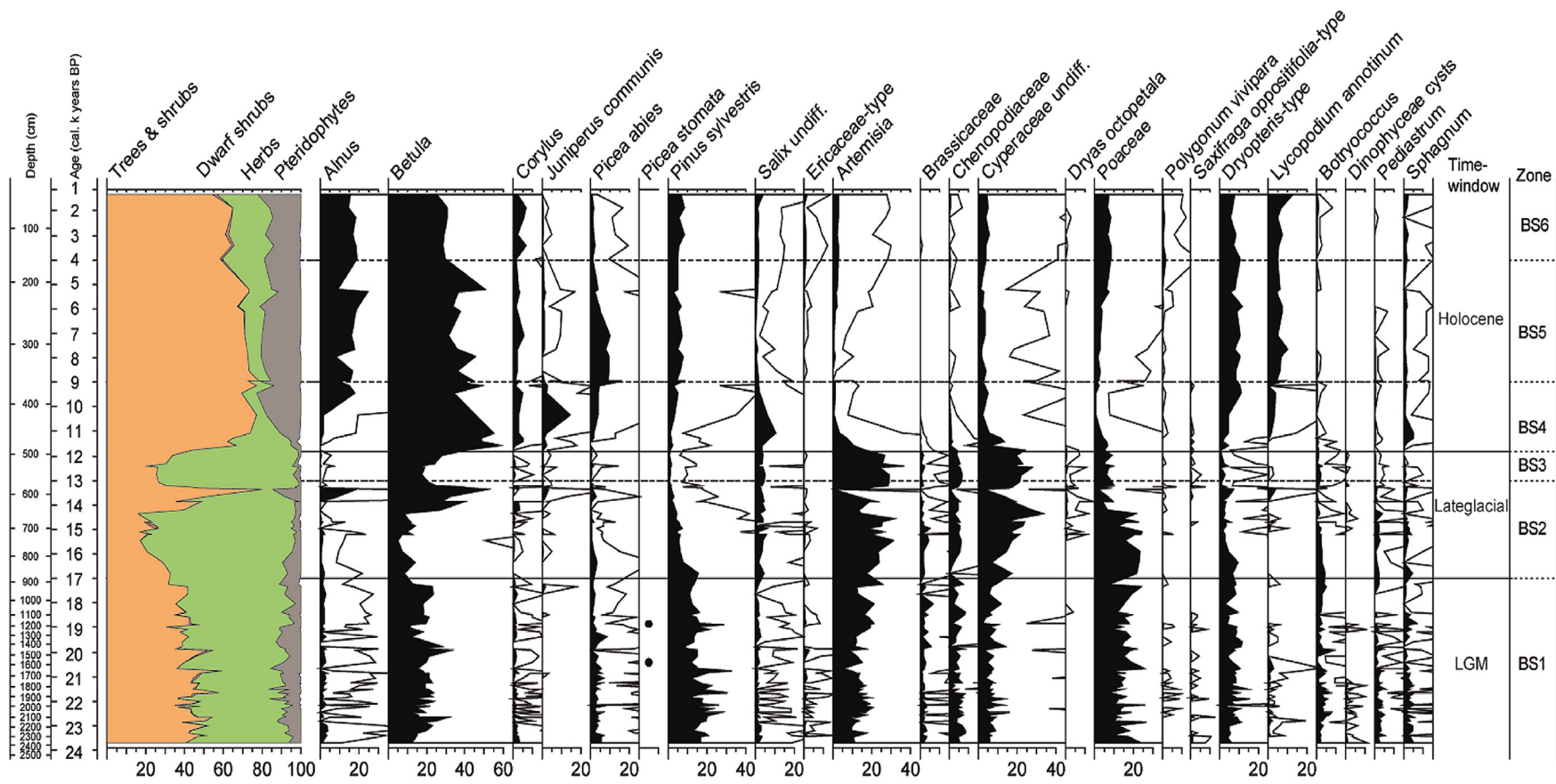


Fig. 4. Summary percentage pollen diagram of key plant taxa for Lake Bolshoye Shchuchye with assemblage zones BS1 to BS6 indicated. Pollen percentages are based on the sum of total terrestrial pollen and spores (ΣP). Proportion of aquatics are calculated based on the sum of total terrestrial pollen and spores plus aquatics ($\Sigma P + \Sigma \text{aquatics}$).

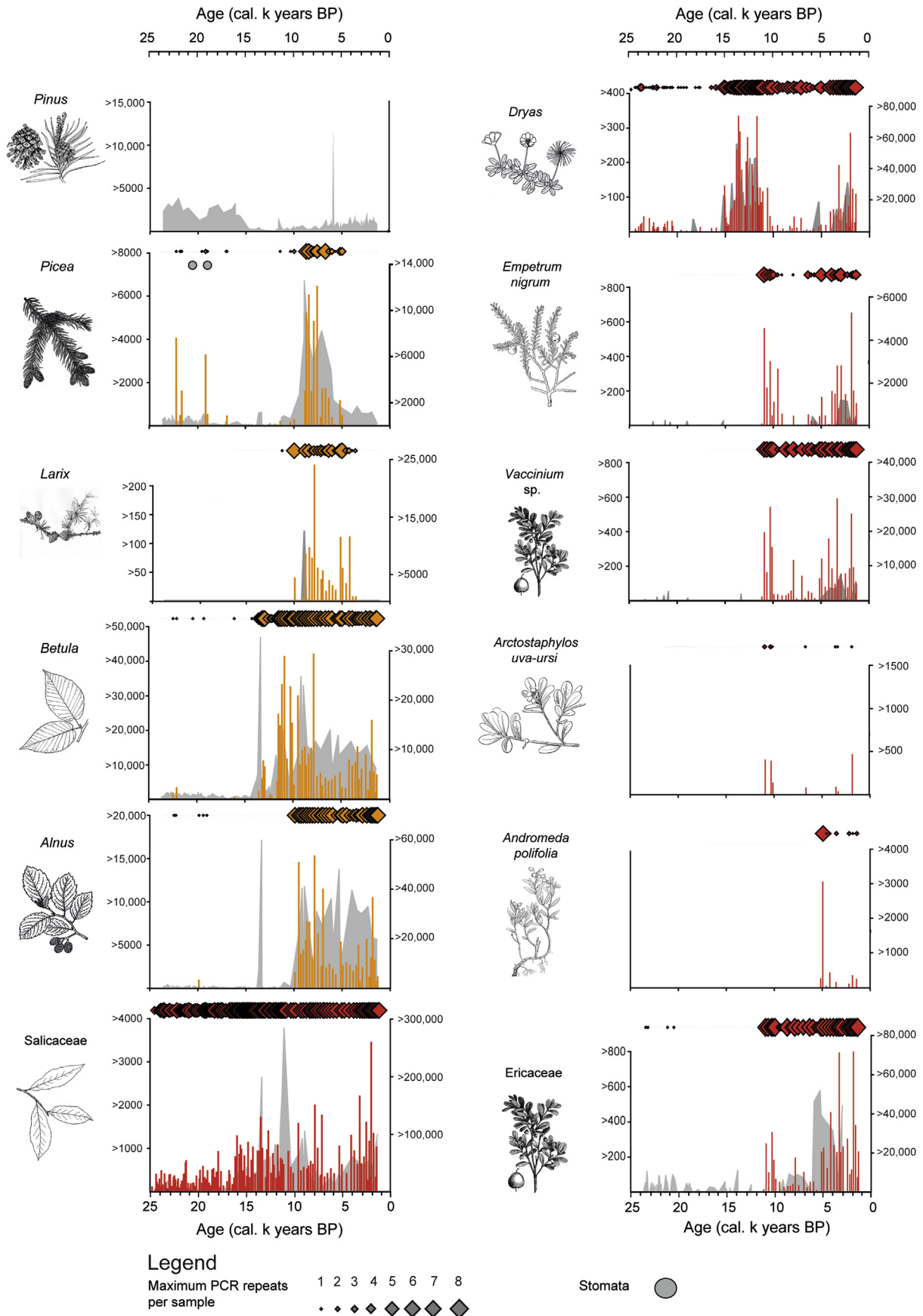


Fig. 5. Selected woody plant taxa presented as total DNA reads per sample (histogram; right-hand y-axis) and maximum number of PCR repeats (diamond symbols) for the Lake Bolshoye Shchuchye record. Grey shaded area depicts pollen concentration (grains/cm³) values (left-hand y-axis). Grey closed circle indicates presence of *Picea abies* stomata. Note that the height of the y-axis varies among panels.

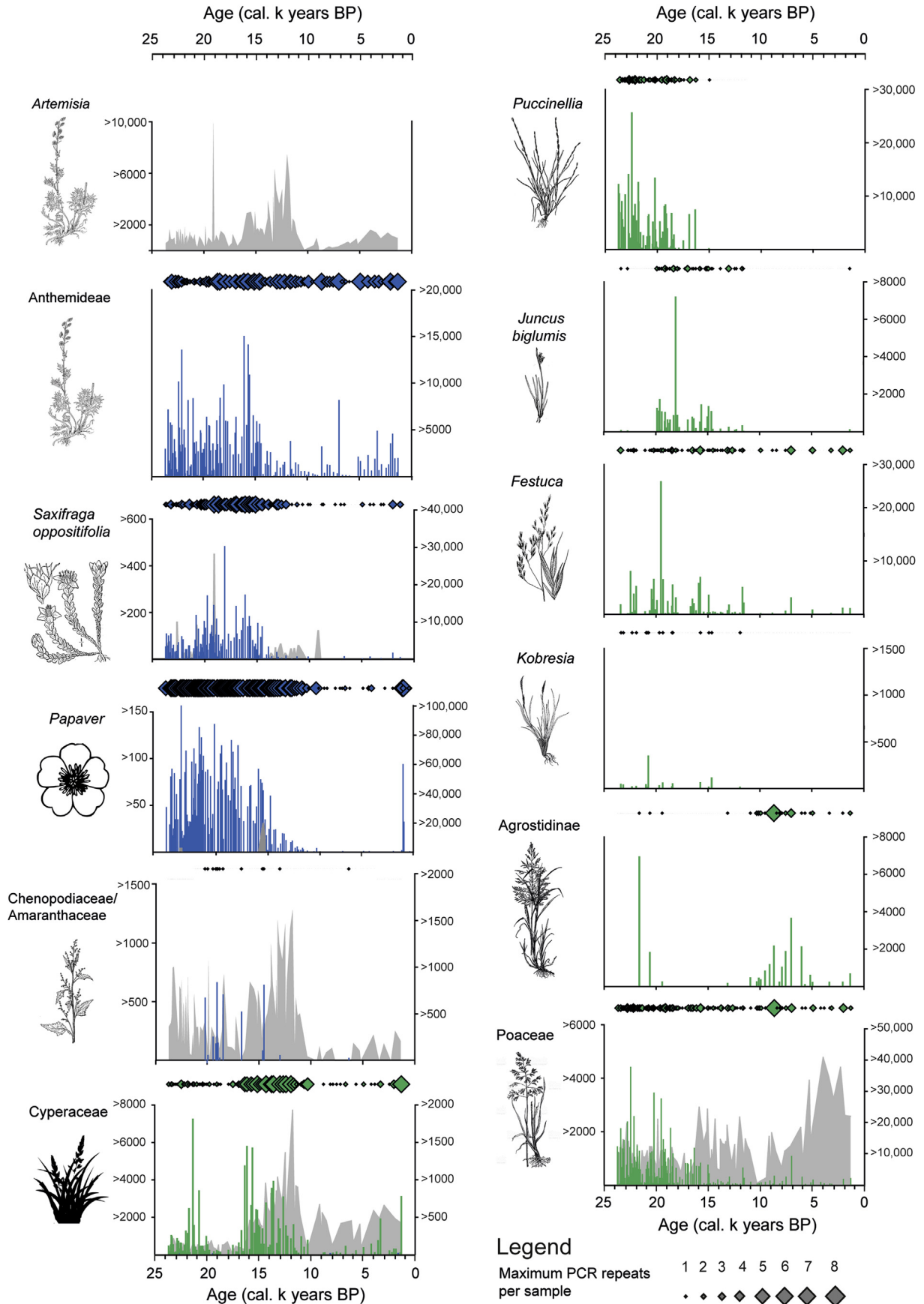


Fig. 6. Selected herbaceous plant taxa presented as total DNA reads per sample (histogram; right-hand y-axis) and maximum number of PCR repeats (diamond symbols) for the Lake Bolshoye Shchuchye record. Grey shaded area depicts pollen concentration (grains/cm³) values (left-hand y-axis). Note that the height of the y-axis varies among panels.

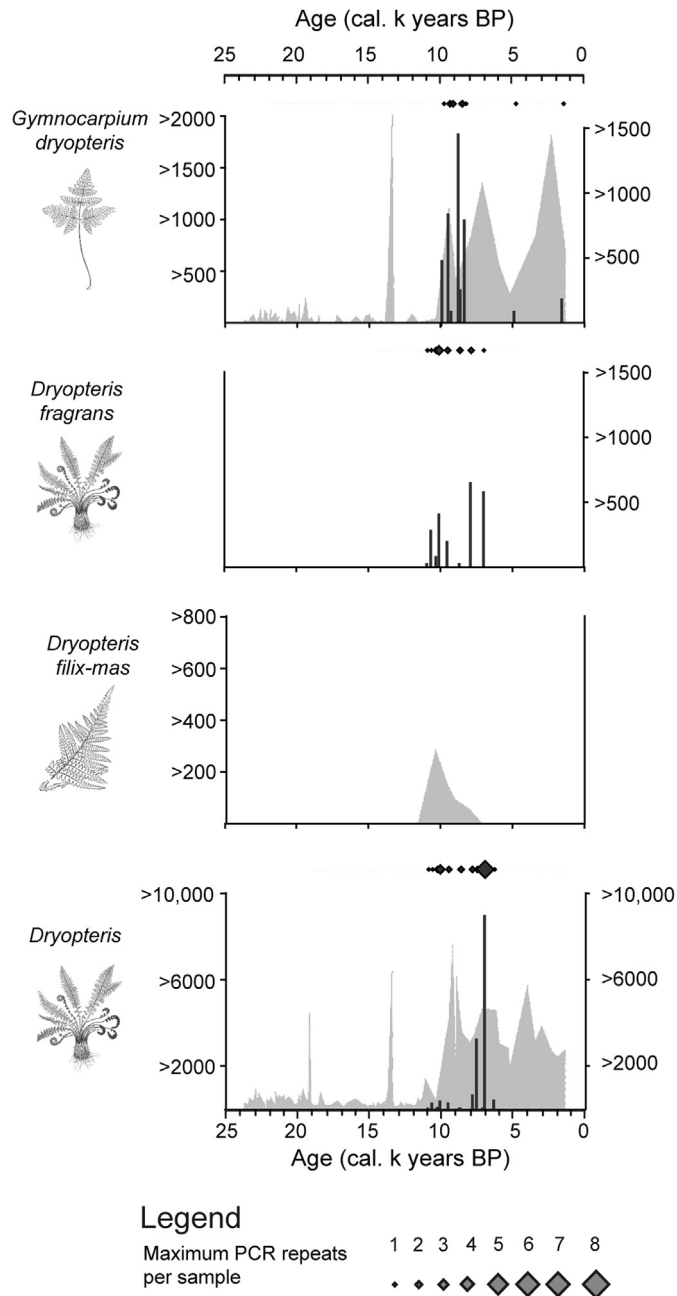


Fig. 7. Selected fern taxa presented as total DNA reads per sample (histogram; right-hand y-axis) and maximum number of PCR repeats (diamond symbols) for the Lake Bolshoye Shchuchye record. Grey shaded area depicts pollen concentration (grains/cm³) values (left-hand y-axis). Note that the height of the y-axis varies among panels.

diversity (32 taxa) of arctic-alpine herbs, such as *Draba pauciflora*, *Saxifraga cespitosa*, *Saxifraga oppositifolia*, *Papaver* and *Juncus biglumis*, are detected within the *sedaDNA* during this interval. Anthemideae is common in all full-glacial *sedaDNA* samples and potentially represents *Artemisia*. *SedaDNA* sequences belonging to *Artemisia* were identified but were subsequently filtered out of the dataset due to their higher average abundance in the negative controls compared to the sediment samples. High pollen percentages are observed for *Artemisia* (15–30%), Poaceae (10–25%) and Chenopodiaceae/Amaranthaceae (5–10%) throughout this interval (Figs. 4 and 6). Notably, the latter taxon only had a few occurrences

in the *sedaDNA*. The coniferous trees *Pinus sylvestris* and *Picea abies* are recorded in the pollen record during the full-glacial interval (average influx rates of ~240 grains cm² year⁻¹ and ~55 grains cm² year⁻¹, respectively; see Supplementary Figs S2 and S3), but percentages do not exceed 20% of the total sum. From ca. 17,000 cal years BP, a distinct increase in *Carex sedaDNA* is evident, followed a little later by an increase in Cyperaceae pollen ca. 16,000 cal years BP (Fig. 6).

The mat-forming dwarf shrub *Dryas* becomes more common in the *sedaDNA* record from ca. 15,000 cal years BP, and the *Dryas* increase is followed by the rise in *Betula sedaDNA* from sporadic occurrence to sustained presences of up to eight PCR repeats and *Betula* pollen from 10% to 55% of the total pollen sum (Fig. 5) from ca. 14,000 cal years BP. Average pollen influx rates of *Betula* increase slightly from ~280 grains cm² year⁻¹ in the full-glacial period (ca. 24,000–17,000 cal years BP) to ~290 grains cm² year⁻¹ between ca. 17,000–13,000 cal years BP, with an anomalous spike (>3000 grains cm² year⁻¹) between ca. 14,000 and 13,000 cal years BP (Supplementary Fig. S4). The rise in *Betula* is interrupted by a rapid but short-lived decline to low values for this taxon in both the *sedaDNA* and pollen between ca. 13,000–12,000 cal years BP, with pollen influx values of ~220 grains cm² year⁻¹ observed. Dwarf shrubs such as *Empetrum*, *Vaccinium* sp. and *Arctostaphylos uva-ursi* first appear in the *sedaDNA* from ca. 11,000, whereas small amounts of Ericaceae pollen is observed from the beginning of the record ca. 24,000 cal years BP (Fig. 5). From ca. 10,000 cal years BP, *Alnus* increases in both the *sedaDNA* and pollen records, with pollen influx values increasing from <10 grains cm² year⁻¹ to >250 grains cm² year⁻¹ during this interval (Fig. 5; Supplementary Fig. S5).

The coniferous tree *Picea* begins to increase in the *sedaDNA* from ca. 10,000 cal years BP, alongside many boreal herbs such as *Alchemilla*, *Anthriscus sylvestris* and *Filipendula ulmaria* and ferns such as *Dryopteris fragrans* and *Gymnocarpium dryopteris* (Figs. 6 and 7). This is followed a little later by an increase in *Larix* in the *sedaDNA* from ca. 9000 cal years BP. Woody taxa such as *Alnus*, *Picea abies* and *Corylus* and the fern *Dryopteris* reach their highest percentages in the pollen record between ca. 10,000 and 4000 cal years BP (Fig. 4). *Picea* reaches pollen influx rates of between 65 and 180 grains cm² year⁻¹ between around 10,000 and 6000 cal years BP (Supplementary Fig. S3). *Corylus* was not detected in the *sedaDNA* record, and the pollen record also includes the continued presence of other woody taxa such as *Betula* and *Pinus sylvestris* since the beginning of the record ca. 24,000 cal years BP. *Betula* pollen influx rates reach ~760 grains cm² year⁻¹, on average, between ca. 10,000 and 4000 cal years BP. *Picea* begins to decline in both the *sedaDNA* and pollen records from ca. 7000 cal years BP, with a complete withdrawal of coniferous forest taxa (e.g. *Picea*, *Larix*, *Dryopteris fragrans*, *Gymnocarpium dryopteris*, *Filipendula ulmaria*) from the *sedaDNA* record altogether by ca. 4000, leaving shrub-tundra taxa (e.g. *Betula*, *Dryas*, *Empetrum*, *Vaccinium* sp.) dominant. In the pollen record, the decline in *Picea* (average pollen influx ~35 grains cm² year⁻¹) is followed by a decline in *Betula* after ca. 4000 cal years BP (average pollen influx ~720 grains cm² year⁻¹), while woody taxa such as *Alnus*, *Corylus* and *Pinus sylvestris* maintain high values (Fig. 4).

3.2. Comparison between taxa recorded by pollen and *sedaDNA*

3.2.1. Woody plant taxa

There is high similarity in the pattern of occurrence of woody taxa, such as *Picea*, *Betula*, *Alnus* and *Dryas* (*D. octopetala*), between pollen concentrations and total DNA sequence reads (Fig. 5), and between pollen percentages and the proportion of *sedaDNA* PCR repeats (out of eight; Supplementary Fig. S6). The distinct, short-lived decline in *Betula* between ca. 12,600–11,500 cal years BP

revealed by *sedaDNA* also occurs in the pollen record. The scattered occurrences of *Picea* in the *sedaDNA* record between ca. 21,000–18,000 cal years BP are mirrored in the pollen record, in addition to two finds of *Picea abies* stomata at ca. 20,400 cal years BP and 18,800 cal years BP, which overlap with this interval (Fig. 5). The *sedaDNA* record shows a clear pattern of occurrence of *Larix sibirica* between ca. 9000 and 3500 cal years BP, whereas only one pollen grain of *Larix* was found throughout the pollen record at ca. 9000 cal years BP (Fig. 5).

SedaDNA detected *Dryas* throughout the record, including prior to ca. 17,000 cal years BP when this taxon first appears in the pollen record. *Dryas* displays its highest values in both the *sedaDNA* and the pollen record between ca. 15,000 and 10,800 cal years BP. Similarly, both records show very low values between 10,800 and 5000 cal years BP and subsequent increases at ca. 4000 cal years BP (Fig. 5). Unlike the *sedaDNA* record, which was able to resolve a range of dwarf shrub taxa (e.g. *Arctostaphylos uva-ursi*, *Empetrum nigrum*, *Vaccinium uliginosum*, *V. vitis-idaea/myrtilus*) within the Ericaceae family, only pollen of Ericaceae-type, *Empetrum nigrum* and *Vaccinium*-type could be resolved (Fig. 5).

3.3. Herbaceous plant taxa

SedaDNA detected a higher diversity of herbaceous plant taxa and, in general, identifications were at a higher taxonomic level than was achieved by pollen (Fig. 6; Supplementary Fig. S7). Of the main herbaceous plant taxa identified by both *sedaDNA* and pollen, many show a similar timing of occurrence. For the grasses, the pollen registers only Poaceae, whereas *sedaDNA* resolved taxa within this family, and the record shows turnover in taxonomic dominance over time (Fig. 6). Spores of *Dryopteris*-type occur in high abundance throughout the record, whereas ferns (including *Dryopteris* sp.) were only detected by *sedaDNA* in the period between ca. 10,000 and 4000 cal years BP (Fig. 7), when the coniferous trees *Picea* and *Larix* were also detected in the *sedaDNA* (Fig. 5; Section 4.2.1).

3.4. Clubmoss and bryophyte taxa

Only spores belonging to the genus *Sphagnum* were detected whereas *sedaDNA* detected a diverse bryophyte flora which varied over time (Supplementary Fig. S8). For clubmosses

(Lycopodiopsida), *sedaDNA* detected only Lycopodiaceae whereas pollen analysis detected five taxa (*Diphasiastrum*, *Selaginella selaginoides*, *Lycopodium annotinum*, *Lycopodium undiff.* and *Huperzia selago*), although many of them at low abundances (Supplementary Fig. S8).

3.5. Compositional changes in plant communities over time

Ordination using an NMDS revealed a distinct clustering of *sedaDNA* samples for three different time-windows (Fig. 8a; LGM, Lateglacial and Holocene) across the record, with the exception of five Holocene-aged samples which display considerable variability from the remaining samples in this time-window. These five samples (56.5 cm, 202 cm, 282 cm, 401 cm, 349 cm) represent anomalously high peaks in floristic richness values compared to the rest of the *sedaDNA* samples analysed (see Section 4.4). The same metric for pollen revealed a less pronounced grouping of samples, with a larger overlap observed between samples belonging to the different time-windows than was observed for the *sedaDNA* (Fig. 8b).

Several shifts in the dominance of plant functional groups occur in both the *sedaDNA* and pollen records over the past 24,000 years (Fig. 9). Terrestrial forbs (e.g. *Papaver*, *Draba*, *Bistorta vivipara*) dominate the *sedaDNA* between ca. 24,000 and 17,000 cal years BP, accounting for 72% of total DNA reads on average. In contrast, forbs (e.g. *Artemisia*, Chenopodiaceae/Amaranthaceae, Brassicaceae, *Rumex acetosa*, *Thalictrum*) accounted for only 25% of the total pollen sum, whereas trees and/or tall shrubs (e.g. *Betula*, *Alnus*, *Pinus*) account for 45% for the same period.

By ca. 17,000 cal years BP, and lasting until ca. 11,700 cal years BP, the proportional abundance of trees and/or tall shrubs (e.g. *Betula*, *Alnus*, Salicaceae, *Picea*) increases in both the *sedaDNA* and pollen records, with a distinct interval of high dwarf shrub (e.g. *Dryas*, *Vaccinium* sp., *Arctostaphylos uva-ursi*) percentages evident in the *sedaDNA* record between ca. 15,000 and 11,000 cal years BP (Fig. 9). A sustained decline in the *sedaDNA* of forbs from around 67%–10% of total DNA reads is observed between ca. 17,000 and 11,700 cal years BP, which is in contrast to the pollen record where short-lived fluctuations in forb pollen percentages are observed over the same interval until a rapid decline at ca. 11,700 cal years BP. After ca. 11,700 cal years BP, both the *sedaDNA* and pollen records are dominated by trees and tall shrubs with some forbs. The

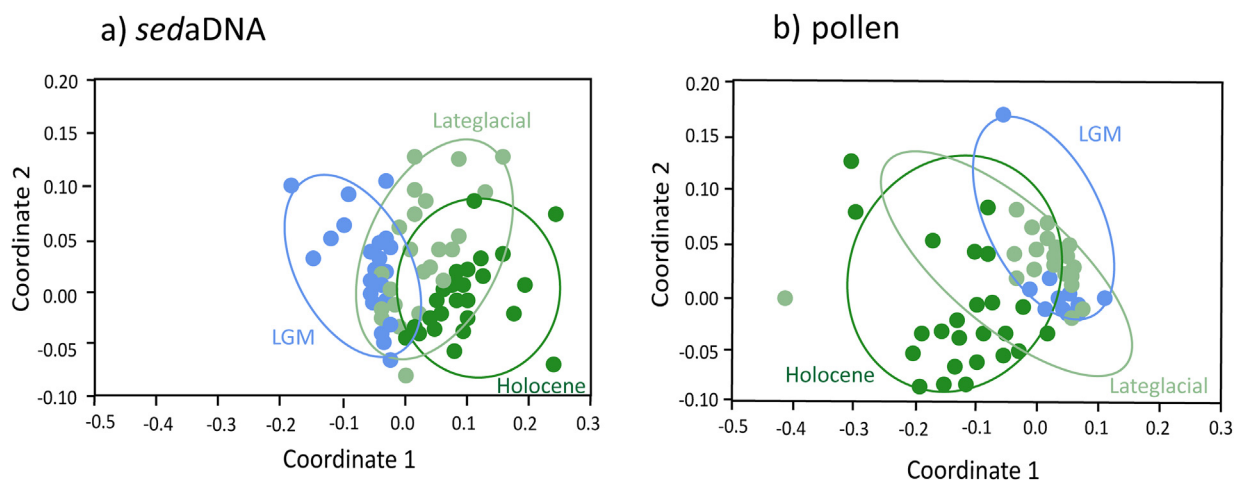


Fig. 8. Non-metric multidimensional scaling (NMDS) scatter plot of *sedaDNA* (a) and pollen samples (b) showing differentiation between samples in terms of plant community composition. Sample are colour-coded according to three time-windows (based on our dataset): Last Glacial Maximum (LGM; 24,000–17,000 cal years BP; 2400–880 cm depth), Lateglacial (17,000–11,700 cal years BP; 880–488 cm depth) and Holocene (11,700–1300 cal years BP; 488–0 cm depth). Ellipses show within-community (each time-window) variability of *sedaDNA* and pollen samples. The ordination plots with taxon names indicated are given in Supplementary Figs S9 and S10.

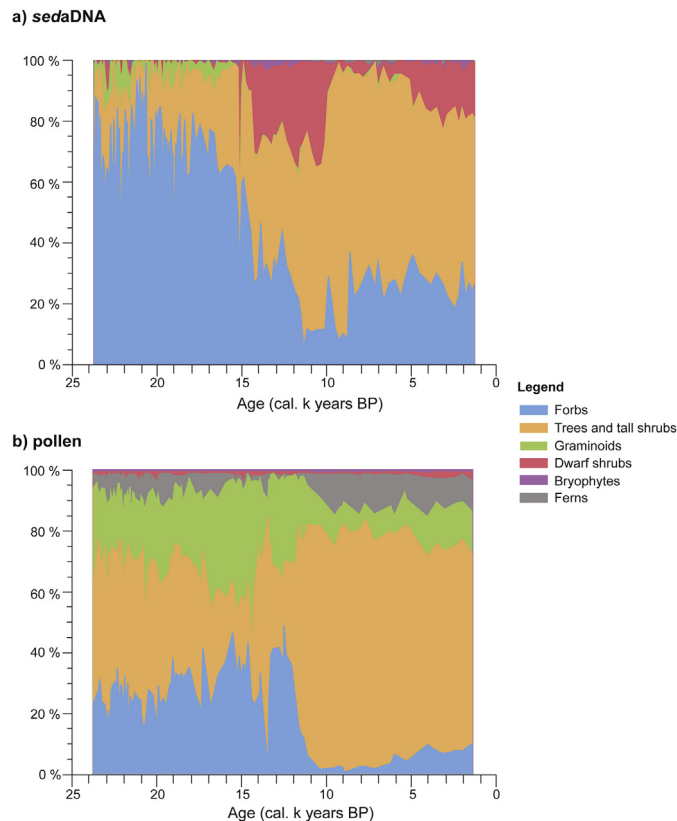


Fig. 9. Summary of the percentage abundance of plant functional groups in the *sedaDNA* and pollen records from Lake Bolshoye Shchuchye. Where a) functional groups as a percentage of total *sedaDNA* reads per sample and b) functional groups as a percentage of the total sum of terrestrial pollen and spores (ΣP).

proportional abundance of graminoids (e.g. Poaceae, Cyperaceae) also remains high in the pollen record (up to 17%), whereas graminoids (e.g. Poaceae, Cyperaceae, Agrostidinae) only encompass 1–2% in the *sedaDNA* after ca. 11,700 cal years BP. *Dryopteris*-type fern spores are found consistently throughout the record, accounting for between 1 and 15% of the total sum, whereas fern taxa such as *Dryopteris fragrans*, *Gymnocarpium dryopteris* and *Thelypteris palustris* are only present within the *sedaDNA* record between ca. 11,000 and 5000 cal years BP and account only for a small percentage (<3%) of total DNA reads during this interval (Fig. 9).

3.6. Floristic richness

The pollen record from Lake Bolshoye Shchuchye demonstrates a relatively stable, rarefied floristic richness over the past 24,000 years (Fig. 10a), although we note that pre-rarefaction richness values show a slight increase towards the later part of the Holocene which is the result of higher overall pollen sums in this part of the record compared to the full-glacial interval when pollen accumulation rates are low. The *sedaDNA* record, on the other hand, demonstrates a sustained, long-term increase in rarefied floristic richness until the early-Holocene (ca. 9000 cal years BP) when it peaks and then levels out into the later part of the Holocene, with the exception of five anomalously high peaks (Fig. 10a). The counts of DNA sequences and pollen grains for each sample differed by several orders of magnitude, with *sedaDNA* samples reaching saturation in all time periods (Supplementary Fig. S11) while those of pollen do not (Supplementary Fig. S12).

For angiosperms and gymnosperms only (Fig. 10b), mean rarefied floristic richness of LGM-aged samples (ca.

24,000–17,000 cal years BP; 2400 - 880 cm) based on *sedaDNA* (16 taxa) is comparable to pollen (14 taxa). After ca. 17,000 cal years BP, a distinct and consistent rise in floristic richness is observed in the *sedaDNA* record, whereas the pollen record shows little change over time (Mean = 13 taxa; Stdev = 1.8; Fig. 10b). For *sedaDNA*, the largest step change in floristic richness occurs between LGM (24,000–17,000 cal years BP; 2400 - 880 cm) and Lateglacial-aged (17,000–11,700 cal years BP; 880 - 488 cm) samples, with a 106% increase observed (Fig. 10b). Floristic richness increased by a further 6% between Lateglacial (17,000–11,700 cal years BP; 488 - 0 cm) and Holocene-aged (11,700–1300 cal years BP) samples.

In all three of the time-windows investigated (Fig. 10c), *sedaDNA* detected a greater number of forbs (61–81 taxa) than pollen (40–46 taxa) and resolved more graminoid and bryophyte taxa (Fig. 10c). For woody taxa, *sedaDNA* identified more dwarf shrub taxa within the Holocene interval than were identified by pollen, but pollen detected a number of trees and/or tall shrub taxa across all three time-windows (15–20 taxa) that were not detected by *sedaDNA* (6–8 taxa).

3.7. Comparison to existing pollen records from the Polar Urals and adjacent regions

The high sedimentation rate (2.2–2.6 mm year⁻¹) between ca. 24,000–17,000 cal years BP (Svendsen et al., 2019) in Lake Bolshoye Shchuchye (Fig. 3) allows an investigation of plant community composition at high temporal resolution during the LGM. The mean sampling interval was ca. 60 years and ca. 100 years for *sedaDNA* and pollen analysis, respectively, during the LGM interval. This is by far the most continuous and highest resolution record covering the LGM from the Polar Urals and adjacent regions, to date (Fig. 11). The pollen record from Lake Gerdizty, located in the eastern foothills of the Polar Urals, goes back further in time than Lake Bolshoye Shchuchye's record, but it is at low temporal resolution (ca. 65,000 years BP in ~2.6 m of sediment) and the authors could not rule out the possibility of a hiatus during the LGM (Svendsen et al., 2014).

In terms of the nature of key compositional changes, there is a general coherence amongst late Quaternary pollen records from the Polar Urals and adjacent regions and those seen at Lake Bolshoye Shchuchye (Fig. 11). The complexity of compositional changes during the Lateglacial interval, the Holocene establishment of *Picea* and the subsequently reversion back to shrub-tundra communities in the late-Holocene to present-day are seen across all records from the region. There is variation in the timing of compositional changes, however, which is likely the result of the degree of uncertainty in ¹⁴C dating and the different latitude and/or altitude of the sites (Fig. 11). The addition of *sedaDNA* at Lake Bolshoye Shchuchye brings new information which is overlooked by pollen analyses concerning the changing composition and diversity of herbaceous, dwarf shrub and fern communities and the Holocene establishment of *Larix sibirica* (*Larix* is underrepresented by pollen and only one *Larix* pollen grain was identified at Lake Bolshoye Shchuchye; see Section 4.2.1).

4. Discussion

4.1. Comparing the *sedaDNA* and pollen records

4.1.1. Source of *sedaDNA* and pollen

Lake Bolshoye Shchuchye has a large and topographically complex catchment with gentle to steep slopes, high rates of erosion and considerable riverine input (Fig. 2; Svendsen et al., 2019), all of which probably contribute to the floristically rich *sedaDNA* and pollen records obtained from this site. High rates of erosion could result in reworking processes and the redeposition of

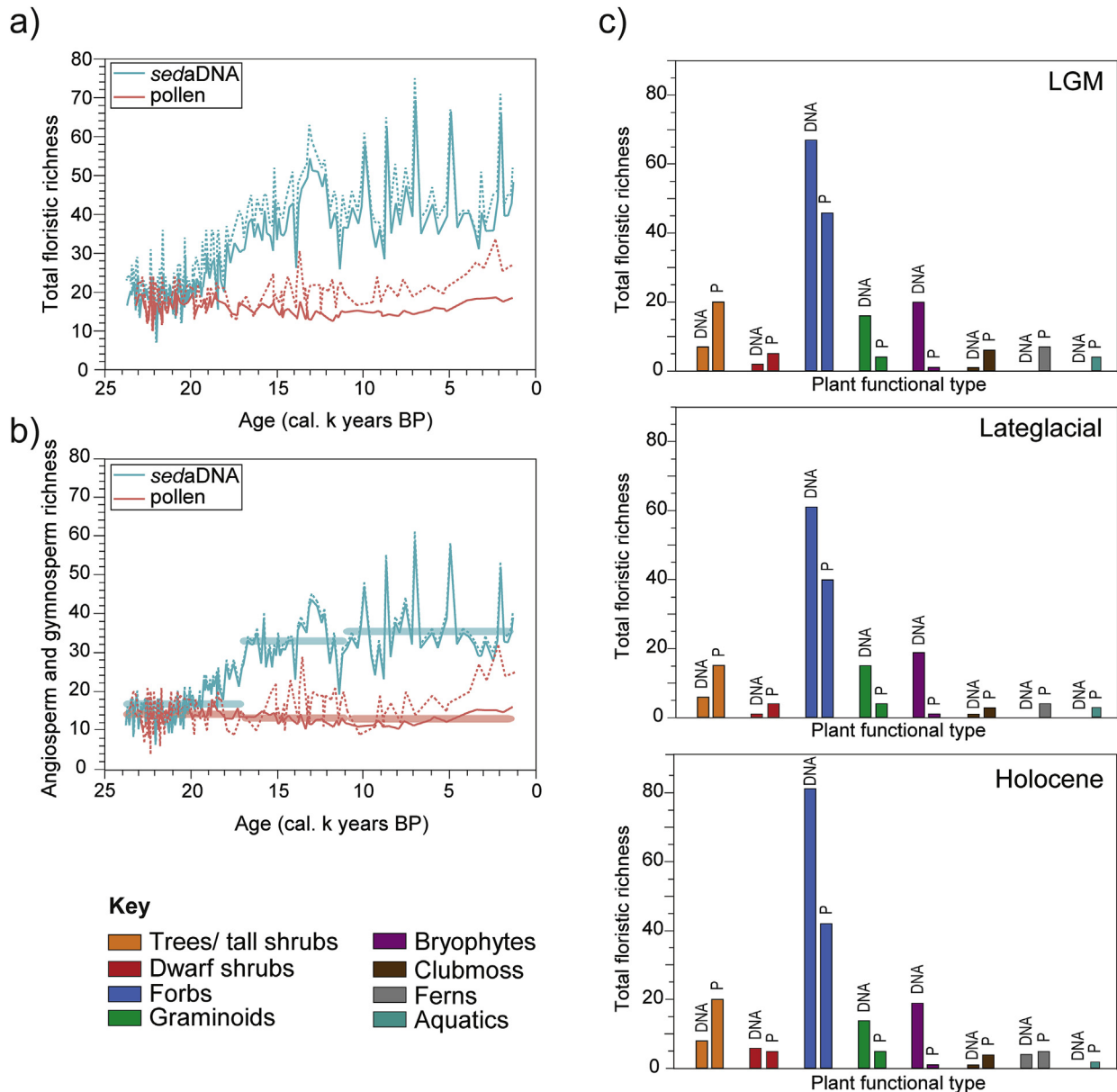


Fig. 10. Measures of floristic richness (number of taxa per sample) based on *sedaDNA* and pollen from Lake Bolshoye Shchuchye. a) Total floristic richness pre-rarefaction (dashed lines) and post-rarefaction (bold lines) for all taxa detected by *sedaDNA* and pollen. b) Floristic richness of angiosperms and gymnosperms pre-rarefaction (dashed lines) and post-rarefaction (bold lines) with mean (colour bars) for three time-windows: Last Glacial Maximum (LGM; 24,000–17,000 cal years BP; 2400–880 cm depth), Lateglacial (17,000–11,700 cal years BP; 880–488 cm depth) and Holocene (11,700–1300 cal years BP; 488–0 cm depth) based on *sedaDNA* and pollen. c) Floristic richness pre-rarefaction within plant functional groups based on *sedaDNA* (DNA) and pollen (P) for three time-windows; Last Glacial Maximum (LGM; 24,000–17,000 cal years BP; 2400–880 cm depth), Lateglacial (17,000–11,700 cal years BP; 880–488 cm depth) and Holocene (11,700–1300 cal years BP; 488–0 cm depth).

old microfossils, and we note that pre-Quaternary trilete spores are observed (range = 0–0.04% of total pollen sum) in the record prior to ca. 17,000 cal years BP (see Section 4.1). The DNA signal at Lake Bolshoye Shchuchye likely reflects sediment inputs from a much larger source area than lakes used previously in *sedaDNA* studies (e.g. Epp et al., 2015; Pansu et al., 2015; Alsos et al., 2016, 2018). Both the *sedaDNA* and pollen sources likely receive considerable inputs via the river and/or inwash events, which represent catchment-scale rather than regional-scale inputs. In contrast to the *sedaDNA*, the pollen record from Lake Bolshoye Shchuchye also has inputs via long-distance transport of pollen from wind-pollinated, woody taxa that are not present in the lake catchment today but are in the regional flora (e.g. *Pinus*, *Picea*) and others that may be extra-regional (e.g. *Corylus*).

4.1.2. Taxonomic resolution and detection ability

Previous comparisons between *sedaDNA* and pollen have shown limited overlap in taxonomic composition (e.g. Pedersen et al., 2013; Parducci et al., 2015). However, our data from Lake Bolshoye Shchuchye demonstrate considerable overlap in hierarchical clustering (CONISS) analyses (Supplementary Fig. S1), the dominance of plant functional groups over the past 24,000 years (Fig. 9) and in the temporal pattern of occurrence of key plant taxa such as *Picea*, *Betula*, *Alnus*, *Cyperaceae*, *Poaceae*, *Caryophyllaceae*, *Gymnocarpium dryopteris* and *Sphagnum* (Figs. 5–7). The potentially larger source area for *sedaDNA* at Lake Bolshoye Shchuchye, compared with lakes used previously for *sedaDNA* studies, may be one reason for the high overlap observed between the two proxies: at Bolshoye Shchuchye, the *sedaDNA* samples a larger landscape

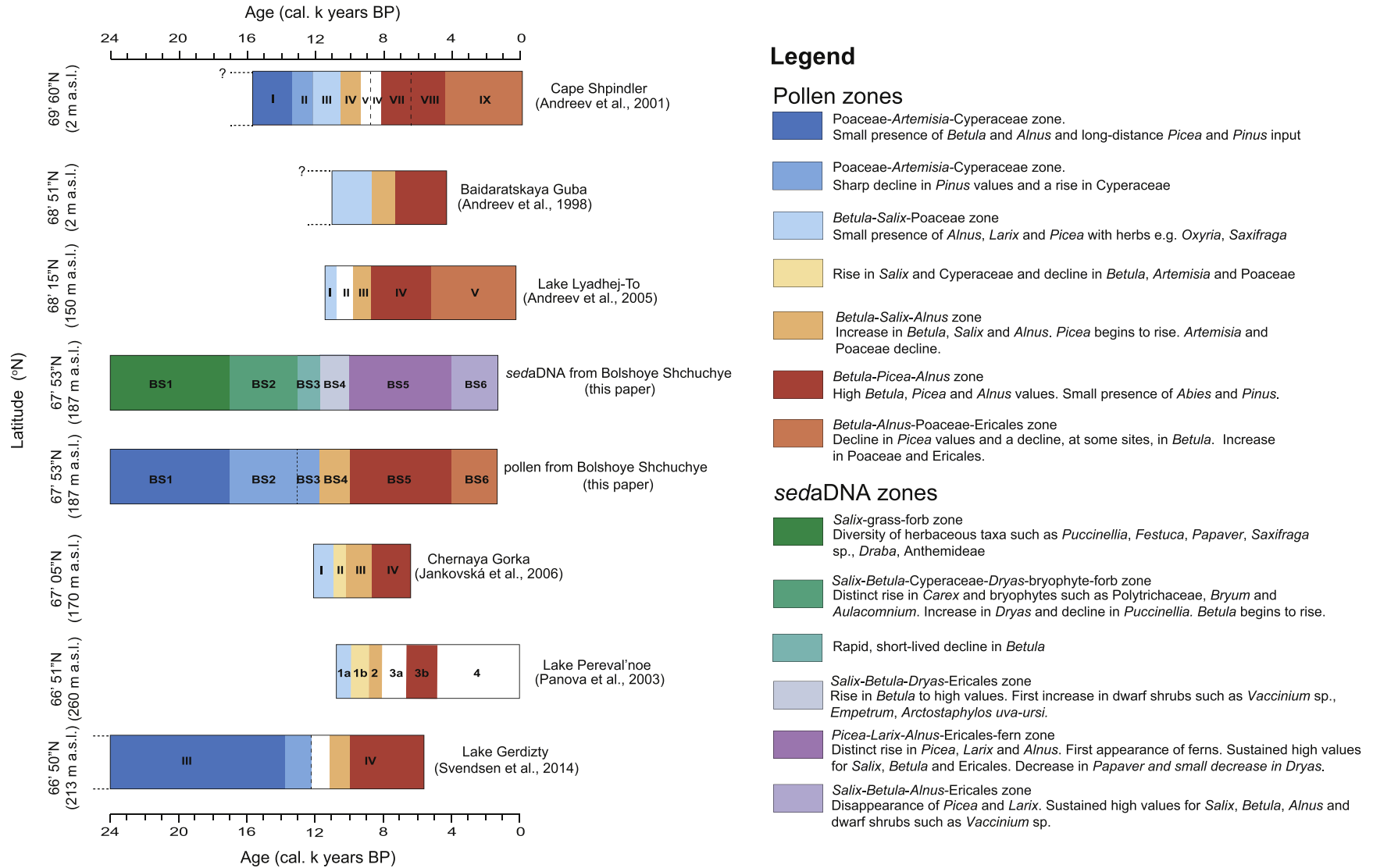


Fig. 11. A comparison of the timing and nature of key changes in floristic composition over the late Quaternary period from Lake Bolshoye Shchuchye (sedaDNA and pollen) and previously published pollen records from the Polar Urals and adjacent regions. The records are ordered from top to bottom based on the latitude of the site. Black dashed line indicates the record goes further back in time, with question mark symbols indicating uncertainty in the chronology of the basal part of the record. White boxes indicate pollen assemblage zones that could not be correlated amongst records. Classification of assemblage zones is predominantly based on those defined by the authors in the original publication and the original names for local pollen assemblage zones (LPAZ's) are given. In some instances, we assigned additional zones to records where similar changes in key plant taxa and/or assemblage composition are evident from the pollen diagrams given in the original publications but were not classified as LPAZ's.

area than is typical via its large hydrologic catchment.

The two proxies differ, however, regarding the functional groups they can identify and/or resolve. *SedaDNA* was found to be superior at detecting forb, graminoid, bryophyte and dwarf shrub taxa (Fig. 10c), functional groups that are typically poorly resolved and/or represented by their pollen. For example, *sedaDNA* was able to resolve taxa within the Ericaceae family (e.g. *Arctostaphylos uva-ursi*, *Vaccinium uliginosum*, *V. vitis-idaea/myrtillus*); these taxa were detected in the *sedaDNA* from ca. 11,000 cal years BP, which is considerably earlier than the main rise in Ericaceae pollen (ca. 5000 cal years BP). On the other hand, the pollen record detected a higher diversity of tall shrub and/or tree taxa than *sedaDNA*; this is, however, primarily the result of long-distance transport of wind-pollinated woody taxa. Thus, comparison of the patterns of occurrence of woody, anemophilous taxa in the pollen record with those in the *sedaDNA* record could help to differentiate between local/catchment presence and long-distance dispersal (i.e., probable local/catchment absence).

Several taxa show limited overlap in their pattern of occurrence in the *sedaDNA* and pollen, of which two (*Dryopteris*-type and *Larix*) are known to have unusually high or low representation in palynological records respectively. *Dryopteris*-type fern spores are detected, often in high abundance, throughout the record whereas fern *sedaDNA* was only detected between ca. 10,000 and 5000 cal years BP. Spores are often not representative of fern abundance as they are highly resistant to breakdown and often mark episodes of erosion (Wilmhurst and McGlone, 2005a, b). *Larix* is notorious for its low pollen productivity and underrepresentation in pollen records (Hansen et al., 1996; Niemeyer et al., 2017). *SedaDNA* was able to clearly resolve the establishment of *Larix sibirica* (Fig. 5) near the lake between ca. 9000 and 4000 cal years BP, whereas only one pollen grain of *Larix* was identified (see Section 4.2.1).

4.1.3. Floristic richness and dominance of plant functional groups

Another difference between the *sedaDNA* and pollen records is their long-term trends in floristic richness (Fig. 10a–b), with *sedaDNA* demonstrating a sustained, long-term increase until the early-Holocene (ca. 9000 cal years BP), while the pollen record showed little change in rarefied floristic richness over time. It is possible that the observed pattern in floristic richness based on *sedaDNA* could be controlled by DNA preservation levels in the sediments. The dataset from Lake Bolshoye Shchuchye suggests this is not the case however, as richness appears to stabilise from the early Holocene (with the exception of a few anomalous peaks) towards the most recent samples, with little change that could be attributed to better DNA preservation (Clarke et al., 2019b). The rarefaction curves for *sedaDNA* and pollen indicate that sequencing depth was sufficient for *sedaDNA* as all samples reached saturation (Supplementary Fig. S11), whereas the pollen samples did not reach saturation (with the exception of one sample at 22,214 cal years BP; Supplementary Fig. S12) and thus there was insufficient sampling effort which likely leads to an underestimation of floristic richness based on pollen. Our dataset highlights the challenge of obtaining reliable estimates of floristic richness based on pollen from large lakes that have large hydrologic catchments, high rates of sedimentation, and are situated within a predominantly treeless, thin and patchy vegetation cover.

There are very few records that reconstruct floristic richness from pollen data (palynological richness) spanning as far back in time as the LGM. Paus et al. (2003) estimated palynological richness for the past ca. 20,000 cal years BP from lake and peat deposits from the Timan Ridge but conclude that richness estimates were strongly affected by long-distance dispersal and/or reworking of pollen. Records from northern Scandinavia span the Lateglacial to

Holocene and demonstrate a rapid increase in floristic richness over the Pleistocene-Holocene transition (ca. 12,000–8000 cal years BP), with spatially and temporally inconsistent trends characterizing the later Holocene interval (Seppä, 1998; Berglund et al., 2008a, 2008b; Birks and Birks, 2008; Felde et al., 2017). Records from central Scandinavia show that species richness has remained rather stable, with no long-term trends observed over the Holocene interval (Giesecke et al., 2012). We calculated palynological richness from the detailed pollen record of Ager (2003) from Zagoskin Lake situated on St. Michael Island in northeast Bering Sea (Supplementary Fig. S13). The record extends back to the LGM and the lake is located beyond the present-day forest limit. Changes in palynological richness (pre- and post-rarefaction) at Zagoskin Lake show a similar pattern to those observed based on pollen from Lake Bolshoye Shchuchye (Fig. 10) with little change in palynological richness over the late Pleistocene to Holocene interval, with the exception of a step-change increase in richness observed ca. 29,000 cal years BP (~110 cm; see Supplementary Fig. S11).

A dominance of woody taxa producing high amounts of pollen (e.g. *Pinus*, *Picea*, *Betula*) at the expense of insect-pollinated, entomophilous forbs is a common issue in pollen records from high northern latitudes and likely leads to an underestimation (and muted signal) of floristic richness based on pollen (Lamb and Edwards, 1988; Gajewski, 2015). Moreover, in large lakes with large source areas for pollen such as Lake Bolshoye Shchuchye, the probability of detecting insect-pollinated taxa is even more reduced than in smaller lakes. The analysis of *sedaDNA* may provide improved estimates of floristic richness compared to those based on pollen. As the *sedaDNA* signal is less sensitive to 'swamping' by dominant woody plant taxa, it can often resolve plant taxa within groups that are poorly represented by pollen (e.g. dwarf shrubs, grasses, bryophytes) and total richness estimates are not limited by counting time (Clarke et al., 2019a). A *sedaDNA* record from Bolshoy Lyakhovsky Island (New Siberian Archipelago) demonstrates similar trends to those observed from *sedaDNA* at Lake Bolshoye Shchuchye, with a distinct increase in floristic richness over the Pleistocene-Holocene transition (MIS 2–1; Zimmermann et al., 2017b).

The diversity patterns shown by the *sedaDNA* from Lake Bolshoye Shchuchye are also consistent with those of Willerslev et al. (2014) who document an increase in floristic diversity between the time windows of the LGM and Holocene and highlight a predominance of forbs in the LGM vegetation mosaic. Willerslev et al. (2014) used data from disparate sites representing different periods of time, the identity of which changed considerably between the late Pleistocene and the Holocene (predominantly yedoma sites in the former, but additional lake and mire sites in the latter). These locality changes may have contributed to the observed increase in diversity. In contrast, the dataset from Lake Bolshoye Shchuchye provides a geographically consistent and continuous record of floristic richness changes from a single landscape represented by a single site.

Consistent with the findings of Willerslev et al. (2014), forbs remain the most dominant plant functional group in the *sedaDNA* for each of the time windows (LGM, Lateglacial and Holocene; see Fig. 10c) at Lake Bolshoye Shchuchye. Whether the forb dominance in such *sedaDNA* records is proportional to that in the vegetation is less clear. Current thinking from DNA calibration studies suggests that forbs are overrepresented in the DNA signal within sediments. Explanations, which are not mutually exclusive, include greater fine-root turnover in forbs (Yoccoz et al., 2012), and the observation that the polymerase used during PCR has a bias in favour of the amplification of forb DNA (Nichols et al., 2018). In contrast, forbs are often underrepresented in pollen records (see above) but, in steppe environments, dense forest cover can be masked by the dominance

of herbaceous pollen such as *Artemisia*, Chenopodiaceae and Poaceae (Beer et al., 2007). We note these taxa are highly abundant in our pollen record while they are either entirely absent (sequences belonging to *Artemisia* were filtered out of the *sedDNA* dataset due to their high abundance in the negative controls) or only present in small amounts in the *sedDNA*. Until biases related to the representation of certain functional groups within the DNA signal are understood, interpretations of their dominance within the full-glacial vegetation mosaic will remain tentative. The actual abundance of forbs on the landscape likely lies somewhere between the pollen and the *sedDNA* estimates. Pollen has the potential to uncover more information on plant abundance with the use of pollen calibration studies (Sugita, 2007; Hellman et al., 2008; Niemeyer et al., 2015).

Our results from Lake Bolshoye Shchuchye demonstrate that *sedDNA* can significantly augment the information gained by pollen analysis and *vice versa*. In the following sections, we bring together the insights gained from the two records, addressing aspects of plant community composition during the LGM and through the dynamic environmental changes of the late-Quaternary interval.

4.2. Vegetation history inferred from the combined record

4.2.1. A diverse arctic-alpine herb flora during the Last Glacial Maximum (LGM) which comprised more tundra taxa than steppe taxa

An open, treeless vegetation characterises the LGM interval (ca. 24,000–17,000 cal years BP) at Lake Bolshoye Shchuchye, with a high diversity of arctic-alpine forbs plus grasses in the *sedDNA*, high Poaceae and *Artemisia* in the pollen and with the sub-shrubs *Dryas* (assumed here to be *D. octopetala*) and *Salix* (assumed to be a dwarf form) also consistently present in the *sedDNA* (Figs. 5–7). The floristic composition of *sedDNA* and pollen samples within this period is broadly consistent with the two previous LGM records from the region (Fig. 11), with the exception that *sedDNA* at Lake Bolshoye Shchuchye contributes more detail on the composition of a highly diverse arctic-alpine herbaceous flora. The vegetation mosaic at Lake Bolshoye Shchuchye also included a few taxa that hint at a steppic element in the flora: *Ephedra* and *Puccinellia* in the *sedDNA* and a dominance of graminoids, Chenopodiaceae/Amaranthaceae and *Artemisia* in the pollen record - though *Artemisia* is also common in some tundra communities (Edwards and Armbruster, 1989). *Artemisia* pollen is found in high abundance during this interval at Lake Gerdzity on the eastern foothills of the Urals (Svendsen et al., 2014) and Cape Shpindler on the Taymyr Peninsula much further to the east (Fig. 11; Andreev et al., 2001). Sequences belonging to the tribe Anthemideae are well represented in the *sedDNA* record during this interval, yet Chenopodiaceae/Amaranthaceae is rare in the *sedDNA* suggesting that, for the most part, Chenopodiaceae/Amaranthaceae pollen is likely long-distance dispersed (Fig. 6). *Kobresia*, which occurs sporadically in this portion of the *sedDNA* record, characterises a macrofossil flora dated to ca. 20,000 cal years BP from northwest Alaska described by Goetcheus and Birks (2001) as “dry tundra”. Several *Kobresia* species are also dominant in high-elevation, herbaceous plant communities of the Tibetan Plateau: “arctic-alpine pastures” and “alpine steppe” (Miehe et al., 2019), characterized by cool, dry growing seasons. The *sedDNA* also includes grass genera such as *Festuca*, but such genera have large ecological ranges that encompass both steppe and tundra and are thus harder to characterise. *SedaDNA* detected several forbs and graminoid taxa (Fig. 6) that were rare or even absent in the pollen record (e.g. *Papaver*, *Draba*, *Saxifraga oppositifolia*, *Bistorta vivipara*, *Puccinellia*, *Festuca* and *Juncus biglumis*). Many of these reflect arctic-alpine environments.

The balance of the evidence from both proxies is that the flora was characterised more by tundra forbs than steppe forbs, thus challenging previous interpretations based on pollen of a predominance of cold- and drought-adapted steppe taxa across unglaciated Eurasia (e.g. Kaplan et al., 2003; Sher et al., 2005; Bezrukova et al., 2010; Kuzmina, 2015; Chytrý et al., 2019).

4.2.2. A full-glacial *Picea* population?

The scattered occurrence of *Picea* pollen and *sedDNA* between 21,000 and 18,000 cal years BP (~1700 - 1010 cm depth), together with the observation of two *Picea abies* stomata (Fig. 5), raises questions. It is possible that the occurrence of *Picea* pollen during the LGM interval originates from long-distance dispersal (Hicks, 1994; Gajewski et al., 1995). The present-day northern limit for *Picea* is approximately 40–50 km south of Lake Bolshoye Shchuchye, and isolated stands occur in the lowlands of the Pechora basin ca. 600–650 km to the southwest of the lake (Pravdin, 1975; Kremenetski et al., 1998). Studies of *sedDNA* and pollen suggest that *sedDNA* of *Picea* does not derive from pollen (Niemeyer et al., 2017; Parducci et al., 2017; Sjögren et al., 2017), and finds of its stomata within sediments are considered to represent strong evidence for local presence (Ammann et al., 2014). Pollen grains of *Picea* do contain cpDNA, however, so there is a finite possibility that this could be introduced into the sediment matrix. The average frequency of *Picea* in negative controls in the *sedDNA* clean laboratory at Tromsø University Museum over the past few years is 1.99% (SD = 2.52, range 0–6.25 for n = 1360 PCR repeats of 170 negative control samples; Alsos et al., 2020). Thus, while the frequency of *Picea* in the Holocene part of the Lake Bolshoye Shchuchye core is far above the background contamination rate and most likely represents local presence of trees within the catchment, the *sedDNA* record from the LGM interval is inconclusive, due to low numbers of DNA reads in LGM samples. However, the average DNA reads of *Picea* within the sediment samples it was present (3194 DNA reads) was considerably higher than its average reads across all of the negative controls analysed for the Lake Bolshoye Shchuchye dataset (986 DNA reads) and thus, *Picea* is included in the final dataset (see Supplementary Table S1).

A survey of plant macrofossils from across northern Eurasia demonstrates early finds of *Picea* from 25,000 cal years BP in the southern part of the Ural Mountains, but sites in the Polar Urals do not show *Picea* presence until around 13,000 cal years BP (Binney et al., 2009). *Picea* macrofossils dated to ca. 19,500 cal years BP have been documented from a floodplain site located ~500 km east at the same latitude as Lake Bolshoye Shchuchye, but as Binney et al. (2009) caution, macrofossils from floodplain sites have a higher probability of being reworked or transported a long distance. Except for Saliceae, the *sedDNA* detected no tree and/or tall shrub taxa during this interval nor any other thermophilic taxa that could support the necessary inference of favourable growing conditions for *Picea* at this time.

Although we cannot discount the evidence of *Picea* presence during this interval, there are several reasons why its occurrence could be an artefact of contamination. The *Picea* *sedDNA* could represent contamination by DNA reagents, laboratory materials or by pollen carried into the DNA laboratories (Alsos et al., 2020), and in this study, *Picea* DNA was found in the negative extraction and water controls (Supplementary Table S1). However, this does not explain the presence of stomata. Unfortunately, the preservation of plant macrofossil remains is poor within our core, with examination yielding only fragmented, unidentifiable plant remains, so the *Picea* data remain equivocal.

Re-sedimentation of older material might explain the scattered occurrences of its pollen, *sedDNA* and stomata at roughly the same time (but not exactly the same sample depths). Reworked

microfossils (Dinophyceae cysts and pre-Quaternary trilete spores) are present in this part of the record, indicating reworking of older sediment deposits. These scattered occurrences of *Picea* pollen, *sedaDNA* and the stomata do occur within a continuous sequence of varves (Fig. 3), but we cannot discount the possibility that older sediment particles containing *Picea* remains (the catchment remained ice-free for most of the last glaciation was certainly ice-free during the Eemian interglacial) and reworked microfossils were washed into the lake from the catchment and upstream valley and eventually became incorporated into the varve sequence.

Based on the available data, we are uncertain whether *Picea* was locally present during the LGM but it is certainly a possibility that needs to be confirmed with new investigations. If it was growing locally, it was most probably in the form of cold- and wind-resistant krumholz individuals. The data from Lake Bolshoye Shchuchye suggest that the population did not persist, as it disappears again in the *sedaDNA* until the Holocene (Fig. 5).

4.2.3. Compositional changes in vegetation through the Pleistocene-Holocene transition

Large changes in the importance of plant functional groups (Fig. 9) and numerous species additions (Fig. 10) accompanied the Pleistocene-Holocene transition at Lake Bolshoye Shchuchye. A distinct increase in Cyperaceae is observed in the *sedaDNA* from ca. 17,000 cal years BP and in the pollen record from ca. 16,000 cal years BP (Fig. 6). In the *sedaDNA* record, this rise is coincident with an increase in bryophyte taxa such as *Bryum*, *Aulacomnium*, Polytrichaceae and Dicranaceae and a distinct decline in the potentially salt-tolerant grass *Puccinellia*. A rise in Cyperaceae pollen is also documented at Cape Shpindler and Lake Gerdzity from ca. 14,000 cal years BP (Fig. 11). This may reflect an early (by hemispheric standards) shift to moister conditions and the onset of a prolonged postglacial transition. At this time, most of Barents Sea was ice-free (Hughes et al., 2016; Brendryen et al., 2020). It seems likely that this deglaciation led to an increase in moisture availability within the Polar Urals, with our data from Lake Bolshoye Shchuchye suggesting the climate became increasingly moist around 17,000 to 16,000 cal years BP. The timing of this change does indeed fall within the overall cold Heinrich Stadial 1, but given the complexity and age uncertainty of the different “events” within this stadial (e.g. Hodell et al., 2017; Camuera et al., in review) we have chosen not to include a more detailed discussion at this stage on the potential linkages between our record and these ice-rafting events in the North Atlantic.

Communities of *Salix* and *Betula*, with *Dryas* (assumed to be *D. octopetala*) began to establish at Lake Bolshoye Shchuchye from ca. 15,000 cal years BP, with a remarkable similarity in the timing of the increase in these taxa between *sedaDNA* reads and pollen concentration (Fig. 5). At ca. 14,500 cal years BP, pollen percentages of *Betula* increased from around 15% and reaching up to 60% of the total pollen sum by ca. 13,500 cal years BP (Fig. 5). The main increase in this taxon occurs a little later in the *sedaDNA* (ca. 13,700 cal years BP) than in the pollen record, likely due to long-distance transport of its pollen to the lake from regional populations occupying lower elevations before populations established within the lake's catchment. By ca. 13,300 cal years BP, *Betula* pollen influx values reach ~500–700 grains cm² year⁻¹, which many authors have taken to indicate local presence of *B. pubescens* forest (Paus, 1995; Seppä and Hicks, 2006; Jensen et al., 2007). A rise in *Alnus* (assumed to be *A. viridis*) pollen is observed during the Lateglacial interval between ca. 17,000–11,700 cal years BP, yet *Alnus* is not detected in the *sedaDNA* until the early-Holocene interval at ca. 10,000 cal years. Thus, in the Lateglacial to early Holocene interval, the first signals of *Betula* and *Alnus* values are seen in the pollen record and represent long-distance transport of their

pollen prior to their local establishment as shown by their appearance in the *sedaDNA* and increase in pollen influx rates (Fig. 5; Supplementary Figs S4 and S5).

A rapid yet short-lived decline in *Betula* between ca. 13,000 and 12,000 cal years BP is evident in both the *sedaDNA* and pollen records (Fig. 5). At the same time, *Alnus* disappears from the pollen record and percentages of *Artemisia* increase. We also note a small increase in the *sedaDNA* of forbs such as *Geum*, *Cardamine*, *Valeriana*, *Hedysarum hedysaroides* and *Castilleja* during this interval (see Clarke et al., 2019b). The timing of these changes coincides approximately with the Younger Dryas (YD) chronozone (ca. 12,700–11,700 cal years BP (Lohne et al., 2014); and Greenland Stadial 1 (ca. 12,800–11,600 before 1950; Björck et al., 1998; Rasmussen et al., 2006). Although a well-known climatic event in the Northern Hemisphere, the YD differs in its strength and extent across European Russia and Siberia (Andreev et al., 1997, 2003; Khotinsky and Klimanov, 1997; Paus et al., 2003; Henriksen et al., 2008; Svendsen et al., 2014; Välranta et al., 2006; Binney et al., 2017). The compositional changes seen at Lake Bolshoye Shchuchye are not particularly clear in earlier pollen records from the region (Fig. 11), although Svendsen et al. (2014) do note a small decline in *Betula* around this time, but the temporal resolution is too poor to be able to see the pattern of the changes. Lake Bolshoye Shchuchye potentially has a detailed record of the YD event, but the signal is muted in this record. In the current analysis, only five *sedaDNA* samples and three pollen samples span the YD; however, the YD interval spans around 80 cm of sediment (Regnell et al., 2019; Svendsen et al., 2019). Analysis of more pollen and *sedaDNA* samples from this interval are underway and will be presented in a future paper.

The recovery of *Betula* to high values in both the *sedaDNA* and pollen records around ca. 11,500 cal years BP coincides with the first appearance of the dwarf shrubs *Arctostaphylos uva-ursi*, *Empetrum*, *Vaccinium uliginosum* and *V. vitis-idaea/myrtillus* in the *sedaDNA* (Fig. 5). This probably reflects warmer and/or moister conditions, and possibly the establishment of more stable soils. Detectability of dwarf shrubs in the pollen record from Lake Bolshoye Shchuchye and other records from the region is limited (Fig. 11); at Lake Bolshoye Shchuchye, Ericaceae pollen is recorded but shows its main increase much later than in the *sedaDNA* ca. 5000 cal years BP (Fig. 5). Even though there is little evidence of a distinctive decline in *Betula* around the YD interval in the pre-existing pollen records from the region, the recovery of *Betula* to high values at Lake Bolshoye Shchuchye is concurrent with the main increase in *Betula* and *Salix* pollen in the region from ca. 12,000 cal years BP (Fig. 11).

In addition to shifts in the dominance of plant functional groups over time (Fig. 9), the *sedaDNA* record reveals compositional turnover within plant functional groups themselves (Figs. 5–7). For example, there is turnover between the different graminoid taxa detected; a dominance of *Puccinellia*, Poaceae, *Kobresia* and *Festuca* in the full-glacial, *Juncus biglumis*, *Festuca* and *Bromus* spp. in the Lateglacial, and a dominance of Agrostidinae during the Holocene interval. This is rarely, if ever, detected in traditional palaeorecords; pollen of graminoids are barely distinguishable below family level, as demonstrated in the pollen stratigraphy from Lake Bolshoye Shchuchye and pre-existing records from the region (Fig. 11).

4.2.4. Expansion of trees in the Holocene

The early-to middle-Holocene interval (ca. 11,700–4000 cal years BP) saw an increasing dominance of woody taxa in both the *sedaDNA* and pollen records from Lake Bolshoye Shchuchye. High influx rates of *Betula* pollen (~500–800 grains cm² year⁻¹), considered to represent the tree *B. pubescens*, are recorded during this period which indicates a continued presence of forest (Paus, 1995; Seppä and Hicks, 2006; Jensen et al., 2007). The coniferous

trees *Picea* and *Larix* established within the lake's catchment from ca. 10,000 and 9000 cal years BP, respectively, along with several fern taxa (*Dryopteris fragrans*, *Gymnocarpium dryopteris* and *Thelypteris palustris*). At the same time, many boreal tall herbs, such as *Aconitum lycoctonum*, *Chamerion angustifolium*, *Filipendula ulmaria*, and *Galium boreale* show first appearances in the *sedaDNA*, suggesting a change in the composition of the understory linked to moister and nutrient-rich soils associated with forest presence. The timing of forest tree establishment (from 10,000 cal years BP and continuing until ~4000 cal years BP) in the early-to middle-Holocene is broadly concurrent with *Picea* and *Alnus* reaching their highest values in pre-existing pollen records from the region (Fig. 11). The composition of *sedaDNA* and pollen records from Lake Bolshoye Shchuchye is broadly consistent with the assemblage composition of other pollen records from the region (Fig. 11), with the added benefit that *sedaDNA* is able to resolve the establishment of *Larix sibirica* and a range of tall, boreal herbs which are poorly represented or entirely absent from the pollen record from the same site and others from the region (Fig. 11). Analyses of *sedaDNA* from the Taymyr Peninsula indicate a *Larix* population increase and range expansion between around 7000 and 5000 cal years BP (Epp et al., 2018; Schulte et al., 2020) which falls within the time interval when *Larix* is present in the *sedaDNA* at Lake Bolshoye Shchuchye.

Many authors consider the high *Picea* and *Alnus* pollen percentages in the early to mid-Holocene (Fig. 11) to represent a northward treeline expansion into the Polar Urals and surrounding lowlands in response to warmer summer temperatures during the regional Holocene Thermal Maximum (Surova et al., 1975; Kremenetski et al., 1998; Kaakinen and Eronen, 2000; Kultti et al., 2003; Binney et al., 2009; Salonen et al., 2011). There is also evidence from northern Europe for an early Holocene Thermal Maximum, with peak summer temperatures reached as early as ca. 10,000 cal years BP (Paus, 2013; Välijärvi et al., 2015; Paus and Haugland, 2017; Mangerud and Svendsen, 2018). During this period, when cold-adapted taxa would have been most disadvantaged, most arctic-alpine taxa were detected, at least in small quantities, in the *sedaDNA* from Lake Bolshoye Shchuchye, strongly suggesting their persistence in the lake catchment from full-glacial times (Clarke et al., 2019b).

Coniferous forest (*Larix*, *Picea*) and certain elements of the understory or tall-meadow vegetation (e.g. *Dryopteris fragrans*, *Gymnocarpium dryopteris*, *Filipendula ulmaria*, *Anthriscus sylvestris*, *Galium boreale*) started to withdraw from the catchment of Lake Bolshoye Shchuchye from ca. 7000 cal years BP. By ca. 4000 cal years BP, the vegetation had subsequently reverted to shrub-tundra with *Betula*, *Alnus*, *Salix* and dwarf shrubs such as *Arctostaphylos uva-ursi*, *Vaccinium uliginosum*, *Empetrum* and *Dryas*. A diverse herb flora persisted following the withdrawal of forest, characterised by taxa such as *Aconitum lycoctonum*, *Bistorta vivipara*, *Lagotis glauca*, *Oxyria digyna* and graminoids such as *Carex*, *Agrostidinae*, *Eriophorum* and *Festuca*. This change marks the establishment of a vegetation mosaic similar to that of the present-day. Pollen (Fig. 11) and plant macrofossil records from the region also indicate the loss of forest taxa from ca. 7000–6000 cal years BP (Surova et al., 1975; Andreev et al., 1998; Serebryanny et al., 1998; Koshkarova et al., 1999; Panova and Jankovska, 2000).

5. Conclusions

The 24-m long sediment sequence obtained from Lake Bolshoye Shchuchye enabled a detailed reconstruction of long-term plant community dynamics during and since the Last Glacial Maximum (LGM) without any apparent breaks in sedimentation over the 24,000-year period investigated. Herb-tundra vegetation with a rich diversity of forbs, such as *Papaver*, *Draba*, *Bistorta vivipara* and

Saxifraga oppositifolia, and graminoids such as *Puccinellia*, *Festuca* and *Juncus biglumis* characterises the full-glacial (ca. 24,000–17,000 cal years BP) part of the record. By ca. 17,000 cal years BP, mesic sedge communities established when climate became moister, followed by a warming a little later that caused the establishment of *Dryas* from 15,000 cal years BP, followed by *Betula* ca. 14,000 cal years BP, with pollen influx rates indicating local presence of *B. pubescens* at this time. This was interrupted by a short-lived response to Younger Dryas cooling around 12,500 cal years BP, although the low temporal resolution of samples during this chronozone limits an interpretation of vegetation response. The coniferous trees *Picea* and *Larix* became dominant elements of the vegetation from ca. 10,000 and 9000 cal years BP, respectively, alongside ferns and many boreal herbs. *Picea* began to decline from ca. 7000 cal years BP, with a complete withdrawal of coniferous forest accomplished by ca. 4000 cal years BP when the vegetation subsequently reverted to shrub-tundra with a diverse herb flora, similar to the present-day vegetation of the Polar Urals.

Contrary to earlier comparative *sedaDNA* studies, we show considerable overlap in compositional changes and the pattern of occurrence of key taxa identified by *sedaDNA* and pollen. We demonstrate that the information gained by *sedaDNA* and pollen augment each other, with the two proxies differing in terms of their ability to detect and/or resolve taxa within different plant functional groups and the dominance of these functional groups over time. It is especially during the Holocene interval that we can clearly see the valuable contribution *sedaDNA* can make for reconstructing past community composition: ability to identify a range of herbaceous taxa, little or no “swamping” by dominant woody taxa and estimates of floristic richness not limited by pollen-counting time.

Taken together, the *sedaDNA* and pollen records from Lake Bolshoye Shchuchye show how the local vegetation mosaic has built up over the past 24,000 years in considerable detail. The *sedaDNA* record reveals several important features that the pollen stratigraphy fails to detect: a turnover in grass and forb genera over the Pleistocene-Holocene transition, the Holocene establishment of *Larix sibirica* populations, a diverse and temporally variable bryophyte flora, and a sustained increase in floristic richness since the LGM until the early-Holocene. We demonstrate how *sedaDNA* can provide improved estimates of floristic richness as the same metric reconstructed from pollen is often limited by differential pollen productivity, dispersal and often low taxonomic resolution. However, joint use of the proxies enabled a distinction to be made between long-distance transport of pollen and local presence of the taxon. The record from Lake Bolshoye Shchuchye demonstrates promise for retrieving floristically informative and detailed *sedaDNA* records from mineral-rich silty sediments and large lakes with topographically diverse catchments.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Ludovic Gielly is one of the co-inventors of patents related to the g and h primers and the use of the P6 loop of the chloroplast *trnL* (UAA) intron marker used for plant identification using sedimentary ancient DNA templates. These patents restrict commercial applications only and have no impact on the use of this marker in academic research.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2020.106564>.

Author contributions

IGA, JIS and JM developed the idea and concept of the study and obtained the funding. JIS cored Lake Bolshoye Shchuchye. Pollen analysis was conducted by AB, with contributions from AP. CLC subsampled the sediment core and extracted the DNA and LG amplified the DNA and performed the initial sequence analysis and taxa assignment. CLC further analysed the DNA data and performed the post-identification filtering with contributions from IGA and ME. Ecological and methodological expertise was contributed by AB, IGA, ME, AP and PDMH. Information on the geomorphological background and glacial history of the site, along with sediment analyses and dating of the core, was contributed by JIS, HH, JM and CR. Lastly, CLC compared the *sedDNA* and pollen data and wrote the manuscript, which all co-authors commented on.

Data availability

The forward and reverse raw DNA reads for the four amplicon libraries analysed from Lake Bolshoye Shchuchye, along with the primer and tag sequence information, are publicly accessible within the DRYAD database at <https://doi.org/10.5061/dryad.jdfn2z378>. The final *sedDNA* and pollen datasets that form the basis of the figures presented in this paper will be made available on the Neotoma Paleocology Database at <https://www.neotomadb.org/>.

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