



## Sedimentary ancient DNA and pollen reveal the composition of plant organic matter in Late Quaternary permafrost sediments of the Buor Khaya Peninsula (north-eastern Siberia)

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15 **Abstract.** Organic matter deposited in ancient, ice-rich permafrost sediments is vulnerable to climate change and may contribute to the future release of greenhouse gases; it is thus important to get a better characterization of the plant organic matter within such sediments. From a Late Quaternary permafrost sediment core from the Buor Khaya Peninsula, we analysed plant-derived sedimentary ancient DNA (sedaDNA) to identify the taxonomic composition of plant organic matter, and undertook palynological  
20 analysis to assess the environmental conditions during deposition. Using sedaDNA we identified 154 taxa and from pollen and non-pollen palynomorphs we identified 86 taxa. In the deposits dated between 54 and 51 kyr BP, sedaDNA records a diverse low-centred polygon plant community including recurring aquatic pond vegetation while from the pollen record we infer terrestrial open-land vegetation with relatively dry environmental conditions at a regional scale. A fluctuating dominance of either  
25 terrestrial or swamp/aquatic taxa in both proxies allowed the local hydrological development of the polygon to be traced. In deposits dated between 11.4 and 9.7 kyr BP (13.4–11.1 cal kyr BP), sedaDNA shows a taxonomic turnover to moist shrub tundra and a lower taxonomic richness compared to the older samples. Pollen also records a shrub tundra spectrum, mostly seen as changes in relative proportions of the most dominant taxa, while a decrease in taxonomic richness was less pronounced  
30 compared to sedaDNA. Our results show the advantages of using sedaDNA in combination with



palynological analyses when macrofossils are rarely preserved. The high resolution of the sedaDNA record provides a detailed picture of the taxonomic composition of plant-derived organic matter throughout the core and palynological analyses prove valuable by allowing for inferences of regional environmental conditions.

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## 1. Introduction

Decomposition of soil organic carbon from ancient permafrost deposits may augment ongoing global warming, but how intensely will depend on the character of the organic matter. Most soil organic carbon in permafrost was deposited during the Late Pleistocene and Holocene (cf. Schirrmeister et al., 2011a). Throughout the last glacial (Marine Isotope Stages 4 to 2, ca. 71–10.5 kyr BP), much of north-eastern Siberia was non-glaciated (Hubberten et al., 2004). The region was exposed to extremely cold conditions, which resulted in the formation of deep permafrost with an estimated thickness of 500 m (Duchkov et al., 2014) and in lowlands of polygonal tundra environments. Ice-wedge polygons developed after many cycles of wintertime frost cracking and subsequent springtime melt-water infiltration into these cracks. Ice-wedges create ridges surrounding polygonal depressions (e.g. Lachenbruch, 1962; Leffingwell, 1915; Minke et al., 2007). The cold and water-saturated conditions in the depressions caused the accumulation of organic matter in soil horizons, as decomposition rates were low (Davidson and Janssens, 2006; Hugelius et al., 2014). Over time, ice- and organic matter-rich permafrost containing massive syngenetic ice-wedges was formed (Schirrmeister et al., 2011b). These Late Pleistocene deposits are called Ice Complex or Yedoma and are estimated to store  $83 \pm 12$  Pg organic carbon (Hugelius et al., 2014), which accounts for more than 10 % of the total organic carbon pool in permafrost globally.

Permafrost is susceptible to future climate change-induced increases in ground temperatures, which can lead to active layer deepening (Romanovsky et al., 2010) and thermoerosion (Grosse et al., 2011). When permafrost sections thaw, microbial-driven decomposition rates increase and release climate relevant greenhouse gases that further enhance climate warming in a positive feedback loop (Knoblauch



et al., 2013; Wagner et al., 2007). To improve assessments of the potential greenhouse gas release from organic matter, knowledge about its composition is of great relevance as it allows for the inference of organic matter decomposability (Cornwell et al., 2008; Hobbie, 1992). Furthermore, knowledge about the conditions under which the organic matter accumulated in the past can help us understand how it accumulates today (Lyell, 1830). Recently, the sediments, cryolithology and stratigraphy of outcrops on the western coast of the Buor Khaya Peninsula in north-eastern Siberia were described, including organic carbon quantity, quality and degradability (Günther et al., 2013b; Schirrmeister et al., 2016; Stapel et al., in review; Strauss et al., 2012, 2013, 2015). However, the palaeobotany of the site has not been studied. It represents a more southerly example of highly degraded Ice Complex in the central Laptev region between the Lena Delta to the west and the Indigirka lowlands to the east. The closest palaeobotanical reconstruction was carried out at the north-eastern coast of the peninsula using palaeolake sediments, but only of Mid Holocene origin (Willerslev et al., 2014). Hence a record which describes the floristic composition of organic matter from the last glacial is needed to complete our understanding of the source and quality of organic carbon in these deposits.

Plant macrofossil and/or pollen are the palaeobotanical records usually used to study the permafrost soil organic matter composition and environmental conditions during its deposition. Plant macrofossils, which can often be identified to species level, mostly originate directly from former vegetation at the study site, allowing past local environmental conditions to be inferred (Birks, 2001). However, identifiable macrofossils are usually preserved in low quantities and preservation varies strongly among taxa, which hinders a quantitative exploitation of this proxy data (Kienast et al., 2001). Pollen, in contrast, is preserved in sufficient amounts to quantify its composition, but in arctic treeless ecosystems it originates from across a variable extent from extra-local to local sources (Birks, 2001; van der Knaap, 1987) and taxonomic resolution is mostly limited to genus- and family level (Beug, 2004; Moore et al., 1991). A comparatively new proxy is the analysis of sedimentary ancient DNA (sedaDNA), which originates from disseminated material within sediments (Haile et al., 2009; Rawlence et al., 2014). Its application to permafrost sediments was introduced by Willerslev et al. (2003) who reported the successful retrieval of plant DNA as old as 300,000 to 400,000 years. Since then, several studies prove that DNA is exceptionally well preserved in permafrost sedimentary archives with respect to vascular



plants (Willerslev et al., 2003), bryophytes (Epp et al., 2012), fungi (Bellemain et al., 2013; Epp et al., 2012; Lydolph et al., 2005), bacteria (e.g. Wagner et al., 2007; Willerslev et al., 2004b), invertebrates (Epp et al., 2012), birds (Epp et al., 2012), and mammals (e.g. Arnold et al., 2011; Haile et al., 2009; Willerslev et al., 2003, 2014). The constantly cool temperatures of permafrost lead to reduced microbial and enzymatic degradation (Levy-Booth et al., 2007) and limited hydrolytic damage, since up to 97 % of the water is frozen (Willerslev et al., 2003, 2004a). SedaDNA is supposed to be of local origin (Boessenkool et al., 2014; Haile et al., 2007; Jørgensen et al., 2012; Parnetti et al., 2013) and can be preserved extracellularly, even when macrofossil evidence is absent (Arnold et al., 2011; Willerslev et al., 2003). In comparison to arctic pollen and macrofossils, the taxonomic resolution of sedaDNA exceeds that of pollen in almost all groups of higher plants and is close to the resolution of macrofossils (Jørgensen et al., 2012; Pedersen et al., 2013; Sørensen et al., 2010).

The purpose of this study is to combine sedaDNA and pollen analyses to reconstruct past local and regional flora from a Late Quaternary permafrost sediment core, which was recovered from the western coast of the Buor Khaya Peninsula, a sparsely investigated region of the Late Pleistocene Ice Complex. The sediments contain moderate organic carbon content generally 2–5 % (Schirrmeister et al., 2016; Stapel et al., in review; Strauss et al., 2015). Given that organic matter is the substrate for microbial turnover and the future release of greenhouse gases, it is crucial to get a better characterization of the plant organic matter within those sediments. At the same time it is necessary to understand the environmental conditions that prevailed when the organic matter was deposited to allow for inferences of modern and future processes under comparable environmental conditions. We therefore aim to answer the following questions: (1) What is the taxonomic composition of plant organic matter stored locally in the ancient permafrost sediments? (2) What were the environmental conditions during the time of organic matter accumulation?

## 2. Geographical settings

The Buor Khaya Peninsula belongs to the north-east Siberian Yana-Indigirka lowlands and is surrounded by the Buor Khaya Bay and the Yana Bay in the southern Laptev Sea (Fig. 1). It is underlain by continuous permafrost with ground temperatures of less than -10°C (Schirrmeister et al., 2016). The



study area has a subarctic continental climate with a short growing season and long severe winters. Mean annual precipitation is 321.5 mm, and the mean annual air temperature is  $-12.8^{\circ}\text{C}$  (mean temperature of the warmest month:  $8.7^{\circ}\text{C}$ , mean temperature of the coldest month:  $-32.5^{\circ}\text{C}$ ) at the closest meteorological station in Tiksi (WMO 218240) based on data between 1981 and 2010.

- 5 The treeless landscape is covered by polygonal tundra and a mosaic of thermokarst and alas depressions and Yedoma ‘hills’ up to 37 m above sea level (Günther et al., 2013a). Thermokarst depressions formed by permafrost thaw and ground subsidence as a consequence of increasing temperatures after the Last Glacial Maximum (Czudek and Demek, 1970), whereas Yedoma hills and uplands are relicts of Late Pleistocene accumulation plains (Schirrmeister et al. 2013). According to the Circumpolar Arctic
- 10 Vegetation Map (CAVM Team, 2003) the modern vegetation cover can be classified mostly as erect dwarf-shrub tundra, in places tussock-sedge, dwarf-shrub, moss tundra and the northernmost part of the peninsula as sedge, moss, dwarf-shrub wetlands. On raised microsites, such as ridges of low-centred ice-wedge polygons, sedge, moss, dwarf-shrub wetlands also include components of non-tussock sedge, dwarf-shrub, moss tundra.

## 15 **3. Material and Methods**

### **3.1 Core material**

- In April 2012, an 18.9-m long core with frozen sediment (BK-8) was drilled from the top of an eroding Yedoma hill at 34 m a.s.l. (Fig. 1) located at about 100 m from the cliff edge on the western coast of the Buor Khaya Peninsula ( $71.420^{\circ}\text{ N}$ ,  $132.111^{\circ}\text{ E}$ ). Detailed descriptions of the fieldwork and
- 20 cryolithological properties (i.e. ground ice and sediment features) are published in Günther et al. (2013) and Schirrmeister et al. (2016). Radiocarbon dating was performed on bulk plant macro remains by accelerator mass spectrometry at the Cologne AMS laboratory, Germany (Schirrmeister et al., 2016) and radiocarbon ages are given in Table 1. Based on field observations, core descriptions and analytical data sets, Schirrmeister et al. (2016) subdivided the core into six cryolithological units (Table 1).
  - 25 Absolute ice-contents varied between 66 and 84 wt %, which is typical for Yedoma (Schirrmeister et



al., 2011b, 2016). Plant remains were sparsely distributed throughout the core and were composed mainly of fine rootlets, grass fragments, small woody pieces and very few seeds and fruits.

### 3.2 Subsampling of the permafrost core

In January 2014 the core segments were cut into two halves. One was stored as an archive and the  
5 second was subsampled. The opening of the core and the subsampling took place at the German  
Research Centre for Geosciences Helmholtz Centre Potsdam in the climate chamber at a temperature of  
-10°C, where no genetic experiments were performed either before or after. The drilling mud was  
removed using a band saw. Approximately 3 mm of the surface was removed with a clean straight draw  
knife of 225 mm length (Wilh. Schmitt & Comp. GmbH & Co. KG, Germany). Before use, the draw  
10 knife was cleaned with 5 % Deconex-solution (Th. Geyer, Germany), rinsed in purified water, followed  
by DNA-ExitusPlus treatment (VWR, Germany) and rinsing in purified water. Finally, the draw knife  
was soaked in 96 % technical Ethanol (Carl Roth GmbH & Co. KG, Germany) and flamed. Then, about  
1 mm of the newly exposed sediment was removed with a small clean knife (Th. Geyer, Germany).  
Each knife was used for one draw only. Before use, the small knife was cleaned with 5 % Deconex-  
15 solution, rinsed in purified water, followed by DNA-Away® (Carl Roth GmbH & ca. KG, Germany)  
treatment, and rinsed in purified water. Finally, each side of the knife was UV-irradiated, at close  
distance for 10 minutes in a CL1000 ultraviolet crosslinker (UVP, USA), as recommended by Champlot  
et al. (2010).

The samples were drilled through the clean surface using a TCT hole saw with one tooth and an outer  
20 diameter of 25 mm (Esska.de GmbH, Germany). Before use, they were cleaned in the same manner as  
the small knives. The ends of the retrieved cylindrical sediment pieces were cut using sterile disposable  
scalpel tips. After cutting the first end, the scalpel tip was cleaned using Deconex, rinsed with purified  
water and Ethanol, and finally flamed to prevent contamination from one end to the other. The DNA  
samples were stored at -20°C and the pollen samples were stored at 4°C. In total, 54 samples were  
25 drilled (approximately 3 to 4 samples per metre) for each kind of analysis. The ice-wedge segment was  
not sampled for DNA analyses, because it was shattered into pieces, which were too small for an intact  
piece from the inside to be drilled out.



### 3.3 Molecular genetic laboratory work

Total DNA was isolated from approximately 5 g of frozen permafrost sediment using the PowerMax® Soil DNA Isolation Kit (Mo Bio Laboratories, Inc. USA). For the initial lysis and homogenization step, 0.8 mg peqGOLD proteinase K (VWR, Germany), 0.5 ml 1M Dithiotreitol (VWR, Germany) and 1.2 ml C1 solution and samples were added to 15 ml PowerBead solution, vortexed for 10 minutes and incubated overnight at 56°C on a nutating mixer (VWR, Germany) under gentle agitation. All following steps were carried out according to the kit manufacturer's recommendations, using 1.6 ml elution buffer and extending the incubation time to 10 minutes for the final elution. One extraction blank was included for each isolation batch of 11 samples and processed in the same way as the samples.

The PCR reactions were performed with the trnL g and h primers (Taberlet et al., 2007). Both primers were modified on the 5' end by unique 8 bp tags which varied from each other in at least five base pairs to distinguish samples after sequencing (Binladen et al., 2007) and were additionally elongated by NNN tagging to improve cluster detection on the sequencing platform (De Barba et al., 2014). The PCR reactions contained 1.25 U Platinum® *Taq* High Fidelity DNA Polymerase (Invitrogen, USA), 1 x HiFi buffer, 2 mM MgSO<sub>4</sub>, 0.25 mM mixed dNTPs, 0.8 mg Bovine Serum Albumin (VWR, Germany), 0.2 mM of each primer and 3 µl DNA in a final volume of 25 µl. PCRs were carried out in a TProfessional Basic thermocycler (Biometra, Germany) with initial denaturation at 94°C for five minutes, followed by 50 cycles of 94°C for 30 s, 50°C for 30 s, 68°C for 30 s and a final extension at 72°C for 10 min. To trace possible contamination one No Template Control (NTC) was included in each PCR and treated identically to the samples and the extraction blanks. 2 % agarose (Carl Roth GmbH & Co. KG, Germany) gels were used to check if the PCR was successful and whether the products matched the expected size.

All samples were subjected to up to four PCR runs. Once two positive amplifications were obtained, while the associated NTC and extraction blank remained negative, they were used for sequencing. The two positive amplifications were pooled and purified using the MinElute PCR Purification Kit (Qiagen, Germany), following the manufacturer's recommendations. Elution was carried out twice with DEPC-treated ultra-purified water to a final volume of 40 µl. The DNA concentrations were estimated with the dsDNA BR Assay and the Qubit® 2.0 fluorometer (Invitrogen, USA) using 1 µl of the purified





amplifications. To avoid bias based on differences in DNA concentration between samples, they were pooled in equimolar concentrations. All extraction blanks and NTCs were included in the sequencing run, using a standardized volume of 10 µl, even though they were negative in the PCRs. Library preparation and sequencing on the Illumina HiSeq platform (2 x 125 bp) were performed by the Fasteris

5 SA sequencing service (Switzerland).

DNA isolation and PCR setup was performed in the palaeogenetic laboratory of the Alfred-Wegener-Institute Helmholtz Centre for Polar and Marine Research in Potsdam, Germany. This lab is dedicated to ancient DNA isolation and PCR setup and is located in a building devoid of any molecular genetics lab work. The lab is cleaned frequently by the researchers and subjected to nightly UV-irradiation. All laboratory work was performed in a UVC/T-M-AR DNA/RNA cleaner-box (BIOSAN, Latvia). DNA isolations and PCR setups were performed on different days using dedicated sets of pipettes and equipment. Further precautions to reduce contamination included UV-irradiation of 10x buffer, BSA, MgSO<sub>4</sub> and DEPC-treated water for 10 minutes in a UV crosslinker in thin-walled PCR reaction tubes approximately 1 cm below the UV light bulbs (similar to recommendations of Champlot et al. (2010)).

### 15 3.4 Analysis of sequence data and taxonomic assignments

The sequence quality was checked using FastQC (Andrews, 2010) (S1, Fig. S3.1). Filtering, sorting and taxonomic assignments of the sequences were performed using OBITools (Boyer et al., 2016). Forward and reverse reads were aligned to produce single sequences using *illumina-paired-end*. These sequences were assigned to their samples based on exact matches to their tag-combination using *ngsfilter*, followed by *obigrep* to exclude sequences shorter than 10 bp and *obiuniq* with which duplicated sequences were merged while keeping the information to which sample the sequences originally belonged. Rare sequences occurring with less than 10 read counts across the dataset were excluded as probable artefacts using *obigrep*. Sequence variants probably attributable to PCR or sequencing errors were excluded by *obiclean* (Boyer et al., 2016).

25 Two reference databases were used for taxonomic assignments as described in Epp et al. (2015): the first is based on the quality-checked and curated Arctic and Boreal vascular plant and bryophyte reference libraries (composed of 1664 vascular plant and 486 bryophyte species) published by Sønstebo





et al. (2010), Willerslev et al. (2014) and Soininen et al. (2015); the second is based on the EMBL Nucleotide Database standard sequence release 117 (Kanz et al., 2005; [www.ebi.ac.uk/embl/](http://www.ebi.ac.uk/embl/)). The sequences were assigned to taxon names based on sequence similarity to each of the reference databases using *ecotag*. When the same taxonomic names were given more than once to different sequences we  
 5 attached the affix MOTU (Molecular Operational Taxonomic Unit).

To further remove noise in the dataset, sequences occurring less than 10 times in a sample were excluded using R v. 3.0.3 (R Core Team, 2014). Only sequences that displayed a best identity value of 1.0 to an entry of a reference database were kept and assigned its taxonomic name (S4, PANGAEA doi: follows). Sequences which were assigned to cultivated plants or those highly unlikely to occur in the  
 10 Arctic were excluded from our analyses as probable contamination (S5). As a conservative measure we excluded sequences assigned to the PACMAD-clade (including *Muhlenbergia richardsonis*), since they are identical with *Zea mays* and authentic sequences cannot be distinguished from probable contamination. Nevertheless, the excluded sequences comprised only a small proportion (3.3 %) of all Poaceae sequences and an under-representation would thus have only a minor impact. Sequences  
 15 appearing in the extraction blanks and NTCs comprised 3.4 % of all sequence counts and were also excluded (S6). In most cases these sequences were only found in the extraction blanks (55.6 %) or NTCs (33.3 %) and not in the samples, while approximately 10 % of were probably derived from wrong sample assignment through tag-jumps.

### 3.5 Pollen sample treatment and analysis

20 Thirty-two samples were selected for pollen analysis. From each sample approximately 3 g (wet weight) were taken for sample preparation. For fluid samples (unfrozen due to storage at 4°C) 1 ml of sediment was taken using a syringe. Standard preparation following Faegri and Iversen (1989) including KOH, HCl and HF treatment was used to extract pollen, spores and non-pollen palynomorphs (NPPs) from the sediment. Pollen of terrestrial and aquatic plants as well as common NPPs were analysed using a light  
 25 microscope (Zeiss Axioskop 2) under 400–600x magnification (S7). At least 300 pollen grains and NPPs were identified in each sample following sample sizes in Andreev et al. (2011). Published pollen atlases (Beug, 2004; Kupriyanova and Alyoshina, 1972, 1978; Moore et al., 1991; Savelieva et al.,



2013; Sokolovskaya, 1958) and a pollen reference collection at the Arctic and Antarctic Research Institute (Sankt-Petersburg) and the Alfred Wegener Institute were used for taxonomic identification of pollen and spores. NPPs were determined according to van Geel (2001), van Geel et al. (1983), van Geel and Aptroot (2006). Freshwater algae were determined using Jankovská and Komárek (2000) and Komárek and Jankovská (2001).

### 3.6 Statistical analyses and visualization

Analyses for sedaDNA and pollen were carried out in the same manner. After first inspection of the data we assigned Cyperaceae to the local component (Moore et al., 1991) of the swamp and aquatic taxa to get a better picture about changes in the terrestrial sedaDNA and pollen signals. We thus separated the data of both proxies into two datasets: (1) terrestrial and (2) swamp and aquatic. Recorded bryophytes for sedaDNA and NPPs for pollen were described, but since they were sparse, they could not be analysed statistically. Due to the higher taxonomic resolution of the sedaDNA, *Kobresia* (Cyperaceae) remained in the terrestrial sedaDNA set, while Poinae – either *Arctophila fulva* or *Dupontia fisheri* – were included in the swamp and aquatic set as both can occur within low-centred polygons (Aiken et al., 2007). Rarefaction curves were produced and rarefied taxon richness calculated using *rarecurve* and *rarefy*, to compare taxon richness at a particular number of sequences or pollen grains, determined by the lowest number of retrieved sequences or pollen grains among all samples (Heck et al., 1975; Hurlbert, 1971). This was performed for the terrestrial and swamp and aquatic datasets separately.

For statistical analyses only taxa that were present in at least six samples in the terrestrial and in three samples in the taxonomically-poorer swamp and aquatic datasets were included. Relative proportions of taxa within a sample were calculated on the basis of their sequence count or pollen sum in each dataset. A double square-root transformation was performed on the relative proportions of the sedaDNA dataset to mitigate the effect of overrepresented and rare sequences, while square-root transformation was applied to the pollen dataset, since differences between counts were not as pronounced. A constrained hierarchical clustering approach (CONISS (Grimm, 1987)) was performed with clusters constrained by depth using *chclust*. The relative proportions were thereafter transformed to Euclidean distances by



*vegdist*. Zoning was guided by the broken-stick model (Bennett, 1996; MacArthur, 1957) using *bstick*, but with the condition that a minimum of five samples was necessary to assign a zone for the DNA datasets to avoid inflation of several very small zones. For pollen analysis a minimum of four samples was necessary to assign a zone, since fewer samples were taken compared to the DNA dataset. The stratigraphs were plotted for each dataset separately with *strat.plot*.

Ratios of terrestrial to swamp and aquatic taxa and Poaceae to Cyperaceae were built (Mensing et al., 2008) to assess which contributed most to a sample, following Eq. (1) and Eq. (2):

$$\text{ratio} = \frac{\text{terrestrial-aquatic}}{\text{terrestrial+aquatic}}, \quad (1)$$

$$\text{ratio} = \frac{\text{Poaceae-Cyperaceae}}{\text{Poaceae+Cyperaceae}}, \quad (2)$$

For this, the sums of sequence counts or pollen grains of (1) all terrestrial, (2) all swamp and aquatic taxa, (3) Poaceae and (4) Cyperaceae in a sample were built. The ratios range between -1.0 and 1.0 with negative values indicating dominance of swamp and aquatic or Cyperaceae sequences or pollen grains and positive values indicating dominance of terrestrial or Poaceae sequences, while a value of zero indicates an equal contribution of both.

A Principal Component Analysis (PCA) was applied on the double square-root transformed relative proportions for sedaDNA and square-root transformed relative proportions for pollen using *rda* in order to portray the major structure in the multivariate dataset. Loadings for PC1 and PC2 axes were extracted and visualized in biplots. For better visibility, only terrestrial taxa that explained the most are plotted (n = 20 for sedaDNA; n = 25 for pollen).

The statistical analyses were performed in R v. 3.0.3 (R Core Team 2014) using the packages “vegan” (Oksanen et al., 2011), “rioja” (Juggins, 2012) and “analogue” (Simpson, 2007; Simpson and Oksanen, 2016). The datasets are deposited at <https://www.pangaea.de/> (doi: follows after acceptance).



## 4. Results

### 4.1 SedaDNA

#### 4.1.1 SedaDNA of terrestrial plants

- In total, 7,238,506 sequence counts were assigned to 113 terrestrial plant taxa, of which 40 were identified to species level, 49 to genus level, 22 to sub-tribe or family level, and one to order level. Rarefaction analysis to compare richness on a similar level of sampling effort is based on the minimum number of observed sequence counts ( $n = 1064$ , 14.85 m depth). All curves of samples reach an asymptotic state indicating a sufficient sampling effort in all samples (Fig. S3.2). The complete taxa-list is available in S3.
- No tree taxa were detected, although Saliceae, *Betula* and *Alnus* occurred there as shrub form. 64.5 % of all terrestrial sequence counts are from shrubs (Saliceae, *Betula*, *Alnus*), while 18.1 % are from graminoids and 17.4 % herbs. The dataset is particularly dominated by Saliceae sequences, which comprise 64 % of all terrestrial sequence counts, followed by Pooideae (13 %), Agrostidinae MOTU1 (3 %), *Ranunculus* MOTU1 (3 %) and *Betula* (3 %).
- According to the CONISS results the terrestrial plant sedaDNA dataset can be divided into three zones (TerrDNA Zone) (Fig. 2). TerrDNA Zone 1 (18.48–10.15 m) displays low to high rarefied richness ranging from 2–26 taxa, with a median of 11 taxa. The lowest richness is found among the deepest samples from 14.85 m downwards. TerrDNA Zone 1 is dominated by Saliceae ranging from 22–99.8 % with a median of 91 % accompanied by low proportions of Pooideae up to 24 % with a median of 1 %.
- The most frequent herbaceous and graminoid taxa are *Dryas* (up to 20 %), *Festuca* MOTU1 (up to 19 %), Anthemideae MOTU1 (up to 7 %) and *Potentilla* (up to 6 %).
- TerrDNA Zone 2 (9.9–3.3 m) frames the ice-wedge (8.35–3.4 m) and exhibits the highest rarefied taxonomic richness, especially among graminoids, while herbs range from 6–24 taxa, median 17. Similar to TerrDNA Zone 1, Saliceae sequences dominate ranging from 0–83 %, median 60 % while Anthemideae (up to 50 %), Pooideae (up to 56 %), Poeae MOTU1 (up to 36 %), *Potentilla* (up to 31 %) and *Dryas* (up to 13 %) have the highest proportions among graminoids and herbs. The sample at 3.3 m depth is the only sample of this zone above the ice-wedge and shows an intermediate composition



between TerrDNA Zone 2 and 3. It has lower richness in comparison to the samples below the ice-wedge, but contains sequences of Anthemideae, *Oxytropis*, *Festuca* MOTU2 and *Plantago*, which are absent in TerrDNA Zone 3. However, it is the only sample of this zone to record *Betula*, although at a lower proportion than samples of TerrDNA Zone 3.

- 5 TerrDNA Zone 3 (2.85–0.1 m) displays a low to intermediate taxonomic richness ranging from 2–13 taxa, median 8 taxa. Several graminoid (e.g. Poeae MOTU1, *Festuca*, *Pleuropogon sabinei*) and herbaceous taxa (e.g. Anthemideae, *Potentilla*, *Hulteniella integrifolia*) are not recorded. Characteristic is the presence of *Betula* sequences with proportions ranging from 0–63 % with a median of 2 %. Pooideae (up to 96 %) and Saliceae (up to 86 %) sequences dominate with median proportions of 16 %  
 10 and 8 %, respectively. Taxonomic composition is further characterized by Agrostidinae MOTU1 and 2 (up to 100 % in the uppermost sample), *Ranunculus* MOTU1 (up to 74 %), *Parrya* (up to 44 %), *Pyrola grandiflora* (up to 26 %), *Delphinium* (up to 25 %), Ranunculaceae (up to 22 %) and Asteraceae (up to 20 %).

The PCA biplot of the first two axes (Fig. 3), jointly explaining 41.5 % of the variance in the dataset,  
 15 reveals the major structure of the terrestrial sedaDNA. Along PC1 Saliceae and *Potentilla* exhibit the highest loadings of 0.67 and 0.63, respectively, while *Betula* and Agrostidinae MOTU1 have the lowest negative loadings of -0.54 and -0.46, respectively. Along PC2 Saliceae and *Potentilla* have the highest loadings of 0.52 and 0.23, while Pooideae and Poeae MOTU1 show the lowest negative loadings of -1.14 and -0.53, respectively. Samples of TerrDNA Zone 1 are placed mostly in the upper right quadrant  
 20 and are partly intermixed with those of TerrDNA Zone 2, which are mostly placed in the lower right quadrant. TerrDNA Zone 3 samples are located in the upper and lower left quadrants and intermix only with the sample from 3.3 m.

#### 4.1.2 SedaDNA of swamp and aquatic plants

- 25 In total, 4,591,277 sequence counts were assigned to 21 swamp or aquatic taxa, of which five were assigned to species level, 15 to genus level and one to sub-tribe level. The most dominant sequences of the dataset are *Carex aquatilis* comprising 66 % of all sequence counts, followed by *Eriophorum*



- MOTU1 (11 %), *Carex* MOTU1 (8 %), *Caltha palustris* (5 %) and Poinae (*Arctophilla fulva* or *Dupontia fisheri*) (4 %). Rarefaction is based on the minimum number of 20 sequence counts at 1.2 m depth. The rarefaction curves for all samples reach an asymptotic state indicating sufficient sampling effort in all samples (Fig. S3.3).
- 5 The swamp and aquatic plant DNA dataset is divided into two zones (Fig. 4). AquaDNA Zone 1 (18.48–3.3 m) comprises all samples below the ice-wedge plus a single sample above the ice-wedge at 3.3 m. The rarefied taxonomic richness of this zone ranges between zero and five with a median of one. In the deepest part of this zone (14.85–18.48 m) three out of ten samples exhibit aquatic sequences from
- 10 *Caltha palustris* up to 97 %, *Carex* MOTU1 up to 100 % and *Carex aquatilis* up to 100 %. Hydrophytes such as *Stuckenia* and *Hippuris* are characteristically present with proportions up to 63 % and 4 %, respectively.
- AquaDNA Zone 2 (2.85–0.1 m) comprises all samples above the ice-wedge, except for the sample at 3.3 m depth. This zone exhibits a lower rarefied taxonomic richness than AquaDNA Zone 1 (Fig. 4).
- 15 Samples between 2.4 and 1.2 m display high proportions of *Equisetum* up to 100 % with a median of 54 % followed by *Eriophorum* MOTU1 up to 99 %, median 12 %. Near surface parts at 1.1–0.1 m depth are dominated by Poinae up to 50 %, *Carex* MOTU1 up to 45 % and *Tephroseris* up to 17 %. Hydrophytes are not present whereas *Caltha palustris* is present at 0.55 m with a proportion of less than 1 %. Sedges are only represented by *Carex aquatilis* and *Carex* MOTU1.
- 20 The PCA biplot of the first two axes (Fig. 5), jointly explain 48.79 % of the variance in the dataset. Along PC1 *Caltha palustris* and *Carex aquatilis* demonstrate the highest loadings of 0.86 and 0.85, respectively, while *Equisetum* exhibits the only negative loading of -1.11. Along PC2 Poinae and *Caltha palustris* exhibit the highest loadings of 0.91 and 0.62, respectively, while *Carex* MOTU1 and *Carex aquatilis* have the lowest negative loadings of -0.79 and -0.46, respectively. AquaDNA Zone 1
- 25 samples are located mostly in the right quadrants and partly intermix with those of AquaDNA Zone 2, which are mostly located in the left quadrants.



### 4.1.3 SedaDNA of bryophytes and algae

In total, 8,482 sequence reads were assigned to 19 bryophyte taxa and one alga (Table 2), which constitutes 0.07 % of all sequences. Seven taxa were assigned to species level, including the freshwater alga *Cosmarium botrytis* (John et al., 2002), four to genus level, five to family level and four to order level. The observed number of taxa varies between one and six. 82.31 % of all cryptogam sequence reads are assigned to *Sphagnum* (37.39 %) and *Sphagnum russowii* (44.92 %) at 3.3 m; the depth at which the highest number of bryophyte taxa is recorded.

## 4.2 Pollen

### 4.2.1 Pollen of terrestrial plants

A total of 8,881 terrestrial pollen grains were counted and ascribed to 53 taxa, including indeterminable and pre-Quaternary pollen. Seven taxa were assigned to species type or section level, 24 taxa to genus level, 21 to family level, and one to order level. Rarefaction is based on the minimum number of 137 pollen counts at 11.7 m depth. The rarefaction curves did not reach saturation implying that the sampling effort was insufficient to display the sample diversities (Fig. S3.4, Fig. S3.5).

The core is divided into three terrestrial palynological zones (Fig. 6). TerrPZ 1 (18.48–17.2 m) displays the highest rarefied richness ranging from 18 to 21 taxa, with a median of 20 taxa. This zone is distinguished by the presence of pollen from shrubs, especially *Betula* sect. *Nanae* with proportions up to 15 %, *Alnus fruticosa*-type up to 8 % and *Salix* up to 11 %. Poaceae with proportions up to 50 %, Brassicaceae up to 10 % and *Artemisia* up to 7 % dominate among the graminoid and herbaceous taxa. Pollen from trees comprise, among others, *Pinus Haploxylon*-type up to 3 % and *Larix* up to 2 %.

For TerrPZ 2 (17.05–8.75 m) relatively high taxonomic richness is registered ranging from 15–26 taxa, median 19 taxa. This zone is characterized by a decrease in pollen from trees and shrubs with decreasing depth and a dominance of herbaceous and graminoid taxa, especially Poaceae with proportions up to 79 %. *Artemisia*, Asteraceae, Caryophyllaceae, Brassicaceae, Ranunculaceae and Saxifragaceae dominate among other herbs. Furthermore, a remarkable proportion of cf. *Dryas* of up to 2 % is seen in this zone.





TerrPZ 3 (2.85–0.1 m) displays a lower rarefied richness of 11–19 taxa, median 14 taxa. This zone is dominated by *Betula* sect. *Nanae* (up to 54 %), *Salix* (up to 38 %) and Poaceae (up to 51 %). In the samples of 0.85 m and 1.3 m large proportions of *Salix* are present of 30 % and 38 %, respectively. The proportion of *Artemisia* decreases and ranges between 1 % and 2 %. The uppermost sample is  
 5 characterized by large increases of *Alnus fruticosa*-type (up to 17 %) and Ericales (up to 18 %) reflecting the recent pollen spectrum.

The first two axes in the biplot (Fig. 7), jointly explain 55 % of the variance in the dataset. Along PC1 Poaceae and *Artemisia* exhibit the highest loadings of 0.44 and 0.23, respectively, while *Betula* sect. *Nanae* and *Salix* have negative loadings of -0.94 and -0.17, respectively. Along PC2 the highest positive  
 10 loadings belong to Poaceae and *Salix* with 0.31 and 0.28, respectively, while Brassicaceae and *Alnus fruticosa*-type exhibit the lowest negative loadings of -0.37 and -0.31, respectively. The upper right quadrant includes mostly shrub taxa, the upper left quadrant mostly coniferous trees and the lower quadrants mostly open-land taxa. Samples of TerrPZ 1 plot mostly in the lower left and right quadrants, samples of TerrPZ 2 plot in the upper and lower left quadrants and samples of TerrPZ3 plot in the upper  
 15 and lower left quadrants, without intermixing.

#### 4.2.3 Pollen and spores of swamp and aquatic plants

A total of 2,816 aquatic pollen grains and spores were counted and ascribed to eight taxa, of which six were assigned to genus level and two to family level. The numbers of aquatic pollen grains are low and vary between 15 and 220 per sample. Rarefaction curves, based on the minimum number of pollen  
 20 grains ( $n = 15$ ; 16 m depth), do not reach saturation, implying insufficient sampling effort and an underestimate of the sample's diversity (Fig. S3.6). The broken-stick model recommends three zones, but under the condition that each zone must consist of at least four samples, two aquatic palynological zones are assigned (Fig. 8).

AquaPZ 1 (18.48–16.0 m) consists of the deepest part of the core. Rarefied richness ranges from one to  
 25 two with a median of two. Cyperaceae dominate with proportions of 73–96 % and a median of 92 %. The sum of proportions from other taxa accounts for less than 10 %, except for the sample at 16.0 m,



which was co-dominant with *Equisetum* at 27 %, while the sample at 17.0 m is co-dominant with cf. *Potamogeton* at 13 %.

AquaPZ 2 (15.2–0.1 m) comprises nearly the whole core. Rarefied richness ranges from one to two with a median of one. The proportions of Cyperaceae range from 92 % up to 100 % with a median of 98 %.

5 The sum of all further taxa account for less than 10 % in each sample.

The first two axes in the biplot (Fig. 9), jointly explain 75 % of the variance in the aquatic pollen dataset. *Equisetum* displays the only positive loading along PC1 of 0.67, while cf. *Potamogeton* has the lowest negative loading of -0.42. Along PC2 cf. *Potamogeton* has the highest positive loading of 0.58 and Cyperaceae has the lowest negative loading of 0.17. Samples from AquaPZ 1 are located in the  
 10 upper quadrants of the biplot while most of the samples from AquaPZ 2 are located in the lower quadrants.

### 4.2.3 Non-pollen palynomorphs

A total of 1,092 NPPs were counted and assigned to 25 taxa, comprising four mosses, two spikemosses, six clubmosses, three ferns, six fungi and four green algae (Table 3). In samples below the ice-wedge  
 15 the most abundant NPPs are green algae, especially *Pediastrum*, *Botryococcus* and *Zygnema*-type and Bryales. The most abundant fungal spores are *Sporormiella* and *Glomus*, with *Glomus* being only recorded in the deepest parts of the core, except for the sample at 8.9 m. Above the ice-wedge *Gelasinospora*, *Zygnema*-type, *Botryococcus*, Bryales and *Sphagnum* are relatively abundant.

### 4.3 Ratios of terrestrial to swamp and aquatic taxa and Poaceae to Cyperaceae

20 Ratios were built for the sedaDNA and pollen datasets to assess whether terrestrial or swamp and aquatic taxa contributed more sequences or pollen grains to a sample and were compared to the corresponding Poaceae-Cyperaceae ratios to identify drier (positive values) and wetter phases (negative values) (Fig. 10). Generally, sedaDNA and pollen show similar trends for both ratios, with an exception between 11.7 m and 12.12 m depth. The Poaceae-Cyperaceae ratio of the sedaDNA exhibits highly  
 25 fluctuating ratios across the core and mostly follows the pattern of the terrestrial-aquatic ratio. Eighteen sedaDNA samples are dominated by swamp and aquatic taxa: four above the ice-wedge and 14 below.



The pollen ratios show more moderate fluctuations and only two samples are dominated by swamp and aquatic taxa at 11.7 m and 12.12 m depth. However, in six samples Cyperaceae dominate over Poaceae, one at 2.85 m and five between 11.7 m and 14.65 m, whilst samples between 13.0 m and 14.0 m have equal contributions of Poaceae and Cyperaceae pollen.

## 5 Discussion

### 5.1 Quality and proxy value of sedaDNA and pollen data

All samples from the BK-8 sediment core contained plant-derived DNA and pollen. The two proxies are known to complement each other (e.g. Jørgensen et al., 2012) and differences in the obtained data result mostly from the spatial scale at which sedaDNA and pollen originate (local vs. regional signal) and technical biases, which lead to variations in the taxonomic richness, the level of taxonomic resolution and the strength of taphonomic processes in both proxies.

The different spatial scales of sedaDNA (local) and pollen (local to extra-regional) records are an important aspect of the differences identified in the taxa spectra and thus indicate complementarity rather than direct comparability of the proxies. Our results agree with several other studies which demonstrate first, that sedaDNA originates mainly locally (Haile et al., 2007, 2009; Jørgensen et al., 2012; Parducci et al., 2013; Yoccoz et al., 2012) and, second, that it is predominantly derived from roots and other plant parts rather than from pollen (Jørgensen et al., 2012; Levy-Booth et al., 2007; Willerslev et al., 2003). The sedaDNA record does not contain conifer-derived DNA (Birks, 2001; van der Knaap, 1987), although they display high proportions in the pollen record, presumably from long-distance dispersed pollen. Overall, we find a steady dominance of Saliceae (which we interpret as *Salix*), Poaceae and Cyperaceae sequences across all samples of the core. This is likely caused by the huge below-ground biomass of these taxa in tundra environments, which can far exceed the above-ground biomass. According to Iversen et al. (2015), the ratio of below-ground to above-ground biomass in tundra is highest for sedges and grasses, followed by shrubs, and is lowest for forbs. They also showed that these ratios are larger in tundra compared to other biomes such as forests (Iversen et al., 2015). Accordingly Yoccoz et al. (2012) propose that a higher biomass above-ground than below-ground led to



the under-representation of *Salix* in comparison to other plant functional types in the soil of boreal environments. Since *Salix* is also found throughout the pollen record, we assume that it was locally present throughout the investigated time frame and is not only a result of *Salix* roots, which can grow down to depths of 30 to 40 cm (Iversen et al., 2015). Hence, our results support the general view that  
 5 sedaDNA mainly presents a local signal.

Technical and taphonomic biases of pollen data are well known. For example, standard pollen sample preparation, as applied in this study, may (partly) destroy *Luzula* and *Larix* pollen grains (Moore et al., 1991). Hydrophytes are largely under-represented in the pollen dataset when compared to the sedaDNA results, which may be caused by low pollen production or insufficient sedimentation, as pollen from  
 10 *Potamogeton*, for example, tends to float on the water surface for pollination (Cox, 1988; Preston and Croft, 1997). The technical biases of sedaDNA during DNA isolation, PCR and sequencing are also known and have been reviewed (Hansen et al., 2006; Schnell et al., 2015; Thomsen and Willerslev, 2015). In this study, we found an inflation of unique sequence types, attributable to PCR-errors, across the whole dataset, except for those taxa which we deemed as possible contamination (cultivated and  
 15 non-Arctic plants). Otherwise, our dataset shows low probabilities for erroneous base-calls indicated by high sequencing qualities. We therefore assume that the taxa included in the analyses are authentic and the PCR-errors are caused by template age. A more detailed technical evaluation can be found in S2. Taphonomic biases in sedaDNA are still not well understood and part of ongoing research, especially for lake sediments (Alsos et al., 2015).

20 Compared to the number of vascular plant taxa (58) and bryophytes (20) recorded by pollen analysis, the sedaDNA approach recorded a higher number of vascular plants (134) and a similar number of bryophytes (20). After technical biases and taphonomy, the lower number of taxa recorded by pollen can be explained by two major reasons: sampling effect and taxonomic resolution. First, the counts of sequences and pollen grains differed by several orders of magnitude, which is reflected in rarefaction  
 25 curves of sedaDNA reaching saturation while those of pollen do not. This indicates that our sequencing depth was adequate for sedaDNA. The number of pollen counts was guided by pollen records for the Laptev region usually ranging between 100 and 600 counts (Andreev et al., 2011). However, for future studies a higher sampling effort should be considered to mitigate the effect of the low taxonomic



richness. Second, the recorded richness depends on the taxonomic resolution. For sedaDNA the resolution depends on the marker employed. In our study, the resolution of the *trnL* P6 loop marker (Taberlet et al., 2007) made it possible to assign 78 % of the retrieved sequences to species or genus level, while 71 % of pollen and spores were identified to a similar taxonomic level. This is similar to other sedaDNA studies focusing on Arctic vegetation from permafrost sediments (Taberlet et al., 2007: 90 % up to genus level, Sønstebo et al., 2010: 83 % for the oldest and 68 % for the youngest sample, Jørgensen et al., 2012: 81 %, Willerslev et al., 2014: 80 %). SedaDNA analysis was able to distinguish between 18 sequence types from Poaceae and 12 from Cyperaceae, although several closely related taxa within Poaceae and Cyperaceae and especially Saliceae, could not be distinguished because there is not enough interspecific variation in the marker target region. Most of these closely related taxa, especially in the Poaceae and Cyperaceae, cannot be distinguished by pollen analysis either and the resolution is often restricted to family level (Birks, 2001). A higher resolution would be able to provide a better estimate of the taxonomic richness and thus greater insight into local environmental conditions since different species of the same genus can have different habitat preferences. Additionally, we found that bryophytes are highly under-represented in our datasets, despite being reported to be highly abundant, diverse and functionally very important members of modern polygonal landscapes (Zibulski et al., 2013, 2016). Epp et al. (2012) developed a more specific marker for bryophyte metabarcoding with an approximately 10 % higher resolution than the marker used in this study. Their marker, however, suffered from a low amplification success rate in late Pleistocene samples. They highlighted two probable causes, which may also hold true for the *trnL* P6 marker. First, the main bryophyte biomass is typically found above-ground, whereas roots are suspected to contribute the majority of vascular plant DNA in soil (Levy-Booth et al., 2007; Willerslev et al., 2003; Yoccoz et al., 2012), and second, the presence of secondary metabolites may increase DNA degradation rates after cell lysis (e.g. Xie and Lou, 2009).

In addition to sequence counts, richness in the sedaDNA sequence data depends highly on the completeness of the reference database used to assign the taxonomic name (Jørgensen et al., 2012; Parducci et al., 2013; Pedersen et al., 2013). By using the Arctic-Boreal reference database (Soininen et al., 2015; Sønstebo et al., 2010; Willerslev et al., 2014) we were able to increase the resolution for many



taxa, plus the EMBL database allowed us to examine our sequences for possible contamination by food or cultivated plants.

## 5.2 Environmental conditions during the pre-LGM (54–51 kyr BP, 18.9–8.35 m) and composition of deposited organic matter

- 5 The major part of the core below the ice-wedge encompasses sediments deposited before the LGM. According to sedaDNA and pollen this part can be divided into two zones; however the boundary between these zones slightly differs between the terrestrial and swamp and aquatic datasets and lies between 15 m and 17 m. The pollen record from the whole core portrays an open landscape at the regional scale.
- 10 The deepest part of the core from 18.9 m to ~16 m matches well with the deepest cryolithological unit presented in Schirrmeister et al. (2016). SedaDNA reflects a local terrestrial flora with low taxonomic richness, comprising taxa such as *Plantago*, *Puccinellia* and *Potentilla*, with *Carex aquatilis* as the only wetland plant retrieved at 18.15 m depth. The pollen record of this zone is characterized by high proportions of shrub, Poaceae and tree pollen, but with low proportions of *Larix*. As *Larix* pollen has a
- 15 very limited dispersal capacity owing to its size, weight and low quantity (Niemeyer et al., 2015; Sjögren et al., 2008), *Larix* stands are inferred to have been in the vicinity of the coring site and possibly even closer than they are today. In contrast to sedaDNA, high proportions of *Pediastrum*, *Botryococcus* and *Zygnema*-type algae and highest proportions of *Potamogeton* pollen overall imply the presence of a shallow pond (Andreev et al., 2002; Kienast et al., 2005). Only in this zone do the
- 20 sedaDNA and pollen records show such distinct differences.

At depths from approximately 16 m until the ice-wedge at 8.35 m, sedaDNA and pollen reveal high taxonomic richness. SedaDNA portrays high diversity among grasses, a rich herbaceous flora including swamp and aquatic taxa and high proportions of *Salix*. In several samples the sedaDNA record is dominated by Cyperaceae and other swamp and aquatic taxa, indicating wet conditions and probably

- 25 enhancing organic matter accumulation, as cold and anoxic conditions reduce decomposition rates (Davidson et al., 2000). These findings are supported by the sedimentary, hydrogeochemical (Schirrmeister et al., 2016) and biomarker analyses (Stapel et al., in review) performed on the same core. Schirrmeister et al. (2016) and Stapel et al. (in review) identified less decomposed organic matter





- at depths of 10 m and between 11.2 m and 15 m from higher total organic carbon (TOC) content, higher hydrogen index, lower  $\delta^{13}\text{C}$  values and high concentrations of branched Glycerol dialkyl glycerol tetraether (br-GDGTs, microbial membrane compounds). The taxonomic composition of sedaDNA comprised typical taxa of low-centred polygonal depressions such as *Stuckenia*, *Hippuris* and *Caltha*
- 5 *palustris* indicating the presence of a shallow pond (Kienast et al., 2008). Intermittently, the absence of hydrophytes and increasing proportions of Poinae (*Arctofila fulva* / *Dupontia fisheri*) and Cyperaceae indicate times without a pond and hence point towards temporal fluctuations in the hydrology of the depression. The temporal scale on which these fluctuations occurred however cannot be assessed due to cryoturbation in the sediments and the large uncertainties of the dating results.
- 10 As shown by recent studies of low-centred polygons, microtopographical differences resulting from the moisture gradient between the dry uplifted ridge and the wet depression shape the local plant community (de Klerk et al., 2009, 2011; Zibulski et al., 2016). According to the sedaDNA results, *Carex* probably occupied the major part of the polygon, whereas the ridge was likely covered by *Salix* shrubs along with Poaceae and herbs (de Klerk et al., 2009, 2011, 2014, Minke et al., 2007, 2009;
- 15 Teltewskoi et al., 2016). The transitional zone from the ridge to the depression is characterized by an increase in moisture and was probably occupied by taxa such as *Carex*, *Eriophorum*, *Saxifraga hirculus*, *Comarum* and *Pedicularis* (de Klerk et al., 2009, 2014; Savelieva et al., 2013; Zibulski et al., 2016). However, vegetation surveys along transects through modern low-centred polygons and temporal reconstructions from short cores (de Klerk et al., 2009, 2011, 2014, Minke et al., 2007, 2009;
- 20 Teltewskoi et al., 2016; Zibulski et al., 2016) show high proportions of Ericales (e.g. *Vaccinium* spp., *Ledum palustre*, *Empetrum nigrum*) and *Betula nana* ssp. *exilis* and therefore display a different plant assemblage to Holocene polygons in comparison to our findings. This indicates that Holocene polygon mires may differ from those of the pre-LGM.
- The pollen and NPP record in this zone (16–8.35 m) comprises *Potamogeton* pollen and *Pediastrum*,
- 25 *Botryococcus* and *Zygnema*-type algae, which supports the sedaDNA results and the presence of a shallow pond (Andreev et al., 2002; Kienast et al., 2005). Taxa such as *Artemisia*, *Dryas*, Papaveraceae and *Saxifraga* indicate overall dry environmental conditions with probably more severe winters than today, while *Potamogeton* indicates warmer summers (Kienast et al., 2001, 2005). Annual precipitation





of less than 250 mm and rapidly falling temperatures in winter must have occurred to allow thermal cracking of the soil to keep the active layer sufficiently shallow for the formation of ice-wedges and ridges that enclose low-centred polygons (Minke et al., 2007). Low relative proportions of trees (also derived by long-distance dispersal from extra-regional stands (Birks, 2001; van der Knaap, 1987)) and shrubs with high proportions of grasses, sedges and herbs are consistent with other published pollen and macrofossil analyses in this time interval and region (Andreev et al., 2011; Kienast et al., 2001; Sher et al., 2005). The recorded pollen spectrum from our core furthermore tallies with studies from Bol'shoy Lyakhovsky island, Bykovsky Peninsula and Kurungnakh Island, which present pollen records dominated by Cyperaceae and Poaceae with a constant presence of *Salix* and high abundances of *Artemisia* and Caryophyllaceae for 55 to 40 kyr BP (Andreev et al., 2011 and references therein). The decreasing proportions of *Larix* pollen with decreasing depth presented here may point towards a southward retreat of *Larix* stands or a reduction in pollen productivity through unfavourable environmental conditions.

### 5.3 Environmental conditions during the post-LGM (11.4–9.7 kyr BP (13.4–11.1 cal kyr BP)) and composition of deposited organic matter

The upper part of the core from the ice-wedge up to approximately 0.25 m depth includes the late glacial transition to the early Holocene (approximately 11.4 to 9.7 kyr BP, (13.4–11.1 cal kyr BP)). As emphasized in Andreev et al. (2011) records of the late glacial transition are rare because of active thermoerosion. Hence, our results provide valuable information about the vegetation history in this region and organic matter composition.

The sedaDNA results imply profound changes after the LGM. First, the local taxonomic richness decreased strongly. Second, the taxonomic composition of the local flora changed towards shrub tundra and was mainly characterized by high proportions of *Betula*, *Salix* and *Equisetum* with a low diversity among Poaceae and herbaceous plants with only a subset of the formerly present Cyperaceae. Highly fluctuating proportions, especially between Poaceae and Cyperaceae, indicate fluctuating moisture conditions but not the presence of a pond. In drier periods the organic matter comprises mostly Poaceae, which were represented by a different composition in comparison to the pre-LGM, with Agrostidinae



and *Poa* MOTU2. During moister periods, increased proportions of wetland plants such as *Eriophorum*, *Equisetum* and *Ranunculus* were recorded. The high proportions of *Equisetum* in this time interval are supported by our spore-pollen record and were recorded in six post-LGM samples with a median proportion of 38 % in the palaeogenetic study of Willerslev et al. (2014) and the palynological review of Andreev et al. (2011) with NPP percentages below 1 %.

The pollen analysis shows that the same dominant taxa detected by the sedaDNA approach characterize the area on a regional scale and implies shrub tundra with dwarf willow, dwarf birch and alder (Andreev et al., 2011). The equal relative proportions between pollen from trees and shrubs and pollen from herbs, grasses and sedges indicate climate amelioration during the early Holocene (Andreev et al., 2011) with increased humidity after the marine transgression (Kienast et al., 2001). Published pollen records for 11.7–10.6 kyr BP are dominated by Cyperaceae and Poaceae. Shrub pollen increased at approximately 9 kyr BP (Andreev et al., 2011), with up to 60 % of *Betula* in the Khorogor Valley near Tiksi (Andreev et al., 2011; Grosse et al., 2007). These results match well with the pollen data presented here.

The uppermost samples are dominated by Poaceae followed by Cyperaceae pollen and show high proportions of alder, dwarf birch and dwarf willow shrubs, along with Ericales and Ranunculaceae and low proportions of *Artemisia*, reflecting the modern pollen spectrum (Andreev et al., 2011; CAVM Team, 2003). In contrast, the sedaDNA surface sample is characterized by *Agrostidinae* MOTUs 1 and 2, *Eriophorum* MOTU1 and *Carex aquatilis*. This most likely reflects their high below-ground biomass in this sample. Taken together, both proxies reflect the tussock-sedge, dwarf-shrub, (moss) tundra according to the division of the Circumarctic Vegetation Map (CAVM Team, 2003).

## 6. Conclusions

We demonstrate that combining sedaDNA with pollen and NPPs for palaeobotanical reconstructions offers valuable insights into the taxonomic composition of plant organic matter and its accumulation conditions. The proxies complement each other and differences between the records result mainly from differences in the spatial resolution, the taxonomic resolution capacities and the sampling effort.



The sedaDNA record presents a high number of taxa at a high resolution throughout the core allowing a detailed characterization of plant community changes in the deposited sediments. Furthermore, the high taxonomic resolution allowed for inferences of hydrological changes at the coring site. Our findings support the general view that sedaDNA represents the local flora and predominantly local below-ground biomass.

Pollen and NPPs prove to be important for a more complete representation of the taxonomic composition on a local to regional scale and to assess the environmental conditions. They are suitable in tracing hydrological changes at the coring site, even though the signal can be buffered by the regional and extra-regional pollen input and hence not as pronounced as with sedaDNA.

For sediments deposited from 54 to 51 kyr BP, the pollen record suggests an open landscape shaped by relatively dry environmental conditions. Plant organic matter composition, derived from sedaDNA, reveals high taxonomic richness among grasses, sedges and herbs, including hydropytes with a constant presence of dwarf willows. The fluctuating dominance of swamp and aquatic taxa in both proxies suggests the presence of a low-centred polygon, which frequently carried a pond in the depression, implying that severe winters prevailed, which allowed for frost cracking and polygon development. Comparisons with studies of Holocene polygons indicate that pre-LGM plant communities of low-centred polygons differed from Holocene ones.

During the post-LGM (11.4–9.7 kyr BP (13.4–11.1 cal kyr BP)), sedaDNA shows an almost complete taxonomic turnover to shrub tundra with less taxonomic richness in comparison to the pre-LGM deposits. Similar to the sedaDNA record, pollen also implies shrub tundra during the post-LGM, but in contrast to sedaDNA, the taxonomic richness decreased only to a minor extent while proportional changes among dominant taxa are more decisive.

Future developments will probably comprise technical refinements to reduce biases in sedaDNA data as the relevant sequencing technologies are progressing quickly and sequence databases are continuously enhanced with new genomic reference sequences. Biases currently introduced through the PCR step will potentially be reduced as DNA extracts will increasingly be sequenced directly - all together providing a more comprehensive understanding of past ecosystems.



## Data availability

<https://www.pangaea.de/> (follows after acceptance and includes the DNA and pollen and NPP datasets)

## Supplement

1. Supplement\_Zimmermann.pdf
- 5
  - S1 Sequencing and sequence filtering
  - S2 Technical evaluation and authenticity of the data
  - References
  - S3 Figures
2. S4\_DNA\_dataset.xlsx
- 10
  - 3. S5\_cultivated\_nonArctic\_plants.xlsx
  - 4. S6\_negative\_controls.xlsx
  - 5. S7\_Pollen\_counts.xlsx

## Author contributions

H. H. Zimmermann performed the core sub-sampling, the genetic laboratory work and all  
15 bioinformatics and statistical analyses, guided by L. S. Epp, U. Herzsuh and K. R. Stoof-  
Leichsenring. E. Raschke counted pollen and NPPs. P. P. Overduin coordinated the field work in 2012  
and collected the core. G. Schwamborn and L. Schirrmeister opened the core and advised on sub-  
sampling. H. Zimmermann wrote the manuscript that all co-authors commented on.

## Competing interests

20 The authors declare that they have no conflict of interest.



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## 10 References

- Aiken, S. G., Dallwitz, M. J., Consaul, L. L., McJannet, C. L., Boles, R. L., Argus, G. W., Gillett, J. M., Scott, P. J., Elven, R., LeBlanc, M. C., Gillespie, L. J., Brysting, A. K., Solstad, H. and Harris, J. G.: Flora of the Canadian Arctic Archipelago: Descriptions, Illustrations, Identification, and Information Retrieval. NRC Research Press, National Research Council of Canada, Ottawa, [online] Available from:  
 15 <http://nature.ca/aaflora/data/index.htm> (Accessed 20 July 2016), 2007.
- Alsos, I. G., Coissac, E., Edwards, M., Foreid, M. K., Gielly, L., Sjoegren, P., Taberlet, P. and Yoccoz, N.: Plant DNA in sediments: to which degree do they represent the flora?, *GENOME*, 58(5), 186, 2015.
- Andreev, A., Schirrmeister, L., Siegert, C., Bobrov, A. A., Demske, D., Seiffert, M. and Hubberten, H. W.: Paleoenvironmental changes in Northeastern Siberia during the Late Quaternary - evidence from  
 20 pollen records of the Bykovsky Peninsula, *Polarforschung*, 70, 13–25, 2002.
- Andreev, A. A., Schirrmeister, L., Tarasov, P. E., Ganopolski, A., Brovkin, V., Siegert, C., Wetterich, S. and Hubberten, H.-W.: Vegetation and climate history in the Laptev Sea region (Arctic Siberia) during Late Quaternary inferred from pollen records, *Quat. Sci. Rev.*, 30(17–18), 2182–2199, doi:10.1016/j.quascirev.2010.12.026, 2011.
- 25 Andrews, S.: FastQC A Quality Control tool for High Throughput Sequence Data, [online] Available from: <http://www.bioinformatics.babraham.ac.uk/projects/fastqc>, 2010.
- Arnold, L. J., Roberts, R. G., MacPhee, R. D. E., Haile, J. S., Brock, F., Möller, P., Froese, D. G., Tikhonov, A. N., Chivas, A. R., Gilbert, M. T. P. and Willerslev, E.: Paper II – Dirt, dates and DNA:



- OSL and radiocarbon chronologies of perennially frozen sediments in Siberia, and their implications for sedimentary ancient DNA studies, *Boreas*, 40(3), 417–445, doi:10.1111/j.1502-3885.2010.00181.x, 2011.
- Bellemain, E., Davey, M. L., Kauserud, H., Epp, L. S., Boessenkool, S., Coissac, E., Geml, J., Edwards, M., Willerslev, E., Gussarova, G., Taberlet, P. and Brochmann, C.: Fungal palaeodiversity revealed using high-throughput metabarcoding of ancient DNA from arctic permafrost, *Environ. Microbiol.*, 15(4), 1176–1189, doi:10.1111/1462-2920.12020, 2013.
- Bennett, B.: Determination of the number of zones in a biostratigraphical sequence, *New Phytol.*, 132, 155–170, 1996.
- 10 Beug, H.-J.: *Leitfaden der Pollenbestimmung*, Verlag Dr. Friedrich Pfeil, München, 2004.
- Binladen, J., Gilbert, M. T. P., Bollback, J. P., Panitz, F., Bendixen, C., Nielsen, R. and Willerslev, E.: The Use of Coded PCR Primers Enables High-Throughput Sequencing of Multiple Homolog Amplification Products by 454 Parallel Sequencing, *PLoS ONE*, 2(2), e197, doi:10.1371/journal.pone.0000197, 2007.
- 15 Birks, H. H.: Plant macrofossils, in *Tracking Environmental Change Using Lake Sediments*, vol. 3 Terrestrial, Algal, and Siliceous Indicators, edited by J. P. Smol, H. J. B. Birks, W. M. Last, R. S. Bradley, and K. Alverson, Springer Netherlands, Dordrecht. [online] Available from: <http://link.springer.com/10.1007/0-306-47668-1> (Accessed 29 July 2016), 2001.
- Boessenkool, S., McGlynn, G., Epp, L. S., Taylor, D., Pimentel, M., Gizaw, A., Nemomissa, S., 20 Brochmann, C. and Popp, M.: Use of ancient sedimentary DNA as a novel conservation tool for high-altitude tropical biodiversity, *Conserv. Biol.*, 28(2), 446–455, doi:10.1111/cobi.12195, 2014.
- Boyer, F., Mercier, C., Bonin, A., Le Bras, Y., Taberlet, P. and Coissac, E.: OBITools: a Unix-inspired software package for DNA metabarcoding, *Mol. Ecol. Resour.*, 16, 176–182, doi:10.1111/1755-0998.12428, 2016.
- 25 CAVM Team: Circumpolar Arctic Vegetation Map (1:7,500,000 scale), Conservation of Arctic Flora and Fauna (CAFF) Map No. 1. U.S. Fish and Wildlife Service, Anchorage, Alaska. [online] Available from: <http://www.geobotany.uaf.edu/cavm/>, 2003.
- Champlot, S., Berthelot, C., Pruvost, M., Bennett, E. A., Grange, T. and Geigl, E.-M.: An efficient multistrategy DNA decontamination procedure of PCR reagents for hypersensitive PCR applications, 30 *PLoS ONE*, 5(9), e13042, doi:10.1371/journal.pone.0013042, 2010.



- Charkin, A. N., Dudarev, O. V., Semiletov, I. P., Kruhmalev, A. V., Vonk, J. E., Sánchez-García, L., Karlsson, E. and Gustafsson, Ö.: Seasonal and interannual variability of sedimentation and organic matter distribution in the Buor-Khaya Gulf: the primary recipient of input from Lena River and coastal erosion in the southeast Laptev Sea, *Biogeosciences*, 8(9), 2581–2594, doi:10.5194/bg-8-2581-2011, 5 2011.
- Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H. M., Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R., Allison, S. D., Van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T. V., Díaz, S., Garnier, E., Gurvich, D. E., Kazakou, E., Klein, J. A., Read, J., Reich, P. B., 10 Soudzilovskaia, N. A., Vaieretti, M. V. and Westoby, M.: Plant species traits are the predominant control on litter decomposition rates within biomes worldwide, *Ecol. Lett.*, 11(10), 1065–1071, doi:10.1111/j.1461-0248.2008.01219.x, 2008.
- Cox, P. A.: Hydrophilous pollination, *Annu. Rev. Ecol. Syst.*, 19(1), 261–279, doi:10.1146/annurev.es.19.110188.001401, 1988.
- 15 Czudek, T. and Demek, J.: Thermokarst in Siberia and its influence on the development of lowland relief, *Quat. Res.*, 1(1), 103–120, doi:10.1016/0033-5894(70)90013-X, 1970.
- Davidson, E. A. and Janssens, I. A.: Temperature sensitivity of soil carbon decomposition and feedbacks to climate change, *Nature*, 440(7081), 165–173, doi:10.1038/nature04514, 2006.
- Davidson, E. A., Trumbore, S. E. and Amundson, R.: Biogeochemistry: soil warming and organic 20 carbon content, *Nature*, 408(6814), 789–790, 2000.
- De Barba, M., Miquel, C., Boyer, F., Mercier, C., Rioux, D., Coissac, E. and Taberlet, P.: DNA metabarcoding multiplexing and validation of data accuracy for diet assessment: Application to omnivorous diet, *Mol. Ecol. Resour.*, 14(2), 306–323, doi:10.1111/1755-0998.12188, 2014.
- Duchkov, A. D., Zheleznyak, M. and Sokolova, L. S.: Electronic geothermal atlases of Asian Russia, 25 *Sci. Cold Arid Reg.*, 6(5), 0479–0483, doi:10.3724/SP.J.1226.2014.00479, 2014.
- Epp, L. S., Boessenkool, S., Bellemain, E. P., Haile, J., Esposito, A., Riaz, T., Erséus, C., Gusarov, V. I., Edwards, M. E., Johnsen, A., Stenøien, H. K., Hassel, K., Kauserud, H., Yoccoz, N. G., Bråthen, K. A., Willerslev, E., Taberlet, P., Coissac, E. and Brochmann, C.: New environmental metabarcodes for analysing soil DNA: potential for studying past and present ecosystems, *Mol. Ecol.*, 21(8), 1821–1833, 30 doi:10.1111/j.1365-294X.2012.05537.x, 2012.





- 5 Epp, L. S., Gussarova, G., Boessenkool, S., Olsen, J., Haile, J., Schröder-Nielsen, A., Ludikova, A., Hassel, K., Stenøien, H. K., Funder, S., Willerslev, E., Kjær, K. and Brochmann, C.: Lake sediment multi-taxon DNA from North Greenland records early post-glacial appearance of vascular plants and accurately tracks environmental changes, *Quat. Sci. Rev.*, 117(318), 152–163, doi:10.1016/j.quascirev.2015.03.027, 2015.
- Fægri, K. and Iversen, J.: Textbook of pollen analysis, Fourth Edition by K. Fægri, P.E. Kaland, and K. Krzywinski., Blackburn Press, Caldwell, NJ., 1989.
- van Geel, B.: Non-pollen palynomorphs, in *Tracking Environmental Change Using Lake Sediments: Terrestrial, Algal, and Siliceous Indicators*, edited by J. P. Smol, H. J. B. Birks, W. M. Last, R. S. Bradley, and K. Alverson, pp. 99–119, Springer Netherlands, Dordrecht. [online] Available from: [http://dx.doi.org/10.1007/0-306-47668-1\\_6](http://dx.doi.org/10.1007/0-306-47668-1_6), 2001.
- 10 van Geel, B. and Aptroot, A.: Fossil ascomycetes in Quaternary deposits, *Nova Hedwig.*, 82(3–4), 313–329, doi:10.1127/0029-5035/2006/0082-0313, 2006.
- van Geel, B., Hallewas, D. P. and Pals, J. P.: A late Holocene deposit under the Westfriese Zeedijk near  
15 Enkhuizen (Prov. of Noord-Holland, The Netherlands): Palaeoecological and archaeological aspects, *Rev. Palaeobot. Palynol.*, 38(3), 269–335, doi:10.1016/0034-6667(83)90026-X, 1983.
- Grimm, E. C.: CONISS : A FORTRAN 77 Program for stratigraphically constrained cluster analysis by the method of incremental sum of squares, *Comput. Geosci.*, 13(I), 13–35, 1987.
- Grosse, G., Schirrmeister, L., Siegert, C., Kunitsky, V. V., Slagoda, E. A., Andreev, A. A. and  
20 Dereviagn, A. Y.: Geological and geomorphological evolution of a sedimentary periglacial landscape in Northeast Siberia during the Late Quaternary, *Geomorphology*, 86(1–2), 25–51, doi:10.1016/j.geomorph.2006.08.005, 2007.
- Grosse, G., Romanovsky, V., Jorgenson, T., Walter Anthony, K., Brown, J. and Overduin, P. P.: Vulnerability and feedbacks of permafrost to climate change, *EOS Trans. Am. Geophys. Union*, 92(9),  
25 73–80, doi:10.1002/ppp.689.Rowland, 2011.
- Günther, F., Overduin, P. P., Makarov, A. S. and Grigoriev, M. N.: Russian-German cooperation SYSTEM LAPTEV SEA : the expeditions Laptev Sea - Mamontov Klyk 2011 & Buor Khaya 2012, Alfred Wegener Institute for Polar and Marine Research, Bremerhaven. [online] Available from: [hdl:10013/epic.41834](http://hdl:10013/epic.41834), 2013a.



- Günther, F., Overduin, P. P., Sandakov, A. V., Grosse, G. and Grigoriev, M. N.: Short- and long-term thermo-erosion of ice-rich permafrost coasts in the Laptev Sea region, *Biogeosciences*, 10, 4297–4318, doi:10.5194/bg-10-4297-2013, 2013b.
- Gustafsson, Ö., van Dongen, B. E., Vonk, J. E., Dudarev, O. V. and Semiletov, I. P.: Widespread  
5 release of old carbon across the Siberian Arctic echoed by its large rivers, *Biogeosciences*, 8(6), 1737–1743, doi:10.5194/bg-8-1737-2011, 2011.
- Haile, J., Holdaway, R., Oliver, K., Bunce, M., Gilbert, M. T. P., Nielsen, R., Munch, K., Ho, S. Y. W., Shapiro, B. and Willerslev, E.: Ancient DNA chronology within sediment deposits: Are Paleobiological reconstructions possible and is DNA leaching a factor?, *Mol. Biol. Evol.*, 24(4), 982–989,  
10 doi:10.1093/molbev/msm016, 2007.
- Haile, J., Froese, D. G., MacPhee, R. D. E., Roberts, R. G., Arnold, L. J., Reyes, A. V., Rasmussen, M., Nielsen, R., Brook, B. W., Robinson, S., Demuro, M., Gilbert, M. T. P., Munch, K., Austin, J. J., Cooper, A., Barnes, I., Möller, P. and Willerslev, E.: Ancient DNA reveals late survival of mammoth and horse in interior Alaska, *Proc. Natl. Acad. Sci.*, pnas.0912510106, doi:10.1073/pnas.0912510106,  
15 2009.
- Hansen, A. J., Mitchell, D. L., Wiuf, C., Paniker, L., Brand, T. B., Binladen, J., Gilichinsky, D. A., Rønn, R. and Willerslev, E.: Crosslinks rather than strand breaks determine access to ancient DNA sequences from frozen sediments, *Genetics*, 173(2), 1175–1179, doi:10.1534/genetics.106.057349, 2006.
- 20 Heck, K. L., van Belle, G. and Simberloff, D.: Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size, *Ecology*, 56(6), 1459–1461, doi:10.2307/1934716, 1975.
- Hobbie, S. E.: Effects of plant species on nutrient cycling, *Trends Ecol. Evol.*, 7(10), 336–339, doi:10.1016/0169-5347(92)90126-V, 1992.
- 25 Hubberten, H. W., Andreev, A., Astakhov, V. I., Demidov, I., Dowdeswell, J. A., Henriksen, M., Hjort, C., Houmark-Nielsen, M., Jakobsson, M., Kuzmina, S., Larsen, E., Lunkka, J. P., Lyså, A., Mangerud, J., Möller, P., Saarnisto, M., Schirrmeister, L., Sher, A. V., Siegert, C., Siegert, M. J. and Svendsen, J. I.: The periglacial climate and environment in northern Eurasia during the last glaciation, *Quat. Sci. Rev.*, 23(11–13), 1333–1357, doi:10.1016/j.quascirev.2003.12.012, 2004.



- Hugelius, G., Strauss, J., Zubrzycki, S., Harden, J. W., Schuur, E. A. G., Ping, C.-L., Schirrmeister, L., Grosse, G., Michaelson, G. J., Koven, C. D., O'Donnell, J. A., Elberling, B., Mishra, U., Camill, P., Yu, Z., Palmtag, J. and Kuhry, P.: Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps, *Biogeosciences*, 11(23), 6573–6593, doi:10.5194/bg-11-6573-2014, 2014.
- Hurlbert, S. H.: The nonconcept of species diversity: A critique and alternative parameters, *Ecology*, 52(4), 577–586, doi:10.2307/1934145, 1971.
- Iversen, C. M., Sloan, V. L., Sullivan, P. F., Euskirchen, E. S., McGuire, A. D., Norby, R. J., Walker, A. P., Warren, J. M. and Wullschleger, S. D.: The unseen iceberg: plant roots in arctic tundra, *New Phytol.*, 205(1), 34–58, doi:10.1111/nph.13003, 2015.
- Jankovská, V. and Komárek, J.: Indicative value of *Pediastrum* and other coccal green algae in palaeoecology, *Folia Geobot.*, 35(1), 59–82, doi:10.1007/BF02803087, 2000.
- John, D. M., Whitton, B. A. and Brook, A. J., Eds.: The freshwater algal flora of the British Isles: An identification guide to freshwater and terrestrial algae, Cambridge University Press, Cambridge, 2002.
- Jørgensen, T., Haile, J., Möller, P., Andreev, A., Boessenkool, S., Rasmussen, M., Kienast, F., Coissac, E., Taberlet, P., Brochmann, C., Bigelow, N. H., Andersen, K., Orlando, L., Gilbert, M. T. P. and Willerslev, E.: A comparative study of ancient sedimentary DNA, pollen and macrofossils from permafrost sediments of northern Siberia reveals long-term vegetational stability, *Mol. Ecol.*, 21(8), 1989–2003, doi:10.1111/j.1365-294X.2011.05287.x, 2012.
- Juggins, S.: rioja: Analysis of Quaternary science data, R package version 0.7-3., 2012.
- Kanz, C., Aldebert, P., Althorpe, N., Baker, W., Baldwin, A., Bates, K., Browne, P., van den Broek, A., Castro, M., Cochrane, G., Duggan, K., Eberhardt, R., Faruque, N., Gamble, J., Garcia Diez, F., Harte, N., Kulikova, T., Lin, Q., Lombard, V., Lopez, R., Mancuso, R., McHale, M., Nardone, F., Silventoinen, V., Sobhany, S., Stoeck, P., Tuli, M. A., Tzouvara, K., Vaughan, R., Wu, D., Zhu, W. and Apweiler, R.: The EMBL nucleotide sequence database, *Nucleic Acids Res.*, 33(DATABASE ISS.), 29–33, doi:10.1093/nar/gki098, 2005.
- Kienast, F., Siebert, C., Dereviagin, A. and Mai, D. H.: Climatic implications of Late Quaternary plant macrofossil assemblages from the Taymyr Peninsula, Siberia, *Glob. Planet. Change*, 31, 265–281, 2001.



- Kienast, F., Schirrmeister, L., Siegert, C. and Tarasov, P.: Palaeobotanical evidence for warm summers in the East Siberian Arctic during the last cold stage, *Quat. Res.*, 63(3), 283–300, doi:10.1016/j.yqres.2005.01.003, 2005.
- Kienast, F., Tarasov, P., Schirrmeister, L., Grosse, G. and Andreev, A. A.: Continental climate in the East Siberian Arctic during the last interglacial: Implications from palaeobotanical records, *Glob. Planet. Change*, 60(3–4), 535–562, doi:10.1016/j.gloplacha.2007.07.004, 2008.
- de Klerk, P., Donner, N., Joosten, H., Karpov, N. S., Minke, M., Seifert, N. and Theuerkauf, M.: Vegetation patterns, recent pollen deposition and distribution of non-pollen palynomorphs in a polygon mire near Chokurdakh (NE Yakutia, NE Siberia), *Boreas*, 38(1), 39–58, doi:10.1111/j.1502-3885.2008.00036.x, 2009.
- de Klerk, P., Donner, N., Karpov, N. S., Minke, M. and Joosten, H.: Short-term dynamics of a low-centred ice-wedge polygon near Chokurdakh (NE Yakutia, NE Siberia) and climate change during the last ca 1250 years, *Quat. Sci. Rev.*, 30(21–22), 3013–3031, doi:10.1016/j.quascirev.2011.06.016, 2011.
- de Klerk, P., Teltewskoi, A., Theuerkauf, M. and Joosten, H.: Vegetation patterns, pollen deposition and distribution of non-pollen palynomorphs in an ice-wedge polygon near Kytalyk (NE Siberia), with some remarks on Arctic pollen morphology, *Polar Biol.*, 37(10), 1393–1412, doi:10.1007/s00300-014-1529-3, 2014.
- van der Knaap, W. O.: Transported pollen and spores on Spitsbergen and Jan Mayen, *Pollen Spores*, 24, 449–453, 1987.
- Knoblauch, C., Beer, C., Sosnin, A., Wagner, D. and Pfeiffer, E.-M.: Predicting long-term carbon mineralization and trace gas production from thawing permafrost of Northeast Siberia, *Glob. Change Biol.*, 19(4), 1160–1172, doi:10.1111/gcb.12116, 2013.
- Komárek, J. and Jankovská, V.: Review of the Green Algal Genus *Pediastrum*; Implication for Pollenanalytical Research, Schweizerbart Science Publishers, Berlin, Stuttgart, Germany. [online] Available from: [http://www.schweizerbart.de//publications/detail/isbn/9783443600358/Bibliotheca\\_Phycologica\\_Band\\_108\\_Komar](http://www.schweizerbart.de//publications/detail/isbn/9783443600358/Bibliotheca_Phycologica_Band_108_Komar), 2001.
- Kupriyanova, L. A. and Alyoshina, L. A.: Pollen and spores of plants in the flora of the European part of the USSR (Vol. 1), Academy of Sciences USSR, Komarov Botanical Institute, Leningrad, 1972.



- Kupriyanova, L. A. and Alyoshina, L. A.: Pollen and spores of plants from the flora of European part of USSR. Lamiaceae-Zygophyllaceae, Academy of Sciences USSR, Komarov Botanical Institute, Leningrad, 1978.
- Lachenbruch, A. H.: Mechanics of thermal contraction cracks and ice-wedge polygons in permafrost,  
5 Geol. Soc. Am. Spec. Pap., 70, 1–66, doi:10.1130/SPE70-p1, 1962.
- Leffingwell, E. de K.: Ground-ice-wedges: The dominant form of ground-ice on the north coast of Alaska, J. Geol., 23(7), 635–654, 1915.
- Levy-Booth, D. J., Campbell, R. G., Gulden, R. H., Hart, M. M., Powell, J. R., Klironomos, J. N., Pauls, K. P., Swanton, C. J., Trevors, J. T. and Dunfield, K. E.: Cycling of extracellular DNA in the soil  
10 environment, Soil Biol. Biochem., 39(12), 2977–2991, doi:10.1016/j.soilbio.2007.06.020, 2007.
- Lydolph, M. C., Jacobsen, J., Arctander, P., Gilbert, M. T. P., Gilichinsky, D. A., Hansen, A. J., Willerslev, E. and Lange, L.: Beringian paleoecology inferred from permafrost-preserved fungal DNA, Appl. Environ. Microbiol., 71(2), 1012–1017, doi:10.1128/AEM.71.2.1012-1017.2005, 2005.
- Lyell, C.: Principles of geology: Being an inquiry how far the former changes of the earth's surface are  
15 referable to causes now in operation, Murray, London, 1830.
- MacArthur, H.: On the relative abundance of bird species, Proc. Natl. Acad. Sci. USA, 43, 293–295, 1957.
- Mensing, S., Smith, J., Burkle Norman, K. and Allan, M.: Extended drought in the Great Basin of western North America in the last two millennia reconstructed from pollen records, Quat. Int., 188(1),  
20 79–89, doi:10.1016/j.quaint.2007.06.009, 2008.
- Minke, M., Donner, N., Karpov, N. S., de Klerk, P. and Joosten, H.: Distribution, diversity, development and dynamics of polygon mires: Examples from NE Yakutia (NE Siberia), Peatl. Int., 1, 36–40, 2007.
- Minke, M., Donner, N., Karpov, N., de Klerk, P. and Joosten, H.: Patterns in vegetation composition,  
25 surface height and thaw depth in polygon mires in the Yakutian Arctic (NE Siberia): a microtopographical characterisation of the active layer, Permafr. Periglac. Process., 20(4), 357–368, doi:10.1002/ppp.663, 2009.
- Moore, P. D., Webb, J. A. and Collison, M. E.: Pollen Analysis, 2nd ed., Blackwell Scientific Publications, Oxford, UK, 1991.



- Niemeyer, B., Klemm, J., Pestryakova, L. A. and Herzsuh, U.: Relative pollen productivity estimates for common taxa of the northern Siberian Arctic, *Rev. Palaeobot. Palynol.*, 221, 71–82, doi:10.1016/j.revpalbo.2015.06.008, 2015.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L.,  
5 Solymos, P., Stevens, M. H. H. and Wagner, H.: *vegan: Community Ecology Package*. R package version 2.0-2., 2011.
- Parducci, L., Matetovici, I., Fontana, S. L., Bennett, K. D., Suyama, Y., Haile, J., Kjaer, K. H., Larsen, N. K., Drouzas, A. D. and Willerslev, E.: Molecular- and pollen-based vegetation analysis in lake sediments from central Scandinavia, *Mol. Ecol.*, 22(13), 3511–3524, doi:10.1111/mec.12298, 2013.
- 10 Pedersen, M. W., Ginolhac, A., Orlando, L., Olsen, J., Andersen, K., Holm, J., Funder, S., Willerslev, E. and Kjær, K. H.: A comparative study of ancient environmental DNA to pollen and macrofossils from lake sediments reveals taxonomic overlap and additional plant taxa, *Quat. Sci. Rev.*, 75, 161–168, doi:10.1016/j.quascirev.2013.06.006, 2013.
- Preston, C. D. and Croft, J. M.: *Aquatic plants in Britain and Ireland: a joint project of the Environment  
15 Agency Institute of Terrestrial Ecology and the Joint Nature Conservation Committee*, Harley, Colchester, 1997.
- R Core Team: *R: A language and environment for statistical computing*, Vienna, Austria. [online] Available from: <http://www.r-project.org/>, 2014.
- Rawlence, N. J., Lowe, D. J., Wood, J. R., Young, J. M., Churchman, G. J., Huang, Y.-T. and Cooper,  
20 A.: Using palaeoenvironmental DNA to reconstruct past environments: progress and prospects, *J. Quat. Sci.*, 29(7), 610–626, doi:10.1002/jqs.2740, 2014.
- Romanovsky, V. E., Drozdov, D. S., Oberman, N. G., Malkova, G. V., Kholodov, A. L., Marchenko, S. S., Moskalenko, N. G., Sergeev, D. O., Ukraintseva, N. G., Abramov, A. A., Gilichinsky, D. A. and Vasiliev, A. A.: Thermal state of permafrost in Russia, *Permafr. Periglac. Process.*, 21(March), 136–  
25 155, doi:10.1002/ppp.683, 2010.
- Savelieva, L. A., Raschke, E. A. and Titova, D. V.: *Photographic Atlas of Plants and Pollen of the Lena River Delta*, St. Petersburg State University, Saint-Petersburg, 2013.
- Schirrmeister, L., Grosse, G., Wetterich, S., Overduin, P. P., Strauss, J., Schuur, E. A. G. and Hubberten, H.-W.: Fossil organic matter characteristics in permafrost deposits of the northeast Siberian  
30 Arctic, *J. Geophys. Res.*, 116, doi:10.1029/2011JG001647, 2011a.



- Schirrmeister, L., Kunitsky, V., Grosse, G., Wetterich, S., Meyer, H., Schwamborn, G., Babiy, O., Derevyagin, A. and Siegert, C.: Sedimentary characteristics and origin of the Late Pleistocene Ice Complex on north-east Siberian Arctic coastal lowlands and islands – A review, *Quat. Int.*, 241(1–2), 3–25, doi:10.1016/j.quaint.2010.04.004, 2011b.
- 5 Schirrmeister, L., Schwamborn, G., Overduin, P. P., Strauss, J., Fuchs, M. C., Grigoriev, M., Yakshina, I., Rethemeyer, J., Dietze, E. and Wetterich, S.: Yedoma Ice Complex of the Buor Khaya Peninsula (southern Laptev Sea), *Biogeosciences Discuss.*, 1–36, doi:10.5194/bg-2016-283, 2016.
- Schnell, I. B., Bohmann, K. and Gilbert, M. T. P.: Tag jumps illuminated – reducing sequence-to-sample misidentifications in metabarcoding studies, *Mol. Ecol. Resour.*, 15(6), 1289–1303, doi:10.1111/1755-0998.12402, 2015.
- 10
- Sher, A. V., Kuzmina, S. A., Kuznetsova, T. V. and Sulerzhitsky, L. D.: New insights into the Weichselian environment and climate of the East Siberian Arctic, derived from fossil insects, plants, and mammals, *Quat. Sci. Rev.*, 24(5–6), 533–569, doi:10.1016/j.quascirev.2004.09.007, 2005.
- Simpson, G. L.: Analogue methods in palaeoecology: Using the analogue package, *J. Stat. Softw.*, 22(2), 1–29, doi:10.18637/jss.v022.i02, 2007.
- 15
- Simpson, G. L. and Oksanen, J.: analogue: Analogue and weighted averaging methods for palaeoecology. [online] Available from: <http://cran.r-project.org/package=analogue>, 2016.
- Sjögren, P., van der Knaap, W. O., Huusko, A. and van Leeuwen, J. F. N.: Pollen productivity, dispersal, and correction factors for major tree taxa in the Swiss Alps based on pollen-trap results, *Rev. Palaeobot. Palynol.*, 152(3–4), 200–210, doi:10.1016/j.revpalbo.2008.05.003, 2008.
- 20
- Soininen, E. M., Gauthier, G., Bilodeau, F., Berteaux, D., Gielly, L., Taberlet, P., Gussarova, G., Bellemain, E., Hassel, K., Stenøien, H. K., Epp, L., Schröder-Nielsen, A., Brochmann, C. and Yoccoz, N. G.: Highly overlapping winter diet in two sympatric lemming species revealed by DNA metabarcoding, *Plos One*, 10(1), e0115335, doi:10.1371/journal.pone.0115335, 2015.
- 25
- Sokolovskaya, A. P.: Vegetation of Far North and its development, in *Pollen of the Arctic Plants*, pp. 245–292, Komarov Botanical Institute, Academy of Sciences USSR, Moscow-Leningrad, 1958.
- Sønstebo, J. H., Gielly, L., Brysting, a K., Elven, R., Edwards, M., Haile, J., Willerslev, E., Coissac, E., Rioux, D., Sannier, J., Taberlet, P. and Brochmann, C.: Using next-generation sequencing for molecular reconstruction of past Arctic vegetation and climate., *Mol. Ecol. Resour.*, 10(6), 1009–1018, doi:10.1111/j.1755-0998.2010.02855.x, 2010.
- 30





- Stapel, J. G., Schirrmeister, L., Overduin, P. P., Horsfield, B. and Mangelsdorf, K.: Present and past microbial lipid signatures and substrate potential of the organic matter in permafrost deposits from Buor Khaya: implications for future greenhouse gas production, in review.
- 5 Strauss, J., Schirrmeister, L., Wetterich, S., Borchers, A. and Davydov, S. P.: Grain-size properties and organic-carbon stock of Yedoma Ice Complex permafrost from the Kolyma lowland, northeastern Siberia, *Glob. Biogeochem. Cycles*, 26, 1–12, doi:10.1029/2011GB004104, 2012.
- Strauss, J., Schirrmeister, L., Grosse, G., Wetterich, S., Ulrich, M., Herzsuh, U. and Hubberten, H.-W.: The deep permafrost carbon pool of the Yedoma region in Siberia and Alaska, *Geophys. Res. Lett.*, 40, 6165–6170, doi:10.1002/2013GL058088, 2013.
- 10 Strauss, J., Schirrmeister, L., Mangelsdorf, K., Eichhorn, L., Wetterich, S. and Herzsuh, U.: Organic-matter quality of deep permafrost carbon – a study from Arctic Siberia, *Biogeosciences*, 12(7), 2227–2245, doi:10.5194/bg-12-2227-2015, 2015.
- Taberlet, P., Coissac, E., Pompanon, F., Gielly, L., Miquel, C., Valentini, A., Vermat, T., Corthier, G., Brochmann, C. and Willerslev, E.: Power and limitations of the chloroplast trnL (UAA) intron for plant  
 15 DNA barcoding, *Nucleic Acids Res.*, 35(3), doi:10.1093/nar/gkl938, 2007.
- Teltewskoi, A., Beermann, F., Beil, I., Bobrov, A., de Klerk, P., Lorenz, S., Lüder, A., Michaelis, D. and Joosten, H.: 4000 years of changing wetness in a permafrost polygon peatland (Kytalyk, NE Siberia): A comparative high-resolution multi-proxy study, *Permafr. Periglac. Process.*, 27(1), 76–95, doi:10.1002/ppp.1869, 2016.
- 20 Thomsen, P. F. and Willerslev, E.: Environmental DNA – An emerging tool in conservation for monitoring past and present biodiversity, *Biol. Conserv.*, 183, 4–18, doi:10.1016/j.biocon.2014.11.019, 2015.
- Wagner, D., Gattinger, A., Embacher, A., Pfeiffer, E.-M., Schlöter, M. and Lipski, A.: Methanogenic activity and biomass in Holocene permafrost deposits of the Lena Delta, Siberian Arctic and its  
 25 implication for the global methane budget, *Glob. Change Biol.*, 13(5), 1089–1099, doi:10.1111/j.1365-2486.2007.01331.x, 2007.
- Willerslev, E., Hansen, A. J., Binladen, J., Brand, T. B., Gilbert, M. T. P., Shapiro, B., Bunce, M., Wiuf, C., Gilichinsky, D. A. and Cooper, A.: Diverse Plant and Animal Genetic Records from Holocene and Pleistocene Sediments, *Science*, 300(5620), 791–795, doi:10.1126/science.1084114, 2003.



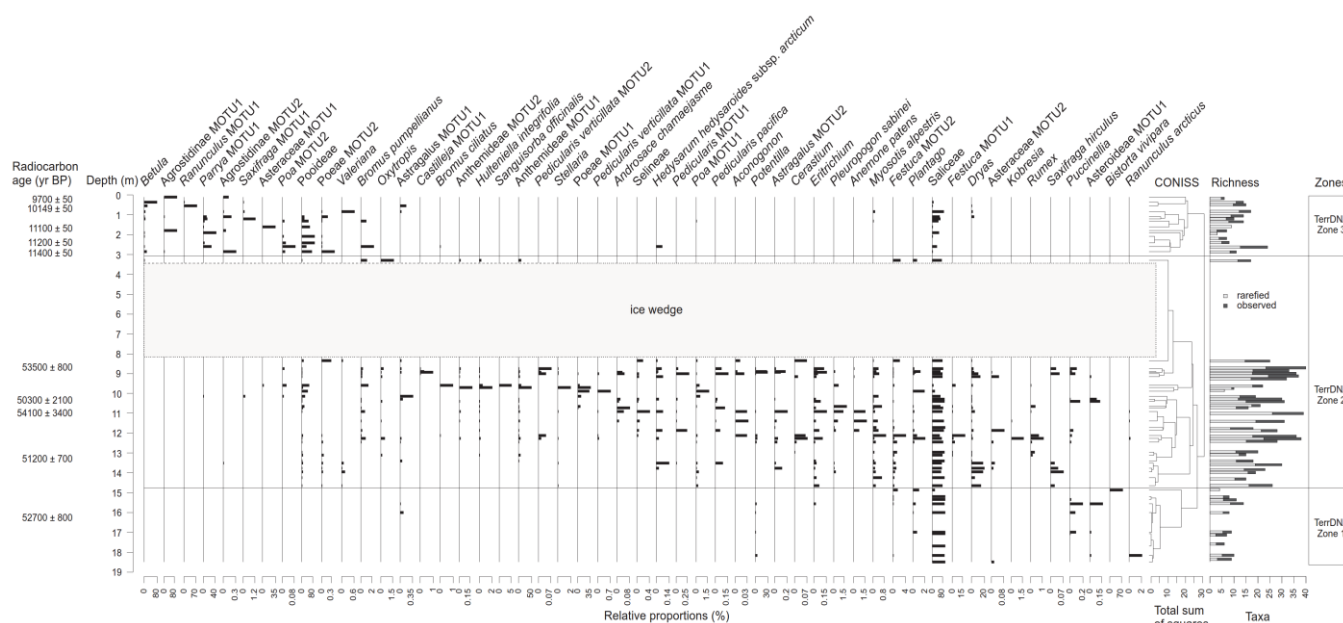
- Willerslev, E., Hansen, A. J. and Poinar, H. N.: Isolation of nucleic acids and cultures from fossil ice and permafrost, *Trends Ecol. Evol.*, 19(3), 141–147, doi:10.1016/j.tree.2003.11.010, 2004a.
- Willerslev, E., Hansen, A. J., Rønn, R., Brand, T. B., Barnes, I., Wiuf, C., Gilichinsky, D., Mitchell, D. and Cooper, A.: Long-term persistence of bacterial DNA, *Curr. Biol.*, 14(1), R9–R10, doi:10.1016/j.cub.2003.12.012, 2004b.
- Willerslev, E., Davison, J., Moora, M., Zobel, M., Coissac, E., Edwards, M. E., Lorenzen, E. D., Vestergaard, M., Gussarova, G., Haile, J., Craine, J., Gielly, L., Boessenkool, S., Epp, L. S., Pearman, P. B., Cheddadi, R., Murray, D., Brathen, K. A., Yoccoz, N., Binney, H., Cruaud, C., Wincker, P., Goslar, T., Alsos, I. G., Bellemain, E., Bryisting, A. K., Elven, R., Sonstebo, J. H., Murton, J., Sher, A., Rasmussen, M., Ronn, R., Mourier, T., Cooper, A., Austin, J., Moller, P., Froese, D., Zazula, G., Pompanon, F., Rioux, D., Niderkorn, V., Tikhonov, A., Savvinov, G., Roberts, R. G., MacPhee, R. D. E., Gilbert, M. T. P., Kjaer, K. H., Orlando, L., Brochmann, C. and Taberlet, P.: Fifty thousand years of Arctic vegetation and megafaunal diet, *Nature*, 506(7486), 47–51, doi:10.1038/nature12921, 2014.
- Xie, C.-F. and Lou, H.-X.: Secondary metabolites in bryophytes: An ecological aspect, *Chem. Biodivers.*, 6(3), 303–312, doi:10.1002/cbdv.200700450, 2009.
- Yoccoz, N. G., Bråthen, K. A., Gielly, L., Haile, J., Edwards, M. E., Goslar, T., Von Stedingk, H., Bryisting, A. K., Coissac, E., Pompanon, F., Sønstebo, J. H., Miquel, C., Valentini, A., De Bello, F., Chave, J., Thuiller, W., Wincker, P., Cruaud, C., Gavory, F., Rasmussen, M., Gilbert, M. T. P., Orlando, L., Brochmann, C., Willerslev, E. and Taberlet, P.: DNA from soil mirrors plant taxonomic and growth form diversity, *Mol. Ecol.*, 21(15), 3647–3655, doi:10.1111/j.1365-294X.2012.05545.x, 2012.
- Zibulski, R., Herzsuh, U., Pestryakova, L. A., Wolter, J., Müller, S., Schilling, N., Wetterich, S., Schirrmeister, L. and Tian, F.: River flooding as a driver of polygon dynamics: modern vegetation data and a millennial peat record from the Anabar River lowlands (Arctic Siberia), *Biogeosciences*, 10(8), 5703–5728, doi:10.5194/bg-10-5703-2013, 2013.
- Zibulski, R., Herzsuh, U. and Pestryakova, L. A.: Vegetation patterns along micro-relief and vegetation type transects in polygonal landscapes of the Siberian Arctic, *J. Veg. Sci.*, 27(2), 377–386, doi:10.1111/jvs.12356, 2016.



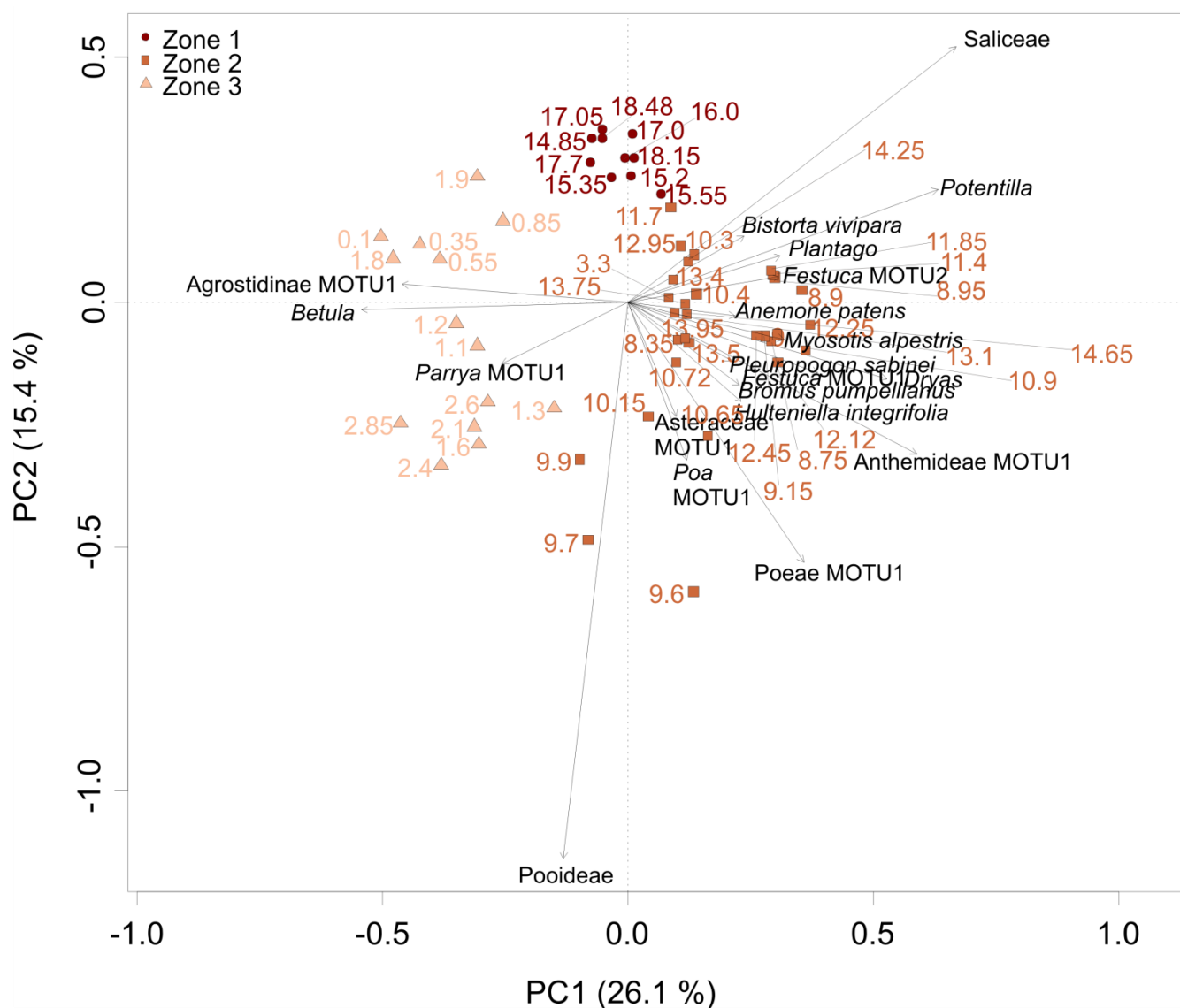
Figure 1 consists of two panels. Panel A is a map of the Laptev Sea region, showing the Taymyr Peninsula, the Lena Delta, the Lena River, and the New Siberian Islands. A scale bar indicates distances from 0 to 300 km. A dashed box highlights the area shown in Panel B. Panel B is a detailed map of the Buor Khaya Peninsula, showing the coastline, inland features, and the location of the BK-8 site marked with a yellow square. A scale bar indicates distances from 0 to 30 km.

**Figure 1:** (A) Geographical setting of the study site in the southern Laptev Sea with the Buor Khaya Peninsula framed by dashed lines and (B) the position of the BK-8 drilling site on the western coast of the peninsula (compiled by Bennet Juhls).

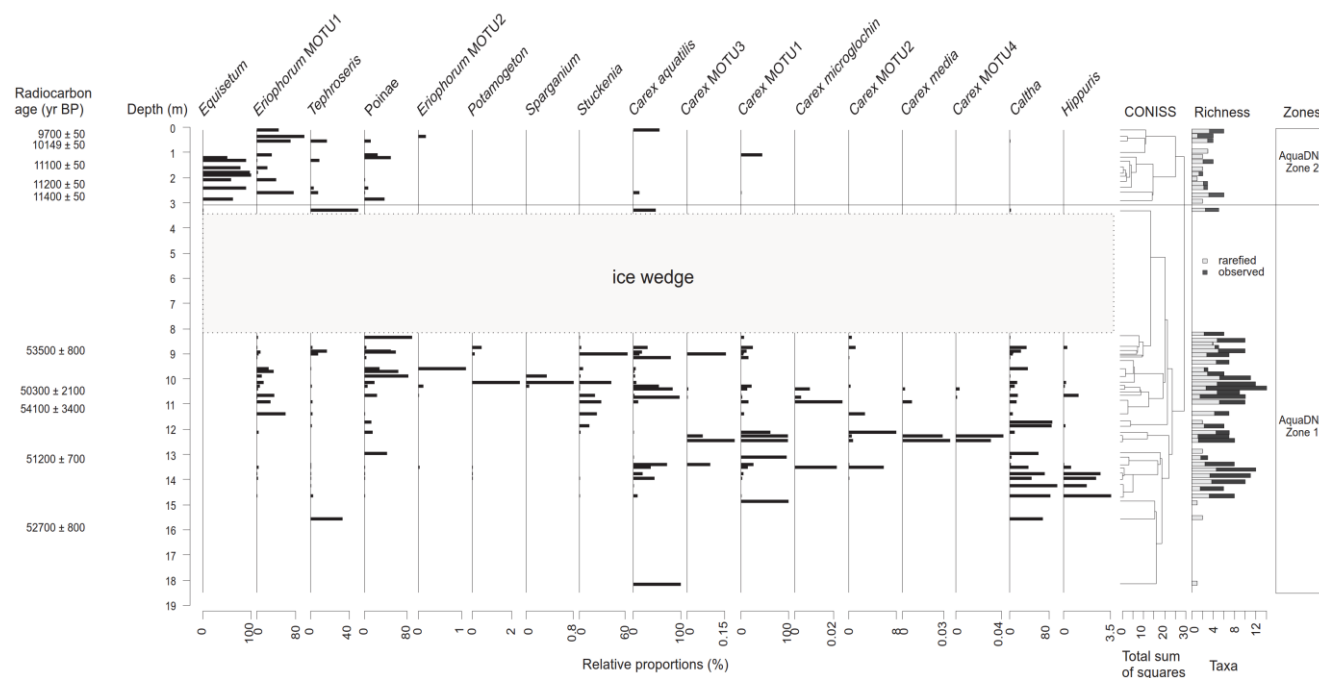
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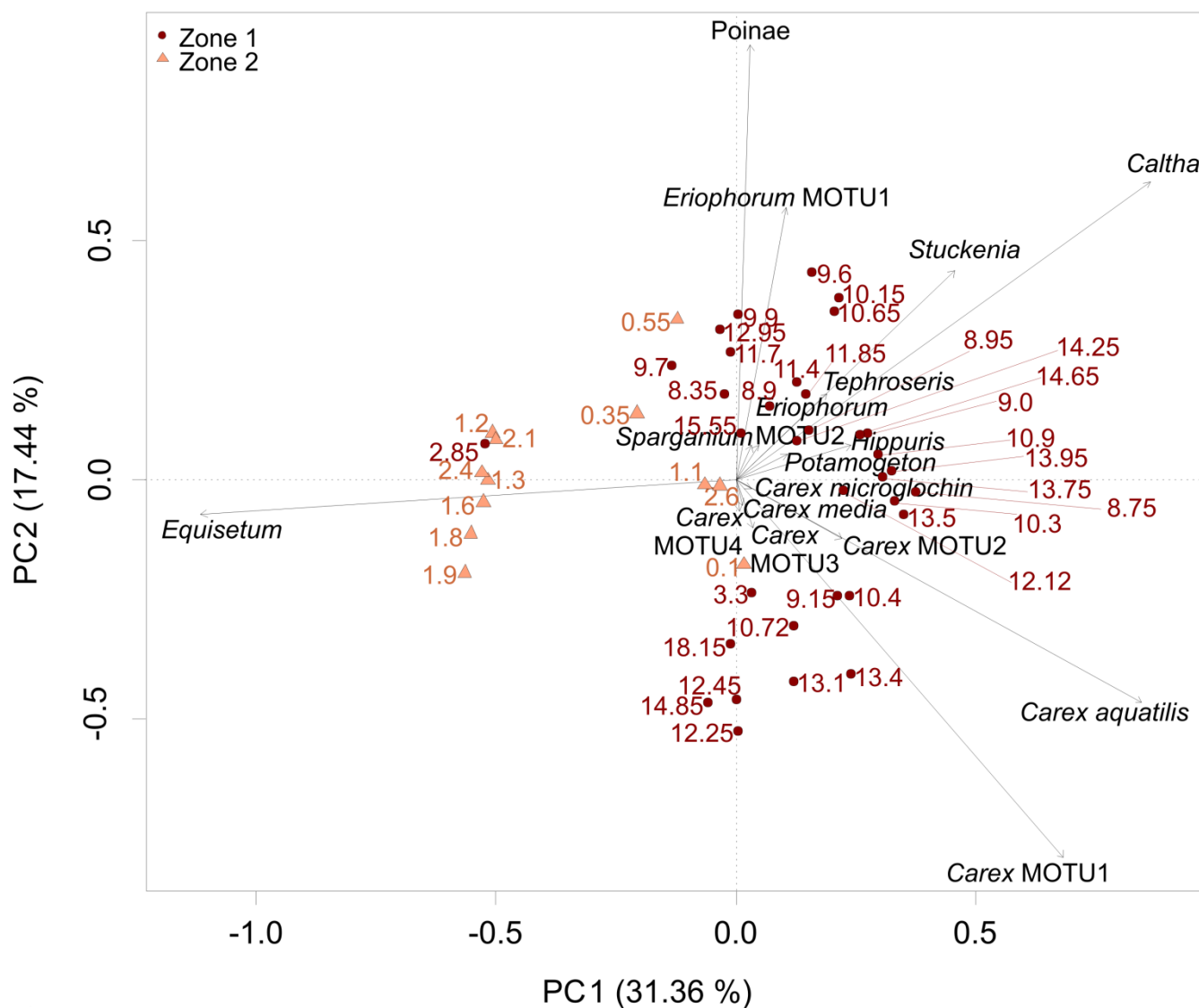
**Figure 2:** Stratigram of terrestrial sedaDNA (subset for statistical analyses) with relative proportions in percent of the taxa in each sample as horizontal bars, CONISS dendrogram, observed (dark grey) and rarefied (light grey) taxonomic richness. The grey area indicates the ice-wedge where no samples were taken. Horizontal lines indicate borders between zones. Scaling is taxon specific for better visibility of low percentages. Uncalibrated radiocarbon ages are given in years before present (yr BP).



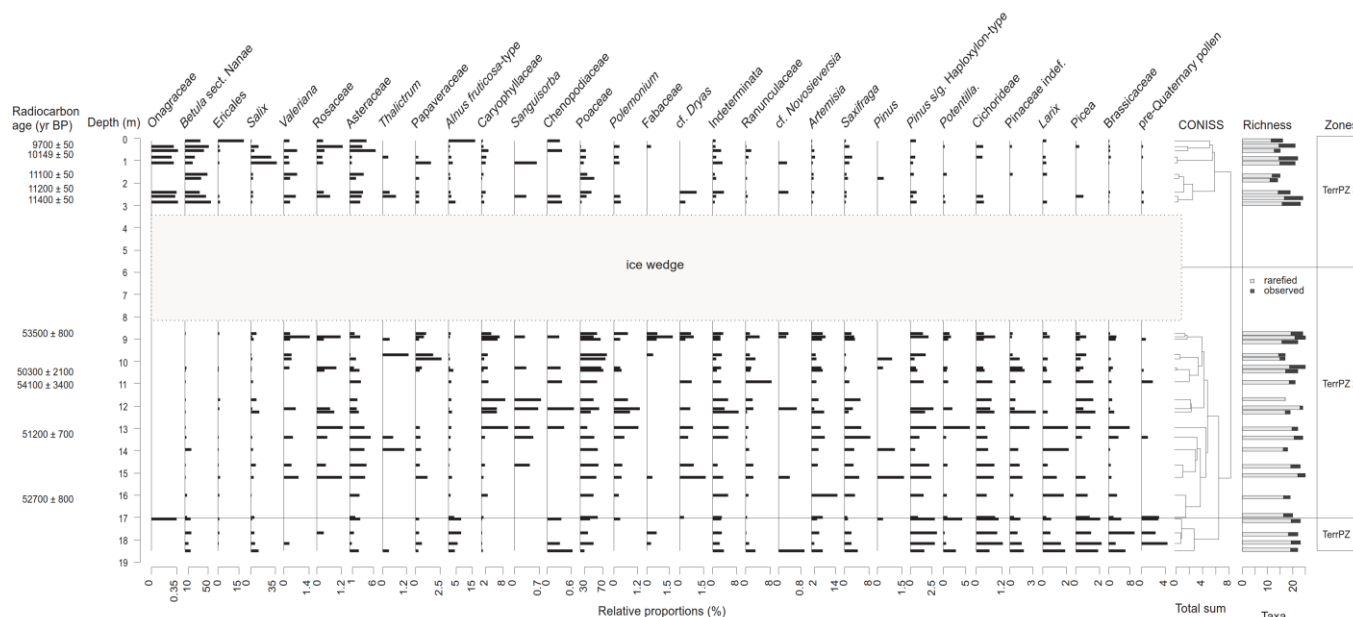
**Figure 3:** PCA biplot of terrestrial taxa from plant sedaDNA, showing a subset of 20 taxa which explained most of the variance in the dataset. Sample depths (m) are coloured according to their corresponding zone. Explained variances of the two principal components (PC) are shown in brackets.



**Figure 4:** Stratigram of swamp and aquatic sedaDNA (subset for statistical analyses) with relative proportions in percent of the taxa in each sample as horizontal bars, CONISS dendrogram, observed (dark grey) and rarefied (light grey) taxonomic richness. The grey area indicates the ice-wedge where no samples were taken. The horizontal line indicates the border between the zones. Scaling is taxon specific for better visibility of low percentages. Uncalibrated radiocarbon ages are given in years before present (yr BP).

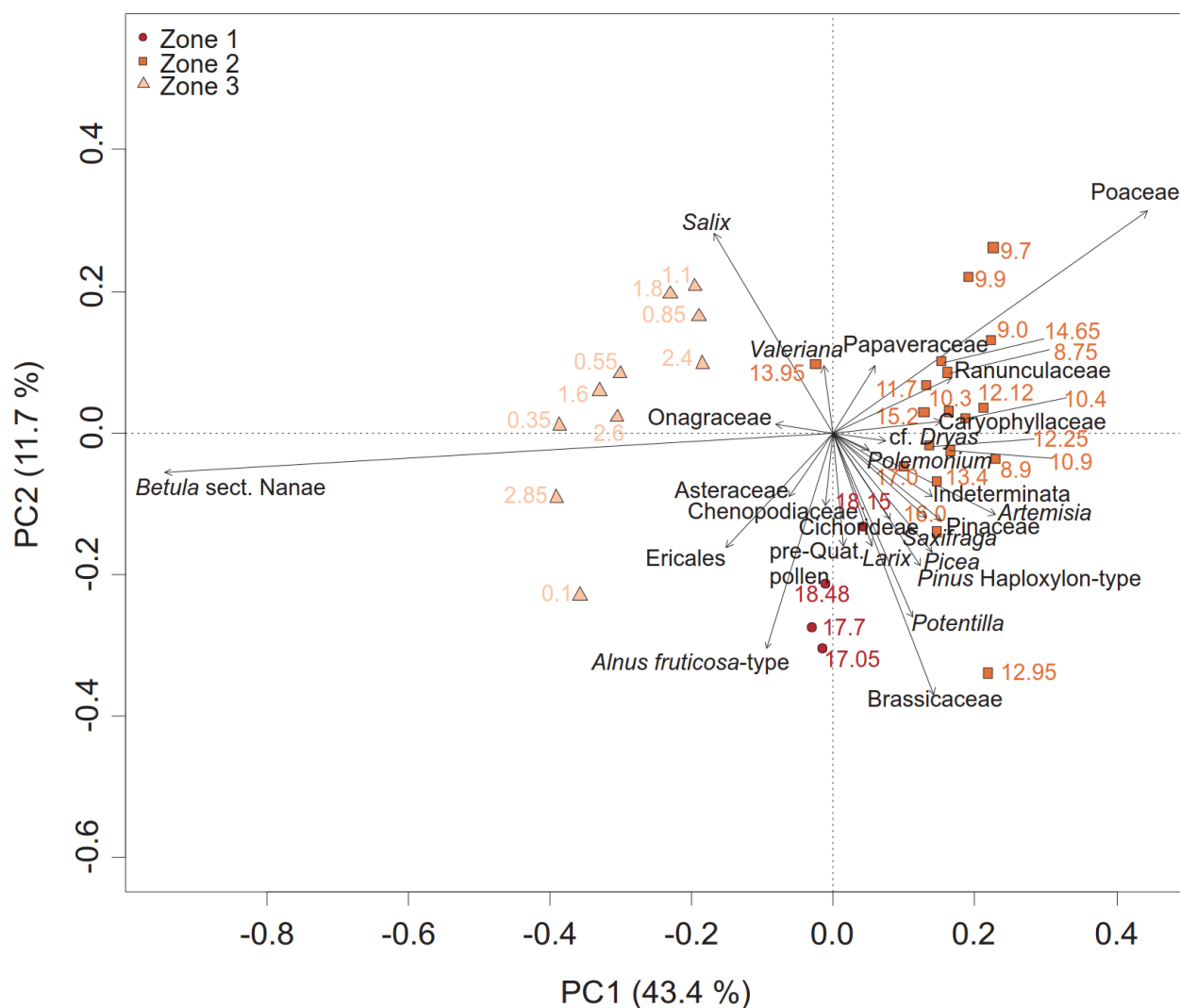


**Figure 5:** PCA biplot of swamp and aquatic taxa from plant sedaDNA. Sample depths (m) are coloured according to their corresponding zone. Explained variances of the two principal components (PC) are shown in brackets.

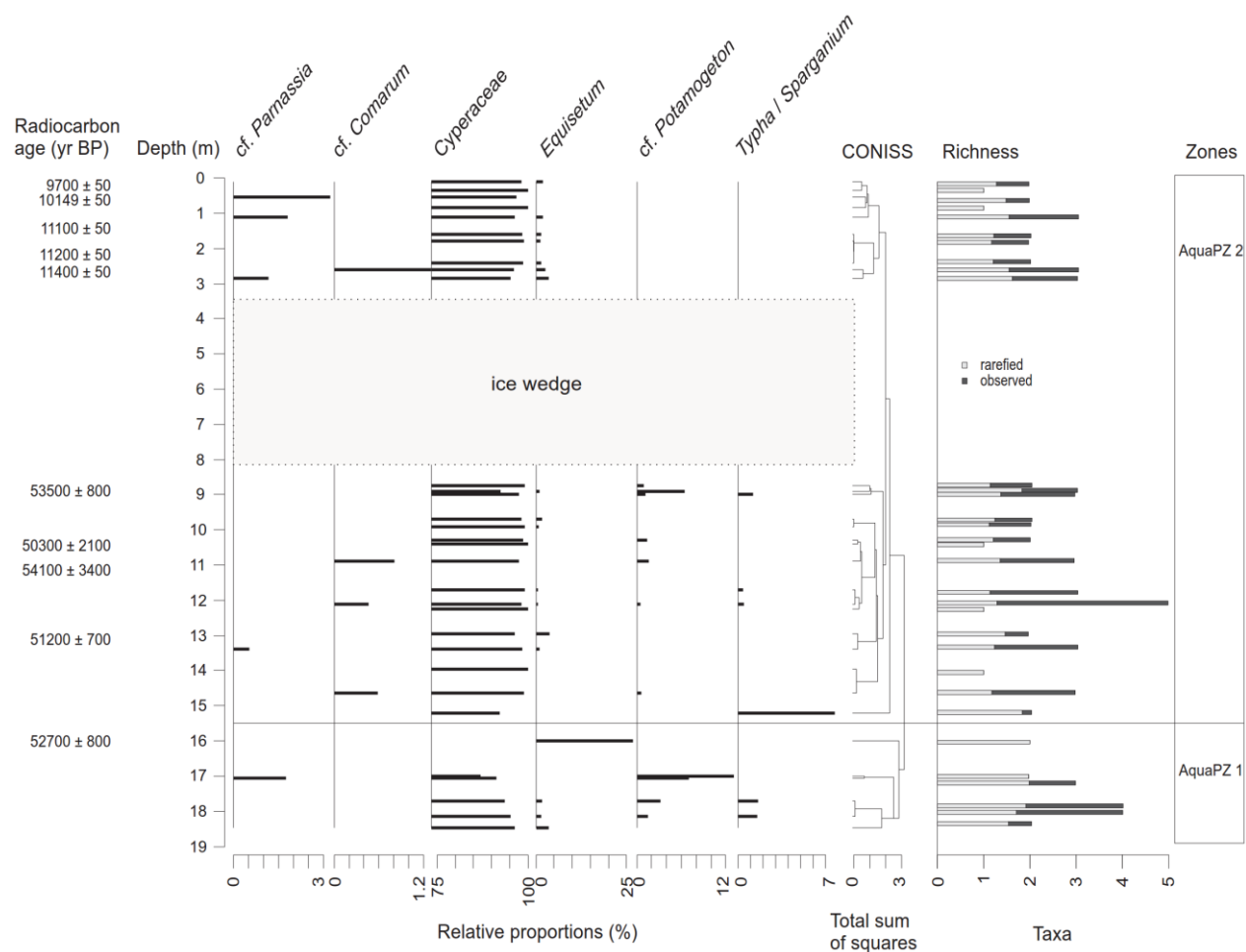


**Figure 6:** Stratigram of terrestrial pollen (subset for statistical analyses) with relative proportions in percentage of the taxa in each sample as horizontal bars, CONISS dendrogram, observed (dark grey) and rarefied (light grey) taxonomic richness. The grey area indicates the ice-wedge where no samples were taken. Horizontal lines indicate borders between palynological zones. Scaling is taxon specific for better visibility of low percentages. Uncalibrated radiocarbon ages are given in years before present (yr BP).

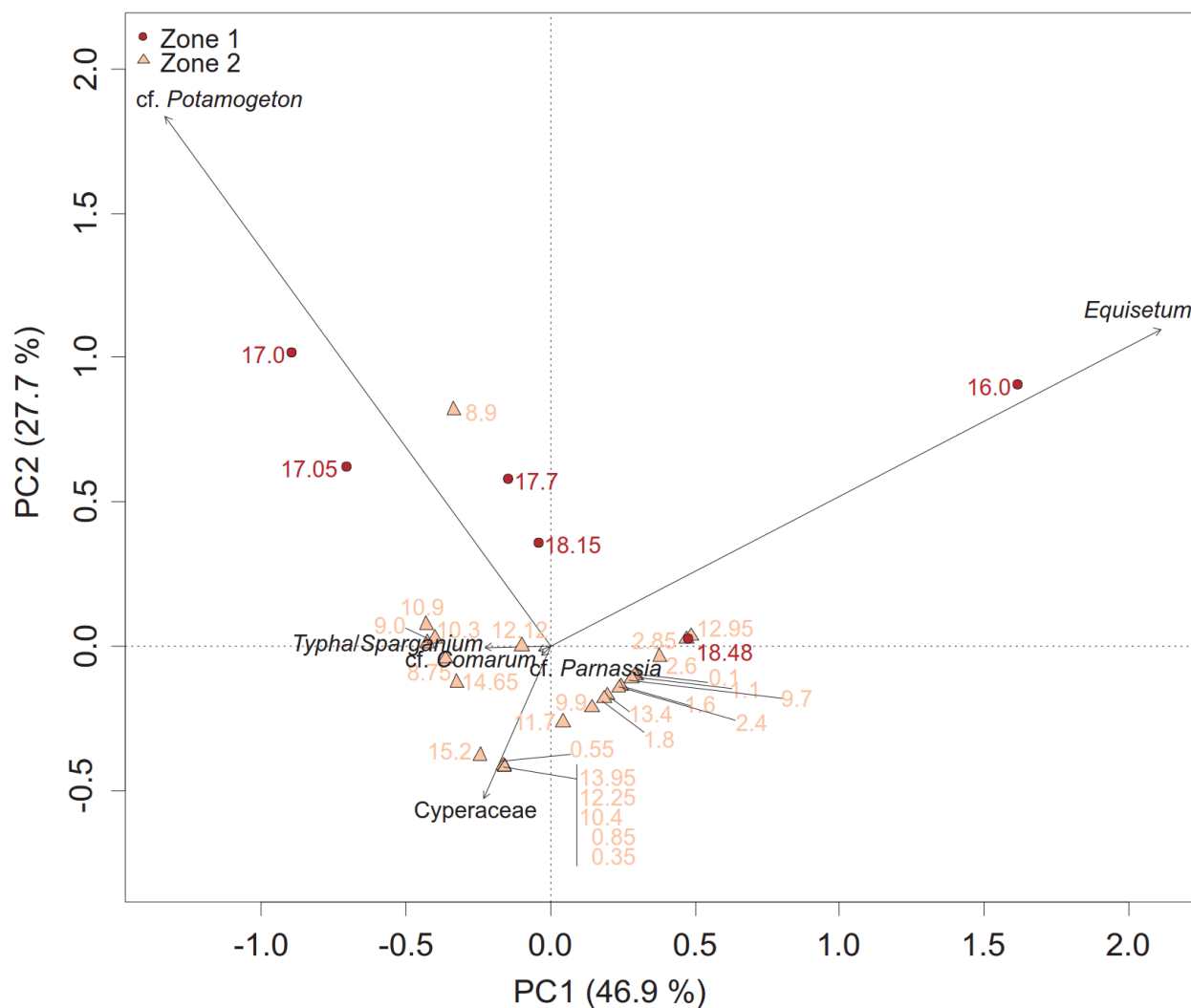




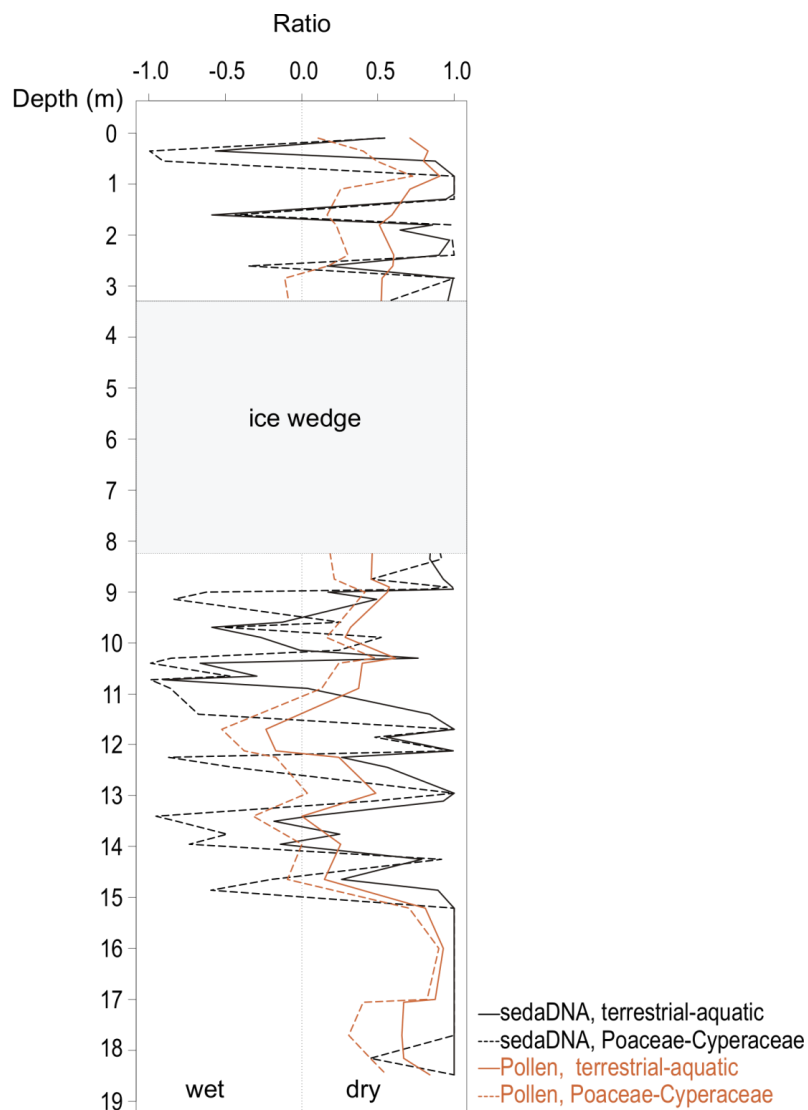
**Figure 7:** PCA biplot of terrestrial taxa from pollen analysis, showing a subset of 25 taxa, which explained most of the variance in the dataset. Sample depths (m) are coloured according to their corresponding zone. Explained variances of the two principal components (PC) are shown in brackets.



**Figure 8:** Stratigraphic diagram of swamp and aquatic pollen/spores with relative proportions of the taxa in each sample as horizontal bars and CONISS dendrogram. The grey area indicates the ice-wedge where no samples were taken. The horizontal line indicates the border between the palynological zones. Scaling is taxon specific for better visibility of low percentages. Uncalibrated radiocarbon ages are given in years before present (yr BP).



**Figure 9:** PCA biplot of swamp and aquatic taxa from pollen analysis. Sample depths (m) are coloured according to their corresponding zone. Explained variances of the two principal components (PC) are shown in brackets.



**Figure 10:** Terrestrial-aquatic (Eq. 1) (line) and Poaceae-Cyperaceae ratios (Eq. 2) (dashed line) of plant sedaDNA (black) and pollen (red). Positive ratios indicate a higher contribution of terrestrial or Poaceae sequence counts or pollen grains and hence drier conditions. Negative ratios indicate a higher contribution of swamp and aquatic or Cyperaceae sequence counts or pollen grains and hence wetter conditions.



## Tables

**Table 1:** Cryolithological units from the bottom to the top with sample depths below surface (m), radiocarbon ages given as years before present (yr BP), calibrated radiocarbon ages (cal kyr BP) and characteristics according to Schirrmeister et al. (2016).

Unit	Depth (m)	Radiocarbon ages (yr BP)	± (yr)	Calibrated ages (2σ) (cal yr BP)	Cryolithological characteristics
1 (18.9–16.0 m)	16.13	52,700	800	not calculable	horizontally bedded grey-brown, silty fine-grained sand; electric conductivity up to 14 mS cm <sup>-1</sup> resulting from downward freezing of the ground from the surface
2 (16.0–9.95 m)	13.03	51,200	700	not calculable	horizontally bedded grey-brown, silty fine-grained sand
	11.15	54,100	3,400	not calculable	
	10.53	50,300	2,100	not calculable	
3 (9.95–8.35 m)	8.83	53,500	800	not calculable	inclined contact zone between the ice-wedge and encasing sediment, grey-brown, silty fine-grained sand
4 (8.35–3.4 m)					ice-wedge
5 (3.4–0.35 m)	2.93	11,400	50	13,096–13,304	grey-brown, silty, fine-grained sand
	2.5	11,200	50	12,996–13,199	
	1.7	11,100	50	12,827–13,090	
	0.7	10,149	50	11,603–12,048	
6 (0.35–0.0 m)	0.3	9,700	50	11,075–11,238	active layer, brown, silty fine-grained sand, and modern top
	0.1	modern			



**Table 2:** Number of sequence counts for bryophyte taxa detected by sedaDNA in the corresponding sample depths.

Depth (m)	Brachytheciaceae	Bryaceae MOTU1	Bryaceae MOTU2	Bryum MOTU1	Cosmarium botrytis	Dicranales	Drepanocladus	Funaria	Hamatocaulis vernicosus	Hypnales MOTU1	Hypnales MOTU2	Hypnales MOTU3	Leptobryum pyriforme	Platydictya confervoides	Polytrichaceae	Pottiaceae	Ptychostomum pendulum	Sanionia uncinata	Sphagnum	Sphagnum russowii
0.35	0	0	0	14	0	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2.60	0	0	0	27	60	0	0	0	0	0	0	12	42	0	0	0	0	0	0	0
2.85	0	0	0	0	0	0	0	0	82	0	0	0	0	0	0	0	0	0	0	0
3.30	0	0	0	0	0	0	0	0	0	0	148	0	0	0	39	0	157	89	3171	3810
8.35	0	12	0	41	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0
8.75	0	14	19	203	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8.90	10	0	0	27	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0
8.95	0	0	0	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9.00	0	0	0	17	0	0	15	0	0	236	0	0	0	56	0	0	0	0	0	0
9.60	0	0	0	0	0	0	0	0	0	75	0	0	0	0	0	0	0	0	0	0
10.40	0	0	0	0	0	0	0	30	0	0	0	0	0	0	0	0	0	0	0	0



**Table 3:** Number of non-pollen palynomorphs for each sample.

Depth (m)	<i>Botrychium</i>	<i>Osmunda</i>	Polypodiaceae	Bryales	<i>Encalypta</i>	<i>Riccia</i>	<i>Sphagnum</i>	<i>Huperzia selago</i>	<i>Lycopodium</i> sp.	<i>L. annotinum</i> -type	<i>L. clavatum</i> -type	<i>L. complanatum</i>	<i>L. pungens</i>	<i>Selaginella involvens</i>	<i>S. rupestris</i>	<i>Cercophora</i>	<i>Gelasinospora</i>	<i>Sordaria</i>	<i>Sporormiella</i>	<i>Valsaria</i>	<i>Glomus</i>	<i>Botryococcus</i>	<i>Pediastrum</i>	<i>Spirogyra</i>	<i>Zygnema</i> -type	pre-Quaternary spores
0.10	0	0	0	0	0	0	6	0	0	0	0	1	1	0	0	0	0	0	0	0	0	2	1	0	1	0
0.35	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	0	1	0	4	2
0.55	0	0	0	4	0	0	0	0	0	0	0	0	0	0	1	0	38	0	0	0	1	0	0	0	4	0
0.85	0	2	2	0	2	1	0	0	0	0	0	0	0	0	1	0	37	0	0	0	0	1	0	0	1	0
1.10	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	9	0	0	0	0	1	0	0	13	0
1.60	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	3	0	0	0	0
1.80	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
2.40	0	0	0	8	0	1	2	1	0	0	0	0	0	0	0	1	5	0	0	0	0	2	0	0	2	0
2.60	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	3	0	0	0	0	0	1	0	1	0
2.85	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	1	10	0	0	0	0	1	1	0	0	0
8.75	0	0	2	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	7	3	0	1	0
8.90	1	0	0	2	1	0	3	0	0	1	0	0	0	0	5	1	0	0	1	0	5	7	5	0	1	1
9.00	0	0	0	1	0	0	0	1	0	1	0	0	0	0	2	0	0	0	0	0	0	3	2	0	6	0
9.70	0	0	0	8	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	2	0	3	0
9.90	0	0	0	25	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	6	0
10.30	1	0	1	0	1	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	6	5	0	4	0
10.40	0	0	1	4	1	0	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0	6	5	0	3	0
10.90	0	0	3	0	1	1	2	1	0	0	0	0	0	0	1	0	0	0	0	0	0	9	8	0	2	0
11.70	0	0	0	4	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	8	0
12.12	0	0	1	3	1	1	1	1	0	0	0	0	0	0	2	0	0	0	1	0	0	2	12	0	2	1
12.25	0	0	2	7	1	0	0	0	1	0	0	0	0	0	4	0	0	0	0	0	0	6	5	0	4	0
12.95	0	1	2	16	0	2	1	0	0	0	0	0	0	0	1	0	0	0	27	0	0	3	49	0	3	0
13.40	0	0	1	10	1	1	3	1	1	0	0	0	1	0	1	0	0	0	2	0	0	5	4	0	4	1
13.95	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	6	0	0	2	0
14.65	1	0	4	0	2	1	2	0	0	0	0	0	1	0	1	0	0	0	0	0	3	8	0	0	2	0
15.20	0	0	1	10	4	1	2	0	0	0	0	0	1	0	1	0	0	4	0	0	2	4	3	0	7	0
16.00	0	1	2	4	1	0	7	0	0	0	0	0	1	3	0	0	0	0	0	0	3	4	1	0	1	0
17.00	0	0	2	9	0	0	6	0	0	0	2	0	1	0	2	0	0	0	9	1	1	7	10	0	0	0
17.05	0	0	5	1	4	0	7	0	0	0	0	0	0	0	1	0	0	0	2	0	7	9	12	0	2	1
17.70	0	0	2	2	2	0	7	0	0	0	0	1	0	0	1	0	0	0	2	0	1	13	16	0	1	3
18.15	1	1	4	0	1	1	6	0	1	0	2	0	1	0	3	0	0	0	7	0	1	17	63	0	3	1
18.48	1	1	4	20	3	0	8	0	1	0	1	0	0	0	1	0	0	0	7	0	12	14	21	0	3	0