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Terrestrial vegetation and lake aquatic community diversity under climate change during the mid–late Holocene in the Altai Mountains

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ABSTRACT

Using pollen analysis and metabarcoding of plant sedimentary ancient DNA (sedaDNa), we infer the floristic diversity in the vicinity of Lake Balyktukel, Ulagan Plateau, the Altai Mountains, over the last 7 kyr. The SedaDNA method identified 200% more taxa than found by morphological pollen analysis. In particular, it revealed that the dominant tree for the last 7 kyr was *Larix* rather than *Pinus*, which was less frequent in the vicinity of Lake Balyktukel. About 7 ka, larch forest mixed with dwarf birch was widespread on the Ulagan Plateau. The period between 5.3 and 3.4 kyr BP was characterized by the maximal spread of larch forest with an understorey cover of *Vaccinium vitis-idaea*. Pollen-based annual precipitation reconstruction indicates the most humid phase was between 6.95 and 4.3 ka, and generally coincides with maximal phytodiversity. The most bioproductive period of the lake was from 7 to 6 ka. After that, the trophicity of the lake decreased until 4.5 ka. The appearance of *Hippuris vulgaris* and increase in *Ranunculus* subgen. *Batrachium* at about 5.3–5 ka may indicate the extension of shallow-water ecotopes. Between 3.7 and 3.5 ka, the cyanobacterium *Anabaena* – an indicator of increased organic matter and algal blooms – was widespread. A planktic thermophilic cladoceran *Bosmina longirostris* appeared after 1.8 ka and colonized the lake, suggesting an increase in lake trophicity. The last 100 years have been characterized by dramatic changes in the cladoceran community reflecting significant warming of climate.

1. Introduction

Evidence from recent decades shows that growing populations, changes in food and energy consumption strategies, habitat destruction, invasive species, pollution, and climate change have contributed to loss of natural ecosystems and declining biodiversity (IPCC, 2019). Nowadays, numerous studies of biodiversity focus on the last 200 years (the Anthropocene). However, it is also important to study trends in biodiversity during the Holocene to understand whether current trends in biodiversity are a continuation of Holocene trends or whether they are novel and unprecedented (McGill et al., 2015; Birks et al., 2016).

The traditional approach for discovering past plant diversity is by pollen analysis. To reconstruct past alpha and beta diversity from pollen data, a standard set of statistical methods is used, although with some limitations. For the estimation of alpha diversity, we use Hill numbers (Chao et al., 2014), but this does not map species diversity in full because it is not always possible to identify pollen grains to species level (Birks and Line, 1992). Therefore, estimates based on pollen counts

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reflect a diversity of pollen taxa or pollen types over complete representation of the vegetation.

The extent to which the estimation of plant diversity from pollen data can adequately reflect the trends of actual phytodiversity both in the past and in the present has been the focus of a number of methodological studies (Odgaard, 1994; Seppä, 1998; Berglund et al., 2008; Overland and Hjelle, 2009; Meltsov et al., 2011, 2013; Jantz et al., 2014; Felde et al., 2016; Reitalu et al., 2019). For example, Meltsov et al. (2011, 2013) have shown that, for a single climatic region, pollen diversity provides an adequate estimate of floristic diversity. It must be remembered that the application of statistical methods to reveal the phytodiversity to reconstruct vegetation from pollen data may be limited for territories dominated by a taxon whose pollen accumulation in sediments does not fully reflect the degree of its distribution in the territory. This occurs when reconstructing vegetation and phytodiversity for landscapes dominated by *Larix* (larch), which includes vast territories in Siberia (260 million ha according to Abaimov, 2010).

Larch pollen is very poorly preserved in sediments and its productivity is extremely low (Niemeyer et al., 2015). Subrecent samples taken in larch forest demonstrate that the proportion of larch pollen in palynological spectra is about 1–3% (Giterman, 1963; Braitseva et al., 1968; Korotkii, 2002; unpublished data from the Altai Mountains). This results in rare findings of *Larix* pollen in sediments and a possible misclassification of larch taiga as pine forest or as treeless tundra (Bigelow et al., 2003).

Another problem that arises in pollen analysis is the dominance of taxa that produce high amounts of pollen (*Pinus, Picea, Betula*) at the expense of entomophilous forbs, leading to the underestimation of floristic richness (Clarke et al., 2019a). A further limitation of the pollen method's application for estimating floristic richness is its low taxonomic resolution (only 23% at species-level; Giesecke et al., 2012).

Plant DNA from lake sediments enables us to establish with high accuracy the presence of larch in the vegetation and show its dominance as well as detecting more species per sample than other palaeoecological methods and reflecting better the local plant community composition than pollen (Pansu et al., 2015; Clarke et al., 2019b; Heinecke et al., 2017; Epp et al., 2018; Voldstad et al., 2020; Huang et al., 2021a; Schulte et al., 2021; Li et al., 2021; Liu et al., 2020, 2021).

In the present study, we used the standard pollen method and metabarcoding of sedimentary ancient DNA (sedaDNA) to establish the floristic diversity in the vicinity of Lake Balyktukel, Ulagan Plateau, the Altai Mountains, over the last 7 kyr. It has been shown that metabarcoding often identifies more species at higher taxonomic resolution than pollen records (Niemeyer et al., 2015; Liu et al., 2020) and that the DNA signal is highly local compared to the more regional pollen signal (Parducci et al., 2017; Alsos et al., 2018). However, some researchers point out that metabarcoding does not always identify rare species (Alsos et al., 2018; Shirazi et al., 2021); for example, Schulte et al. (2021) relied on target enrichment by hybridization capture to isolate larch DNA from sediments. Since our goal is to obtain the maximum floristic diversity from the palaeoenvironmental record, metabarcoding proved to be a suitable method. The metabarcoding also revealed the diversity of aquatic higher plant taxa, the presence of which are typically poorly reflected in pollen research.

This paper, in addition to reconstruction of vegetation cover and phytodiversity of the Ulagan Plateau and the composition of Lake Balyktukel's aquatic habitats, focuses on the issue of whether pollen analysis adequately reflects the composition of the main dominant forests of the Ulagan Plateau in the Holocene. Plant sedaDNA is used to test the hypothesis that pollen analysis is of limited utility for vegetation and climate reconstruction in areas dominated by larch.

Our studies are supplemented by the analysis of Cladocera and non-pollen palynomorphs. The cladoceran community is affected by multiple biological and limnological interactions as well as climatic factors. The complex responses of Cladocera to environmental and climate change may be interpreted in relation to ongoing and future climate warming

(Nevalainen et al., 2015). Blooms of blue-green algae provide palaeoecological information about the status of the lake, as well as about the palaeoenvironmental conditions in general.

2. Site setting

Lake Balyktukel (N 50.53°, E 87.70°, 1842 m asl) is located on the high-mountain Ulagan Plateau in the north-eastern part of the Altai Mountains. The Ulagan Plateau is restricted to the east by the Chulyshman Upland, to the south by the Kurai Ridge, to the west by the Tongosh Ridge, and to the north by Lake Teletskoye (Fig. 1). It is a plateau with elevations from 1500 to 2500 m, deeply eroded by rivers.

The Ulagan Plateau experiences a diverse climate. The upper courses of the Bashkaus and Chulyshman Rivers are influenced by dry south-easterly winds, with a mean annual temperature of −3.7 °C and mean annual precipitation of 270 mm. The lower course of the Chulyshman River receives a warming effect from the nearby Lake Teletskoye and has a mean annual temperature of +4 °C and mean annual precipitation of 460 mm (Blyakharchuk et al., 2004). Mean annual precipitation in the vicinity of Lake Balyktukel is 390 mm with most precipitation falling in May–July (SamSamWater Foundation); mean annual temperature is −3.8 °C, while the mean temperature for January is −20.5 °C and for July is +12 °C (WorldClim).

The lake is mainly fed by meltwater, with a small river flowing into the lake and an outflowing unnamed river flowing into the Saryachik River. The lake is fresh and ultra-oligotrophic with a maximum depth of 23.9 m. The water is characterized as very clean (saprobic index is 0.81) with pH = 8.3; we recorded a surface-water temperature of 17.6–17.7 °C and bottom water of 15.5–16.4 °C in mid-July (2021, our data).

The phytoplankton of the lake is rather poor, represented by diatoms and dinophytes. The survey, carried out on 18 July 2021 at two locations (at depths of 23.7 m and 8.1 m), recovered 36 diatom species belonging to 25 genera, 19 families, 12 orders, and three classes of Bacillariophyta. Relatively rich families were Staurosiraceae, Rhopalodiaceae (4 species each), Achnanthidiaceae, Gomphonemataceae, and Aulacoseiraceae (3 species each). The remaining 56% of the families had 1–2 species each. The dominant species were *Aulacoseira alpigena* (Grunov) Kramer (89.6% of the total number of valves), *Staurosira venter* (Ehrenberg) Grunow (49.7%), *Fragilaria construens* (Ehrenberg) Grunow, (10.5%), and *Staurosirella pinnata* (Ehrenberg) D.M.Williams & Round (10.2%), while *Aulacoseira subarctica* (Otto Müller) E.Y.Haworth (6.7%) and *Pseudostaurosira brevistriata* (Grunow) D.M.Williams & Round (5.3%) were subdominant. The distribution of diatom species diversity across the two locations differs. In the deep part of the lake (23.7 m), ten species were recorded, with high abundance of the planktic species *Aulacoseira alpigena*, and in the second sampling location (8.1 m), 31 species were recorded with a dominance of epiphytic "fragilarian" forms (*Staurosira venter, Fragillaria construens, Staurosirella pinnata, Pseudostaurosira brevistriata*). The revealed diatom flora comprises typical species of oligotrophic Arctic lakes with *Aulacoseira alpigena, A. subarctica* etc.

The blue-green alga *Microcystis wesenbergii* (Komárek) Komárek ex Komárek dominates the lake in abundance, while the dinophyte *Glochidinium penardiforme* (Lind.) Boltwoskoy and the blue-green *Anabaena spiroides* (Woronichin) Elenkin subdominate. The biomass is based on the large-celled *Glochidinium penardiforme*, followed by the dinophyte *Peridiniopsis cunningtonii* Lemmerm. and *Microcystis wesenbergii* (Popov et al., 2003).

The zooplankton of the lake samples comprises Cladocera, copepods, and rotifers. Among the Cladocera, *Bosmina longirostris* O.F.Müller, *Ceriodaphnia quadrangula* O.F.Müller, and *Polyphemus pediculus* L. dominate. *Keratella cochlearis* Gosse dominates among rotifers, and *Acanthocyclops viridis* Jurine dominates among copepods. Copepoda is represented mainly by nauplii and copepodites (Popov et al., 2003; Burmistrova and Ermolaeva, 2013).

Plant macrophytes are represented by several species of *Potamogeton*
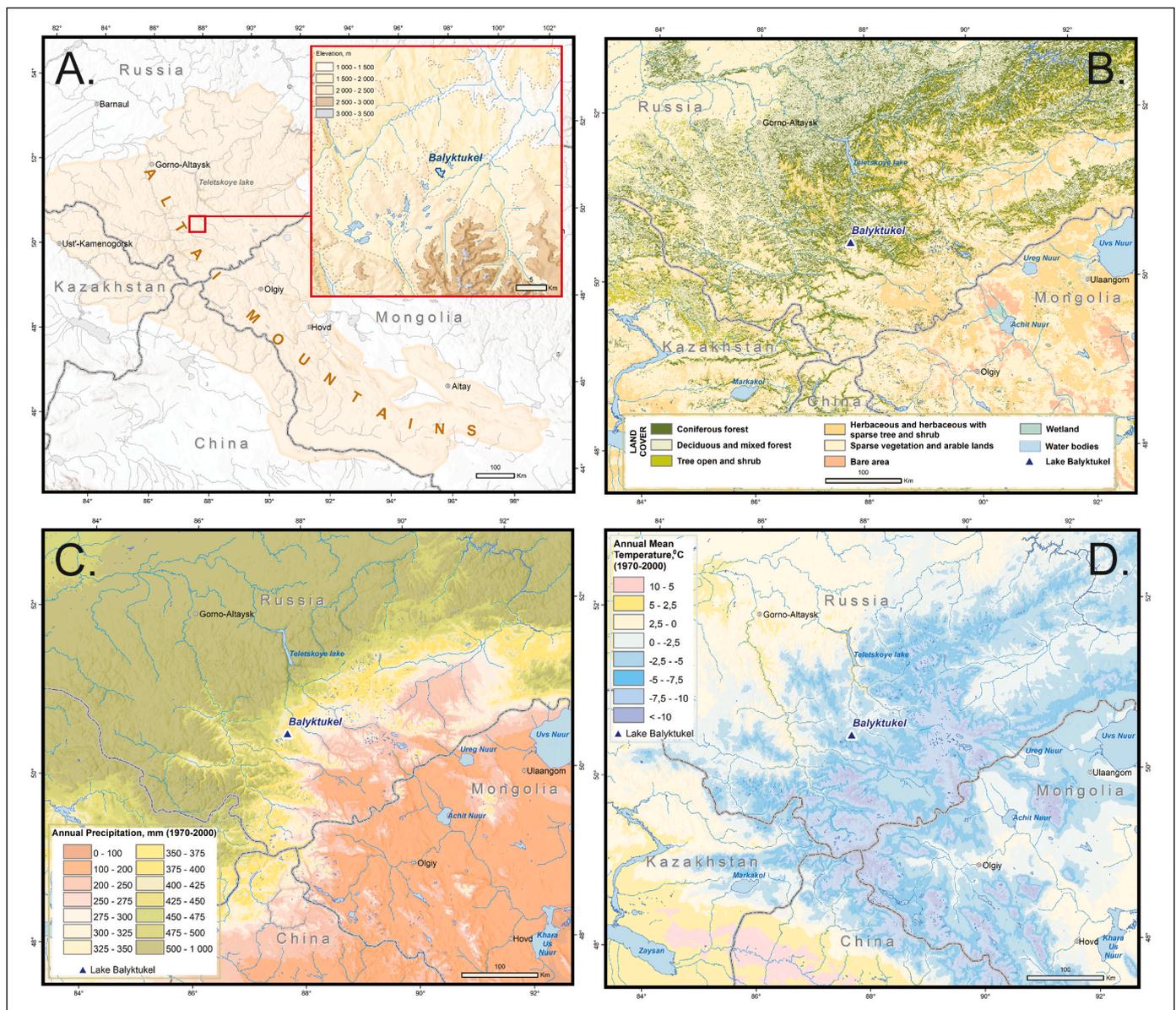
Fig. 1. Map of the studied area. A. Lake Balyktukel on the map of the Altai Mountains. B. Land cover of the studied area. C. Map of the modern annual amount of precipitation (mm). D. Map of modern annual mean temperature distribution (°C). Sources http://goto.arcgisonline.com/maps/NatGeo_World_Map; https://globalmaps.github.io/glcnmo.html; https://www.worldclim.org/data/worldclim21.html.

(*P. perfoliatus* L., *P. alpinus* Balb., *P. gramineus* L., *P. berchtoldii* Fieber), *Ceratophyllum demersum* L., and *Myriophyllum sibiricum* Kom.

Larch forest with *Larix sibirica* Ledeb. covers most of the area, whereas the upper limit of continuous forest is formed of *L. sibirica–Pinus sibirica* Du Tour open woodland at about 2100-m elevation. Steppe is extensive below 1400-m elevation in the valleys of the Karakudyur, Kubardu, and Ulagan Rivers near Ust'-Ulagan village, 20 km north-east of the study area. Dark-coniferous taiga with *Abies sibirica* Ledeb., *Picea obovata* Ledeb., and *Pinus sibirica* occurs north of the study area near Lake Teletskoye, in the lower valley of the Chibitka River, and on the slopes around Lake Cheibekol. *Picea obovata* grows locally admixed in the larch forest on northern slopes, but it generally predominates in the river valleys (Kuminova, 1960; Blyakharchuk et al., 2004).

3. Data and methods

3.1. Coring and subsampling

Bottom sediment core *BK2018–1* (2.35 m, 50.53411°N, 87.70788°E) was retrieved in July 2018 from the lake's deepest point of 23.9 m (Fig. 2) using a hammer-modified UWITEC gravity corer. The core was transported to the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research (AWI) in Potsdam. In November 2019, the core was subsampled at the climate chamber of the German Research Center for Geosciences (GFZ). Subsampling was performed at a constant temperature of 15 °C in a previously cleaned room using UV-sterilized tools (knives, spatulas, spoons) and sterile 8 ml tubes for sedaDNA samples and unsterile boxes for samples of other analyses.

3.2. Dating and age modelling

The age-depth model is based on 12 radiocarbon dates obtained from
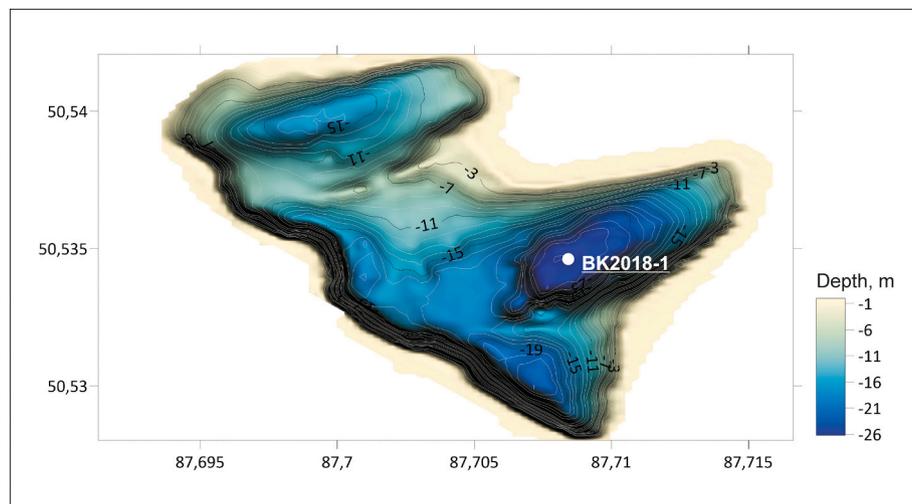
Fig. 2. Bathymetric map of Lake Balyktukel with coring site BK2018–1.

bulk sediments (Table 1). The age-depth model was created in Bacon 2.2 (R Core Team, 2018; Blaauw and Christen, 2011) using the IntCal20 calibration curve (Reimer et al., 2020).

3.3. Plant sedaDNA analysis

In total, 57 samples were taken for sedaDNA analysis; the interval between samples is 4 cm covering approximately 100 years. Total DNA from samples (3–5 g) was isolated using the DNeasy PowerMax Soil Kit (Qiagen) with the addition of dithiothreitol (VWR International) and Proteinase K (VWR International) in the initial lysis and homogenization step. Then tubes were vortexed for 10 min and incubated at 56 °C overnight in a rotating incubator. The remaining protocol was conducted according to the manufacturer's instructions, and final extracts were eluted in 2 ml of solution C6. Each extraction batch included nine samples and one negative control to assess extraction purity.

After extraction each sample was purified and concentrated using the GeneGet KIT. Then, the amount of extracted DNA was measured using a Qubit Fluorometric Quantification instrument (Thermo Fisher Scientific) and a Qubit BoardRange KIT (Thermo Fisher Scientific). All samples were further diluted to the same concentration (3 ng/µL) and underwent polymerase chain reaction (PCR). The PCRs were performed with universal primers g and h with additional tags (Coissac, 2012) for the P6 loop of the chloroplast trnL (UAA) intron (Taberlet et al., 2007). Each batch also included a negative control. The total volume of PCR was 25 µL per sample, comprising 12.75 µL of distilled water, 2.5 µL of 10× buffer, 2.5 µL of 2.5 mM dNTP, 1 µL 0.8 mg bovine serum albumin, 50 mM MgSO$_4$, 0.25 µL of 1× Platinum® High Fidelity Taq DNA Polymerase, 3 µL of sedaDNA template, and 1 µL of 5 µM for forward and reverse primers. All PCRs were taken to the post-PCR laboratory for amplifying using a Thermo Cycler with the following program: 94 °C for 5 min; 40 cycles of 94 °C for 30 s, 50 °C for 30 s, 68 °C for 30 s; 72 °C for 10 min. Gel electrophoresis was performed on all amplicons and negative controls to control the length of the bands (100–200 bp) (Liu et al., 2021).

After obtaining three successful PCRs for each sample, the PCR-products were further purified using the MinElute KIT (Qiagen) with the addition of ethanol. The samples were then equimolarly combined into one pool and sent to Fasteris SA (Geneva, Switzerland) for Next-Generation DNA sequencing. Paired-end sequencing (2*150 bp) was performed on an Illumina NextSeq sequencing platform with a NextSeq Mid kit.

3.4. Plant sedaDNA statistical analyses

Primary data processing was performed in OBITools, which includes a large set of simple tools for the efficient processing of text data (Boyer et al., 2016). A feature of OBITools is its ability to take into account taxonomic information, which allows the sorting and filtering of sequence records based on taxonomy. Primary sequences were merged via overlapping paired end sequences; oligonucleotide combinations separated; matched to databases; and assigned a taxonomic identity and type according to PCR batches. Reads were classified to a taxonomic level using two reference databases: the first database is based on the quality-checked and curated arctic and boreal vascular plant and bryophyte reference database (best_identity.arctborbryo_gh) published by Sønstebø et al. (2010), Willerslev et al. (2003, 2014), and Soininen et al. (2015). The second database is based on the EMBL Nucleotide Database standard sequence release 143 (Kanz et al., 2005). Sequences shorter than ten base pairs were excluded from the dataset.

Taxa identified to a species level that is non-typical for the study area were grouped to the genus or family level. We also excluded PCR-batches that were unsuccessful and differed significantly from the other two for the same sample. With two unsuccessful PCRs, the sample was excluded from the analysis entirely. The data were regrouped according to the samples and summed up before being rarefied. Rarefaction to the least number of reads was performed in the R-environment (R Core Team, 2018) using an adapted script (https://github.com/Stefan Kruse/R_Rarefaction), which resulted in standardized samples for further analysis.

The taxa were divided into two groups: terrestrial and aquatic (Appendix 1). DNA diagrams were constructed using the Tilia software, and cluster analysis and stratigraphical zonation were performed by CONISS (Grimm, 1987, 2004). The diagrams present the percentage of the total

Table 1
Radiocarbon dates of the core *BK2018–1*.

Sample and Lab ID	14C age	Error (±)	Depth, cm	Material
AWI-5334.1.1	1283	20	24.5	bulk
AWI-5335.1.1	1858	20	44.5	bulk
NTUAMS-5947	2292	80	64.5	bulk
AWI-5336.1.1	2921	22	84.5	bulk
AWI-5337.1.1	3873	19	104.5	bulk
AWI-5338.1.1	4350	23	124.5	bulk
AWI-5339.1.1	4495	23	144.5	bulk
AWI-5340.1.1	4881	20	164.5	bulk
NTUAMS-5948	5400	85	184.5	bulk
AWI-5341.1.1	6111	25	204.5	bulk
AWI-5342.1.1	6579	26	224.5	bulk
NTUAMS-5949	6626	91	234.5	bulk

number of reads per sample (terrestrial and aquatic separately).

3.5. Pollen analysis

A total of 61 samples (0.8–1.2 g of dry sediment) with an interval of 2–4 cm and time resolution of about 50–100 years were used for pollen and non-pollen palynomorph analyses (Appendix 1). The samples were chemically treated according to the methodology of Faegri and Iversen (1989), including treatment with a 10% solution of hydrochloric acid to dissolve carbonates, a 10% solution of potassium hydroxide to remove humic acids, and high concentration hydrofluoric acid to remove silicates. Acetolysis was not performed. A *Lycopodium* spore tablet was added to each sample to calculate the total palynomorph concentration. Pollen grains mounted in glycerine were analysed under a transmitting light microscope AxioImagerD2 with x400 magnification. In addition to pollen and spores, non-pollen palynomorphs (NPPs) were counted, and are included in the total sum. Pollen percentages are calculated based on the pollen sum of all detected taxa, taken as 100%. NPP percentages are calculated based on the total sum taken as 100%.

3.6. Biomization of pollen data

We used a quantitative approach to reconstruct vegetation types (biomes) based on fuzzy logic introduced by Prentice et al. (1996). Biomization is a powerful tool for objective vegetation reconstruction from late-Quaternary pollen data of Europe and Asia (Tian et al., 2018; Cao et al., 2019). The method is based on an objective assignment of pollen taxa with plant functional types (PFTs) and to biomes based on modern ecology, bioclimatic tolerance, and the geographical distribution of pollen-producing plants. The result of classification into particular PFTs is presented as a PFT–taxa matrix. The PFTs are combined to form biomes and a PFT–biome matrix. A particular biome is characterized by a particular set of PFTs. Finally, a taxon–biome matrix is formed, in which every palynotaxon is correlated with one or several biomes. Scores were calculated for ten biomes, but three were used to interpret the data: TAIGA, STEPPE, and TUNDRA, as the most informative.

3.7. Cladoceran analysis

Fifty-nine sediment samples with an interval of 2–4 cm and average temporal resolution of ~50–100 years were processed for cladoceran analysis. Cladoceran remains were prepared following the methods outlined in Korhola and Rautio (2001): 0.2 g of freeze-dried sediments were disaggregated using a heated (75 °C) 10% KOH solution for 30 min, rinsed through a 50-μm mesh sieve, and concentrated into a 12.5 ml plastic vial. A small amount of 96% ethanol was added to the concentrated solution to prevent fungal growth, and one to two drops of safranin solution were added to stain the remains. Cladoceran remains were examined at 100–400 magnification under brightfield illumination with a Carl Zeiss Axiolab microscope.

Each fragmented remain was identified to a species or genus level following Smirnov (1971), Sinev (2002), Szeroczyńska and Sarmaja-Korjonen (2007), and Kotov et al. (2010). The most commonly encountered body part of each cladoceran taxon was used to calculate the number of individuals (Szeroczyńska and Sarmaja-Korjonen, 2007). A minimum of 100 individuals was counted per sample (Kurek et al., 2010).

The stratigraphy for all bioproxies was done with the software TILIA and divided into local zones using CONISS and TILIAGRAPH (Grimm, 2004).

3.8. Estimating the diversity of plant and cladoceran assemblages – comparison of multivariate datasets of bioproxies

The richness and diversity of all bioproxies were calculated as the effective taxon numbers of Hill: $N0$ (total taxa richness), $N1$ (common

taxa richness), and $N2$ (dominant taxa richness) proposed by Hill (1973) and adapted by Chao et al. (2014) (Appendix 1). Diversity analyses for pollen were conducted using the iNEXT package version 2.0.12 (Chao et al., 2014; Hsieh et al., 2016) for R (R Core Team, 2018).

We evaluated the similarity in temporal evolutions of pollen, terrestrial, and aquatic plant sedaDNA, and Cladocera using Procrustes rotation and tested the significance of any relationship found with the associated PROTEST permutation test (Peres-Neto and Jackson, 2001) for the non-metric multidimensional scaling (NMDS) results of these datasets. Procrustes rotation assesses the overall degree of correlation between two or more ordination results through a Procrustean superimposition approach, where the results of the ordination are scaled and rotated to find an optimal superimposition that maximizes their fit. PROTEST is a permutation-based procedure, which assesses the degree of concordance between two matrices, producing a correlation-like statistic derived from the symmetric Procrustes sum of squares and an associated p-value indicating the likelihood of the relationship occurring by chance (Wischnewski et al., 2011).

Detrended canonical correspondence analysis (DCCA) with species assemblage changes constrained to sediment age as the sole environmental variable, was used to develop quantitative estimates of compositional turnover (beta diversity), scaled in standard deviation (SD) units for each taxonomic group (according to Birks, 2007). The change in weighted average sample scores reflects compositional change or turnover in SD units along the temporal gradient (Felde et al., 2020). The analysis was performed in CANOCO 5 (Šmilauer and Lepš, 2014).

3.9. Quantitative reconstruction of the amount of annual precipitation (PANN)

Our newly completed modern pollen data from south-west Siberia (unpublished) and the modern pollen data from arid central Asia (Bordon et al., 2009) was homogenized and combined with the modern pollen dataset of Cao et al. (2014). In this study, 637 modern pollen sites within 1000-km around Lake Balyktukel were selected to establish pollen-climate calibration-sets. PANN was taken as the target climatic variable for past climate reconstruction. The model performance of cross-validation for the pollen-PANN calibration-set has a high R^2 (0.8) and a low RMSEP (74 mm). A quantitative PANN reconstruction was made using the WAPLS function in the rioja R-package version 0.7–3 (Juggins, 2012) with square-root transformed pollen data.

4. Results and interpretation

4.1. Chronology

Twelve dates were used to construct an age-depth model for the *BK2018–1* core (Table 1, Fig. 3). Linear regression was applied to calculate the reservoir effect (=797.5 years), which was then subtracted from the radiocarbon ages. The core, according to the age-depth model, covers the last 6.95 kyr. The rate of sedimentation is estimated at 0.35 mm per year. Calibrated (modelled) ages before present (where present = 1950 CE) will be given in thousand years as "ka".

4.2. Pollen analysis and biomization

A total of 43 pollen taxa of higher terrestrial vascular plants and just two aquatic taxa were identified (Appendix 1). The pollen record can be divided into three pollen zones. In general, the pollen record is monotonous and characterized by the dominance of *Pinus sibirica* and *P. sylvestris* L. Among other woody species, the percentage of *Betula* pollen is relatively high and there is a constant presence of *Larix*. Herbaceous pollen is mainly represented by *Artemisia*, Poaceae, Cyperaceae, and forbs (Fig. 4).

PZI (237–150 cm; 6.95–4.3 ka) is characterized by a dominance of *P. sibirica* and *P. sylvestris*; the percentage of *Betula,* Artemisia, Poaceae,
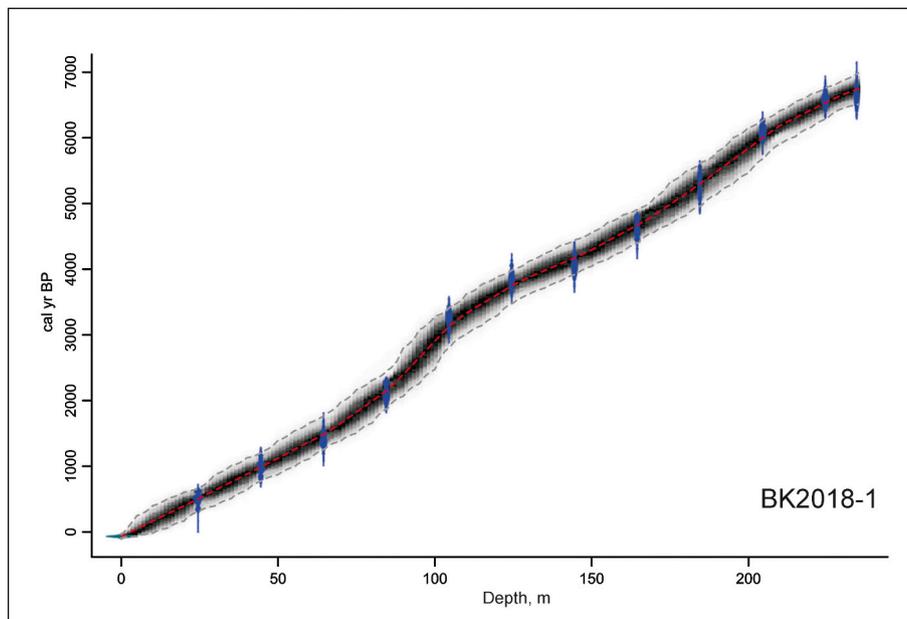
Fig. 3. Age-depth model based on the radiocarbon dates for the core BK2018–1 from Lake Balyktukel (constrained in Bacon 2.2: Blaauw and Christen, 2011).
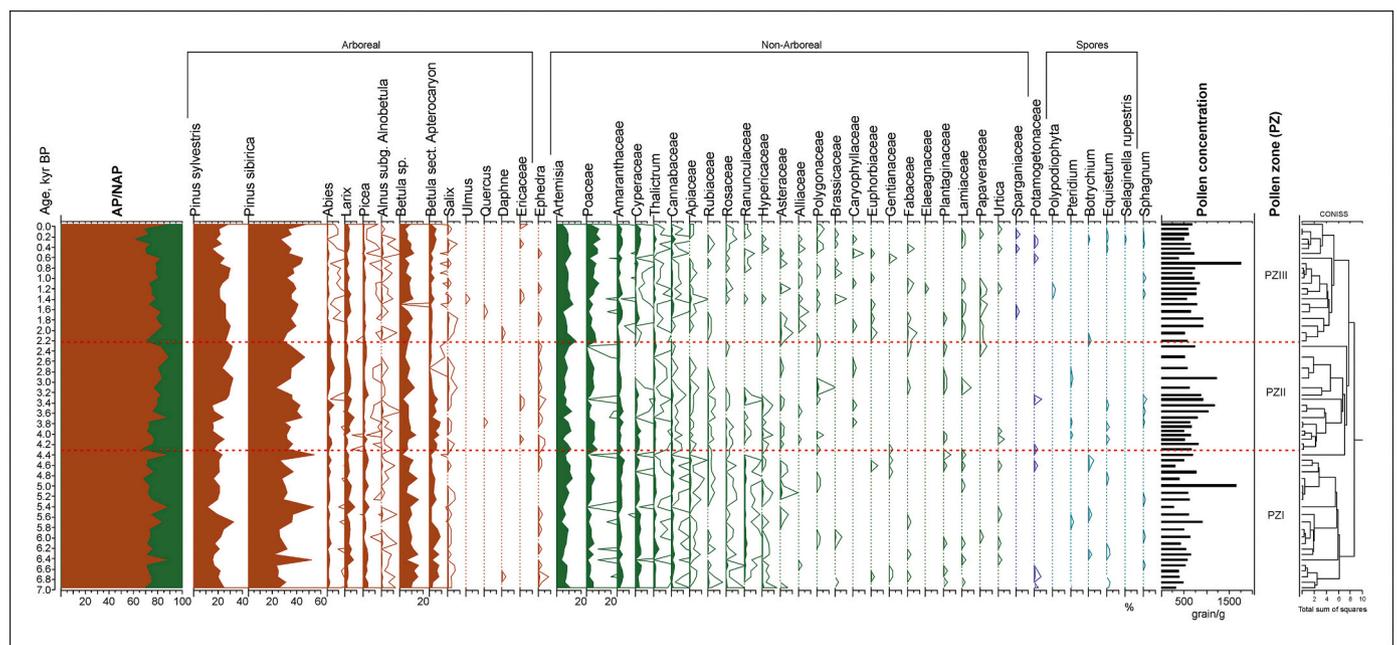
Fig. 4. Pollen diagram for core BK2018–1 from Lake Balyktukel.

and Amaranthaceae is rather high. PZI is also characterized by the abundant remains of the green alga *Botryococcus*, suggesting relatively warm lake water.

PZII (150–85 cm; 4.3–2.2 ka) is characterized by a slight increase in the abundance of Poaceae, a slight decrease in *Picea* pollen, and a marked decrease in the abundance of *Botryococcus*. Stomata of *Larix* are found in this zone. *Pinus* is also dominant in this zone; after 3.3–3 ka, *Pinus sylvestris* increases its abundance. In contrast, the percentage of *Betula* sect. *Apterocaryon* decreases.

PZIII (85–0 cm; 2.2 ka −2018 CE) is characterized by a slight decrease in the share of arboreal pollen, a slight decrease in the abundance of *Abies* pollen, and an increase in the abundance of Poaceae. *Pinus* also prevails in this zone; evidence of the presence of pine and fir close to the lake is provided by their stomata. *Betula* sect. *Apterocaryon*

increases slightly after 0.5 kyr BP.

The dominant reconstructed biome throughout the pollen record is TAIGA (Fig. 5). Minimum values of the TAIGA biome are seen between 4.2 and 3.8 and 0.23–0.05 ka; while maximum values occur at 3.1–2.3 ka. The evolution of the STEPPE and TUNDRA biomes are noteworthy: they increase during 6.95–3.7 ka, and then decrease until 0.4 ka. The maximum values of the STEPPE biome are found for 5.2–4.5 and 0.23 ka, while maximum TUNDRA biome values occur at 6.5 and 6.3 ka. Increases of TUNDRA biome at 4.3–3.8 ka and 0.4–0.2 ka can be associated with the "4.2 ka event" and the Little Ice Age, respectively. The values of indicator biomes by pollen zones are given in Table 2.
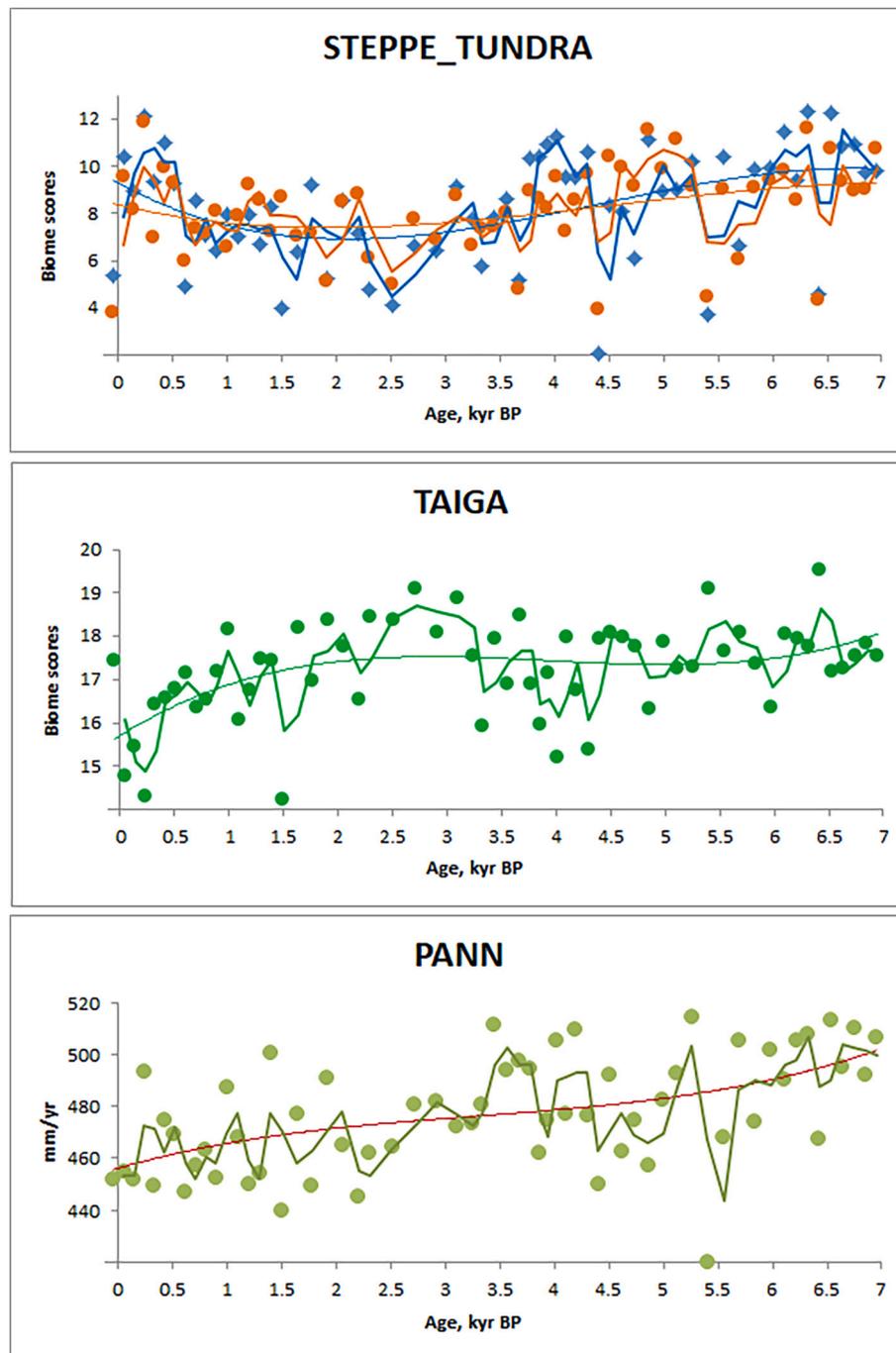
Fig. 5. Biome reconstruction and amount of annual precipitation (PANN) for core BK2018–1 from Lake Balyktukel. Biomes: STEPPE – orange curve, TUNDRA – blue curve, and TAIGA – green curve. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Values of indicator biomes (in scores): TAIGA (TA), STEPPE (ST), DESERT (DE), TUNDRA (TU); value of plant diversity indices (N0,N1,N2); mean annual precipitation (PANN) for different pollen zones (PZ) *BK2018–1*.

PZ	Age, kyr BP	TA	ST	DE	TU	N0	N1	N2	PANN
III	2,2–0	16,7	7,8	4.2	7,8	19,2	7	4,7	464.2
II	4,3-2,2	17,3	7,7	4.4	8,1	18,0	7,4	4,9	481.3
I	6,95-4,3	17,7	8,9	4.4	8,9	19,9	8,7	5,8	485.6

4.3. Non-pollen palynomorphs

Fifteen non-pollen palynomorph types were identified in this study including cyanobacteria, Chlorophyta, Charophyta, dinocysts, Rotifera eggs, Tardigrada eggs, spores of fungi, and conifer stomata (Fig. 6; Appendix 1). The NPP palaeorecord is subdivided into four zones. The diagram reflects the concentration of the NPPs.

NPZI (237–223 cm; 6.95–6.5 ka) is characterized by a relatively high abundance of Cyanobacteria, especially planktic *Aphanizomenon* and *Microcystis*. *Anabaena* is not abundant but is constant throughout this zone. Chlorophyta are represented by constant levels of *Botryococcus braunii* Kütz. and *Transeauina*, as well as *Pseudopediastrum boryanum* (Turpin) E.Hegewald in the lower part of the zone and *Tetraedron*
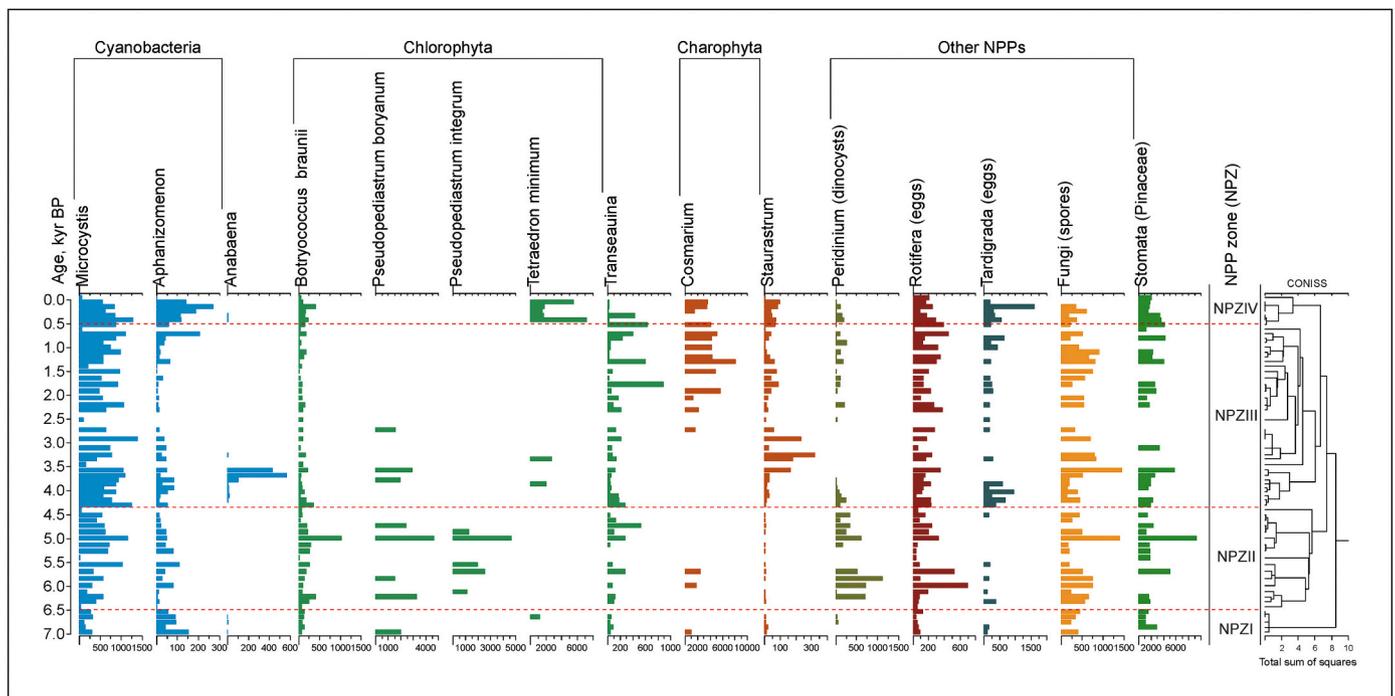
Fig. 6. Non-pollen palynomorph diagram for core BK2018–1 from Lake Balyktukel.

minimum (A.Braun) Hansg. in the upper part of the zone. *Staurastrum* represents the Charophyta and is constant here. Relatively low concentrations of rotifer eggs are found. Among other NPPs, spores of fungi and conifer stomata occur.

In NPZII (223–150 cm; 6.5–4.3 ka) the concentrations of *Microcystis,* Chlorophyta*, Peridinium,* Rotifera, and fungal spores increase*. Pediastrum integrum* Nägeli appears in this zone (from 6.1 ka) only, possibly reflecting the occurrence of a cold and oligotrophic lake (Komarek and Jankovska, 2001).

An increase in *Microcystis,* planktic *Staurastrum*, and Tardigrada egg concentrations is noted in NPZIII (150–24 cm; 4.3–0.5 ka). *Anabaena,* mostly a planktic genus, occurs from the beginning of the zone until 3 ka with a high peak in about 3.7–3.6 ka (with *Pseudopediastrum boryanum)*. After about 2.7 ka, *Pseudopediastrum boryanum* disappears but

Cosmarium from the Charophyta appears. *Peridinium* disappears from 3.7 ka and appears again from 2.7 ka. The appearance of *Peridinium* and *Cosmarium* can be evidence of acidification of the water (Zippi et al., 1991).

The upper NPZIV (24–0 cm; 0.5 ka–2018 CE) is notable for a sharp increase in planktic *Aphanizomenon* and *Tetraedron minimum* that only occurred once; *Botryococcus braunii* increases slightly. *Aphanizomenon* can form blooms. The upper modern samples contain only single remnants of *Aphanizomenon* and *Microcystis* suggesting clean water without blooming.
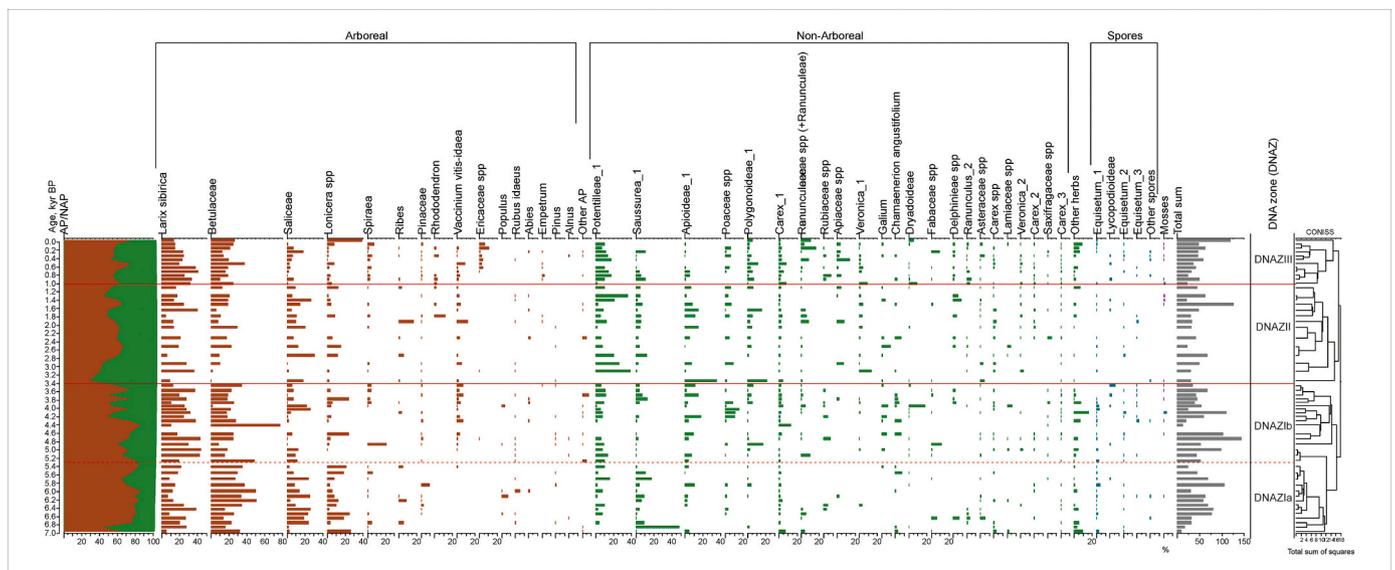
Fig. 7. Terrestrial plants identified from sedimentary ancient DNA for core BK2018–1 from Lake Balyktukel.

4.4. Plant sedaDNA analysis

4.4.1. Terrestrial plants

A total of 118 taxa were identified (Appendix 1). The terrestrial plant sedaDNA record forms three DNA zones (Fig. 7). The palaeosequence is dominated by woody taxa: *Larix sibirica*, *Betula* sp., Salicaceae, and *Lonicera*. Herbaceous taxa are mainly represented by Potentilleae (Rosaceae), Asteraceae, and Apiaceae, although the tribe Potentilleae also contains the widespread shrubby species *Dasiphora fruticosa* (L.) Rydb.

DNAZI (237–112 cm; 6.95–3.4 ka) is characterized by the highest percentages of tree taxa comprising *Larix sibirica*, Betulaceae, Salicaceae, and *Lonicera*. Abundances of other conifers are low; *Pinus* is constant but at very low abundance and *Abies* occurs sporadically in the upper part of the zone. *Populus* (likely *P. tremula* L.) occurs only in this zone. Among herbaceous taxa, *Saussurea* and Potentilleae are abundant. In subzone DNAZIa (237–184 cm; 6.95–5.3 ka) the palaeorecord is dominated by Betulaceae and *Larix sibirica*; the percentages of Salicaceae and *Lonicera* are also high. *Saussurea* has the highest percentage throughout the core. DNAZIb (184–112 cm; 5.3–3.4 ka) is distinguished by an increase of *Larix sibirica* and a slight decrease of Betulaceae, Salicaceae, and *Lonicera*. *Vaccinium vitis-idaea* L. and Dryadoideae (*Dryas*) appear in the upper part of DNAZIa and became common in this subzone. Mosses occur in this subzone after 4.8 ka.

In DNAZII (112–45 cm; 3.4–1 ka) the abundance of herbaceous taxa significantly increases especially at the border between zones DNAZI and DNAZII, and the abundance of Betulaceae decreases. Among herbaceous taxa, the abundance of Potentilleae increases sharply. After 2 ka, *Rhododendron* (likely *R. tomentosum* (Stokes) Harmaja) appears, *Vaccinium vitis-idaea* becomes more abundant, and *Empetrum* (likely

E. nigrum s.l.) occurs at low abundance but is constant. Mosses are absent in this zone from the bottom until 2 ka. *Dryadoideae* almost disappears in this zone.

DNAZIII (45–0 cm; 1 ka–2018 CE) is characterized by an increase of *Larix sibirica*, especially until 0.6 ka and Betulaceae after 0.2 ka. After 0.7 ka Ericaceae appears in the record; *Dryadoideae* reappears here. *Pinus* is absent in DNAZIII.

4.4.2. Higher aquatic plants

In total, 19 macrophyte taxa were determined, of which ten were assigned to species level, eight to genus level, and one to family level (Appendix 1). Assignment to a genus or a family level was caused by the incompleteness of the EMBL142 database, which thus limited the interpretation of the data obtained. Nevertheless, probable species for four samples are suggested: (1) *Potamogeton*_1 as *P. alpinus*, (2) *Myriophyllum* as *M. sibiricum*; both species currently occur in the lake (Popov et al., 2003); (3) *Hippuris* as *H. vulgaris* L., because other species of this small genus occur only at high latitudes in Siberia (Baikov, 2012); (4) *Ranunculus*_1 likely to be the aquatic subgenus *Batrachium* (DC.) Ser. as other groups of this genus are represented in the regional flora exclusively by terrestrial plants (Schegoleva, 2008).

The macrophyte sedaDNA palaeorecord is divided into three zones (DNAZa) (Fig. 8). DNAZaI (237–205 cm; 6.95–6.0 ka) is dominated by eutrophic *Ceratophyllum demersum* and mesotrophic *Myriophyllum* (*sibiricum*) (Hejný and Sytnik, 1993; Wilmanns, 1998; Chepinova and Rosbakh, 2012). The development of communities with *Myriophyllum* (*sibiricum*) can also be an indicator of the transition of a water body to higher trophic level (Kuzmichev et al., 2009). Oligo-mesotrophic *Potamogeton*_1 (*alpinus*) and mesotrophic *P. praelongus* Wulfen (Hejný and Sytnik, 1993; Didukh, 2011; Chepinoga et al., 2013) are abundant as
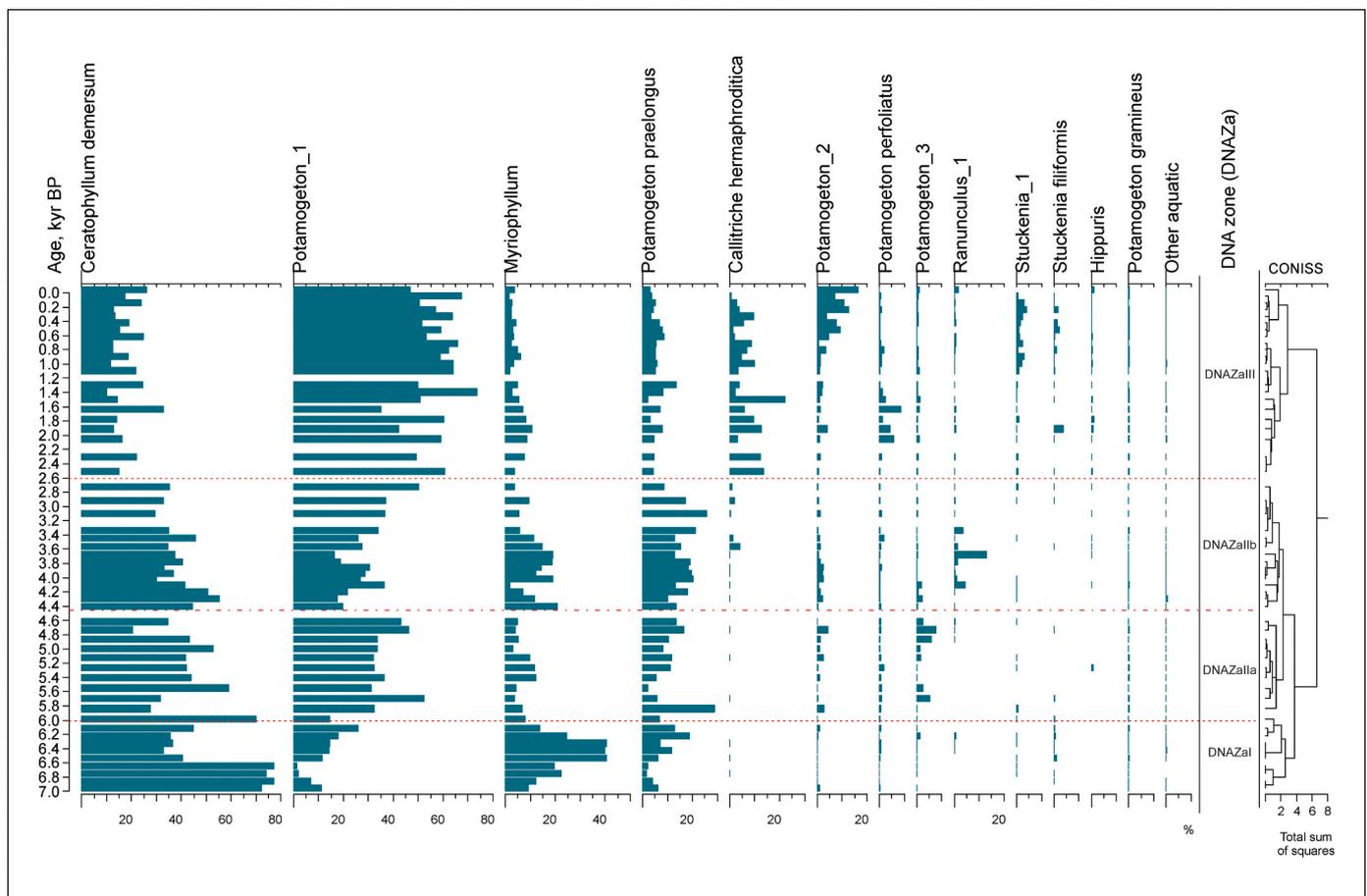
Fig. 8. Aquatic plants identified from sedimentary ancient DNA for core BK2018–1 from Lake Balyktukel.

well. As we get closer to the present, the percentages of *Ceratophyllum demersum* and *Myriophyllum* (*sibiricum*) decrease, but *Potamogeton*_1 (*alpinus*) and *P. praelongus* increase, which may reflect a gradual decline of trophicity.

DNAZaII (205–94 cm; 6.0–2.6 ka) is characterized by the dominance of *Potamogeton*_1 (*alpinus*) and *Ceratophyllum demersum*. Percentages of *Potamogeton*_1 (*alpinus*), the oligo-mesotrophic species, significantly increase in subzone DNAZaIIa (205–158 cm; 6.0–4.5 ka), however, *Ceratophyllum demersum* is still abundant in this zone; and *Myriophyllum* (*sibiricum*) decreases. *Hippuris* (*vulgaris*) appears for the first time at 5.3 ka and after 3.7 ka becomes more or less constant. In DNAZaIIb (158–94 cm; 4.5–2.6 ka), *Ceratophyllum demersum* abundance gradually decreases to the end of the zone. Within the zone, we find a decrease of oligo-mesotrophic *Potamogeton*_1 (*alpinus*), a slight increase of meso-trophic *Myriophyllum* (*sibiricum*), and the highest proportion of meso-trophic *Potamogeton praelongus*. *Ranunculus*_1 (subgen. *Batrachium*) becomes constant after 5 ka with the highest peak at about 3.7 ka. The pronounced presence of *Ranunculus*_1 (subgen. *Batrachium*) might suggest a broad distribution of shallow waters in the lake (Hejný and Sytnik, 1993; Chepinoga, 2015). After 3.6 ka, the oligo-mesotrophic *Callitriche hermaphroditica* occurs at considerable abundance.

DNAZaIII (94–0 cm; 2.6 ka–2018 CE) has a minimum amount of eutrophic *Ceratophyllum demersum* and mesotrophic *Myriophyllum* (*sibiricum*), whereas oligo- mesotrophic *Potamogeton*_1 (*alpinus*) and *Callitriche hermaphroditica* (Hejný and Sytnik, 1993) have maximum percentages. A wide-ranging aquatic species, *Potamogeton perfoliatus*, becomes abundant between 2 and 1.4 ka, while a shallow water species, *Stuckenia filiformis,* becomes relatively abundant in the last millennium.

4.5. Plant diversity

Alpha diversity indices of the terrestrial plants based on the pollen and sedaDNA data reveal large amplitudes among dominant (*N*2) and common (*N*1) species (Appendix 1). The highest *N*1 and *N*2 indices are observed in 6.95–3.7 ka (Fig. 9) and coincide with the dynamics of STEPPE and TUNDRA biomes (Table 2). Similarly, the indices of plant diversity based on the pollen data, along with the STEPPE and TUNDRA biome scores, increase during 0.4–0.2 ka (Little Ice Age). However, Hill numbers calculated from the sedaDNA dataset do not show any visible fluctuation after about 3.7 ka.

The highest values of Hill indices for aquatic plant alpha diversity are at 4.7–4.5 (*N*1,*N*2), 3.8–3.6 (*N*2), 1.3 (*N*2), and 0.5–0.3 (*N*1, *N*2) ka and lowest values are at 0.9–0.6 (*N*1, *N*2) ka (Fig. 9).

Taxonomic diversity relative to the time gradient (species turnover) based on the pollen data has relatively high values from the beginning of the palaeorecord to about 3.2 ka with maxima at 6.2 ka (0.7 SD) and 3.3 ka (0.6 SD). Thereafter, the indices decrease to a minimum and only in the last 0.8 ka increase steadily (Fig. 9). In the period between 3 and 1 ka BP, beta diversity indices are minimal.

Beta diversity based on the terrestrial plant sedaDNA data shows a gradual decrease from its highest point (1.1 SD) at 6.6 ka to a minimum close to zero at 1–0.1 ka. A short peak with a relatively high SD (0.8) is calculated for 3.9–3.7 ka. Species turnover calculated from the aquatic plant sedaDNA data has a similar trend to that for terrestrial taxa with
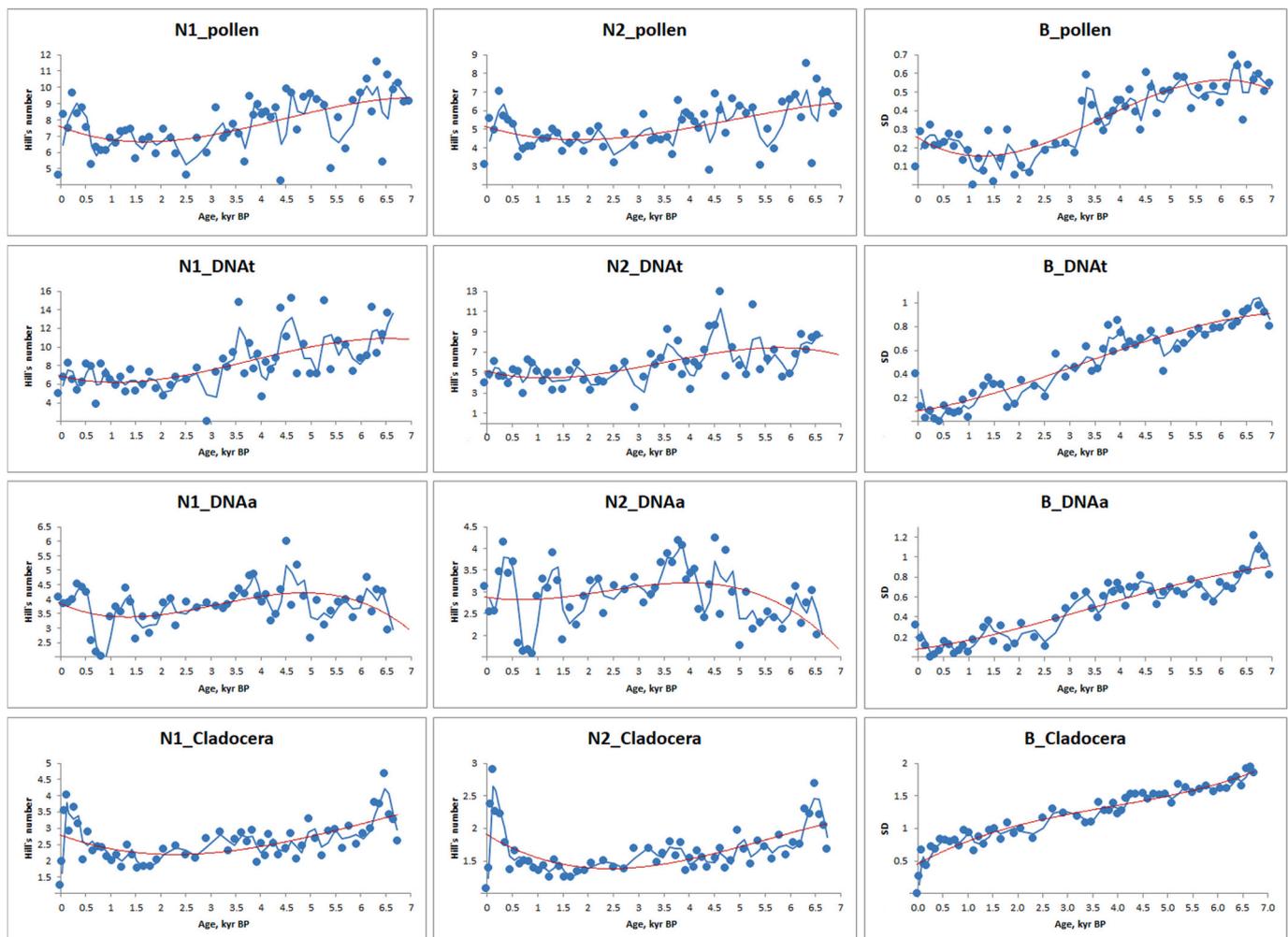
Fig. 9. Alpha and beta diversity of plants (based on pollen and terrestrial and aquatic sedaDNA) and Cladocera.

Table 3

Correlation coefficients (r2) for indicator biomes (in scores): TAIGA (TA), STEPPE (ST), DESERT (DE), TUNDRA (TU); mean annual precipitation (PANN) and values of pollen-based plant diversity indices (N0, N1, N2) for *BK2018–1*. The statistical correlation coefficients are marked in red.

Hill number	TA	ST	DE	TU	PANN
N0	−0.2	0.6	0.3	0.7	0.4
N1	−0.2	0.9	0.5	0.9	0.5
N2	−0.2	0.9	0.5	0.9	0.5

the highest value (1.2 SD) at 6.6 ka and a minimum between 1 and 0.2 ka (Fig. 9).

The calculated pollen diversity indices show significant positive correlations with the amount of annual precipitation (Table 3) for N1 and N2. Correlation analysis between biodiversity indices and the major biomes shows strong positive correlations between all indices and biomes of open vegetation – STEPPE and TUNDRA (Table 3). In addition, Hill numbers obtained by both sedaDNA and pollen analyses show strong positive correlations with beta diversity. For the results obtained by sedaDNA analysis, a strong positive correlation is found between taxonomic richness (N0) and beta diversity ($r^2 = 0.6$), and for pollen data between common (N1) and dominant (N2) taxa and beta diversity ($r^2 = 0.7$ and $r^2 = 0.6$, respectively).

4.6. Cladocera

A total of 15,225 cladoceran remains were identified. Twenty-four Cladocera taxa are encountered from the sediment profile, of which 17 relate to Chydoridae, and the others to *Daphniidae, Bosminidae, Eurycercidae* and *Ophryoxidae* (Appendix 1). This expands the taxonomic list of Cladocera to 24 taxa from the 18 noted in Burmistrova and Ermolaeva (2013). Most cladoceran assemblages are dominated by *Daphnia longispina* agg. Pelagic organisms dominate the record in abundance.

The cladoceran community of Lake Balyktukel is similar to arctic and subarctic lakes in terms of species composition (Harmsworth, 1968; Nevalainen et al., 2013; Frolova et al., 2014). Cold-water oligosaprobic taxa of the northern complex (*Daphnia longispina* agg., *Alonella nana* Baird, *Alona affinis* Leydig, *A. guttata/Coronatella rectangula* Sars) are predominant. Warm-water species (e.g. *Leydigia leydigi* Schödler, *Pleuroxus uncinatus* Baird, *Graptoleberis testudinaria* Fischer) are found in insignificant proportions. Only in the last 300 years, has the thermophilic taxon *Bosmina longirostris* increased and even become dominant in the last 100 years.

Remains of *Polyphemus pediculus* which is noted in the modern zooplankton are not found throughout the core. Remains of *P. pediculus* can, however, be absent in the bottom sediments, even if they are well represented in the modern samples, due to its poorly preserved soft-shelled chitinous body (Davidson et al., 2007; Kattel et al., 2007; Cakiroglu et al., 2014).
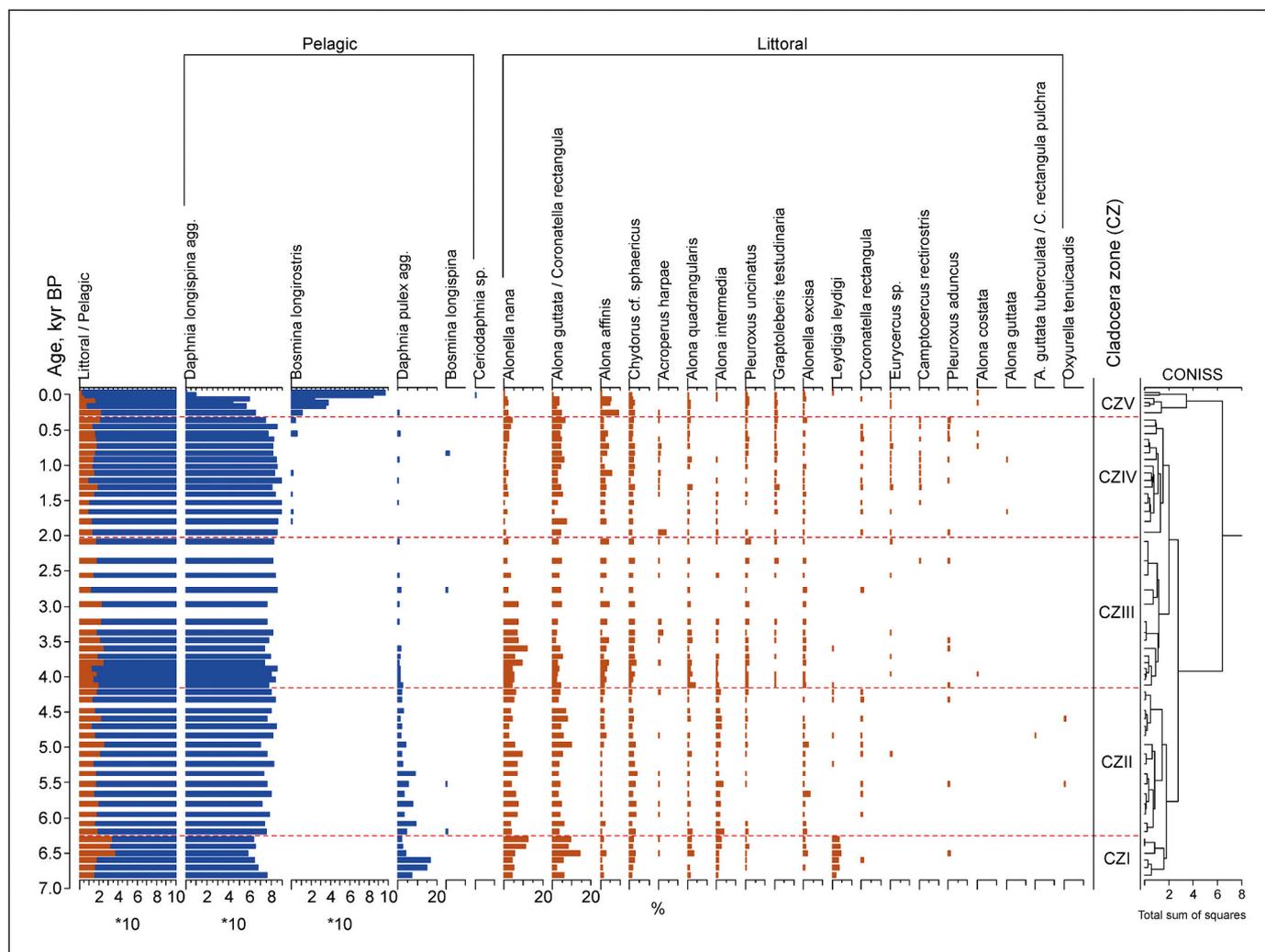
Fig. 10. Cladoceran diagram for core BK2018–1 from Lake Balyktukel.

The diagram is divided into five cladoceran zones (CZ; Fig. 10). CZI (234–212 cm; 6.95–6.2 ka) is characterized by the dominance of pelagic taxa *Daphnia longispina* agg. and *D. pulex* agg.; although the littoral taxa reach their maximum abundance. Towards the top of the zone, an increase of littoral phytophilous macrophyte-associated *Alonella nana* and *Alona guttata/Coronatella rectangula* (Fryer, 1968; Smirnov, 1974) is observed. Littoral species *Alona quadrangularis* O.F.Müller and *Leydigia leydigi* have a constant and high abundance only in this zone. *Alona quadrangularis* shows a preference for muddy deep-water localities (profundal) and prefers waters rich in fine organic matter (Smirnov, 1974; Flössner, 2000; Błędzki and Rybak, 2016). It is considered likely that the relatively warm-water species *Leydigia leydigi* is distributed in eutrophic/productive waters (Duigan, 1992). It is a true bottom dweller, often reported on the muddy bottom with rich detritus and dead leaves and prefers water with low oxygen saturation. This zone is the most productive throughout the core.

Daphnia longispina agg. is dominant in CZII (212–146 cm; 6.2–4.2 ka); the *D. pulex* group decreases to very low values in the upper part of the zone. *Alonella nana* and *Alona guttata /Coronatella rectangula* are present at lower abundances. Percentages of *Alona intermedia* Sars increase; *Oxyurella tenuicaudis* and *Alona guttata tuberculata /Coronatella rectangula pulchra* occur in this zone. There is a slight increase in the proportion of pelagic:littoral taxa.

Dominant *Daphnia longispina* and *Alona affinis* slightly increase in CZIII (146–80 cm; 4.2–2.0 ka). *Alonella nana* is constantly present while the pelagic *Daphnia pulex* decreases to very low values.

In CZIV (80–16 cm; 2.0–0.3 ka) *Daphnia longispina* is still dominant; it increases significantly in the upper part of the zone. *Alona guttata/Coronatella rectangula* is subdominant. The small *Alonella nana* decreases markedly and *Alona affinis* increases slightly towards the zone top. *Camptocercus rectirostris,* associated with low productivity non-polluted lakes (Whiteside, 1970), appears at low but constant abundance only in this zone.

The planktic cladoceran *Bosmina longirostris,* that is absent in the lower zones, appears for the first time at 1.8 ka and gradually becomes dominant in the upper zone towards the core top. *B longirostris* is characterized as a thermophilic species (Nevalainen et al., 2013). The species occurs throughout the Holarctic and is an inhabitant of nutrient-rich lakes and an indicator of eutrophication. However, it is not typical for high-latitude or high-elevation lakes (Kamenik et al., 2007; Brancelj et al., 2009; Perga et al., 2010; Nevalainen et al., 2013).

Dramatic changes in the planktic cladoceran assemblages occur in CZV (16–0 cm; 0.3 ka–2018 CE). *Daphnia longispina* decreases to near extirpation in the uppermost layer. *Bosmina longirostris* increases significantly in the upper samples of the core belonging to the 20th century. This relative increase is coincident with a decrease in the abundance of pelagic *Daphnia longispina* and littoral cold water taxa *Alonella nana* and *Alona affinis.*

Alpha diversity of Cladocera is highest at ca 6.5 ka and about 0.12 ka (1830 CE); and lowest in modern times when the community becomes monodominant (Fig. 9). Highest beta diversity (>1SD) is recorded from the beginning of the record to ca 1.8 ka with a maximum (1.8 SD) at about 6.7 ka (Fig. 9).

4.7. Annual precipitation

The general trend of the reconstructed PANN decreases over the last 6.95 ka; it is especially noticeable after 3.3 ka (Fig. 5; Appendix 1). The lowest value (420 mm yr^{-1}) is reconstructed for 5.4 ka; the highest values are at 5.3 and 3.5 ka (515 and 510 mm yr^{-1}, respectively).

The most humid phase of the *BK2018–1* core corresponds to PZIII (6.95–4.3 ka) with an average PANN of 485 mm yr^{-1}; and the driest phase is in PZI (2.2–0 ka) with an average PANN of 465 mm yr^{-1} (Table 2).

4.8. Comparison of the different bioproxy datasets

Fig. 11 illustrates the goodness-of-fit between ordination results from two different datasets. The size of the residuals for each time slice between 6.95 and 0 ka is shown. Low residuals indicate a good agreement between datasets, while high residuals indicate a poor agreement (Wischnewski et al., 2011). Procrustes and PROTEST results indicate that the best fit is between the cladoceran and sedaDNA of aquatic plants datasets ($r = 0.6$) throughout the entire core except for the upper modern samples. Comparison of the pollen and sedaDNA of terrestrial plants do not agree so well ($r = 0.3$). Better agreement between these two datasets occurs from 6.95 to 3 ka with two exceptions at 5.4 and 4.4 ka.

5. Discussion

5.1. The environmental history of the Ulagan Plateau for the last 7 ka

At about 7 ka, boreal larch forest mixed with *Betula fruticosa* Pall, *Salix, Ribes, Lonicera, Rubus idaeus*, and *Spiraea* was distributed across the Ulagan Plateau. *Pinus* grew in much lower abundance around the lake than *Larix*; however, it was represented regionally in this part of the Altai Mountains. Up to 3.5 ka, according to the sedaDNA data, *Populus* grew sporadically in the forest stands. Plant diversity was greatest between 7 and 3.7 ka. In both records for terrestrial plants (sedaDNA and pollen), increased taxonomic diversity (Hill numbers) is positively correlated with beta diversity. This suggests the existence of a mosaic vegetation under a favourable climate between 7 and 3.5 ka. The period between 5.3 and 3.4 ka is characterized by the maximum spread of larch in the vicinity of the lake and maximum amount of annual precipitation. A maximum distribution of larch has also been recorded near the high
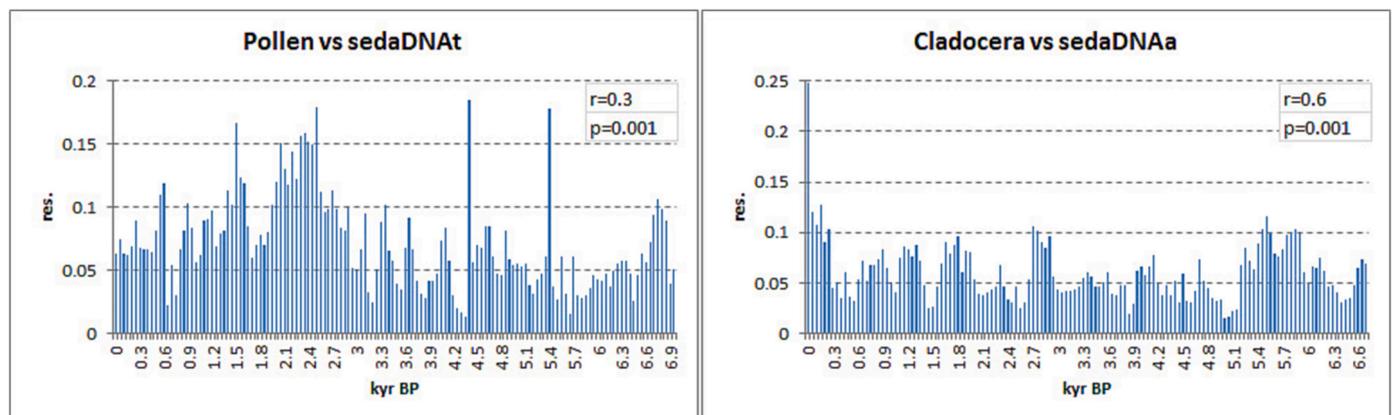
Fig. 11. Procrustus analysis for the bioproxies from Lake Balyktukel records.

mountain Lake Kanas in the Mongolian Altai at around 4–3.8 ka (Huang et al., 2018). A short period of increased tundra vegetation at 4.3–3.8 ka on the Ulagan Plateau could correspond to the severe "4.2 ka event" recorded in both hemispheres (Mayewski et al., 2004; Seppä et al., 2009). The cooling climate during 4.2–4.1 ka is also evidenced by the significant decrease or absence of the thermophilic green alga *Pediastrum simplex* in the palaeorecord from Lake Boston in Xinjiang Province, north-western China (Huang et al., 2021b).

From 5.3 ka, a cover of *Vaccinium vitis-idaea* begins to develop in the larch forest. After 3.4–3.3 ka, communities with dwarf birch – so called *yernik* – decrease in abundance. A ground cover of small shrubs such as *Rhododendron tomentosum, Empertrum nigrum,* and *Vaccinium vitis-idaea* and mosses became widespread around the lake from about 2–1.8 ka, which may indicate swamping of the area. Indirect evidence of swamping includes a significant increase of *Potamogeton perfoliatus* between 2 and 1.4 ka as communities of *P. perfoliatus* with *Ceratophyllum demersum* grow in muddy, swampy areas with slow flow or still water (Kuzmichev et al., 2009).

After 0.8 ka the pine pollen decreases in the pollen record and *Pinus* totally disappears from the terrestrial plant sedaDNA record. Ericaceae and Dryadoideae become constant after 1–0.8 ka, and after 0.6 ka the abundance of dwarf birch increases. This reflects the establishment of different types of alpine tundra on the Ulagan Plateau similar to the modern vegetation. The maximum tundra development, coinciding with increased terrestrial and aquatic plant diversity, is inferred for between 0.5 and 0.2 ka and can be associated with the Little Ice Age.

Plant diversity has been decreasing for the last three thousand years according to both pollen and sedaDNA palaeorecords. At the same time, beta diversity, falling to a minimum level at 1.5–1 ka in the pollen record, begins to increase in the last thousand years. The sedaDNA palaeorecord reveals an increase in beta diversity only in the modern sample, which spans the last decades. The same trend is revealed for plant macrophytes by sedaDNA. This may indicate a change in environmental conditions in recent decades.

5.2. Aquatic population of the lake and its fluctuations

The beginning of the palaeorecord around 7 ka is the most productive time according to the cladoceran and higher aquatic plant composition. The mesosaprobic taxon *Leydigia leydigi,* associated with relatively warm climate and high organic content, is present only in the lowermost part of the core until 6.3 ka. However, the lowering of lake trophicity at 6 ka BP is reflected by a decrease in *Ceratophyllum demersum* and *Myriophyllum sibiricum* and increase in *Potamogeton alpinus* and *P. praelongus*. The appearance of *Pseudopediastrum integrum* from 6.1 ka also suggests a cold and oligotrophic lake environment. The trophicity of the lake continued to decrease until 4.5 ka.

The appearance of *Hippuris vulgaris* and the increase in *Ranunculus* subgen. *Batrachium* around 5.3–5 ka may indirectly indicate the extension of shallow-water ecotopes due to an increase in lake area. The cladoceran composition supports this suggestion. The interval of 3.7–3.5 ka is marked by growth of the cyanobacteria *Anabaena* with probable blooms. During the same period, an increase of *Ranunculus* subgen. *Batrachium* suggests a sharp rise in organic matter in the lake.

Callitriche hermaphroditica is a northern species (<53°N) typically found in shallow lakes and slow-moving rivers (Clarke et al., 2019a): it became notable after 3.5 ka. After 2.6 ka the lake trophicity continued to reduce as suggested by the maximum occurrence of oligo-mesotrophic species (*C. hermaphroditica, Potamogeton alpinus)*. At the same time, the acidity in the lake probably increased, as evidenced by the appearance of *Peridinium* and *Cosmarium* (Zippi et al., 1991). The planktic thermophilic *Bosmina longirostris* colonized the lake after 1.8 ka BP, suggesting a rise in lake trophicity. Active algal blooms are inferred from a high abundance of the cyanobacteria *Aphanizomenon* and *Microcystis* in the last 500 years. However, the most recent decades are characterized by clean water with almost an absence of cyanobacteria. The presence of

cyanobacteria can cause dramatic changes in the composition of Cladocera, as cyanobacteria suppress the growth of bacteria that small-bodied Cladocera feed on.

Bosmina longirostris has become dominant in the cladoceran community during the last 100 years. The species is considered a typical thermophilic inhabitant of nutrient-rich lakes (Brancelj et al., 2009). It has a small body size compared to *Daphnia longispina*, which is a preferred food item for many predators. Sudden changes in the food web of Lake Balyktukel, such as an increase in visually feeding fish that prey on *D. longispina* and a decrease in cyanobacteria could be the cause for the success of *B. longirostris*. The chronology of the palaeorecord, however, indicates that the *B. longirostris* shift occurred at about 0.3 ka and prior to an artificial stocking of the lake. Nevalainen et al. (2015) also show that a sharp increase in the abundance of *B. longirostris* in Lake Stortṛäsk (southern Finland) in the last century is likewise unrelated to artificial stocking, because it does not coincide chronologically and no significant statistical relationship was found between the abundance of predators and the abundance of *B. longirostris*. Accordingly, *B. longirostris* can be an indicator of a warming climate and its distribution might be expanding under ongoing climate warming (Nevalainen and Luoto, 2012; Nevalainen et al., 2013).

5.3. Advantages of plant sedaDNA over pollen analysis

Even though the calculated mean Hill numbers for the sedaDNA palaeorecord of terrestrial plants and the pollen record are almost identical ($N0 = 19$, $N1 = 8$, $N2 = 6$ and $N0 = 19$, $N1 = 8$, $N2 = 5$, respectively), the numbers of identified taxa differ significantly. The sedaDNA analysis provides close to three times as many terrestrial higher plant taxa as the pollen study (118 and 43, respectively) and 19 aquatic plant taxa compared to two in the pollen analysis (Appendix 1).

The modern vegetation of the Lake Balyktukel basin is larch forest with occasional trees of *Pinus sibirica*; open sites and along the shores of the lake are covered by y*ernik* with *Betula fruticosa. Salix* spp., *Lonicera altaica* Pall*., Ribes petraeum* Wulfen, and *Dasiphora fruticose* are widespread in the undergrowth. The herbaceous and semi-shrub modern vegetation around the lake includes *Dasiphora fruticosa, Vaccinium vitis-idaea, V. uliginosum* L., *Empetrum nigrum, Rhododendron tomentosum,* and *Poa sibirica* Roshev.

The use of the sedaDNA metabarcoding not only clarifies the floristic composition of the Ulagan Plateau vegetation, but also provides a completely new perspective on the composition of dominant taxa. Taxonomic lists obtained by sedaDNA and pollen analyses differ considerably in their composition, including the dominant taxa (Fig. 12). The main dominant arboreal taxa by sedaDNA are *Larix sibirica, Betula* sp., Salicaceae, Ericales, *Lonicera,* and Potentilleae (presumably *Dasiphora fruticosa*), with *Pinus* occurring rarely and with very few reads (Fig. 7). In contrast, *Pinus sibirica* and *P. sylvestris* dominate in the pollen record with a rather high percentage of *Betula* sp., while *Larix* occurs only sporadically (Fig. 4).

A dominance of pine pollen and sparsity of larch pollen is found in all pollen records from the Ulagan Plateau for the last 7 kyr published in Blyakharchuk et al., 2004. Figs. 4 and 7 demonstrate the difference in larch abundance according to sedaDNA metabarcoding and pollen analysis and confirms that larch is underrepresented in palynological studies.

Based on the sedaDNA data, Rosaceae, Asteraceae, and Apiaceae are dominant among non-aquatic herbaceous taxa; by pollen data, the dominant herbaceous taxa are *Artemisia*, Amaranthaceae, Cyperaceae, and Poaceae (Figs. 4, 7). Amaranthaceae and *Artemisia* do not dominate or play a significant role in the modern land cover of the high-mountain Ulagan Plateau, but they are the common components of the lowland vegetation belt of the Altai Mountains. This demonstrates that the pollen record provides a regional signal, reflecting the vegetation of the broader steppe and even semi-desert mountain zones and overrepresents the contribution of Amaranthaceae and *Artemisia* to the Holocene
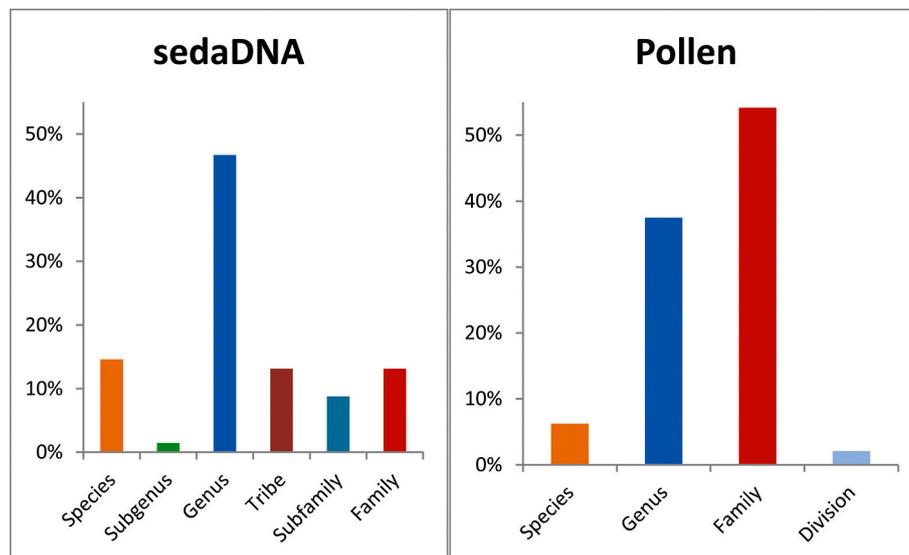
Fig. 12. Comparison of taxonomic diversity results obtained by two methods: sedDNA metabarcoding and palynological.

vegetation of the Ulagan Plateau. The local signal obtained by the sedaDNA metabarcoding reflects, among other things, the floristic diversity of a specific alpine zone, while the study of pollen gives a mixed signal combining several elevational belts.

Comparing the sets of dominant taxa, we can see that DNA metabarcoding better reflects the plant composition near the lake. Likewise, in the modern flora of the Ulagan Plateau, *Artemisia* and Amaranthaceae are not present in the sedaDNA record, while in the pollen record they dominate among herbaceous plants.

These biases introduce errors in the reconstruction of biomes, where methodologically only pollen content above 0.5% is taken into account, but preservation in sediments and pollen production of the taxon are not considered. Consequently, the presence of taxa whose pollen content is low (e.g. *Larix*) due to accumulation and preservation problems is underestimated.

6. Conclusions

The estimations of floristic diversity based on both pollen and sedaDNA data show identical trends with maximum plant diversity between 7 and 3.7 ka. However, compared to morphological pollen analysis, the sedaDNA metabarcoding reveals three times more terrestrial higher plant taxa and eight times more aquatic plant taxa.

In plant communities dominated by larch, pollen analysis does not accurately reflect the composition of dominant taxa; for example, in the Altai Mountains taiga zone, the larch-dominated communities show a dominance of pine. Plant sedaDNA analysis of the bottom sediments of Lake Balyktukel reveals a more accurate composition of the tree taxa with a predominance of larch. This means that in landscapes where larch was dominant or had significant cover, reconstruction methods, including the biomization method, and estimations of climatic variables based on pollen data, should all be treated with great caution because of the possible underestimation of the contribution of larch to the vegetation cover.

In the last century, the abundance of thermophilic small-sized Cladocera (*Bosmina longirostris*) has increased remarkably indicating both recent climate warming and a dramatic change in the food-web structure of Lake Balyktukel.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Appendix 1

Numerical datasets for the Lake Balyktukel sediment core A. Counts of pollen and spores; B. Counts of non-pollen palynomorphs (NPPs); C. Reads of plant sedaDNA; D. Counts of Cladocera; E. Plant diversity indices based on the pollen data; F. Plant diversity indices based on the DNA data. G. Cladoceran diversity indices; H. PANN: reconstructed annual precipitations, mm yr^{-1}

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