

Sedimentary DNA identifies modern and past macrophyte diversity and its environmental drivers in high-latitude and high-elevation lakes in Siberia and China

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Abstract

Arctic and alpine aquatic ecosystems are changing rapidly under recent global warming, threatening water resources by diminishing trophic status and changing biotic composition. Macrophytes play a key role in the ecology of freshwaters and we need to improve our understanding of long-term macrophytes diversity and environmental change so far limited by the sporadic presence of macrofossils in sediments. In our study, we applied metabarcoding using the *trnL* P6 loop marker to retrieve macrophyte richness and composition from 179 surface-sediment samples from arctic Siberian and alpine Chinese lakes and three representative lake cores. The surface-sediment dataset suggests that macrophyte richness and composition are mostly affected by temperature and conductivity, with highest richness when mean July temperatures are higher than 12°C and conductivity ranges between 40 and 400 $\mu\text{S cm}^{-1}$. Compositional turnover during the Late Pleistocene/Holocene is minor in Siberian cores and characterized by a less rich, but stable emergent macrophyte community. Richness decreases during the Last Glacial Maximum and rises during wetter and warmer climate in the Late-glacial and Mid-Holocene. In contrast, we detect a pronounced change from emergent to submerged taxa at 14 ka in the Tibetan alpine core, which can be explained by increasing temperature and conductivity due to glacial runoff and evaporation. Our study provides evidence for the suitability of the *trnL* marker to recover modern and past macrophyte diversity and its applicability for the response of macrophyte diversity to lake-hydrochemical and climate variability predicting contrasting macrophyte changes in arctic and alpine lakes under intensified warming and human impact.

Climate warming is amplified in high-latitude (Walter et al. 2006) and high-elevation regions (Mountain Research Initiative EDW Working Group 2015). Lakes are an important feature in these landscapes as they not only provide habitats for aquatic life but also a resource for terrestrial life (Williamson

et al. 2008). Biodiversity is changing more rapidly in aquatic systems than in the surrounding terrestrial landscapes (Collen et al. 2014), but to what extent freshwater systems will respond to future climate warming is largely not understood. Physical properties of lakes, such as the length of the open-water duration and strength of thermal stratification, are affected by warmer and drier climate (Rühland et al. 2008). These affect water-column mixing processes, light availability, and nutrient distribution (Smol 1988), which impact the biodiversity of the aquatic systems.

Macrophytes, aquatic plants growing in or near water bodies, play a key role in the ecology and function of freshwater ecosystems by providing habitat and nutrition for aquatic life (Sayer et al. 2010) and stable clear-water conditions (Hilt and Gross 2008). Macrophytes are sensitive to environmental

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changes which can alter physical (water depth and erosional processes) and chemical parameters (nutrient level, water clarity, and primary productivity) of lakes (Wrona et al. 2013). Thus, changes in macrophyte diversity, including richness and composition, are indicative of lake-level changes, trophic status, and the health of freshwater ecosystems (Bennion et al. 2000). Generally, macrophyte species richness tends to decrease along latitudinal and elevational gradients by following a gradient of decreasing temperature and nutrient availability (Squires et al. 2009). Although total richness of macrophytes is an important ecological indicator, there are three growth forms of macrophytes (floating, submerged, and emergent) and their ecological roles in response to environment are not uniform (Akasaka et al. 2010). Floating and emergent macrophytes are more directly affected by climate than by water conditions, while submerged species are more dependent on water nutrients and depth. Under warming climatic conditions, arctic lakes, for example, show an increase in submerged macrophyte abundance due to rising temperatures (Lauridsen et al. 2019) and increased nutrient levels caused by permafrost melt. In alpine lakes, knowledge about changes in macrophyte diversity in relation to climate warming is still very scarce, especially for climate-sensitive areas such as high-latitude and high-elevation lakes.

Past changes in the macrophyte diversity during the transition from the Late Pleistocene to the Holocene (Birks et al. 2000) or during the Holocene thermal maximum (Väliranta et al. 2015) are scarce and more investigations would improve our understanding of macrophyte responses under warming climate conditions. Past changes in macrophytes are traditionally investigated by macrofossil assemblages extracted from lacustrine sediment cores (Birks et al. 2000; Heino and Toivonen 2008; Väliranta et al. 2015). However, the technique risks restricting the detection of a more complete diversity due to the limited dispersal of heavy seeds and the local but patchy distribution of vascular macrophytes (Birks and Birks 2006). Plant metabarcoding using the P6 loop of the *trnL* gene (Taberlet et al. 2007) on sedimentary DNA (sedDNA) is an established proxy that can provide taxonomic information about terrestrial and aquatic plant composition and detect plant diversity from lake sediments (Niemeyer et al. 2017; Alsos et al. 2018; Parducci et al. 2019; Liu et al. 2020).

Macrophytes seldom have airborne seeds and rely on water vectors for long-distance dispersal (Sawada et al. 2003). The plant sedDNA proxy captures local plant diversity by detecting plant DNA of extra- and intra-cellular sources, which do not necessarily require the presence of seeds or pollen. A previous study using the *trnL* P6 loop marker successfully recovered the productivity changes of submerged *Potamogeton* mats from lake sedimentary DNA in eastern Pamir (Heinecke et al. 2017). This study will provide new insights into past macrophyte diversity as inferred from sedimentary DNA and related environmental relationships.

Our surface-sediment dataset originates from lakes covering a broad environmental gradient that spans a wide latitudinal

and elevational range. We analyzed macrophyte data from modern lake sediments and sediment cores to uncover present and past macrophyte richness and composition from Siberian high-latitude and Chinese (including Tibetan) high-elevation lakes. We aim to understand (1) the feasibility of the universal plant sedDNA proxy for assessing macrophyte diversity, (2) which environmental drivers best explain modern macrophyte richness and composition, and (3) how macrophyte diversity changed through the climate transition from the Late Pleistocene to Holocene.

Materials

Study area

The study area comprises two main regions of high-latitude Siberia and high-elevation Asia. The investigated lakes cover a broad environmental gradient, with a focus on the treeline areas from the Taymyr peninsula in northeastern Siberia, Yakutia in central Siberia, Chukotka in far-eastern Siberia, the central and eastern Tibetan Plateau, and northern and north-western China (Fig. 1). Siberian localities are characterized by continuous permafrost of up to several hundred meters (Andreev et al. 2011) with a mean January temperature of -41.6°C . Hence, Siberian lakes are partly formed by thermokarst processes or are of glacial origin. The Siberian lakes have an average elevation of 122.8 m with average July temperatures of about 12°C and low mean annual precipitation of 234 mm. Investigated Siberian lakes have, on average, a water depth of 6.1 m and electrical conductivity of $147.4 \mu\text{S cm}^{-1}$. The Chinese and Tibetan sites belong to mountainous areas of the Eurasian continent, which are considered a key biodiversity hotspot for conservation priorities (Myers et al. 2000). Mean July temperature is also about 12°C and mean January temperature is -22°C . Chinese and Tibetan lakes are at higher elevations (mean: 3324 m) and have a slightly higher mean annual precipitation of about 540 mm compared to Siberian lakes. The lakes have a mean water depth of about 10 m and mean electrical conductivity of $2908 \mu\text{S cm}^{-1}$. Recent environmental parameters of the three cored lakes are as follows: Lake 14-OM-02—water depth 3.5 m, pH 6.11, and conductivity $17 \mu\text{S cm}^{-1}$; Lake Ilirney 16-KP-01-L02—water depth 37 m, pH 7.6, and conductivity $13 \mu\text{S cm}^{-1}$; and Lake Naleng—water depth about 17.8 m, no measurements for pH or conductivity available.

Field sampling and environmental data collection

The surface-sediment data, including the environmental parameters, are from the dataset of Stoof-Leichsenring et al. 2020 and comprises 117 lakes from Siberia and 62 lakes from China. We excluded 84 lakes from the full dataset (262 lakes) because they contained no detectable DNA from macrophytes. The collection of the environmental data is described in detail in Supplementary Information. The three lake cores—core 14-OM-02B from the Omoloy region in

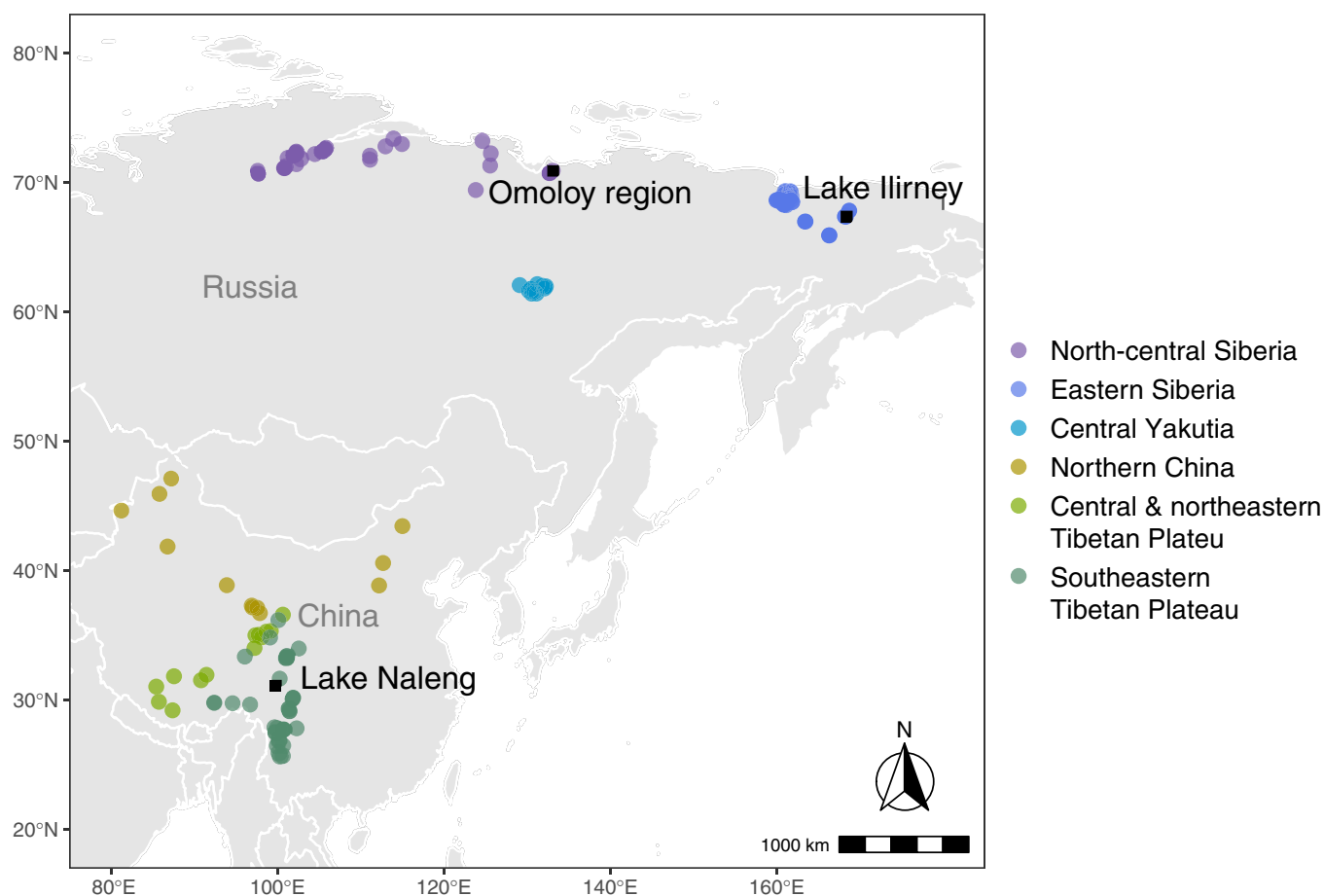


Fig. 1. Map of the regions in Siberia and China where lake surface-sediments were sampled (colored points). The surface dataset comprises 117 lakes from Siberia and 62 lakes from China that range in latitude between 25.64°N and 78.38°N and in longitude between 81.24°E and 168.7°E and range in elevation between 0 and 5156 m. The three core sites (Lake Ilirney, Lake 14-OM-02, Lake Naleng) are shown as black squares.

Siberia, core 16-KP-01-L02_Long3 from Lake Ilirney in Siberia, and Lake Naleng core in China—investigated in this study were sampled during previous Russian-German and Chinese-German field trips. A chronology for the Lake Ilirney core is published in Andreev et al. (2021): for lake 14-OM-02, see Liu et al. (2021) and for Lake Naleng, see Kramer et al. (2010). Coring, transportation, preservation, and subsampling of the core for ancient DNA are described in detail in Supplementary Information.

Molecular genetic laboratory work

DNA extraction of initially 262 lakes' surface-sediment samples was carried out in the molecular genetic laboratories equipped for environmental DNA work at the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Potsdam (Stoof-Leichsenring et al. 2020). DNA extraction was done by using the PowerMax Soil DNA Isolation kit[®] (Mo Bio Laboratories) and PCR amplification were performed with the *g* and *h* universal plant primers of the P6 loop (Taberlet et al. 2007)

modified with randomized 8 bp nucleotide tags and three additional unidentified bases (NNN) for improved sample separation during sequencing. PCRs were run using the Platinum[™] Taq DNA Polymerase High Fidelity (Invitrogen), purification of PCR products was done with Min Elute (Qiagen), followed by equimolar pooling of PCR products and preparation for Illumina next-generation sequencing. Sequencing of four PCR pools was realized in four independent HiSeq2500 runs with a read length of 2×125 bp at sequencing service (Fasteris SA). A more detailed description of the lab procedures and bioinformatic analyses are given in Stoof-Leichsenring et al. (2020).

The DNA extraction for downcore samples was performed in the paleogenetic laboratories at AWI in Potsdam, which is in a building separate from the normal genetic and post-PCR area. Precautions were taken in all the experimental steps to avoid potential contaminations (Champlot et al. 2010; Epp et al. 2019). DNA extraction of core samples was conducted with the same extraction kit. A detailed description of the metabarcoding pipeline to generate the plant DNA data of the

core from Lake 14-OM-02B is described in Liu et al. (2020), Lake Ilirney is summarized in Huang et al. (2021), and Lake Naleng is described in Liu et al. (2021).

Bioinformatic analyses

Sequence data processing and macrophyte sequence fetching is described in detail in Supplementary Information. Raw sequence data, reference databases, and scripts can be downloaded from Dryad repository (<https://doi.org/10.5061/dryad.k6djh9w4r>). For the taxonomic assignment, a sequence reference database for Arctic and Boreal vascular plants (Sønstebø et al. 2010; Willerslev et al. 2014; Soininen et al. 2015) and a reference database generated from the EMBL standard sequences (<http://www.ebi.ac.uk/ena>, release 138) were used. After filtering for macrophytes only, our final surface-sediment dataset includes data from 179 lakes and 88 unique macrophyte amplicon sequence variants (ASVs), which had an exact match of 100% sequence identity to entries in either the EMBL or Arctic and Boreal database. The number of read counts differed greatly between the samples (570–356,613). The three lake cores generated 55 unique macrophyte ASVs, which varied in read counts from 4190 to 75,478 for Lake 14-OM-02, from 133 to 15,708 for Lake Ilirney, and from 259 to 191,145 for Lake Naleng (Supplementary Table S2).

Statistical analyses

Prior to any statistical analyses of the surface-sediment dataset, macrophyte sedDNA data were resampled to 570 reads without replacement to reduce biases produced by sampling size differences occurring through PCR amplification, pooling samples, and sequencing. The following analyses were conducted in R (R Core Team 2020). Resampling was repeated 100 times and the average resampled read counts and resampled richness were used in further analysis (https://github.com/StefanKruse/R_Rarefaction). The effective number of species was calculated based on the resampled plant sedDNA data using the function *diversity* in the package “vegan” (Oksanen et al. 2019). In the same way, the core data were resampled to the minimum read count of each core dataset (Lake 14-OM-02 $N_{\text{Min}} = 4190$, Lake Ilirney $N_{\text{Min}} = 133$, Lake Naleng $N_{\text{Min}} = 259$). A boosted regression tree (BRT) model was applied to resampled taxa richness estimated from the surface-sediment data and to test their response to environmental variables in the package “dismo” (Hijmans et al. 2011). The correlation analyses between all pairs of environmental parameters helped to select the least inter-set correlated parameters for the BRT analyses. The model was run using the settings of a default bag fraction of 0.5, a Gaussian error distribution, a slow learning rate of 0.001, and a tree complexity of 2 for all analyses. Resampled plant sedDNA data were reduced to those ASVs with a minimum relative abundance of $\geq 0.5\%$ per sample and occurring at least five times in the dataset. The following analyses were conducted using the “vegan” package (Oksanen et al. 2019). The data subset was $\log(1+x)$

transformed and normalized using the *decostand* function. With the transformed and normalized data, we ran a principal component analysis (PCA) using the function *prcomp* in the package “stats” (<http://www.r-project.org/>). We fitted $\log(1+x)$ transformed explanatory variables including electrical conductivity, water depth, and July temperature (untransformed) to the ordination plot using the *envfit* function. We further used the function *varpart* to partition the variation in the community data with respect to the three explanatory variables and extracted the individual fractions of explained variance. ASVs in the resampled core datasets with a minimum relative abundance of $\geq 0.5\%$ per sample were kept in the dataset and the data were $\log(1+x)$ transformed and normalized prior to ordination analyses. We used the *predict* function in the package “stats” (<http://www.r-project.org/>) to plot the core datasets onto the ordinations of the surface-sediment dataset.

Results

Modern macrophyte community inferred from sedDNA in surface sediments

After filtering the raw sequence data from the modern datasets, we retrieved 5,406,846 reads with 88 unique ASVs from the 179 lakes (Supplementary Table S1). The majority of macrophyte ASVs (57) is identified to species level, 30 are identified to genus only, and 1 is assigned to family level. The identified ASVs come from 19 families, dividing into 32 genera and 48 species. Submerged Potamogetonaceae (24 different ASVs) and wetland Cyperaceae (20 ASVs) are the most diverse families detected, followed by Juncaceae and Ranunculaceae. Our surface data reveal six ASVs of floating taxa, 36 submerged, and 46 emergent macrophytes (Supplementary Table S1). Only a sporadic occurrence of floating macrophytes is detected in the Siberian and Tibetan lakes (Fig. 2). Submerged macrophytes of the genera *Potamogeton* and *Stuckenia* are dominant in most of the lakes investigated. The Siberian lakes are dominated by *Hippuris* and *Potamogeton*, whereas Tibetan lakes are dominated by *Myriophyllum* and *Stuckenia*. The final resampled macrophyte data from sediment surface samples is provided as Supplementary data (final_macrophyte_DNA_data.xlsx).

Modern macrophytes and their relationship to environmental variables

Macrophyte richness varies between 1 and 27 ASVs detected in the 179 Siberian and Chinese lake samples analyzed. The northern Siberian lake 13-TY-16 has the highest richness of 27 unique ASVs, followed by the central Siberian lake 05-Yak-17 and northern Siberian lake 13-TY-13, whereas the eastern Siberian lake 16-KP-03 and the southern Tibetan lake Daze Co have the lowest richness with only one macrophyte ASV present. In general, the Siberian lakes (mean richness: 13.9 ± 6.2) have higher macrophyte richness than the Chinese lakes (mean richness: 8.7 ± 4.5). Mean July

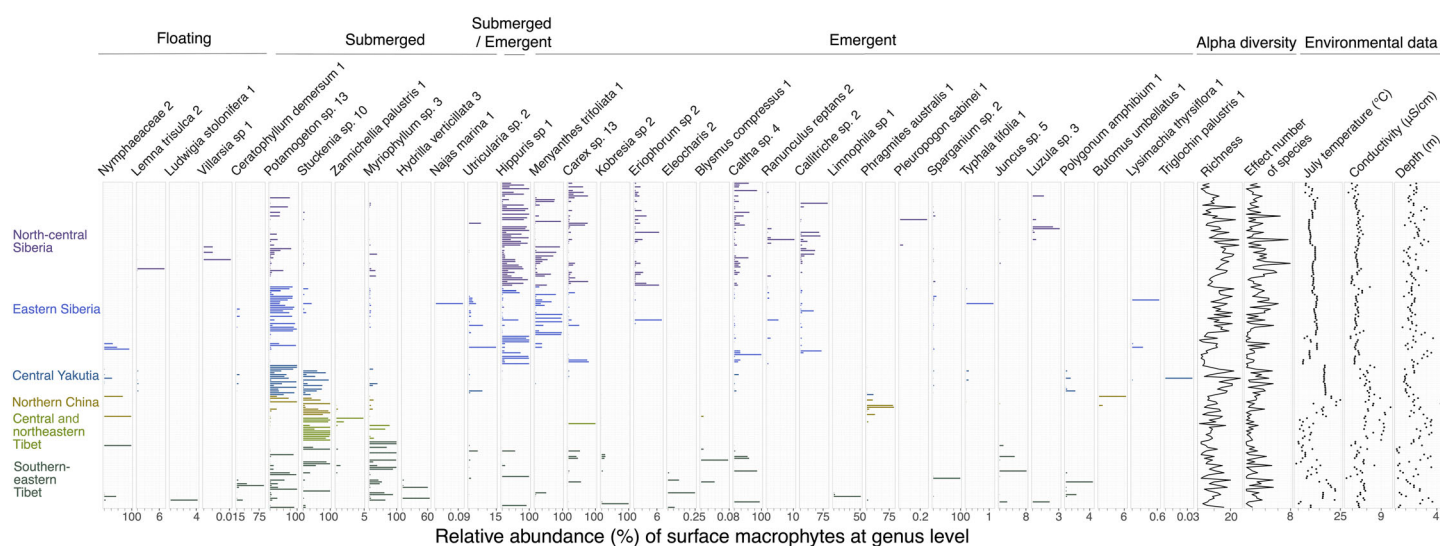


Fig. 2. Compilation of macrophyte taxonomically summed ASVs, resampled richness, effective number of species derived from the metabarcoding of surface sediments, and environmental factors derived from 179 lakes. Conductivity and lake depth are $\log(1 + x)$ transformed. Totally 88 ASVs were detected, but summed up according taxon name resulting in 33 different taxa. The number after the taxonomic name relates to the number of unique ASVs identified according this taxon.

temperature, electrical conductivity, and sample depth were selected as the most uncorrelated and explanatory variables for BRT analyses (see the pairwise correlations in Supporting Information Fig. S1). In the BRT analyses, July temperature (40.8%) explains macrophyte species richness best, followed by lake conductivity (35.2%) and lake water depth (24%) (Fig. 3). Environmental parameters and fitted values and functions are shown in Supporting Information Figs. S2, S3. The interaction plots indicate that highest species richness occurs when July temperatures are higher than 12°C and conductivity ranges between 40 and 400 $\mu\text{S cm}^{-1}$.

The first axis of the PCA explains 21.9% and the second explains 12.3% of the variance in the macrophyte community obtained from sedDNA (Fig. 4a). Samples from Siberian lakes disperse extensively, whereas the Tibetan samples form a cluster along the negative PC1 axis. There is no clear differentiation within the Siberian and Tibetan lakes from their geographic distribution. According to the variation partitioning analyses, 14.5% of the variance is explained by all variables. A significant proportion of the variance (7.6%, $p = 0.001$) in macrophyte composition from all analyzed lakes is uniquely explained by conductivity (Fig. 5), and 4.1% of the variance is significantly uniquely explained by July temperature. Lake water depth, however, explains little (0.4%) of the macrophyte compositional signal. Only 0.5% of the explained variation is shared by the three variables.

Past macrophyte community inferred from sedaDNA of sediment cores

Two of the three investigated lake sediment cores cover the late-glacial to Holocene with the third core covering most of the Holocene. They vary in macrophyte read count from

144,860 reads in Lake Ilirney, 445,459 reads in Lake 14-OM-02 in the Omoloy region, to 571,688 reads in Lake Naleng. The minimum counts per sample vary strongly, with a minimum count of 133 reads in one sample from Lake Ilirney to a minimum count of 4190 reads in a sample from Lake 14-OM-02 (Supplementary Table S2). Maximum counts vary between 15,708 (Lake Ilirney) and 191,145 (Lake Naleng) reads. Twenty-seven and 20 unique macrophyte ASVs are detected in Lake Ilirney and Lake 14-OM-02, respectively. The highest number of ASVs (34) is in the Naleng core. In total, 55 unique ASVs are detected in the three cores. They mostly comprise emergent plants from Cyperaceae (23 ASVs), followed by submerged plants, for example, Potamogetonaceae (11 ASVs). Altogether, we identified 103 unique macrophyte ASVs in the surface-sediment and core samples, whereof 40 ASVs (38.6%) are found in both surface-sediment and core samples, and 48 (40%) and 15 (14.4%) ASVs exclusively occur in surface-sediment and core samples, respectively. The final resampled macrophyte data from sediment core samples are provided as Supplementary data (final_macrophyte_DNA_data.xlsx).

Past macrophytes and their relationship to environmental changes

The variations in past macrophyte richness and composition show large differences in the Siberian and Tibetan cores (Supporting Information Fig. S4). The downcore richness of Siberian Lake 14-OM-02 varies subtly between 6 and 12 taxa over the past 7000 yr. Highest macrophyte richness is noted between 5–4 and 2–1.3 ka, whereas richness decreases to a few taxa at 2.8 ka and during 0.9–0.1 ka. Periods of higher richness are dominated by the aquatic taxon *Hippuris*, co-occurring with low abundances of emergent wetland types such as

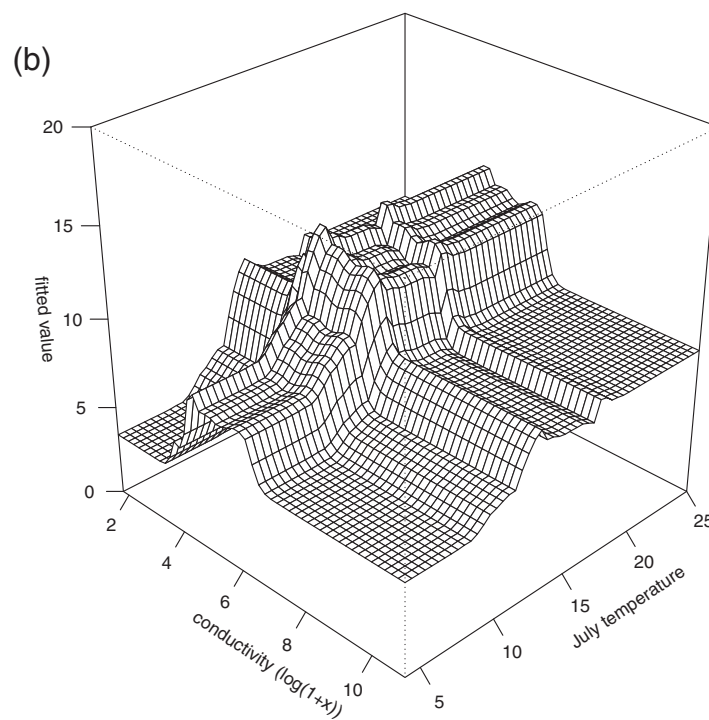
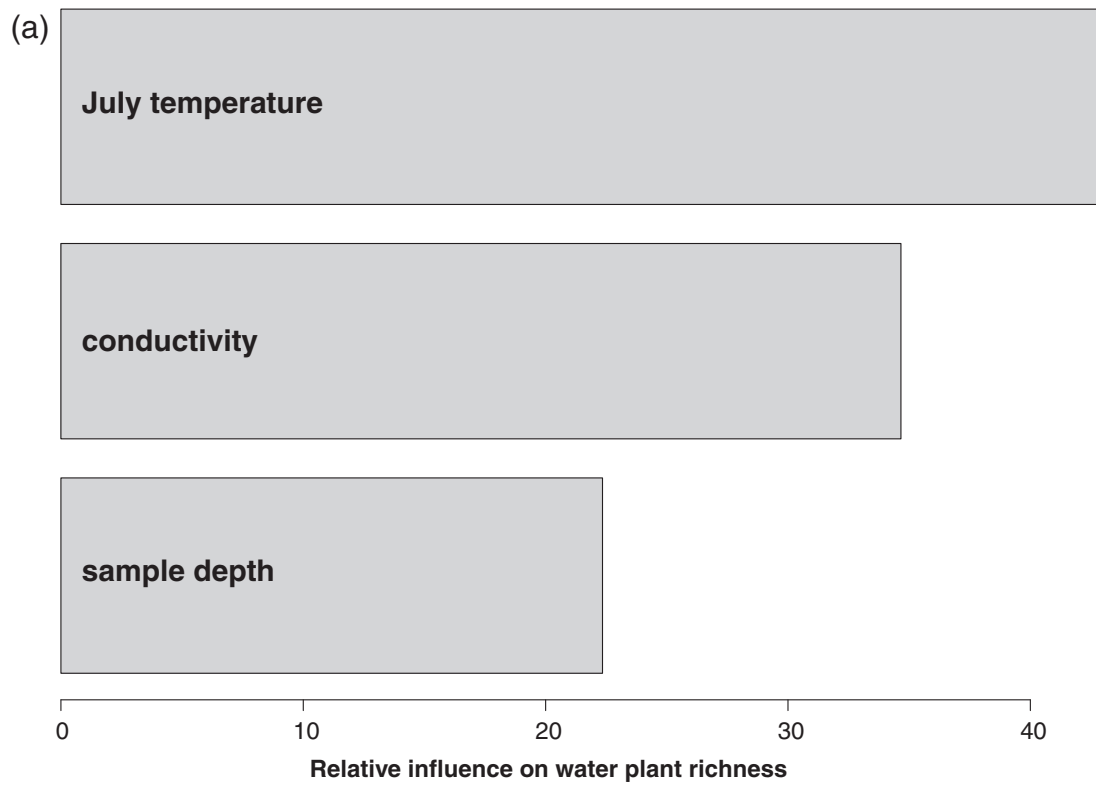


Fig. 3. Three-dimensional partial dependence plots showing the interaction between the tested environmental variables and macrophyte species richness in the BRT model (a). July temperature and water conductivity have the largest relative influences on the richness, whereas sample depth (water depth at sampling location) is of minor influence (b).

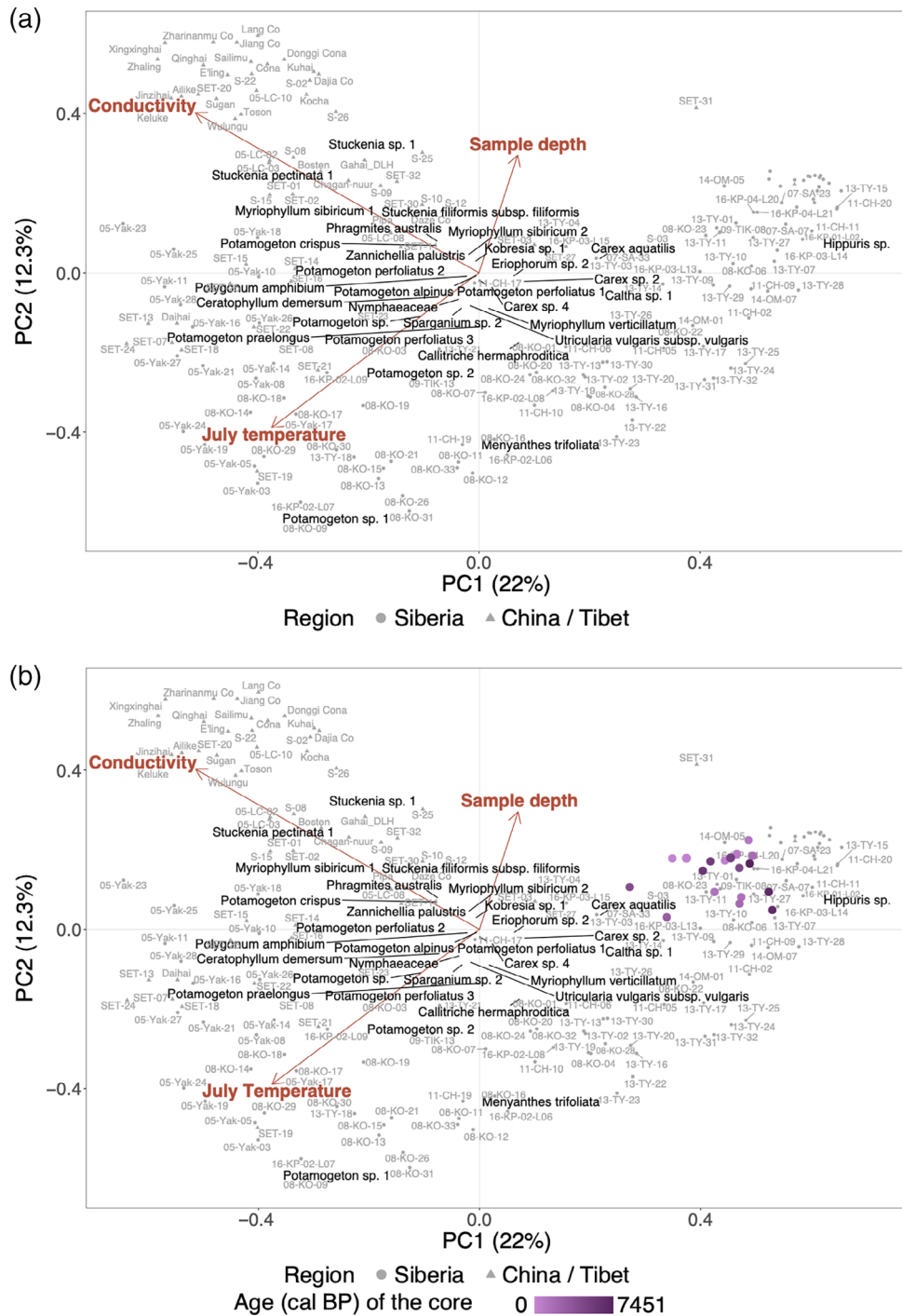


Fig. 4. PCA biplots of (a) macrophyte taxa from sedimentary DNA, showing a subset of the dominant taxa which explain most of the variance in the dataset. Surface-sediment ordinations were fitted to data from three lake sediment cores: downcore age of samples from (b) Lake 14-OM-02 are presented in purple, (c) Lake Ilirney in blue, and (d) Lake Naleng in green. Siberian sites are shown as circles; Chinese and Tibetan sites are shown as triangles. Environmental factors that explain the most significant variance in the macrophyte composition are indicated in red.

Comarum, *Ranunculus*, and *Caltha* (Supporting Information Fig. S4a). Between 4 and 2 ka only a few emergent taxa (*Carex*, *Eriophorum*, *Menyanthes trifoliata*) are present while *Hippuris*

nearly completely disappears. Recent (last 500 yr) macrophyte assemblages are largely dominated by *Comarum* and co-occurring wetland taxa resulting in an increasing trend in

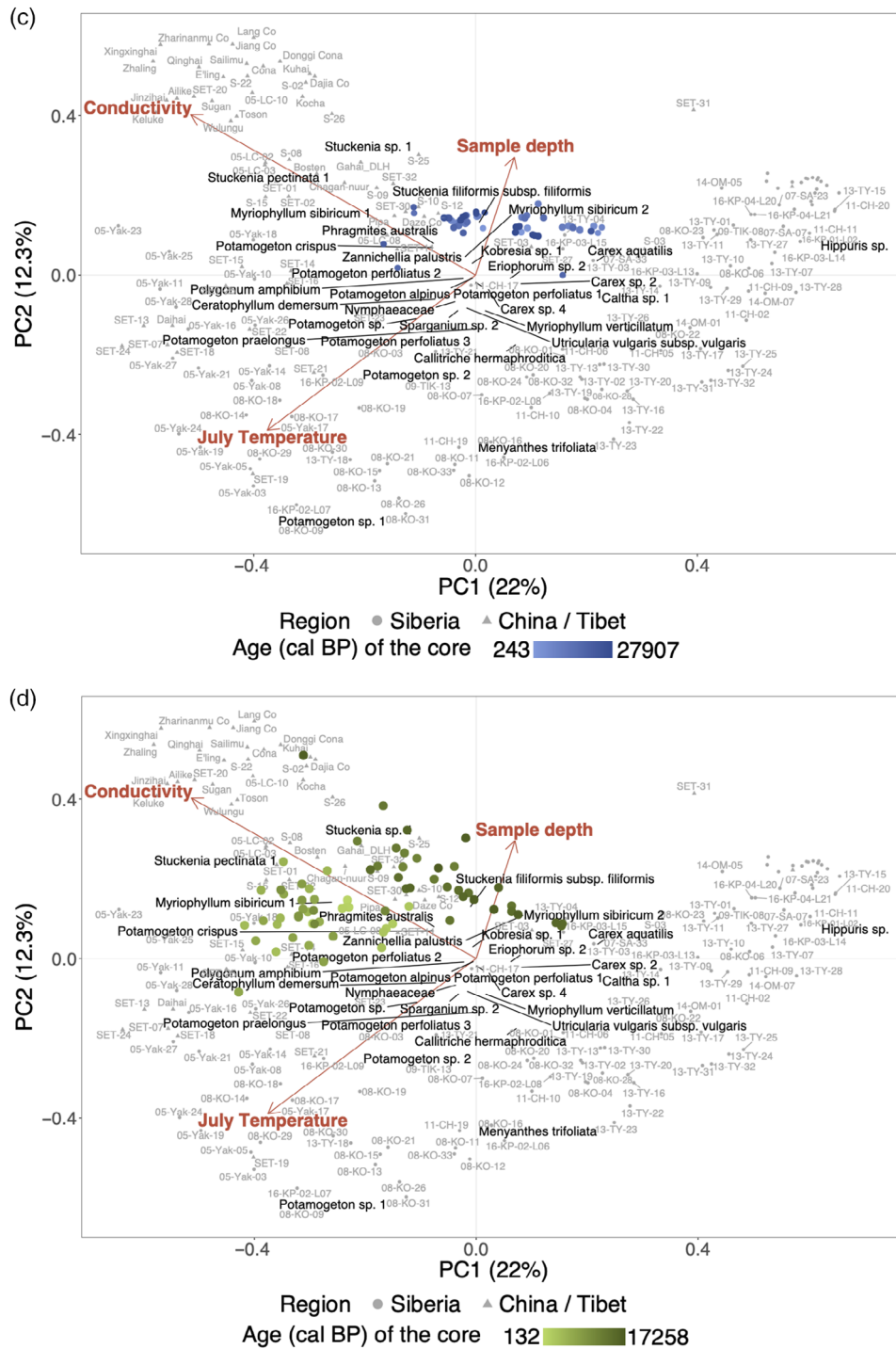


Fig. 4 (Continued)

overall macrophyte richness toward the present. Unique ASVs that are found only in this sediment core are assigned to *Ranunculus sceleratus* and *Stellaria* (Caryophyllaceae).

The macrophyte richness of the Lake Ilirney core varies between 1 and 13 ASVs over the past 28 ka (Supporting Information Fig. S4b). Lower richness is detected during the Last

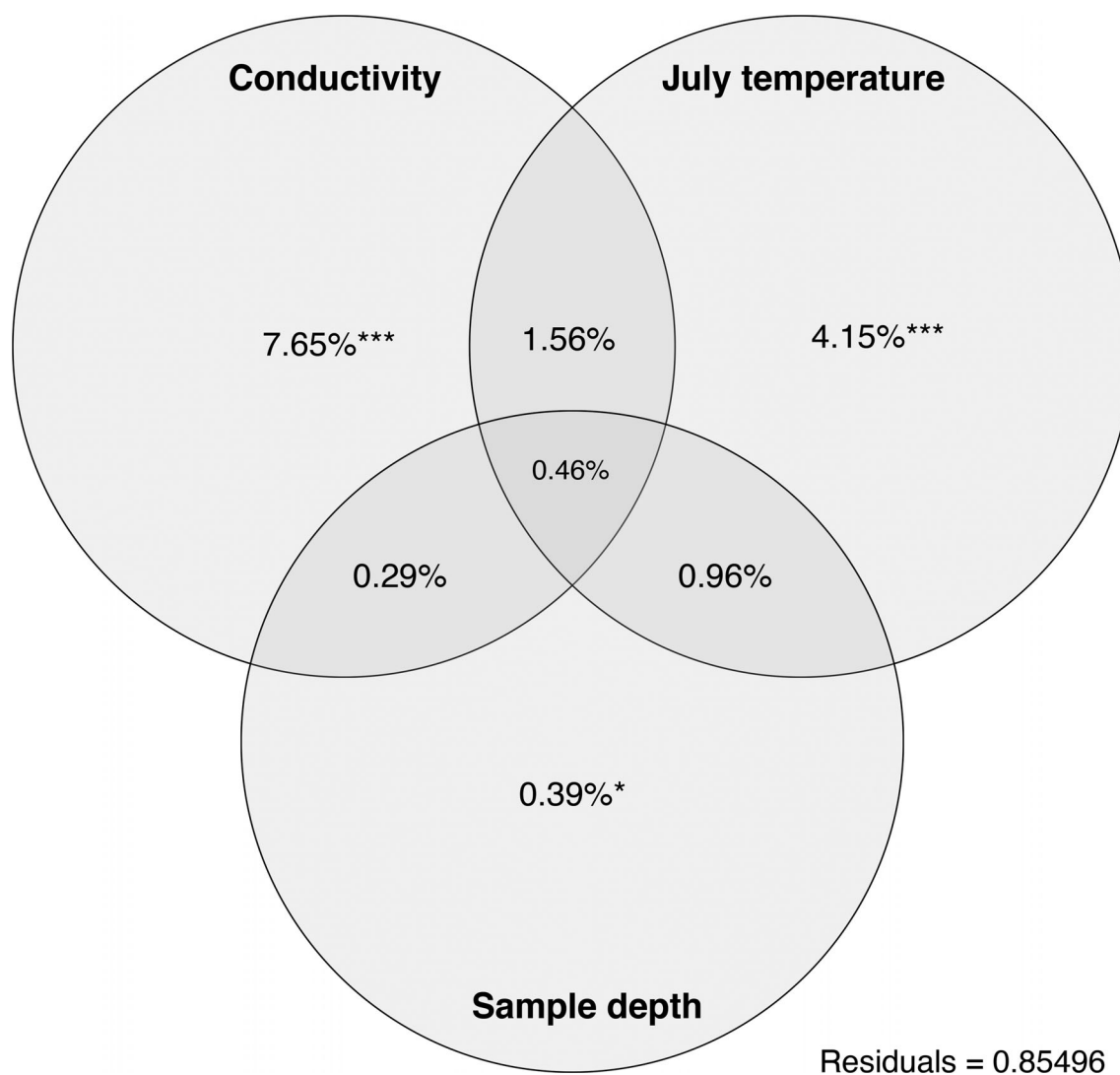


Fig. 5. Venn diagram showing the percentage of explained variance for electrical conductivity, July temperature, and sample depth (= lake depth at sampling localities) revealed by the constrained ordination analyses for all lakes in the surface-sediment dataset. *p* values are coded in ***0.001 and *0.05.

Glacial Maximum at 21–19 and 13–12 ka, whereas higher richness is detected at 28–26, 16–15, 11 ka and steadily increases since 6 ka. The macrophyte assemblages are mainly composed of emergent wetland plants dominated by *Carex*, *Caltha*, and *Luzula*. The Ilirney core has high *Carex* diversity with 13 different ASVs including seven *Carex* species, whereof four *Carex* ASVs are only detected in this lake core. Submerged plants (*Potamogeton perfoliatus*, *Callitriche hermaphroditica*) are present but are only dominant between 17.5 and 16.5 ka.

The Lake Naleng core shows greater richness (up to 24 ASVs) and turnover in macrophyte richness in the past 18 ka compared to Siberian cores (Supporting Information Fig. S4c). We find low richness (3–10 ASVs) between 18 and 14 ka, followed by a prominent increase after 14 ka of up to 24 ASVs. The macrophyte assemblages remain rich but with

fluctuations after 11 ka and peaks at 8, 5, and 0.7 ka. Lake Naleng was dominated by emergent macrophytes between 18 and 15 ka, mainly *Carex* and *Caltha*, whereas submerged plants (a few *Potamogeton* and *Stuckenia* types) rarely occurred. Since 14 ka both emergent—mostly *Caltha*—and submerged plants—mostly *Myriophyllum sibiricum* and *Potamogeton*—are common.

We projected the core data onto the surface-sediments ordination. Although the highest sample counts are detected in Lake 14-OM-02, the core shows little variation in past macrophyte diversity as the samples mostly cluster together (Fig. 4b). Downcore samples from 14-OM-02 reflect surface samples from thermokarst lakes currently located in forest-tundra to forest vegetation in Siberia. Similarly, little variation in past macrophyte composition is detected in the large,

glacially formed Siberian Lake Ilirney (Fig. 4c). In contrast, the macrophyte composition from the Tibetan Lake Naleng is much more diverse through time (Fig. 4d). The past macrophyte compositional change in Lake Naleng is putatively mostly impacted by temporal changes in electrical conductivity of the lake water.

Discussion

The *trnL* plant metabarcode as a proxy of macrophyte diversity

Aquatic plants, which grow along the shoreline or on the bottom of a lake are a suitable target for metabarcoding approaches on sedaDNA as they may contribute more to the plant sedimentary DNA signal compared to terrestrial catchment vegetation (Alsos et al. 2018). In our study, we detected 103 unique macrophyte ASVs from floating, submerged, and wetland taxa by using the *trnL* P6 loop as a metabarcode applied to surface and core sediments from Siberian and Chinese lakes. Despite the overall high number of recovered ASVs in our dataset, the macrophyte richness in the surface-sediment data varies strongly, which can be either caused by differences in DNA quality of the samples (Jia et al. 2021) and related differences in metabarcoding success and/or by assembly rules that naturally affect macrophyte richness. The taxonomic resolution of the 103 ASVs is very good with a detection of 99% of ASVs to genus (67%) or species (32%) level, although the taxonomic resolution of the *g-h* amplified *trnL* P6 loop (Taberlet et al. 2007) is lower compared to its encompassing longer *trnL* fragment (Zhu et al. 2015). In addition, cryptic diversity, which is a well-known phenomenon in aquatic plant genera such as *Potamogeton* (Bobrov et al. 2018), *Stuckenia* (Volkova et al. 2017), and *Hydrilla* (Zhu et al. 2015) is partly represented in our data. For example, submerged taxa such as *Potamogeton* and *Stuckenia* and emergent taxa including *Carex* and *Juncus* show intra-generic (and partly intra-specific) variation revealed by the short marker (Supporting Information Fig. S4), with few ASVs of the genera *Carex* and *Potamogeton* being solely present in core samples.

The *trnL* P6 loop metabarcode has rarely been used to recover (past) macrophyte diversity from environmental DNA (Heinecke et al. 2017). Despite its good performance with the vascular plants, it may have a problem in capturing all other macrophyte categories (Chambers et al. 2007), except for stonewort types such as *Chara*, which were successfully detected by the *trnL* P6 loop in a previous study (Heinecke et al. 2017). In this case, traditional barcoding of aquatic plants using chloroplast markers such as *rbcL/matK* (Weigand et al. 2019), *rpl32-trnL* (Volkova et al. 2017) or *trnL-F* (Zhu et al. 2015), and nuclear ITS (Bobrov et al. 2018) are preferred, but cannot be used directly on sedimentary or environmental DNA because of the length of the barcode, amongst other reasons. So far, a *rbcL* marker established by (Coghlan et al. 2021) has been used successfully for the identification of

macrophyte diversity on environmental DNA from water samples, but this marker has not been tested on sediments yet.

In summary, the overall high richness and good inter- and intra-generic diversity recovered by the *trnL* P6 loop in our data support the usage of this well-established metabarcode in future studies. This method can recover greater past macrophyte diversity than macrofossil analysis can and it enables the comparison of macrophyte diversity patterns from the many available *trnL* P6 loop datasets (citations within Capo et al. 2021).

Temperature and conductivity are significant predictors of macrophyte diversity

The results of our study align with previous results and indicate that macrophyte richness over a large spatial and environmental gradient (spanning arctic to boreal and high-elevation lakes in Tibet) is significantly predicted by July air temperature and secondly by lake-water conductivity.

Other studies on arctic and boreal lakes support our findings by reporting a negative relationship between latitude (a surrogate for temperature) and richness (Heino and Toivonen 2008) and find richness to be highly dependent on climate variables such as snow cover and the length of the ice-free period (Alahuhta et al. 2012). In our study, highest macrophyte richness is detected in lakes with a mean July air temperature higher than 10–12°C and low to moderate conductivity of 40–400 $\mu\text{S cm}^{-1}$, which are mostly shallow and oligo- to mesotrophic due to their thermokarst origin. Deviations from moderate conductivity result in lower richness at similar July temperatures (Fig. 3). In particular, slump-disturbed thermokarst lakes in permafrost areas have a higher macrophyte richness, which might be a result of nutrient input and benthic habitat development (Mesquita et al. 2010). The overall high plant richness in Siberian lakes can also be explained by the fact that northeastern Siberia was largely ice-free during most of the Pleistocene (Brubaker et al. 2005). This will have provided a glacial refugium for many types of vegetation (Brubaker et al. 2005), which could have led to the relatively higher number of macrophyte species present in Siberia.

Our study also supports that macrophyte compositional patterns are mainly explained by conductivity and temperature. Macrophyte composition in our study lakes is dominated by various submerged types such as *Potamogeton* and *Stuckenia* and emergent taxa including *Carex* and *M. trifoliata*. Interestingly, our data from eastern Siberian lakes show a lower richness compared to northern or central Siberian lakes. Because lakes from eastern Siberia are larger, glacially formed, and hyper-oligotrophic, macrophyte diversity is reduced and might be hindered by steep shorelines which putatively prevent macrophyte development (Mesquita et al. 2010). Macrophyte composition in these lakes is characterized by a few emergent types including *Carex*, *Caltha*, and *Hippuris* as well as the submerged plant *Callitriche*.

Our study finds that mean macrophyte richness is lower in Chinese lakes than in Siberian lakes. Although Chinese and Siberian lakes in our study have very similar July air temperatures on average (Chinese lakes: $N_{\text{Lakes}} = 62$, $T_{\text{July,median}} = 11.2^{\circ}\text{C}$; Siberian lakes: $N_{\text{Lakes}} = 117$, $T_{\text{July,median}} = 12.5^{\circ}\text{C}$), most of the investigated lakes have higher conductivity than the Siberian lakes (Chinese lakes: $\text{cond}_{\text{median}} = 2980 \mu\text{S cm}^{-1}$; Siberian lakes: $\text{cond}_{\text{median}} = 147 \mu\text{S cm}^{-1}$). High ion concentrations contributing to the high conductivity in the Tibetan lakes result in the dissolution of evaporites from the basin or weathering of basin rocks (Sun et al. 2020). Because only some macrophytes prefer high ion concentrations, the overall macrophyte richness is reduced compared to Siberian lakes. Several other studies from different geographic areas covering shorter conductivity gradients also find that conductivity is significantly related with macrophyte richness and note decreased richness with increasing lake conductivity, as exemplified in alpine lakes (Hinden et al. 2005) and in Baikal Siberia lakes (Alahuhta et al. 2020). Our study also finds that moderate conductivity has a positive effect on macrophyte richness, whereas eutrophic to hypertrophic conditions favor only a few saline-tolerant species such as the submerged *Stuckenia* (in our data putatively ASV *Stuckenia* sp. 1) and *Phragmites australis* which reduces the overall richness in several Tibetan lakes and also in some central Yakutian lakes. For example, *Stuckenia pectinata* shows increased productivity under high levels of conductivity (Herzschuh et al. 2010) and it outcompetes other macrophytes under very high levels of hydrogen carbonate (James 2008). Besides the dominance of a specific *Stuckenia* ASV, the globally distributed emergent macrophyte *P. australis* (common reed) is abundant in lakes with the highest conductivity (up to $57,000 \mu\text{S cm}^{-1}$) because it can withstand saline conditions (Köbbing et al. 2013) and also because of the co-occurrence of beneficial rhizospheric microbial communities (Srivastava et al. 2014). Differences in DNA preservation tested on a larger metabarcoding data of 219 surface samples (Stoof-Leichsenring et al. 2020) that include aquatic and terrestrial plants indicate that conductivity and lake size significantly explain recovered total plant richness from surface sediment DNA (Jia et al. 2021). Specifically, at high ion concentrations and partly warmer winter temperatures detected in a few Chinese lakes, poor sedDNA preservation might cause a decrease the recovery of the plant DNA signal in general (Jia et al. 2021).

Our study provides evidence of higher mean macrophyte richness in high-latitude Siberian lakes than in the high-elevation Tibetan lakes. Additionally, our data indicate that summer temperature during the growing and ice-free season of arctic lakes is the best predictor of macrophyte richness in Siberia. Under future climate warming, habitable depths for aquatic organisms are likely to increase as lakes thaw and thus enhance aquatic plant survival (Prowse et al. 2011). Rapid ice loss can lead to an earlier open-water season, which likely will enhance freshwater productivity (Arp et al. 2019) and might lead to increased macrophyte richness in Siberian lakes. However, lake thawing can also diminish submerged macrophyte

growth, because increasing DOC values can result in a decrease of water clarity reducing light availability (Beall et al. 2016). Macrophyte richness in Tibetan lakes is mostly affected by water conductivity with high levels of dissolved evaporites including inorganic carbon in the lake water favoring those few macrophytes adapted to the uptake of hydrogen carbonate for photosynthesis. Under future warming, we expect an increase in evaporation which will probably shift conductivity to higher levels resulting in a further decrease of macrophyte richness in high-elevation Tibetan lakes.

Macrophyte response to past environmental change

Past macrophyte community changes are traditionally assessed using macrofossil analyses revealing temporal environmental changes that affected the lake and its catchment. Lake type and habitat development (Mesquita et al. 2010), variations in productivity (Poikane et al. 2020), human influence (Lindholm et al. 2020), and natural climatic changes (Väliranta et al. 2015) are major factors that can influence the macrophyte communities. In our study, temporal changes in macrophyte richness and community composition show different patterns in Siberian and Tibetan lake-sediment records. The two Siberian lake cores originate from different lake types. Lake 14-OM-02, located in the Omoloy region, is a thermokarst lake whereas Ilirney is a glacially formed lake. Although the past richness of aquatic plants is generally low in the sediment core from Lake 14-OM-02, the composition shows pronounced changes altering between the aquatic type *Hippuris* and wetland plants such as *Comarum*, *Carex*, and *Eriophorum*. Periods of *Hippuris* dominance (7.6–4.6 and 2–0.5 ka) coincide with a higher abundance of Salicaceae (Liu et al. 2020) suggesting open water and generally cooler conditions. The typical circumboreal taxon *Hippuris* is a heterophyllous aquatic plant tolerant of water-level variations (Mjelde et al. 2013). It is known to live as both a submerged and emergent type and mainly occurs in areas of the lake no deeper than 1 m (Mariash et al. 2018). The shift from *Hippuris* to *Comarum* and *Carex* dominance occurred from around 4–2 ka and during the last 500 yr, reflecting the development of an extensive wetland surrounding the lake. This wetland development is likely linked to increased permafrost thaw and thus low-centered polygon expansion in the vicinity of the lake (Liu et al. 2020).

Past macrophyte composition in Lake Ilirney core is largely characterized by emergent wetland taxa, which grew in the vicinity of the lake. Only a few submerged taxa occurred, which is likely due to its far north geographic location, large size, and glacial origin as well as its rather stony lake shore, which might limit the growth of submerged macrophytes due to low nutrient levels. In addition, the great lake depth does not allow for the growth of submerged plants due to limitations in light availability. Past macrophytes were poorly reflected in the pollen data from Lake Ilirney. The pollen-based reconstruction suggests cold and dry climate in the lake

Iirney region between 28 and 14 ka (Andreev et al. 2021). Interestingly, there is only one period between about 17.5 and 16.5 ka during which submerged *Potamogeton* types persist. This period coincides with a sharp decrease in *Alnus* and *Betula* pollen from the same sediment core inferring harsh conditions exemplified by a drop in reconstructed July temperature at around 17 ka to temperatures similar to those during the Last Glacial Maximum (Andreev et al. 2021). As the richness of terrestrial plants (Andreev et al. 2021) and macrophytes (our study, Supporting Information Fig. S4) generally decreased during this period, it is likely that a few submerged plants dominate the sedaDNA signal while the rare terrestrial vegetation was not recovered. Except this period, the Iirney sediment core is dominated by emergent wetland plants with a great diversity recovered within the *Carex* genus. *Carex* diversity is highest between 28 and 26 ka and increases again with the onset of the late-glacial climate amelioration at about 16 ka (Andreev et al. 2021) and peaks at the onset of the Early Holocene 10.5 ka and the warmer mid-Holocene period at 6 ka. *Carex* diversity mainly drives the overall macrophyte richness in the sediment record and correlates with periods of higher reconstructed precipitation inferred from pollen data of the same core (Andreev et al. 2021) implying wetter and also warmer conditions favoring the establishment of wetland taxa in the lake vicinity. During the LGM (21–19 ka) and the cooler Younger Dryas period (13–12 ka), macrophyte richness is lowest with only a few *Carex* taxa present.

Overall, submerged plants are generally in low abundance in the Siberian lakes. The rich and diverse *Potamogeton* assemblages reported by studies on other arctic lakes during the early Holocene (Birks et al. 2000; Väliiranta 2006; Väliiranta et al. 2011) are not reflected in our results. Harsh winter conditions can severely limit macrophyte growth, especially in boreal regions (Alahuhta et al. 2011). Ice erosion and freezing of bottom sediments may destroy the macrophyte beds (Heino and Toivonen 2008) and a short growing-season (Mariash et al. 2018) can result in poor macrophyte productivity. Although warming leads to extended ice-free periods, the isothermal mixing and elevated turbidity in the absence of ice cover can reduce light availability (Beall et al. 2016) thus inhibiting the growth of macrophytes.

Generally, the variation in the past macrophyte assemblages detected in the two Siberian lake cores is small. The macrophyte composition appears to be largely explained by variations in temperature and water depth, based on the relationships seen in the larger surface-sediment data that cover a greater environmental gradient (Fig. 4b–d).

The Lake Naleng core has the highest past macrophyte richness compared to the Siberian cores. The record shows a strong shift from low macrophyte richness between 18 and 14 ka to an increasing macrophyte richness after 14 ka, which could be explained by rising temperature and changes in lake-water conductivity due to glacier retreat and the subsequent dissolution of evaporites and weathering of basin rocks (Sun et al. 2020). The

low richness during the Late Pleistocene can be explained by the cold and dry climate conditions with low biomass productivity, as the inferred precipitation and temperature decreased based on palynological reconstructions of Lake Naleng (Opitz et al. 2015).

During the Late Pleistocene, macrophyte composition is richer in emergent plant types including *Carex*, *Kobresia*, *Caltha*, and *Juncus*, whereas the submerged community is dominated by *Stuckenia* sp. and *Potamogeton crispus* (abundance peak 15–14 ka). *P. crispus* is known to tolerate different nutrient levels but is less tolerant of temperature increase (Hao et al. 2018), which might explain its nearly complete disappearance after 14 ka. The overall increased macrophyte richness after 14 ka corresponds with an increase in nonpollen palynomorphs in the same core (Kramer et al. 2010) and characterizes the onset of an aquatic ecosystem after the glacial period. This warmer period known as the Bølling/Allerød in the North Atlantic region (Mischke et al. 2008; Kramer et al. 2010) led to increased nutrient supply resulting in higher productivity in Lake Naleng (Opitz et al. 2015).

The macrophyte assemblages during the early Holocene are dominated by both emergent and submerged plants. Emergent plants mainly comprise *Kobresia* and *Caltha scorbosa*, which are known to co-occur in swamp meadows and are indicators of permafrost degradation and soil wetting (Yang et al. 2010). Submerged taxa include mainly *Myriophyllum sibiricum* and, at lower abundance, *Potamogeton* types, *Stuckenia filiformis*, and *S. pectinata*. *M. sibiricum* is a typical circumboreal species with a disjunctive distribution between northeast China and the Qinghai-Tibetan Plateau (Wu et al. 2015). *Myriophyllum sibiricum* and sister/hybrid species are known to be invasive and exclude/suppress the growth of other macrophytes once they are established (Lindholm et al. 2008), which is reflected in our data as it retains a stable dominance once it was established in the lake.

In contrast, the mid-Holocene richness peak at 5 ka coincides with the frequent occurrence of various submerged macrophytes with a dominance of *P. perfoliatus* instead of *Myriophyllum*. This aligns with the present-day situation where the organic matter content in Lake Naleng is high (Opitz et al. 2015) suggesting that easy nutrient availability alongside increased conductivity favored specific submerged taxa such as *Stuckenia* and *Potamogeton*. Toward the present, richness of submerged taxa decreases, as does overall macrophyte richness, which possibly indicates eutrophic conditions under which submerged taxa struggle to survive. Declining richness is also detected in the terrestrial vegetation based on local sedaDNA analyses of the same core (Liu et al. 2021), which is explained by increasing human impact via livestock and land use. This could also affect trophic conditions in the lake.

Inferring aquatic plant richness and composition using sedimentary ancient DNA improves our understanding of how richness and compositional change respond to environmental factors and, at the same time, provides a less sporadic picture of taxa assembly compared to macrofossil data (Parducci

et al. 2015; Bishop et al. 2018). From our results we conclude that high-latitude and high-elevation lakes are strongly susceptible to environmental change and macrophyte richness and composition are particularly sensitive to temperature, conductivity, and lake-level changes. According to our records, macrophyte diversity increased during the Late Pleistocene/Holocene transition due to a warming climate. Until today, warming has increased macrophyte diversity and abundance in arctic lakes which are also assumed to be a carbon sink counteracting the increased greenhouse gases. Tibetan lakes are more affected by mineral and nutrient concentrations, which restrict macrophytes to saline-tolerant taxa. However, further warming and increased human impact may exceed optimal temperatures and ion/nutrient levels leading to a decrease and putative loss of macrophyte taxa, which would have a positive feedback to climate warming. This will eventually threaten the health of these important freshwater ecosystems and their function as freshwater resources in these remote areas.

Data availability statement

Environmental meta data related to sediment surface samples from the lakes investigated are available at PANGAEA (<https://doi.pangaea.de/10.1594/PANGAEA.920866>). Raw DNA sequence data, reference databases and scripts to analyze metabarcoding data from sediment surface samples can be downloaded from Dryad repository (<https://doi.org/10.5061/dryad.k6djh9w4r>). The final resampled macrophyte data from sediment surface and core samples are provided as Supplementary data (final_macrophyte_DNA_data.xlsx).

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Conflict of Interest

None declared.

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