

The link between climate change and biodiversity of lacustrine inhabitants and terrestrial plant communities of the Uvs Nuur Basin (Mongolia) during the last three millennia

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Abstract

The paper is focused on changes in biodiversity, the environment, and human activity in the Uvs Nuur Basin during the last three millennia based on biological and geochemical proxies from the lake Bayan Nuur. Regions with high biodiversity and relatively low anthropogenic pressures are typically the most vulnerable to both climate change and human activities. One such area is the Uvs Nuur Basin located on the north of the Great Lake Depression of Mongolia. The main objective of this study is to assess changes in the past biodiversity of the lake's microflora and microfauna, and surrounding vegetation biodiversity in the Uvs Nuur Basin, and to determine the main drivers of diversity change. Based on the analysis of pollen and chironomids we conclude that the most humid and afforested phase was between 1400 and 1800 CE. We assume that the Little Ice Age in the Uvs Nuur Basin was humid with mean annual precipitation ca. 305 mm/year and mean July temperature about 13°C. Conversely, the warmest and most arid period was between 650 and 1350 CE with mean annual precipitation ca. 280 mm/year and mean July temperature of about 16°C, attributed to the Medieval Warm Period. The biodiversity of terrestrial plants, chironomids, and Cladocera positive react to changes in annual precipitation and July temperature, whereas diatoms do not correlate directly to the climatic factors. The diversity and the evenness of plants are strongly correlated with the change in the leading biomes. The calculated species turnover suggests no significant changes in plant and Cladocera taxa composition, but significant changes in diatom and chironomid communities. This may be explained by the instability of lake ecology due to the fluctuation of the salinity and acidity of the water. An additional aim was to assess if dung fungi in lacustrine sediments reflect changes in human population density around the lake. We found that neither historical sources of human presence nor the influx of coprophilous fungi are correlated with the inferred climate changes. Coprophilous fungi can be used as individual or additional sources of assessment for the peopling and human-related herbivore density including overgrazing of the studied area.

Keywords

anthropogenic activity, biodiversity, chironomids, Cladocera, diatoms, dung fungi, late-Holocene, LIA, Mongolia, paleoclimate, pollen

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Introduction

The issue of global biodiversity decline has recently been actively discussed in both scientific and public communities (Engels et al., 2020; Tilman et al., 2012; WWF, 2016). Regions with high biodiversity are of interest for investigations on the biodiversity change and causes that affect biodiversity. Such regions are typically the most vulnerable to both climate change and human activities.

The Uvs Nuur Basin located in the north of the Great Lake Depression of Mongolia is an UNESCO World Heritage because it includes the major biomes of Central Asia with corresponding high floral and faunal diversity. The Uvs Nuur Basin is also unique in different forest types and vegetation that are highly specialized for high altitudes, alpine tundra, and dryland ecosystems, including species and communities adapted to saline conditions (Uvs Nuur Basin, 2003).

Since the 1990s, processes related to human activities (logging and overgrazing) have become the most important factors

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changing the landscapes and biota of this region (Hilker et al., 2014; Uvs Nuur Basin, 2003). At the same time, there are studies suggesting that mainly recent climate change has caused desertification and biodiversity loss in Mongolia (Hoshino et al., 2009). Assessment of the current biodiversity of the neighboring Russian Altai also revealed the strong climate dependence of this indicator (Chytry et al., 2017). However, both climate and human activities are expected to affect biodiversity change.

The degree to which present-day biodiversity is impacted by climate change is difficult to assess because of the short history of observations. An approach that helps to clarify the impact of climate on biodiversity could be an estimate of past diversity and simultaneous quantitative reconstruction of climate. An important criterion for such a study is the high resolution of the paleorecords. Lake sediments containing proxies such as pollen and remains of organisms that lived in the lake can be analyzed using statistical methods and at a high resolution. Lake paleorecords are the most appropriate objects for studying past biodiversity and factors acting on biodiversity.

The taxonomical composition of lacustrine biotas such as diatoms, chironomids, and cladoceran can provide valuable information not only about environmental changes in the lakes but also about biodiversity changes and species turnover over time (Frolova et al., 2013; Nazarova et al., 2020; Smol et al., 2005; Syrykh et al., 2017). Pollen data is an important proxy for studying the terrestrial vegetation biodiversity over long time scales (Birks et al., 2016; Felde et al., 2016, 2020; Giesecke et al., 2019; Jackson and Blois, 2015; Rudaya et al., 2020). Pollen as fossil data provides also important information about long-term fluctuations, non-linear responses, time-lags, stability, and the resilience of ecosystems for human land use and climate change (Rudaya et al., 2016; Willis et al., 2010; Zhilich et al., 2017).

Even though many climatic reconstructions of the Holocene in Mongolia and Central Asia have been published (Felauer et al., 2012; Feng et al., 2013; Gunin et al., 1999; Peck et al., 2002; Rudaya et al., 2009; Sun et al., 2013; Tian et al., 2014; Unkelbach et al., 2017, 2019, 2020, etc.), there is no uniform picture of the climate history and vegetation successions in the region. This was demonstrated in the recent excellent review by Klinge and Sauer (2019). Reasons for these inconsistencies include the complex structure of landscapes in the territory, microclimatic variability, insufficient dating of records, and different resolutions of sampling. ^{14}C -dating from most of the Mongolian lakes have a reservoir effect caused by old carbon that is not considered by age-depth construction in any case. The dating error derived from the reservoir effect particularly occurs in the upper part of the records for the last millennia. Furthermore, the last millennia are often considered in the context of the entire Holocene record and are studied at low resolution in comparison with other Holocene periods (Rudaya et al., 2009; Tian et al., 2014).

A further issue related to the estimation of past and present biodiversity change relates to the impact of human activity on it. It is also difficult to estimate the human impact on the environment of the Uvs Nuur Basin over the last three millennia since there is limited historical and archaeological evidence of human presence.

The eastern part of Uvs aimag (province) remains under-researched archaeologically, even though many researchers have passed through the area since the expedition of Potanin in the second half of the 19th century CE (Potanin, 1948). There is also little data on the population density of the Uvs Nuur Basin during the late-Holocene. Only archaeological sites in Khovd and Bayan-Ulgii aimags and the western part of Uvs aimag have been explored relatively well where many sites of Paleolithic, Bronze, Early Iron, and Middle Ages have been found (Derevyanko et al., 1990; Iderkhangay, 2017; Novgorodova, 1989; Volkov, 1967;

Yevtyukhova, 1952). In the eastern part of the Uvs Nuur Basin the number of burial, ritual, and settlement-related sites, presumably dating to the late Paleolithic until the Hunnu periods, has been registered but not investigated in detail by participants of the Mongolian-American research project in 2015–2016 (Barton, personal communication).

In this study, we focus on changes in biodiversity, environment, and human activity in the Uvs Nuur Basin during the last three millennia. The main objective is to assess changes in the biodiversity of the lake's microflora and microfauna, and surrounding vegetation biodiversity in the Uvs Nuur Basin, and to determine the main drivers of diversity change (e.g. climatic, human-induced). A related task is to check whether the total abundance of dung fungi in lacustrine sediments reflects changes in population density around the lake. Archaeological and historical evidence is used as a source of human population density. We consider the fluctuation of coprophilous fungi influx and concentration as an indicator of grazing intensity and hence evidence of human activity in the area.

Site setting

Bayan Nuur (49.98 N, 93.95 E, 932 m a.s.l.) is part of the Uvs Nuur Basin, and is one of the northern lakes in the Great Lake Depression of Mongolia (Figure 1). It is located in the north of the Boorog Deliyin Els dunes in Zuun Govi Soum, Uvs aimag. The lake fills a graben depression which is created by a fault that runs SW-NE through the inner basin (Paul, 2012). Khan Khokhiyn Ridge separates the Uvs Nuur Basin from the Khirgis Nuur Basin in the south and the Tannu-Ola Mountains that are located in the north. The high elevated Turgen-Kharkhiraa Mountain system lies in the northernmost part of the Mongolian Altai and is situated southwest of the Uvs Nuur Basin. Dunes stretch about 200 km in an ESE direction in adaptation to the prevailing wind system, seasonally strong westerlies (Grunert and Lehmkuhl, 2004).

The Bayan Nuur has only one inflow, the Khoit-Gol, a tributary of the Narin-Gol which rises in the East Tannu-Ola Ridge, and one outflow, the Tsagaan-Gol. The climate is continental, with a mean annual precipitation of about 200 mm at an altitude of 2000 m a.s.l., and ca. 400 mm in the high mountain areas, whereas precipitation in the basin is less than 100 mm per year. Around Bayan Nuur maximum rainfall takes place in July (74 mm/year) and in August (58 mm/year), and precipitation is lowest in January and February, at 8, and 7 mm/year, respectively (SamSamWater, 2020). The rain shadow of the Altai and Sayan Mountains in the northwest strongly contributes to the aridity of this area by capturing precipitation from the westerlies (Klinge and Sauer, 2019; Rudaya et al., 2009).

The mean annual temperature is 3.7°C. The climate is characterized by very cold dry winters ($T_{\text{Jan}} = -32.5^\circ\text{C}$) with a minimum temperature of -56°C and relatively warm summers ($T_{\text{Jul}} = 19.5^\circ\text{C}$) (Ulaangom meteorostation; National Atlas of Mongolian People's Republic, 1990). The study lake is located close to the southern limit of the permafrost that extends until 47°N in Northwestern Mongolia.

Bayan Nuur is a freshwater oligo- to mesotrophic lake. The maximal depth of the lake is 29.2 m with an average of 10.2 m; the open water area is 32 km² (Tian et al., 2014). Other modern water features of Bayan Nuur are given in Supplemental Table S1. The bottom of the lake consists of muddy, calcareous sediments. From the shallow epilittoral down to the sublittoral, the bottom is covered by a dense carpet of Characeae, *Stuckenia pectinata*, *Myriophyllum spicatum*, and *Najas marina* ssp. *intermedia*. The *Chara* species have thick lime coverings due to strong biogenic calcite precipitation. *Phragmites australis* grows only sparsely at a few sites (Paul, 2012).

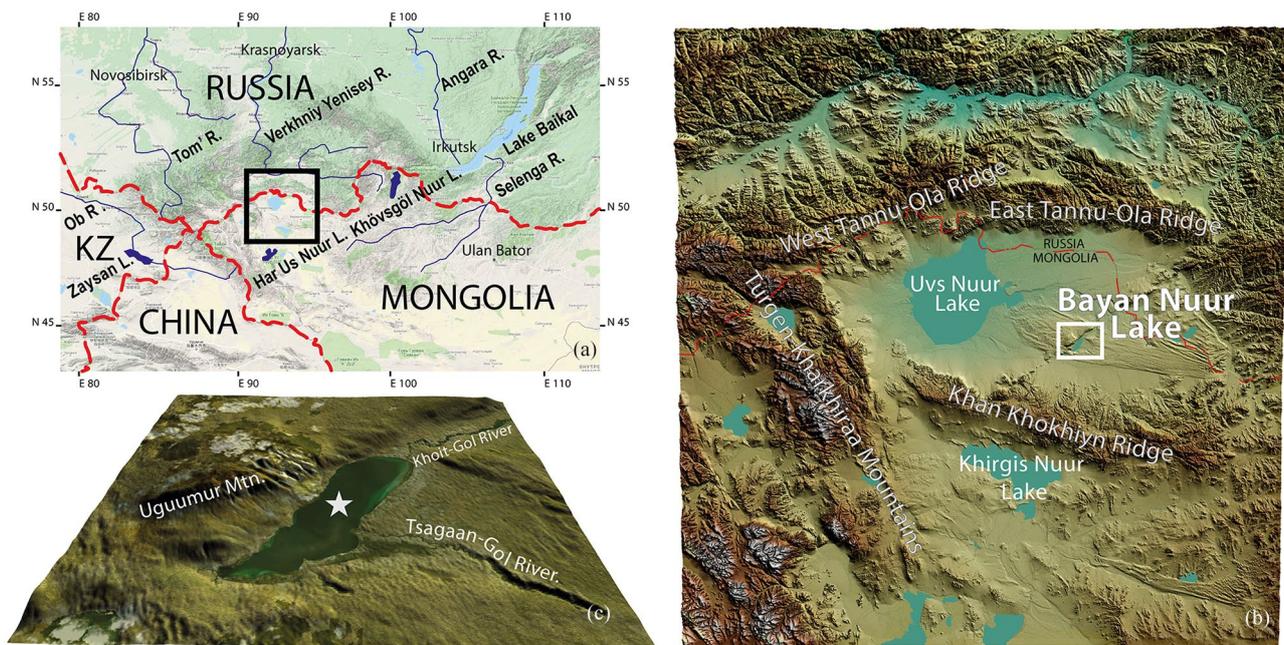


Figure 1. Map of the study area. (a) Overview map. (b) Geographical setting of the Uvs Nuur Basin. (c) Map of Bayan Nuur. Star marks a coring site.

Modern phytoplankton is taxonomically and functionally diverse. It is characterized by a co-dominance of Dinophyta, Bacillariophyceae (with the dominance of *Pantocsekiella ocellata*, *Fragilaria ulna*, *Cyclotella radiosa*) and Cyanobacteria. Chrysophyceae, Chlorophyceae, and Cryptophyta are subdominant groups. The benthic cladoceran fauna consists of *Alona affinis*, *A. quadrangularis*, *Scapholeberis rammeri*, *Iliocryptus sordidus*, and *Rhynchotalona falcata* (Paul, 2012).

The species-rich zoobenthos is dominated by oligotrophic Ephemeroptera, Gastropoda, Hirudinea, *Gammarus lacustris*, and mesotrophic and phytophilic Chironomidae (*Ablabesmyia monilis*, *A. phatta*, *Psectrocladius sordidellus*, *Chironomus tentans*, *Cryptochironomus supplicans*, *Endochironomus tendens*, *Polypedilum nubeculosum*, *Xenochironomus xenolabis*, *Cladotanytarsus* sp., *Paratanytarsus dimorphus*, *P. inopertis*, *Tanytarsus glabrescens*) (Paul, 2012).

Bayan Nuur belongs to the Uvs Nuur desert-steppe district of the North-Gobi desert-steppe botanical province (Yunatov, 1950). Around the lake, dunes are covered by steppe vegetation. Wormwood and wormwood-grass steppe with *Artemisia arenaria*, *Agropyron cristatum*, and *Stipa capillata* cover the small interdune depressions. *Caragana bunge* grows on the borders of the sand massive, with undergrowth of *Eragrostis minor*, *Salsola ruthenica*, *Cardiospermum*, and *Agropyron cristatum*. *Elymus giganteus*, *Hedysarum mongholicum*, and *Pugionum dolabratum* grow on the top of dunes and the downwind slopes. Larch forest spreads above the steppe mountain belt on the ridges of Kharkhiraa and Turgen. Alpine meadows and small patches of moss tundra are typical in the alpine belt of Kharkhiraa and Turgen. Larch, mixed larch, and Siberian pine forests are abundant on the northern slope of the Khan Khokhiyn Ridge. Desert steppe spreads across the lower part of the southern slope of Tannu Ola, which is replaced by steppe above 1500 m a.s.l. Between 1500 and 2300 m a.s.l. small patches of larch forest have developed, sometimes with *Pinus sibirica* and *Picea*. The alpine belt of Tannu Ola is characterized by mountain tundra (Namzalov and Mongush, 2010).

The modern ecosystems of the Uvs Nuur Basin suffer from overgrazing. The livestock population increased by 2.5–4 times between 2002 and 2012 leading to a decline in vegetation density. There are roughly 2 million units of livestock in the Uvs Nuur Basin (Hilker et al., 2014).

Data and methods (detailed description of methods in Supplemental Material I)

Coring and age-depth modeling

A 112-cm-long sediment core (BN2016-1) was obtained from a small platform using a 60-mm gravity corer UWITEC in August 2016. The core location (50.01072N, 93.97450E) was in a water depth of 29 m at the deepest part of the lake. Six AMS radiocarbon measurements for bulk sediment samples were used for the age modeling (Supplemental Table S2).

Stable carbon isotopes and total organic carbon (TOC) for bulk sediments

We measured TOC (39 sediment samples) and $\delta^{13}\text{C}$ (42 samples) from the BN2016-1. The sediment samples were leached by 0.5 N HCl to remove inorganic carbon, then washed with distilled water and freeze-dried. The TOC and $\delta^{13}\text{C}$ were measured using the (IRMS) Delta V Advantage with EA 2000 HT.

Pollen analysis

A total of 94 samples were used for pollen and non-pollen palynomorphs analysis (Supplemental Appendix 1). The samples were chemically treated according to the methodology suggested by Faegri and Iversen (1989). In the pollen diagram, dung fungi *Sordaria*, *Sporormiella*, and single coprophilous Ascomycetes (*Podospora* and *Gelasinospora*) are combined in one group, “coprophilous fungi.” The coprophilous fungi were calculated in the pollen slides simultaneously with pollen.

Diatom analysis

Twenty-five samples from the sediment core BN2016-1 were processed for diatom analysis in the range from 0 to 110.4 cm (Supplemental Appendix 2). The pH and total phosphorus ($\mu\text{g/l}$) values were reconstructed using the European diatom algae database (Battarbee et al., 2001). The trophic status was assessed according to the reconstructed value of total phosphorus (Reynolds, 2003). Biogeographical and ecological characteristics of the taxa concerning preferences of habitat, pH, water salinity, geographical

distribution were described following Van Dam et al. (1994) and Barinova et al. (2006).

Chironomid analysis

A total of 42 samples were studied for chironomid analysis (Supplemental Appendix 3). Treatment of sediment samples for chironomid analysis followed the standard techniques described in Brooks et al. (2007).

Cladocera analysis

Twenty-five samples were prepared for cladoceran analysis using the methods described in Korhola and Rautio (2001) (Supplemental Appendix 4). The chitinous remains of cladoceran were identified with both subfossil (Frey, 1959, 1973; Szeroczyńska and Sarmaja-Korjonen, 2007) and modern (Flössner, 2000; Kotov et al., 2010) cladoceran identification keys. Cladocera were subdivided into two groups based on their habitats (planktonic and benthic).

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

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 the late Quaternary pollen data of Europe and Asia (Tarasov et al., 1998; Tian et al., 2018). 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.

Estimating of diversity of aquatic and pollen-assemblages. Comparison of multivariate datasets of bioproxies

To evaluate the similarity or dissimilarity of aquatic (lacustrine) and pollen assemblages, and their response to environmental changes, different datasets were compared using the statistical methods applied in modern species ecology. The richness and diversity of all bioproxies (pollen, diatoms, cladoceran, and chironomids) were calculated as the effective taxon numbers N_0 (total taxa richness), N_1 (common taxa richness), and N_2 (dominant taxa richness) proposed by Hill (1973). Evenness (E) was calculated as the N_2/N_0 ratio (Hill, 1973; Jost, 2007).

We evaluated the similarity in temporal evolutions among pollen, diatom, chironomid, and cladoceran 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.

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, scaled in standard deviation (SD) units for each taxonomic group (according to Birks, 2007). The change in weighted average (WA) sample scores reflects compositional change or turnover in SD units along the temporal gradient (Felde et al., 2020).

Method for quantitative reconstruction of mean July air temperatures (T_{July}) and the amount of annual precipitation (PANN)

Mean T_{July} temperatures were inferred using a model based on a modern calibration data set of 193 lakes and 162 taxa from East

and West Siberia (Nazarova et al., 2015). Mean T_{July} of the lakes for the calibration data set was derived from New et al. (2002). Chironomid-based reconstructions were performed in C2 version 1.7 (Juggins, 2007).

In this study, the 808 modern pollen sites 1000-km around Bayan Nuur (Supplemental Figure S1) were selected to establish pollen-climate calibration-sets (Cao et al., 2014, 2020). A quantitative PANN reconstruction was performed using the WAPLS function in rioja package version 0.7-3 (Juggins, 2012) for R (R Development Core Team, 2018) with square-root transformed pollen data.

Results and interpretation

Chronology of the BN2016-1

The age-depth includes five dates, however, one date 2258 ± 57 14C years BP from the depth of 32 cm seems to be an outlier because it is too old (Supplemental Figure S2). The average sediment accumulation rate is estimated at 0.37 mm/year. The reservoir effect calculated as 736 years was subtracted from the age-depth model. According to Paul (2012), bottom samples from Bayan Nuur are rich in calcium carbonate that may be a source of old carbon and the reason for the reservoir effect. Core BN2016-1 covers the last 2885 cal. years BP.

TOC, $\delta^{13}\text{C}$ of TOC

The composition of organic matter (TOC, $\delta^{13}\text{C}$) in lacustrine sediments is a powerful tool for reconstructions of lake environments and climate fluctuations. In lacustrine sediments, organic matter is comprised of detritus which arises from terrestrial and aquatic vascular plants and algae, as well as other organic producers (cladoceran, chironomids, etc.). Carbon isotopic compositions indicate changes in lake productivity and carbon recycling (Meyers and Ishiwatari, 1993).

The mean value of TOC in the BN2016-1 is 4.46 ± 0.8 wt% ($n=39$; Supplemental Appendix 5). The content of TOC throughout the core is relatively high when compared with some other Central Asian lake records. The late-Holocene section of the high mountain Hoton Nuur record (Mongolian Altai; 2083 m a.s.l.) reveals the mean value of TOC in 1.2% (Rudaya and Li, 2013) and from Lake Teletskoye (Russian Altai, mountain taiga, 434 m a.s.l.) – 0.88% (our data). The TOC contents of the surface sediments from the five lakes located in the hyper-arid Badain Jaran Desert (China) are 0.03%–1.01% (Dong et al., 2018).

The $\delta^{13}\text{C}$ values of bulk samples from BN2016-1 vary between -26.4‰ and -20.4‰ , with a mean of $-23.2\text{‰} \pm 1.2\text{‰}$ ($n=42$) (Figure 2b) and reveal several phases: at depths of 112–65 cm (ca. 2885–1470 year BP) the average $\delta^{13}\text{C}$ is -23.05‰ ; at depths of 65–43 cm (ca. 1470–1075 year BP) – -21.75‰ ; at depths of 43–12 cm (ca. 1075–340 year BP) – -23.89‰ ; 12–1.2 cm (1775–1966 CE) – -26.1‰ (Figure 2b). Maximal values of $\delta^{13}\text{C}$ coincide with minimums of TOC (Supplemental Appendix 5). The lowest TOC value occurs about 1400 CE, probably indicating diminished bioproductivity due to the cold climate. The lightest values of $\delta^{13}\text{C}$ (av. -26.1‰) during the last ca. 200 year are for the most organic-rich phase in the BN2016-1.

Rudaya and Li (2013) reported that the average $\delta^{13}\text{C}$ value measured in pollen samples of Hoton Nuur record of the taiga-biome group is $-27.85\text{‰} \pm 2.01\text{‰}$ whereas the average $\delta^{13}\text{C}$ value of samples from the steppe biome group is heavier, at $-25.50\text{‰} \pm 3.43\text{‰}$.

Smith and Epstein (1971) demonstrated that aquatic, desert, and salt marsh plants have the highest $\delta^{13}\text{C}$ values (-6‰ to -19‰). Low $\delta^{13}\text{C}$ values (-24‰ to -34‰) have high plant species from different ecological groups mostly with mesophytic features. The algae have generally intermediate $\delta^{13}\text{C}$ values (-12‰ to -23‰).

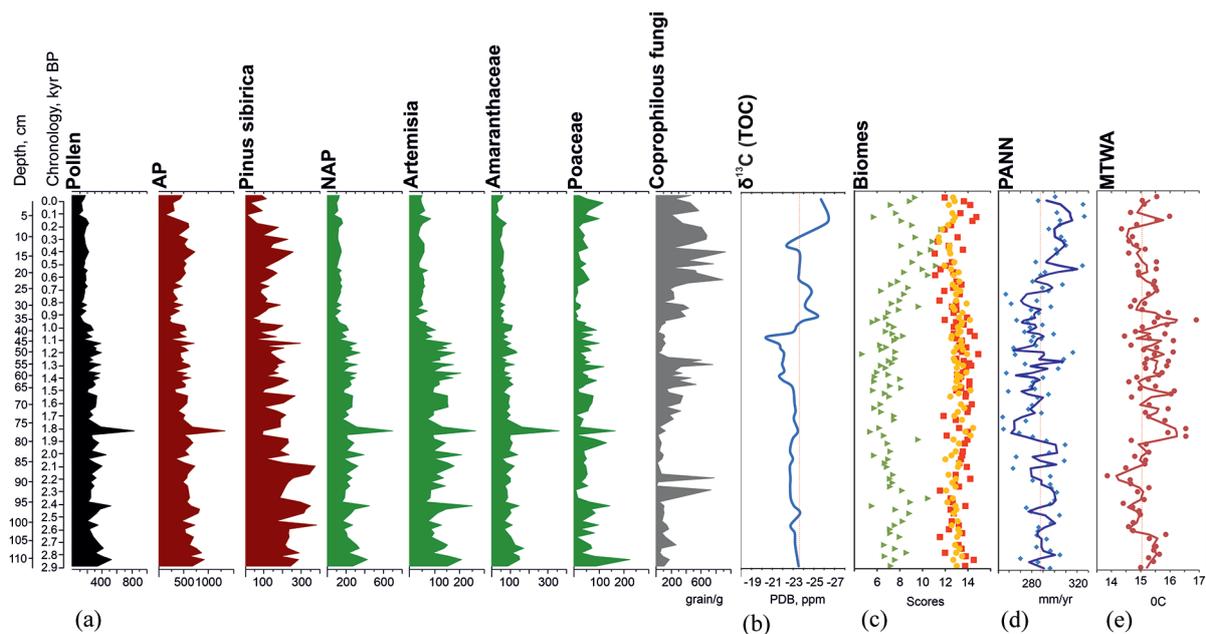


Figure 2. Main reconstructed parameters for the core of the lacustrine bottom sediments of Bayan Nuur. (a) Pollen and coprophilous fungi concentrations. (b) Fluctuations of the $\delta^{13}\text{C}$ ratios of TOC. (c) Biomization of the pollen data (orange dots: STEPPE scores; yellow dots: DESERT scores; green dots: TAIGA scores). (d) Reconstruction of the amount of annual precipitation based on the pollen data. (e) Reconstruction of the July temperatures based on the chironomid data.

Modern bottom and sublittoral aquatic plants from northwestern Mongolian lakes are represented by *Chara* spp. and *Stuckenia pectinata* (Dgebuadze, 2014). The $\delta^{13}\text{C}$ of their species varies between -10.11‰ and -16.8‰ and between -6.61‰ and -15.29‰ , respectively (Liu et al., 2018).

The heavier values of the $\delta^{13}\text{C}$ ratios in BN2016-1 may reveal periods when the spread of littoral zones covered by macrophytes under the dry climate. The additional source of heavier $\delta^{13}\text{C}$ is desert terrestrial plants.

Pollen and biome reconstruction

The sampling resolution of the pollen spectra is, on average, 40 years/sample. The pollen diagram is subdivided into seven pollen zones (PZ) based on changing pollen taxa composition and abundances (Figure 3, Supplemental Appendix 1). Concentration curves are added for several important taxa (*Pinus sibirica*, *Artemisia*, Amaranthaceae, and Poaceae) (Figure 2a). Concentration is a more independent indicator that is calculated exclusively by the weight of samples and the amount of *Lycopodium* spores. The qualitative interpretation of the pollen diagram is supported by the quantitative reconstruction of the dominant biomes (Figure 2c, Supplemental Table S3).

PZI (112–95 cm; 2885–2380 year BP) is characterized by high percentages of Amaranthaceae and *Artemisia*. The concentration and percentages of *Pinus sibirica*, *Artemisia*, Amaranthaceae, and Poaceae pollen are highest throughout the record (Figure 2a). The dominant biomes are STEPPE and DESERT, however, in the upper part of PZI TAIGA scores start to increase, with the highest peak at the upper border of PZI (ca. 2380 year BP).

The percentages of *Artemisia* significantly increase in PZII (95–80 cm; 2380–1910 year BP). *Ephedra* pollen percentages and pollen concentrations slightly decrease. The STEPPE biome dominates over DESERT, and TAIGA scores decrease to the minimum.

PZIII (80–74 cm; 1910–1725 year BP) shows a distinct sharp decrease of *Artemisia* and an increase of Amaranthaceae and *Ephedra*. This zone is characterized by the highest total concentration and peaks of concentration for *Pinus*, *Betula*, *Ephedra*,

and Amaranthaceae. The highest scores for the DESERT biome (13.7) belong to this PZ.

PZIV (74–40 cm; 1725–1020 year BP) is characterized by the return of percentages of *Artemisia*, Amaranthaceae, and *Ephedra* to previous limits, as in PZII. The lowest percentages of Cyperaceae are in PZIV, at least up to the depth of 48 cm (ca. 1160 yr BP). The concentration of *Artemisia* and Amaranthaceae decreases from the upper border of this zone, onwards. DESERT scores decrease and STEPPE becomes dominant.

PZV (40–20 cm; 1020–570 year BP) has the highest percentages of Amaranthaceae and gradually decreases in *Artemisia*. Cyperaceae returns to a similar abundance to PZI, PZII, and PZIII. *Ephedra* and *Betula* pollen start increasing at a depth of 36 cm (ca. 945 year BP) and of 28 cm (ca. 775 year BP), respectively. The concentration of *Pinus* spp., *Betula*, and Poaceae noticeably increases. The dominant biomes are STEPPE and DESERT.

PZVI (20–6 cm; 570–200 year BP) is characterized by the lowest amount of *Artemisia*, and higher percentages of arboreal pollen, especially *Pinus* and *Betula*. At the depth of 12 cm (340 year BP) *Ephedra* pollen slightly decreases. Biomization reveals the highest score for TAIGA (9.9) that starts to increase greatly throughout the core between ca. 570 and 210 year BP.

The upper PZVII (6–0 cm; 200–0 year BP) is distinguished by a sharp increase of *Artemisia* and Poaceae percentages, however, the concentration of *Artemisia* is at the same level. STEPPE scores significantly increased and TAIGA scores decreased.

Coprophilous fungi

Only two genera were identified by pollen analysis (*Sporormiella* and *Sordaria*) in high abundances; *Podospora* and *Gelasinospora* were found in single spores. Concentrations and abundances of the coprophilous fungi have high values at 94–86 cm (2300–2200 year BP), 74–52 cm (1725–1250 year BP), and 30 cm (820 year BP), with maximal concentration after ca. 620 year BP. Very low or low concentrations are recorded between 2070 and 1790 year BP and 1200–950 year BP (Figures 3a and 5; Supplemental Figure S3). The calculation of the influx (cm/year) shows

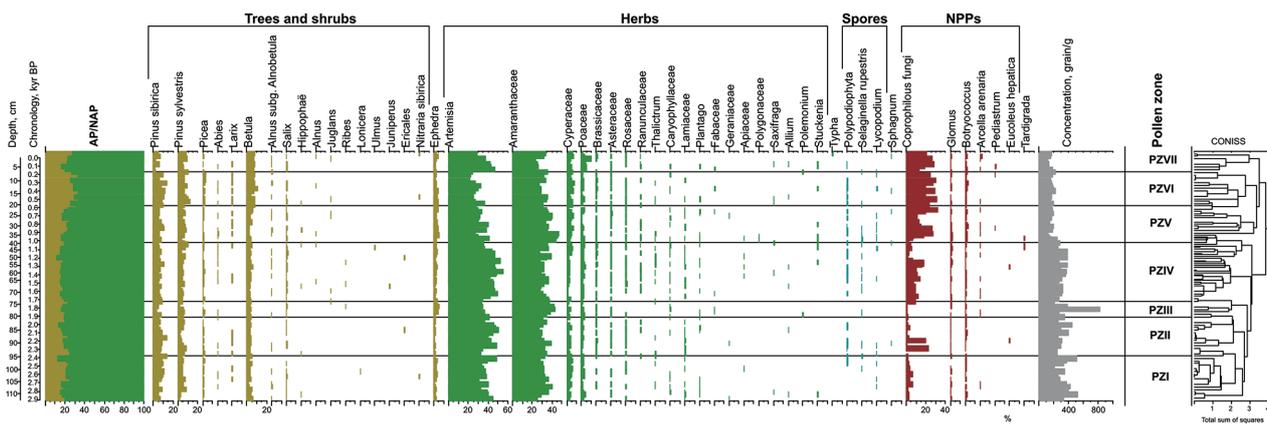


Figure 3. Pollen diagram for the Bayan Nuur sediments.

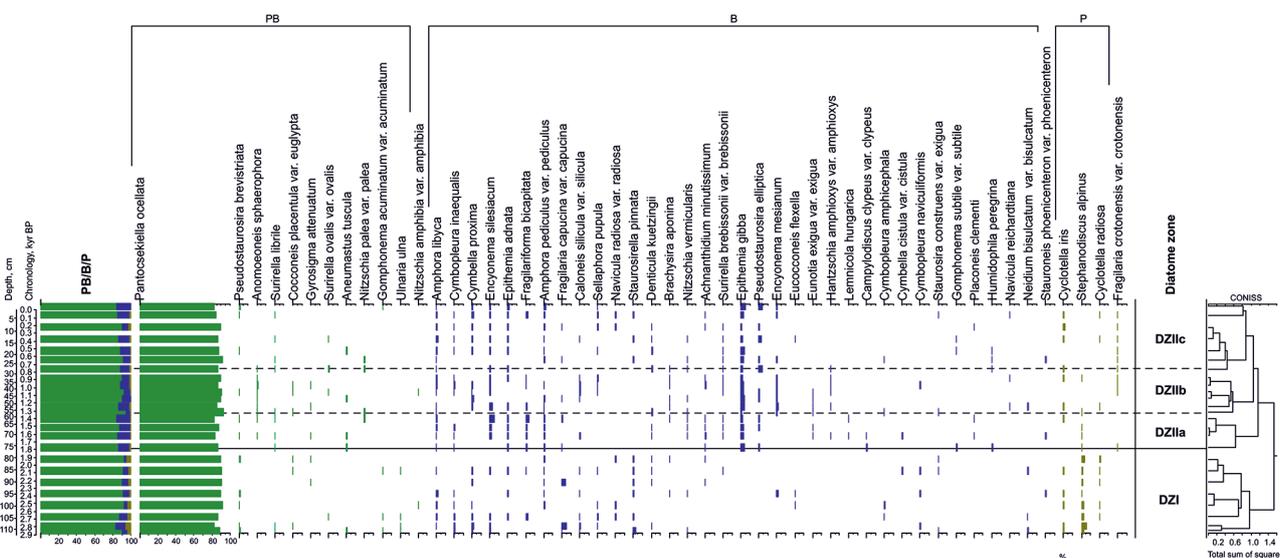


Figure 4. Diatom diagram for Bayan Nuur sediments.

a slightly different picture. The highest peak is 1290 year BP and the highest values are between 1450 and 1250 year BP; there are two peaks at 2285 and 2190 year BP, and increased values are calculated for the interval between 930–820 year BP and 620–400 year BP.

Diatoms

We identified 66 diatom taxa (Supplemental Appendix 2) in BN2016-1; however, only 10 have been found at abundancies $\geq 2\%$ (Figure 4). The planktonic-benthic species *Pantocsekiella ocellata* dominates throughout the entire record with a mean abundance of 87%. The paleorecord is divided into two diatom zones (DZ).

DZI (110.4–75 cm; 2840–1755 year BP). The dominant species is *Pantocsekiella ocellata*; the subdominants are the benthic *Fragilaria capucina* var. *capucina* and planktonic freshwater *Stephanodiscus alpinus*. A slight increase in planktonic-benthic species and a gradual decrease in benthic species were noted within DZI. This may indirectly indicate a gradual increase in the water level of the lake. A notable proportion of valves of flowing water diatoms such as *Eucoconeis flexella*, *Denticula kuetzingii*, *Neidium bisulcatum* var. *bisulcatum* suggest an effect from the river runoff into the lake. Indifferent species prevailed, but several halophob-acidophilic species (*Staurosira construens* var. *exigua*,

Eunotia exigua var. *exigua*) and halophilic-alkaliphilic species (*Amphora libyca*, *Staurosirella pinnata*, *Sellaphora pupula*) were also found. The arctic-alpine mezogalobic *Eucoconeis flexella* is found at about 2500–2400 year BP.

We recorded in DZIIa (75–56 cm; 1755–1310 year BP) an increase in the benthic species, and species preferring standing water. That may indicate a decrease in water level and reflect the formation of the lake with shallow littoral. An increase of halophob *Fragilariforma bicapitata* and acidophilic *Eunotia exigua* reflects the waterlogging of the littoral. A slight increase in the species developing on aquatic vegetation is recorded. *Amphora pediculus* var. *pediculus* and epiphytic *Epithemia gibba*, which can grow on *Phragmites* (Müller, 1999), appears for the first time and is then present continuously in DZII.

DZIIb (56–27 cm; 1310–750 year BP) is characterized by the highest number of species; increased percentages of planktonic and planktonic-benthic valves and an increase in thermophilic species and species that are indicators of flowing waters. The halophob species decrease; halophilic, including *Anomooneis sphaerophora*, species are noted. This reflects the higher salinity and productivity of the lake under climate warming.

DZIIc (27–0 cm; 750–0 year BP) is characterized by an insignificant increase of benthic and decrease of planktonic species; the disappearance of thermophilic *Anomooneis sphaerophora* and *Planolithidium borneolanceolatum*. An increase in halophob

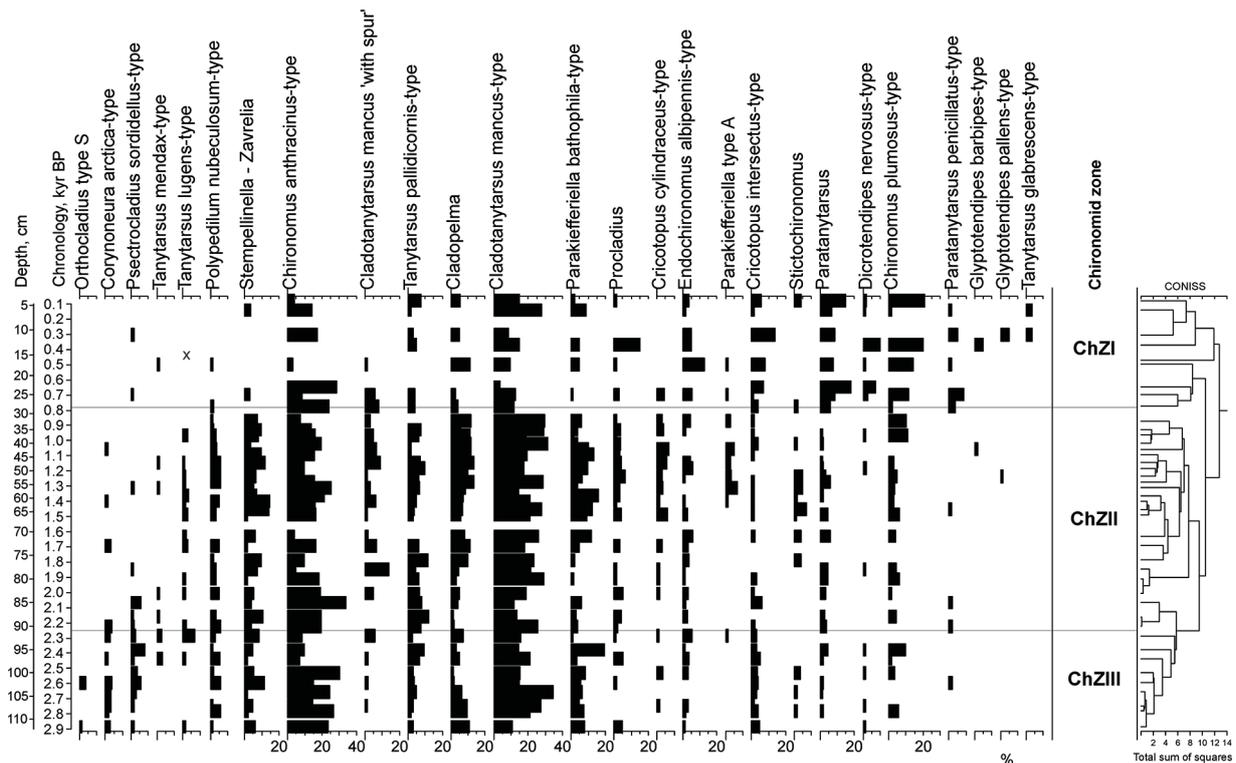


Figure 5. Chironomid diagram for Bayan Nuur sediments.

Cymbella proxima and *Fragilariforma bicapitata*; the disappearance of the Mediterranean *Brachysira aponina* and reappearance of the arctic-alpine *Eucoconeis flexella* reflect climate cooling and the desalinization of lake water.

Reconstructed pH fluctuates between 8.38 and 8.44. Total phosphorus shows an increased interval between 1400 and 600 year BP, which may indicate the eutrophication of the lake under a relatively warm climate.

Chironomids

We identified 60 chironomid taxa (Supplemental Appendix 3). The down-core changes in the chironomid assemblages led to the identification of three chironomid zones (ChZ) (Figure 5).

ChZI (112–90 cm; 2885–2220 year BP). Chironomid communities are dominated by eurytopic taxa indicative of cool conditions. The highest abundances include the *Cladotanytarsus mancus*-type and *Chironomus anthracinus*-type. *C. anthracinus* is a ubiquitous taxon mostly confined to the profundal but can also be found in the littoral. It is tolerant of low oxygen concentrations, pH, and high salinity. *Chironomus* species are often early colonizers after significant environmental changes and can withstand suboptimal conditions (Brooks et al., 2007; Stief et al., 2005). Abundances of *Cladotanytarsus mancus*-type, which is typical in the littoral of productive lakes and can tolerate acidic conditions, increase until 104 cm (ca. 2655 year BP) and strongly decline thereafter. Several other littoral taxa, some of which can be found in lotic environments, have noticeable abundances until 104 cm and also decline shortly after this: *Cladopelma*, photophilic *Cricotopus intersectus*-type, *Corynoneura arctica*-type, *Tanytarsus mendax*-type, acid-tolerant *Psectrocladius sordidellus*-type, and shallow water *Stempellinella – Zavrelia*.

ChZII (90–27 cm; 2220–750 year BP). Abundances of cold-tolerant *Chironomus anthracinus*-type vary considerably throughout this zone. The strong decline of the *C. anthracinus*-type around 97–92 cm (2440–2285 year BP), 70.8 cm (1560 year BP), 51.6–46.8 cm (1235–1145 year BP), and 15.6–13.2 cm (460–370 year BP) alongside with the increase of some taxa characteristic for

warmer conditions (*Tanytarsus mendax*-type, *T. pallidicornis*-type, *Psectrocladius sordidellus*-type, *Parakiefferiella bathophila*-type) indicate climatic amelioration. High abundances of the *Chironomus anthracinus*-type between 90 and 80.4 cm (ca. 2220–1920 year BP), 58.8–56.4 cm (ca. 1360–1310 year BP), and around 39.6–37.2 cm (ca. 1010–965 year BP) suggest slight cooling. Cooling between 60 and 55 cm (ca. 1380–1290 year BP) is further supported by the appearance of cold-stenotherm *Parakiefferiella triquetra*-type and *Parakiefferiella* type A.

Between 60 and 27 cm (ca. 1380–750 year BP) several lotic taxa have the highest abundances in the entire core: *Stictochironomus*, *Cladopelma*, *Parakiefferiella* type A and *P. triquetra*-type, *Cricotopus cylindraceus*-type, *Paratendipes*, and *Stempellinella – Zavrelia*. This prevalence of taxa preferring the littoral zones suggests that under varying climatic conditions, this period could be characterized by lower water levels. All these taxa strongly decline or disappear above 27 cm, which, alongside a sharp decline in the dominant littoral *Cladotanytarsus mancus*-type, could be a response to a rise in the water level and thus the flooding of the littoral zone of the lake.

ChZIII (27–0 cm; 750–0 year BP). Between 27.6 and 22.8 cm (770–646 year BP) abundances of the cold-tolerant eurytopic taxa *Chironomus anthracinus*-type and *Paratanytarsus penicillatus*-type increase considerably, indicating cooling.

Between 27 and 6 cm (750–200 year BP) *Chironomus plumosus*-type and other thermophilic taxa decline or disappear; cold-tolerant *C. anthracinus*-type and *Paratanytarsus penicillatus*-type became dominant again, reflecting climatic cooling. After 200 year BP the *C. anthracinus*-type is replaced by the thermophilic *C. plumosus*-type.

There is a short interval between 15.6 and 13.2 cm (435–370 year BP) that is characterized by the decline or disappearance of the cold-tolerant *P. penicillatus*-type. *Chironomus anthracinus*-type is replaced by a *C. plumosus*-type, which is indicative of warm conditions, alongside an increase in several other more thermophilic and eutrophic taxa (*Cladopelma*, *Procladius*, *Endochironomus albipennis*-type, *Dicrotendipes nervosus*-type, *Glyptotendipes barbipes*-type).

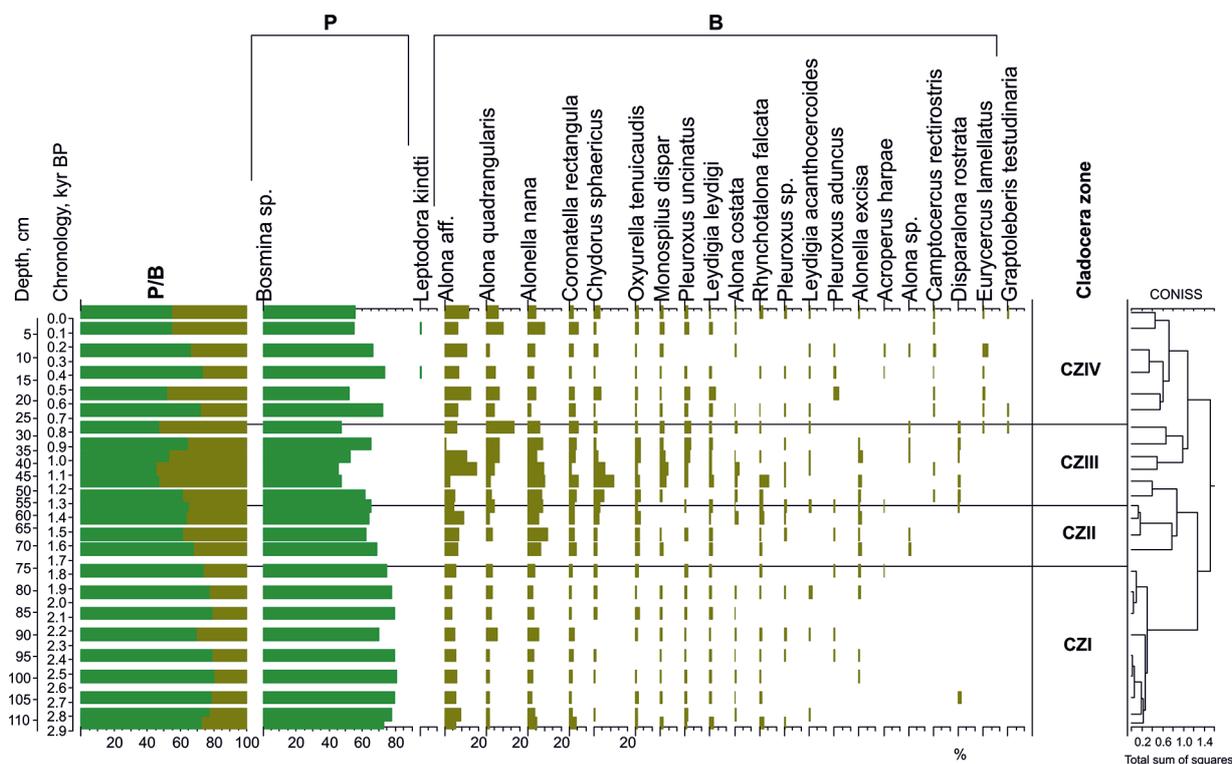


Figure 6. Cladocera diagram for Bayan Nuur sediments.

Cladocera

A total of 27 cladoceran taxa were identified in BN2016-1 (Figure 6; Supplemental Appendix 4). The paleorecord is divided into four Cladocera zone (CZ).

CZI (112–75 cm; 2885–1755 year BP) is characterized by the dominance of planktonic species *Bosmina longirostris*. The abundance of *B. longirostris* attains minimal occurrence (approx. 70%) close to the middle part of the zone (90 cm; 2225 year BP) and begins to increase afterwards. Simultaneously littoral taxa *Alona quadrangularis* and *Alonella nana* increase. Percentages and taxa composition suggest a higher water level in comparison with upper zones.

CZII (75–56 cm; 1755–1310 year BP). The most common taxon is *Bosmina longirostris*, which decrease slightly at 67 cm (ca. 1500 year BP). The abundance of littoral taxa increases. *Alonella nana*, preferred oligotrophic to mesotrophic water, increases distinctly in sandy littoral vegetation as well as *Alona affinis*, *Coronatella rectangularis*, *Chydorus cf. sphaericus*, and *Oxyurella tenuicaudis*. They are often associated with vascular plants and marginal vegetation (Bledzki and Rybak, 2016).

CZIII (56–27 cm; 1310–750 year BP) is characterized by a continuing decrease in *Bosmina longirostris* and by a distinct increase in *Alona affinis* in the middle of the zone. *Alona quadrangularis* increases sharply. *A. affinis* and *A. quadrangularis* are two taxonomically close species, however, *A. quadrangularis* seems to be restricted to soft mud, while *A. affinis* occupies the littoral near the bottom among vegetation (Flössner, 2000; Smirnov, 1999). *Chydorus cf. sphaericus* has maximal occurrence throughout the record close to the bottom of the zone (47 cm; ca. 1145 year BP) and begins to decline afterwards. Increased *C. cf. sphaericus* suggests that the lake had enhanced productivity (de Eyto and Irvine, 2001; Szeroczyńska, 1998). This is also indicated by the presence of mesotrophic *Pleuroxus uncinatus*, *Alona costata*, and *Disparalona rostrata* (Røen, 1995; Szeroczyńska, 1991). Indicators of bare littoral with sandy or muddy bottoms *Monospilus dispar*, *Rhynchotalona falcata*, and *Pleuroxus uncinatus* have their maximum in CZIII. The percentages of littoral taxa continue increasing and reach maximal values at 42 cm (ca. 1055 year BP).

CZIV (27–0 cm; 750–0 year BP) is characterized by a high variation of percentages of dominant *Bosmina longirostris* (50%–75%) and increase of pelagic taxa that suggests an increasing water level. Littoral *Alona affinis* increases slightly toward the top of CZIV. *Eurycerus lamellatus* appears in CZIV and has maximal occurrence in the middle. *E. lamellatus* inhabits the oligotrophic and eutrophic lake littoral with *Myriophyllum*, *Nymphaea*, *Nuphar*, and *Chara*. However, it may occur on plant-free bottoms together with another photophilic taxon, *Camptocercus rectirostris*. *Alonella nana*, *Alona quadrangularis*, and *Coronatella rectangularis* increase at the top of the zone (3.6 cm; 1890 CE) and begin declining afterwards, which suggests a decrease in the littoral.

Diversity and comparison of aquatic and terrestrial communities

Taxonomical richness (N_0) shows a trend to increase in species richness for pollen, diatoms, especially for cladoceran from the bottom to the top of the core; the total diversity N_0 of chironomids slightly decreases throughout the core (Figure 7).

The diversity of pollen common (N_1) and dominant (N_2) species decreases between ca. 2300 and 1100 year BP and increases between ca. 670 and 200 year BP, which correlates well with the decrease in TAIGA biome scores (Figure 2c); both results may reflect annual precipitation changes. The evenness curve has a deflection between 1600 and 900 year BP, slopes from 2780 to 2290 year BP and there is a general increase from 600 year BP with a short dip at about 140–80 year BP. This dip coincides with a decrease in N_1 and N_2 diversity. The correlation between Hill numbers, evenness, and dominant biome scores shows a strong positive correlation between N_1 , N_2 , E , and TAIGA score ($r^2=0.8$); a strong negative correlation between N_1 , N_2 , and DESERT scores ($r^2=-0.7$), and a significant negative correlation between N_2 , E , and STEPPE score ($r^2=-0.5$) (Supplemental Table S4).

Measures of N_1 and N_2 of diatoms reveal a decrease in the diversity of common and dominant species between ca. 2500 and 1900 year BP, and significant increases between ca. 1700 and

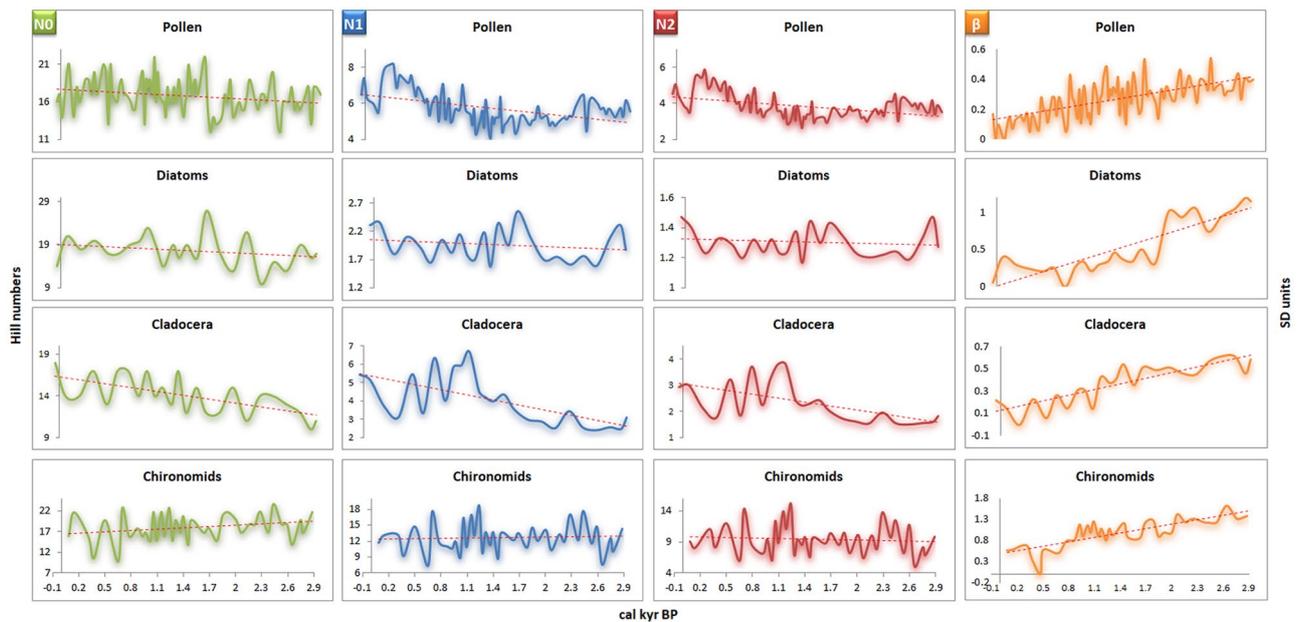


Figure 7. Diversity of plant, diatoms, chironomids, and cladocera, obtained from Bayan Nuur palaeorecord: N0 - total species richness; N1 - richness of common taxa; N2 - richness of dominant taxa. SD - individual sample scores (standard deviation units) of detrended canonical correspondence analysis (DCCA) axis I for Bayan Nuur pollen, diatom, chironomid, and cladoceran records along the temporal gradient.

1200 year BP and in modern times. The highest evenness for diatoms is recorded from 2850 and until ca. 1500 year BP, then the curve is deflected, and we can only see a sharp increase in evenness in the modern sample.

The chironomid community shows the highest diversity of common (N1) and especially dominant (N2) species between ca. 2600 and 2300 year BP and around 1200–1000 year BP, and the lowest in ca. 2650 year BP and ca. 600 year BP. The evenness curve follows the *E* curve of pollen, however, the fluctuations are more pronounced. The coinciding peaks and dips on both curves (Figure 7) suggest a common reaction by plant and chironomid communities to the environment.

The common and dominant species diversity of Cladocera is low between ca. 2800 and 1700 year BP and sharply increases from ca. 1250 to 900 year BP. Evenness is relatively low until 1500 year BP and follows an increasing trend thereafter with only a decrease in the modern sample.

Generally, the trends of evenness changes are similar in pollen, chironomid, and Cladocera datasets, whereas the diatoms show the opposite pattern.

Overall changes in species composition (species turnover) involve 0.3 SD units for pollen; 0.5 SD units for cladoceran; and 1 SD units for diatoms and chironomids. According to Legendre and Legendre (2012), there is a complete turnover in species composition in about 4 SD units and no turnover in about 0 SD. A half-change in species composition is within 1–1.4 SD units. The maximum difference of WA sample scores within paleorecords is a relative turnover measure (Figure 7; Felde et al., 2020). WA results show that the maximal relative turnover for the diatom community was observed until 1925 year BP, whereas the maximal turnover for chironomids was from the bottom of the core to 930 year BP. The low SD units for pollen and Cladocera suggest no significant changes in taxa composition during the last 2885 years.

Procrustes results indicate that the best fit was produced between lacustrine datasets: diatoms and cladoceran ($p=0.001$); diatoms and chironomids ($p=0.002$), cladoceran, and chironomids ($p=0.01$) (Supplemental Figure S4). The fit between pollen and other lacustrine bioproxies produced high p values, suggesting a poor match between data sets (Supplemental Table S5).

The best fit between diatoms and cladoceran is observed after 550 year BP and between diatoms and chironomids after 650 year BP which means they respond in analogous ways to climate and/or atmospheric-induced changes, such as the beginning of the Little Ice Age (LIA).

Mean July temperatures and amount of annual precipitation

The application of transfer functions inferred from the pollen and chironomid datasets resulted in PANN and T_{July} estimates, respectively (Figure 2d and e). The calculated precipitation and T_{July} reflect the regional features of the studied area and are cumulative for the mountains and lowland parts of the Uvs Nuur Basin.

All fossil chironomid taxa were represented in the modern training sets. Goodness-of-fit statistics for T_{July} reconstruction revealed that only two samples had a “poor” fit with temperature. The rest of the samples showed a “good or moderate fit.”

The average mean of T_{July} is 15.8°C, with a maximal 19.1°C (900 year BP) and minimal 12.4°C (670 year BP). The highest values are in 1400–700 year BP and there is a drop in T_{July} immediately after that. An increase in the T_{July} is observed after 150 year BP. Pollen zones PZIII, PZIV, and PZV demonstrate the highest average meaning of T_{July} – 16.3°C, 16.2°C, and 16.1°C, respectively. The minimal average T_{July} meaning is 13.2°C in PZ VI (Supplemental Table S3).

The average value of PANN is 288.3 ± 16 mm/year with maximal 325 mm/year (14 year BP) and minimal 254 mm/year (1692 year BP). The highest values of PANN were reconstructed for PZVII and PZVI – 307.5 ± 15.6 mm/yr and 303.9 ± 11.4 mm/year, respectively (Supplemental Table S3). The lowest PANN is in PZIII – 274.5 ± 14 year BP. In general, there is a tendency for PANN curve to increase between 2885 and 1880 year BP and after 700 year BP.

The most arid and warm interval coincides with PZIII, and the most humid and warm period that began from PZVII. PZVI was relatively humid and cold.

The correlation coefficients calculated between diversity indices of all datasets, and PANN and T_{July} reveal a significant correlation between N1, N2 of pollen, and PANN (both $r^2=0.5$); *E* of

chironomids and PANN ($r^2=0.5$); $N0$, $N1$, and $N2$ of cladoceran and PANN ($r^2=0.5$ for all); and $N1$, $N2$ of chironomids, and T_{july} ($r^2=0.6$ and $r^2=0.5$, respectively) (Supplemental Table S6). The diversity indices and evenness of diatoms didn't reveal any significant correlation with calculated climatic variables. It should be emphasized here that the calculated climate indicators are completely independent only for diatoms and cladoceran, as their data did not contribute to the quantitative reconstruction of precipitation and temperatures.

Correlation coefficients (r^2) between concentrations of dung fungi and environmental variables are $r^2=0.3$ both for PANN and T_{july} . These results show the independence of the coprophilous fungi fluctuation throughout the core.

Discussion

Bayan Nuur environments: Lake level fluctuations and climate for the past three millennia

Lacustrine species such as diatoms, chironomids, and cladoceran are reliable indicators of palaeoclimate and aquatic environments, including fluctuations of water level (Meyer et al., 2015; Nazarova et al., 2011; Nevalainen et al., 2011; Wolin and Stone, 2010). The highest water level of Bayan Nuur for the last three millennia is reconstructed from 2885 to 1760 year BP and during the last ca. 800 years; the lower water stand was in intervals of 1760–700 year BP. The main trends of the T_{july} and PANN fluctuation correlate well with the reconstructed water level changes. High water levels are associated with increased precipitation and cooler July temperatures; low water levels are associated with periods of reduced precipitation and warmer temperatures. Based on geomorphic changes in the landforms of the Uvs Nuur Basin, Grunert et al. (2000) assumed that after the arid phase in the late-Holocene there was a rise in water level at 3000–2000 year BP in Bayan Nuur; and they also distinguished the modern rise of lake level.

Based on the chironomid taxa composition, we suggest that between ca. 2885 and 2700 year BP under a relatively cool climate the lake received more water from inflowing tributaries and surface runoff, which led to the expansion of littoral and facilitated the development of diverse littoral fauna. After 2700 year BP the littoral and lotic chironomid taxa did not indicate the shrinking of shallow coastal areas.

The period from 2800 to 2500 year BP is characterized by a prominent cooling and increase of humidity in northern Europe (Wanner et al., 2008). At the same time, glaciers were advancing in the northern hemisphere, which is associated with a minimum of solar activity (van Geel et al., 2000) and strengthened westerlies over the North Atlantic and Siberia (Mayewski et al., 2004). An et al. (2008) suggested that increased humidity in response to a decrease in solar radiation is the result of decreased evaporation due to dropping temperatures in Mongolia. The historical stage of glacial advances in the Russian Altai under the cool and humid climate is documented between 2300 and 1700 year BP and the subsequent period of warm climate lasted until the early 12th century (Agatova et al., 2012). The late-Holocene record from Lake Teletskoye (Rudaya et al., 2016) suggests that after ca. 3500 year BP, the coniferous mountain taiga spread significantly, with the maximum between ca. 2700 and 1600 year BP, indicating increased humidity.

A period between 1400 and 600 year BP is associated with a maximal littoral with a sandy and muddy bottom, high lake productivity, and increased July temperatures. The interval of ca. 1470–1075 year BP with the heaviest values of $\delta^{13}\text{C}$ may reflect a shallow lake with large littoral covered by macrophytes with heavier stable carbon isotope ratios than conifers or mesophytic terrestrial plants. It is agreed with the diatom and cladoceran results. A similar pattern was also established for the Bosumtwi

(Ghana) and Walker (USA) lakes (Meyers and Ishiwatari, 1993). The desiccation of these lakes and deposition under the drier climatic conditions were documented in $\delta^{13}\text{C}$ shifts to heavier values. A dendrochronological study from the Russian Altai reveals that a lessening of tree ring anomalies from the mid-10th to 13th centuries corresponded to the warm Medieval Period (MWP) and the significant increase in tree-ring anomalies from the onset of the 16th to the onset of the 20th centuries corresponded to the LIA (Barinov et al., 2017).

After about 700 year BP the TAIGA biome scores and precipitation start to increase significantly with lowering of $\delta^{13}\text{C}$ values in BN2016-1 (Figure 2b). This reflects the increase of humidity and development of forest at least between 1400 and 1810 CE in the catchment area of the lake. After 700–750 year BP the lake became deeper, with a reduction of the littoral zone. In the northern hemisphere, the advance of glaciers and strengthened westerlies over the North Atlantic and Siberia suggest that the climate change from 1350 to 1800 CE had the fastest and strongest onset of any in the Holocene (Mayewski et al., 2004). The intensification of the Siberian High after 1350 CE, calculated from the content of potassium from ice cores obtained by Greenland Ice Sheet Project Two (GISP2) for the Northern Hemisphere (Mayewski et al., 2004; Figure 8a), confirms the cooling of the climate.

Chronologically, the period of 1400–1810 CE is attributed to the LIA (Grove, 2004; Wanner et al., 2008). We can thus assume that the LIA in the Uvs Nuur Basin was humid. The Aktru stage of the last glacier advance in the Russian Altai lasting from the 13th to 19th centuries (Agatova et al., 2012) confirms the presence of cold and humid conditions. A new period of cooling in the northern Russian Altai started around 1100 CE with minimum July temperatures occurring between 1450 and 1800 CE (Rudaya et al., 2016). According to Chen et al. (2010), northwestern China within the context of an overall cold LIA climate was characterized by relatively increased humidity. Yang et al. (2009) also noted that the LIA in arid Central Asia was cold and humid. Chen et al. (2019) linked the higher humidity and moisture instability during the LIA to the North Atlantic Oscillation (NAO) fluctuations which affected northwestern China via westerlies. Considering the reconstruction of negative winter NAO (Trouet et al., 2009) for the last millennium, this pattern seems reasonable. Negative NAO phases are associated with the air mass southward migration; some of the storms continue to track eastwards across western Asia, causing increased precipitation in arid Central Asia (Chen et al., 2019). There is a high probability that the same processes took place in the Uvs Nuur Basin.

The T_{july} reconstruction suggested in this study reveals warming of the climate for the last 100 years. For this period the stable carbon isotope record shows the lightest value, confirming a more humid phase. This assumption is also confirmed by increased precipitation. However, the TAIGA biome curve has a significant deflection, probably due to human logging. Pollen data obtained from the Tsambagarav ice core (Brugger et al., 2018), located 270 km to the southwest, shows the maximum deforestation after 1700 CE and an increase of forest only during the last 60 years due to the spread of birch, a pioneer plant after fires and logging. Our study also showed a recent increase in tree percentages in modern times, however, this was mainly Scotch pine.

Bayan Nuur environments: Biodiversity changes for the past three millennia

The diversity of terrestrial plants react positively to the increased precipitation after 700 year BP and generally reflects the lowering of humidity in 2300–1100 year BP as a decrease in the diversity of common and dominant species (Figure 8). The evenness of terrestrial plant communities correlates negatively with the decrease in precipitation, an increase in July temperatures and a lowering

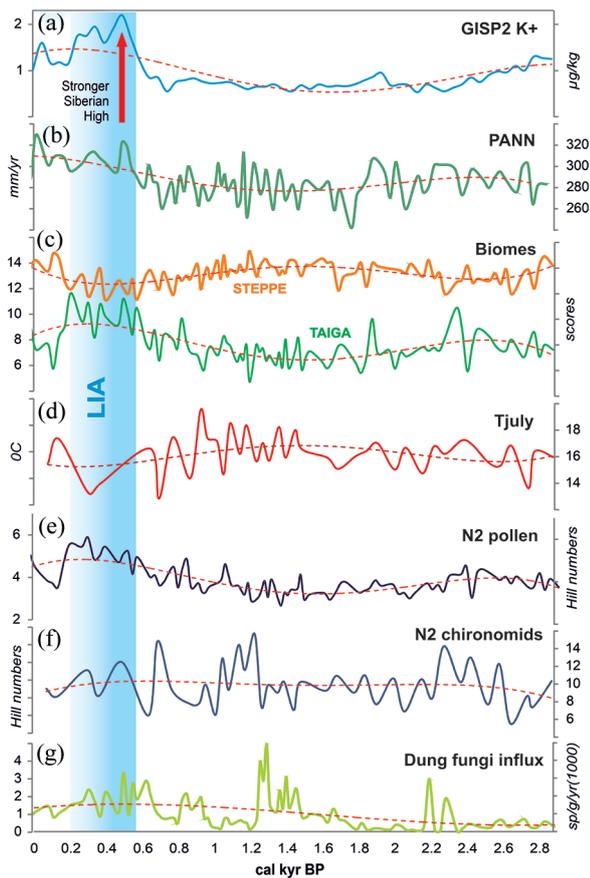


Figure 8. Summary chart of changes in climate, vegetation, and biodiversity in the Uvs Nuur Basin for the late-Holocene and comparison with proxy for intensification of the Siberian High. (a) Content of potassium (K⁺) from ice cores obtained by GISP2 for the northern hemisphere (Mayewski et al., 2004). (b) Reconstruction of the amount of annual precipitation in the lacustrine sediments of Bayan Nuur (this study). (c) Biomization of the pollen data (this study). (d) Reconstruction of the July temperatures based on the chironomid data (this study). (e) Diversity of plant, expressed in richness of dominant taxa (this study). (f) Diversity of chironomids, expressed in richness of dominant taxa (this study). (g) Influx of coprophilous fungi (this study).

of the water level between 1600 and 900 year BP, and correlates positively with the increased precipitation around 2700–2300 year BP and during the last 700 years, but with a short but significant decrease in plant diversity and evenness around 1810–1870 CE.

The increase in woody vegetation in the region also enhanced the diversity of terrestrial plants at the level of dominant and common species and is positively correlated with the evenness of communities. Desertification, in contrast, leads to a sharp decline in plant diversity. The effect of the steppes expansion on plant diversity and evenness is negative, although not as strong. LIA is accompanied by an increase in plant diversity despite lower mean July temperatures (Figure 8). This suggests that in arid regions, precipitation is a crucial factor for the development of diverse plant communities and increased taxonomic diversity, even at low temperatures.

Changes in chironomid biodiversity and evenness show high positive similarities with changes in average July temperatures. The change in WA sample scores reflecting species turnover is on average above 1 SD (Figure 7) between 2885 and 930 year BP. After 930 year BP the WAs are low, reflecting the unchanged taxonomical structure of chironomids as a result of more stable ecological conditions in the lake. The water level increased again from approximately this time.

Although the correlation coefficients between the diversity of cladoceran and precipitation are positive and significant (Supplemental Table S6), the diversity indices are relatively low between ca. 2800 and 1700 year BP where the precipitation is relatively high, and they have sharp increases in an interval of ca. 1250–900 year BP when the precipitation generally decreased. The evenness of cladoceran tends to increase with strong fluctuations after 1500 year BP.

The behaviour of the cladoceran evenness curve is opposite to that of the diatom, which has been decreasing since 1500 year BP. This means that communities of Cladocera and diatoms responds to an environmental factor in opposite ways. Our environmental reconstruction suggests that a period between 1400 and 600 year BP was relatively warm; the lake had a maximal littoral and productivity. We can conclude that the cladoceran respond positively to all or one of these factors by leveling out the composition of the communities, while the diatoms are stressed, which has a negative effect on evenness. Based on the Procrustes analysis (Supplemental Figure S4), Cladocera and diatoms reacted to the environmental changes in a similar way only after 550 year BP, with the beginning of the LIA. This was because one factor, or a combination of factors, was beginning to have a stronger impact on the community of these aquatic inhabitants.

The diversity and evenness of diatoms show a different pattern to that of other proxies, and do not correlate directly to temperatures or precipitation changes. The highest common and dominant diatom species diversity is recorded from ca. 1700 to 1200 year BP and in modern times; the lowest diversity is similar to cladoceran – between ca. 2500 and 1900 year BP, whereas the highest evenness is recorded from 2850 to ca. 1500 year BP during the humid phase. A sharp increase in diatom evenness is documented in a modern sample. The maximal relative turnover for the diatom community reflected in WA sample scores was found at 1925 year BP. This may be explained by the instability of lake ecology due to the fluctuation of the salinity and acidity of the water. Against the background of the dominance of indifferent species at this time, species preferring salty and unsalted, acidic and non-acidic conditions were also found in the sediment. We, therefore, cannot single out the leading factor that most affects the biodiversity and species turnover of diatoms. For comparison, the leading factor in this region for terrestrial vegetation is precipitation, and for chironomids it is July temperatures. Despite the diversity and evenness fluctuations, however, no dramatic species turnover has been documented during the last ca. 2900 years, neither in terrestrial plants nor in aquatic inhabitant communities.

Bayan Nuur environments: People in the past three millennia

In this study we use the influx of coprophilous fungi to reconstruct the peopling around Bayan Nuur; this is particularly important in the absence of archaeological data. Coprophilous fungi are used in palaeoenvironmental studies as an indicator of grazing and overgrazing due to pastoral human activity (Brugger et al., 2018; Dietre et al., 2012; van Geel et al., 2003). The strong correlation with the main Central Asian cultural events helps us to understand the reasons for the population fluctuations of Bayan Nuur surroundings.

The first peak of the coprophilous fungi influx at 335 BCE is probably connected with the expansion of carriers of the Ulan-gom culture from the north. At the same time, the Pazyryk people entered the Mongolian Altai and the eastern Turkestan (Novgorodova, 1989; Tsevendorzh, 2008; Volkov and Novgorodova, 1974). A sharp drop to the minimum of coprophilous fungi in the Bayan Nuur sediments is recorded in 300–270 BCE. We haven't documented any extreme climatic events at this time, and this may

indicate that the end of the Ulangom culture was due to socio-cultural reasons.

The second peak of the coprophilous fungi is recorded at the boundary of the third-second centuries BCE (about 240 BCE). This is undoubtedly due to the expansion of the Central Asian Hunnu (Danilov, 2004; Rudenko, 1962). The lack of archaeological data means that it is impossible to say who inhabited the surroundings of the lake; the Hunnu themselves, or the population that fled from them.

At the beginning of the second century BCE, the number of coprophilous fungi began to decline sharply throughout the Hunnu and half of the Xianbei period, until the first half of the third century CE, when the Xianbei Empire split into several states. The influx of fungi then continued almost at a minimum, with minor fluctuations in the range of 210–160 BCE. This minimum in coprophilous fungi is highly unexpected here, as during this period large masses of the Hunnu state population were concentrated in the neighbouring northern and central Mongolia, cities, and king's tombs were built. According to the climate reconstruction presented in this study, the first centuries CE in the Uvs Nuur area were characterized by dry climate and a decreased amount of precipitation. At least one extremely hot and dry event was recorded around 160 CE. The lands around Bayan Nuur were probably uninhabitable. Another explanation for the low influx of coprophilous fungi is that the population was mobilized for numerous military campaigns against Xianbei occupation and that northwestern Mongolia was thus largely depopulated.

Only in the first half of the third century CE, after the collapse of the Xianbei Empire (in 234 CE) and during the period of the scattered states headed by the Xianbei dynasties (Kradin, 2007), was there a trend toward (from 230 CE) a gradual increase in the number of dung fungi, continuing almost throughout the first half of the fourth century CE, reflecting the demographic changes after a long period of low population around the Bayan Nuur.

The Khaganate of Jujani, which defeated the Xianbei states, appeared in 330 CE in Central Asia (Mongol *ulsyn tyikh tergyyn bot'*, 2004). This event was probably associated with a short-term decrease in population, reflected in a decrease in the number of coprophilous fungi in the record, which began to increase again in the fifth century (about 480 CE).

The cessation of the influx of dung fungi in the middle of sixth century CE correlates with the defeat of Jujani by the Turks and the establishment of the First Turkic Khaganate (552 CE). From the second half of the sixth until the second half of the seventh centuries CE, dramatic changes are recorded in the coprophilous fungi influx and a steady upward trend. In the second half of the seventh century CE, with the formation of the Second Turkic Khaganate (682 CE), the influx of coprophilous fungi reached its absolute maximum and decreased only after the defeat of the Turks in 744 CE by Chinese troops and their allies, the Karluks and Uigurs.

In Uigur Khaganate time, since 744 Uigurs CE (Klyashtorny and Sultanov, 2009), the sandy lands around the Bayan Nuur were not in demand, because they were not suitable for agriculture, which actively developed in the Khaganate. The whole period was therefore characterized by a decrease in the number of coprophilous fungi (750–960 CE), which reached a minimum at the beginning of the 9th century CE and remained at a low level until the middle of the 11th century CE. The situation did not change by the fall of the Uigur Khaganate in 840 CE and the territory's transition to Yenisei Kyrgyz.

The number of coprophilous fungi in Kyrgyzs time did not change dramatically in the middle of the ninth-middle of the 11th centuries CE, showing some fluctuations close to the minimum values, which still indicates a small degree of exploration of the Bayan Nuur surroundings. Only in the second half of the 11th century CE a noticeable increase in the number of fungi occurred

(1020–1130 CE), which may be associated with some destabilization in the political situation in the region due to the conquests of Mongolian-speaking Kidans after they entered the Central Asian steppes from the forest region (Kyzlasov, 1984).

A certain increase in the influx of fungi was recorded at the beginning of the 13th century CE, but the amount stabilized, which was probably associated with the cessation of population growth due to the mobilization to participate in the Mongolian invasions. From the beginning of the 14th century CE, there was an increasing trend in the number of coprophilous fungi that reached its peak in 1330–1450 CE, which correlates with the collapse of the Yuan Empire in 1368 CE and the return of Mongolian emperors from China to their historical homeland (Bazarov et al., 2004).

The cause of the reduction in fungi quantity from the end of the 14th century CE and a considerable part of the 15th century CE is difficult to determine, because this period of Mongolia, including the Uvs Nuur Basin, is poorly described in the historical literature due to a scarcity of sources. The Khotogoid state of Altan-Khans arose between the Hubsugul and Uvs Nuur lakes at the boundary of the 16th–17th centuries CE (Shastina, 1949). The considerable cattle-breeding population of that time is reflected in the increased content of coprophilous fungi.

In the first half of the 18th century CE a long period of reduction in the coprophilous fungi in the vicinity of the Bayan Nuur (min at 1840 CE) occurred. There is a great temptation, however, to link this event to the LIA and depopulation of the area. The drop in plant diversity is also observed in 1810–1870 CE, which could have been the result of the cold climatic event.

Comparing the historical evidence of settlement in northern Mongolia over the past 2885 years suggests a pronounced correlation in the number of dung fungi and the historically explained population increases in the region. At the same time, we do not observe any noticeable connection with climate fluctuations, either with the number of dung fungi or with the assumed episodes of population growth, while terrestrial vegetation and aquatic organisms respond to climate change. It is only in the last 100 years that woody vegetation has been decreasing despite increased precipitation. We can therefore assume that forests were logged by people in modern times.

Conclusions

1. The most humid and afforested phase in the Uvs Nuur Basin during the last three millennia was between 1400 and 1800 CE. Chronologically, this period can be attributed to the LIA. We can thus assume that the LIA in the Uvs Nuur Basin was humid. Conversely, the warmest and most arid period was between 650 and 1350 CE, attributed to the MWP.
2. The biodiversity of terrestrial plants, chironomids, and Cladocera react to climatic variables, at least at the level of typical and dominant species, whereas diatoms show another pattern and do not correlate directly to the climatic factors calculated in this study.
3. The diversity of typical and dominant species, as well as the evenness of plants, are strongly correlated with the change in the leading biomes. They have a strong positive correlation with TAIGA biome scores and a strong negative correlation with DESERT biome scores. These interdependencies relate directly to the amount of precipitation that controls the spread and composition of vegetation in arid areas.
4. Procrustes analysis reveals that when we use different datasets of lake sediment biological proxies for any natural reconstructions, we can expect a common reaction to the environmental factors between lacustrine organisms and a different reaction between lake organisms and ter-

restrial vegetation. This means that the interpretation of these proxies should be independent.

5. The calculated species turnover suggests no significant changes in plant and Cladocera taxa composition during the last 2885 years, but significant changes in diatom and chironomid communities.
6. Historical sources and the influx of coprophilous fungi as a proxy of peopling around the lake have not revealed direct connections with climate changes.
7. Coprophilous fungi appear to be independent of climate indicators and only reflect pasture pressure. They can be used as an individual or additional sources of assessment for the peopling and human-related grazing pressure in the studied area.

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Supplemental material

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