



Aquatic ecosystem responses to Holocene climate change and biome development in boreal, central Asia

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ABSTRACT

Boreal ecosystems are highly vulnerable to climate change, and severe ecological impacts in the near future are virtually certain to occur. We undertook a multiproxy study on an alpine lake (ESM-1) at the modern tree-line in boreal, southern Siberia. Steppe and tundra biomes were extensive in eastern Sayan landscapes during the early Holocene. Boreal forest quickly expanded by 9.1 ka BP, and dominated the landscape until c 0.7 ka BP, when the greatest period of compositional turnover occurred. At this time, alpine meadow landscape expanded and *Picea obovata* colonised new habitats along river valleys and lake shorelines, because of prevailing cool, moist conditions. During the early Holocene, chironomid assemblages were dominated by cold stenotherms. Diatoms for much of the Holocene were dominated by alkaliphilous, fragilarioid taxa, up until 0.2 ka BP, when epiphytic species expanded, indicative of increased habitat availability. C/N mass ratios ranged between 9.5 and 13.5 (11.1–15.8 C/N atomic ratios), indicative of algal communities dominating organic matter contributions to bottom sediments with small, persistent contributions from vascular plants. However, $\delta^{13}\text{C}$ values increased steadily from -34.9‰ during the early Holocene (9.3 ka BP) to -24.8‰ by 0.6 ka BP. This large shift in magnitude may be due to a number of factors, including increasing within-lake productivity, increasing disequilibrium between the isotopic balance of the lake with the atmosphere as the lake became isotopically 'mature', and declining soil respiration linked to small, but distinct retreat in forest biomes. The influence of climatic variables on landscape vegetation was assessed using redundancy analysis (RDA), a linear, direct ordination technique. Changes in July insolation at 60 °N significantly explained over one-fifth of the variation in species composition, while changes in estimates of northern hemisphere temperature and ice-rafted debris events in the North Atlantic were also significant, but considerably less important. The potential importance of climate and biome development (tundra, steppe, cold deciduous forest and taiga) on different trophic levels (i.e. chironomid and diatom communities) in lake ESM-1 was also assessed using RDA. Climate predictors had a more significant influence on Holocene chironomid assemblages, especially July insolation at 60 °N, estimates of regional precipitation and estimates of northern hemisphere temperature, while only the development of the taiga biome had a significant impact on these primary consumers. Diatom communities also had a small, but significant influence on Holocene chironomid populations, perhaps linked to variation in faunal feeding strategies. In contrast, climatic and biome predictors explained similar amounts of variation in the Holocene diatom assemblage (approximately 20% each), while chironomids themselves as predictors explained just under 7% of diatom variation. Lake acidity was inferred using a diatom inference model. Results suggest that after deglaciation, the lake did not undergo a process of gradual acidification, most likely due to the presence

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of continuous permafrost and low levels of precipitation, preventing base cations and dissolved organic carbon entering the lake (except for the period between 1.7 and 0.7 ka BP). We conclude that lakes in continental, boreal regions undergo different models of lake ontogeny than oceanic boreal regions. Unlike other regions discussed, climate is a more important driver of ecosystem change than catchment changes. We also demonstrate that the start of the period coincident with the onset of the Little Ice Age resulted in important thresholds crossed in catchment vegetation and aquatic communities.

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1. Introduction

Our knowledge of how lakes develop over long timescales in different regions is rather poor; monitoring records are generally short, so models of lake ontogeny are usually inferred from palaeolimnological data. Early studies suggested temperate lakes underwent a process of natural enrichment over time (Deevey, 1942). In contrast, boreal and arctic lakes in base-poor catchments have been shown to undergo acidification, linked to gradual leaching of base cations (Ford, 1990; Bradshaw et al., 2000; Briner et al., 2006; Michelutti et al., 2007). Ontogeny has also been tracked in lakes of different ages, and these studies confirm the close connection between natural acidification and long-term soil development (Matthews, 1992; Engstrom et al., 2000; Fritz et al., 2004). Lake communities are influenced by a variety of drivers, including climate change (e.g. Baulch et al., 2005; Michelutti et al., 2007; Moore et al., 2009; Reuss et al., 2010), catchment development (Renberg, 1990; Engstrom et al., 2000; Boyle, 2007), and biotic interactions (Parker and Schindler, 2006). Communities living in mountain ecotones are especially sensitive to changes in climate and biome development (Lotter and Birks, 2003). For example, long periods of ice cover, promoted by cool temperatures, can greatly inhibit primary production and habitat availability (Douglas and Smol, 2010). Changes in catchment processes such as vegetation succession and soil leaching are important because these result in the supply of e.g. dissolved organic carbon (DOC) and nutrients to lakes, which in turn influence aquatic communities and biological productivity (Birks et al., 2000; Engstrom et al., 2000; Engstrom and Fritz, 2006; Michelutti et al., 2007; Reuss et al., 2010).

Engstrom et al. (2000) proposed that boreal lakes (derived from glaciation) may undergo limnological change similar to that described for Glacier Bay in Alaska. However, limnological change after deglaciation shows considerable variation, even in a relatively small geographical area (Fritz et al., 2004). The area covered by boreal forests is vast (between 12 and 15 millions km²), and post-glacial ontogeny likely to be varied too. The central Asian region of southern Siberia and northern Mongolia is one of the most continental regions on earth, and experiences some of the coldest winter temperatures in the Northern Hemisphere. However, the region has also experienced some of the most pronounced increases in surface temperature in the last 90 years, which in recent decades is linked to anthropogenic warming (IPCC, 2007). The boreal landscape of southern Siberia is dominated by forest growing above continuous permafrost, which is expected to undergo considerable degradation and in the eastern Sayan Mountains is predicted to thaw altogether by 2100 AD (IPCC, 2007). These changes will have major impacts on lacustrine ecosystems, yet few detailed studies investigating central Asian lakes exist, resulting in considerable scientific uncertainties.

The principal aim of this study was to investigate landscape change and lake ontogeny in the climatically sensitive, alpine region of boreal, southern Siberia. To do this, trends in acidification were reconstructed using a diatom-inferred pH transfer function. Changing vegetation sources of organic matter to the lake were investigated using organic geochemistry. The relative importance

of factors that drive long-term limnological change were evaluated using constrained ordination techniques (Lotter and Birks, 2003; Anderson et al., 2008). Given the importance of vegetation succession on catchment processes in boreal (Engstrom et al., 2000) and alpine regions (Lotter and Birks, 2003), pollen-based biome scores were used as predictors of both producers (diatoms) and primary consumers (larval Chironomidae). However, given that climate is also likely to be an important driver influencing limnological change in this region, the importance of July insolation at 60 °N (Berger and Loutre, 1991), palaeo-temperatures inferred from the GRIP borehole at the summit of the Greenland ice sheet (Dahl-Jensen et al., 1998), ice-rafted debris events in North Atlantic sediments (Bond et al., 1997), and pollen-inferred annual precipitation from Hoton-Nur, a lake situated to the west of the study region, in the Mongolian Altai (Rudaya et al., 2009), were also evaluated. Within-lake processes, such as aquatic food-web interactions, were explored, to the extent that top-down influence of consumers (chironomids) on primary producers (diatoms) through the Holocene was estimated using partial constrained ordination. However, different chironomid species have different feeding strategies (e.g. some are collector–filterers and construct nets; others have known associations with plants (Berg, 1994)), and so bottom-up influence of primary producers on chironomid assemblages was also explored using ordination techniques. Multiproxy approaches offer a much more holistic approach in determining e.g. direct climatic (Briner et al., 2006) or indirect catchment influences on aquatic organisms (Birks et al., 2000; Lotter and Birks, 2003; Anderson et al., 2008). Multivariate analyses, such as constrained ordination, also allow specific hypotheses to be tested, such as the importance of palaeo-temperatures (Anderson et al., 2008) or catchment vegetation (Lotter and Birks, 2003) in influencing aquatic ecosystem change.

2. Regional setting

The Sayan Mountains straddle the geographical boundaries between southern Siberia and northern Mongolia (Fig. 1). They extend east to Lake Baikal, and to the west they form a continuation with the Altai Mountains. Precipitation is associated with the Asian low-pressure cell, and falls mainly during June, July and August (JJA). The mountains lie to the north of the Asian monsoon boundary, and rainfall comes from the North Atlantic via the Westerlies (Lydolph, 1977). Rainfall declines in August as the intensity of the Siberian High develops, which remains dominant in the region until April. Winters are therefore long, cold and dry, resulting in lakes and rivers freezing over every year. Holocene records have been published for a few lakes in neighbouring regions, e.g. Lake Baikal (Demske et al., 2005; Tarasov et al., 2007) and several smaller lakes in the Altai Mountains (Blyakharchuk et al., 2004; Westover et al., 2006; Rudaya et al., 2009). Drilling campaigns have also been undertaken in Lake Hovsgol, a large, deep lake, which lies in a rift basin to the southwest of ESM-1 in Mongolia (Prokopenko et al., 2007).

The study site belongs to a group of lakes of glacial origin located in the Ilyuchirsky graben in the eastern Sayan mountain range. The catchment consists of Pre-Cenozoic, metamorphic and Neogenic

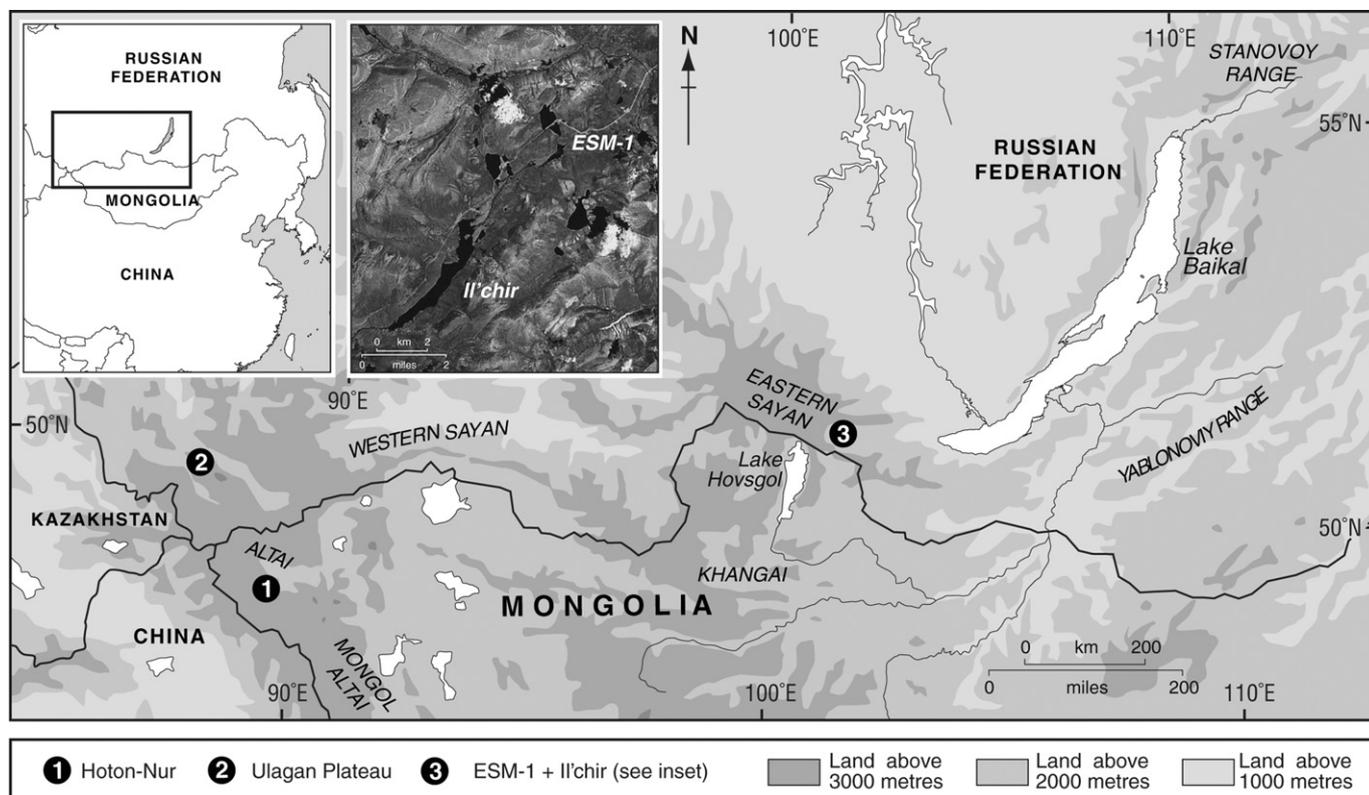


Fig. 1. Map of central Asia focussed on southern Siberia and northern Mongolia. Principal sites highlighted in study are annotated on the map. The insert is a satellite image of lake ESM-1, with nearby Lake Il'chir highlighted.

volcanic rocks, overlain by debris of Late Pleistocene basal moraines. The graben base is at an elevation of 1950–2000 m a.s.l., which also delimits the tree-line. The alpine lake sampled for this study does not appear to have an official name, so for the purposes of this study we have called it ESM-1 (52.02695 °N, 101.05908 °E; 1992 m a.s.l.) (Fig. 1). Using a Garmin® eTrex GPS, the area of the lake was calculated to be approximately 0.3 km². It is very close to Lake Il'chir, whose outlet is the Irkut River, an important tributary of the Angara River, Lake Baikal's outflow.

The Ilyuichirsky graben is surrounded on all sides by high ridges, resulting in a particular type of climate regime. Modern climate variables for the region were estimated using an interpolation method, which uses monthly precipitation and temperature data representing the 1961–1990 interval and covering the global land surface at 0.5° × 0.5° resolution (New et al., 2002; Mitchell and Jones, 2005; Schneider et al., 2008). The climate is characterized by mean July temperature of +11 °C, and mean January temperature of –26 °C. Minimum temperatures often fall below –40 °C, while maximum summer temperatures can exceed +25 °C, resulting in an average annual temperature of –6.6 °C. Mean annual precipitation is approximately 400 mm, of which only 10% falls during the cold season from October to March. Radiation balance is about 32 kcal/cm². We have no direct monitoring records for ESM-1, but for nearby Lake Il'chir (Fig. 1), surface waters can reach over 15 °C in July (Bondarenko et al., 2002), and the lake freezes over between October and June (Bondarenko et al., 2002).

Modern vegetation in the eastern Sayan has clear altitudinal zones. *Abies* (fir), *Picea* (spruce) and *Pinus sibirica* (Siberian pine) trees dominate mountain boreal forest at elevations below 1000 m a.s.l. *P. sibirica* and *Larix sibirica* dominate forests between 1000 and 1800/2000 m a.s.l. Shrubs including species of *Betula*, *Alnus*, and *Ericales* are abundant in the under-storey of the dark-coniferous forest and in the subalpine belt above the tree-line. Forests of *Pinus*

sylvestris (Scots pine) occupy drier habitats in the eastern part of the Sayan mountains. Vegetation in the immediate catchment of the lake is dominated by sparse larch forest (*L. sibirica*), with an understory of dwarf birch (*Betula nana*), and carpeted lichen (*Cladonia*) and moss floor. In the lake, there are abundant littoral aquatic macrophytes including *Carex* and *Potamogeton* spp.

3. Material and methods

3.1. Fieldwork

Fieldwork took place between 20th–22nd July 2006. pH and conductivity were measured in situ using a Fisher Scientific accumet AP85 pH/conductivity meter. The pH of the surface water was 8.2 pH units, and conductivity values were moderate (360 μS/cm). Due to time constraints, it was not possible to conduct a detailed bathymetry of the lake, although a Plastimo Echotest II handheld depth sounder was used to estimate the deepest region at 7 m. Cores were extracted from 4.5 m water depth, in a region far from shore with a flat bottom. A 71 mm diameter Livingstone core was initially extracted (1.03 m length), which maintained the surface sediment–water interface, followed by a series of overlapping Livingstone drives down to a depth of 3.71 m within the sediment.

3.2. Chronology

Extracted lake sediments were highly humified and it was not possible to obtain any sizeable macrofossils for radiocarbon analyses. Radiocarbon dating was instead performed on 13 bulk sediment samples using accelerator mass spectrometry (AMS) at the Poznan Radiocarbon Laboratory, Poland. The amount of radiocarbon reservoir effect (i.e. shift towards older ages) was estimated on the basis of ¹⁴C dating of two contemporary plant macrophytes.

The results were very similar, c 105 percent modern carbon (pMC), and suggest a reservoir age of approximately 200 years (Mackay, unpublished data). We have therefore added this reservoir effect to our age model for ESM-1. All dates were calibrated using IntCal09 radiocarbon calibration curve (Reimer et al., 2009). Construction of the age–depth model was prepared with use of the clam program (Blaauw, 2010). Age–depth relationship was estimated using a smooth spline approximation, with additional mixed-effect uncertainty (Heegaard et al., 2005).

3.3. Palynology

Seventy-eight 1 cm³ sediment samples were processed for pollen analysis using standard laboratory methods, including HCl and KOH treatments, heavy-liquid separation and subsequent acetolysis (Berglund and Ralska-Jasiewiczowa, 1986). Pollen and spores were mounted in glycerin and counted using light microscopy at $\times 400$ – $\times 1000$ magnification. Identification of fossil pollen and spores was assisted with the use of regional pollen atlases (Kuprianova and Alyoshina, 1972; Bobrov et al., 1983; Moore et al., 1991) and the reference collection held at the Institute of the Earth Crust, Irkutsk. A total of 100–1200 grains were counted at each level. Relative abundances of individual taxa were based on the sum of all terrestrial pollen grains. Spore percentages for cryptogam plants were calculated in relation to the total sum of counted pollen and spores. Haploxyton-type pine pollen (*P. sibirica*, *Pinus pumila*) were separated from Diploxyton-type pine pollen (*P. sylvestris*) based on the position of the sacchi in polar view. Overall, very few *P. pumila*-type grains were identified and counted, and these were included in the *P. sibirica* category. We used the pollen-based biome reconstruction method and equation presented in Prentice et al. (1996) and a regionally approved biome-taxon matrix (Müller et al., 2010), which assigns all selected pollen taxa to appropriate biomes. Calculations of biome scores (taiga = TAIG; cold deciduous forest = CLDE; steppe = STEP; tundra = TUND) were performed using the PPPBase software (Guiot and Goeury, 1996). Quantitative palaeoenvironmental reconstructions have not been attempted from ESM-1 pollen fossils, because too few close modern analogues exist from the eastern Sayan Mountains.

3.4. Chironomids

Thirty samples for chironomid analysis were prepared and mounted using standard techniques (Brooks et al., 2007). Chironomid larval head capsules were mounted, ventral side uppermost, in Euparal[®]. Between 36 and 244 head capsules from each sample were counted and identified at $\times 200$ – $\times 400$ magnification using Wiederholm (1983), Makarchenko and Makarchenko (1999), Rieradevall and Brooks (2001), Brooks et al. (2007) and the national Chironomidae collection at The Natural History Museum, London. Previous studies have shown that a minimum of 50 head capsules is required for robust palaeoenvironmental reconstructions (Heiri and Lotter, 2001), although this number may be reduced if taxon richness is low. There was insufficient material available to isolate 50 head capsules from 4 of the subsamples (8, 125, 135 and 175 cm). Mean July air temperature was reconstructed using an 81-lake training set from European Russia – central Siberia (Self et al., 2011) and the reliability of the reconstruction was assessed using the criteria proposed by Velle et al. (2005) and Engels et al. (2008). Mean July air temperatures were estimated using a weighted-averaging partial least squares (WA-PLS) 2 component model based on an 81-lake training set located along a transect from European Russia to central Siberia, with a present-day temperature gradient of 8.8–18.9 °C (Self et al., 2011).

3.5. Diatoms

Forty-three diatom samples were prepared for counting using standard procedures (Battarbee et al., 2001). Approximately 0.1 g of wet sediment per sample was heated in 30% H₂O₂ until all organic material was oxidised, and any carbonates were removed with the addition of a few drops of 10% HCl. Diatom suspensions were diluted to a suitable concentration for counting, pipetted onto a coverslip and left to dry overnight, before being mounted on slides with Naphrax[®] (refractive index = 1.73). Diatoms were counted at $\times 1000$ magnification under an oil-immersion objective and phase contrast on a Zeiss Axiostar Plus light microscope. A minimum of 300 valves were counted in each sample. Diatoms were identified according to a range of published literature (Krammer and Lange-Bertalot, 1986, 1988, 1991a, 1991b; Williams and Round, 1987; Krammer, 2000; Lange-Bertalot, 2001). Long-term trends in acidification were explored using a diatom-inferred pH reconstruction undertaken using combined training sets available from the European Diatom Database. Reconstructed pH values were generated using ERNIE (v.1.2), a software package within EDDI (Juggins, 2001). Reconstructions were undertaken using weighted-averaging (WA) with classical deshrinking, because this technique gave a reconstructed value of 8.1 pH units at the very top of the core, which agreed well with measured pH values from the lake (8.2 pH units). Prediction error of the model (root mean square error of prediction (RMSEP_{jack})) was 0.5 pH units, with an r^2 0.757.

3.6. Isotope geochemistry

Thirty-six sediment subsamples were prepared for organic geochemical analyses (¹³C/¹²C, %TOC and %TN) to determine possible sources of organic matter within the lake sediments (Leng and Marshall, 2004). Calcites were removed from the sediments by leaving them overnight in 50 ml of 5% HCl. Samples were then washed with deionised water through Whatman No. 41 filter papers, and air-dried at 40 °C before being ground into a fine powder. %TOC and %TN were measured using a Carlo Erba elemental analyser (with internal acetanilide standards used for calibration). Replicate analyses of well-mixed samples showed that precision was $\pm <0.1\%$ (1 S.D.). C/N in our study refers to the weight ratio of organic carbon to total nitrogen for each sample. Weight percentages can be multiplied by 1.167 (the ratio of atomic weights of nitrogen and carbon) to yield C/N atomic ratios. Both weight and mass ratios are used and it is necessary to compare like with like. Atomic ratios are often preferred because they reflect biochemical stoichiometry (Meyers and Teranes, 2001). Stable isotope analyses (¹³C/¹²C) were undertaken by combustion using a Carlo Erba NA1500 (series 1) on-line to a VG Triple Trap and Optima dual-inlet mass spectrometer, with $\delta^{13}\text{C}$ values calculated to the VPDB scale using a within-run laboratory standard calibrated against NBS19 and NBS22. Analyses of replicates of sample material revealed a precision of $\pm <0.1\%$ (1 SD). Two soil and six vegetation samples close to the vicinity of the lake were also analysed (after acid washing, drying and freezer milling), to aid interpretation of the sediment core data.

3.7. Statistical analyses

Detrended correspondence analysis (DCA) was initially undertaken on relative abundances of each of the three biological datasets to establish the magnitude of species turnover. Relative abundance data were $\log(x + 1)$ transformed in order to stabilize species variance and rare species were down-weighted. In each case, the axis 1 gradient length (standard deviation units) was

under 2, indicating that linear ordination techniques were more appropriate for analyses. Principal components analysis (PCA) with symmetric scaling of the ordination scores to optimise scaling for both samples and species was undertaken (Gabriel, 2002). Species data were $\log(x + 1)$ transformed and both species and samples were centred to give a log-linear contrast PCA, appropriate for closed relative abundance data (Lotter and Birks, 1993). Significance of PC axes were tested with a broken stick model (Jolliffe, 1986) using BSTICK v1.0 (Line and Birks, 1996). Compositional change in biological data (β -diversity) was estimated using detrended canonical correspondence analysis (DCCA) (Birks, 2007), with the biological data constrained using dates obtained from the age–depth model. Explanatory variables used to explain variation in biological proxy data include: July insolation at 60 °N (W/m^2 ; insolation), palaeo-temperatures inferred from the GRIP borehole at the summit of the Greenland ice sheet ($^{\circ}C$; GRIPT), ice-rafted debris events in North Atlantic sediments (% hematite stained grains (%HSG)), pollen-inferred annual precipitation at Hoton-Nur (mm/yr ; P_{ann}), and pollen-based biome scores.

The aims of the study were addressed by estimating the unique influence of each variable, using a series of partial redundancy analyses, with the remaining variables, and time, partialled out as co-variables. Significant PCA axes sample scores of species assemblages were further used as predictors to test the following hypotheses in lake ESM-1: (i) changes in catchment vegetation (pollen PCA scores) significantly influenced primary producers and consumers; (ii) chironomids (chironomid PCA scores) had a significant top-down impact on primary producers; (iii) diatoms (diatoms PCA scores) had a significant bottom-up influence on primary consumers. All ordination analyses were undertaken using Canoco v. 4.5 (ter Braak and Šmilauer, 2002). Monte Carlo permutation tests for temporally ordered data were used to determine significance levels ($n = 499$). Stratigraphical profiles were constructed using C2 Data Analysis Version 1.5.1 (Juggins, 2007). Stratigraphical zones for each proxy were delimited by optimal partitioning (Birks and Gordon, 1985) using the unpublished programme ZONE (version 1.2) (Juggins, 1991).

4. Results

4.1. Core description and chronology

The lithology of the parallel cores consisted of 351 cm of dark brown, highly humified, gyttja, overlying 20 cm of more peaty, but still dark and humified sediments. All dates are given as calibrated thousands of years before present (ka BP). We acknowledge that dating of bulk sediments can be problematic, but several studies have shown that errors are likely to be small in highly organic sediments as reviewed in Björck and Wohlfarth (2001). The complete ESM-1 sediment sequence spans 11.2 ka BP (Fig. 2; Table 1). Between the base of the core and 4.0 ka BP, sediment accumulation was rather slow (0.16 mm/yr), and increased from 4.0 ka BP to the top of the core (0.77 mm/yr).

4.2. Pollen stratigraphy

Four distinct zones were delimited from the Holocene pollen profile (Figs. 3 and 6).

- Poll-1 (370–347.5 cm; 11.2–9.1 ka BP). The bottom of this zone was characterised by highly fluctuating abundance of *P. sylvestris* pollen, together with the highest relative abundances of *Alnus*, *B. nana*-type and *Artemisia*. At 360 cm (10.2 ka BP), *P. sylvestris* was almost absent from the record. Pollen N2 diversity was highest in this zone.

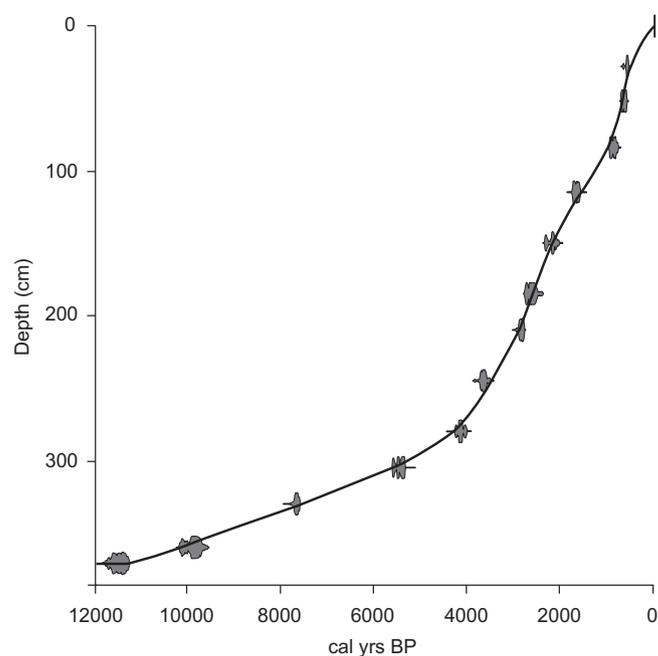


Fig. 2. Age-depth model based on calibrated radiocarbon AMS dates from ESM-1 sediments, constructed using the clam program (Blaauw, 2010). Grey-shaded area represents 95% confidence intervals of modelled ages (black line).

- Poll-2 (347.5–122.5 cm; 9.1–1.7 ka BP). This zone was dominated throughout by fluctuating relative abundance of *P. sylvestris*. Up to 3.0 ka BP, a small increase in *P. sibirica* occurred during periods of increasing *P. sylvestris*. Other taxa including *B. nana*-type, *Salix* spp., and *Picea obovata* all gradually declined in abundance, although *Artemisia* and Cyperaceae pollen showed small but distinct increases.
- Poll-3 (122.5–55.5 cm; 1.7–0.7 ka BP). This zone was characterised mainly by peak relative abundance of *P. sylvestris* pollen.
- Poll-4 (55.5–0 cm; 0.7 ka BP – present). There was a marked change in PCA axis 1 sample scores between zones poll-3 and poll-4, indicative of a decline in *P. sylvestris* and *B. nana*, concomitant with increased *P. obovata*, *Larix*, and several non-arboreal pollen taxa, especially Poaceae and Cyperaceae. In this zone there was also the first appearance of *Thalictrum* pollen and *Sphagnum* and Polypodiaceae spores. Also of note, *P. obovata* peaked at c 0.6 ka BP, before declining in the uppermost sediments.

Table 1

Results of AMS radiocarbon dating for core ESM-1. Depth range and mid-depth are the original depths of samples from core. Calibration was performed using IntCal09 radiocarbon calibration curve (Reimer et al., 2009).

Date code	Depth range, cm	Mid-depth, cm	^{14}C age BP	Calibrated age range, 95.4% probability	Calibrated age mid-point, 95.4% probability	
Poz-22126	27.5–28	27.75	720 ± 30	373	497	458
Poz-21076	51.5–52	51.75	820 ± 30	580	694	641
Poz-22158	83.5–84	83.75	1105 ± 30	862	1003	936
Poz-21077	114–115	114.5	1920 ± 35	1452	1626	1543
Poz-22127	149–150	149.5	2345 ± 35	2049	2250	2136
Poz-21078	184–185	184.5	2700 ± 35	2474	2645	2555
Poz-22160	209–210	209.5	2920 ± 35	2773	2949	2855
Poz-21080	244–245	244.5	3580 ± 40	3219	3559	3439
Poz-22159	279–280	279.5	3955 ± 35	4111	4402	4245
Poz-21081	304–305	304.5	4900 ± 40	5404	5679	5537
Poz-22161	329–330	329.5	7010 ± 50	7306	7582	7479
Poz-21082	359–360	359.5	9010 ± 60	9950	10,315	10,126
Poz-22162	370–371	370.5	10190 ± 60	10,935	11,394	11,159

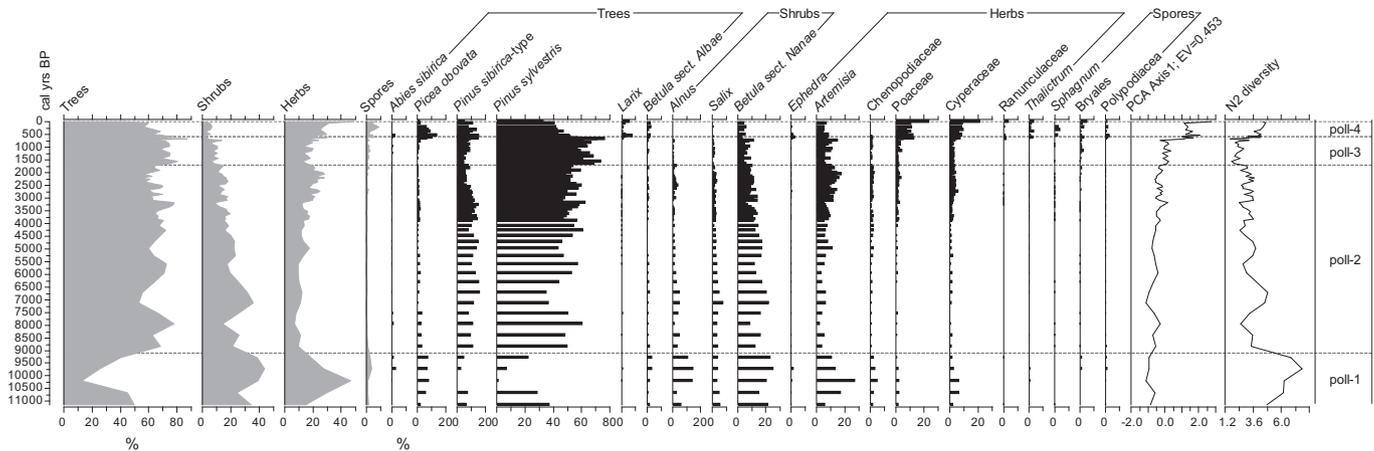


Fig. 3. Pollen and spore relative abundance stratigraphy plotted on the calibrated age scale. Pollen and spore taxa have been grouped according to growth form (trees, shrubs, herbs and cryptogams). Significant PCA axis 1 sample scores (+eigenvalue; EV) and N2 diversity values are also shown. Pollen zones have been delimited using optimal partitioning.

4.3. Chironomid stratigraphy

Of the 53 taxa present in the sub-fossil samples, the assemblages were dominated by six morphotypes (*Tanytarsus lugens*-type, *Sergentia coracina*-type, *Tanytarsus mendax*-type, *Psectrocladius sordidellus*-type, *Procladius* and *Tanytarsus pallidicornis*-type), which occurred in over 80% of the samples (Fig. 4). Taxa able to construct webs dominated Holocene assemblages, although predatory taxa and taxa associated with aquatic macrophytes were common too. Although eight taxa were not represented in the Russian training set, these unrepresented taxa typically only formed minor components of the assemblages (1–3 occurrences at less than 1.5%). Four distinct zones were delimited from the Holocene profile (Figs. 4 and 6). Chironomid taxa are arranged according to their PCA axis 1 species scores.

- Chir-1 (370–339.5 cm; 11.2–8.4 ka BP). This zone was dominated by *T. lugens*-type and *Chironomus anthracinus*-type. *Prosilocerus lacustris*-type and *Glyptotendipes pallens*-type also reached their highest abundances in this zone, and only occurred rarely in the remainder of the core.
- Chir-2 (339.5–249.5 cm; 8.4–3.5 ka BP). *T. lugens*-type remained abundant in this zone, and reached peak values at c 5.0 ka BP. *S. coracina*- and *T. pallidicornis*-type both increased in relative abundances, while other taxa such as *C. anthracinus*-type and *Paratanytarsus* declined.
- Chir-3 (249.5–43.8 cm; 3.5–0.6 ka BP). *S. coracina*-type remained dominant in this zone while *T. lugens*-type declined. *P. sordidellus*-type increased in abundance to highest values at between 2.4 and 2.2 ka BP.
- Chir-4 (43.8 cm–0 cm; 0.6 ka BP – present). *Hydrobaenus conformis*-type and *Zavrelia* increased in abundance towards the top of the zone. *S. coracina* declined to low values near the top of this zone, while both *T. lugens*-type and *T. pallidicornis*-type both remained moderately abundant.

Sample specific RMSEP errors ranged between 0.95 °C–1.14 °C for chironomid-inferred (CI) July air temperatures. Mean July air temperatures were estimated at 14.9 °C at the base of the core (370 cm; 11.2 ka BP), and declined throughout zones chir-1 and chir-2–12.1 °C at 5.0 ka BP (295 cm) (Fig. 4). A notable prolonged warmer period of 13.8–14.1 °C occurred between 1.7 and 0.9 ka BP (124–80 cm). Cooler intervals occurred at 4.9 ka BP (294 cm) and at 0.2 ka BP (7 cm). In recent decades, mean July air temperatures increased to 13.4 °C at 35 yrs BP (4 cm), values typical of the late Holocene.

4.4. Diatom stratigraphy

Four distinct zones were delimited from the Holocene diatom profile (Figs. 5 and 6). Diatom taxa are arranged according to their PCA axis 1 species scores, and fragiliarioid taxa and planktonic taxa have also been summed (Fig. 5). Diatom counts (and organic geochemical values) were only measured from 10.2 ka BP (360 cm). N2 diversity fluctuated between 3 and 4 for most of the Holocene, but increased steadily from 1.4 ka BP. Reconstructed pH values ranged between 7.6 and 8.1 pH units.

- Diat-1 (360–149.5 cm; 10.2–2.2 ka BP). Diatoms were dominated by fragiliarioid taxa (60–85%), especially *Staurosira construens* and *S. construens* f. *venter*. Up until c 3.1 ka BP (225 cm) many littoral species were also common. The number of planktonic taxa also increased in this zone between 7.1 and 3.1 ka BP (324.5–224.5 cm) and again between 2.3 and 2.2 ka BP (164.5–154.5 cm). Diatom-inferred pH values ranged between 7.8 at the base of the core and 7.7 at 3.1 ka BP, and then increased to the top of the zone
- Diat-2 (149.5–107 cm; 2.2–1.4 ka BP). Fragiliarioid taxa still dominated the diatom assemblage, with few other littoral taxa apparent. Diatom-inferred pH initially reached its highest value for the whole of the profile (8.1 at c 1.9 ka BP).
- Diat-3 (107–39.75 cm; 1.4–0.6 ka BP). *S. construens* declined to low levels in this zone, although *S. construens* f. *venter* and *Navicula diluviana* were both abundant. *Pinnularia divergensissima* appeared in the record for the first time in appreciable abundances. Diatom-inferred pH values declined to the lowest value (7.6) for the whole Holocene at c 0.9 ka BP.
- Diat-4 (39.75–0 cm; 0.6 ka BP – present). Fragiliarioid taxa, especially *S. construens* f. *venter*, declined to lowest abundances for the complete profile from 0.2 ka BP to the present. Concomitant with this decline were increases in *Achnanthes minutissimum*, *Psammodium abundans* f. *rosenstockii*, and *Denticula kuetzingii*. Diatom-inferred pH values fluctuated at high values in this zone, reaching 8.1 pH units in the surface sample.

4.5. Isotope stratigraphy

Contemporary soil and vegetation samples have C/N ratios under 21 and $\delta^{13}\text{C}$ values between -24 and -28‰ (data not shown). For the majority of the profile, %TOC fluctuated around 30%, until 4.3 ka BP (Fig. 5). After this date, %TOC values were much

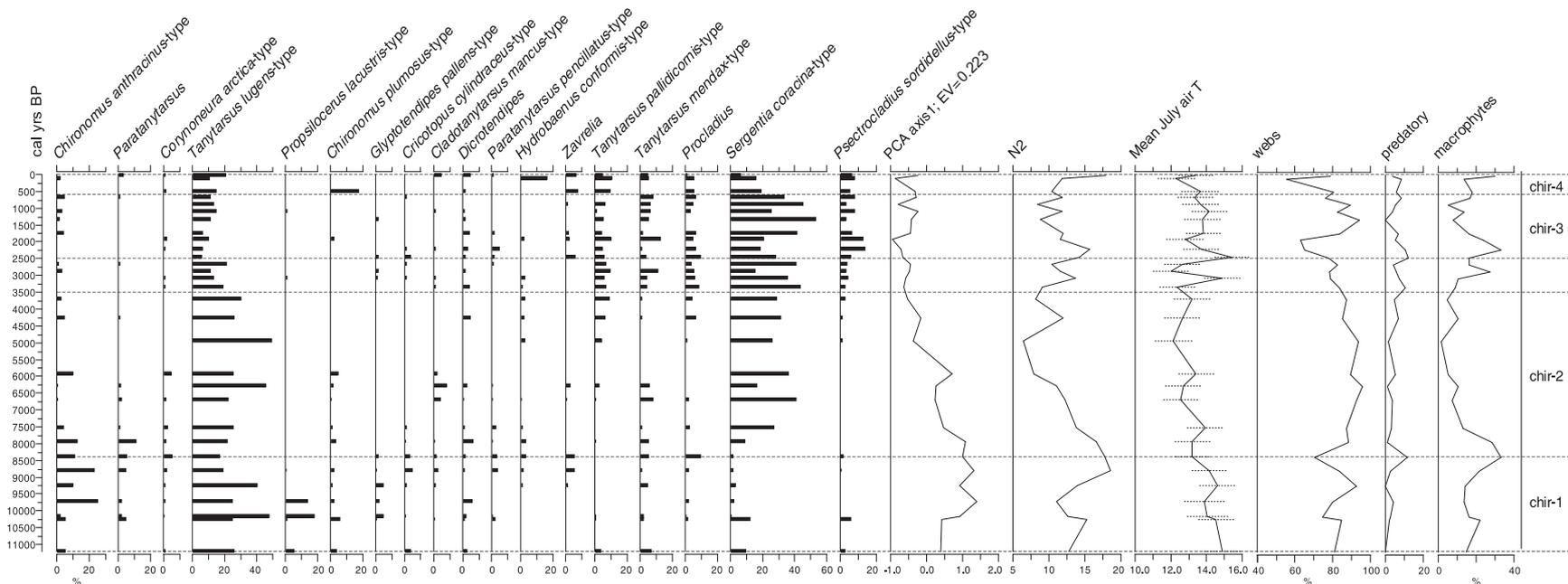


Fig. 4. Chironomid relative abundance stratigraphy plotted on the calibrated age scale. Chironomid taxa have been arranged according to their PCA axis 1 species scores. Significant PCA axis 1 sample scores (+eigenvalue; EV), N2 diversity values, reconstructed mean July air temperatures and selected feeding strategies are also shown. Chironomid zones have been delimited using optimal partitioning.

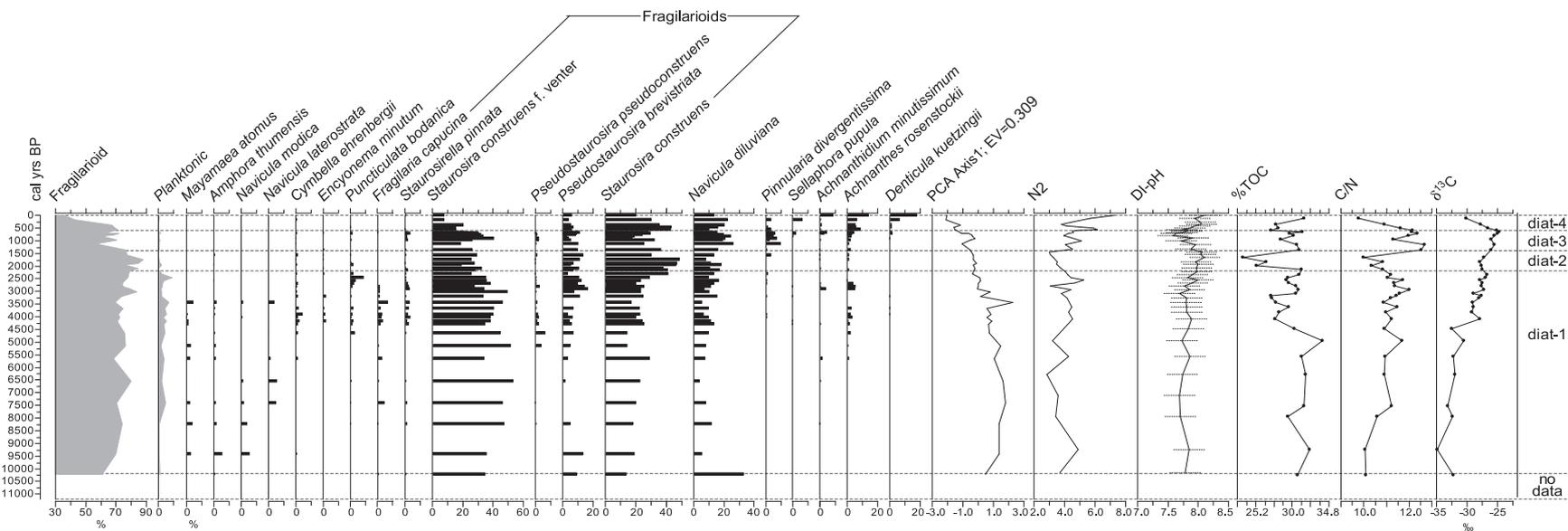


Fig. 5. Diatom relative abundance stratigraphy plotted on the calibrated age scale. Also shown are: (i) Fragilarioid and plankton groups; (ii) diatom taxa arranged according to their PCA axis 1 species scores; (iii) Significant PCA axis 1 sample scores (+eigenvalue; EV) and N2 diversity values; (iv) reconstructed diatom-inferred pH values; (v) %TOC; (vi) C/N ratios and (vii) $\delta^{13}\text{C}$ values. Diatom zones have been delimited using optimal partitioning.

more variable, with lows occurring especially between 2.0 and 1.6 ka BP (i.e. zone diat-2). C/N ratios ranged between 9.5 and 13.5 (11.1–15.8 atomic ratios), and $\delta^{13}\text{C}$ values between -24 and -35‰ . $\delta^{13}\text{C}$ increased steadily from -34.9‰ at c 9.3 ka BP to -24.8‰ at 0.7 ka BP, and declined by 5.3‰ towards the top of the profile (0.1 ka BP).

4.6. Multivariate analyses

Through the series of constrained, partial ordinations, several significant relationships are apparent (Fig. 7). Climate variables were important in influencing vegetation change: changes in insolation accounted for most variation (22.8%; $p = 0.002$) followed by GRIPT (8.5%; $p = 0.002$) and %HSG (4.0%; $p = 0.012$). Only P_{ann} did not result in significant change (2.8%; $p = 0.056$). Vegetation changes in the catchment significantly accounted for just under 20% of variation in diatom assemblage data. CLDE and TAIG explained most variation (6.9% and 6.8%; $p = 0.002$ and 0.004 respectively). Variation explained by TUND was marginally significant (4.6%; $p = 0.046$), while variation explained by STEP was not significant (2.7%; $p = 0.406$). The four climatic variables (insolation, %HSG, P_{ann} and GRIPT) explained 22.4% variation in the diatom data ($p = 0.002$). However, only insolation (13.8%; $p = 0.002$) and GRIPT (6.2%; $p = 0.006$) were uniquely significant (P_{ann} and %HSG were not significant in explaining any variation) (Fig. 7). Vegetation changes in the catchment had much less influence on chironomid assemblages, and only TAIG was significant in explaining any variation (6.3%; $p = 0.024$). However, past climate was substantially more important: insolation (7.4%; $p = 0.01$); P_{ann} (6.5%; $p = 0.018$); GRIPT (6.5%; $p = 0.024$). %HSG only accounted for 4% of variation ($p = 0.546$). Chironomids themselves accounted for a significant amount of variation in the diatom assemblage data (7.4%; $p = 0.002$). However, varying diatom assemblages also had a significant, albeit weaker, influence on chironomid assemblages through the Holocene period (4.9%; $p = 0.014$), and potential reasons for these observations are discussed below.

5. Discussion

5.1. Ecosystem stability and lake ontogeny

Compositional turnover in all three biological proxies was significant (Fig. 6), highlighting that major Holocene changes occurred both in the catchment and within the lake (Fig. 7). Vegetation turnover was similar to that observed for relatively species-poor boreal ecosystems in Sweden (Birks, 2007). However, diatom turnover gradient length was relatively low in comparison to other Holocene sequences (e.g. Michelutti et al., 2007), perhaps due to extreme continentality in central Asia and persistence of fragilarioid taxa (Westover et al., 2006). Zone boundaries indicate possible thresholds crossed for the different groups of organisms. At ESM-1, pollen and chironomid thresholds were crossed for the first time during the early Holocene, while for diatoms, thresholds were not crossed until much later. The significance of the dates when zones were delimited are discussed in detail below. We believe that our data also allows us to conclude that grazing pressures from chironomids had a significant influence on diatom communities, at least as important as vegetation-mediated changes in the catchment (Fig. 7). However, using diatoms as response variables also reveals that as a food source, they can also have a smaller, but still significant influence on chironomid assemblages, possibly influencing feeding strategies (Berg, 1994), which we have shown to vary through the Holocene at key periods (Fig. 4).

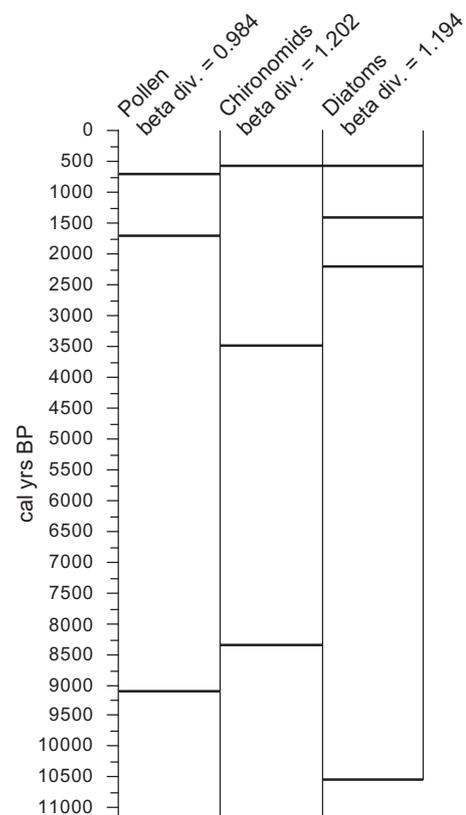


Fig. 6. Zones for each biological proxy delimited using optimal sum of squares partitioning. Significant compositional turnover (beta diversity; SD units) values for each proxy dataset are also given ($p = 0.05$; $n = 499$).

Deglaciated lakes in boreal regions have been shown to undergo directional change associated with the progressive loss of alkalinity and concomitant decline in pH (Renberg, 1990; Bradshaw et al., 2000; Engstrom et al., 2000; Bigler et al., 2002; Briner et al., 2006; Michelutti et al., 2007). These limnological processes are associated with changes in catchment soil properties, notably primary terrestrial succession, although the leaching of apatite from catchment soils has been put forward as an alternative theory (Boyle, 2007). However, limnological change at lake ESM-1 showed a markedly different response, highlighted by persistent, high diatom-inferred pH (DI-pH) values, due in the main to the dominance of alkaliphilous fragilarioids (Fig. 5). In the nearby Altai Mountains, diatom records from three shallow lakes exhibited broad similarities to ESM-1 (Westover et al., 2006). It is likely therefore that the ESM-1 ontogeny may be indicative of a regional pattern in shallow lakes that does not involve a progressive leaching of base cations from catchment soils (Fig. 5). The Glacier Bay region in Alaska experiences heavy rainfall, and although hydrological setting governs variation in ontogeny, lakes became more dilute and acid due to a reduction in groundwater discharge and increased surface run-off containing DOC (Engstrom et al., 2000). The eastern Sayan Mountains are semi-arid, and low precipitation levels may be important in the lack of hardened soil horizons and deep accumulations of peat (Engstrom et al., 2000). Alternatively, pH and conductivity measurements from ESM-1 suggest that the lake is well buffered (e.g. see Jones et al., 2011).

In Arctic and alpine regions, climate is suggested to be the principal driver of pH in poorly buffered lakes (Psenner and Schmidt, 1992; Michelutti et al., 2007), through variation in ice cover regulating dissolved inorganic carbon dynamics. A reduction

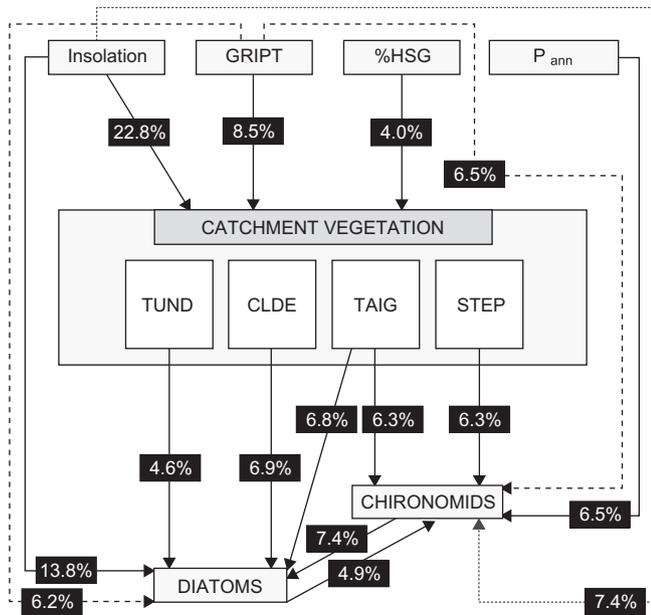


Fig. 7. Conceptual figure detailing only significant variances explained by (i) climate drivers on catchment vegetation, (ii) climate and biome drivers on aquatic organisms living in lake ESM-1. Climatic drivers were: July insolation at 60°N (W/m²) [insolation] (Berger and Loutre, 1991), palaeo-temperatures inferred from the GRIP borehole (°C) [GRIPT] (Dahl-Jensen et al., 1998), ice-rafted debris events in North Atlantic sediments [%HSG] (Bond et al., 1997), and pollen-inferred annual precipitation from Hoton-Nur, a lake situated in the Mongolian Altai (mm) [P_{ann}] (Rudaya et al., 2009). Catchment vegetation biomes were tundra [TUND], steppe [STEP], cold deciduous forest [CLDE] and taiga [TAIG].

in catchment ice cover is associated with an increase flux of base cations, and increased within-lake photosynthesis, leading to reconstructed increases in pH (e.g. Koinig et al., 1998). Fragilarioid taxa are opportunistic species and dominate assemblages in cold, alkaline, oligotrophic lakes, which have prolonged ice cover and short growing season (Lotter and Bigler, 2000; Michelutti et al., 2007). In sub-humid, European alpine lakes, mean July air temperature and length of ice cover have been shown to have significant influence on the distribution of fragilarioid species (Schmidt et al., 2004). We demonstrate that diatom assemblages at ESM-1 were significantly influenced by climatic variables, especially insolation and to a lesser degree northern hemisphere temperatures (Fig. 7). These variables have a direct influence on e.g. ice cover (Schmidt et al., 2004), which in turn influences availability of habitat for diatom colonisation. Modulation of pH in lake ESM-1 is also indirectly influenced by climate, via catchment mediation processes regulating the influence of catchment weathering on lake alkalinity and export of DOC from forest soils.

The longest held model of lake ontogeny is that of natural enrichment (Deevey, 1942). Long-term changes in primary production in lakes can be inferred by a variety of methods including spectrally inferred chlorophyll a (Chl a) concentrations (e.g. Michelutti et al., 2007), photosynthetic pigments (e.g. Leavitt and Hodgson, 2001), and stable isotope ratios of ¹³C/¹²C (δ^{13} C) in organic sediments (Leng and Marshall, 2004). In ESM-1, after an initial decline, δ^{13} C values gradually increased through the early to late Holocene by over +10‰. During periods of enhanced productivity, the availability of dissolved CO₂ in lakes becomes limited, and autotrophs such as algae increasingly use HCO₃ as a source of carbon, which results in elevated δ^{13} C values (Leng and Marshall, 2004). However, such a large shift in values at ESM-1 is unlikely to have occurred due to enhanced primary production alone (Meyers and Lallier-Vergès, 1999). We can rule out any significant

contribution of routinely higher δ^{13} C values (c -8‰ to -15‰) from C₄ land vegetation, because of the lack of pollen evidence for these plants (Fig. 3). However, progressively less negative δ^{13} C values have also been observed from lake sediments as lakes mature, because of burial of ¹²C-enriched organic matter into bottom sediments (Meyers and Lallier-Vergès, 1999).

δ^{13} C values in sedimentary organic matter may also be controlled by changes in catchment vegetation and the extent of soil respiration. For example, the development of stable, mature soils during the early Holocene can result in increased soil respiration and the supply of δ^{13} C-depleted dissolved CO₂ to lakes, leading to lower δ^{13} C values (Hammarlund, 1992; Wolfe et al., 2003; Reuss et al., 2010). This may be the reason for the observed decline in δ^{13} C values in ESM-1 sediments prior to 9 ka BP. Conversely, increasing δ^{13} C values has been interpreted due to forest retreat and subsequent reduction in catchment soil respiration (e.g. Reuss et al., 2010). At ESM-1, pollen evidence is inconclusive; pine forests dominate the landscape, and show little sign of retreat. However, over the period of increasing δ^{13} C values, the extent of taiga and cold deciduous forests show distinct declines, especially after 5 ka BP, perhaps associated with gradually declining chironomid-inferred mean July temperature, leading to a reduction in catchment soil respiration. Low C/N ratios highlight the importance of autochthonous sources of carbon to the lake (Meyers, 1994), although continuous delivery of allochthonous matter cannot be ruled out either.

5.2. Early Holocene environmental change (11.2–9.1 ka BP)

During the very early Holocene, pollen indicative of extensive tundra-steppe vegetation (*Betula* and *Artemisia*) were at highest values (Fig. 3). *P. sylvestris* pollen therefore, although initially very common, was most probably transported from wood-stands at lower elevation, or from the western region of the Sayan Mountains. Pollen indicative of a more open landscape rapidly replaced pine, and initially consisted of steppe vegetation (e.g. *Artemisia*), followed by mountain tundra communities, including *B. nana* and *Alnus fruticosa*. Opening up of the landscape also resulted in a more diverse flora (Fig. 3). This increase in steppe community has been observed elsewhere in northern Mongolia and the Lake Baikal region between c 11–10 ka BP (Tarasov et al., 2007). Reconstructed annual precipitation at nearby Hoton-Nur was at first very low, and although increased to peak amounts by 9.0 ka BP, between 11 and 10 ka BP, abrupt fluctuations were apparent (Fig. 8), concurrent with rapid increases in %HSG, indicative of a major ice-rafted debris (IRD7) event in the North Atlantic (Bond et al., 1997). Mackay et al. (2011) determined a significant shift in δ^{18} O_{diatom} values from Lake Baikal of +8‰ between c 10.3–10.2 ka BP, which they associated with increased Siberian High activity. Constrained RDA shows that %HSG played a small, but significant role in influencing vegetation in the Sayan Mountains (Fig. 7). Forest expansion resulted in the earliest pollen-delimited zone, indicating that a major threshold was crossed in catchment vegetation communities. Lowest δ^{13} C values were also observed (-34.9‰), which may be a result of forest expansion and concomitant increased soil respiration (Hammarlund, 1992; Reuss et al., 2010).

Chironomid assemblages were initially dominated by *T. lugens*, a cold stenotherm (Brundin, 1956; Brodin, 1986) typical of oligotrophic, subarctic and subalpine lakes. By 9.7 ka BP however, *C. anthracinus*, a thermophilic taxon, associated with relatively deep waters, replaced *P. lacustris*-type larvae, which typically occur in littoral zones of relatively warm, shallow lakes (Walker and MacDonald, 1995). At this time, there is a modest, but temporary increase in taxa with known associations with aquatic macrophytes, indirectly suggesting at least the presence of plants at this

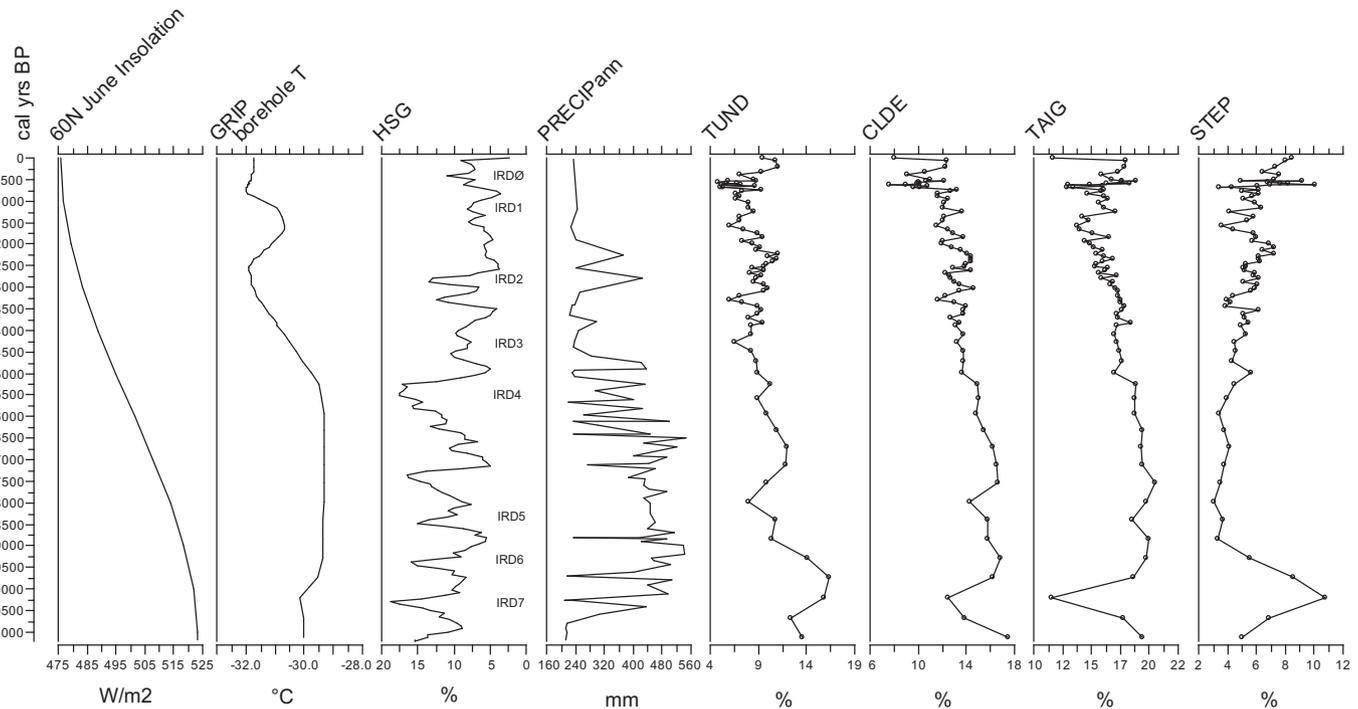


Fig. 8. Explanatory variables used in Fig. 7 above plotted on the calibrated age scale. July insolation at 60° N (W/m^2) (Berger and Loutre, 1991), palaeo-temperatures inferred from the GRIP borehole ($^{\circ}C$) (Dahl-Jensen et al., 1998), ice-rafted debris events in North Atlantic sediments (%HSG) (Bond et al., 1997), and pollen-inferred annual precipitation from Hoton-Nur (mm), a lake situated in the Mongolian Altai (Rudaya et al., 2009). Calculations of biome scores were performed using the PPPBase software (Guiot and Goegy, 1996).

time. Chironomid analysis from two other Mongolian lakes also suggests elevated lake levels prior to c 8.5 ka BP (Ilyashuk and Ilyashuk, 2007). Partial RDA revealed that changes in the taiga biome had a significant influence on chironomid assemblages, which may account for the observation that chironomid N2 diversity is highest during the initial period of forest expansion (Fig. 4). However, analyses revealed much stronger climatic influences on chironomids at ESM-1, especially insolation, northern hemisphere temperatures and regional precipitation. Overall, catchment changes, unlike climate, seemed not to be a major influence on chironomid populations in lake ESM-1. This is in contrast to findings from Sagistalsee, a remote mountain lake in the European Alps, where only catchment variables were found to have a significant influence on aquatic communities, not past climate (Lotter and Birks, 2003).

5.3. Early–late Holocene environmental change (9.1–0.7 ka BP)

Boreal forest communities dominated the landscape surrounding lake ESM-1 during much of the Holocene (Fig. 3). The rapid expansion of Scots pine (*P. sylvestris*) and Siberian pine (*P. sibirica*) (a major component of dark, coniferous taiga) at c 9.1 ka BP is similar to the expansion observed in nearby Mongolian lakes e.g. Hovsgol (Prokopenko et al., 2007). Forest expansion at ESM-1 occurred slightly later than in other sequences from lakes with a more westerly location on the Ulagan plateau of the Altai Mountains (Blyakharchuk et al., 2004) but at a substantially earlier date than observed in Lake Baikal to the east (Demske et al., 2005) (Fig. 1). Reconstructed annual precipitation from Hoton-Nur remained high until c 4.5 ka BP, while GRIP borehole temperatures were highest up to c 5.0 ka BP. Relatively humid environments resulted in maximum taiga biome reconstructed between c 9 and 5 ka BP (e.g. see also Bezrukova et al., 2005; Prokopenko et al., 2007). Up until 0.7 ka BP, forest tundra communities persisted in the catchment of ESM-1, characterised especially by *P. sibirica* and

B. nana, although tundra shrubs gradually declined up until 0.7 ka BP. Climate change likely drove these long-term trends, especially changing insolation associated with orbital forcing (e.g. Bush, 2005), which accounts for over a fifth of the variation in vegetation communities (Fig. 7). However, what we have not accounted for in our study is the influence of wildfire, which is an important process in driving ecological change in boreal regions (e.g. Bonan and Shugart, 1989; Soja et al., 2007).

Chironomid assemblages in ESM-1 were still dominated throughout the early to late Holocene by fluctuating cold stenothermic species (Brundin, 1956; Brodin, 1986). Diatom communities were dominated by fragilarioid taxa, which are well-adapted to growing in cold, ice-covered lakes. However, there were some interesting and subtle changes. The presence of the planktonic diatom *Punctulata bodanica* likely suggested that during summer months the lake was relatively deep, and together with *Fragilaria capucina* that ice cover duration was relatively short (Schmidt et al., 2004). This may account for the presence of abundant aquatic macrophytes, indirectly suggested through the increase in chironomid taxa with known plant associations between c 3.0–2.0 ka BP. Prior to c 3.5 ka BP, a diverse naviculoid flora dominated by *N. diluviana* and *Mayamaea atomus* highlighted a minor but persistent influence of marshy, littoral habitats on diatom assemblage composition (Van Dam et al., 1994; Robertsson, 1995). Higher C/N values between 8.0 and 3.0 ka BP may be indicative of small quantities of terrestrial carbon having entered the lake.

Between 1.7 and 0.7 ka BP, light-coniferous taiga forest dominated the landscape. Vegetation diversity was low (Fig. 3), because light-coniferous forests are less productive and floristically rich than dark-coniferous forests (Soja et al., 2007). These observations tie in well with reconstructed climate parameters: a relatively short-lived peak in northern hemisphere temperatures (GRIP) and low amounts of precipitation (Fig. 8). These climatic patterns are consistent with a period of warmer temperatures and hydrological anomalies experienced in the northern hemisphere, sometimes referred to as

the Medieval Climate Anomaly (Stine, 1998; IPCC, 2007). Climatic changes at this time resulted in significant changes to the aquatic ecosystem of ESM-1. A major shift in diatom assemblage composition occurred (Fig. 6), with a marked decline in fragilarioid taxa and concomitant increase in species diversity indicative of greater habitat availability (e.g. Douglas and Smol, 2010). The decline in pH between 1.4 and 0.6 ka BP occurs at the same time as a small peak in northern hemisphere temperatures, and relatively high CI-July temperatures at ESM-1. It may well be that permafrost melted to a degree, and allowed increased concentrations of DOC to enter the lake to reduce pH. During this period, *P. divergentissima* is abundant, and although it not a common species, in northern alpine and arctic regions it prefers aerial habitat locations such as forest mosses (Krammer, 2000; Van Kerckvoorde et al., 2000). Its presence, together with peak C/N ratios, suggests increased allochthonous transport to the lake between 1.5 and 0.6 ka BP.

5.4. Recent environmental change (0.7 ka BP – present)

Zonation of each proxy provides the strongest evidence for a major period of landscape disturbance occurring c 0.7 ka BP, quickly followed by lacustrine change at 0.6 ka BP (Fig. 6). The start of this period occurs at the same time as measured increases in % HSG, linked to the slow down in North Atlantic THC (IRD 0; Bond et al., 1997, Fig. 8). Geomorphological evidence exists in the Sayan Mountains for young moraines at this time, associated with re-advancing glaciers (Ivanovsky and Panychev, 1978 in Shahgedanova et al., 2002), indicative of cooler, regional environments (Krenke and Chernavskaya, 2002). Chironomid-inferred temperatures also showed a distinct cooling, reaching a low value of 12.3 °C at 0.2 ka BP, although we acknowledge that the temporal resolution was low.

At c 0.7 ka BP, alpine meadow vegetation (e.g. Poaceae, *Thalictrum* spp.) expanded, followed shortly by increased *P. sibirica* and *P. obovata* (Siberian spruce). Siberian spruce pollen is deposited locally, and likely represents real increases in tree abundance along river valleys and the lake shoreline (Bezrukova et al., 2005). Siberian spruce is characteristic of soils with elevated moisture content (e.g. which are frequently water-logged) and along with *Larix*, can tolerate cold climates associated with a high degree of continentality (Bezrukova et al., 2005). Other taxa indicative of more moist conditions include increases in sedge pollen, and the appearance for the first time of *Sphagna* bog mosses. These changes are similar to changes in vegetation composition reconstructed from peat bog sequences from the northern shore of Lake Baikal (Bezrukova et al., 2006). There are a number of factors that may have caused significant changes to these upland ecosystems, such as climate, human impact and wildfires although at present we are unable to evaluate the latter two conclusively. Climatically, colder temperatures likely resulted in increased cloud formation and precipitation due to the exponential decline of saturation vapour pressure (Bush, 2005). Domestication of reindeer is thought to have taken place in the Sayan Mountains thousands of years ago, and for at least the last 100 years reindeer, along with other animals including horses and cattle, have been extensively utilised (Ingold, 1986). Wildfires are an important factor in governing floristic diversity in boreal forests (Bonan and Shugart, 1989), and wildfires may have declined during this period, although we have no charcoal evidence to confirm the influence of fire at this time. The decline in $\delta^{13}\text{C}$ values from c 0.6 ka BP to present coincides with major shifts in catchment vegetation and aquatic communities. The decline in $\delta^{13}\text{C}$ values may represent a decline in overall aquatic productivity (Leng and Marshall, 2004). However, values may also have been influenced by increased hydrological delivery of ^{13}C -depleted dissolved CO_2 (Wolfe et al., 2003), linked to pollen

evidence for the expansion of spruce forests, which may have resulted in increased soil respiration. In all likelihood there will be multiple influences on the $\delta^{13}\text{C}$ record, and estimating their relative importance remains a significant challenge.

In the last c 0.15 ka BP, CI-July temperatures increased, in line with prevailing warming temperatures experienced globally since the end of the LIA. Although *Denticula kuetzingii* appeared in the record for the first time at c 0.6 ka BP, valves only occurred in substantial abundances after c 0.2 ka BP. This is an epiphytic diatom commonly found growing on aquatic mosses, usually in the littoral region of lakes and ponds (Round, 1959). Its occurrence in lake sediments has been interpreted as an indicator of increased moss epiphytes (linked to shorter ice cover duration) (Keatley et al., 2008). An increase in aquatic macrophytes is also indirectly indicated by the increase in chironomids with known plant associations. Elsewhere in the region, recent warming trends have been linked to, for example, the expansion of Siberian pine (*P. sibirica*) into the mountain tundra belt of the Western Sayan Mountains (Kharuk et al., 2008), and to significant increases in surface water temperature (Hampton et al., 2008) and decline in ice cover thickness (Todd and Mackay, 2003) in Lake Baikal. Over the past 150 years, observations of $\delta^{13}\text{C}$ in atmospheric CO_2 have shown a decline in values (of c 1.7‰) linked directly to increasing CO_2 emissions into the atmosphere from fossil fuel combustion (i.e. Suess effect; Keeling, 1979). However, the initial decline at c 0.7 ka BP precludes significant impact from fossil fuel combustion, and therefore a decline in aquatic productivity or increase in delivery of ^{13}C -depleted dissolved CO_2 are the most likely causes, at least for the period concurrent with the Little Ice Age.

In conclusion, our observations provide no evidence for long-term oligotrophication and natural acidification at lake ESM-1 in the eastern Sayan Mountains. This is in contrast to many other boreal lakes of glacial origin, where buffering capacity is low, or precipitation levels are high. Major ecosystem change is apparent in the lake and its catchment at between 0.7 and 0.6 ka BP, indicative of thresholds crossed for all three groups of organisms. This period is concurrent with IRD0, and generally cooler, more moist conditions in the eastern Sayan Mountains. In the last 150 years however, there are distinct increases in measures of aquatic diversity, which are likely linked to increasing regional temperatures and the opening up of new habitats in and around the margins of the lake, similar to other high latitude and high altitude sites.

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