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Millennial-scale vegetation history of the north-eastern Russian Arctic during the mid-Pliocene inferred from the Lake El'gygytgyn pollen record

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ABSTRACT

The 318-m long sediment record from Lake El'gygytgyn, NE Russia situated in the present-day herb tundra zone, provides a unique archive of high Arctic environmental changes since ca 3.6 million years ago (Ma). This paper focuses on pollen-derived vegetation change during the mid-Pliocene Warm Period (mPWP) and in particular during Marine Isotope Stage (MIS) M2, which is known to represent the coldest interval of the Pliocene. Building on initial pollen studies, we provide a more complete record and a more detailed discussion of climatically-driven vegetation and environmental changes in the northeastern Russian Arctic, spanning the 203-thousand-year interval between 3.383 and 3.180 Ma ago. Pine-spruce-fir-larch-Douglas fir forests dominated the area around Lake El'gygytgyn between 3.383 and 3.330 Ma (MIS MG4 - MIS MG2). Colder and drier climate caused a decrease of coniferous forests and widespread *Sphagnum* habitats around the lake between 3.370 and 3.357 Ma. After 3.3 Ma, the presence of spruce, fir and Douglas fir decreased again. A very pronounced cooling took place at the first half of MIS M2 (3.312–3.283 Ma), when treeless tundra- and steppe-like habitats became common in the regional vegetation. Climate conditions were similar or only slightly warmer and wetter to those of the Holocene. Numerous coprophilous fungi spores identified in the MIS M2 pollen samples suggest the presence of grazing mammals around the lake. Larch-pine forests with some spruce started to dominate the area again after ca. 3.282 Ma, thus pointing to a significant climate amelioration during the mPWP. However, the forested area decreased, while herb- and shrub-dominated vegetation spread again during MIS KM6 (especially 3.235–3.223 Ma), suggesting a noticeable climatic deterioration and relatively cold and dry conditions.

1. Introduction

Realistic predictions of future climatic change and its regional and global consequences depend on a profound understanding of the climatic and environmental variability on geological timescales, when boundary conditions may have been different from today. One focus of the paleoclimatic research has been put on Late Pliocene (i.e., the Piacenzian, ~3.6–2.6 Ma), especially driven by the Pliocene Research Interpretations and Synoptic Mapping (PRISM) project (e.g. Dowsett et al., 2010, 2016 and references therein) and the Pliocene Model Intercomparison Project, the so-called PlioMIP (e.g. Haywood et al., 2013, 2016 and references therein). The Piacenzian Stage spans a critical period in Earth climate history, with the transition from the relatively warm Pliocene climate to the substantially cooler Pleistocene one (e.g. Schepper et al., 2014 and references therein). The mid-Pliocene (mid-Piacenzian), ~3.3–3.0 Ma has been defined as the most recent period in Earth history with an atmospheric CO_2 concentration comparable to today but a global air temperature 2–3 °C higher than modern (e.g. Dowsett et al., 2010; De Schepper et al., 2013; Willeit et al., 2013 and references therein). With widespread recognition that human activity has been the dominant driver of observed recent climate change, understanding the Pliocene climate without anthropogenic influence became especially important (e.g. Dowsett et al., 2016 and references therein).

The so-called mid-Pliocene (mid-Piacenzian) Warm Period (mPWP; ~3.3–3.0 Ma) has rather intensively been studied by numerical climate modelling, since it is regarded as an analogue of future global climate (e.g. Haywood et al., 2013, 2016; Schepper et al., 2014; Prescott et al., 2014; Dolan et al., 2015 and references therein). In contrast, relatively little is known about natural processes during this interval, which may help to understand the long-term effect of increasing CO_2 levels on environmental conditions. The data-model comparisons for the mPWP

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interval have identified specific regions of concordance and discordance between climate model outputs and the proxy data as yet available (e.g. Prescott et al., 2014; Howell et al., 2016). In the Northern Hemisphere, the model-predicted surface air temperatures reveal a substantial cold bias, with particularly strong data-model mismatches occurring in annual temperatures in Northern Russia (Salzmann et al., 2013). Moreover, the proxy data suggest an interval with a climate similar or even cooler than modern during the mPWP. For example, De Schepper et al. (2013) interpreted a sharp increase in oxygen isotopes over 20 kyr (~3.312–3.285 Ma) as an intensive glaciation within the longer relatively cold interval of MIS M2 (~3.312–3.264 Ma), and referred this event as a failed attempt of the climate to reach a full glacial state. The M2 lasted 50 kyr with corresponding sea-level drop of ca 20–60 m, therefore the M2 ice sheets were not only confined to Greenland but must have broader spread out over Northern Hemisphere (Tan et al., 2017).

The existing oxygen isotope data and temperature reconstructions are mostly based on marine geological records. Although these records tend to detect the MIS M2 cooling, the exact nature of this event remains enigmatical (Dolan et al., 2015 and references therein). An important prerequisite for the better understanding of long-term climate trends during the mPWP warm interval, which includes the significant MIS M2 cooling, is the multiproxy investigation of high-resolution terrestrial records.

The sediment record from Lake El'gygytgyn, situated in a meteorite impact crater in northeastern Russian Arctic (67°30′ N, 172°05′ E, Fig. 1), is such an archive, which has stored the information about environmental changes since ~3.6 Ma in high sensitivity and temporal resolution (for details see Melles et al., 2012 and references therein). A first, although low temporarily-resolved compilation of multiproxy data obtained from the Pliocene part of the El'gygytgyn sediment record was provided by Brigham-Grette et al. (2013). The lake sediments continuously trapped pollen from a several thousand square-kilometer catchment, thus providing reliable insights into the history of regional and over-regional vegetation and climate changes. The data suggest extreme warmth and polar amplification during the middle Pliocene (~3.6–3.4 Ma), when summer temperatures were ~8 °C higher then today (Tarasov et al., 2013). The relatively high sedimentation rate in Lake El'gygytgyn during the Pliocene (Melles et al., 2012; Brigham-Grette et al., 2013) allows for sub-Milinkovic pollen-based environmental reconstructions for the mPWP. Building on the previous pollen studies (Brigham-Grette et al., 2013; Andreev et al., 2014), we present here a high-resolution, millennial and/or even centennial-scale pollen record with an average temporal resolution of ca. 400 yr for intervals with sufficient recovery. The new data enable a more detailed zonation of the revealed pollen assemblages and more precise boundaries between pollen zones resulting in more precise chronology of the reconstructed environmental changes. The record is documenting climatically-driven environmental changes in the northeastern Russian Arctic between ~3.383 and 3.180 Ma, with particular focus on the paleomagnetic Mammoth Subchron including the coldest Pliocene interval, MIS M2. Such unique high-resolution terrestrial record is an important step for the better understanding of long-term environmental trends and forms a reliable basis for improvements of climate simulation scenarios.

2. Lake setting

Lake El'gygytgyn is located in an impact crater of 18 km diameter, which was formed about 3.58 Ma in an Upper Cretaceous volcanic plateau of the northeastern Russian Arctic (Fig. 1; for details see Melles et al., 2012 and references therein). The modern lake is 170 m deep and 12 km wide, being situated at 492 m above sea level. The lake is covering an area of 110 km^2 within a 293 km^2 large catchment that is defined by the crater rim.

The study region is characterized by an extremely harsh climate.

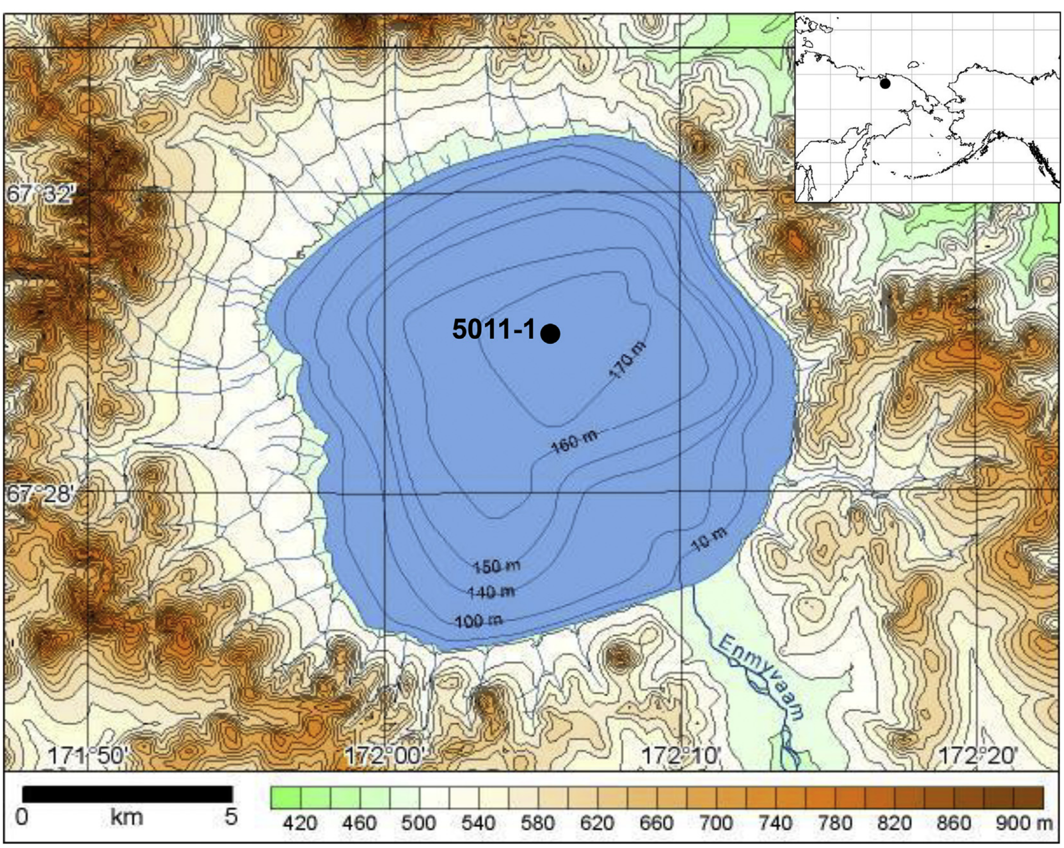

Fig. 1. Location of Lake El'gygytgyn in northeastern Russia (inserted map) and position of ICDP Site 5011–1 in the lake center.

Mean annual air temperatures amount to ca. -10 °C, with mean January temperatures and mean July temperatures ranging between −32 and − 36 °C and 4 and 8 °C, respectively (Nolan and Brigham-Grette, 2007). The precipitation consists of ca. 70 mm summer rainfall and ca. 110 mm water equivalent of snowfall. The study area is located in the continuous permafrost zone with a mean annual ground temperature of −10 °C at 12.5 m below the ground surface (Schwamborn et al., 2008).

Lake El'gygytgyn is located in the subzone of southern shrub and typical tundra (Galanin et al., 1997). The modern tree line (northern larch taiga) is positioned roughly 100 km to the south and west of the lake. Although the northern boundary of shrub alder and stone pine distribution is reported to be located further to the north of the lake, only dwarf birches and willows were observed in the lake vicinity growing in more protected habitats. For a more detailed description of the local vegetation, see Andreev et al. (2012), Lozhkin and Anderson (2013) and references therein.

3. Material and methods

Within the scope of the International Continental Scientific Drilling Program (ICDP), in 2009 three holes were drilled in the center of the Lake El'gygytgyn (site 5011–1), penetrating about 318 m of lake sediments and additional 200 m into the underlying impact rocks (Melles et al., 2011; Melles et al., 2012). Unfortunately, the core recovery in the Pliocene part of the ICDP core was only about 52% in average, with some major recovery gaps within complete sediment units of high temporal resolution (for details see Melles et al., 2011; Wennrich et al., 2016). High-resolution pollen analyses were conducted in the interval from 220.13 to 169.17 m depth below lake floor of the core composite, corresponding to the time interval from ~3.383 to ~3.180 Ma. The age model is based on magnetic polarity stratigraphy and cyclostratigraphy of various climatically-controlled sedimentological and geochemical parameters (for details see Haltia and Nowaczyk, 2014; Nowaczyk et al., 2013). The pollen record presented in this study includes 242 pollen spectra with a time resolution of about 400 years or higher where possible.

For pollen preparation on subsamples of ca. 1 g, a standard HF technique was applied (Berglund and Ralska-Jasiewiczowa, 1986). A tablet of *Lycopodium* marker spores was added to each sample for calculating total pollen and spore concentrations following Stockmarr (1971). Water-free glycerol was used for sample storage and preparation of the microscopic slides. Pollen and spores were identified at magnifications of 400×, with the aid of published pollen keys and atlases (Kupriyanova and Alyoshina, 1972, Kupriyanova and Alyoshina, 1978; Bobrov et al., 1983; Reille, 1992, 1995, 1998). In addition to pollen and spores, a number of non-pollen-palynomorphs, such as fungi spores, as well as microscopic remains of algae and invertebrates were also identified when possible and counted, since they are valuable indicators of past environments (van Geel, 2001 and references therein).

At least 250 terrestrial pollen grains were counted in each sample. The relative frequencies of individual pollen taxa were calculated from the sum of terrestrial pollen taken as 100%. Spore percentages are based on the sum of pollen and spores. The percentages of non-pollen palynomorphs are based on the sum of pollen and non-pollen palynomorphs, and the percentages of algae are based on the sum of pollen and algae. The TGView software (Grimm, 2004) was used for the calculation of percentages and for drawing the diagram (Fig. 2). The diagram was zoned by a qualitative inspection of significant changes in pollen assemblages, pollen concentrations, and occurrence of particularly indicative taxa. The software Adobe Illustrator was used for preparation of the final version of the diagram.

For quantitative interpretation of the pollen record, the biome reconstruction method, also known as "biomization" (Prentice et al., 1996) was used. The method's key advantages are twofold. First, it performs an ecologically/climatically-defined translation of the pollen data into numerical scores of the major regional vegetation types (i.e. biomes) and thus allows for an objective vegetation reconstruction around the study site (Prentice et al., 1996; Tarasov et al., 2013). Second, it facilitates the data-model comparisons, as the pollen-derived and climate-simulated biomes are defined based on the same set of bioclimatic parameters (Prentice et al., 1992, 1996). Both these advantages have been proven in several studies in northern Eurasia (e.g. Tarasov et al., 1998, 2000; Bigelow et al., 2003) and on Lake El'gygytgyn (Melles et al., 2012; Brigham-Grette et al., 2013; Tarasov et al., 2013; Zhao et al., 2015; Zhao et al., 2018; Zhao et al., 2019). For comparison with these studies, we followed the same reconstruction protocol and applied the same biome-taxon matrix as in these publications. Tarasov et al. (2013) further exploited the potential of the biome reconstruction approach. By calculating the difference between the maximal forest biome score and the maximal non-forest biome score, a qualitative assessment of the landscape openness can be achieved with a higher confidence compared to a more traditional approach using arboreal and non-arboreal pollen percentage variations (see Tarasov et al., 2013 for details of the method and validation).

4. Results

4.1. Pollen analysis

A total of 115 different pollen, spore, and non-pollen-palynomorph types have been found in the studied samples (Fig. 2). The revealed pollen assemblages were subdivided into 6 main pollen zones (PZ), which were partly further subdivided into subzones, keeping the zone numbering introduced by previous pollen studies of the core (Brigham-Grette et al., 2013; Andreev et al., 2014).

PZ-6 (~3.383–3.348 Ma) assemblages are dominated by pollen of *Pinus* (up to 50%), *Picea* (up to 25%), *Larix/Pseudotsuga* (up to 20%), *Alnus* (up to 20%), *Betula* sect. *Nanae* (up to 18%), Poaceae (up to 25%), and Cyperaceae (up to 20%). Spores of *Sphagnum* are also an important component in this zone. The pollen concentration reaches up to 24,540 grains/g. PZ-6 is subdivided into 3 subzones, with PZ-6b differing from PZ-6a and PZ-6c by notably lower concentrations of coniferous pollen and *Sphagnum* spore percentages, while percentages of Poaceae pollen and coprophilous fungi spores are distinctly higher.

PZ-7 (~3.348–3.312 Ma BP) is subdivided into 2 subzones. PZ-7a (~3.348–3.329 Ma BP) is distinguishable by higher contents of *Picea* and *Larix/Pseudotsuga* pollen, lower contents of *Alnus* and *Betula*, and low pollen concentration (up to 2030 grains/g). Contents of Poaceae are relatively high (up to 35%) and coprophilous fungi spores are also rather abundant in the subzone. In PZ-7b (~3.329–3.312 Ma BP), *Larix/Pseudotsuga* pollen percentages drastically decrease, while contents of *Alnus* and *Betula* pollen significantly increase. This subzone is also noticeable for a much higher pollen concentration (up to 11,450 grains/g) compared to PZ-7a.

PZ-8 (~3.312–3.283 Ma BP) is characterized by a further decrease in coniferous pollen percentages, while the amounts of Poaceae, Cyperaceae, *Artemisia*, Caryophyllaceae, and other herb pollen as well as *Selaginella rupestris* and coprophilous fungi spores distinctly increase. PZ-8 is also noticeable by a small peak of cysts of *Zygnema* (green algae). The pollen concentration, in general, is relatively low (up to 5690 grains/g).

PZ-9 (~3.283–3.237 Ma BP) shows a gradual increase in coniferous pollen percentages, while the amounts of *Artemisia* and Caryophyllaceae pollen, *Selaginella rupestris,* and coprophilous fungi spores drop significantly. The pollen concentration is significantly higher (up to 25,380 grains/g) than in PZ-8.

PZ-10 (~3.237–3.223 Ma BP) is distinguishable by a pronounced decrease in the percentages of coniferous (*Picea*, *Pinus*, *Larix/Pseudotsuga*) and *Alnus* pollen as well as *Sphagnum* spores, while contents of herbs (mostly Poaceae, *Artemisia*) and *Selaginella rupestris* spores increase. The pollen concentration is low (in average ca 2310 grains/g) in this zone.

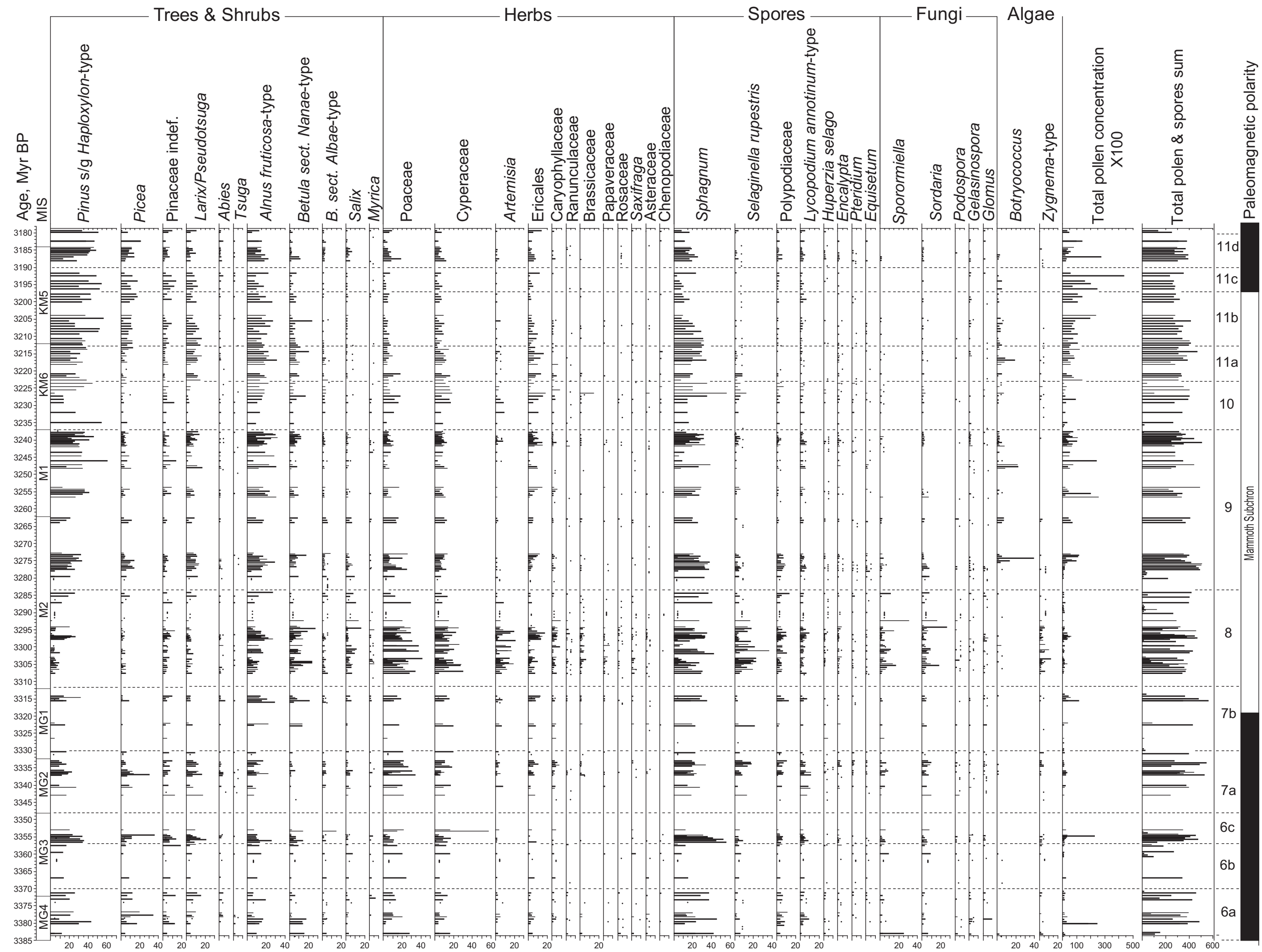

Fig. 2. Percentage pollen, spore, and non-pollen-palynomorph diagram of the time interval 3.382 to 3.198 Ma ago of the Lake El'gygytgyn record. The first graph shows the most common pollen and spores types and the second graph shows the minor pollen and spores types.

In PZ-11 (~3.223–3.180 Ma BP), the pollen concentrations are distinctly higher than in PZ-10 (up to 24,580 grains/g). This zone is additionally characterized by a further increase in *Pinus s/g Haploxylon*, *Picea*, and *Larix/Pseudotsuga* pollen contents. Also notable is a higher abundance of *Botryococcus* (green algae) colonies. PZ-11 can be subdivided into 4 subzones: PZ-11a (~3.223–3.212 Ma BP) is distinguishable by low contents of *Picea* and a relatively low pollen concentration (up to 4340 grains/g), PZ-11b (~3.212–3.197 Ma BP) demonstrates higher contents of *Picea* (up to 18%) and an increase in pollen concentration, PZ-11c (~3.197–3.190 Ma BP) differs by lower contents of herb pollen and the highest pollen concentrations (up to 40,540 grains/g), and PZ-11d (~3.19–3.18 Ma BP) is characterized by distinctly higher percentages of herb pollen.

4.2. Biome and landscape openness reconstruction

The results of the biome reconstruction and distribution of the non-biomized samples with low pollen counts (40 of 155 analyzed levels) are shown in Fig. 3A. Five biomes are reconstructed to have been dominant in the regional vegetation at least once during the study period: cool conifer forest (COCO), taiga (TAIG), cold deciduous forest (CLDE), tundra (TUND), and cold steppe (COST). While CLDE biomes are predominant during the whole study interval (assigned to 73 of 115 analyzed spectra), the TAIG (11 spectra) and TUND (25 spectra) occupied much shorter time intervals. The COCO biome is reconstructed only five times. One pollen spectrum, dated to 3.2981 Ma, reveals a highest score for the COST biome. Spectra with low pollen contents build three clusters in the lower, middle and upper part of the record, in close association with the TUND and COST biomes. The landscape openness curve (Fig. 3B) demonstrates a well-visible shift from the predominantly open or mixed vegetation landscape prior to 3.2885 Ma to the landscape covered with woody vegetation (i.e. mainly cold deciduous forest and taiga biomes) after this date. The maximum openness of the landscape around Lake El'gygytgyn and predominantly tundra vegetation are reconstructed during the coldest interval of the M2 glaciation (ca. 3.3100–3.2885 Ma), as indicated by the marine isotope record (Fig. 3C).

4.3. Discussion and interpretation

4.3.1. Environmental conditions prior to 3.383 Ma ago

The vegetation at Lake El'gygytgyn prior to 3.383 Ma BP, during MIS MG7, MG6 and MG5, was discussed in detail by Andreev et al. (2014). They found highest contents (up to 40%) of *Larix/Pseudotsuga* pollen type in the respective sediments. This could be traced back to a dominance of larch in the region. However, it is also possible that these pollen grains are at least partly produced by *Pseudotsuga* (Douglas fir). This suggestion is indirectly supported by relatively high percentages of

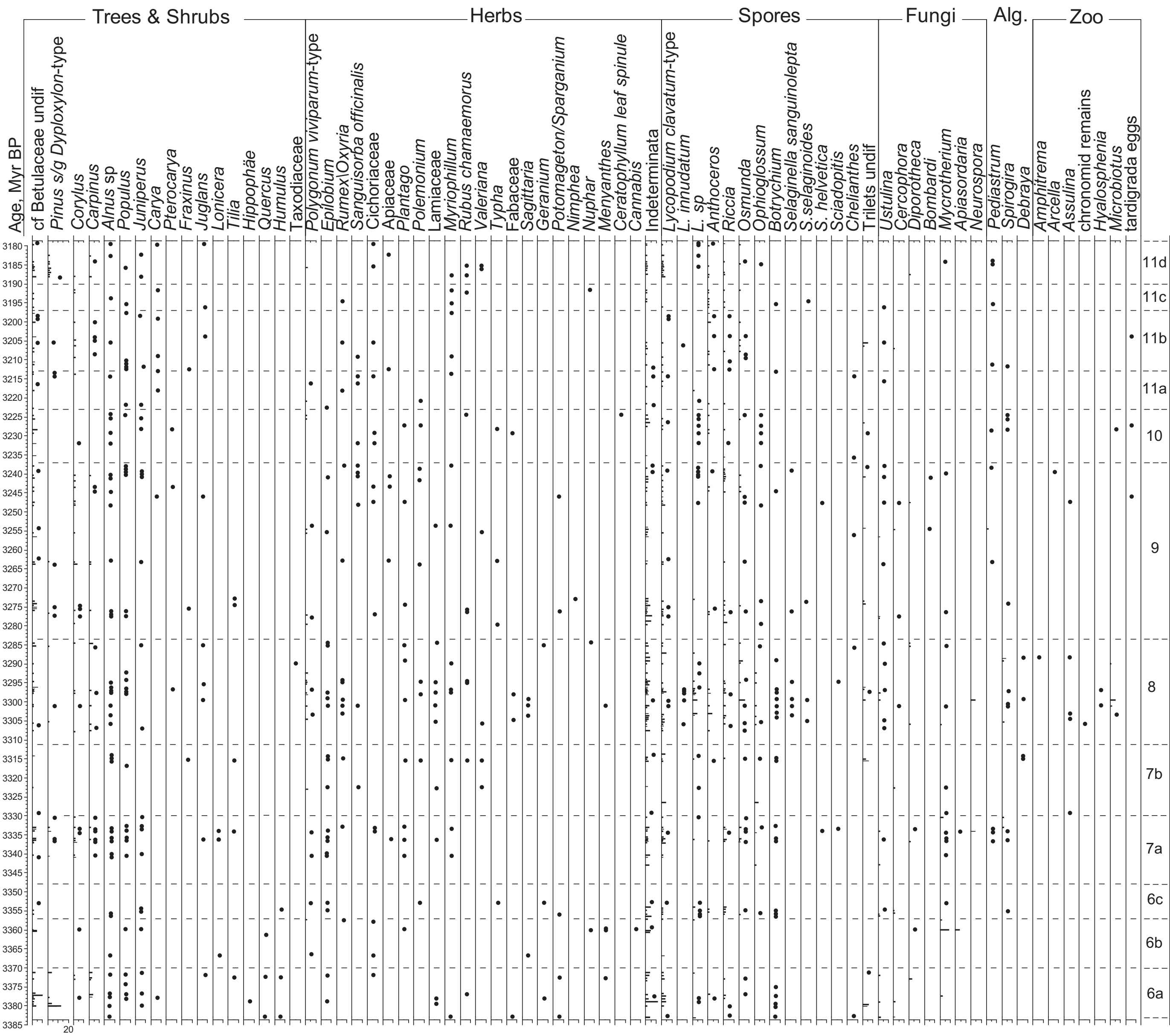

Fig. 2. (*continued*)

Picea, *Abies*, and *Tsuga* pollen (up to 40, 25, and 5%, respectively), as well as the presence of single pollen grains of some relatively thermophilic taxa, such as *Corylus, Quercus, Carpinus, Tilia*, Taxodiaceae, *Juglans,* and *Carya* (Andreev et al., 2014). Wood remains of firs in the sediments accumulated during MIS MG5, between 3.413 and 3.395 Ma BP (Fig. 4), suggest that firs were rather numerous around the lake during this period.

Pine stands were also abundant in the local vegetation before 3.383 Ma BP (Andreev et al., 2014). However, it is difficult to conclude whether pollen of *Pinus* s/g *Haploxylon* type was produced by tree pines, (such as the modern taxa *P. sibirica* and *P. koraiensis,* belonging to this subgenus and today growing in southern Siberia and southern Far East), or by shrub pines (namely *P. pumila,* which is broadly distributed today in northeastern and southeastern Siberia, Kamchatka and northern Japan). Because of the high pollen contents of *Picea* and *Abies* as well as the permanent presence of *Tsuga* (up to 5% in some samples), we assume that a high proportion of the *P.* s/g *Haploxylon* pollen was produced by tree pines. However, the relatively high content of *Alnus fruticosa*-type pollen, reflecting that shrub alder was also common in the regional forests, is an indirect evidence that stone pine also might have grown in the area, probably at higher elevations.

4.3.2. Environmental conditions between 3.383 and 3.312 Ma ago

After 3.383 Ma BP, a significant decrease in *Picea* and *Abies* pollen percentages along with an increase in dwarf *Betula* and herbs (mainly Poaceae, Cyperaceae and *Artemisia*; PZ-6a, Fig. 2), point to colder and drier climate conditions in the study area during MIS MG4. The pollen assemblages indicate that forests with pine, larch and possibly Douglass fir dominated the vegetation, but open, herb-dominated habitats were also common around the lake. This suggests a significant climate deterioration at the onset of MIS MG4, which coincides well with a respective deterioration deduced from pollen assemblages in sediments deposited in Lake Baikal around 3.39 Ma BP (Demske et al., 2002).

Between 3.370 and 3.357 Ma BP (PZ-6b, first part of MIS MG3), pollen assemblages show a significant decrease in percentages of coniferous pollen along with an increase in dwarf *Betula* and herbs (mainly Poaceae, Cyperaceae, and *Artemisia*; Fig. 2). Furthermore, spores of *Selaginella rupestris* (an important indicator of dry environments)

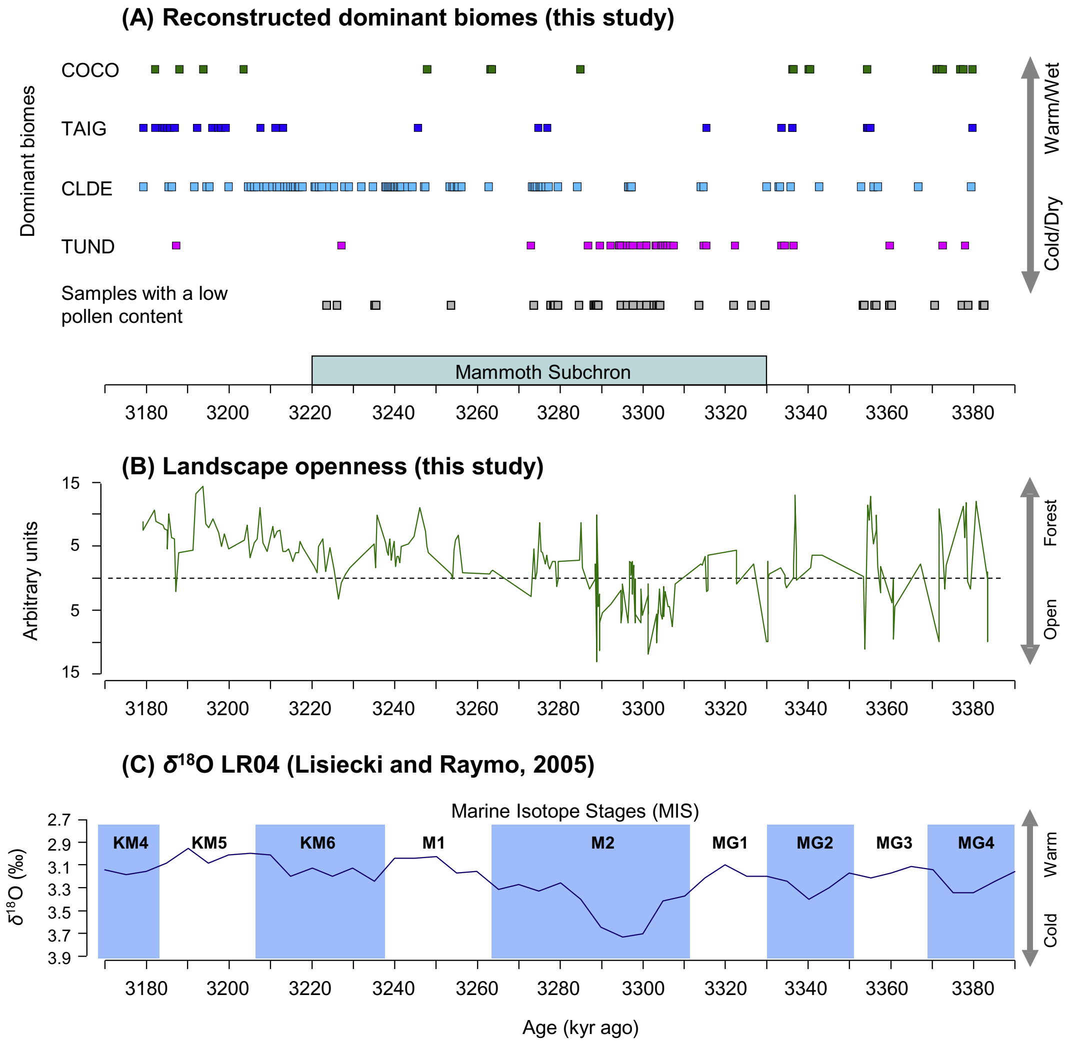

Fig. 3. A - Reconstructed dominant biomes (this study), B - Landscape openness (this study), C– Marine Isotope Stages according (Lisiecki and Raymo, 2005).

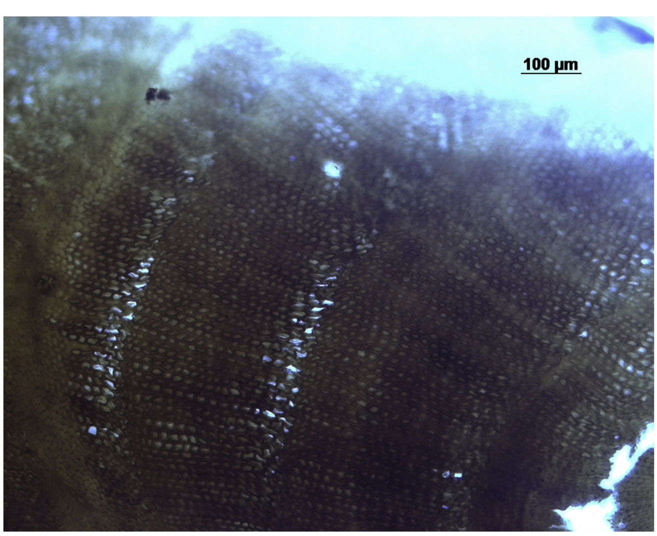

Fig. 4. Microtome sections of an *Abies* sp. twig found in the lake El'gygytgyn core. Photo by V.R. Filin (Moscow State University).

became more common in pollen assemblages, while amounts of *Sphagnum* spores decrease. Some increase in coprophilous fungi spores also indirectly documents that open herb-dominated habitats became more common in vegetation. In total, these changes in pollen spectra reflect a trend to relatively dry and cold climate conditions. Between 3.357 and 3.348 Ma BP (PZ-6c, second part of MIS MG3) coniferous stands (especially *Picea* and *Larix/Pseudotsuga*) and *Sphagnum* habitats further increased (Fig. 2), reflecting warmer and wetter climate conditions.

After ~3.348 Ma BP (PZ-7a, Fig. 2), pollen assemblages show increases in herb (Poaceae, Cyperaceae, *Artemisia*, Caryophyllaceae, *Artemisia*) contents. These changes suggest the presence of treeless habitats in the area and indicate that environmental conditions became much cooler and dryer than before in the course of the MIS MG2 cooling. A significant increase in *Selaginella rupestris* and a simultaneous decrease in *Sphagnum* spore contents also suggest open habitats and drier climate conditions. Significant amounts of coprophilous fungi spores (primarily *Sporormiella*, *Sordaria* and *Podospora*) indirectly point to the presence of grazing animals in the lake vicinity, thus confirming that open habitats became more common. Nevertheless, coniferous forests with pine, spruce, larch, and possibly Douglass fir still dominated the area, although open, grass-dominated habitats were probably also common around the lake. A synchronous pollen record from Norwegian Sea (site ODP 642) suggest a wide distribution of pine-dominated boreal forest in northern Norway (Panitz et al., 2016). The Norwegian record demonstrates an increase in herb pollen (especially Asteraceae) between 3.47 and 3.35 Ma BP interpreted as the interval with relatively cool and dry climate conditions. The further decrease in

Pinus pollen after 3.35 Ma BP reflecting climate cooling in Norway (Panitz et al., 2016) well coincides with our pollen record also pointing to a climate deterioration at this time.

The pollen assemblages that accumulated between ~3.330 and 3.312 Ma BP (PZ-7b, Fig. 2) have significantly higher contents of *Alnus*, *Betula*, and *Sphagnum*, although *Pinus* remains an important component of the pollen spectra. The data indicate that coniferous forests with birch-alder brushwood dominated the vegetation. The presence of *Abies* pollen suggests that fir might have resettled the lake catchment. In total, the revealed changes in pollen assemblages point to some climate amelioration in the course of MIS MG1. This suggestion is supported by the noticeable presence of microfossil remains of coniferous wood (vascular tracheids) in the pollen samples, which can be traced back to a higher input of coniferous wood to the lake.

The Lake El'gygytgyn pollen assemblages between 3.387 and 3.312 Ma BP (PZ-6 and 7, Fig. 2) can be compared with pollen spectra from till sediments found on the northeastern Chukchi Peninsula. The till pollen spectra suggest significant cooling about 3.5–3.2 Ma ago during the so-called Zhuravlinean Glaciation, the first local alpine glaciation in this region, when mountain glaciers extended far into the lowlands (Laukhin et al., 1999; Fradkina et al., 2005; Laukhin, 2014). Unfortunately, the age control of these sediments is poor and based only on diatom stratigraphy (Pushkar and Cherepanova, 2001), making precise correlations difficult. Pollen-based climate reconstructions using the so-called information-statistical method (Klimanov, 1984) suggest mean July and January temperatures of 14 to 18 °C and about −25 to −18 °C, respectively, and annual precipitation in the range of 425 to 500 mm (Laukhin et al., 1999). Generally, these estimations are in range of the climate reconstructions from our Lake El'gygytgyn pollen record, however, according to our reconstructions, temperatures of the warmest month between 3.387 and 3.312 Ma BP were not higher than 15 °C and annual precipitation ranged between 300 and 600 mm (Brigham-Grette et al., 2013; Tarasov et al., 2013). Furthermore, the biome reconstruction shows a predominance of the boreal forest biomes, mainly CLDE, reflecting spread of the cold resistant summergreen trees, shrubs, and eurythermic conifers into the region (Prentice et al., 1992). The tundra biome reconstructed for the relatively cold MIS MG4 (Fig. 3) is in line with somewhat stadial glacial conditions as visible in the $\delta^{18}O$ LR04 record (Lisiecki and Raymo, 2005). However, three spectra with the assigned TUND biome appear during the warm MIS MG1 (Fig. 3). Since the robustness of the biomization approach used for distinguishing between forest and non-forest biomes is rather high (see discussion in Tarasov et al., 2013), this may be due to a greater sensitivity of the El'gygytgyn pollen record to millennial-scale climatic variability in comparison to the stacked marine record of Lisiecki and Raymo (2005).

4.3.3. Environmental conditions ca. 3.312–3.282 Ma BP

The lower percentages of coniferous pollen in PZ-8 (Fig. 2) and the increased percentages of Poaceae, Cyperaceae, *Artemisia*, Caryophyllaceae, Brassicaceae, Ranunculaceae, Rosaceae, and other herb pollen as well as *Selaginella rupestris* and coprophilous fungi spores reflect the dominance of open, mostly treeless tundra- and steppe-like habitats during this interval synchronous with the older part of MIS M2 (Fig. 3). De Schepper et al. (2013) also distinguish an interval of intensive glaciation in the Northern Hemisphere with characteristics similar to early Quaternary glaciations at the beginning of MIS M2 (3.305 to 3.285 Ma BP). The extent of this glaciation was smaller than those of typical Quaternary glaciations, but it may have been larger than today (De Schepper et al., 2013). The Norwegian pollen record demonstrates a high proportion of *Sphagnum* spores around 3.3 Ma BP interpreted as a spread of peatlands due to high precipitation at that time in Norway (Panitz et al., 2016). Based on their record, Panitz et al. (2016) suggested boreal to alpine vegetation and climate conditions cold enough to establish mountain glaciation in northern Norway.

Very pronounced changes in the PZ-8 pollen assemblages point to dry and cold climate conditions similar to those during the Late Pleistocene. However, relatively high contents of *Alnus*, *Betula*, *Pinus*, and *Larix* pollen document that trees and shrubs survived in the area during the PZ-8 interval, probably at more protected localities (e.g. in sheltered microhabitats). It is likely that during MIS M2 for the first time permafrost expanded in the study area similar to modern northern taiga and forest-tundra zones.

Relatively high contents of green algae cysts (*Zygnema*) in the sediments suggest the increased presence of shallower-water environments, possibly as a result of a lake-level lowering. However, high contents of *Sphagnum* spores indicate the existence of wetlands in the lake vicinity, probably along the inlet streams similar to modern *Sphagnum* habitats around the lake.

Large amounts of coprophilous fungi spores in the El'gygytgyn sediments indirectly imply a permanent presence of numerous grazing animals, such as mammoths, bisons, and horses in the lake vicinity, thus confirming that open habitats became broadly distributed in the study area. Interestingly, this episode corresponds to the beginning of the so-called Mammoth paleomagnetic Subchron. The reconstructed climatic and environmental conditions at Lake El'gygytgyn at the beginning of MIS M2 coincide well with colder and drier climatic conditions documented in the Lake Baikal pollen assemblages, which likely reflect a mosaic character of the vegetation during this time interval (Demske et al., 2002). Environmental records from western Beringia also indicate more open forest conditions during this period as well as the existence of permafrost (ice wedge casts; Schweger et al., 2011 and references therein).

The cold and dry early M2 interval revealed in the Lake El'gygytgyn sediments might also be linked to the final (coldest) stage of the Zhuravlinean Glaciation recorded in eastern Chukotka (Laukhin et al., 1999; Fradkina et al., 2005; Laukhin, 2014). The relatively dry and cold conditions during the PZ-8 interval are presumably simultaneous with the coldest stage of this glaciation, when diatom-based climate reconstructions show climate conditions similar to modern ones, but slightly wetter (Pushkar and Cherepanova, 2001; Laukhin, 2014). However, the poor age control in the Zhuravlinean till sediment records does not allow precise correlations.

Marine records also provide consistent evidence for the intensification of continental glaciations in the Northern Hemisphere during this Middle Pliocene cold interval (e.g. Matthiessen et al., 2009; De Schepper et al., 2013 and references therein). The first major pulse of ice-rafted detritus in cores from the North Atlantic, which suggests a distinct expansion of Greenland glaciation, is dated to around 3.3 Ma (Jansen et al., 2000; Flesche Kleiven et al., 2002). Sea-level estimates for this glacial maximum vary from > −10 to −65 ± 15–25 m (Schepper et al., 2014 and references therein). De Schepper et al. (2013) propose that sufficiently cooler surface waters in northern high latitudes were crucial for the glaciation in the Northern Hemisphere during MIS M2. The development of significant ice sheets during this interval was unlikely due to sea-surface temperatures approaching present day values. Climate-model data do not preclude the possibility of the existence of larger ice masses during M2 event, consistent with a global sea-level fall of about 40–60 m (Dolan et al., 2015). The mechanisms causing the onset and termination of the M2 glaciation are still not completely understood. Recent studies suggest that the closing and re-opening of the Central American Seaway might have played a key role (Tan et al., 2017 and references therein), nevertheless its significance remains heavily debated (e.g. Lunt et al., 2008; Brierley and Fedorov, 2016).

The calculated biome scores from Lake El'gygytgyn support the qualitative interpretation of the pollen data. The TUND biome assigned to the majority of the analyzed pollen spectra and the reconstructed highest values of landscape openness between 3.3100 and 3.2885 Ma attest this interval as driest and coldest of the entire record. A single spectrum with the highest COST biome scores is dominated by *Artemisia* (21%) and Poaceae (31%) pollen and reflects the spread of cold and drought-resistant herbaceous vegetation communities, i.e. tundra-steppe or dry graminoid and forb tundra (Edwards et al., 2000). It corroborates with MIS M2 interval in the marine record (Lisiecki and Raymo, 2005).

4.3.4. Environomental conditions ca. 3.282–3.180 Ma BP

A distinct increase of coniferous pollen percentages (mostly *Pinus* s/g *Haploxylon*) at about 3.282 Ma BP (PZ-9, Fig. 2) reflects the further dominance of pine stands in the region. It is not clear whether the pine pollen was produced by trees or shrubs, since the respective *Pinus* pollen cannot be differentiated. It might have been at least partly produced by shrub pine (*P. pumila*), which nowadays is indicative for higher elevations with deep snow in southeastern Siberia and Japan, but is also common at low elevations in northeastern Siberia. The spectra also contain *Larix/Pseudotsuga* pollen type grains. It is unclear whether this pollen type in the pollen spectra is produced by the relatively thermophilic Douglas fir (*Pseudotsuga*) or by larches (*Larix*). Taking into consideration the lower contents of *Picea* pollen and the presence of only very few pollen of relatively thermophilic coniferous trees, such as *Abies* and *Tsuga,* however, we may suppose that the *Larix* pollen grains after 3.282 Ma BP are mostly originated from *Larix*. Based on these findings and the occurrence of *Picea* in the pollen spectra, we assume that pine-larch-spruce forests dominated the area between ca. 3.282 and 3.236 Ma BP. Besides, large amounts of *Alnus fruticosa* and *Betula* sect. *Nanae* pollen suggest that these shrubs were common in the local forests. The high contents of pollen of shrubby taxa may also be an indirect evidence that shrub stone pine (*P. pumila*) might have grown in the area as well. The El'gygytgyn pollen data are in good agreement with a pollen record from Norwegian Sea that reflects the remigration of deciduous and mixed forests with thermophilous coniferous taxa, such as *Tsuga* and *Sciadopitys,* to northern Norway after 3.29 Ma BP suggesting a climate warming (Panitz et al., 2016, 2017). A re-establishment of warmer conditions around 3.290–3.285 Ma BP is also documented in North Atlantic sea surface temperature (SST) records (e.g. Naafs et al., 2010; De Schepper et al., 2013 and references therein). Based on dinoflagellate record from Norwegian Sea (ODP Site 642), Panitz et al. (2017) estimated that SST around 3.285–3.283 Ma BP became at least 5 °C warmer than during MIS M2.

Modelling studies suggest that the ice sheets, which have existed during the M2 event, retreated after 3.27 Ma (during mPWP) to become considerably smaller than today (Schepper et al., 2014 and references therein). A significant reduction in global ice volume is also reflected by a higher-than-modern sea level, which is estimated to up to +40 m (Raymo et al., 2011), averaging around +20 to +25 m (Miller et al., 2012).

Coniferous pollen contents, and especially *Picea*, further increase in the upper part of PZ-9 (ca. 3.250–3.236 Ma), thus pointing to persistent climate amelioration, which coincides well with the MIS M1 climate optimum. However, some increase of *Betula* sect. *Nanae*, *Artemisia*, and Caryophyllaceae pollen as well as *Selaginella* and coprophilous fungi spores in the uppermost part of PZ-9 (starting around 3.240 Ma BP) suggest the onset of some climate deterioration obviously connected with the beginning of the subsequent MIS KM6.

Peaks of *Botryococcus* green algae colonies in the sediments dated to about 3.275, 3.263, and 3.248 Ma BP, and generally rather high *Botryococcus* contents in the upper part of PZ-9, suggest the widespread occurrence of shallow-water environments in the lake during the PZ-9 interval.

The contents of coniferous, *Alnus*, and *Betula* pollen as well as *Sphagnum* spores are significantly lower in PZ-10 (ca. 3.236–3.223 Ma BP), while the assemblages contain rather large amounts of pollen of Poaceae, Cyperaceae, and other herbs, such as *Artemisia*, Ericales, Caryophyllaceae, and Chenopodiaceae as well as spores of *Selaginella rupestris* and coprophilous fungi. These pollen assemblages reflect that open herb-dominated habitats again became more common in the landscape than during MIS M1. The revealed changes suggest drier and colder climate conditions during MIS KM6. Our pollen data are in good agreement with the Lake Baikal pollen record, which also reveals colder and drier climate conditions during this time (Demske et al., 2002). The pollen and dinoflagellate records from the Norwegian Sea also reflect a change from boreal to cool temperate climate conditions during MIS KM6 (Panitz et al., 2017).

Coniferous pollen contents drastically increase again in PZ-11 (ca. 3.223–3.180 Ma BP), reflecting a dominance of pine-larch-spruce forests in the lake area during this interval. The highest *Picea* pollen and *Sphagnum* percentages in the PZ-11b-d subzones point to warmer and wetter climate conditions, which presumably coincide with MIS KM5. Higher contents of *Botryococcus* green algae colonies in PZ-11a-c subzones suggest widespread occurrence of shallow-water environments in the lake. The Norwegian Sea pollen record demonstrate high presence of cool temperate taxa reflecting warmer-than-present climate conditions along the northern Norwegian coast during MIS KM5 (Panitz et al., 2017).

The biome reconstruction for MIS KM5 shows that the CLDE biome returns to be the dominant vegetation type and the TAIG biome appears more frequently in the uppermost part of the interval. This suggests progressive amelioration of the regional climate towards warmer and wetter conditions. Higher moisture availability (particularly winter snow accumulation) may have promoted a strengthening of the boreal evergreen conifers in the regional vegetation, thereby leading to the reconstruction of the TAIG biome.

The reconstructed biomes and landscape openness scores suggest a predominantly forested landscape around Lake El'gygytgyn during the long interval between ca. 3.285 and 3.180 Ma, which includes the younger half of MIS M2, M1, KM6, KM5 and the older part of KM4. During this 105 kyr long interval a dominance of the tundra biome accompanied by the greater landscape openness scores are reconstructed only three times, at ca. 3.2730, 3.2264 and 3.1875 Ma BP, suggesting generally warmer and wetter conditions during the second half of the Mammoth Subchron (including the later part of the M2 glaciation) compared to the first half.

5. Conclusions

The results of this study demonstrate that the pollen record from Lake El'gygytgyn well reflects the global paleoenvironmental fluctuations during the mPWP. Our data showing that mPWP was not an environmentally homogenous interval can be also used to validate modelling experiments simulating Pliocene climate and environmental changes.

According to the revealed pollen assemblages, pine-spruce-larch forests dominated the study area between ca. 3.383 and 3.180 Ma BP. Climate conditions were the warmest at about 3.383–3.350, 3.250–3.235, and 3.222–3.180 Ma BP. Most pronounced environmental changes (first appearance of tundra and steppe-like habitats) have occurred at about 3.31–3.28 Ma BP, pointing to cold and dry climate conditions and probably first permafrost in the area. A relatively cold interval has also occurred between 3.235 and 3.222 Ma BP.

Non-pollen-palynomorphs, such as green algae and spores of coprophilous fungi, during the investigated time interval provide important information concerning lake-level changes and the presence of herbivores around the lake.

Declaration of Competing Interest

There is no conflict of Interest.

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