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# Millennial-scale vegetation changes in the north-eastern Russian Arctic during the Pliocene/Pleistocene transition (2.7–2.5 Ma) inferred from the pollen record of Lake El'gygytyn

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## ABSTRACT

The sediment record of Lake El'gygytyn (67°30'N, 172°05'E) spans the past 3.6 Ma and provides unique opportunities for qualitative and quantitative reconstructions of the regional paleoenvironmental history of the terrestrial Arctic. Millennial-scale pollen studies of the sediments that accumulated during the Late Pliocene and Early Pleistocene (ca. 2.7 to 2.5 Ma) demonstrate orbitally-driven vegetation and climate changes during this transitional interval. Pollen spectra show a significant vegetation shift at the Pliocene/Pleistocene boundary that is, however, delayed by a few thousand years compared to lacustrine response. About 2.70–2.68 Ma the vegetation at Lake El'gygytyn, currently a tundra area was mostly dominated by larch forests with some shrub pine, shrub alder and dwarf birch in understory. During the marine isotope stages G3 and G1, ca. 2.665–2.647 and 2.625–2.617 Ma, some spruce trees grew in the local larch-pine forests, pointing to relatively warm climate conditions. At the beginning of the Pleistocene, around 2.588 Ma, a prominent climatic deterioration led to a change from larch-dominated forests to predominantly treeless steppe- and tundra-like habitats. Between ca. 2.56–2.53 Ma some climate amelioration is reflected by the higher presence of coniferous taxa (mostly pine and larch, but probably also spruce) in the area. After 2.53 Ma a relatively cold and dry climate became dominant again, leading to open steppe-like and shrubby environments followed by climate amelioration between ca. 2.510 and 2.495 Ma, when pollen assemblages show that larch forests with dwarf birch and shrub alder still grew in the lake's vicinity. Increased contents of green algae colonies (*Botryococcus*) remains and *Zygnema* cysts around 2.691–2.689, 2.679–2.677, 2.601–2.594, 2.564–2.545, and 2.532–2.510 Ma suggest a spread of shallow-water environments most likely due to a lake-level lowering. These events occurred simultaneously with dry climate conditions inferred from broad distribution of steppe habitats with *Artemisia* and other herbs.

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## 1. Introduction

The transition from the late Pliocene into the earliest Pleistocene is an interval of dynamic environmental changes. During this transition glacioeustatic sea-level changes markedly increased in amplitude in response to intensification and increased fluctuation of Northern Hemisphere glaciation (Bailey et al., 2012). Generally, this interval at about 2.588 Ma covers the termination of the

Pliocene, the most recent geological epoch with global temperatures several degrees higher than today, and the onset of the Pleistocene, the epoch of increasing climate extremes.

The high Arctic is particularly sensitive to climate changes. Recent studies have shown that during the last few decades the Arctic has experienced significant warming, more dramatic than in other parts of the globe (e.g. Sundqvist et al., 2010 and references therein). The rate of temperature increase of 2 °C since 1961 significantly exceeds that of the global mean (IPCC, 2007). With further temperature rise, the permafrost-dominated Siberian Arctic will likely turn from a main methane sink into a significant source of greenhouse gases (e.g. Schuur et al., 2009; Nisbet et al., 2014).

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For a better understanding of climate and environmental processes in the Arctic long, high-resolution paleoenvironmental records are required. Such records are also an important prerequisite for the validation and improvement of climate simulation scenarios. Unfortunately, long-term, continuous records are extremely rare in the Arctic. It took until 2009 for the first terrestrial sediment record that continuously penetrates beyond the Pliocene/Pleistocene boundary to become available from Lake El'gygytyn, which was drilled under the auspices of the International Continental Scientific Drilling Program (ICDP) (Melles et al., 2011, 2012; Brigham-Grette et al., 2013).

Lake El'gygytyn was formed following a meteorite impact  $3.58 \pm 0.04$  Ma ago (Layer, 2000), in an area of northeastern Russia that remained afterwards free of continental glaciations, despite its location approximately 100 km to the north of the Arctic Circle ( $67^{\circ}30'N$ ,  $172^{\circ}05'E$ , Fig. 1). The unique, 318-m thick, sedimentary record of Lake El'gygytyn provides excellent opportunities for time-continuous reconstructions of past environments. Multi-proxy results from the upper part (back to 2.8 Ma) of the lake sediment succession have provided a complete record of glacial/interglacial changes in the Arctic throughout the Pleistocene (Melles et al., 2012). A first compilation of data and paleoenvironmental interpretations obtained from the lower part of the record ( $\sim 3.6$ – $\sim 2.2$  Ma ago) was published by Brigham-Grette et al. (2013). More detailed results have recently become available in a special issue of the journal *Climate of the Past: Initial results from Lake El'gygytyn, western Beringia: first time-continuous Pliocene-*

*Pleistocene terrestrial record from the Arctic* ([http://www.clim-past.net/special\\_issue48.html](http://www.clim-past.net/special_issue48.html)).

Amongst the large number of sediment proxies applied to the El'gygytyn record, palynological proxies turned out to be of particular importance (Melles et al., 2012; Andreev et al., 2012, 2014; Brigham-Grette et al., 2013; Lozhkin and Anderson, 2013; Tarasov et al., 2013). Modern pollen studies indicate that the lake record provides reliable insights into regional and/or even over-regional vegetation changes, since the lake traps pollen from a source area of several thousand square-kilometers (Lozhkin and Anderson, 2013 and references therein). Taking the sensitivity of the vegetation to climate, the pollen assemblages can also be used to reconstruct climate parameters and to validate and improve climate model scenarios.

According to initial palynological results, the Pliocene/Pleistocene boundary (at 2.558 Ma during Marine Isotope Stage (MIS 103) marks an important change in vegetation at Lake El'gygytyn from generally interglacial to glacial environmental conditions (Andreev et al., 2014). However, the understanding of the vegetation and climate change at this globally important boundary was hampered by the rather low temporal resolution of ca. 2000 yr/sample of the preliminary palynological data. Here, we present a more detailed reconstruction of climatically and environmentally driven vegetation changes in the northeastern Russian Arctic between  $\sim 2.7$  and  $\sim 2.5$  Ma, based upon palynological data from the Lake El'gygytyn record in a temporal resolution of ca. 800 yr/sample in average.

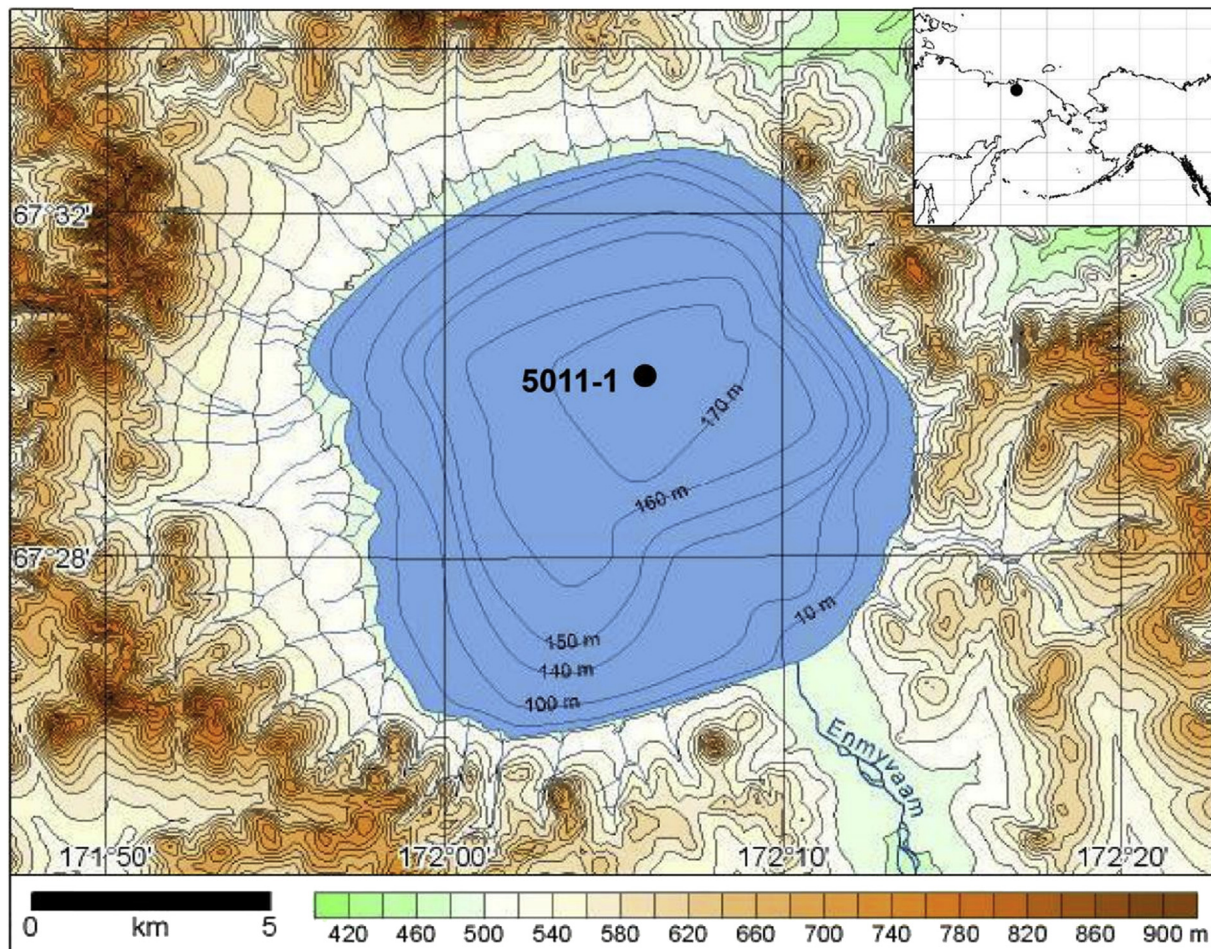


Fig. 1. Map of Lake El'gygytyn showing the location of ICDP Site in the central, deepest part of the lake (for location of the lake in north-eastern Russia see inserted map).



## 2. Lake setting

Lake El'gygytyn is located in a meteorite impact crater of 18 km in diameter, which was formed about 3.58 Ma ago in an Upper Cretaceous volcanic plateau in NE Russia (Layer, 2000, Fig. 1). Today the 170-m deep and 12 km wide lake covers an area of 110 km<sup>2</sup> within a 293 km<sup>2</sup> large catchment that is defined by the crater rim comprising peaks between 600 and 930 m above sea level (a.s.l.). The modern lake level is situated at 492 m a.s.l.

The region is characterized by an extremely harsh climate with mean annual air temperatures of ca. –10 °C, mean July temperatures of 4–8 °C and mean January temperatures of –32 to –36 °C. The precipitation consists of 70 mm summer rainfall (June–September) and ca. 110 mm water equivalent of snowfall (Nolan and Brigham-Grette, 2007). The local climate variables are strongly dependent on oceanic influence, as expressed in relatively low summer temperatures (Kozhevnikov, 1993). Predominant wind directions at Lake El'gygytyn are from the south and north. The study area is located in the zone of continuous permafrost with a mean annual ground temperature of –10 °C at 12.5 m below the ground surface (Schwamborn et al., 2008).

The study area belongs to the subzone of southern shrub and typical tundra. The modern treeline for larch and shrub stone pine is positioned roughly 100 km to the south and west of the lake. Only dwarf birches and willow grow in the lake vicinity. Although the northern boundary of shrub alder is reported to be located further to the north of the lake, the only few shrub alder stands grow approximately 10 km from the lake, in the more protected river valley habitats (Andreev et al., 2012; Lozhkin and Anderson, 2013 and references therein). For a more detailed description of the local vegetation see Belikovich and Galanin (1994), Andreev et al. (2014) and references therein.

Recent pollen assemblages from the sediments of Lake El'gygytyn contain significant amounts of tree and shrub pollen grains that have been transported to the lake by air over long distances (Lozhkin et al., 2001; Matrosova et al., 2004; Matrosova, 2006, 2009; Andreev et al., 2012; Lozhkin and Anderson, 2013). Hence, for interpretations of fossil pollen assemblages it has to be taken into consideration that parts of the pollen may have originated from dozens, or for some rare pollen types perhaps hundreds, of kilometers away.

## 3. Material and methods

Drilling at ICDP site 5011-1 in central Lake El'gygytyn (Fig. 1) was conducted in spring 2009 using the lake ice as a platform (for details see Melles et al., 2011). The 318-m long composite record retrieved from the lacustrine sediments overlaying impact rocks represents the complete history following lake formation soon after the impact event ~3.6 Ma ago. The record was investigated using non-destructive scanning and logging techniques along with multiproxy investigations on discrete subsamples (for details see Melles et al., 2012; Brigham-Grette et al., 2013 and papers in a special issue of *Climate of the Past*). The age model for the record is primarily based on paleomagnetic stratigraphy and subsequent cyclostratigraphy of various climatically-controlled sedimentological and geochemical parameters. As the time interval presented in this paper includes the paleomagnetic Gauss/Matuyama polarity change at 2.588 Ma (Nowaczyk et al., 2013) the age model is well constrained for the Pliocene/Pleistocene transition. Further details can be found in Haltia and Nowaczyk (2014) and Nowaczyk et al. (2013).

Pollen subsamples of ca. 1 g were investigated in the composite depth from 130.57 to 117.66 m below lake floor corresponding to the time interval from ~2.7 to ~2.5 Ma at a resolution of about 0.8

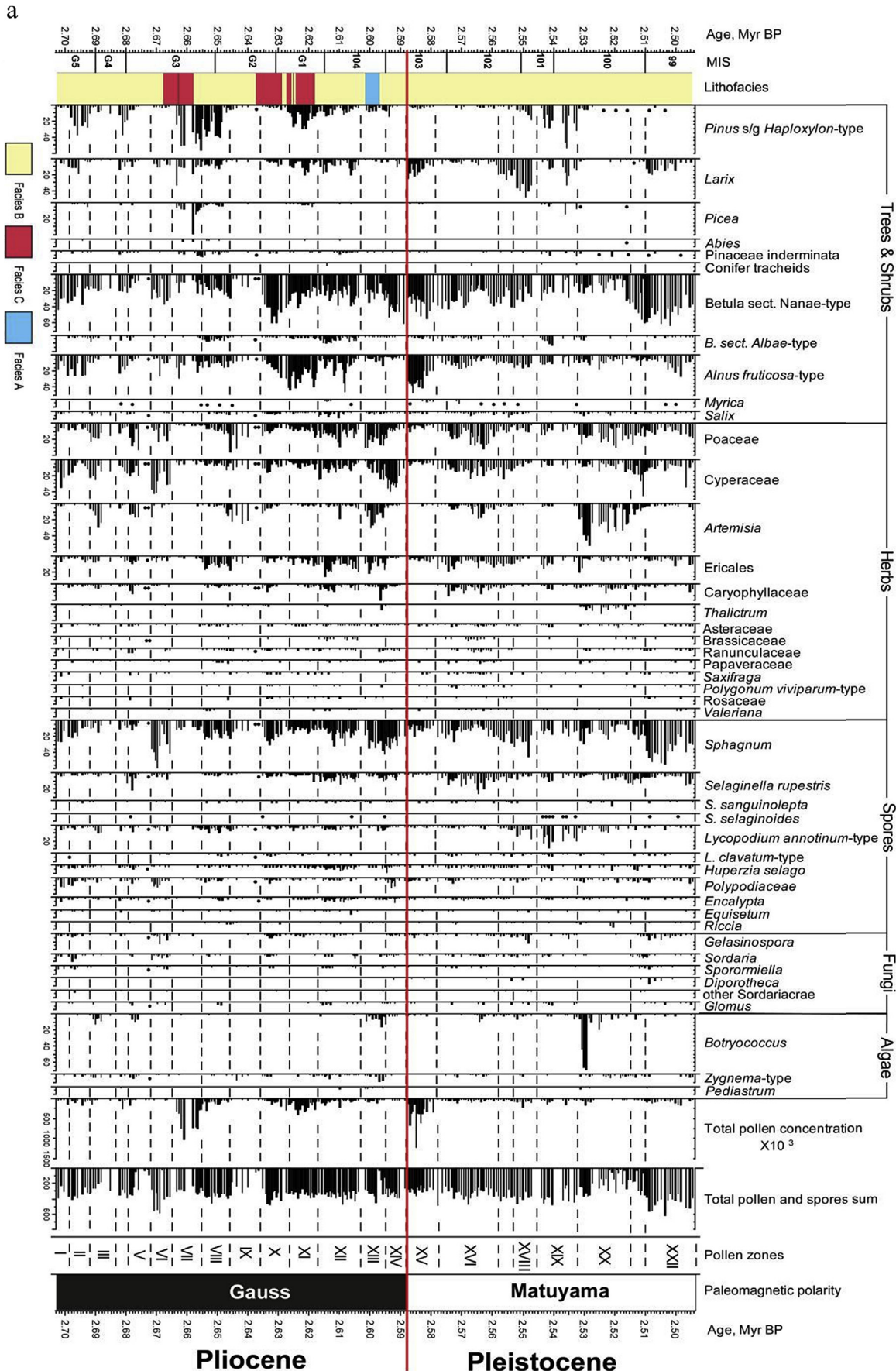
kyr or higher. The samples were processed following a standard HF technique for pollen preparation (Berglund and Ralska-Jasiewiczowa, 1986). The procedure includes KOH, HCl, HF, and acetolysis treatments as well as fine sieving (112 µm) to remove clay-sized particles. A tablet of *Lycopodium* marker spores was added to each sample for calculating total pollen and spore concentrations following Stockmarr (1971). Glycerol was used for sample storage and preparation of the microscopic slides. Pollen and spores were identified under a light microscope at 400× magnification, with the aid of published pollen keys and atlases (e.g., Kupriyanova and Alyoshina, 1978; Bobrov et al., 1983; Reille, 1992, 1995, 1998). Non-pollen-palynomorphs (NPPs), such as fungi spores, remains of algae and invertebrate, were also identified and counted when possible following van Geel (2001 and references therein).

At least 250 pollen grains of terrestrial plants were counted in each sample. Exceptions are samples with extremely low pollen concentration, in which the number of counted pollen grains might be less. Such samples were excluded from the paleoenvironmental reconstructions or only used with special precaution. The relative frequencies of pollen taxa were calculated from the sum of the terrestrial pollen taxa. Spore percentages are based on the sum of pollen and spores. The percentages of non-pollen palynomorphs are based on the sum of the 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 diagrams (Fig. 2a–b). Adobe Illustrator software was used for the compilation of the final pollen diagrams.

Pollen-based biome reconstruction (also known as the 'biomization' approach), using the numerical method first introduced by Prentice et al. (1996), facilitates interpretation of pollen data and data-model comparison (e.g., Brigham-Grette et al., 2013). This approach assigns identified pollen taxa to principal vegetation types (biomes) on the basis of the modern ecology, bioclimatic tolerance and spatial distribution of pollen-producing plants. The method was successfully tested using extensive surface pollen data sets and regionally adapted biome-taxa matrices from northern Eurasia (Tarasov et al., 1998; Edwards et al., 2000), and applied to the last glacial-interglacial pollen records from the vast regions of Siberia and the Far East (e.g. Tarasov et al., 1998, 2000; 2005; Edwards et al., 2000; Mokhova et al., 2009; Müller et al., 2010). It was also applied to lower-resolution Lake El'gygytyn pollen records (Melles et al., 2012; Brigham-Grette et al., 2013; Tarasov et al., 2013) using the same biome-taxon matrix as in this study.

The biome-taxon matrix (Table 1) was constructed using all identified terrestrial pollen taxa assigned to the main vegetation types found in Siberia and the Far East regions. The biome score calculation was performed using standard equation and reconstruction procedures published by Prentice et al. (1996) and PPPBase software (Guiot and Goeury, 1996). Square root transformation was applied to the pollen percentage values to increase the importance of the minor pollen taxa and the 0.5% threshold was universally used as suggested by Prentice et al. (1996). The biome with the highest affinity score or the one defined by a smaller number of taxa/plant functional types (when scores of several biomes are equal) was assigned for each pollen spectrum as the dominant biome (Fig. 3).

Bigelow et al. (2003) suggested an alternative biome-taxon matrix and modified biomization approach in an attempt to refine reconstructions of different types of tundra (Table 1) and to get closer to the real vegetation described in botanical literature and to the BIOME4 model output (Kaplan, 2001). Their approach differs in some principal aspects from the original biomization procedure published by Prentice et al. (1996) and accepted in the



**Fig. 2.** Percentage pollen, spore, and non-pollen-palynomorph diagram for the time interval ca. 2.7 to 2.5 Ma of the Lake El'gygytyn sediment record, showing A) the most common pollen, spores and non-pollen-palynomorphs types and B) the minor pollen, spores and non-pollen-palynomorphs types.

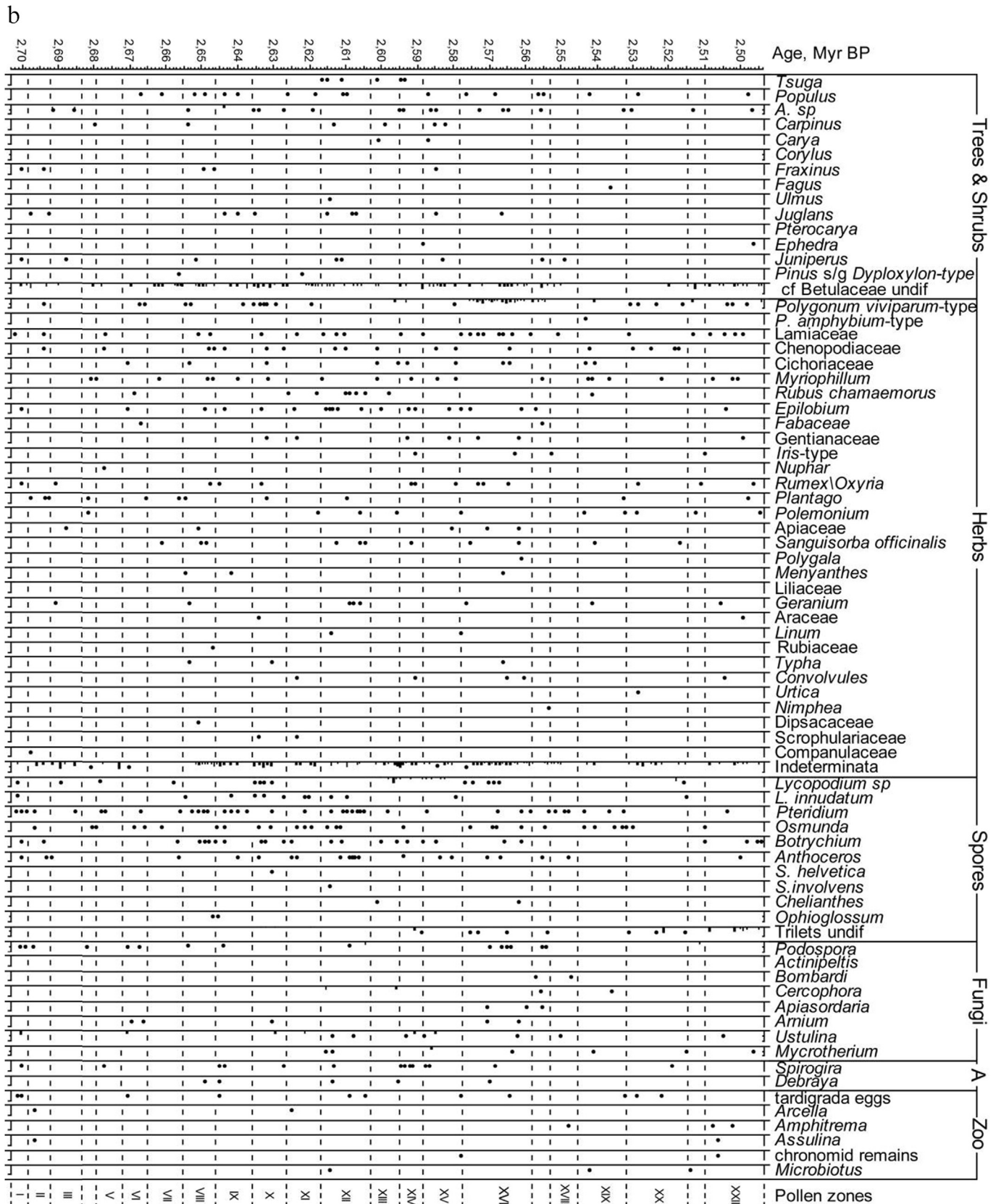


Fig. 2. (continued).



**Table 1**  
Biome–taxon matrixes used in the biome reconstructions. All terrestrial pollen taxa identified in the fossil pollen spectra from the analyzed core are attributed to one or several potentially present biomes.

Biome name	Abbr.	Attributed pollen taxa
After Tarasov et al. (2013)/Brigham-Grette et al. (2013)		
Tundra	TUND	<i>Alnus fruticosa</i> -type (shrub), <i>Betula</i> sect. <i>Albae</i> -type (tree), <i>B.</i> sect. <i>Nanae</i> -type (shrub), <i>B.</i> undif., Cyperaceae, Ericales, Poaceae, Polemonium, <i>Polygonum bistorta</i> -type, <i>Rubus chamaemorus</i> , <i>Rumex</i> , <i>Salix</i> , Saxifragaceae, Valerianaceae
Cold deciduous forest	CLDE	<i>Alnus fruticosa</i> -type (shrub), <i>A.</i> sp. (tree), <i>Betula</i> sect. <i>Albae</i> -type (tree), <i>B.</i> sect. <i>Nanae</i> -type (shrub), <i>B.</i> undif., Cupressaceae/Taxodiaceae, Ericales, <i>Larix/Pseudotsuga</i> , <i>Pinus</i> s/g <i>Diploxylon</i> , <i>P.</i> s/g <i>Haploxylon</i> , Pinaceae undif., <i>Populus</i> , <i>Rubus chamaemorus</i> , <i>Salix</i>
Taiga	TAIG	<i>Abies</i> , <i>Alnus</i> sp. (tree), <i>Betula</i> sect. <i>Albae</i> -type (tree), <i>B.</i> sect. <i>Nanae</i> -type (shrub) <i>B.</i> undif., Cupressaceae/Taxodiaceae, Ericales, <i>Larix/Pseudotsuga</i> , <i>Lonicera</i> , <i>Picea</i> , <i>Pinus</i> s/g <i>Diploxylon</i> , <i>P.</i> s/g <i>Haploxylon</i> , Pinaceae undif., <i>Populus</i> , <i>Rubus chamaemorus</i> , <i>Salix</i>
Cool conifer forest	COCO	<i>Abies</i> , <i>Alnus</i> sp. (tree), <i>Betula</i> sect. <i>Albae</i> -type (tree), <i>B.</i> sect. <i>Nanae</i> -type (shrub), <i>B.</i> undif., <i>Carpinus</i> -type, <i>Corylus</i> , Cupressaceae/Taxodiaceae, Ericales, <i>Larix/Pseudotsuga</i> , <i>Lonicera</i> , <i>Picea</i> , <i>Pinus</i> s/g <i>Diploxylon</i> , <i>P.</i> s/g <i>Haploxylon</i> , Pinaceae undif., <i>Populus</i> , <i>Salix</i> , <i>Tilia</i> , <i>Tsuga</i> , <i>Ulmus</i>
Temperate deciduous forest	TEDE	<i>Abies</i> , <i>Alnus</i> sp. (tree), <i>Betula</i> sect. <i>Albae</i> -type (tree), <i>B.</i> sect. <i>Nanae</i> -type (shrub), <i>B.</i> undif., <i>Carpinus</i> -type, <i>Carya</i> , <i>Corylus</i> , Cupressaceae/Taxodiaceae, Ericales, <i>Juglans</i> , <i>Larix/Pseudotsuga</i> , <i>Lonicera</i> -type, <i>Pinus</i> s/g <i>Diploxylon</i> , Pinaceae undif., <i>Populus</i> , <i>Pterocarya</i> , <i>Quercus</i> deciduous, <i>Salix</i> , <i>Tilia</i> , <i>Ulmus</i>
Cool mixed forest	COMX	<i>Abies</i> , <i>Alnus</i> sp. (tree), <i>Betula</i> sect. <i>Albae</i> -type (tree), <i>B.</i> sect. <i>Nanae</i> -type (shrub), <i>B.</i> undif., <i>Carpinus</i> -type, <i>Corylus</i> , Cupressaceae/Taxodiaceae, Ericales, <i>Larix/Pseudotsuga</i> , <i>Lonicera</i> -type, <i>Picea</i> , <i>Pinus</i> s/g <i>Diploxylon</i> , <i>P.</i> s/g <i>Haploxylon</i> , Pinaceae undif., <i>Populus</i> , <i>Tsuga</i> , <i>Quercus</i> deciduous, <i>Salix</i> , <i>Tilia</i> , <i>Ulmus</i>
Warm mixed forest	WAMX	<i>Alnus</i> sp. (tree), <i>Carpinus</i> -type, <i>Carya</i> , <i>Corylus</i> , Cupressaceae/Taxodiaceae, Ericales, <i>Juglans</i> , <i>Lonicera</i> , <i>Pinus</i> subgenus <i>Diploxylon</i> , Pinaceae undif., <i>Populus</i> , <i>Pterocarya</i> , <i>Quercus</i> deciduous, <i>Salix</i> , <i>Tilia</i> , <i>Ulmus</i>
Cold steppe	COST	Apiaceae, <i>Artemisia</i> , Asteraceae Asteroideae, Asteraceae Cichorioideae, Brassicaceae, <i>Cannabis</i> -type, Caryophyllaceae, Chenopodiaceae, Fabaceae, Lamiaceae, <i>Linum</i> , Onagraceae, Papaveraceae, Plantaginaceae, Poaceae, <i>Polygonum bistorta</i> -type, Ranunculaceae, Rosaceae, <i>Rumex</i> , <i>Sanguisorba</i> , <i>Thalictrum</i> , Urticaceae, Valerianaceae
After Bigelow et al. (2003)		
Temperate grassland and xerophytic shrubland	STEP	Apiaceae, <i>Artemisia</i> , Asteraceae undif., Brassicaceae, Caryophyllaceae, Chenopodiaceae, Gentianaceae, Lamiaceae, Papaveraceae, Plantaginaceae, Poaceae, Ranunculaceae, Rosaceae, <i>Rumex</i> , <i>Sanguisorba</i> , <i>Thalictrum</i> , Valerianaceae
Cushion-forb tundra	CUSH	Apiaceae, <i>Artemisia</i> , Asteraceae undif., Brassicaceae, Caryophyllaceae, <i>Epilobium</i> , Gentianaceae, Papaveraceae, Plantaginaceae, Poaceae, Polemoniaceae, <i>Polygonum bistorta</i> -type, Ranunculaceae, Rosaceae, <i>Rumex</i> , <i>Sanguisorba</i> , Saxifragaceae, <i>Thalictrum</i> , Valerianaceae
Graminoid and forb tundra	DRYT	Apiaceae, <i>Artemisia</i> , Asteraceae undif., Brassicaceae, Caryophyllaceae, Cyperaceae, <i>Epilobium</i> , Gentianaceae, Papaveraceae, Plantaginaceae, Poaceae, Polemoniaceae, <i>Polygonum bistorta</i> -type, Ranunculaceae, Rosaceae, <i>Rumex</i> , <i>Sanguisorba</i> , Saxifragaceae, <i>Thalictrum</i> , Valerianaceae
Prostrate dwarf- shrub tundra	PROS	Apiaceae, <i>Artemisia</i> , Asteraceae undif., Brassicaceae, Caryophyllaceae, EPILOBIUM <i>Epilobium</i> , Gentianaceae, Papaveraceae, Plantaginaceae, Poaceae, Polemoniaceae, <i>Polygonum bistorta</i> -type, Ranunculaceae, Rosaceae, <i>Rumex</i> , <i>Salix</i> , <i>Sanguisorba</i> , Saxifragaceae, <i>Thalictrum</i> , Valerianaceae
Erect dwarf- shrub tundra	DWAR	<i>Betula</i> sect. <i>Nanae</i> -type (shrub), <i>B.</i> undif., Cyperaceae, Ericales, Poaceae, <i>Salix</i>
Low- and high- shrub tundra	SHRU	<i>Alnus fruticosa</i> -type (shrub), <i>Betula</i> sect. <i>Nanae</i> -type (shrub), <i>B.</i> undif., Cyperaceae, Ericales, <i>Juniperus</i> , <i>Pinus</i> undif., <i>Rubus chamaemorus</i> , <i>Rumex</i> , <i>Salix</i> , <i>Sphagnum</i>
Cold deciduous forest	CLDE	<i>Alnus fruticosa</i> -type (shrub), <i>A.</i> sp. (tree), <i>Betula</i> sect. <i>Albae</i> -type (tree), <i>B.</i> sect. <i>Nanae</i> -type (shrub), <i>B.</i> undif., <i>Corylus</i> , Ericales, <i>Juniperus</i> , <i>Larix</i> , <i>Maica</i> , <i>Pinus</i> undif., <i>Populus</i> , <i>Rubus chamaemorus</i> , <i>Salix</i> , <i>Sphagnum</i>
Cold evergreen needle-leaved forest	TAIG	<i>Abies</i> , <i>Alnus fruticosa</i> -type (shrub), <i>A.</i> sp. (tree), <i>Betula</i> sect. <i>Albae</i> -type (tree), <i>B.</i> sect. <i>Nanae</i> -type (shrub) <i>B.</i> undif., <i>Corylus</i> , Ericales, <i>Juniperus</i> , <i>Maica</i> , <i>Picea</i> , <i>Pinus</i> undif., <i>Populus</i> , <i>Rubus chamaemorus</i> , <i>Salix</i> , <i>Sphagnum</i>

following publications on northern Eurasia related to the BIOME6000 project (e.g., Tarasov et al., 1998, 2000). In order to compare our results with those of Bigelow et al. (2003), we applied their taxa to biome assignment (Table 1) and biome reconstruction steps to the Lake El'gygytyn pollen record presented in this paper. Both result sets are discussed in section 4.8.

#### 4. Results

A total of 259 samples have been investigated from the Pliocene/Pleistocene transition between 130.57 m (~2.7 Ma) and 117.66 m (~2.5 Ma) depth of the composite core from ICDP site 5011-1 in the center of Lake El'gygytyn (Fig. 1). Almost 120 different pollen, spore, and non-pollen-palynomorph types have been found in the studied samples (Fig. 2). The most important pollen, spore, and non-pollen-palynomorph types are presented on Fig. 2a, the minor types on Fig. 2b. The revealed pollen assemblages can be subdivided into 22 main pollen zones (PZ), based upon a qualitative inspection of significant changes in pollen associations, pollen concentrations, and on the occurrence of particularly indicative taxa. PZ-I (ca. 2.702–2.698 Ma) shows high *Betula* and Cyperaceae pollen contents, while *Pinus* pollen is almost absent. This zone is also characterized by rather high contents of fungi spores (mainly *Gelasinospora* and *Sordaria*). Pollen concentration reaches 9750

grains/g.

PZ-II (ca. 2.698–2.692 Ma) is noticeable by a significant increase in *Pinus* (up to 38%) and *Larix* (up to 20%) pollen contents, while Cyperaceae pollen are drastically decreased. *Sordaria* spore contents also show an increase. Pollen concentration is slightly higher (up to 12,840 grains/g) than in PZ-I.

PZ-III (ca. 2.692–2.684 Ma) is characterized by a significant decrease in coniferous and *Alnus* pollen, while *Artemisia*, Poaceae, and Cyperaceae pollen drastically increase. The zone is also noticeable for the relatively high presence of *Botryococcus* green algae colonies and *Zygnema* cysts. Pollen concentration is lower (up to 6090 grains/g) than in PZ-II.

Significant increases in *Pinus* (up to 40%), *Larix* (up to 18%), and *Alnus* (up to 22%) pollen are characteristic for PZ-IV (ca. 2.684–2.679 Ma). Pollen concentration in this zone is significantly higher (up to 27,240 grains/g) than in PZ-III.

In PZ-V (ca. 2.679–2.672 Ma) coniferous pollen contents gradually decrease, while *Artemisia*, Poaceae, and Cyperaceae pollen and *Selaginella* spore contents increase. The zone is also noticeable for the rather high presence of *Botryococcus* green algae colonies and *Zygnema* cysts. Pollen concentration is much lower (up to 2340 grains/g) than in PZ-IV.

In PZ-VI (ca. 2.672–2.665 Ma) *Pinus* pollen is almost absent, while *Betula* and Cyperaceae pollen and *Sphagnum* spores are

drastically increased. Characteristic of this zone are rather high contents of *Larix* pollen (up to 12%) and very low pollen concentrations of mostly <1000 grains/g.

PZ-VII (ca. 2.665–2.655 Ma) is characterized by a drastic increase in *Pinus*, *Picea*, and *Larix* pollen contents. Pollen concentration of up to 98,850 grains/g is very high.

In PZ-VIII (ca. 2.655–2.646 Ma) *Picea* pollen contents gradually decrease, while *Betula*, *Artemisia*, Poaceae, and Cyperaceae pollen as well as *Selaginella*, *Sphagnum*, and *Lycopodium* spore contents increase. This zone is also noticeable for the rather high presence of Ericales, Caryophyllaceae, Ranunculaceae, Brassicaceae, and Asteraceae pollen. Pollen concentration is lower (up to 14,500 grains/g) than in PZ-VII.

PZ-IX (ca. 2.642–2.636 Ma) is characterized by the disappearance of coniferous pollen, while *Artemisia* pollen contents increase at the beginning of the zone and *Betula* in its upper part. Pollen concentration is lower (up to 4010 grains/g) than in PZ-VIII.

PZ-X (ca. 2.636–2.626 Ma) pollen assemblages are characterized by a drastic increase in *Betula* pollen contents (up to 62%). This zone is also noticeable for gradual increases in *Alnus*, *Larix*, *Pinus*, and *Sphagnum* contents, while Poaceae, Cyperaceae *Artemisia*, and *Thalictrum* decrease. In addition, it is characterized by relatively high contents of *Gelasinospora*, *Sporormiella*, and *Sordaria* fungi spores. Pollen concentration reaches 15,030 grains/g in the upper part of the zone.

PZ-XI (ca. 2.626–2.617 Ma) is distinguishable by high contents of coniferous (*Pinus*, *Larix*) and Ericales pollen. Pollen concentration is higher (up to 30,600 grains/g) than in PZ-X.

In PZ-XII (ca. 2.617–2.603 Ma) *Pinus* pollen contents gradually decrease, while percentages of Poaceae, Cyperaceae, Caryophyllaceae, Ericales pollen and *Sphagnum* spores increase.

PZ-XIII (ca. 2.603–2.595 Ma) is noticeable by the disappearance of *Larix* pollen and a further decrease of *Pinus* and *Alnus* pollen contents, while *Artemisia*, Poaceae, and Cyperaceae pollen and *Sphagnum* spores contents increase. This zone is also characterized by rather high presence of *Botryococcus* colonies and *Zygnema* cysts. Pollen concentration with up to 9140 grains/g is relatively high.

In PZ-XIV (ca. 2.595–2.588 Ma) coniferous pollen is almost absent. Characteristic for this zone is also the low content of *Alnus* pollen, while percentages of *Betula* and Cyperaceae remarkably increase. Pollen concentration is rather low (up to 4750 grains/g).

PZ-XV (ca. 2.588–2.578 Ma) pollen assemblages differ from PZ-XIV by peaks in *Larix* and *Alnus* pollen. Furthermore, the pollen concentration is much higher (up to 142,650 grains/g) than in PZ-XIV.

PZ-XVI (ca. 2.578–2.558 Ma) is noteworthy for a significant increase in Poaceae, Cyperaceae, Ericales, *Artemisia*, Caryophyllaceae, Ranunculaceae, Brassicaceae, and Asteraceae pollen and *Selaginella* spores percentages. In contrast, contents of *Larix* and *Alnus* pollen as well as the pollen concentration, drastically decrease.

Characteristic for PZ-XVII (ca. 2.558–2.553 Ma) is a distinct peak in *Larix* pollen percentages, while Poaceae, Cyperaceae, and other herbs decrease.

In PZ-XVIII (ca. 2.553–2.546 Ma) *Pinus* pollen contents increase significantly once a. This zone is also noticeable for the further increase in *Larix* pollen and in spores of *Lycopodium* and *Gelasinospora*.

*Pinus* pollen contents are further increased in PZ-XIX (ca. 2.546–2.532 Ma), reaching a maximum of 54%. Characteristic of this zone is also the increase in *Lycopodium* spore contents (up to 29%).

Coniferous pollen disappear again in PZ-XX (ca. 2.532–2.515 Ma). Additional characteristics for this zone are large amounts of *Artemisia* pollen and numerous remains of *Botryococcus*

colonies.

PZ-XXI (ca. 2.515–2.510 Ma) is characterized by a significant increase in *Betula* pollen contents (up to 56%), while *Artemisia* pollen are reduced.

PZ-XXII (ca. 2.510–2.492 Ma) is notable for the significant increase in *Larix* pollen and *Sphagnum* spore contents. *Alnus* pollen percentages also show some increase. Pollen concentration is much higher (up to 16,300 grains/g) than in PZ-XXI.

## 5. Discussion and interpretation

The changes revealed in the pollen and non-pollen-palynomorph records, as well as their paleoecological significance for the reconstruction of local and regional vegetation changes, are discussed below, along with their possible relationship with globally and regionally known paleoenvironmental events. Such relations, however, are not always clearly pronounced and visible in pollen records, for instance due to delays in vegetation response to climate changes. For example, plants, such as *Pinus pumila*, might need millennia to reach their ecologically-determined northern distribution limit. Another possible reason is a possible discrepancy between the age model of the Lake El'gygytyn record and age models developed for the individual paleoenvironmental records.

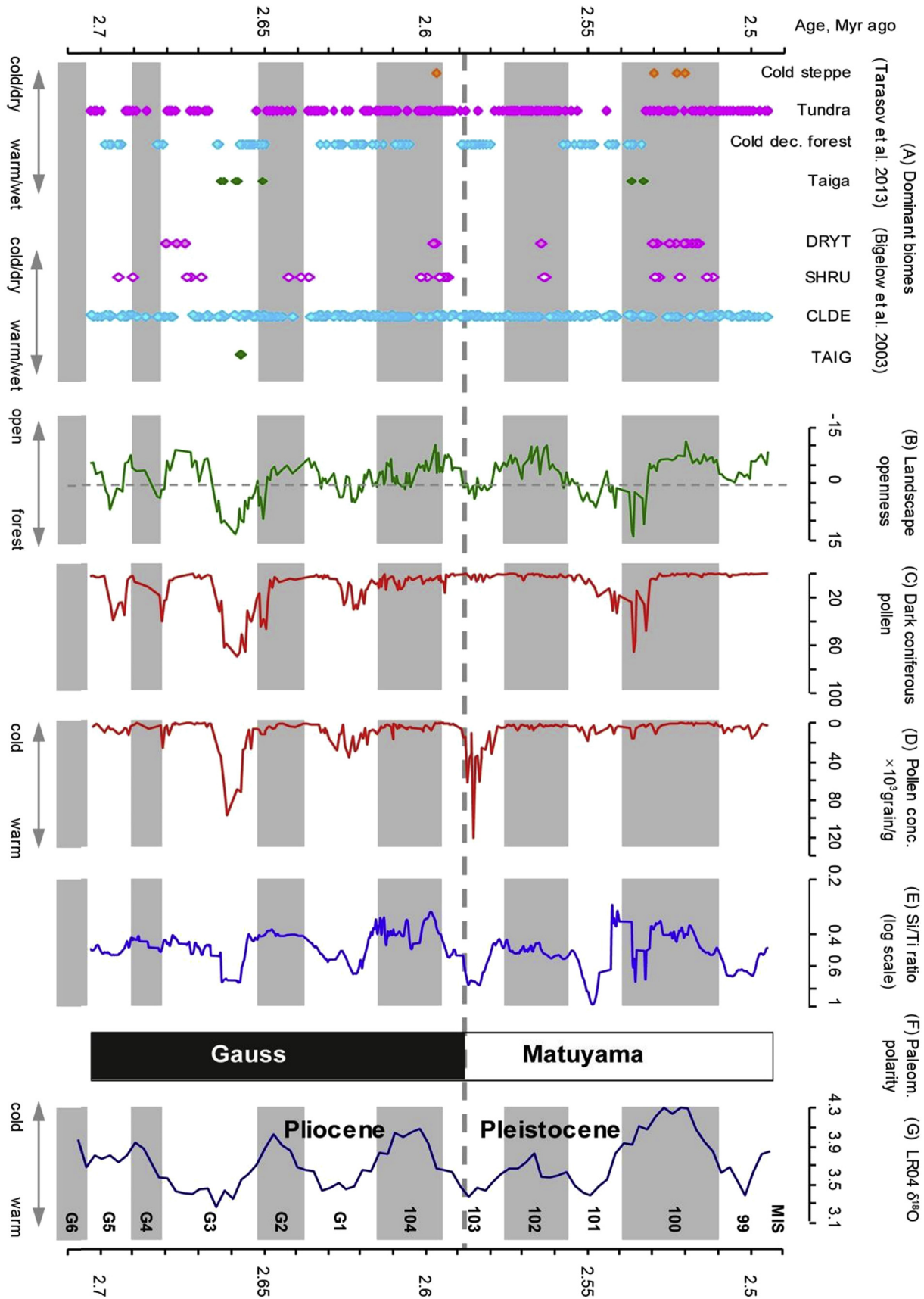
The time slices discussed in this chapter were chosen according to the importance of the revealed pollen changes for the paleoenvironmental reconstructions and their possible relation to globally known events.

### 5.1. The biome reconstruction results: an overview and climatic implication

Two sets of the biome reconstruction results derived from the Lake El'gygytyn pollen record are presented in Fig. 3A. The two approaches differ from each other in several aspects, including tundra biome classification, taxon to biome assignment (for example, *Larix* and *Corylus*), involvement of *Sphagnum* spores (for details see Table 1), and a number of steps for the biome score calculations. Despite the differences in approach, the results obtained demonstrate basically the same set of the dominant biomes and the predominance of the cold deciduous forest biome during the investigated time interval.

The taiga biome characterized by a presence of boreal evergreen and deciduous tree and shrub taxa appears only once in the reconstruction based on the Bigelow et al. (2003) approach (Fig. 3A, right panel) and a few more times in the reconstruction based on the Tarasov et al. (2013)/Brigham-Grette et al. (2013) approach (Fig. 3A, left panel). According to the bioclimatic limits applied by the BIOME family vegetation models (Prentice et al., 1992; Kaplan, 2001), the reconstruction of the taiga biome suggests the most favorable climate conditions for the boreal evergreen conifer forest growing, including relatively mild winter temperatures and higher precipitation or moisture availability than required by the cold deciduous forest biome. The relatively low landscape openness (Fig. 3B), percentages of dark coniferous pollen (Fig. 3C), and the relatively high pollen concentration values (Fig. 3D) revealed in the El'gygytyn record seem to support such interpretation.

The test of the method performance using modern surface samples from the Arctic by Bigelow et al. (2003), has demonstrated a relatively low percentage of correct reconstructions versus observations, i.e., 49.4% for the CLDE and 74.2% for the TAIG biome. In turn, the test of the biomization approach applied in the current study using representative modern pollen sample sets from eastern Siberia (Müller et al., 2010) and from Lake El'gygytyn (Tarasov et al., 2013), shows much better performance in distinguishing cold deciduous forest from tundra and taiga vegetation in the study



**Fig. 3.** Temporal changes in (A) dominant biomes and (B) landscape openness reconstructed from the Lake El'gygytgyn pollen record presented in Fig. 2, compared to the values of (C) dark coniferous (*Abies*, *Picea*, *Pinus* s/g *Haploxyton*) pollen sum, (D) total pollen concentration in the Lake El'gygytgyn pollen record (this study), (E) Si/Ti ratio, (F) paleomagnetic polarity, and (G) global marine isotope stack (after Lisiecki and Raymo, 2005). Gray bands indicate cold MIS. For technical details of the biome score and landscape openness



region (e.g., Lozhkin and Anderson, 2013). A weighting ( $\times 15$ ) of the *Larix* pollen percentages prior to calculating the affinity score and an exclusive assignment of this taxon to cold deciduous forest (Table 1), as applied by Bigelow et al. (2003), could be a main reason for overrepresentation of the CLDE biome in the reconstruction from Lake El'gygytgyn (Fig. 3A, right panel).

The Bigelow et al. (2003) approach reveals the reconstruction of two (of five potentially possible) types of tundra (Table 1), thus allowing for a more detailed understanding of the reconstructed vegetation and the underlying climate conditions. The graminoid and forb tundra (i.e. DRYT = dry tundra) biome is reconstructed several times through the record (Fig. 3A, right panel), i.e., during the relatively warm early MIS G3, and during the coldest intervals of the MIS 104, MIS 102, and MIS 100 (Fig. 3G). This reconstruction coincides well with the reconstruction of cold steppe (Fig. 3A, left panel) during MIS 104 and 100, suggesting that both approaches are able to catch phases with relatively dry environments, which could occur in both warm and cold intervals. The fact, that the temperate grassland and xerophytic shrubland (STEP) biome does not appear in the reconstruction using the Bigelow et al. (2003) approach supports our interpretation of the Pliocene/Pleistocene transition as an interval with relatively severe boreal environments.

Low- and high-shrub tundra (SHRU) is another tundra biome revealed by the Bigelow et al. (2003) approach (Fig. 3A, right panel). In reality such vegetation is very close in appearance to the cold deciduous forest and often referred to as forest-tundra. We assume that the reconstruction of SHRU is underestimated for the reasons explained above. On the other hand, we can be more or less confident that most of the tundra biome reconstructions (Fig. 3A, left panel) represent low- and high-shrub tundra, which requires relatively moist environments and snow cover sufficient to protect woody plants from the extreme winter frost and icy winds.

## 5.2. Environmental conditions 2.702–2.698 Ma

Previous pollen studies of the El'gygytgyn sediments have revealed that 2.735 Ma ago coniferous forests started to disappear from the regional vegetation (Andreev et al., 2014). The climate-driven environmental changes culminated between 2.710 and 2.695 Ma, when open steppe- and tundra-like habitats dominated the vegetation around the El'gygytgyn crater, thus implying much drier and colder conditions. Significant climate deterioration after ca 2.71 Ma was also reconstructed from the pollen record of Lake Baikal, which reflects that hemlock almost disappeared from the local vegetation (Demske et al., 2002).

The climate deterioration after ca 2.71 Ma documented in the El'gygytgyn and Baikal pollen records coincides well with the intensification of Northern Hemisphere Glaciation during the MIS G6. For example, Duk-Rodkin et al. (2010) found evidence for the build-up of regional ice caps in north-western Canada and an early Cordilleran ice sheet around 2.74 Ma. Also the Greenland, Scandinavian and Arctic ice sheets expanded after 2.75 Ma (e.g., Kleiven et al., 2002; Matthiessen et al., 2009 and references therein). According to Jansen et al. (2000) the expansion of large-scale ice sheets in the Northern Hemisphere is reflected by a significant increase of ice-rafted debris. Studer et al. (2012) assume that a rapid decline in diatom opal accumulation flux in North Pacific marine sediment cores is also associated with the development of glacial cycles at the Pliocene/Pleistocene transition. It is also notable that

dust and disseminated volcanic ash deposition in the subarctic Pacific increased markedly  $\sim 2.75$  Ma (Bailey et al., 2011).

The higher resolution pollen record presented here very well confirms the previously revealed paleoenvironments. The sediments deposited in Lake El'gygytgyn between ca 2.702 and 2.698 Ma (PZ-I of Fig. 2) suggest that open shrub tundra (mostly dwarf birch) dominated the vegetation in the lake's vicinity. This interpretation is supported by the biome reconstruction (Fig. 3A) for this interval, which also reveals tundra to have the highest affinity scores. However, relatively high percentages of *Larix* pollen in the fossil assemblages point to the persistent presence of larch around the lake. The presence of arboreal vegetation in the study area is also indicated in the relatively small difference between the maximum score of forest biomes and the maximum score of open biomes (a qualitative indicator of landscape openness, Fig. 3B). High contents of Cyperaceae pollen and *Sphagnum* spores imply extended wetland habitats in the lake vicinity. Generally, the PZ-I vegetation, corresponding with the lower part of MIS G5, is similar to a modern forest-tundra ecotone.

Thus, our pollen data point to still relatively warm, but rather wet climate conditions on Chukotka between ca. 2.702 and 2.698 Ma. This is in a good accordance with other records which for instance suggest the synchronous rise of western subarctic Pacific Ocean summer sea surface temperatures (SSTs), while winter SSTs cooled (Haug et al., 2005). The latter is hypothesized to have caused more abundant floating ice during winter times in the subarctic Pacific. Haug et al. (2005) suggested that the observed summer warming extended into the autumn, providing water vapor to northern North America, where it precipitated and accumulated as snow, and thus triggered the intensification of Northern Hemisphere Glaciation around 2.7 Ma ago. This interpretation is supported by data from Europe, which suggest that a significant Scandinavian glaciation did not occur before ca 2.7 Ma (e.g., De Schepper et al., 2014 and references therein), and that aeolian input of terrestrial material to the North Atlantic also drastically increased synchronously with enhanced glaciation (Naafs et al., 2012). A significant climate change at  $\sim 2.7$  Ma is also documented in pollen data from fluviolacustrine sediments in central China, where the onset of dominant steppe vegetation at 2.7 Ma reflects the change from a long-lasting warm and dry climate to cold-dry and warm-wet oscillations responding to global glacial-interglacial forcing (Han et al., 1997).

## 5.3. Environmental conditions 2.698–2.665 Ma

A significant increase in *Pinus*, *Larix*, and *Alnus* pollen contents between ca. 2.698–2.692 Ma (PZ-II, Fig. 2, upper part of MIS G6, Fig. 3G) reflects climate amelioration and a return of pine to the local vegetation, which was probably similar to modern northern larch forests with dense stone pine and shrub alder understory. This interpretation is in line with the biome reconstruction (Fig. 3A) demonstrating the highest affinity scores for the cold deciduous forest biome. The difference between the maximum score of forest biomes and the maximum score of open biomes (Fig. 3B) is relatively large, thus indicating the dominance of arboreal vegetation in the area. Rather high contents of some coprophilous fungi spores (*Gelasinospora*, *Sordaria*, and *Sporormiella*) point indirectly to the presence of herbivores (Baker et al., 2013) in the lake vicinity.

Open tundra and steppe-like herb communities with *Artemisia*,

(difference between the maximum score among forest biomes and the maximum score among non-forest biomes at each level) calculations see Tarasov et al. (2013). Changes in dominant biomes (A) are reconstructed using two biome-taxa matrixes discussed in details in Tarasov et al. (2013)/Brigham-Grette et al. (2013) and in Bigelow et al. (2003), respectively. The abbreviated biome names in Bigelow et al. (2003) are DRYT for graminoid and forb tundra (i.e. dry tundra), SHRU for low- and high-shrub tundra and CLDE for cold deciduous forest and TAIG for cold evergreen needle-leaved forest (i.e. taiga).

Poaceae, and Cyperaceae dominated in the local vegetation between ca. 2.692 and 2.684 Ma (PZ-III, Fig. 2, central part of MIS G4) thus pointing to rather dry and cold climate conditions. However, forested habitats (larch stands mixed with stone pine, shrub alder and birch) still survived in more protected places like river valleys. The biome reconstruction also shows that tundra has the highest affinity scores (Fig. 3A). A rise in the landscape openness (Fig. 3B) reflects significant strengthening of non-arboreal vegetation in the area. The relatively high presence of *Zygnema* cysts and a small peak of *Botryococcus* remains in the sediments point to an expansion of shallow-water environments, likely as a result of lake-level lowering due to dry climate.

Larch forest with stone pine and shrub alder in the understory dominated the local vegetation between ca. 2.684 and 2.679 Ma (PZ-IV, Fig. 2, transition from MIS G4 to MIS G3, Fig. 3G). Climate amelioration is also indicated by a slight increase in forestation (Fig. 3B) and the spread of cold deciduous forest biome in the area (Fig. 3A).

Starting at 2.679 Ma (onset of PZ-IV, Fig. 2, lower part of MIS G3, Fig. 3G), however, forested habitats quickly disappeared, and steppe-like coenoses with *Artemisia*, Poaceae, Cyperaceae, Caryophyllaceae, *Thalictrum*, and *Selaginella* increased again, suggesting climate deterioration. Consequently, the tundra biome exhibits the highest affinity scores (Fig. 3A), thus reflecting a significantly open, treeless landscape (Fig. 3B). The relatively high presence of *Zygnema* cysts and small *Botryococcus* peaks in the sediments accumulated at the beginning of this interval (low part of PZ-V, Fig. 2) again pointing to more shallow-water environments.

The geochemical data from the lake sediments also exhibit changes interpreted as the onset of a pronounced glacial-to-interglacial cyclicity (for details see Wennrich et al., 2014; Wennrich et al., in this issue). These changes display an overall change not only in the lake but also in its catchment that just slightly postdates a drop in precipitation and winter temperatures at 2.73 Ma reconstructed from pollen data (Brigham-Grette et al., 2013; Tarasov et al., 2013). Some climate deterioration is also reflected in the Lake Baikal pollen record pointing to the expansion of dry forest types with pine after 2.68 Ma (Demske et al., 2002).

Larch stands appear again in the lake vicinity between 2.672 and 2.665 Ma (PZ-VI of Fig. 2, central part of MIS G3, Fig. 3G), suggesting climate amelioration. Drastically increased pollen contents of *Betula* and Cyperaceae, as well as *Sphagnum* and Polypodiaceae spores likely reflect a broader distribution of wetter habitats in the lake area. Most likely, the vegetation resembles the modern open larch forests close to the northern limit of larch distribution. Rather high contents of *Gelasinospora* and other coprophilous fungi spores indirectly point to presence of numerous grazing animals around the lake, and therefore, also indicate a relatively open landscape.

#### 5.4. Environmental conditions ca. 2.665–2.626 Ma

Larch forest with some spruce and numerous shrub pines in the understory dominated the Lake El'gygytyn area between 2.665 and 2.655 Ma (PZ-VII and PZ-VIII, Fig. 2, upper part of MIS G3, Fig. 3G). The biome reconstruction (Fig. 3A) shows that cold deciduous forest and taiga have the highest affinity scores in line with the qualitative interpretation of pollen data. The landscape openness significantly decreased (Fig. 3B). All these data suggest that the climate conditions became much warmer and wetter than before and that this climate amelioration reflects the climatic optimum of MIS G3.

Spruce pollen disappear from the spectra between 2.648 and 2.646 Ma (the uppermost part of PZ VII, Fig. 2, transition from MIS G3 to MIS G2, Fig. 3G), pointing to a successive deterioration of climate conditions. A very cold and dry climate prevailed at Lake

El'gygytyn between ca. 2.646 and 2.636 Ma (PZ-IX, Fig. 2, middle part of MIS G2, Fig. 3G), when coniferous taxa (*Pinus*, *Larix*) disappeared. Instead, steppe-like herb communities dominated the local vegetation during this interval. The biome reconstructions (Fig. 3A–B) also point to a treeless environment. This period may be correlated with the onset of the most extensive Cordilleran ice sheet in north-western Canada, which was dated to 2.64 Ma (Hidy et al., 2013). This also coincides with evidence for the first ice-rafted debris in Northern Atlantic marine sediment cores, which originate from an ice sheet on the North American continent and were dated at around 2.64 Ma (De Schepper et al., 2014 and references therein).

Birch and alder shrub thickets again became common in the region between 2.636 and 2.626 Ma (PZ-X, Fig. 2, transition from MIS G2 to MIS G1, Fig. 3G) thus hinting on warmer and wetter climate conditions. Rather high percentages of *Larix* document that larch has also grown in the vicinity of the lake. The biome reconstruction (Fig. 3A) is in line with these interpretations, and shows the highest affinity scores for cold deciduous forest and taiga. The landscape openness reconstruction also supports these interpretations and indicates an increased role of trees around the lake (Fig. 3B). However, a relatively high presence of *Artemisia* in the lower part of PZ-X reflects a rather dry climate, still favorable for the cold steppe habitats.

Cold steppe habitats with *Artemisia* completely absent from the pollen assemblages around 2.63 Ma at the onset of MIS G1 (upper part of PZ-X, Fig. 2) reflect further climate amelioration. The simultaneously rather high contents of *Gelasinospora* spores and other coprophilous fungi reflect the presence of grazing animals around the lake, which coincides with the existence of steppe habitats in lake's vicinity.

#### 5.5. Environmental conditions ca. 2.626–2.595 Ma

According to the pollen spectra pine and larch returned to the area between 2.626 and 2.617 Ma (PZ-XI, Fig. 2, middle part of MIS G1, Fig. 3G), when the regional vegetation was dominated by larch forests with stone pine, shrubby alder, and numerous ericaceous plants in the understory. Single spruces might also have grown in more protected places such as river valleys. The biome reconstruction (Fig. 3A) shows that cold deciduous forest, which has the highest affinity scores, was the dominant vegetation type. Some forestation of the landscape is also indicated by the difference between the maximum score of forest biomes and the maximum score of open biomes (Fig. 3B). The vegetation changes clearly reflect that the climate was significantly warmer and wetter than during the previous interval.

Drier and colder environmental conditions between 2.617 and 2.603 Ma (PZ-XII, Fig. 2, transition from MIS G1 to MIS 104 and middle MIS 104, Fig. 3G) are suggested by a gradual decrease of *Pinus* and especially by the rather high presence of *Artemisia*, Caryophyllaceae, Brassicaceae, and other herb and *Selaginella* spores in pollen assemblages. Vegetation during this interval was characterized by larch forests with some stone pine, shrubby alder and birch in understory, alternating with open steppe- and tundra-like habitats. The biome reconstructions (Fig. 3A–B) are in good accordance with this interpretation.

A reduction of forested areas and strong expansion of sage-grass steppe communities and dry rock-steppe habitats with *Selaginella*, which point to dry and cold conditions, are also notable in the Baikal region after 2.62 Ma (Demske et al., 2002). At about the same time, around 2.6 Ma, dry climate conditions were established on the Chinese Loess Plateau as well (Kukla and Cilek, 1996; Ding et al., 1997 and references therein).

Between 2.603 and 2.595 Ma (PZ-XIII, Fig. 2, upper part of MIS 104, Fig. 3G) steppe-like communities with *Artemisia*, Poaceae, and

Cyperaceae became dominant in the regional vegetation, thus reflecting further climate deterioration. The biome reconstruction for this interval shows that tundra has the higher affinity scores and cold steppe appears as a biome for the first time (Fig. 3A). In parallel the landscape openness increased (Fig. 3B). The upper boundary of the interval corresponds well to the transition from MIS 104 to MIS 103 (Fig. 3G). A relatively high presence of *Zygnema* cysts and remains of *Botryococcus* colonies point a stronger influence of shallow-water environments on the sedimentations at site 5011-1, which may be due to a lowered lake level in consequence of the dry climate. Nevertheless, high contents of *Sphagnum* spores indicate that swampy habitats were common around the lake. Similar to the present day, *Sphagnum* mosses might locally have grown in wetter habitats along small streams that enter the lake.

PZ-XIII widely coincides with the first occurrence of the so-called facies A in the sediment record of Lake El'gygytgyn (Fig. 2). This facies reflects sedimentation processes under a perennial ice cover (Melles et al., 2012; Wennrich et al., 2014; Wennrich et al., in this issue), whose formation requires mean annual air temperatures of at least  $4 \pm 0.5$  °C lower than today (Nolan, 2013).

#### 5.6. Environmental conditions ca. 2.595–2.558 Ma

Tundra-like coenoses with dwarf birches and sedges became dominant in the regional vegetation between 2.595 and 2.588 Ma (PZ-XIV, Fig. 2, lower part of MIS 103, Fig. 3G). That points to a climate much cooler compared to the previous interval, as also reflected in the biome reconstructions (Fig. 3A–B). Climate cooling at the onset of the Pleistocene may also have led to the formation of permafrost at Lake El'gygytgyn, as indicated by quartz grains in the lake sediments that suggest enhanced cryogenic weathering in the catchment since about 2.55 Ma (Schwamborn et al., 2013). Climate deterioration ca. 2.6 Ma ago was also inferred for eastern Beringia, to the east of the Bering Strait, where pollen and macrofossil records demonstrate that *Pinus* and *Picea* species disappeared or became greatly reduced in the local vegetation, while grasses and other herbaceous taxa increased (Schweiger et al., 2011 and references therein). This cooling may also be associated with the onset of the so-called Okanaanean Glaciation that occurred in eastern Chukotka around 2.6 Ma (Laukhin et al., 1999; Laukhin, 2014). However, the age control of the glacial sediments attributed to the Okanaanean Glaciation is poor and based only on biostratigraphical (pollen and diatom) evidence. In the Baikal area, a remarkable reduction of forested areas took place after 2.61 Ma, while steppe environments expanded strongly (Demske et al., 2002). Furthermore, the first episode of rapid loess deposition in Central China also occurred at ~2.6 Ma, indicating strong intensification of the Siberian cold-high pressure regime, and accordingly, a profound cooling of the regional climate (Han et al., 1997). In the marine realm, sediment records show significant increase of ice-rafted debris around 2.6 Ma (Jansen et al., 2000), which demonstrates that global cooling had a strong influence on the intensification of the northern hemisphere glaciation. This coincides with a southward shift of North Atlantic Current, as reflected in palynological data from the North Atlantic (Hennissen et al., 2014.)

Open larch forests with dense shrub alder and birch understory dominated in the region from 2.588 to 2.579 Ma (PZ-XV, Fig. 2, middle part of MIS 103, Fig. 3G). Somewhat more favorable climate conditions, reflecting the MIS 103 optimum, are also suggested by a slight increase in *Pinus* pollen, although pine probably did not grow in the lake vicinity. The biome reconstruction shows that cold deciduous forest became the dominant vegetation type (Fig. 3A) and forestation increased (Fig. 3B). The transition from a treeless to a forested environment at Lake El'gygytgyn corresponds with the Pliocene/Pleistocene and paleomagnetic Gauss/Matuyama

boundaries (Nowaczyk et al., 2013 and references therein).

Between ca. 2.579 and 2.558 Ma (PZ-XVI, Fig. 2, upper MIS 103 to upper MIS 102, Fig. 3G), larch and especially shrub alder decreased remarkably in the local vegetation, while open grass-herb-sage-*Selaginella* dominated habitats became common around the lake. These changes point to rather dry and cold climate conditions. Accordingly, tundra has the highest affinity scores (Fig. 3A). A small increase in the *Botryococcus* remains and *Zygnema* cysts again suggests enhanced influx from shallow-water environments, which likely were due to the dry climate that resulted in lake-level lowering.

#### 5.7. Environmental conditions ca. 2.558–2.533 Ma

Larch forest with few shrub pines became more wide-spread around the lake between ca. 2.558 and 2.533 Ma (PZ-XVII, Fig. 2, upper part of MIS 102, Fig. 3G), thus pointing to a slightly more favorable (wetter and probably warmer) climate. Wetter local environments are also suggested by the increased presence of alder and *Sphagnum*. The biome reconstruction reveals a strengthening of the cold deciduous forests (Fig. 3A) and increased forestation of the landscape (Fig. 3B).

Between ca. 2.553 and 2.546 Ma (PZ-XVIII, Fig. 2, transition from MIS 102 to MIS 101, Fig. 3G) the vegetation was dominated by larch forests with some stone pine, shrubby alder, and birch in understory. This suggests significant climate amelioration, which is in good accordance with the biome reconstructions (Fig. 3A–B). Furthermore, relatively high contents of *Gelasinospora* and spores of some other coprophilous fungi, indirectly point to the presence of grazing animals around the lake during this period.

In the interval from ca. 2.546 to 2.532 Ma (PZ-XIX, Fig. 2, transition from MIS 101 to MIS 100, Fig. 3G) the understory (stone pine, shrubby alder, dwarf birch) of the larch forests became denser. Club mosses also increased in the local vegetation. The vegetation changes suggest that climate conditions remained rather warm and wet, as supported also by the biome reconstruction which shows that forest biomes (i.e. cold deciduous forest and taiga) have the highest affinity scores (Fig. 3A) and the landscape openness significantly decreased at that time (Fig. 3B).

#### 5.8. Environmental conditions ca. 2.533–2.465 Ma

In the interval ca. 2.533 and 2.515 Ma (PZ-XX, Fig. 2, middle part of MIS 100, Fig. 3G), Coniferous trees and shrubs completely disappeared in the region, while open, steppe-and meadow-like habitats with *Artemisia*, *Thalictrum*, Poaceae and Caryophyllaceae became broadly distributed. In the biome reconstruction tundra and cold steppe have the highest affinity scores (Fig. 3A), and the landscape openness also increased drastically (Fig. 3B). Numerous *Botryococcus* remains, especially at the beginning of the PZ, reflect abundant shallow-water habitats, likely due to lake lowering. The revealed changes clearly point to particularly dry and cold climate conditions at Lake El'gygytgyn during MIS 100. During this glacial, the closure of the Panamanian Gateway commenced, and sea level dropped by 60–90 m as a result of increased ice volume (Groeneveld et al., 2014 and references therein). Bailey et al. (2012) deduced from marine records from the North Atlantic Ocean that this earliest large-amplitude Pleistocene glacial, ~2.52 Ma, was arguably a key glacial characterized by abundant iceberg calving from large ice-sheets on multiple continents in the high northern latitudes.

Subsequently, between 2.515 and 2.510 Ma (PZ-XXI, Fig. 2; MIS 100 to MIS 99 transition, Fig. 3G), tundra and landscape openness kept highest affinity scores and high values, respectively, (Fig. 3A and B). However, dwarf birch coenoses became more common,



while steppe-like communities with *Artemisia* started to decline from the vegetation, thus suggesting some climate amelioration. An increase of *Sphagnum* may point to wetter soil conditions.

Between 2.515 and 2.492 Ma (PZ-XXII, Fig. 2, middle MIS 99, Fig. 3C) open larch forest with numerous dwarf birches and some shrub alders in understory dominated the area. Together with a distinct reduction in landscape openness (Fig. 3B) this suggests further climate amelioration. Increased presence of *Sphagnum* may be traced back to a paludification and wetter soil conditions during this interval. A shift to relatively favorable environmental conditions at about 2.5 Ma ago was also reconstructed from the contemporaneous Baikal pollen record which suggest the growth of moisture-dependent fir and even broadleaved taxa in the area (Demske et al., 2002).

### 5.9. Climate-vegetation lag and climate trends crossing the Pliocene/Pleistocene boundary

Both the qualitative pollen-based (Fig. 2) and the biome (Fig. 3A–B) reconstructions reveal some lags between global climate change, highlighted by the benthic oxygen isotope stack (Fig. 3G), and the vegetation responses in the study area. As sedimentary proxies from Lake El'gygytgyn argue against significant redeposition of older material (i.e. contamination of the pollen-poor glacial sediment by pollen reworked from the previous interglacial, Wennrich et al., in this issue), the observed lags suggest a delay in the response of the regional vegetation to climate change, at least during the transition from the warmest interglacials (i.e. MIS G3 and 103) to glacials (i.e. MIS G2 and 100). An alternative explanation is a possible millennial-scale uncertainty of the age-depth model (Melles et al., 2012), which is based on magnetostratigraphy and tuning of proxy data to the regional insolation and global marine isotope stratigraphy (Fig. 3G). Bearing in mind that not every MIS transition shows delayed response in vegetation, this possibility must be considered. Checking both hypotheses is a task of forthcoming research.

It is interesting to note that the biome reconstruction does not show pronounced differences between the climate cycles presented here prior to and after the Pliocene/Pleistocene boundary (Fig. 3), except distinctly drier and colder vegetation and environments suggested for MIS 100 by the biome (Fig. 3A), landscape openness (Fig. 3B), pollen productivity (Fig. 3D), and marine oxygen isotope record (Fig. 3G). The Pliocene/Pleistocene boundary at 2.588 Ma shows neither a gradual nor a step-wise shift towards a colder and drier climate. This finding is in agreement with results presented by Brigham-Grette et al. (2013) based upon a preliminary, coarser-resolution pollen record from Lake El'gygytgyn that was combined with sedimentary proxies. These data suggested that the major change in regional vegetation and climate at Lake El'gygytgyn occurred earlier, between 2.71 and 2.69 Ma, simultaneous with the onsets of North Pacific stratification (Haug et al., 2005) and Northern Hemispheric glaciation (Brierley et al., 2009). On the other hand, warmer than present Arctic summers existed until ~2.2 Ma ago (Tarasov et al., 2013), indicating that Arctic cooling was insufficient to support large-scale ice sheets until the early Pleistocene (Brigham-Grette et al., 2013).

## 6. Conclusions

Our results demonstrate that the late Pliocene/early Pleistocene pollen record of Lake El'gygytgyn is an excellent archive of vegetation and climate changes in the northeastern Russian Arctic. The quantitative biome reconstructions are in a good accordance with the qualitative interpretation of pollen spectra. The two approaches employed for pollen-based biome reconstructions reveal the same

set of the dominant biomes.

Generally, the record reflects the main paleoenvironmental fluctuations in the region. During the studied time interval the most pronounced environmental changes (appearance of tundra and steppe-like habitats) pointing to cold and dry conditions, occurred around 2.710, 2.645, 2.600, and 2.532 Ma.

Open steppe-like, tundra and shrub tundra vegetation dominated during the early Pleistocene, however, relatively warm intervals with larch forest and stone pine growing around the lake occurred ca 2.587–2.578, 2.558–2.532, and 2.551–2.550 Ma ago. Strong peaks in green algae remains (mostly *Botryococcus* colonies) around 2.695, 2.678, 2.602–2.595, and 2.535–2.515 Ma reflect increased shallow-water conditions coinciding with dry climate intervals reconstructed by pollen indicators.

The biome and qualitative pollen-based reconstructions reveal some lags between the global climate change and regional vegetation responses, however testing of this hypothesis is the task of forthcoming research, which will incorporate all the El'gygytgyn pollen data, including that from the Pleistocene. The same holds true for more detailed investigations of the periodicity of vegetation changes at Lake El'gygytgyn throughout the Late Pliocene and Pleistocene.

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