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The biome reconstruction approach as a tool for interpretation of past vegetation and climate changes: application to modern and fossil pollen data from Lake El’gygytgyn, Far East Russian Arctic

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Abstract

The modern and fossil pollen data obtained under the framework of the multidisciplinary international "El'gygytgyn Drilling Project" represent a unique archive that allows the testing of a range of pollen-based reconstruction approaches and the deciphering of changes in the regional vegetation and climate since ∼ 3.58 Ma. In the current study we provide details of the biome reconstruction method applied to the late Pliocene and Quaternary pollen records from Lake El'gygytgyn. All terrestrial pollen taxa identified in the spectra from Lake El'gygytgyn were assigned to major vegetation types (biomes), which today occur near the lake and in the broader region of eastern and northern Asia and, thus, could potentially have been present in this region during the past. When applied to the modern surface pollen spectra from the lake, the method shows a dominance of the tundra biome that currently characterizes the Lake El'gygytgyn area. When applied to the pollen spectra from the middle Pleistocene to present, the method suggests (1) a predominance of tundra during the Holocene, (2) a short interval during the marine isotope stage (MIS) 5.5 interglacial distinguished by cold deciduous forest, and (3) a long phase of taiga dominance during MIS 31 and, particularly, MIS 11.3. These two latter interglacials seem to be some of the longest and warmest intervals within the past million years.

During the late Pliocene–early Pleistocene interval (i.e., ∼ 3.562–2.200 Ma), there is good correspondence between the millennial-scale vegetation changes documented in the Lake El'gygytgyn record and the alternation of cold and warm marine isotope stages, which reflect changes in the global ice volume and sea level. The biome reconstruction demonstrates changes in the regional vegetation which suggest a step-like transition from generally warmer/wetter environments of the earlier (i.e., Pliocene) interval towards colder/drier environments of the Pleistocene. The reconstruction of most of the species-rich cool mixed and cool conifer forest biomes is particularly noticeable prior to MIS G16, whereas tundra becomes a prominent feature after MIS G6. These results consistently indicate that the study region supported significant tree populations during most of the interval prior to ∼ 2.730 Ma. The biomization results also suggest that the transition from mostly forested to mostly open landscape was not gradual, but rather occurred in step-like fashion. Thus, the cold and drought tolerant steppe biome first appears in the reconstruction ca. 3.298 Ma during the tundra dominated MIS M2, whereas the tundra biome initially occurs between ∼ 3.379 and ∼ 3.378 Ma within MIS MG4. Prior to ∼ 2.800 Ma, several other cold stages during this generally warm Pliocene interval experienced a dominance of tundra and a great reduction of tree populations in the regional vegetation.

1 Introduction

Since the introduction of palynological analysis to the field of geology in 1916, its main purpose has been the objective reconstruction of temporal and spatial changes in vegetation (mainly during the Quaternary period) at local to regional scales (Faegri and Iversen, 1989). Related to this task is the evaluation of the possible roles played by natural factors (e.g., climate change, volcanism, sea-level fluctuations) and/or by human activities (e.g., anthropogenic fires, wood cutting, land use) in affecting the paleovegetation. The fact that the Arctic is poorly populated and human impact on high-latitude vegetation remains virtually insignificant, at least until very recently, makes pollen records from these regions an important source of information concerning the natural factors driving vegetation changes, particularly as related to centennial- and millennial-scale climate variability.

For the first time, sediment cores from Lake El'gygytgyn (Fig. 1) in northern Far East Russia provide a nearly continuous, high-resolution environmental record from the Arctic, a record which spans the past ∼ 3.58 Myr (Melles et al., 2012). Melles et al. (2012) and Brigham-Grette et al. (2013) have presented, in summary form, results of the multi-disciplinary studies of the Lz1024 and 5011-1 (ICDP Site 5011-1) sediment cores recovered from the central part of the lake (Fig. 1b). Among the analyzed proxies, results of the pollen analysis have been presented and used to reconstruct changes in the regional climate through the four Quaternary interglacial intervals, representing marine isotopic stage (MIS) 1, MIS 5, MIS 11 and MIS 31 (Melles et al., 2012; for the MIS 1 to MIS 8 interval, see also Lozhkin et al., 2007), and during the late Pliocene to early Pleistocene interval between ~ 3.58 and ~ 2.2 Ma (Brigham-Grette et al., 2013) by applying the best modern analog (BMA) approach (Overpeck et al., 1985; Guiot, 1990; Tarasov et al., 2005).

The current study provides methodological background and results obtained using a method of biome reconstruction (first introduced by Prentice et al., 1996) applied to the published late Pliocene and Quaternary pollen spectra from Lake El’gygytgyn. The reconstruction results are then discussed in terms of the regional changes in vegetation and as regards the respective bioclimatic variables controlling vegetation dynamics. This method allows a further comparison with the published results obtained using the BMA approach, as well as with the paleoclimate interpretations based on other proxy data.

2 Data and method

2.1 Site setting

Lake El’gygytgyn (67°30′ N, 172°05′ E, 492 m a.s.l.) occupies the central part of a meteorite impact crater situated in the northeastern part of Asia, ~ 100 km north of the northern polar circle, ~ 265 km south of the East Siberian Sea and ~ 390–420 km northwest of the Bering Sea (Fig. 1a). The impact occurred 3.58 ± 0.04 Myr ago (Layer, 2000; see also Melles et al., 2012, and Vogel et al., 2012, for details on the regional geology). The lake has a roughly circular shape with a diameter of 12 km (Fig. 1b) and a maximum water depth of 175 m (Vogel et al., 2012). The lake catchment area, limited by the crater’s outer rim that has a maximum elevation of 857 m a.s.l. (Matrosova, 2009), is drained by numerous short and steep valleys with perennial creeks or ephemeral streams (Fig. 1b). The Enmyvaam River (Fig. 1b) flows from the southeastern part of the basin, connecting the lake with the Anadyr River system and the Bering Sea.

The regional climate is characterized by cold and long winters (September to May) with mean temperatures of the coldest month (MTCM) below −32 °C, and short, cool summers with mean temperatures of the warmest month (MTWM) less than +9 °C according to the gridded ($10' \times 10'$) global dataset of modern climate averaged over a thirty-year (1961–1990) interval (New et al., 2002). Russian sources (e.g., Treshnikov, 1985) provide even lower mean values, i.e., ranging between −32 and −36 °C in January and between +4 and +8 °C in July, though for a different observation period. The mean annual precipitation (PANN) at Lake El'gygytgyn is ∼ 250 mm (New et al., 2002). The relatively low PANN is not a limiting factor for plant growth, as evaporation losses are also low. Snow cover is up to 0.3–0.5 m, a depth sufficient to support growth of perennial shrubs (Kaplan et al., 2003). However, low MTWM prevents the establishment of boreal trees, which require MTWM values of at least +11 °C (e.g., MacDonald et al., 2000; Tarasov et al., 2013). Reflecting the modern regional climate, the vegetation of the Chukchi Uplands, which surrounds Lake El'gygytgyn, belongs to the southern shrub tundra and typical tundra zone (Yurtsev, 1974; Alpat'ev et al., 1976), although vegetation within the lake catchment is dominated by herb-lichen tundra. The uplands is characterized by graminoid (Poaceae and Cyperaceae) and moss tundra communities with occasional shrub thickets of alder (*Alnus viridis* subsp. *fruticosa*, also known as *Duschekia fruticosa*), willow (*Salix*) and birch (*Betula*) (e.g., Matrosova, 2009; see also Lozhkin and Anderson, 2013, and Andreev et al., 2013, for further details and references). Larch (*Larix gmelinii*) and dwarf stone pine (*Pinus pumila*) grow south and west of the lake within the forest-tundra and northern taiga zone. However, tree line is located ∼ 150 km to the southwest of the lake (Lozhkin and Anderson, 2013).

2.2 Pollen data

The pollen data used in the current study include 43 modern pollen spectra representing (1) top samples of the short sediment cores recovered from Lake El'gygytgyn

(Matrosova, 2009; Fig. 1b); and (2) published fossil pollen records, which represent two sediment cores Lz1024 and 5011-1 recovered in the deepest central part of the lake (Fig. 1b). The pollen data for MIS 1 and MIS 5 interglacial intervals are from core Lz1024, whereas core 5011-1 provided samples from MIS 11 and MIS 31 (for detailed results of the pollen analyses and respective pollen diagrams, see Melles et al., 2012, Lozhkin and Anderson, 2013, and Lozhkin et al., 2007). The pollen spectra from the lower part of core 5011-1 represent the late Pliocene and early Pleistocene interval between ∼3.58 and ∼2.2 Ma (for details of the pollen analysis and pollen diagrams, see Brigham-Grette et al., 2013, and Andreev et al., 2013). The fossil pollen spectra used for the biome reconstruction in the current study also were used as the basis for a recently reported quantitative climate reconstruction (see Melles et al., 2012, Brigham-Grette et al., 2013, and Nowaczyk et al., 2013, for the core descriptions and details of the age model).

2.3 Biome reconstruction method

Pollen-based vegetation reconstruction using the quantitative method known as the “biomization” approach enables objective interpretation of pollen data and facilitates discussions of past vegetation dynamics and data–model comparisons (Prentice et al., 1996). The latter is possible because the method provides a systematic way to translate results from paleoclimate models into maps of natural potential vegetation (e.g., Prentice et al., 1992; Kaplan, 2001) by utilizing the same concepts for biome definition in the pollen-based biome reconstructions and climate-based biome simulations (Prentice et al., 1996).

In the biome reconstruction approach, pollen taxa are assigned to plant functional types (PFTs) and to principal vegetation types (biomes) on the basis of the modern ecology, bioclimatic tolerance, and spatial distribution of the pollen-producing plants. The method initially was tested using global-scale modern pollen datasets (e.g., Prentice et al., 1996, 2000), but further modifications of the biome–taxon matrixes were developed for large parts of Siberia and Alaska (e.g., Tarasov et al., 1998; Edwards et al., 2000). A successful validation of the method using modern pollen–vegetation–climate data encouraged an application of the approach to datasets from the mid-Holocene, the last glacial maximum, and the last interglacial in areas of northern Eurasia and North America (Edwards et al., 2000; Tarasov et al., 2000, 2005). Concerns relating to the ability of the method to differentiate cold deciduous forest, taiga, and tundra in these earlier studies (see also Müller et al., 2009) resulted in further testing of the paleodata using a modern pollen dataset from Yakutia (Müller et al., 2010). Based on the results of this study, several modifications (mainly concerning tree and shrub forms of *Betula* and *Alnus/Duschekia*, which represent a wide range of regional vegetation types) were made in the biome–taxon matrix. The modified scheme became more consistent with the authors' field observations, regional botanical studies (Müller et al., 2010, and references therein), and with the taxa to biome attribution suggested for northeastern Siberia (i.e., Edwards et al., 2000; Anderson et al., 2002).

The biome–taxon matrix (Table 1) used in the current study employs taxa to biome attribution published by Müller et al. (2010). However, their matrix does not include all terrestrial pollen taxa that have been identified in the sediment samples from Lake El'gygytgyn dated to the late Pliocene and early and middle Pleistocene (Brigham-Grette et al., 2013; Andreev et al., 2013; Lozhkin and Anderson, 2013). These taxa (e.g., *Carpinus*, *Carya*, *Corylus*, *Juglans*, *Pterocarya*, deciduous *Quercus*, *Tilia*, *Ulmus*, *Tsuga* etc.) represent warmer vegetation types (i.e., cool conifer forest, cool mixed forest and temperate deciduous forest), which did not grow in the northern and northeastern parts of Asia under the extremely cold and continental climate conditions of the late Quaternary, but possibly occurred in the region close to Lake El'gygytgyn during the earlier, much-warmer-than-present intervals (Brigham-Grette et al., 2013). In order to consider the whole range of the Lake El'gygytgyn pollen taxa and less continental boreal and temperate forest biomes, which appear in the modern vegetation of the southern Russian Far East (e.g., Mokhova et al., 2009), northern Japan (e.g., Takahara et al., 2010) and China (e.g., Yu et al., 1998), the biome–taxon matrix applied here (Table 1) was extended using the published matrixes tested with the modern surface pollen data from the respective regions of Asia (Yu et al., 2000; Mokhova et al., 2009; Tarasov et al., 2011).

The biome score calculation was performed using standard equation and reconstruction procedures described in Prentice et al. (1996) and the PPPBase software developed by Guiot and Goeury (1996). The sum of all terrestrial pollen taxa (Table 1) identified in the Lake El'gygytgyn records was taken as 100 % for calculating the percentages of an individual taxon.

As suggested by Prentice et al. (1996) and accepted in the global vegetation mapping BIOME6000 Project (Prentice and Webb, 1998), square root transformation was applied to the pollen percentage values. This operation stabilizes variance and increases the method's sensitivity to less abundant taxa (cf. Overpeck et al., 1985). The 0.5 % threshold was applied to all pollen taxa, as recommended by Prentice et al. (1996), to minimize possible noise due to long-distance transport, redeposition and misidentification of single grains representing extremely rare taxa. Edwards et al. (2000) applied a weighting (× 20) to occurrences of *Larix* in individual pollen spectra in order to maximize the chance of reconstructing cold deciduous forest when it was probably present. However, we retain the use of weighting of *Larix* percentages in the current study (see Müller et al., 2010 for discussion of the different approaches).

The biome reconstruction method is based on a fuzzy logic approach, in which each pollen sample is estimated to have a numerical "affinity" with every potential biome listed in Table 1. The final biome identification is based on ranking the affinity scores (Prentice et al., 1996), i.e., the biome with the highest affinity score is assumed to be dominant and is assigned to a given pollen spectrum. A problem can arise at this point if several biomes have an equal maximum score. Prentice et al. (1996) suggested resolving this problem, which happens routinely if the taxa/PFTs of one biome are a subset of those of another biome, by putting the biomes in a particular (though rather straightforward) order so that subsets always come first (see Table 1 for biome ordering).

For distinguishing the cold and warm steppe biomes, the presence of boreal trees and arctic-alpine shrub taxa are used as additional criteria to assign herbaceous pollen taxa to the appropriate biome. This distinction is based on the reasonable assumption that the temperature requirements of the herbaceous taxa may be indicated by associated tree and shrub taxa, which can be identified by pollen analysts at a higher taxonomic level (full details are presented in Tarasov et al., 1998).

The biomization approach provides no quantitative information about vegetation composition or structure and can mask temporal variations in the internal structure and composition of biomes (Williams et al., 2004). It also does not allow the reconstruction of transitional vegetation types, e.g., forest-steppe, tundra-steppe, and forest-tundra (Prentice et al., 1996). However, this missing information can be partly recovered by examining the relative values of the dominant and co-dominant biome scores (e.g., Tarasov et al., 2000; Fig. 2b). Additional (semi-quantitative) information concerning the vegetation cover (i.e., forest versus open vegetation) can be obtained by calculating the distance between the maximum score of forest biomes (MSFB) and the maximum score of open biomes (MSOB) for the analyzed pollen spectra (e.g., Fig. 3c).

3 Results and discussion

3.1 Test with the modern pollen spectra

Palynological results from a set of 43 samples representing surface sediment layers from Lake El'gygytgyn (Matrosova, 2009) indicate only 17 terrestrial pollen taxa exceed the 0.5 % threshold (Fig. 2a). Despite existing variations in the main taxa percentages, all samples are dominated by *Alnus*, *Betula* and *Pinus* subg. *Haploxylon* pollen, representing regional alder, birch and pine shrubs, respectively. Poaceae and Cyperaceae are the most common herbaceous pollen taxa, and reflect local and regional graminoid tundra. These modern pollen spectra support the conclusion that the pollen rain in Lake El'gygytgyn is more indicative of regional than local catchment vegetation with up to 60 % of the pollen (*Alnus*, *Betula*, *Pinus pumila*) coming from the surrounding uplands (Lozhkin et al., 2001). This predominantly regional signal in the modern pollen assemblage strengthens the use of the Lake El'gygytgyn pollen data for paleoclimatic interpretations (Melles et al., 2012; Brigham-Grette et al., 2013; Lozhkin et al., 2007) and quantitative vegetation reconstructions.

The biome reconstruction (Fig. 2b) demonstrates that tundra (TUND) has the highest affinity scores (average of ~ 17.7), followed by cold deciduous forest (CLDE) (~ 15.2 average), and reflects well the main vegetation types in northern Chukotka. On the other hand, affinity scores for cold steppe (STEP) (Table 1), which played a pronounced role across areas of northern Eurasia during the last glacial (e.g., Tarasov et al., 2000; Andreev et al., 2004, 2011; Bezrukova et al., 2010; Müller et al., 2010), are low in the modern surface spectra (~ 6.2 average).

3.2 The last glacial and Holocene interval (~ 24–2 kyr BP)

The results of biomization (Fig. 3) show that the STEP vegetation type displays the highest affinity scores during the last glacial ~ 24–16 kyr BP (Fig. 3a) and remains dominant prior to ~ 14.9 kyr BP (Fig. 3b). This vegetation reconstruction suggests that drought- and cold-tolerant herbaceous communities played a major role in the regional vegetation cover. TUND biome scores for the glacial spectra are substantially lower than in the modern pollen spectra, and the CLDE scores are at minimum, reflecting virtual absence of tree and shrub vegetation in the glacial landscape (Fig. 3c). The interval after ~ 16 kyr BP experiences drastic changes in the biome composition. The Bølling–Allerød (B–A) interstadial (Fig. 3d) is characterized by a marked increase in the TUND and CLDE scores and is accompanied by a decrease in the STEP scores to almost present-day levels. The Younger Dryas (YD) shows biome scores that broadly resemble values reconstructed for the full glacial. However, TUND scores remain dominant, suggesting that YD conditions were less severe than during the interval prior to 14.9 kyr BP. The Holocene biome results are characterized by a continuous dominance of TUND. Between ~ 10.5 and 8 kyr BP, STEP reveals its lowest scores for the entire

El’gygytgyn record. This interval likely corresponds to the early Holocene climatic optimum. Despite a marked increase in CLDE scores, the biome reconstruction suggests that the Holocene landscape remained generally open and that trees did not play an important role in the regional vegetation (Fig. 3c).

High percentages of *Betula* and *Alnus* characterize the late glacial and early Holocene pollen record from Lake El’gygytgyn (Lozhkin et al., 2007). Depending on climatic and ecological conditions, both taxa (and *Salix*) may have substantially different life forms, which represent different biomes. As arctic-alpine shrubs and dwarf shrubs, these taxa are characteristic of the tundra biome, whereas when occurring as tall shrubs and trees they are important constituents of several boreal and boreal-temperate forest biomes (Table 1). Unfortunately, pollen grains representing tree and shrub forms of the same taxon have little morphological difference. This morphological similarity often prevents pollen analysts from distinguishing between the two forms and challenges pollen-based vegetation and climate reconstructions (Prentice et al., 1996). Therefore, our biomization scheme uses a conservative approach and assigns *Alnus* and *Betula* to both TUND and CLDE biomes. Despite these potential limitations, Andreev et al. (2012), who analyzed several Holocene permafrost sequences in the vicinity of Lake El’gygytgyn, assigned pollen of *Alnus* and *Betula* mainly to their shrub forms. Their results indicate the presence of tundra and forest-tundra communities and thus support the conclusions drawn from the biome reconstructions. However, macrofossil analysis of an organic-rich deposit, dated to ~ 9100–8100 ^{14}C yr BP and located ~ 1 km distant from Lake El’gygytgyn, revealed larch needles, tree-sized alder, and taxa that today are restricted to areas to the south of the lake (Shilo et al., 2008). Moreover, larch seeds were found in the P2 core (Andreev et al., 2012) on the northern shore of Lake El’gygytgyn and dated to 9640 ± 60 ^{14}C yr BP, indicating that larch grew in the lake crater during the early Holocene. Furthermore, macrofossil studies to the north of current tree line in Chukotka indicate that alder and willow achieved tree heights during the same interval (Lozhkin, 1993), suggesting that at least during the Holocene thermal maximum cold deciduous woodland was likely present in areas of northern Chukotka.

Climate reconstructions of the early Holocene thermal maximum (Lozhkin et al., 2007) revealed mean July (i.e., MTWM) temperatures that were up to 2 to 4 °C warmer than present. Paleobotanical data suggest the study area perhaps supported vegetation similar to high shrub tundra found today in southern Chukotka. Additionally, gallery birch and willow forests established in protected river valleys and possibly stands of deciduous trees occurred in sheltered areas within the interfluves (Edwards et al., 2005; Lozhkin and Anderson, 2013). More recent climate reconstructions using the BMA approach (Melles et al., 2012) indicate a 2 to 4 °C increase in MTWM (within the reconstruction uncertainty range). These results suggest that the early Holocene warming in the study area was probably less pronounced (Melles et al., 2012 and Fig. 8c) than suggested by Lozhkin et al. (2007), and the more moderate temperatures would prevent significant forest development in the region.

3.3 The penultimate glacial–interglacial transition and the last interglacial interval (~ 138–89 kyr BP)

Biomization results (Fig. 4) show that STEP has the highest affinity score at the end of the penultimate glacial ~ 138–136 kyr BP (Fig. 4a). However, TUND becomes a dominant vegetation type after ~ 135 kyr BP (Fig. 4b). The CLDE affinity scores show a marked increase by ~ 133 kyr BP and a subsequent drop at ~ 130 kyr BP, resembling the interstadial–stadial oscillation during the later part of the last glacial interval (Fig. 3a). The onset of interglacial conditions as indicated by the vegetation reconstruction (Fig. 4c) can be placed ~ 128 kyr BP, or just above the MIS 6/MIS 5 boundary (Fig. 4d). Although maximum CLDE scores are between ~ 128 and ~ 115 kyr BP (MIS 5.5), relatively high TUND scores suggest that this vegetation type was an important landscape element during most of the last interglacial interval. Two samples with CLDE scores slightly higher than those for TUND are dated to ~ 125–123 kyr BP. STEP has its lowest scores for the whole record between ~ 127 and ~ 123 kyr BP. All the evidence marks this interval as the interglacial climatic optimum, which experienced the highest temperature, greatest precipitation, and most extensive establishment of shrub and forest-tundra communities within the region. Although the biome scores (Fig. 4a) suggest that woody plants likely played a more important role in the regional vegetation during the last interglacial as compared to the Holocene, the biome reconstruction indicates that open vegetation predominates on the regional landscape (Fig. 4c). Starting from ∼ 115 kyr BP, the biome reconstruction demonstrates a progressive decrease in CLDE and synchronous increase in STEP scores, marking the interglacial–glacial transition. TUND scores remain important until ∼ 92 kyr BP, and STEP scores achieve their highest values after that, likely indicating the onset of the extremely cold and dry climate of the full glacial.

The pollen record of the MIS 5.5 climatic optimum from Lake El'gygytgyn (Lozhkin et al., 2007; Lozhkin and Anderson, 2013) shows high percentages of *Betula* and *Alnus*, which when combined with the other tree/shrub taxa constitute over 95 % of the pollen assemblage. The MIS 5.5 interglacial pollen spectra reveal substantially lower percentages of herbaceous taxa than recorded in the Holocene spectra. The differences in the paleovegetation suggest that the MIS 5.5 climate optimum was wetter and warmer than the Holocene maximum and that tree and shrub communities were more common in the regional vegetation during MIS 5.5 (Lozhkin and Anderson, 2013). This interpretation agrees with the analog-based climate reconstructions (Lozhkin et al., 2007; Melles et al., 2012; Fig. 8c and d) and with the results of the quantitative biome reconstruction presented here (Fig. 4).

The expansion of trees in the study region during the MIS 5 climate optimum remains under debate. Although woody plant macrofossils assigned to the last interglacial have been found throughout the Siberian Arctic beyond the modern tree line (Lozhkin and Anderson, 1995; Kienast et al., 2011, and references therein), chronological control at many sites is rather weak (Lozhkin and Anderson, 2013).

Evidence from the recently studied site Oyogos Yar (72.68° N, 143.53° E) from northern Yakutia (Kienast et al., 2011) suggests that open forest-tundra with larch (*Larix dahurica*), tree alder (*Alnus incana*), and birch and alder shrubs, interspersed with patches of steppe and meadows, occupied the Yana-Indigirka Lowland in the western-most part of Beringia. The presence of larch indicates that the tree line shifted at least 270 km north of its current position and that the MTWM exceeded 13 °C during the last interglacial optimum (Kienast et al., 2011). The pollen-based climate reconstruction for Lake El'gygytgyn demonstrates a less pronounced increase in summer temperature (Melles et al., 2012) than inferred for Oyogos Yar, which is located ∼ 1200 km to the west of the lake. The temperature differences reconstructed for MIS 5.5 suggest that the central part of the Siberian Arctic perhaps experienced a stronger warming and a greater northward advance of the tree line as compared to northeastern Siberia. A similar situation was noted during the Holocene (e.g., Texier et al., 1997; Binney et al., 2009, and references therein).

3.4 The interval including the MIS 11 interglacial (∼ 428–356 kyr BP)

The biome reconstruction (Fig. 5) displays abrupt changes in the vegetation in the Lake El'gygytgyn region during the MIS 12/MIS 11 transition. The shift in dominance of full glacial steppe/tundra (STEP and TUND) to boreal forest (TAIG) occurs within a rather short time interval (∼ 428 to ∼ 424 kyr BP; Fig. 5a and b). However, the biome reconstruction does not show an event similar to a YD-like oscillation, as seen during the MIS 2/1 (Fig. 3a) and MIS 6/5 (Fig. 4a) transitions. Unlike the two youngest interglacials (MIS 5.5 and MIS 1), the biome results suggest a long phase of TAIG dominance (Fig. 5b) with a major spread of woody vegetation in the study region occurring between ∼ 424 and ∼ 399 kyr BP (i.e., over 25 kyr). The final stage of the MIS 11.3 interglacial (prior to 394 kyr BP) experienced abrupt increases in TUND and STEP scores with an associated decrease in the forest biome scores. This pattern suggests a shift towards colder/drier environments at ∼ 400 kyr BP. TUND becomes a dominant vegetation type during the remaining part of MIS 11 (Fig. 4b), while STEP shows the highest values during MIS 10 between ∼ 374 and ∼ 356 kyr BP. This shift in biome scores indicates a return to an extremely cold and dry full glacial climate.

As expected from both the quantitative biome (this study, Fig. 8a and b) and climate reconstructions (Melles et al., 2012, Fig. 8c and d), the MIS 11 pollen record differs substantially from those of MIS 1 and MIS 5 (Lozhkin and Anderson, 2013). In particular, the MIS 11 spectra contain high percentages of *Picea* and significant amounts of *Larix* pollen (unambiguously defined tree taxa virtually absent in the younger interglacial records), suggesting greater forestation of the region under conditions that were much warmer and wetter than present. The expansion of *Picea* to the Lake El'gygytgyn region is reflected in the dominance of the boreal evergreen conifer forest (i.e., TAIG) biome during the MIS 11.3 interglacial and represents a significant northeastward shift in comparison to its modern distribution (Lozhkin and Anderson, 2013). The biome analysis (Fig. 5b) assigns two pollen spectra to the COCO biome, which corresponds to the appearance of *Corylus* (cool-temperate broadleaf genus) pollen in the MIS 11.3 assemblage. However, the discontinuous presence of this pollen taxon in the El'gygytgyn record has been interpreted as long-distance transport from southern regions, and not indicative of the establishment of the shrub near the lake (Lozhkin and Anderson, 2013). Conventional interpretation of the pollen diagram suggests that shrub tundra did not disappear completely when boreal evergreen coniferous forest was widespread, but rather that tundra likely was restricted to higher elevations (Lozhkin and Anderson, 2013). The latter conclusion is in line with the relatively high biome scores for TUND during the MIS 11.3 (Fig. 5a) and explains the rapid re-establishment of tundra dominance in the region during the later part of MIS 11.

3.5 The interval including the MIS 31 interglacial (∼ 1092–1057 kyr BP)

The biome reconstruction for ∼ 1092–1057 kyr BP (Fig. 6) provides another example of a long interglacial interval (∼ 1084 to ∼ 1062 kyr BP; i.e., 22 kyr) dominated by the TAIG biome. The onset of interglacial conditions occurs after ∼ 1088 kyr BP, when STEP biome scores decrease abruptly to ones similar to Holocene levels. At this time, forest biome scores increase (Fig. 6a), although TUND still remains as a dominant vegetation type (Fig. 6b). Extremely low STEP scores characterize the interval between ∼ 1086 and ∼ 1068 kyr BP (Fig. 6a), while the maximum spread of boreal trees occurs from ∼ 1078 to ∼ 1066 kyr BP (Fig. 6c), or during the middle part of MIS 31 (Fig. 6d).

A turn to colder and drier environments is evident by the end of MIS 31. However, TUND replaces TAIG as the dominant vegetation type only at ~ 1062 kyr BP, marking the transition to MIS 30 (Fig. 6d).

A dominance of boreal tree and shrub taxa, including *Picea*, *Larix*, *Abies*, *Pinus* subg. *Haploxylon*, *Pinus* subg. *Diploxylon*, *Betula* and *Alnus*), characterizes the MIS 31 interglacial pollen record. Low percentages of the cool-temperate broadleaved deciduous tree/shrub taxa (e.g., *Corylus*, *Carpinus*, *Acer* and *Quercus*) also appear (Lozhkin and Anderson, 2013). The influence of these more temperate taxa on the biome reconstructions is reflected in the dominance of COCO scores during three periods at the beginning and at the end of the interglacial (Fig. 6b), an interval otherwise dominated by TAIG. According to the biome model and present-day bioclimatic limits for boreal and temperate taxa, COCO requires warmer summer and winter conditions than TAIG (Prentice et al., 1992; Kaplan, 2001). A discontinuous appearance of COCO during the initial and final stages of the interglacial likely indicates that long-distance transport of the temperate pollen taxa from warmer regions accelerated during the transitional intervals, along with a decreased pollen production of the local taxa. Lozhkin and Anderson (2013) also interpreted these warm taxa as being exotic contributors to the MIS 31 record. The latter study further suggested that forests which included temperate taxa possibly occurred in closer proximity to Lake El'gygytgyn as compared to today, implying much warmer and wetter than present conditions (Melles et al., 2012; Fig. 8c and d).

3.6 The late Pliocene and early Pleistocene interval (~ 3562–2200 kyr BP)

Results of the biome reconstructions (Fig. 7a) indicate that the late Pliocene–early Pleistocene can be characterized by six vegetation types. The four biomes representing forest are composed of either boreal (i.e., CLDE and TAIG) or a mixture of boreal and temperate tree taxa (i.e., COCO and COMX). The other two biomes (i.e., TUND and STEP) represent open vegetation dominated by boreal and/or arctic herb and shrub communities. The dominant biome (Fig. 7a) and landscape openness (Fig. 7b) reflect millennial-scale vegetation changes in the Lake El'gygytgyn region that correspond well with shifts in global climate represented by alternating cold and warm marine isotope stages (Fig. 7c).

Biome reconstructions demonstrate a trend in the regional vegetation history, which suggests a step-like transition from generally warmer/wetter environments of the mid to late Pliocene towards colder/drier environments of the early Pleistocene. The COMX and COCO biomes (Fig. 7a) consist of boreal and temperate conifers with a mix of temperate broadleaved trees and shrubs (Table 1). They are particularly noticeable in the lower part of the record prior to MIS G16 (i.e., older than 2937 kyr BP), whereas TUND predominance becomes a prominent feature beginning in MIS G6 (i.e., since 2730 kyr BP). The biome results indicate the study area supported a noticeable tree population during most of the interval prior to ~ 2730 kyr BP, while a generally open landscape became a common feature after that time (Fig. 7b). The biomization further suggests that the transition from mostly forested to mostly open landscape was not gradual and that the regional vegetation responded rapidly to the warmer and colder global climate oscillations seen in the marine isotopic records (Fig. 7c). Biomes characteristic of open landscapes do appear prior to ~ 2730 kyr BP. For example, TUND is noted as early as ~ 3379–3378 kyr BP within MIS MG4 (Fig. 7a). The cold- and drought-tolerant STEP biome is first evident in the reconstruction ~ 3298 kyr BP during the otherwise TUND dominated MIS M2 (~ 3312–3264 kyr BP). Thus, the generally warm Pliocene experienced several cool intervals prior to ~ 2800 kyr BP as shown by TUND dominance (Fig. 7a) and the great reduction of tree populations (Fig. 7b) in the regional vegetation.

Palynological analysis of the lower 216 m of lacustrine sediments (Andreev et al., 2013) provides the most complete terrestrial pollen record of the late Pliocene and early Pleistocene from the Siberian Arctic. Thus, the Lake El'gygytgyn record provides a strong basis for qualitative interpretations of the paleoenvironments (see Andreev et al., 2013) and for quantitative reconstructions of the past vegetation (Fig. 8a and b) and climate (Brigham-Grette et al., 2013; Fig. 8c and d).

Prior to ∼ 3350 kyr BP, the pollen assemblages indicate the presence of a forest dominated by spruce, larch, fir, and hemlock, with lesser amounts of other boreal and temperate taxa (Andreev et al., 2013). The biome-based interpretation suggests the presence of COCO and COMX forests. Deciduous *Quercus* is one of the indicator taxa in the El'gygytgyn pollen record that influenced the reconstruction of a cool mixed forest, which belongs to the temperate deciduous broadleaved tree/shrub plant functional type (Prentice et al., 1996). In the BIOME global vegetation model, the presence of temperate deciduous broadleaved arboreal taxa requires the minimum MTCM to be higher than −15 °C (Prentice et al., 1992). However, this model-based hypothesis contradicts the modern distribution pattern of temperate deciduous broadleaved woody taxa (e.g., *Quercus mongolica*), which grow today in southern areas of the Russian Far East (Mokhova et al., 2009), which experiences much colder winter temperatures (minimum MTCM values going down to −26 °C) than allowed by the model. Mokhova et al. (2009) suggested that sufficiently warm summer temperatures combined with high snow accumulation may outweigh the negative influence of low winter temperatures on the temperate broadleaved tree and shrub taxa.

Reviewing quantitative reconstructions based on terrestrial proxies from the Arctic, summer temperature (MTWM) remains the most confidently reconstructed climate variable (e.g., Andreev et al., 2004; Kienast et al., 2011; Brigham-Grette et al., 2013). Reconstructed values for mean temperature of the coldest month (MTCM) have larger statistical errors and broader uncertainty ranges (Melles et al., 2012) as compared to MTWM. However, the MTCM reconstruction suggests the predominance of warm winter temperatures (i.e., above −26 °C) prior to ∼ 3380 kyr BP (Brigham-Grette et al., 2013), in line with qualitative interpretations of the pollen record (Andreev et al., 2013; Brigham-Grette et al., 2013) and quantitative biome reconstruction results (Fig. 8a).

The pollen records and biome reconstructions suggest that vegetation changes occurred in several steps (Fig. 8a and b). For example, shifts in the composition of boreal forest happen first with the loss of temperate and then later boreal evergreen conifers, followed by transitions from forested habitats to treeless, shrubby and finally herbaceous environments. Estimates of the MTCM, based on changes in the pollen assemblages, suggest predominantly colder-than-present winters since ~ 2940 kyr BP, and especially since ~ 2730 kyr BP (Brigham-Grette et al., 2013). Such winter coolness has important implications for arctic vegetation–climate feedbacks (Levis et al., 1999), such as the expansion of tundra causing increased land surface albedo (thus lowering air temperatures), especially during snow-covered months.

Results of the palynological research and synthesis of the published proxy data from regions of northern Asia and northern North America for the late Pliocene/early Pleistocene presented in the current special issue (see Andreev et al., 2013, for details and references) offer an excellent opportunity for validating quantitative results of the pollen-based biome reconstruction presented here. For example, numerous coprophilous fungi spores revealed in the pollen samples within the Mammoth subchron (MIS M2) suggest open landscape and the presence of grazing animals around the lake, a conclusion that agrees with the pollen-based interpretations. Peaks in green algae (*Botryococcus*) colonies appear well within the intervals for which pollen-inferred reconstructions suggest relatively dry vegetation and climate.

3.7 Data–model comparison

Qualitative or quantitative interpretations of past environments can be challenging, especially during times when modern analogs are weak or nonexistent. However, the expansion of modern datasets and development of more sophisticated models and statistical treatment of the data over the past two decades facilitate the comparison of results from multiple approaches, particularly for reconstructing past climate and vegetation. In the case of Lake El’gygytgyn, there is an opportunity to compare results from the biome reconstructions obtained in the current study (Fig. 8a and b) to (1) the recently published reconstructions of temperature (Fig. 8c) and atmospheric precipitation (Fig. 8d) derived from the El’gygytgyn pollen records using the best modern analog (BMA) approach (Melles et al., 2012; Brigham-Grette et al., 2013); and (2) additional paleoenvironmental reconstructions from other long-term records (e.g., Lisiecki and Raymo, 2005, Fig. 8e). Approaches that have proved useful for interpreting the El'gygytgyn record involve the application of biome reconstruction and BMA. Both methods have their own set of assumptions and shortcomings. For example, the biomization method provides only semi-quantitative and indirect climate information. However, it is "closer" to the actual vegetation and does not suffer as much from the no-analog problem that faces more quantitative approaches (Prentice et al., 1996). Although the modern analog technique may be somewhat limited by analog-related issues, this technique has provided robust climate reconstructions when good analogs exist (e.g., Guiot, 1990; Jackson and Williams, 2004; Tarasov et al., 2007). One of the main advantages of the "biomization" approach, which allows paleovegetation to be reconstructed from either climate or pollen data (Prentice et al., 1992, 1996), is that in both cases the main vegetation types (biomes) are uniformly defined. This consistency is key because it allows the results of model simulations to be directly compared with the pollen-based biome reconstructions. Melles et al. (2012) reported on General Circulation Model (GCM) experiments that included an interactive vegetation component (using GENESIS 3.0 coupled to BIOME4). This paper examined the MIS 1, MIS 5.5, MIS 11.3 and MIS 31 interglacial intervals with a geographic focus on the Arctic. The results of the climate model simulations when converted to vegetation maps show a striking similarity to the pollen-based vegetation reconstructions presented here. Thus, shrub tundra appears around Lake El'gygytgyn in the modern (preindustrial control) and 9 kyr BP runs, whereas deciduous taiga (i.e., CLDE) is simulated in the lake vicinity during the early Holocene thermal optimum. CLDE is also simulated near Lake El'gygytgyn during the warmest phase of the MIS 5.5 interglacial. Evergreen taiga (i.e., TAIG) predominates during MIS 11.3 (ca. 410 kyr BP), and a mixture of TAIG and CLDE vegetation is simulated for the MIS 31 interglacial (~ 1072 kyr BP), corresponding to the timing of peak summer warmth (Melles et al., 2012). Both model simulations and proxy-based reconstructions suggest that MIS 11.3 was the warmest and longest interglacial of the past million years (Melles et al., 2012).

More recently Kleinen et al. (2013) examined climate and vegetation dynamics during the MIS 11.3 using a model of intermediate complexity (CLIMBER2-LPJ; see Kleinen et al., 2010, 2011, for model details and references) and a second comprehensive general circulation model (CCSM3; see Yeager et al., 2006, for a detailed description of the model). Results of the climate modeling were then converted into maps of potential natural vegetation using BIOME4 (a coupled carbon and water flux model that predicts the steady-state vegetation distribution, structure, and biogeochemistry, taking into account interactions between these effects; Kaplan, 2001; Kaplan et al., 2003) for the four selected time slices within MIS 11.3. For comparison, the modern (preindustrial) biome distribution was also simulated using an early twentieth-century climatology. In agreement with the pollen data and pollen-based biome reconstruction, enhanced tree cover occurred for 416 and 410 kyr BP, although the tree cover was more pronounced in CCSM3 as compared to LPJ. Modeling shows (dwarf) shrub tundra as the preindustrial biome, which turns into high shrub tundra and even taiga forest in some locations at 416 and 410 kyr BP. The modeling results indicate a dwarf shrub tundra biome and a reduction in vegetation cover for 400 and 394 kyr BP. These results indicate that there is general agreement about the timing of the interglacial–glacial transition in both models (Kleinen et al., 2013).

Climate and biome models also have been used in a set of sensitivity experiments that focus on the earlier part of the Lake El’gygytgyn record to test the response of temperature and precipitation to the build up of Northern Hemisphere ice sheets (Brigham-Grette et al., 2013). Although results are preliminary, the simulations indicate a drying caused by the presence of large northern hemispheric ice sheets. This simulated PANN decrease and the simulated magnitude in MTCM are similar to ones determined in the proxy-based biome and climate reconstructions after ~ 2900 kyr BP (Fig. 8). These results, while not definitive, suggest that the time-averaged presence of large Northern Hemisphere ice sheets contributed to the marked drying in the Lake El’gygytgyn record after ~ 2730 kyr BP (Brigham-Grette et al., 2013).

Parallels in the reconstructed MTWM values (Fig. 8c) and trends in the benthic marine isotope stack record (Fig. 8e), first noted by Brigham-Grette et al. (2013), are also evident in reconstructed landscape openness (Fig. 8b). The similarities in trends further underscore the importance of the global systematic controls that link colder summer temperatures at Lake El'gygytgyn with oceanic proxies of temperature, global ice volume, and sea level (Brigham-Grette et al., 2013).

4 Conclusions

The terrestrial pollen record from Lake El'gygytgyn, northeastern Asia, represents a unique environmental archive which not only provides a means for deciphering changes in the regional vegetation and climate histories over the last 3.58 Myr at fairly high resolution, but also allows a variety of pollen-based reconstruction approaches to be tested across a wide range of paleoenvironmental conditions. As work progresses with the El'gygytgyn sediments, the temporal resolution of the record will be substantially improved as future studies focus on specific intervals or questions of interest determined by the coarse-resolution analyses, thereby providing additional details on the observed shifts in climate and vegetation and opportunities for further applications of modeling and biome/analog techniques.

Quantitative reconstruction of changes in vegetation cover near Lake El'gygytgyn presented in this paper were obtained using the biome reconstruction method. This approach provides an objectively generated record of vegetation change against which qualitative and quantitative reconstructions generated with other approaches/proxies either from this Arctic site or from other globally distributed sites can be compared.

The objectively generated biome reconstructions are useful for a wide range of paleoenvironmental applications (e.g., data–model comparisons), and they overcome some interpretive difficulties associated with more qualitative approaches. Conventional pollen diagrams contain a great amount of site-specific paleoecological information, and their interpretation requires extensive knowledge of the regional plant ecology and taxonomy. This information often is known primarily by paleobotanical specialists, making pollen diagrams a difficult interpretive tool for other earth scientists. Furthermore, pollen percentages illustrated in diagrams are not directly comparable to climate/vegetation model output, output which is valuable in understanding a variety of earth systems, including atmosphere–biosphere feedbacks. Moreover, comparing spatial and temporal changes in the pollen assemblages among numerous sites and across broad regions is a challenge unless the pollen data are integrated in a systematic manner. The biome reconstruction approach allows diverse pollen data to be compiled more easily within a well-organized analytical framework. In contrast to pollen diagrams, the presentation of results as biomes yields a more understandable format for a majority of geoscientists. The biome approach, although also dependent on understanding ecological relationships, provides a more objectively defined set of natural vegetation types in contrast to the traditional qualitative interpretations. The use of a common set of climatically defined vegetation types in the pollen-based reconstruction and in the model simulations facilitates data–model comparisons. Such comparisons are beneficial for both the data and the modeling communities, as they (1) allow more accurate evaluation of the climate models and of model output; (2) justify the selection of models with a better predictive potential; and (3) help improve knowledge of past developments of the earth system at the global and regional scale.

The current study provides time series of the dominant vegetation types (biomes) and quantitative evaluations of landscape openness between ~ 3.58 and ~ 2.2 Ma and through four shorter glacial–interglacial intervals within the last ~ 1.09 Myr. These results illustrate the timing and nature of the changes that transformed a predominantly forested Pliocene Siberian Arctic ecosystem into a largely forest-free environment, as seen during the early and late Pleistocene. The results also confirm the earlier reported stepwise temperature decline leading to the onset of Northern Hemisphere glacial cycles. Not only does the El'gygytgyn pollen record improve understanding of the Pliocene–Pleistocene transition, it also illustrates the variability within Pleistocene warm intervals. The middle Pleistocene, in particular, provides examples of long interglacial intervals (i.e., 22 and 25 kyr) dominated by taiga, and indicates the extraordinary character of the MIS 31 and MIS 11.3 interglacials.

Biome reconstructions do not rely on modern reference datasets. Thus, this approach provides an independent confirmation of the published quantitative climate reconstructions obtained using the best modern analog method. The results also help to verify the ability of modern coupled climate–vegetation models to simulate past climate and vegetation dynamics in the region. Detailed modeling and analysis of the effect of northern hemispheric ice sheets, vegetation, and sea ice feedbacks on the regional environments around Lake El'gygytgyn, particularly during the "early" intervals of extreme cold (i.e., during MIS M2, G16, G6) and during the "late" intervals of extreme warmth (i.e., during MIS 31 and 11.3), remain the subjects of future work.

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Table 1. Biome–taxon matrix used in the biome reconstruction. All terrestrial pollen taxa identified in the fossil pollen spectra in the Lake El'gygytgyn record are attributed to one or several biomes.

Biome name/ abbreviation	Biome order	Attributed pollen taxa
Tundra/TUND	1	*Alnus fruticosa*-type (shrub), *Betula* sect. *Albae*-type (tree), *B.* sect. *Nanae*-type (shrub), *B.* undif., Cyperaceae, Ericales, Poaceae, Polemoniaceae, *Polygonum bistorta*-type, *Rubus chamaemorus, Rumex, Salix*, Saxifragaceae, Valerianaceae
Cold deciduous forest/CLDE	2	*Alnus fruticosa*-type (shrub), *A.* sp. (tree), *Betula* sect. *Albae*-type (tree), *B.* sect. *Nanae*-type (shrub), *B.* undif., Cupressaceae/Taxodiaceae, Ericales, *Larix/Pseudotsuga, Pinus* subg. *Diploxylon, P.* subg. *Haploxylon*, Pinaceae undif., *Populus, Rubus hamaemorus, Salix*
Taiga/TAIG	3	*Abies, Alnus* sp. (tree), *Betula* sect. *Albae*-type (tree), *B.* sect. *Nanae*-type (shrub), *B.* undif., Cupressaceae/Taxodiaceae, Ericales, *Larix/Pseudotsuga*, *Lonicera, Picea, Pinus* subg. *Diploxylon, P.* subg. *Haploxylon*, Pinaceae undif., *Populus, Rubus hamaemorus, Salix*
Cool conifer forest/COCO	4	*Abies, Alnus* sp. (tree), *Betula* sect. *Albae*-type (tree), *B.* sect. *Nanae*-type (shrub), *B.* undif., *Carpinus*-type, *Corylus*, Cupressaceae/Taxodiaceae, Ericales, *Larix/Pseudotsuga, Lonicera, Picea, Pinus* subg. *Diploxylon*, *P.* subg. *Haploxylon, Pinaceae* undif., *Populus, Salix, Tilia, Tsuga*, *Ulmus*
Temperate deciduous forest/TEDE	5	*Abies, Alnus* sp. (tree), *Betula* sect. *Albae*-type (tree), *B.* sect. *Nanae*-type (shrub), *Betula* undif., *Carpinus*-type, *Carya, Corylus*, Cupressaceae/Taxodiaceae, Ericales, *Juglans, Larix/Pseudotsuga, Lonicera*-type, *Pinus* subg. *Diploxylon*, Pinaceae undif., *Populus, Pterocarya*, *Quercus deciduous, Salix, Tilia, Ulmus*
Cool mixed forest/COMX	6	*Abies, Alnus* sp. (tree), *Betula* sect. *Albae*-type (tree), *B.* sect. *Nanae*-type (shrub), *B.* undif., *Carpinus*-type, *Corylus*, Cupressaceae/Taxodiaceae, Ericales, *Larix/Pseudotsuga, Lonicera*-type, *Picea, Pinus* subg. *Diploxylon*, *P.* subg. *Haploxylon*, Pinaceae undif., *Populus, Tsuga*, *Quercus deciduous, Salix, Tilia, Ulmus*
Warm mixed forest/WAMX	7	*Alnus* sp. (tree), *Carpinus*-type, *Carya, Corylus*, Cupressaceae/Taxodiaceae, Ericales, *Juglans, Lonicera, Pinus* subg. *Diploxylon*, Pinaceae undif., *Populus, Pterocarya, Quercus deciduous, Salix, Tilia, Ulmus*
Cold steppe/STEP	8	*Apiaceae, Artemisia*, Asteraceae Asteroideae, Asteraceae Cichorioideae, Brassicaceae, *Cannabis*-type, Caryophyllaceae, Chenopodiaceae, Fabaceae, Lamiaceae, *Linum*, Onagraceae, Papaveraceae, Plantaginaceae, Poaceae, *Polygonum bistorta*-type, *Ranunculaceae, Rosaceae, Rumex, Sanguisorba*, *Thalictrum*, Urticaceae, Valerianaceae

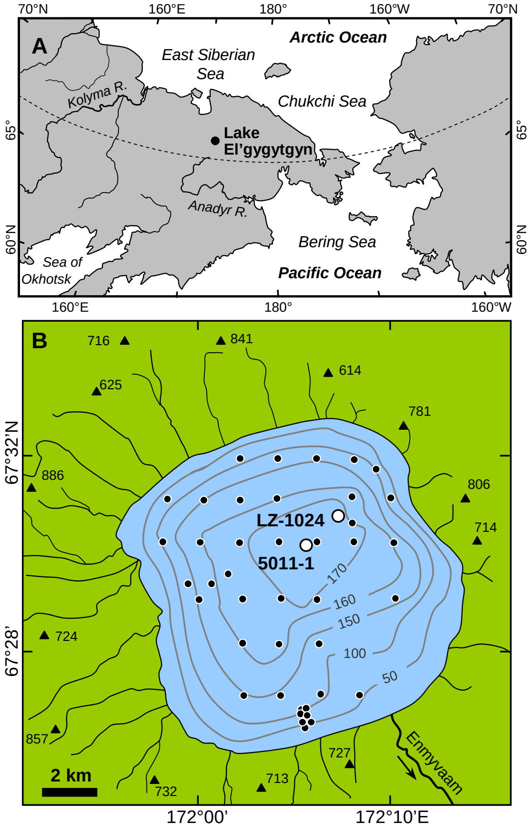

Fig. 1. Maps showing **(A)** geographical location of Lake El'gygytgyn (black dot; 67°30′ N, 172°05′ E, 492 m a.s.l.) in northeastern Siberia, and **(B)** the catchment area of Lake El'gygytgyn with associated hydrological network. The lower map **(B)** also shows the locations of the modern pollen surface samples (closed circles) and fossil pollen records (open circles), bathymetric lines indicating lake water depth (m below modern lake level), and the highest nearby mountain peaks (triangles accompanied with altitude values in m a.s.l.).

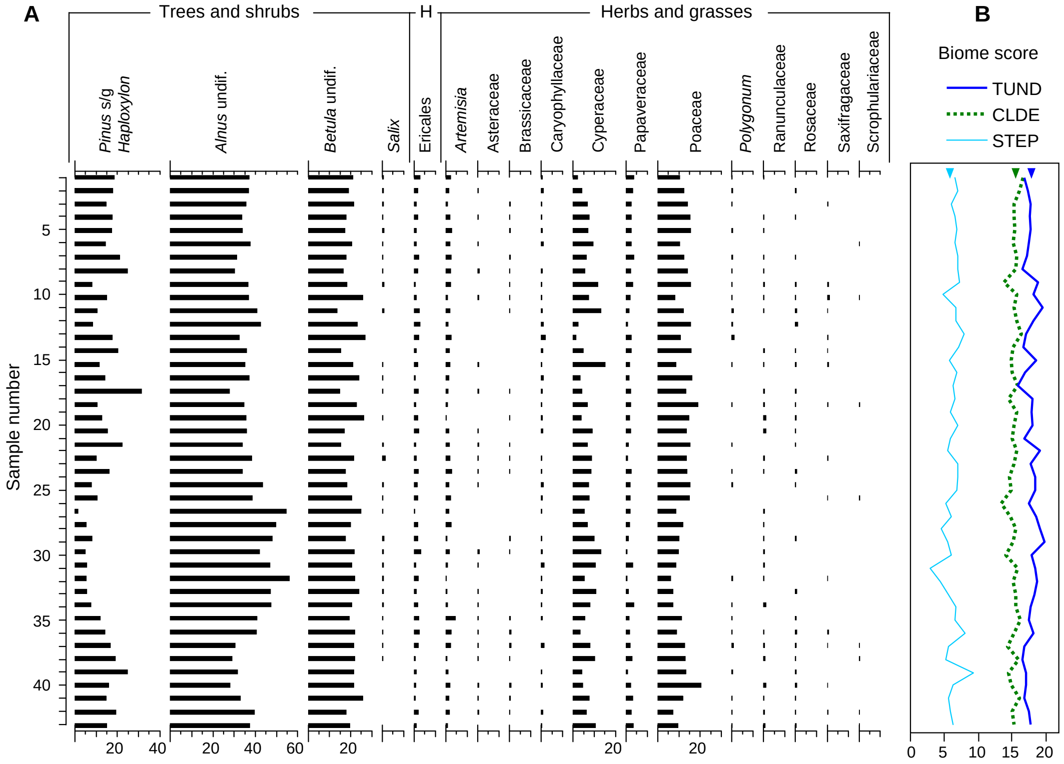

Fig. 2. Diagram of modern data from Lake El'gygytgyn: **(A)** summary pollen percentage diagram of the 43 modern surface pollen spectra (pollen analyst T. Matrosova), and **(B)** calculated affinity scores of individual biomes which dominated in the study area during the late Quaternary. The diagram was constructed using Tilia/Tilia-Graph/TGView software (Grimm, 1993, 2004). Percentages for individual terrestrial pollen taxa at each level were calculated from the sum of arboreal and non-arboreal pollen. Only taxa which exceed the 0.5 % threshold are shown. H indicates heath.

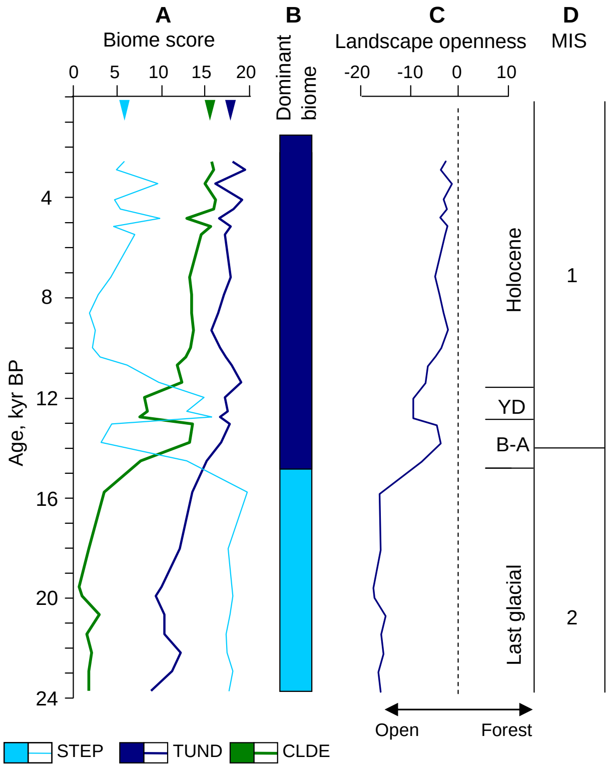

Fig. 3. Summary diagram for the last ~ 24 kyr BP showing the **(A)** time series of individual vegetation types (biomes; triangles indicate the modern average score of each respective biome), **(B)** dominant biomes, **(C)** semi-quantitative characteristic of landscape openness calculated as the difference between the maximum score of forest biomes (MSFB) and the maximum score of open biomes (MSOB) at each level, and **(D)** marine isotope stage (MIS) boundaries (after Lisiecki and Raymo, 2005). The Younger Dryas is indicated by YD and the Bølling–Allerød is indicated by B–A.

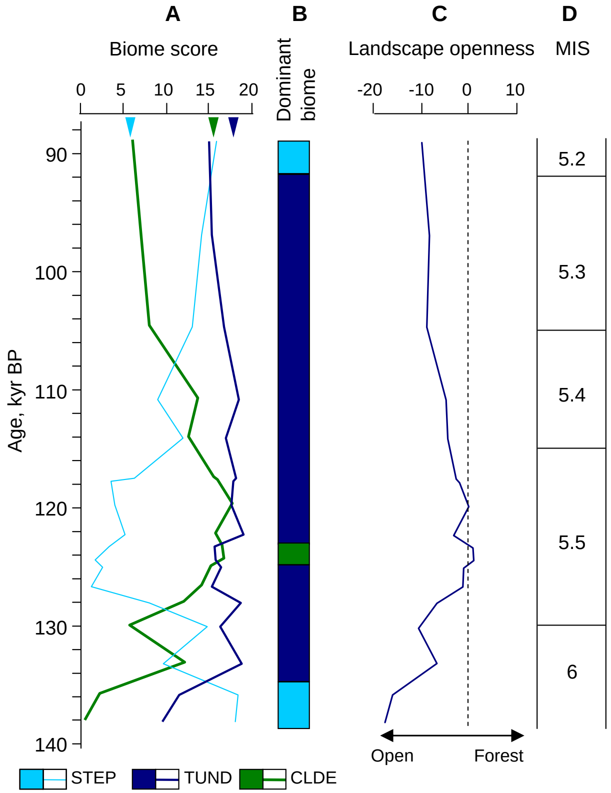

Fig. 4. Summary diagram for ∼ 138 to ∼ 89 kyr BP showing the **(A)** time series of individual vegetation types (biomes; triangles indicate modern average score of each respective biome), **(B)** dominant biomes, **(C)** semi-quantitative characteristic of landscape openness calculated as the difference between the maximum score of forest biomes (MSFB) and the maximum score of open biomes (MSOB) at each level, and **(D)** marine isotope stage (MIS) boundaries (after Lisiecki and Raymo, 2005).

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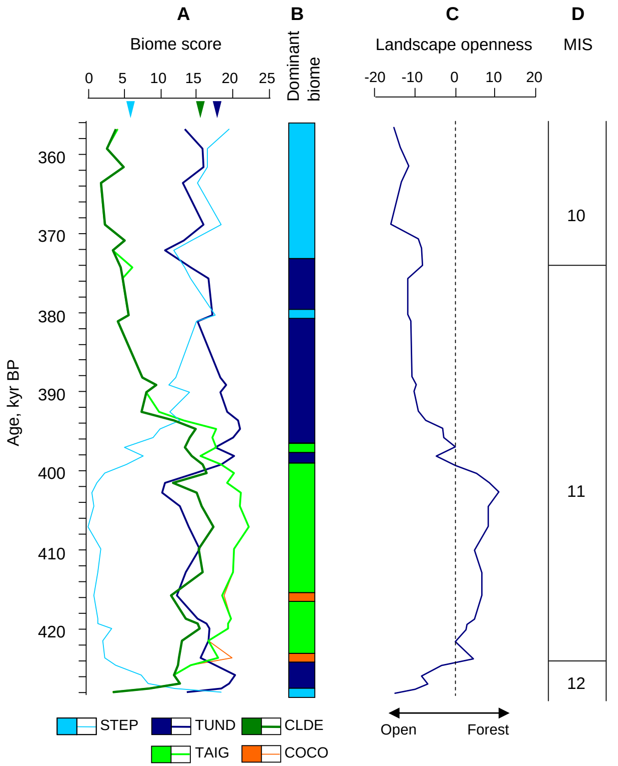

Fig. 5. Summary of paleoenvironmental trends between ∼428 and ∼356 kyr BP showing the **(A)** time series of individual vegetation types (biomes; triangles indicate modern average score of a respective biome), **(B)** dominant biomes, **(C)** semi-quantitative characteristic of landscape openness calculated as the difference between the maximum score of forest biomes (MSFB) and the maximum score of open biomes (MSOB) at each level, and **(D)** marine isotope stage (MIS) boundaries (after Lisiecki and Raymo, 2005). Note that TAIG and COCO biomes are not present in the modern regional vegetation and therefore their score is identical to CLDE in the modern spectra (see Prentice et al., 1996, and Sect. 2.3 for explanations).

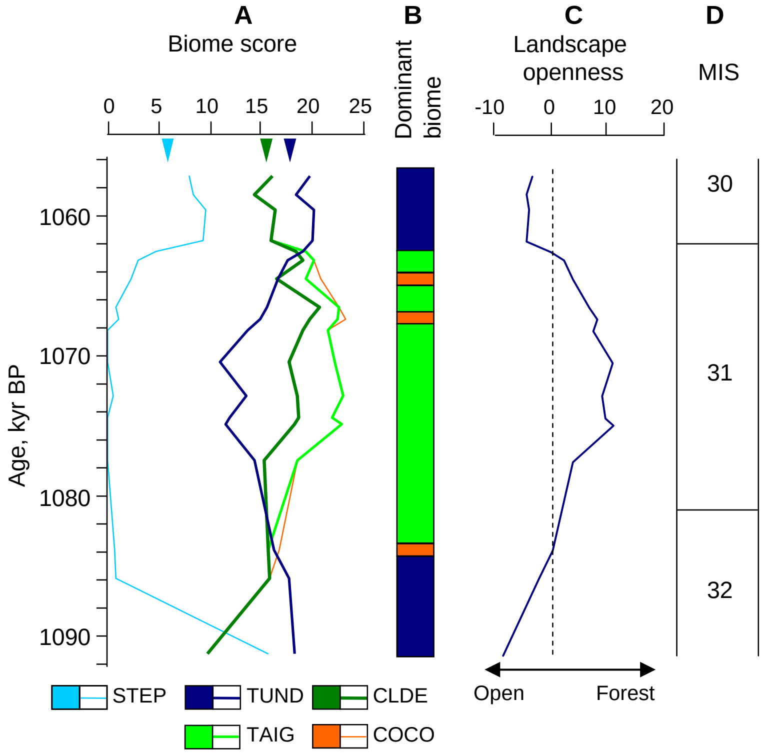

Fig. 6. Summary of paleoenvironmental trends between ∼ 1092 and ∼ 1057 kyr BP showing the **(A)** time series of individual vegetation types (biomes; triangles indicate modern average score of a respective biome), **(B)** dominant biomes, **(C)** semi-quantitative characteristic of landscape openness calculated as the difference between the maximum score of forest biomes (MSFB) and the maximum score of open biomes (MSOB) at each level, and **(D)** marine isotope stage (MIS) boundaries (after Lisiecki and Raymo, 2005). Note that TAIG and COCO biomes are not present in the modern regional vegetation, and therefore their scores are identical to CLDE in the modern spectra (see Prentice et al., 1996, and Sect. 2.3 for explanations).

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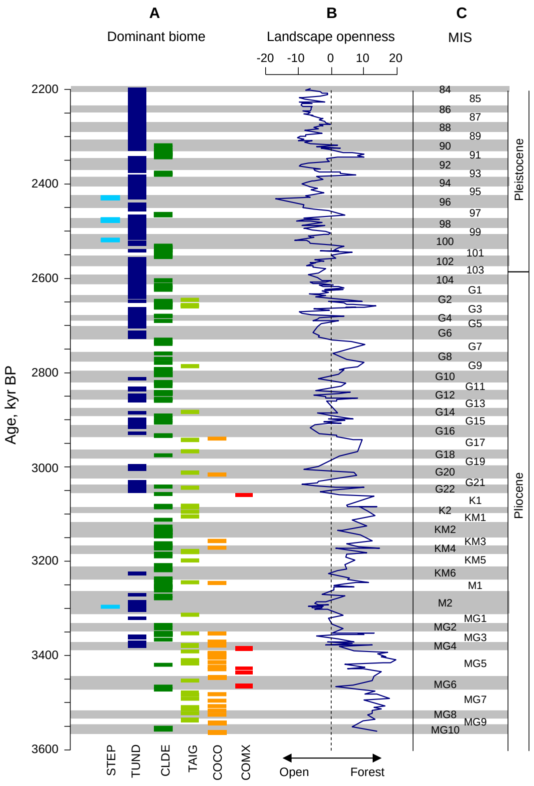

Fig. 7. Summary of paleoenvironmental trends between ~ 3580 and ~ 2200 kyr BP showing the **(A)** time series of the dominant vegetation types (biomes), **(B)** semi-quantitative characteristic of landscape openness calculated as the difference between the maximum score of the forest biomes (MSFB) and the maximum score of the open biomes (MSOB) at each level, and **(C)** marine isotope stage (MIS) boundaries (after Lisiecki and Raymo, 2005). Gray and white bands indicate cold and warm marine isotope stages, respectively.

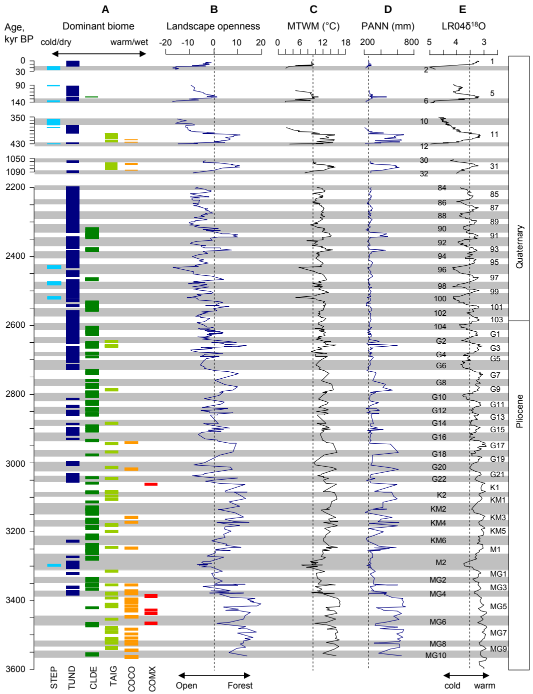

Fig. 8. Summary of paleoenvironmental trends between ~3580 and ~2200 kyr BP showing the **(A)** time series of the dominant vegetation types (biomes), (**B**) semi-quantitative characteristic of landscape openness calculated as the difference between the the maximum score of the forest biomes (MSFB) and the maximum score of the open biomes (MSOB) at each level, **(C)** pollen-based reconstructions of the mean temperature of the warmest month, **(D)** pollen-based reconstructions of mean annual precipitation (after Melles et al., 2012; Brigham-Grette et al., 2013), and **(E)** Pliocene–Pleistocene stack of 57 globally distributed benthic δ^{18}O records with marine isotope stage (MIS) numbers (after Lisiecki and Raymo, 2005). Gray and white bands indicate cold and warm marine isotope stages, respectively.