Quaternary Science Reviews 196 (2018) 38–61

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

# Woodlands and steppes: Pleistocene vegetation in Yakutia's most continental part recorded in the Batagay permafrost sequence

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## ARTICLE INFO

*Article history:*
Received 26 January 2018
Received in revised form
20 July 2018
Accepted 20 July 2018

*Keywords:*
Palaeo-vegetation
Plant macrofossils
Invertebrates
Modern analogues
Pollen
Ground squirrel nest
Last cold stage
Eemian
Beringia

## ABSTRACT

Based on fossil organism remains including plant macrofossils, charcoal, pollen, and invertebrates preserved in syngenetic deposits of the Batagay permafrost sequence in the Siberian Yana Highlands, we reconstructed the environmental history during marine isotope stages (MIS) 6 to 2. Two fossil assemblages, exceptionally rich in plant remains, allowed for a detailed description of the palaeo-vegetation during two climate extremes of the Late Pleistocene, the onset of the last glacial maximum (LGM) and the last interglacial. In addition, altogether 41 assemblages were used to outline the vegetation history since the penultimate cold stage of MIS 6. Accordingly, meadow steppes analogue to modern communities of the phytosociological order *Festucetalia lenensis* formed the primary vegetation during the Saalian and Weichselian cold stages. Cold-resistant tundra-steppe communities (*Carici rupestris-Kobresietea bellardii)* as they occur above the treeline today were, in contrast to more northern locations, mostly lacking. During the last interglacial, open coniferous woodland similar to modern larch taiga was the primary vegetation at the site. Abundant charcoal indicates wildfire events during the last interglacial. Zoogenic disturbances of the local vegetation were indicated by the presence of ruderal plants, especially by abundant *Urtica dioica,* suggesting that the area was an interglacial refugium for large herbivores. Meadow steppes, which formed the primary vegetation during cold stages and provided potentially suitable pastures for herbivores, were a significant constituent of the plant cover in the Yana Highlands also under the full warm stage conditions of the last interglacial. Consequently, meadow steppes occurred in the Yana Highlands during the entire investigated timespan from MIS 6 to MIS 2 documenting a remarkable environmental stability. Thus, the proportion of meadow steppe vegetation merely shifted in response to the respectively prevailing climatic conditions. Their persistence indicates low precipitation and a relatively warm growing season throughout and beyond the late Pleistocene. The

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https://doi.org/10.1016/j.quascirev.2018.07.032

studied fossil record also proves that modern steppe occurrences in the Yana Highlands did not establish as late as in the Holocene but instead are relicts of a formerly continuous steppe belt extending from Central Siberia to Northeast Yakutia during the Pleistocene. The persistence of plants and invertebrates characteristic of meadow steppe vegetation in interior Yakutia throughout the late Quaternary indicates climatic continuity and documents the suitability of this region as a refugium also for other organisms of the Pleistocene mammoth steppe including the iconic large herbivores.



## 1. Introduction

Climatic and associated vegetation changes are considered possible drivers for the extinction of Pleistocene mammoth fauna (Campos et al., 2010; MacDonald et al., 2012; Prescott et al., 2012). In high latitudes, rising temperature and increased humidity triggered, according to this interpretation, the transformation of the Pleistocene nutritious grassland vegetation into birch shrubland, coniferous forest tundra and finally into low-diverse taiga and tundra wetlands (Binney et al., 2009; Edwards et al., 2005; Kienast, 2013). Correspondingly, the demise of mainland mammoth populations coincided with the expansion of coniferous forests and the formation of extensive northern peatlands (MacDonald et al., 2012). The question remains, however, as to why the Pleistocene mammoth fauna survived several warm pulses during the Pleistocene, including full interglacials, but became extinct in particular in the course of the Holocene. Also, it is not fully clear whether the restructuring of late Quaternary vegetation was the cause or, due to herbivore - vegetation interactions, the consequence of the demise of megafauna.

A key region for understanding the mechanisms underlying the late Quaternary biotic impoverishment in northern latitudes is Beringia (Hulten, 1937; Tugarinov, 1929). The sector between the mouths of the Siberian Khatanga River and the Canadian Mackenzie River including entire Yakutia remained free of continental ice caps during the late Quaternary (Barr and Clark, 2012; Svendsen et al., 2004). Beringia, and NE-Siberia in particular, is regarded the last refuge of mammoth fauna (Boeskorov, 2006). Consistently, the latest mainland populations of extinct megaherbivores existed here as indicated by radiocarbon dates of bones from mammoth ($9670 \pm 60$ on the mainland and 3730 uncal. years BP on Wrangel Island; Stuart et al., 2002), woolly rhino (13,978 cal years BP; Stuart and Lister, 2012), steppe bison ($8215 + 45/-40$ uncal. years BP; Murton et al., 2017), and wild horse ($2150 \pm 200$ uncal. years BP; Boeskorov, 2006). The dominance of grazers among Beringian megaherbivores has been taken as evidence for productive, cold-adapted grassland, the tundra-steppe or mammoth steppe being the key vegetation type in the Pleistocene Arctic (Guthrie, 1990). Based on vegetation studies at currently isolated relict steppe stands in Northeast Siberia and Chukotka, Yurtsev (2001) suggested that the Pleistocene palaeo-landscapes were analogously characterized by a codominance of steppe and arcto-alpine plant species. He also showed that modern relict steppe vegetation forms patchy mosaics in response to local environmental conditions such as topography, exposition, disturbances and soil. The existence of modern analogues of Pleistocene vegetation was previously questioned based on non-analogue assemblages of pollen (Cwynar and Ritchie, 1980; Williams et al., 1998), which, due to their constraints in high latitudes, are however of limited use for vegetation reconstruction (Birks and Birks, 2000). In the present paper, the term mammoth steppe is accepted as an ecosystem (or palaeo-biome) supposedly dominating during Pleistocene cold stages as suggested by Guthrie (1990). Tundra-steppe, in contrast, is henceforth regarded here as a certain plant community occurring at dry exposed places in the alpine belt of mountains and subsumed in the plant-sociological class *Carici rupestris-Kobresietea bellardii* (Kucherov and Daniels, 2005). Tundra steppe vegetation is thus regarded as a modern analogue and part of the Pleistocene mammoth steppe and no longer as a synonym. It corresponds to plant communities formerly designated *Kobresia*-meadows (Kienast et al., 2005; Wetterich et al., 2008) or dry arctic upland vegetation (Kienast et al., 2008). We implement this sharp distinction to make palaeo-vegetation reconstructed on the base of diagnostic species comparable with modern vegetation that is analogously classified using diagnostic species.

Palaeontological records from permafrost sections in Northeast Siberia revealed the mosaic-like character of Pleistocene vegetation with a coexistence of steppe, meadow and tundra steppe (Kienast et al., 2005, 2008), which is in line with the descriptions of modern analogues of steppe and tundra-steppe relict vegetation in Yakutia (Yurtsev, 1982, 2001; Reinecke et al., 2017).

Most of the known fossil vegetation records are situated in the coastal lowlands of Yakutia. Due to Quaternary sea level fluctuations, Yakutia's northern lowlands and the adjacent shelves were intermittently hit by tremendous coast line shifts (Bauch et al., 2001; Romanovskii et al., 2004) and correspondingly fluctuating maritime influence on climate. However, inland sections unaffected by maritime climate but with constantly continental climate throughout the Quaternary, were scarcely available so far. A newly formed permafrost exposure near Batagay, Verkhoyansky district in the Yana Highlands, Yakutia is one of the few active permafrost outcrops currently accessible in interior Yakutia (Fig. 1; Ashastina et al., 2017; Murton et al., 2017). The pole of cold - Verkhoyansk, the place with the lowest measured winter temperature in the northern hemisphereis also situated in the Yana Highlands, which thus represent the region with the greatest seasonal temperature gradient, e.g. the most severe climatic continentality in the Northern Hemisphere (USSR Climate Digest, 1989). The region can therefore be considered as a benchmark for northern inland climate. Previous studies on the Batagay permafrost exposure dealt with structure, composition, cryostratigraphical and sedimentological characteristics of the permafrost sequence (Kunitsky et al., 2013; Ashastina et al., 2017; Murton et al., 2017) and expansion rates of the outcrop (Günther et al., 2015) or described megafauna findings, including frozen carcasses of horses (*Equus* sp.) and bison (*Bison priscus*), as well as bone remains of cave lions (*Panthera leo spelaea*), woolly rhinoceroses (*Coelodonta antiquitatis*), mammoths (*Mammuthus primigenius*), and other extinct Pleistocene animals (Novgorodov et al., 2013).

In this paper, we present first results of the analyses of plant macro-fossils, charcoal, pollen and invertebrates obtained from the Batagay permafrost sequence. We provide a reconstruction of palaeo-vegetation from MIS 6 to 2 with a focus on the last interglacial (MIS 5e) and the onset of the last global glacial maximum (LGM), and compare the results with modern vegetation in the area as well as with palaeo-records available from sites in today's coastal zone. Environmental conditions associated with the reconstructed palaeo-vegetation are inferred from the respective macro- and