

# ECOGRAPHY

## Research

### Habitats of Pleistocene megaherbivores reconstructed from the frozen fauna remains

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#### Ecography

43: 703–713, 2020

doi: 10.1111/ecog.04940

Subject Editor: Eric Post

Editor-in-Chief:

Jens-Christian Svenning

Accepted 4 December 2019



The Late Pleistocene landscape in northern Eurasia and North America was inhabited by a specific megafaunal complex, which largely disappeared during the Pleistocene/Holocene transition. Vegetation changes are considered as one of the factors responsible for these extinctions, but the structure and composition of the Pleistocene vegetation are still poorly known. Here we complement previous studies by comparing the taxonomic composition of the plant remains found in the gastrointestinal tracts of the frozen carcasses of Pleistocene megaherbivores with the species composition of the current Siberian vegetation. We compiled a dataset of palaeobotanical records from frozen individuals of Pleistocene megaherbivores found in northern Siberia and Beringia and dated to the period from more than 50 kyr BP to 9 kyr BP. We also compiled a dataset of vegetation plots from several regions in Siberia. We analysed the similarity in taxonomic composition of plants between these two datasets using a novel method that accounts for variable taxonomic resolution in palaeobotanical data. For most megaherbivore individuals, plant remains in their gastrointestinal tracts corresponded to tundra, forest and mire vegetation, while they showed low similarity to steppe. This pattern was relatively constant over time, showing no remarkable differences between the Last Glacial Maximum and the periods before and afterwards. This suggests that during the Upper Pleistocene, a mosaic of mesic and wet vegetation types such as tundra with patches of forests and mires was common in northern Siberia and Beringia. In contrast, the steppe was rare to absent in the landscape or underused by the megaherbivores as a pasture since they found enough food in the widespread mesic and wet habitats with more productive vegetation.

Keywords: mammoth steppe, megafauna habitats, northern Siberia and Beringia, palaeobotany, Pleistocene vegetation, vegetation reconstructions



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## Introduction

The Late Pleistocene landscapes in Eurasia and North America were inhabited by a specific mammalian complex represented most notably by woolly mammoths and other species of megafauna (Vereshchagin and Baryshnikov 1991, Markova et al. 1995, Kahlke 2014). At the end of the Pleistocene (around 10–15 kyr BP), most of the megafauna species went extinct (Stuart 2015). The reasons for such extinctions are complex, including a considerable climate and vegetation change coupled with an increasing human impact (Nogués-Bravo et al. 2008, Allen et al. 2010, Stuart 2015, Pavelková Řičánková et al. 2018), but specific processes and regional differences still remain unclear.

To get a better understanding of these extinction events, palaeoecologists are striving to reconstruct the habitat and vegetation types in which the Pleistocene megaherbivores were living using climate-based modelling (Allen et al. 2010, Janská et al. 2017), pollen (Tarasov et al. 2000), macrofossils (Sher et al. 2005) and recently also DNA analyses of plant remains (Willerslev et al. 2014) or stable isotopes (Rivals et al. 2010, Schwartz-Narbonne et al. 2019). However, each method of palaeovegetation reconstructions suffers from various constraints that can distort interpretations of the past landscape changes. Since the early 20th century, several well-preserved frozen carcasses, some of them being even around 50 000 years old (Willerslev et al. 2014, Kirillova et al. 2016a, b, 2017), have been found scattered across northern Siberia and North America. This gives us a unique opportunity to examine the plant remains found in the gastrointestinal tract of Pleistocene megaherbivores, and to use these data as a proxy in the reconstructions of the Pleistocene vegetation and landscape (Ukrainitseva 2013, Boeskorov et al. 2014, Willerslev et al. 2014).

We compiled two databases to obtain new insights into the Pleistocene vegetation of northern Siberia and Beringia. The first database contains information on plant remains identified in frozen megafauna individuals analysed to date, converted into standardized taxonomy and nomenclature, considering different taxonomic levels to which these plant remains could be identified. The second database contains modern records of plant species composition and cover-abundances in vegetation plots sampled across a broad range of the natural and semi-natural vegetation types in various regions in Siberia. When combined, these two databases make it possible to compare the Late Pleistocene megafaunal diet with current vegetation types of Siberia and to link each animal individual with a set of vegetation types in which it most probably lived shortly before its death. To do so, we developed a new analytical approach enabling a similarity analysis of datasets with different levels of taxonomical identification.

Our aim is to compare the composition of palaeobotanical remains identified in the frozen Pleistocene megaherbivores with modern vegetation types from Siberia and to use this information for reconstructing habitats of these animals and for improving the general reconstruction of the Pleistocene palaeovegetation of northern Siberia and Beringia.

## Material and methods

### Palaeobotanical records from the frozen fauna

We compiled plant records reported from the Pleistocene and early Holocene frozen megaherbivores found in northern Siberia, Alaska and the Yukon Territory (see Fig. 1, Supplementary material Appendix 2 Table A1 for site details). Frozen animals found in the interior parts of North America south of Alaska and the Yukon Territory were not considered in this study due to considerable differences in plant and animal species composition of that region. The palaeobotanical data included pollen + spores, macrofossils and DNA analyses reported from gastrointestinal tracts of frozen fauna or coprolites (for an overview see Supplementary material Appendix 2 Table A2).

The final selection included 27 individuals of Pleistocene megaherbivores including woolly mammoths (*Mammuthus primigenius*: 14 samples), woolly rhinoceroses (*Coelodonta antiquitatis*: 4; and *Stephanorhinus kirchbergensis*: 1), steppe bisons (*Bison priscus*: 4), horses (*Equus lenensis*: 1; and *E. lambei*: 1) and reindeer (*Rangifer tarandus*: 1).

Identification of the plant remains found in the frozen carcasses suffers from several constraints, and it is not always possible to identify plants at the species level (for methodological details see the original publications cited in Supplementary material Appendix 2 Table A2; for an overview of the most frequent plant taxa see Supplementary material Appendix 2 Table A3, A4). To make data on different taxonomical levels (species, genus and family) comparable, we included all these levels to the analyses simultaneously. For example, the species *Abies sibirica* was also included as the genus *Abies* and as the family Pinaceae. Only presence/absence data were used since relative abundances based on palaeobotanical remains suffer from various biases and in several cases, such data were not available at all. We unified plant taxonomy and nomenclature used in the original studies to follow Cherepanov (1995) for vascular plants and Ignatov and Afonina (1992) for bryophytes.

We analysed only plant records directly found within the frozen animal carcass or coprolite, but we did not consider plant remains sampled in the adjacent sediment. We decided so because 1) the data from the sediment were available only for a limited number of megafauna individuals, and 2) plant records from the sediment can be from a different time than the carcass and potentially affected by layer transpositions.

For all but one carcass, radiocarbon dating was available in the original publications (Table 1), which enabled us to sort them by age. In the case of several published age measurements, we used the mean value per animal. All values were then calibrated to the calendar age relative to 1950 using OxCal (Ramsey 2009; ver. 4.3), with calibration curve IntCal13 (Reimer et al. 2013) and probability interval of 95.4%. Following Ukrainitseva (2013) and Willerslev et al. (2014), we used the periods of pre-LGM (50–25 kyr BP; called Kargin in northern Siberia or Wisconsinian Interstadial in North America), LGM (25–15 kyr BP; Sartan Ice Age/

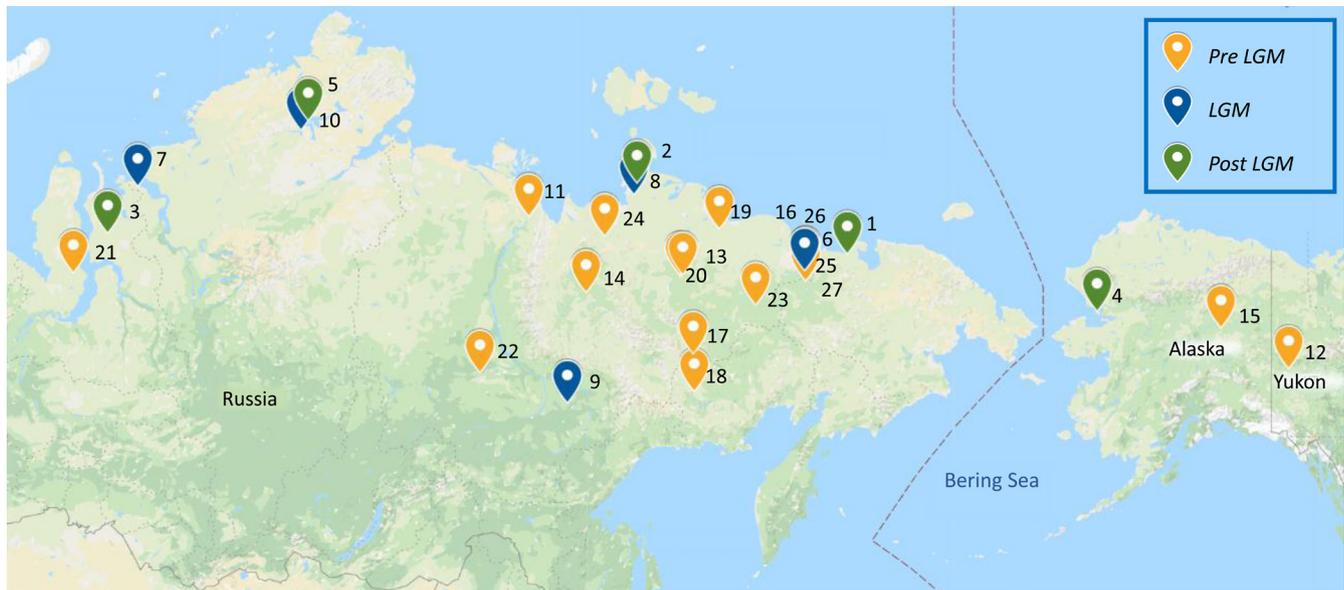


Figure 1. Localities of the frozen fauna finds considered in this study. Different symbols represent the pre-LGM period (Kargin Interstadial), LGM (Last Glacial Maximum) and the post-LGM period (Late glacial and early Holocene).

Table 1. Radiocarbon dating of the megaherbivore individuals according to the originally published data. Most carcasses were found in Siberia; those from Alaska and Yukon are indicated by an asterisk\*. Calendar age was calibrated relative to 1950 using OxCal; calibration curve IntCal13; probability 95.4%, † indicates a mean of more measurements. The dating for Vilyuy rhinoceros is approximate, based on the chronological groups used by Stuart and Lister (2012). The division into the periods follows Ukraintseva (2013) and Willerslev et al. (2014).

ID	Published nickname or (short name)	Radiocarbon date ( <sup>14</sup> C yr BP)	Ref.	Calendar age (calBP)	Period characteristics
1	Rauchua bison	8030 ± 70	8	9091–8643	Holocene; higher temperatures
2	Yukagir bison	9302 ± 45 <sup>†</sup>	3	10 652–10 298	
3	Yuribei mammoth	9730 ± 300	20	12 127–10 261	Glaciers retreat
4	Alaskan Late Glacial mammoth*	12 300 ± 70	5	14 690–14 030	
5	(Reindeer)	13 040 ± 80	15	15 891–15 305	Sartan Ice Age/Late
6	Finish Creek Valley mammoth	17 980 ± 90	20	22 055–21 495	Wisconsinian=Last Glacial
7	Mongochen mammoth	18 370 ± 150	12	22 513–21 865	Maximum; stable cold and dry
8	Yukagir mammoth	18 560 ± 50 <sup>†</sup>	16	22 560–22 318	conditions
9	Churapcha rhinoceros	19 500 ± 120	21	23 686–22 667	
10	Fishhook mammoth	20 620 ± 70	14	25 152–24 509	Kargin/Middle Wisconsinian
11	Chekurovka mammoth	23 220 ± 110	1	27 698–27 281	Interstadial; fluctuating climate
12	Yukon/Last Chance Creek horse*	26 280 ± 210	7	30 977–29 979	
13	Mylakhchin bison	29 500 ± 1000	18	35 693–31 415	
14	Khalbugai rhinoceros	33 000	4	37 496–36 635	
15	Blue Babe bison*	36 425 + 2575–1974	6	47 329–36 830	
16	Kolyma rhinoceros	39 140 ± 390	2	43 641–42 393	
17	Selerikan horse	38 590 ± 1120	20	44 927–41 163	
18	Kirgilyakh mammoth Dima	39 570 ± 870	13	44 997–42 205	
19	Shandrin mammoth	40 350 ± 880	19	45 605–42 684	
20	Mammoth dung F-552	41 813 ± 523 <sup>†</sup>	9	46 185–44 310	
21	Yuribey baby mammoth Lyuba	41 775 ± 625	11	46 393–44 097	
22	Vilyuy rhinoceros	?	17	?	
23	Berezovka mammoth	44 000 ± 3500	19	infinite–43 619	
24	Chondon rhinoceros	> 45 000	10	> 48 000	
25	Mammoth dung F-3447	> 45 000	9	> 48 000	
26	(Bison)	> 52 000	21	infinite	
27	Drevniy Creek mammoth	> 52 000	21	infinite	

References: 1: Boeskorov et al. (2009), 2: Boeskorov et al. (2011), 3: Boeskorov et al. (2014), 4: (Garut et al. 1970), 5: van Geel et al. (2011), 6: Guthrie (1990), 7: Harington (2002), 8: Kirillova et al. (2013), 9: Kirillova et al. (2016a), 10: Kirillova et al. (2017), 11: Kosintsev et al. (2010), 12: Kosintsev et al. (2012), 13: Lozhkin and Anderson (2016), 14: Mol et al. (2001), 15: Mol et al. (2003), 16: Mol et al. (2006), 17: Stuart and Lister (2012), 18: Ukraintseva (1981), 19: Ukraintseva (1993), 20: Ukraintseva (2013), 21: Willerslev et al. (2014).

Late Wisconsinian) and post-LGM (15 kyr BP–present; Late glacial and early Holocene).

### Current vegetation records

We compiled a database of 1658 vegetation-plot records sampled by Masaryk Univ. teams in the years 2003–2014 across Siberia (southern Urals, western Siberian Plain, Salairskii Kryazh, Gornaya Shoriya, Altai, western Sayan and central Yakutia) and Kazakhstan (GIVD code 00-RU-002, Chytrý 2012), and additional 1181 records from various parts of Yakutia (Gogoleva et al. 1987, Mirkin et al. 1992, Telyatnikov et al. 2013, 2014, 2015; and unpublished data from north-eastern Yakutia by E. Troeva). All the records used in this study represent natural or semi-natural vegetation (anthropogenic vegetation was not included). All the plots were of the size of 100 m<sup>2</sup> except grassland plots in the Yakutian database that were of the size of 25 m<sup>2</sup>. Each plot contained a full record of vascular plants, terricolous bryophytes and macrolichens.

All the vegetation-plot records (n = 2839) were assigned to the following broadly defined vegetation groups and types based on their species composition, ecological characteristics and overall physiognomy of the vegetation: group Blackish taiga: vegetation type Blackish taiga (= mixed coniferous–deciduous forest with nemoral species) (75 vegetation plots); Forests: Taiga (204); Hemiboreal forest (278), Alluvial forest and scrub (41), Fen and swamp woodland (51); Mires: Bog (65), Open fen (117); Arctic/alpine tundra: Arctic or alpine deciduous scrub (42), Arctic or alpine heathland (93), Tundra grassland (114), *Betula nana* s.l. scrub (54), Tall forbs (38); Saline grasslands: Saline grassland (212); Marshes: Marsh (217); Meadows: Wet meadow (223), Mesic meadow (76); Steppe: Dry meadow (88), Steppe scrub (75), Meadow steppe (267), Dry steppe (416), Desert steppe (50); Deserts: Semi-desert (17), Desert (26). See Supplementary material Appendix 1 for description of these vegetation types and list of their diagnostic, constant and dominant species.

Like the palaeobotanical records, also the taxa in the current vegetation records were included in analyses at three identification levels, as species, genus and family, in order to make a valid comparison with the palaeobotanical data.

### Analyses

Searching for the similarities between palaeobotanical records (frozen animal individuals) and current vegetation is difficult for several reasons: 1) single palaeobotanical records can be mixed samples of several vegetation types in unknown proportions, 2) some taxa in the palaeobotanical records are often identified at the genus, family or even higher taxon level, rather than at the species level as is the case of the current vegetation-plot data and 3) taxonomic spectrum of the palaeobotanical records is probably incomplete due to faster decomposition of the remains of some taxa. For these reasons, it is inappropriate to use any of the widely used similarity indices. Therefore, for both the vegetation plots and

palaeobotanical records, we prepared presence–absence matrices that contained 1) all the species, 2) all the genera and 3) all the families of recorded taxa. For example, if a vegetation-plot record contained the species *Poa pratensis*, the presence was also recorded for the genus *Poa* and the family Poaceae. If a plant remain (pollen, macrofossil, DNA) was assigned only to a genus or family, its presence in the matrix was recorded only within the same and higher taxonomic rank(s). Then we calculated the number of shared plant taxa in each of the current vegetation plots and each individual of frozen megafauna, and interpreted a higher number of co-occurring taxa as a higher similarity. For each vegetation type, we calculated the mean value of the three most similar vegetation plots to the palaeobotanical record from each frozen animal individual. These mean values were used to sort the vegetation types from the most similar (with the highest number of shared taxa) to the least similar to the palaeobotanical record. This approach was repeated for three categories of palaeobotanical data: 1) separate data on pollen + spores, 2) separate data on macrofossils and 3) pollen + spores, macrofossils and DNA records merged into one data matrix.

To validate our new methodological approach, we tested whether the vegetation plots of a given vegetation type would be most similar to the original vegetation type they were previously assigned by experts. Also in this case, we prepared the matrices combining the species, genus and family levels for all the vegetation plots. Then for each plot, we separately counted the shared taxa between this plot and each of the other plots in the vegetation matrix, like in the case of palaeobotanical records. To calculate the mean number of shared taxa for each vegetation type, we used the three plots with the highest number of shared species; the vegetation type with the highest mean number of shared taxa was considered to be the most similar. The number of plots which had the highest similarity to the vegetation type they were originally classified to, was used as a measure of the reliability of the correct assignment. All the calculations were performed using the JUICE program (Tichý 2002).

### Results

In the analysis based on pollen + spores (Fig. 2), the current vegetation types most similar to the palaeobotanical records were forests (especially taiga and hemiboreal forest), followed by several types of tundra vegetation. Steppe vegetation types showed much lower similarity (with a few exceptions). In contrast, in the analysis based on macrofossils only (Fig. 3), tundra vegetation (including both grasslands and shrublands) was among the most similar vegetation types. The similarity of palaeobotanical records to taiga and hemiboreal forests decreased from the pre-LGM phase (Kargin/Wisconsinian Interstadial; 50–25 kyr BP) through the Last Glacial Maximum (LGM/Sartan/Late Wisconsinian; 25–15 kyr BP) to the post-LGM phase (Late glacial and early Holocene; < 15 kyr BP). However, the post-LGM records were mostly limited to the northernmost parts of the study area, which

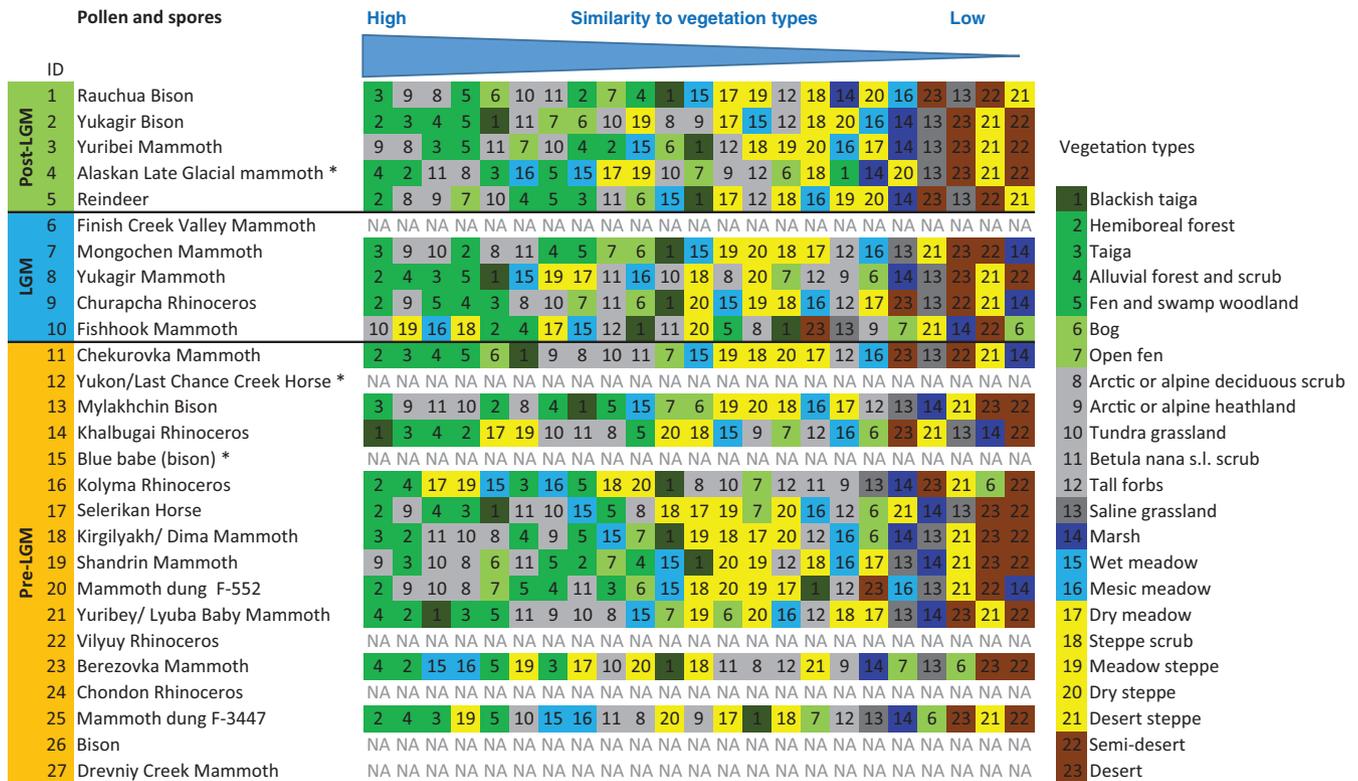


Figure 2. Similarity of pollen and spores (palaeobotanical records) from frozen fauna to current vegetation types. Vegetation types are sorted from those with the highest similarity on the left to those with the lowest similarity on the right side of the graph; numbers represent individual vegetation types, while colours represent broader ecological groups. Frozen fauna carcasses are sorted by age, and colours on the left represent different periods (see Table 1 for details). Most of the finds are from Siberia, while those from Alaska and the Yukon Territory are indicated by an asterisk. NA indicates the animals for which this type of palaeobotanical records is not available.

corresponds to the current tundra zone. An analysis combining pollen + spores, macrofossils and DNA (Fig. 4) showed a pattern similar to that based on pollen + spores only. All the analyses indicated rather wet landscape covered predominantly by vegetation types that require mesic or wet soil. Present-day vegetation of Siberian dry habitats showed a low similarity to the composition of plant material obtained from the frozen megaherbivore remains. The lowest similarity was found for dry steppes, semi-deserts and deserts.

Comparison of the plant remains of different age (Fig. 2–4) did not reveal any substantial difference in the spectrum of most similar/dissimilar vegetation types over time. There were almost no differences between the remains from the LGM (no. 18–22) and the previous and subsequent periods, with the exception of the above-mentioned changes in the similarities to forest vs tundra found in the macrofossil data.

Validation test of our method of similarity calculation revealed that 59% of the vegetation plots were assigned with the highest similarity to the original vegetation type and 78% of the plots had the highest similarity to a vegetation type in the vegetation group which the original type belongs to (Supplementary material Appendix 2 Table A5). As we considered only the highest similarity (not the second or third highest), this test was rather conservative. Most types of forest, tundra and grassland vegetation were classified successfully.

Less satisfactory results were found in the assignment of Fen and swamp woodland, which were often classified as bogs or other forest types, but mostly within the original Forests group. Tall forbs were also frequently misclassified to different forest types. Steppe scrub was most similar to both the original type and Dry steppe, both belonging to the same vegetation group. Finally, Desert steppe and Semi-desert were often misclassified as Dry steppe. Other vegetation types had 40–80% plots correctly assigned to the original vegetation type. The classification success of the vegetation groups ranged between 52 and 92% for all but one group, the Deserts, where only 32% of plots were correctly assigned to the original group.

## Discussion

### Late Pleistocene vegetation of northern Siberia and Beringia

Our analyses suggest that nearly all the individuals of Late Pleistocene megaherbivores preserved in the permafrost of northern Siberia and Beringia grazed or browsed predominantly in mesic, moist and wet habitats, in landscapes with vegetation mosaic containing both tundra vegetation and woodlands along with other vegetation types. This pattern

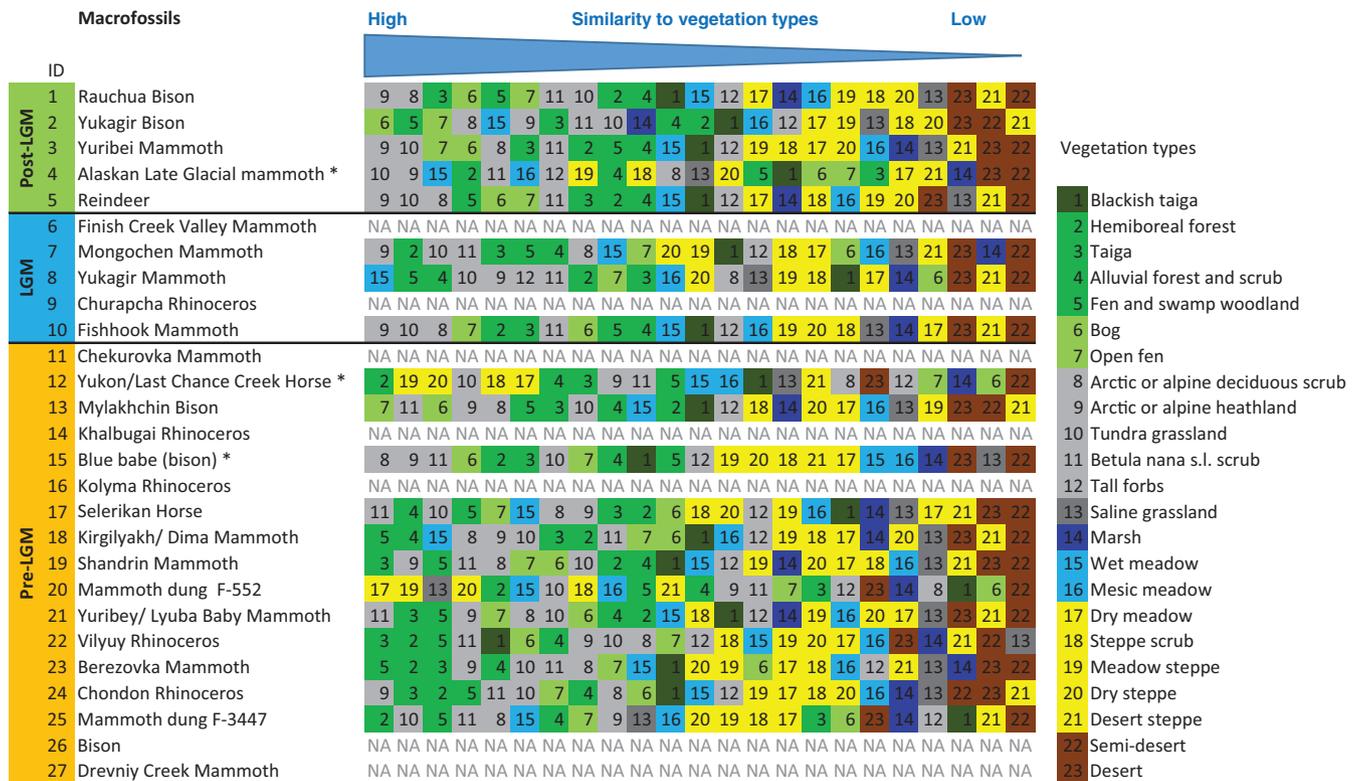


Figure 3. Similarity of macrofossils (palaeobotanical records) from frozen fauna to current vegetation types. See Fig. 2 for details.

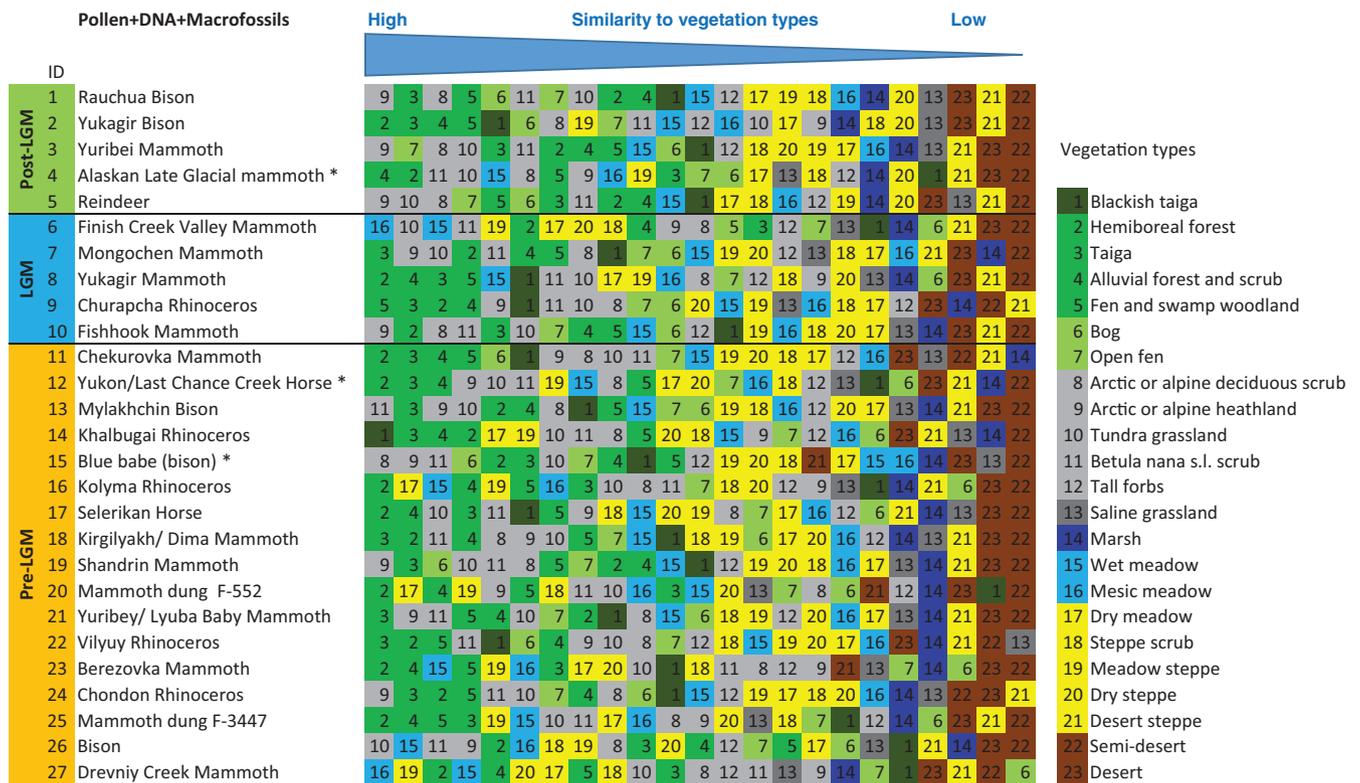


Figure 4. Similarity of all available palaeobotanical records from frozen fauna (pollen + spores, macrofossils and DNA analyses) to current vegetation types. See Fig. 2 for details.

was relatively stable over the time span from > 50 kyr to 9 kyr BP, i.e. from the pre-LGM period through the LGM to the early Holocene (Fig. 2–4).

Palaeoclimatic data and previous palaeobotanical finds suggest that in the pre-LGM period, the climate of northern Siberia and Beringia oscillated between warmer and colder phases. This affected north/south distribution limits of the zonal vegetation types, i.e. different types of taiga and tundra (Hopkins et al. 1982, Zazula et al. 2006, Troeva et al. 2010, Ukraintseva 2013). Drier types of meadows or steppes probably developed only under specific mesoclimatic conditions (Troeva et al. 2010, Ukraintseva 2013). In general, our results are similar to the reconstructions proposed in the previous literature, however, both macrofossils and to a lesser extent also pollen data indicate higher representation of tundra vegetation, while previous reconstructions suggested tundra to be limited to maritime areas (Troeva et al. 2010). It is possible that tundra was not covering the landscape continuously; it may have occurred in discontinuous patches on wind-exposed elevations or in wet depressions (compare Yurtsev 2001, Chytrý et al. 2019).

In contrast, we cannot support the previous reconstructions for the LGM. The LGM was a period of cold, arid and relatively stable climate when north-eastern Siberia was connected with North America through the Beringian Land Bridge (Hopkins et al. 1982). This past connection is reflected in the current distribution of flora (Yurtsev 1982, 2001, Guthrie 2001) and fauna (Hopkins et al. 1982, Guthrie 2001). Evidence gained mainly from pollen data and mammalian fossil finds led scientists to interpret the LGM landscape as the treeless ‘mammoth steppe’ (Guthrie 1990) or a mosaic of different treeless habitats known as the ‘steppe-tundra’ (Hibbert 1982, Yurtsev 1982, 2001, Blinnikov et al. 2011) occurring over a huge area from western Europe to interior Alaska. However, our comparative analysis of pollen data suggests that representation of the main vegetation types did not change substantially between the pre-LGM and LGM periods, indicating forest continuity at least at some topographically suitable mesic or warmer sites (see also Brubaker et al. 2005, Zazula et al. 2006, Ukraintseva 2013). Vegetation with the highest similarity to our LGM palaeobotanical data included different types of forests, especially taiga (probably light woodlands with *Larix* and *Betula*), and tundra. In contrast, the similarity to steppe vegetation types was lower than we could expect if the predominant ecosystem were the steppe-tundra complex. Only recently, Chytrý et al. (2019) proposed the Altai Mountains ecosystem in southern Siberia to be a close modern analogue of the LGM steppe-tundra biome, supporting their suggestion by multi-proxy evidence based on flora, fauna and long-term climate stability. They described the steppe-tundra as a predominantly treeless landscape mosaic of several habitat types (including woodlands) depending on precipitation and topography-related distribution of moisture across the landscape. However, there are several differences between the mountain systems of southern Siberia and northern Siberia and Beringia. Firstly,

northern Siberia and Beringia currently lack many steppe species typical of European and southern Siberian LGM steppe-tundra (Yurtsev 1982, 2001, Chytrý et al. 2019). Similarly, many typical species of the LGM mammalian fauna have never occurred in the north (Pavelková Řičánková et al. 2014, 2018). Secondly, Beringia is affected by a maritime climate, which probably enabled suitable conditions for mesic plant survival also during the otherwise cold and dry LGM (Hopkins et al. 1982, see also the dynamic vegetation model by Allen et al. 2010). Last but not least, the current landscape of northern Siberia and Beringia is characterized by thermokarst processes and relatively low evapotranspiration, supporting mesic habitats despite low precipitation rates. It seems that despite the expectations of a vast biome of the Pleistocene mammoth steppe ranging from Europe to Alaska (Guthrie 1990), northern Siberian and Beringian landscape might have been different from southern areas with relatively stable dry climate. In agreement with our conclusions, palynological evidence of crater-lake sediments also led Lozhkin and Andersson (2006) to propose a prevalence of tundra with some local woodland refugia in northeastern Siberia and Beringia. Similarly, based on palynological, macrofossil and insect evidence, Elias et al. (1996, 1997) reconstructed widespread mesic tundra in central parts of Beringia during the Late Pleistocene, while Goetcheus and Birks (2001) provided evidence for dry steppe-tundra occurrence at other sites in central Beringia during the LGM. All of these findings seem to support the existence of a vegetation mosaic with both wet and dry habitats, depending on the landscape topography.

Palaeoecological reconstructions of the post-LGM period refer to increases in both humidity and temperature, which were reflected in the Early-Holocene spread of forests and establishment of bogs (Ukraintseva 2013). Nowadays the zonal vegetation of northern Siberia and Beringia is tundra and taiga, whereas steppe can be found only azonally, depending on the landscape topography (Edwards and Armbruster 1989, Walker et al. 1991, Yurtsev 2001, Troeva et al. 2010, Reinecke et al. 2017). With considerable climate and vegetation changes at the Pleistocene/Holocene transition, herbivores were forced either to retreat to areas with more suitable conditions (Pavelková Řičánková et al. 2015) or to change their habitats and diets significantly as was evidenced, e.g. by completely changed dental wear of reindeer and moose (Rivals et al. 2010), and by changes in carbon and nitrogen isotopes of European bison, aurochs (Bocherens et al. 2015), and caribou and saiga (Schwartz-Narbonne et al. 2019).

### Methodological considerations

Like in the case of other palaeoecological studies, possible sampling biases and taphonomic issues have to be considered when interpreting our results. Firstly, frozen fauna finds are bound to the permafrost zone of northern Siberia and northern North America. Palaeoclimate studies suggest that this area had specific features that differed from other full-glacial landscapes (Allen et al. 2010). Therefore, conclusions based

on our results cannot be extrapolated to the Pleistocene landscapes in Europe or southern Siberia.

Secondly, only specific environmental conditions allow the preservation of soft tissues for more than fifty thousand years. Most of the animals preserved as frozen carcasses probably died near water bodies where they looked for water or fresh and productive vegetation (Haynes 1991, Kaczensky et al. 2008, Zhang et al. 2015), and thermokarst processes enabled their preservation (Vereshchagin and Tomirdiaro 1999). Therefore, the high similarity of our palaeobotanical data with wet to mesic vegetation types can be partly caused by the fact that shortly before they died, the studied animals grazed in wet areas, while the surrounding landscape could have been much drier.

Thirdly, although different types of plant remains indicated the same general pattern (high similarity to wet and mesic habitats), there were some differences. Taxon spectra from pollen analyses were more similar to forest vegetation, especially to taiga and hemiboreal forest (Fig. 2, 4), while macrofossils mostly indicated treeless vegetation (Fig. 3). Pollen analysis reflects the presence of trees in the wide surroundings of the study site due to wind transport of pollen, and consequently, it can suggest a more forested landscape than it actually was. However, repeated findings of *Larix* macrofossils can also support our conclusions about woodland refugia. Both macrofossils and also DNA represent mainly local plants eaten by the animals. However, as the animals may have been concentrated in more productive habitats in the landscape or around water sources (Hopkins et al. 1982), the reconstruction based on the macrofossils and DNA may provide incomplete picture of the vegetation types in the landscape.

Finally, the interpretation of vegetation from plant remains in frozen animals can be biased by feeding preferences of these animals. Deducing from the number of megafauna finds (Ukrainitseva 2013), it is supposed that northern Siberia and Beringia offered suitable habitats to large populations of megafauna over most of the Pleistocene (Guthrie 1990, Zimov et al. 1995). Although low-productive habitats might have been common in the landscape, we can expect that animals preferentially selected more productive vegetation bound to mesic or wet sites (see also Chytrý et al. 2019, or recent meta-analysis of stable isotopes from mammoth bone collagen by Schwartz-Narbonne et al. 2019). In general, the biology and feeding ecology of extinct megaherbivores can be reconstructed based on the morphology of particular species, biology and ecology of their closest living relatives, although with some degree of uncertainty. The traditional assumption that megaherbivores, especially woolly mammoths, were only grazers and their diet consisted mainly of sedges and grasses (Guthrie 1990, 2001), was already questioned by several authors, who confirmed the surprisingly high abundance of digested twigs (van Geel et al. 2008) and suggested a dietary shift to mixed feeding when the supply of forbs and graminoids was limited (Rivals et al. 2010, Tiunov and Kirillova 2010). Considering our data set, extant reindeer,

the last wild horse *Equus przewalskii* and possibly feral horses *E. caballus* could partly corroborate our results. The habitat and food preferences of extant reindeer fit well to our results (Heggberget et al. 2002). Horses are predominantly grazers with a variable proportion of trees and shrubs in their diet (Putman 1986, Kuiters et al. 2006, Kaczensky et al. 2017, Cromsigt et al. 2018). The wild horse *Equus przewalskii* is considered to be a grazer within desert-steppe habitats, but the isotope evidence suggested a dietary shift from a mixed feeder in winter and grazer in summer to a year-round grazer due to the human persecution (Kaczensky et al. 2017). When its known Pleistocene distribution (Deng 2006) is compared with an LGM vegetation model (Wang et al. 2017), it occupied many various habitats including forested landscapes. The ecological versatility of horses seems to be also supported by their Holocene distribution (Groves 1974, Kuzmina 1997, Naundrup and Svenning 2015). To conclude, our results are fully compatible with the current knowledge about the diet and habitat preferences of reindeer and horses, suggesting that we provide realistic estimations of the megaherbivore habitat preferences.

## Conclusions

Our study presents the vegetation mosaic of the Pleistocene landscape of northern Siberia and Beringia from the megaherbivore point of view. Although the plant data from frozen animal carcasses cannot be used to describe the whole picture of the mammoth steppe, we summarize and complement previous finds and interpretations based on pollen, macrofossil and DNA data, palaeoclimate modelling and other proxies. In contrast to more southern areas covered by the mammoth steppe in the Late Pleistocene, we suggest that northern Siberia and Beringia were characterized by a significant representation of mesic and wet habitats (including tundra, mires and woodlands) at that time.

## Data availability statement

Data available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.sxksn02zs>> (Axmanová et al. 2019).

*Acknowledgements* – We thank all the researchers who participated in vegetation data sampling: El'vira Baisheva, Mikhail Cherosov, Pavel Dřevojan, Nikolai Ermakov, Dmitry German, Paraskovia Gogoleva, Michal Hájek, Petra Hájková, Martin Kočí, Svatava Kubešová, Zdeňka Lososová, Pavel Lustyk, Vassily Martynenko, Nikolai Lashchinsky, Zdenka Preislerová, Philip Resl, Marcela Rezníčková, Jan Roleček, Petr Šmarda and Milan Valachovič. We also thank Věra Pavelková Řičánková for her comments at the beginning of this project.

*Funding* – This study was supported by the Czech Science Foundation (grant no. P504/11/0454 to JR and JD; grant no. 17-15168S to LT and MC), IBPC SB RAS basic research project (no. AAAA-A17-117020110056-0 to ET) and Russian Foundation for Basic Research (grant no. 18-45-140007 p\_a to AP).

*Author contributions* – MC and JR conceived the idea, JR and IA extracted the data on frozen fauna from the literature, MC, JD, IA, LT and ET participated in vegetation sampling, MC, ET and IA compiled the vegetation data, JD and IA unified the plant taxonomy and nomenclature, LT analysed the data, IA prepared graphical outputs and led the writing, all authors participated in interpretation of the results and commented on the manuscript.  
*Conflicts of interest* – The authors declare no competing interest.

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Supplementary material (available online as Appendix ecog-04940 at <[www.ecography.org/appendix/ecog-04940](http://www.ecography.org/appendix/ecog-04940)>). Appendix 1–2.

Ecography

**ECOG-04940**

Axmanová, I., Robovský, J., Tichý, L., Danihelka, J., Troeva, E., Protopopov, A. and Chytrý, M. 2019. Habitats of Pleistocene megaherbivores reconstructed from the frozen fauna remains. – Ecography doi: 10.1111/ecog.04940

**Supplementary material**

## **Supplementary material**

*Habitats of Pleistocene mega herbivores reconstructed from frozen fauna remains.*

### ***Content***

**Appendix 1** Brief characterization of the vegetation types used in this study.

### **Appendix 2**

**Table A1** Localities of the frozen fauna finds.

**Table A2** Overview of the palaeobotanical data from frozen fauna.

**Table A3** Most frequent taxa recorded in the frozen fauna: pollen + spores.

**Table A4** Most frequent taxa recorded in the frozen fauna: macrofossils.

**Table A5** Verification test of the robustness of the similarity calculation method used in this study.

## Appendix 1.

Brief characterization of the vegetation types used in this study with the lists of diagnostic, constant and dominant species. Some descriptions are partly or entirely taken from Janská et al. (2017). All descriptions are based on the expert knowledge of the authors and the references listed below. Species names follow Cherepanov (1995).

Species were considered diagnostic for a given vegetation type when their fidelity value measured as the phi coefficient of association was higher than 0.25 and corresponding Fisher's exact test indicated a significant concentration of species in the vegetation type at the level of 0.05. Highly diagnostic species (highlighted in bold) were those with phi coefficient higher than 0.40. As the fidelity values might be affected by differences in species numbers between vegetation types, we used standardization to equal sizes of all groups before calculation (Chytrý et al. 2002). Constant species or highly constant species (highlighted in bold) are those with a frequency in the dataset over 40% or 50%, respectively. Dominant species were those that reached higher cover values than 25% in at least 5% of plots. All analyses were performed in Juice software (Tichý 2002).

### 1. Blackish taiga

(75 vegetation plots)

Diagnostic species: *Abies sibirica*, *Aconitum septentrionale*, *Aconitum volubile*, *Adoxa moschatellina*, *Aegopodium podagraria*, *Allium microdictyon*, *Angelica sylvestris*, *Anthriscus sylvestris*, *Asarum europaeum*, *Athyrium filix-femina*, *Betula pendula*, *Brachypodium sylvaticum*, *Bupleurum longifolium*, ***Cacalia hastata***, ***Calamagrostis obtusata***, *Carex macroura*, *Circaea alpina*, *Cirsium helenioides*, *Crepis lyrata*, *Crepis sibirica*, *Cruciata krylovii*, *Daphne mezereum*, *Diplazium sibiricum*, *Dryopteris carthusiana*, *Dryopteris dilatata*, *Dryopteris expansa*, *Dryopteris filix-mas*, ***Equisetum sylvaticum***, ***Euphorbia pilosa***, *Festuca altissima*, ***Festuca gigantea***, *Filipendula ulmaria*, ***Galium odoratum***, *Geranium albiflorum*, *Heracleum dissectum*, *Impatiens noli-tangere*, ***Lamium album***, ***Lathyrus gmelinii***, *Lilium pilosiusculum*, *Lonicera xylosteum*, ***Maianthemum bifolium***, ***Matteuccia struthiopteris***, *Melica nutans*, ***Milium effusum***, ***Myosotis krylovii***, ***Oxalis acetosella***, ***Padus avium***, ***Paeonia anomala***, ***Paris quadrifolia***, ***Phegopteris connectilis***, ***Pleurospermum uralense***, *Polemonium coeruleum*, *Polystichum braunii*, *Populus tremula*, *Primula pallasii*, *Pteridium aquilinum*, ***Pulmonaria mollis***, *Ranunculus grandifolius*, *Ranunculus monophyllus*, *Ribes hispidulum*, *Ribes nigrum*, *Ribes spicatum*, *Rubus matsumuranus*, *Saussurea latifolia*, ***Senecio nemorensis***, ***Sorbus sibirica***, *Spiraea chamaedrifolia*, ***Stachys sylvatica***, ***Stellaria bungeana***, *Thalictrum minus*, *Tilia sibirica*, ***Urtica dioica***, *Veratrum lobelianum*, ***Viburnum opulus***, *Vicia sylvatica*, *Viola biflora*, ***Viola uniflora***; *Atrichum undulatum*, *Brachythecium reflexum*, *Brachythecium salebrosum*, *Callicladium haldanianum*, ***Cirriphyllum piliferum***, *Eurhynchium angustirete*, *Eurhynchium hians*, *Fissidens taxifolius*, *Lophocolea heterophylla*, ***Plagiochila porelloides***, *Plagiomnium confertidens*, ***Plagiomnium drummondii***, ***Plagiothecium denticulatum***, ***Rhodobryum roseum***, *Rhytidiadelphus subpinnatus*, *Rhytidiadelphus triquetrus*

Constant species: *Abies sibirica*, *Aconitum septentrionale*, *Aconitum volubile*, *Adoxa moschatellina*, *Aegopodium podagraria*, *Angelica sylvestris*, *Athyrium filix-femina*, ***Betula pendula***, ***Cacalia hastata***, ***Calamagrostis obtusata***, *Crepis lyrata*, *Crepis sibirica*, *Cruciata krylovii*, *Equisetum sylvaticum*, ***Euphorbia pilosa***, *Filipendula ulmaria*, ***Lamium album***, ***Lathyrus gmelinii***, ***Maianthemum bifolium***, ***Milium effusum***, ***Oxalis acetosella***, ***Padus avium***, ***Paris quadrifolia***, *Pleurospermum uralense*, *Polemonium coeruleum*, ***Pulmonaria mollis***, *Senecio nemorensis*, ***Sorbus sibirica***, ***Stellaria bungeana***, *Thalictrum minus*, ***Urtica dioica***, *Viola uniflora*; ***Plagiochila porelloides***, ***Plagiomnium drummondii***, ***Rhodobryum roseum***

Dominant species: *Abies sibirica*, *Aegopodium podagraria*, *Allium microdictyon*, *Athyrium filix-femina*, *Betula pendula*, *Carex macroura*, *Matteuccia struthiopteris*, *Populus tremula*, *Tilia sibirica*; *Hylocomium splendens*

Blackish (in Russian *chernevaya*) taiga is a forest composed of a mixture of coniferous and deciduous trees and both nemoral and boreal species in the herb and shrub layers. They occur especially in the southern subtaiga and southern-taiga zone of western Siberia, but they also occur in the precipitation-rich northern front ranges

of the southern Siberian mountain systems such as the Altai and smaller mountain ranges north of the Altai. These forests are dominated by *Abies sibirica*, *Betula pendula*, *B. pubescens*, *Populus tremula*, with an occasional admixture of *Picea obovata*, especially on the valley bottoms. Unlike in the boreal forests, herb layer is often rather dense and dominated by herbs and grasses, whereas dwarf shrubs, as well as mosses and lichens, are less abundant or even absent.

## 2. Hemiboreal forest

(278 vegetation plots)

Diagnostic species: *Atragea sibirica*, ***Betula pendula***, *Brachypodium pinnatum*, *Calamagrostis arundinacea*, *Calamagrostis pavlovii*, *Carex macroura*, *Cimicifuga foetida*, *Dianthus superbus*, *Fragaria vesca*, *Galium boreale*, *Geranium pseudosibiricum*, *Iris ruthenica*, *Larix sibirica*, *Lathyrus humilis*, *Lathyrus pisiformis*, *Lathyrus vernus*, *Melica nutans*, *Pinus sylvestris*, *Polygonatum odoratum*, *Populus tremula*, *Pulmonaria mollis*, *Rosa majalis*, ***Rubus saxatilis***, *Stellaria holostea*, *Thalictrum minus*, *Vicia sepium*, *Vicia unijuga*, *Viola collina*, *Viola mirabilis*

Constant species: ***Betula pendula***, ***Galium boreale***, ***Rubus saxatilis***, *Thalictrum minus*

Dominant species: *Betula pendula*, *Betula pubescens*, *Carex macroura*, *Larix sibirica*, *Pinus sylvestris*, *Populus tremula*

Hemiboreal forests are either coniferous, dominated by *Pinus sylvestris*, *Larix gmelinii* or *L. sibirica*, or deciduous, dominated by *Betula pendula* or *Populus tremula*. Their tree layer is similar to that of the light taiga, but the herb layer is very different and species-rich, consisting of the herbs and graminoids typical of temperate forests and grasslands. Dwarf shrubs and bryophytes are much less abundant than in boreal forests. This forest type forms a belt stretching approximately from the Southern Urals across the forest-steppe zone of the West Siberian Plain to the mountainous systems of southern Siberia and to the Transbaikal area. To a smaller extent, it also occurs as extrazonal vegetation in dry areas of central Yakutia.

## 3. Taiga

(204 vegetation plots)

Diagnostic species: *Festuca jacutica*, ***Larix cajanderi***, *Ledum palustre*, ***Linnaea borealis***, *Picea obovata*, *Pinus sibirica*, *Trientalis europaea*, *Vaccinium myrtillus*, ***Vaccinium vitis-idaea***

Constant species: ***Pinus sibirica***, ***Vaccinium vitis-idaea***

Dominant species: *Bergenia crassifolia*, *Larix cajanderi*, *Ledum palustre*, *Vaccinium vitis-idaea*; *Hylocomium splendens*, *Pleurozium schreberi*, *Sphagnum balticum*

Taiga is the zonal forest of the boreal zone. In wetter places it is represented by dark taiga dominated by *Abies sibirica*, *Picea obovata* and *Pinus sibirica*, occasionally with an admixture of *Betula pendula*, *B. pubescens* or *Populus tremula*. The herb layer contains abundant dwarf shrubs such as *Ledum palustre*, *Vaccinium myrtillus* and *V. vitis-idaea*, and the soil is usually covered by extensive moss mats. Light taiga is dominated by either *Pinus sylvestris* or different species of *Larix*. *Pinus sylvestris* forests occur in drier places and on poorer soils, especially on sandy deposits, higher rivers terraces and on shallow soils on slopes and crests. The herb

layer is dominated by dwarf shrubs, e.g. *Vaccinium vitis-idaea*, *Empetrum nigrum* and *Arctostaphylos uva-ursi*. Moss layer is usually well developed, with both bryophytes and lichens attaining a high cover. *Larix* forests often occur on permafrost. Their herb layer contains abundant dwarf shrubs such as *Ledum palustre*, *Vaccinium uliginosum*, *V. vitis-idaea* and *Arctous alpina* together with grasses, herbs and abundant mosses and lichens.

#### 4. Alluvial forest and scrub

(41 vegetation plots)

Diagnostic species: *Aconitum septentrionale*, *Adoxa moschatellina*, *Alnus incana*, *Angelica decurrens*, *Anthriscus sylvestris*, *Athyrium filix-femina*, *Cacalia hastata*, *Cardamine impatiens*, *Cardamine macrophylla*, *Carex cespitosa*, *Coccyganthe flos-cuculi*, *Deschampsia cespitosa*, ***Elymus caninus***, *Festuca gigantea*, *Filipendula ulmaria*, *Humulus lupulus*, *Chelidonium majus*, *Impatiens noli-tangere*, *Matteuccia struthiopteris*, *Melilotoides platycarpus*, *Milium effusum*, *Myosotis nemorosa*, *Padus avium*, *Poa remota*, *Populus laurifolia*, *Prunella vulgaris*, *Ranunculus grandifolius*, *Ranunculus repens*, *Ribes nigrum*, *Rubus caesius*, *Salix dasyclados*, ***Salix rorida***, *Salix viminalis*, *Scirpus sylvaticus*, *Scrophularia nodosa*, *Senecio nemorensis*, *Stachys sylvatica*, *Stellaria bungeana*, *Stellaria nemorum*, *Tussilago farfara*, ***Urtica dioica***, *Viburnum opulus*; *Brachythecium rivulare*, *Calliergon cordifolium*, *Climacium dendroides*, *Eurhynchium hians*, *Hypnum lindbergii*

Constant species: *Cacalia hastata*, *Filipendula ulmaria*, *Galium boreale*, *Padus avium*, ***Urtica dioica***

Dominant species: *Aegopodium podagraria*, *Alnus incana*, *Matteuccia struthiopteris*, *Salix rorida*, *Salix viminalis*

Alluvial forests and shrublands occur along streams on mineral alluvial soil with no or only superficial accumulation of peat. They are dominated especially by *Picea obovata*, *Betula pendula*, *B. pubescens*, *Larix* spp., several different species of *Salix* and *Alnus fruticosa*. Their herb layer contains grasses such as *Calamagrostis langsdorffii*, but also herb and dwarf-shrub species occurring in the adjacent forests.

#### 5. Fen and swamp woodland

(51 vegetation plots)

Diagnostic species: *Betula pubescens*, *Carex cespitosa*, *Carex globularis*, *Epilobium palustre*, *Galium palustre*, *Galium uliginosum*, *Chamaedaphne calyculata*, *Ledum palustre*, *Salix bebbiana*, *Salix pyrolifolia*; *Bryum pseudotriquetrum*

Constant species: *Betula pubescens*

Dominant species: *Betula pendula*, *Betula pubescens*, *Calamagrostis langsdorffii*, *Chamaedaphne calyculata*, *Ledum palustre*

Peatland forests occur on the valley bottoms or in shallow depressions that are saturated with water from lateral groundwater flow, as in the case of minerotrophic fens. Dominant trees include *Betula pubescens*, *Picea obovata* and *Pinus sylvestris*. Herb layer is rich in grasses (e.g. *Calamagrostis canescens* and *C. langsdorffii*), sedges (e.g. *Carex cespitosa* and *C. juncella*) and bryophytes including some species of *Sphagnum*.

## 6. Bog

(65 vegetation plots)

Diagnostic species: *Andromeda polifolia*, *Betula nana*, *Betula pubescens*, *Carex globularis*, *Carex lasiocarpa*, *Carex pauciflora*, *Dactylorhiza maculata*, ***Drosera rotundifolia***, *Empetrum nigrum*, ***Eriophorum vaginatum***, ***Chamaedaphne calyculata***, ***Ledum palustre***, ***Oxycoccus microcarpus***, ***Oxycoccus palustris***, *Pinus sylvestris*, ***Rubus chamaemorus***, *Vaccinium uliginosum*, *Vaccinium vitis-idaea*; *Cladonia amaurocraea*, *Cladonia stellaris*, ***Mylia anomala***, *Polytrichum strictum*, ***Sphagnum angustifolium***, ***Sphagnum fallax***, ***Sphagnum fuscum***, ***Sphagnum magellanicum***, *Sphagnum rubellum*, *Sphagnum species*

Constant species: *Andromeda polifolia*, *Betula nana*, ***Eriophorum vaginatum***, ***Chamaedaphne calyculata***, ***Ledum palustre***, *Oxycoccus microcarpus*, *Pinus sibirica*, *Pinus sylvestris*, ***Rubus chamaemorus***, *Vaccinium uliginosum*, ***Vaccinium vitis-idaea***

Dominant species: *Eriophorum vaginatum*, *Ledum palustre*; *Cladonia stellaris*, *Polytrichum species*, *Sphagnum fallax*, *Sphagnum fuscum*, *Sphagnum magellanicum*, *Sphagnum species*

These are rainwater-fed mires occurring mainly in the lowlands of the boreal zone of Siberia, especially on the West Siberian Plain. They are dominated by peat mosses (*Sphagnum* spp.) and contain a significant amount of dwarf shrubs such as *Chamaedaphne calyculata*, *Ledum palustre*, *Rubus chamaemorus*, *Oxycoccus* spp. and *Vaccinium uliginosum*). They are either open or covered by sparse stands of *Pinus sylvestris*. In the permafrost zone of northern Siberia, they often form small elevations with ice cores (palsas).

## 7. Open fen

(117 vegetation plots)

Diagnostic species: *Andromeda polifolia*, ***Carex concolor***, ***Carex chordorrhiza***, *Carex limosa*, ***Carex rotundata***, *Carex williamsii*, ***Comarum palustre***, *Eriophorum polystachyon*, ***Eriophorum russeolum***, *Pedicularis albolabiata*, *Salix fuscescens*, *Utricularia intermedia*

Constant species: ***Carex concolor***, *Carex chordorrhiza*, *Comarum palustre*, *Eriophorum russeolum*

Dominant species: *Hypnum species*, *Tomentypnum nitens*

This type of open mire, occurring in valleys, shallow depressions or around springs, is saturated by groundwater. It is dominated by sedges (e.g. *Carex chordorrhiza*, *C. diandra*, *C. lasiocarpa* and *C. rostrata*), herbs (e.g. *Comarum palustre* and *Menyanthes trifoliata*) and mosses, although the species of the genus *Sphagnum* are less abundant than in ombrotrophic bogs or even absent.

## 8. Arctic or alpine deciduous scrub

(42 vegetation plots)

Diagnostic species: *Arctagrostis arundinacea*, *Arctagrostis latifolia*, *Artemisia tilesii*, *Astragalus alpinus*, ***Duschekia fruticosa***, *Equisetum arvense*, *Pedicularis sceptrum-carolinum*, ***Petasites frigidus***, *Poa alpigena*, ***Polemonium acutiflorum***, *Salix boganidensis*, ***Salix glauca***, *Salix hastata*, *Salix lanata*, *Salix lapponum*, *Salix phylicifolia*, *Salix pulchra*, ***Salix richardsonii***, *Saxifraga hieracifolia*, *Valeriana capitata*, *Viola epipsiloides*, *Wilhelmsia physodes*

Constant species: *Equisetum arvense*, ***Salix glauca***

Dominant species: *Betula exilis*, *Duschekia fruticosa*, *Salix glauca*, *Salix phylicifolia*, *Salix pulchra*, *Salix richardsonii*; *Hylocomium splendens*, *Tomentypnum nitens*

This vegetation type occurs in moist habitats in northern Siberia, especially in the Arctic tundra zone, and in the high mountains in the south. Its characteristic feature is an abundance of deciduous shrubs, especially willows (*Salix glauca*, *S. krylovii*, *S. lanata* and *S. phylicifolia*), *Alnus fruticosa* and *Pentaphylloides fruticosa*.

## 9. Arctic or alpine heatland

(93 vegetation plots)

Diagnostic species: *Aconogonon tripterocarpum*, ***Achoriphragma nudicaule***, *Alopecurus alpinus*, *Arctagrostis latifolia*, *Arctous alpina*, ***Betula exilis***, *Bistorta elliptica*, *Calamagrostis holmii*, *Carex arctisibirica*, *Carex vaginata*, ***Cassiope tetragona***, *Draba species*, ***Dryas punctata***, *Eriophorum vaginatum*, *Festuca brachyphylla*, ***Hierochloa alpina***, *Lagotis minor*, ***Ledum decumbens***, ***Luzula confusa***, ***Luzula nivalis***, *Luzula tundricola*, ***Minuartia arctica***, ***Minuartia macrocarpa***, *Oxytropis nigrescens*, *Pedicularis alopecuroides*, *Pedicularis capitata*, ***Poa arctica***, *Salix glauca*, *Salix polaris*, *Salix pulchra*, ***Saussurea tilesii***, ***Saxifraga nelsoniana***, *Saxifraga nivalis*, *Saxifraga serpyllifolia*, ***Saxifraga spinulosa***, *Sieversia species*, ***Stellaria peduncularis***, *Tephroses heterophylla*, *Tofieldia coccinea*, ***Vaccinium uliginosum***, ***Vaccinium vitis-idaea***, *Valeriana capitata*; ***Alectoria nigricans***, ***Alectoria ochroleuca***, *Aulacomnium turgidum*, ***Bryocaulon divergens***, *Bryoria nitidula*, ***Cetraria laevigata***, *Cetraria nigricans*, ***Dactylina arctica***, *Dicranum species*, ***Flavocetraria cucullata***, *Peltigera aphthosa*, *Polytrichum species*, *Ptilidium ciliare*, *Racomitrium lanuginosum*, *Sphaerophorus globosus*, *Stereocaulon alpinum*, *Stereocaulon species*, ***Thamnia vermicularis***, *Tomentypnum nitens*

Constant species: ***Arctagrostis latifolia***, *Betula exilis*, *Cassiope tetragona*, ***Dryas punctata***, ***Ledum decumbens***, ***Luzula confusa***, *Luzula nivalis*, ***Poa arctica***, *Stellaria peduncularis*, ***Vaccinium uliginosum***, ***Vaccinium vitis-idaea***; *Cetraria laevigata*, *Dactylina arctica*, ***Flavocetraria cucullata***, *Ptilidium ciliare*

Dominant species: *Dryas punctata*, *Eriophorum vaginatum*, *Ledum decumbens*, *Vaccinium vitis-idaea*; *Abietinella abietina*, *Alectoria ochroleuca*, *Aulacomnium species*, *Aulacomnium turgidum*, *Dicranum species*, *Flavocetraria cucullata*, *Hylocomium splendens*, *Ptilidium ciliare*, *Tomentypnum nitens*

Arctic and alpine heathland occurs especially in the tundra zone of northern Siberia as well as in the areas above the timberline of the Siberian mountain systems. It is dominated by dwarf shrubs (e.g. *Empetrum* spp., *Vaccinium myrtillus* and *V. vitis-idaea*) associated with perennial herbs, graminoids, and with significant participation of bryophytes and lichens.

## 10. Tundra grassland

(114 vegetation plots)

Diagnostic species: ***Bistorta vivipara***, *Carex fuscidula*, *Carex redowskiana*, *Carex rupestris*, *Crepis chrysantha*, *Dryas crenulata*, *Dryas punctata*, *Eremogone formosa*, *Eritrichium villosum*, *Eutrema edwardsii*, *Gastrolychnis apetala*, *Gentiana algida*, *Gentiana grandiflora*, *Kobresia species*, *Lagotis minor*, *Luzula nivalis*, *Minuartia arctica*, *Minuartia rubella*, *Minuartia verna*, *Pedicularis amoena*, *Pedicularis oederi*, *Poa glauca*, *Potentilla gelida*, *Salix polaris*, *Saussurea schanginiana*, *Saxifraga hirculus*, *Schulzia crinita*, *Thalictrum alpinum*, *Thymus oxyodontus*; *Cetraria islandica*, *Dactylina arctica*, *Flavocetraria cucullata*, *Thamnolia vermicularis*

Constant species: ***Bistorta vivipara***; ***Flavocetraria cucullata***

Dominant species: *Dryas oxyodonta*, *Dryas punctata*, *Eriophorum polystachyon*, *Eriophorum vaginatum*, *Salix polaris*; *Hylocomium splendens*, *Ptilidium ciliare*, *Tomentypnum nitens*

Grasslands in the tundra zone occur especially at grazed sites or in the surroundings of snow beds. More frequently occurring graminoids include *Kobresia myosuroides* and species of the genera *Carex* and *Festuca*. Herbs include *Bistorta vivipara*, *Gentiana algida* and *Thalictrum alpinum*. Bryophyte and lichens are well developed in these grasslands.

## 11. *Betula nana* s. l. scrub

(54 vegetation plots)

Diagnostic species: *Betula nana*, ***Betula rotundifolia***, *Calamagrostis lapponica*, *Callianthemum sajanense*, *Carex globularis*, *Carex sabynensis*, *Festuca altaica*, *Festuca ovina*, *Festuca sphagnicola*, *Gentiana grandiflora*, *Hedysarum consanguineum*, *Kobresia myosuroides*, *Lagotis integrifolia*, *Luzula sibirica*, *Pachypleurum alpinum*, *Pedicularis compacta*, *Pedicularis labradorica*, *Potentilla gelida*, *Salix glauca*, *Salix phylicifolia*, *Salix rectijulis*, *Saussurea alpina*, *Schulzia crinita*, *Spiraea alpina*, *Swertia obtusa*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea*, *Viola altaica*; *Aulacomnium palustre*, *Aulacomnium turgidum*, *Cetraria islandica*, *Cladonia amaurocraea*, *Cladonia cornuta*, *Cladonia gracilis*, *Cladonia chlorophaea*, *Cladonia rangiferina*, *Cladonia stellaris*, *Dicranum elongatum*, *Dicranum spadiceum*, *Nephroma arcticum*, *Peltigera aphthosa*, *Peltigera scabrosa*, *Pohlia nutans*

Constant species: *Betula rotundifolia*, ***Vaccinium uliginosum***, ***Vaccinium vitis-idaea***; *Cetraria islandica*, *Cladonia rangiferina*

Dominant species: *Betula exilis*, *Betula nana*, *Betula rotundifolia*; *Cladonia stellaris*, *Hylocomium splendens*, *Pleurozium schreberi*, *Ptilidium ciliare*

This dwarf to medium-tall shrub formation, occupying especially the tundra zone in northern Siberia but occurring also in other areas of Siberia, is dominated by shrubby birches from the group of *Betula nana*, in particular *B. nana* in the Arctic tundra of northwestern Siberia, *B. exilis* in the tundra and taiga zone of northern-central and northeastern Siberia as well as Alaska, and *B. rotundifolia* in the alpine tundra of the southern Siberian mountain systems. Associated species include various shrubs and dwarf shrubs (e.g. *Empetrum* spp., *Ledum palustre*, *Salix glauca*, *Vaccinium myrtillus*, *V. uliginosum* and *V. vitis-idaea*), graminoids, dicot herbs, bryophytes and lichens. This vegetation often occurs at topographically wetter sites and in places with distinct snow accumulation in winter.

## 12. Tall forbs

(38 vegetation plots)

Diagnostic species: *Aconitum sajanense*, *Aconitum septentrionale*, *Alchemilla species*, *Allium microdictyon*, *Angelica decurrens*, *Anthoxanthum alpinum*, *Aquilegia glandulosa*, ***Athyrium distentifolium***, *Bistorta major*, *Bupleurum longifolium*, *Calamagrostis langsdorffii*, *Cardamine macrophylla*, ***Carex aterrima***, *Cerastium davuricum*, ***Cerastium pauciflorum***, *Cirsium helenioides*, *Cirsium heterophyllum*, *Crepis lyrata*, *Delphinium elatum*, *Deschampsia cespitosa*, ***Doronicum altaicum***, ***Euphorbia pilosa***, ***Geranium albiflorum***, *Geranium sylvaticum*, *Chamaenerion angustifolium*, *Lamium album*, *Myosotis krylovii*, *Myosotis nemorosa*, ***Pedicularis incarnata***, ***Poa sibirica***, *Primula pallasii*, *Ranunculus grandifolius*, *Rhodiola rosea*, ***Rumex alpestris***, ***Saussurea latifolia***, ***Saxifraga aestivalis***, *Solidago dahurica*, *Stemmacantha carthamoides*, *Swertia obtusa*, *Trisetum altaicum*, *Trollius asiaticus*, ***Veratrum lobelianum***, *Veronica densiflora*, ***Viola biflora***; *Barbilophozia lycopodioides*, *Brachythecium reflexum*, *Conocephalum conicum*, *Hylocomiastrum pyrenaicum*, *Lescurea saxicola*, *Plagiochila porelloides*, *Plagiomnium affine*, *Rhizomnium magnifolium*

Constant species: *Aconitum septentrionale*, *Bistorta major*, *Calamagrostis langsdorffii*, ***Cerastium pauciflorum***, *Euphorbia pilosa*, *Geranium albiflorum*, *Pedicularis incarnata*, ***Poa sibirica***, *Rumex alpestris*, *Trollius asiaticus*, ***Veratrum lobelianum***, ***Viola biflora***

Dominant species: *Allium microdictyon*, *Athyrium distentifolium*, *Calamagrostis langsdorffii*, *Heracleum dissectum*, *Stemmacantha carthamoides*, *Veratrum lobelianum*; *Brachythecium rivulare*

High-productive tall-forb grasslands (also called subalpine meadows) are widespread in the precipitation-rich parts of the high-mountain systems of southern Siberia, particularly in the Altai-Sayan Mountains, but they also occur in the Arctic tundra zone. Dominant species include *Aconitum septentrionale*, *Aquilegia glandulosa*, *Cirsium heterophyllum*, *Doronicum altaicum*, *Pedicularis incarnata*, *Trollius asiaticus* and *Veratrum lobelianum*.

### 13. Saline grassland

(212 vegetation plots)

Diagnostic species: *Glaux maritima*, ***Knorringia sibirica***, ***Puccinellia tenuiflora***, *Saussurea amara*, ***Suaeda corniculata***

Constant species: ***Puccinellia tenuiflora***, *Saussurea amara*

Dominant species: *Alopecurus arundinaceus*, *Artemisia jacutica*, *Elytrigia repens*, *Glaux maritima*, *Hordeum brevisubulatum*, *Puccinellia tenuiflora*, *Suaeda corniculata*

Inland saline grasslands are meadow-like or steppe-like communities on saline soils. More productive types develop on solonchaks, occurring in river valleys, in shallow depressions and in the surroundings of lakes, while the less productive types develop on solonetz soils in flat lowlands and on river terraces. Common species include the herbs *Glaux maritima*, *Halerpestes salsuginosa*, *Potentilla anserina*, *Saussurea amara* and *Triglochin palustre*, the grasses *Agrostis stolonifera*, *Alopecurus arundinaceus* and *Puccinellia* spp., and succulent halophytes of the genera *Salicornia* or *Suaeda*.

### 14. Marsh

(217 vegetation plots)

Diagnostic species: *Beckmannia syzigachne*, *Carex vesicata*, *Eleocharis palustris*, *Equisetum fluviatile*, ***Glyceria triflora***, *Hippuris vulgaris*, *Scirpus lacustris*, *Scolochloa festucacea*, *Sparganium emersum*

Constant species: *Glyceria triflora*

Dominant species: *Beckmannia syzigachne*, *Carex aquatilis*, *Eleocharis palustris*, *Equisetum fluviatile*, *Glyceria triflora*, *Scirpus lacustris*, *Scolochloa festucacea*

This is an azonal vegetation type occurring at topographically wet sites in the lowlands and river valleys. The dominant species include tall wetland grasses, especially *Phragmites australis* and *Typha* spp., and tall sedges. The occurrence of bryophytes and accumulation of moss peat are insignificant features in this habitat.

### 15. Wet meadow

(223 vegetation plots)

Diagnostic species: *Alopecurus arundinaceus*, *Calamagrostis neglecta*, *Caltha palustris*, ***Carex juncella***, ***Carex lithophila***, *Lathyrus pilosus*, *Persicaria amphibia*, ***Poa palustris***, *Potentilla anserina*, *Ptarmica cartilaginea*

Constant species: *Alopecurus arundinaceus*, *Caltha palustris*

Dominant species: *Alopecurus arundinaceus*, *Calamagrostis langsdorffii*, *Calamagrostis neglecta*, *Caltha palustris*, *Carex juncella*, *Carex lithophila*, *Filipendula ulmaria*, *Hordeum brevisubulatum*, *Sanguisorba officinalis*

Wet grasslands are usually confined to bottoms of river valleys in various parts of Siberia, probably being most common in south-western Siberia. They are composed of herbs (e.g. *Filipendula ulmaria*, *Galium boreale*, *Silaum silaus* and *Thalictrum simplex*) and graminoids (e.g. *Carex vulpina*, *Deschampsia cespitosa* and *Poa palustris*).

## 16. Mesic meadow

(76 vegetation plots)

Diagnostic species: *Achillea millefolium*, *Allium schoenoprasum*, *Amoria repens*, *Artemisia mongolica*, *Cnidium davuricum*, *Elytrigia repens*, *Geranium pratense*, *Hordeum brevisubulatum*, *Poa pratensis*, *Potentilla anserina*, *Potentilla stipularis*, *Ptarmica alpina*, *Ranunculus propinquus*, *Rhinanthus vernalis*, *Rumex thyrsoiflorus*, *Sanguisorba officinalis*, *Stellaria dahurica*, *Tanacetum vulgare*, *Taraxacum ceratophorum*, ***Thalictrum simplex***, *Veronica longifolia*, *Vicia cracca*

Constant species: *Achillea millefolium*, ***Elytrigia repens***, ***Galium boreale***, *Galium verum*, ***Geranium pratense***, ***Hordeum brevisubulatum***, ***Poa pratensis***, *Potentilla anserina*, ***Sanguisorba officinalis***, ***Thalictrum simplex***, *Veronica longifolia*, *Vicia cracca*

Dominant species: *Agrostis clavata*, *Elytrigia repens*, *Hordeum brevisubulatum*, *Potentilla anserina*, *Sanguisorba officinalis*, *Thalictrum simplex*, *Vicia cracca*

Mesic meadows typically occur on river terraces which are rarely flooded. Their species composition consists of both graminoids and dicot herbs. Productivity is lower than in the wet meadows, but the swards are often dense and tall and used for grazing or haymaking by local farmers.

## 17. Dry meadow

(88 vegetation plots)

Diagnostic species: *Agrostis trinii*, *Achillea millefolium*, *Anemone sylvestris*, *Artemisia commutata*, *Artemisia mongolica*, *Carex duriuscula*, *Crepis tectorum*, *Elytrigia repens*, *Erigeron acris*, *Hordeum brevisubulatum*, *Linum perenne*, *Pedicularis venusta*, *Plantago canescens*, *Poa pratensis*, *Potentilla conferta*, *Potentilla stipularis*, *Senecio erucifolius*, *Silene repens*, *Taraxacum ceratophorum*, *Thalictrum simplex*

Constant species: *Achillea millefolium*, *Artemisia commutata*, *Carex duriuscula*, ***Elytrigia repens***, ***Galium verum***, ***Hordeum brevisubulatum***, ***Poa pratensis***, *Silene repens*, ***Thalictrum simplex***, *Vicia cracca*

Dominant species: *Agrostis trinii*, *Anemone sylvestris*, *Elytrigia repens*, *Galium verum*, *Hordeum brevisubulatum*, *Puccinellia tenuiflora*

Dry meadow is a vegetation type occurring on the moisture gradient between the mesic meadow and the meadow-steppe. It contains various herbs typical of mesic meadows, dicot herbs and broad-leaved grasses typical of meadow-steppe, but typical steppe species such as those of the genus *Stipa* are missing.

## 18. Steppe scrub

(75 vegetation plots)

Diagnostic species: *Aconogonon alpinum*, *Artemisia armeniaca*, *Artemisia gmelinii*, *Artemisia sericea*, *Caragana frutex*, *Carex supina*, *Fragaria viridis*, *Galium verum*, *Melica transsilvanica*, *Origanum vulgare*, *Phlomooides tuberosa*, *Sedum hybridum*, *Spiraea crenata*, *Spiraea hypericifolia*, *Veronica spuria*

Constant species: *Fragaria viridis*, ***Galium verum***, ***Phlomooides tuberosa***

Dominant species: *Caragana arborescens*, *Caragana frutex*, *Carex pediformis*, *Juniperus sabina*, *Sedum hybridum*, *Spiraea crenata*, *Spiraea media*

This vegetation type is formed of drought-adapted low shrubs, especially those of the genera *Caragana* and *Spiraea*. It occurs in relatively wetter places within the steppe and forest-steppe zones, usually in a mosaic with meadow-steppe or typical steppe, or at the forest edges. Steppe herbs and graminoids occur below the shrub canopy.

## 19. Meadow steppe

(267 vegetation plots)

Diagnostic species: ***Festuca lenensis***, *Pulsatilla flavescens*

Constant species: *Artemisia commutata*, ***Galium verum***

Dominant species: *Pulsatilla flavescens*

Meadow-steppe is a vegetation type occupying an intermediate ecological position on the moisture gradient between dry meadows and dry steppes. This vegetation is common in the forest-steppe zone of the lowland parts of southern Siberia as well as in the mountain forest-steppe belt of the southern Siberian mountain systems. Plant communities of the meadow-steppe consist of a species-rich mixture of broad-leaved herbs and graminoids. Rhizomatous graminoids are more common than tussocky ones.

## 20. Dry steppe

(416 vegetation plots)

Diagnostic species: *Agropyron cristatum*, *Alyssum obovatum*, ***Artemisia frigida***, *Caragana pygmaea*, ***Cleistogenes squarrosa***, *Ephedra monosperma*, *Goniolimon speciosum*, *Chamaerhodos erecta*, *Kitagawia baicalensis*, *Koeleria cristata*, *Orostachys spinosa*, *Poa botryoides*, *Potentilla acaulis*, *Scorzonera austriaca*, *Stipa capillata*, *Stipa krylovii*, *Veronica incana*; *Xanthoparmelia camschadalis*

Constant species: *Artemisia frigida*, ***Koeleria cristata***

Dry (or typical) steppe is the dominant plant formation of the steppe zone of southern Siberia and adjacent areas in Kazakhstan, Mongolia and China. It occurs in drier habitats than meadow-steppe, and it is less productive and less species-rich than meadow-steppe, characterized by a sparser vegetation cover. The typical steppe is dominated by narrow-leaved tussocky grasses such as *Festuca valesiaca*, *Koeleria cristata*, *Stipa* (e.g. *Stipa capillata*, *S. lessingiana*, *S. krylovii*) and *Helictotrichon altaicum*, accompanied by sedges, non-tussocky graminoids, herbs and some low shrubs such as *Caragana* spp.

## 21. Desert steppe

(50 vegetation plots)

Diagnostic species: ***Agropyron cristatum***, *Achnatherum splendens*, *Ancathia igniaria*, ***Artemisia frigida***, *Artemisia obtusiloba*, *Artemisia semiarida*, ***Artemisia schrenkiana***, *Atriplex cana*, *Caragana balchaschensis*, *Caragana bungei*, *Ceratocarpus arenarius*, *Convolvulus ammannii*, *Dontostemon perennis*, *Festuca valesiaca*, ***Kochia prostrata***, *Krascheninnikovia ceratoides*, *Psathyrostachys juncea*, *Ptilotrichum canescens*, *Stellaria dichotoma*, ***Stipa glareosa***, *Stipa orientalis*, ***Stipa sareptana***; *Xanthoparmelia camschadalis*

Constant species: ***Agropyron cristatum***, ***Artemisia frigida***, *Festuca valesiaca*, *Koeleria cristata*, ***Kochia prostrata***

Desert-steppe is open low-productive vegetation currently occurring in the basins of the southern Siberian mountain systems. It is dominated by steppe grasses (e.g. *Festuca valesiaca*, *Psathyrostachys juncea* and *Stipa sareptana*) combined with dwarf shrubs and semi-shrubs, especially various species of *Artemisia* such as *A. frigida*, *A. nitrosa*, *A. schrenkiana* and *A. semiarida*, and *Amaranthaceae* species, e.g. *Kochia prostrata*.

## 22. Semi-desert

(17 vegetation plots)

Diagnostic species: ***Anabasis salsa***, *Anabasis truncata*, *Artemisia gracilescens*, ***Artemisia species***, *Caragana balchaschensis*, ***Ceratocarpus arenarius***, *Ceratocarpus utriculosus*, *Drabopsis species*, ***Ferula species***, *Iris glaucescens*, *Kochia prostrata*, ***Krascheninnikovia ceratoides***, *Lappula spinocarpos*, *Leptaleum filifolium*, ***Megacarpaea megalocarpa***, ***Nanophyton erinaceum***, ***Rheum tataricum***, *Salix arbuscula*, ***Salsola species***, *Scorzonera species*, ***Stipa richteriana***, *Stipa*

*sareptana*, *Tetracme quadricornis*, *Tetracme species*, *Thalictrum isopyroides*, *Tulipa biflora*, *Tulipa species*; *Asperula affinis*, ***Aspicilia desertorum***, ***Aspicilia lacunosa***, ***Aspicilia vagans***, ***Collema species***, *Endocarpon pusillum*, *Endocarpon species*, *Psora decipiens*, *Ramalina species*

Constant species: *Artemisia species*, *Ferula species*, ***Nanophyton erinaceum***, *Rheum tataricum*, ***Salsola species***, ***Stipa richteriana***; *Aspicilia lacunosa*, *Aspicilia vagans*

Dominant species: *Artemisia species*, *Salsola species*, *Stipa richteriana*

Semi-deserts currently occur especially in central Kazakhstan and Mongolia. They are transitional between dry steppes or desert-steppes and true deserts. Steppe grasses (especially tussock species of the genera *Festuca* and *Stipa*) are mixed with dwarf shrubs typical of the true steppe. This vegetation is sparse and has low productivity.

### 23. Desert

(26 vegetation plots)

Diagnostic species: *Aira species*, *Allium iliense*, *Allium sabulosum*, ***Alyssum turkestanicum***, ***Anabasis salsa***, *Anabasis truncata*, *Anisantha tectorum*, ***Arnebia decumbens***, ***Artemisia gracilescens***, *Artemisia pauciflora*, ***Artemisia species***, ***Artemisia turanica***, *Atriplex species*, *Carex physocarpa*, ***Carex physodes***, ***Ceratocarpus utriculosus***, *Ceratocephala falcata*, *Ceratocephala testiculata*, *Climacoptera lanata*, ***Diptychocarpus strictus***, *Drabopsis nuda*, *Ephedra intermedia*, ***Eremopoa species***, ***Eremopyrum species***, *Erysimum czernjajevii*, *Euphorbia blepharophylla*, *Filago species*, ***Gagea species***, ***Girgensohnia oppositiflora***, *Holosteum umbellatum*, *Hypecoum species*, *Chorisporea species*, *Chorisporea tenella*, *Jurinea species*, *Kochia iranica*, *Kochia species*, *Krascheninnikovia ceratoides*, ***Lappula species***, *Lappula spinocarpos*, ***Lepidium perfoliatum***, ***Leptaleum filifolium***, ***Meniocus linifolius***, ***Nanophyton erinaceum***, *Neotorularia brevipes*, ***Petrosimonia sibirica***, ***Poa bulbosa***, *Potentilla astragalifolia*, ***Rheum tataricum***, *Rhinopetalum karelinii*, *Rhinopetalum species*, *Rochelia retorta*, ***Salsola orientalis***, ***Salsola species***, *Scorzonera species*, *Stipa caspia*, ***Streptoloma desertorum***, *Strigosella africana*, *Strigosella species*, ***Tetracme quadricornis***, *Trigonella arcuata*, ***Tulipa species***, ***Veronica species***, *Ziziphora species*, *Ziziphora tenuior*; *Asperula affinis*, ***Aspicilia desertorum***, *Aspicilia lacunosa*, ***Collema species***, *Psora decipiens*

Constant species: *Artemisia species*, ***Ceratocarpus utriculosus***, *Eremopoa species*, ***Leptaleum filifolium***, *Meniocus linifolius*, *Poa bulbosa*, *Salsola species*, *Tetracme quadricornis*

Dominant species: *Salsola species*

Deserts currently occur especially in southern Kazakhstan and Mongolia. They have a very sparse vegetation cover characterized by dwarf shrubs, some of them succulent (e.g. the genera *Anabasis*, *Artemisia* and *Salsola*), and spring geophytes and therophytes.

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## Appendix 2

**Table A1.** Localities of the frozen fauna finds. Most carcasses were found in Siberia; those from Alaska and the Yukon Territory are indicated by an asterisk\*. If available, geographic coordinates were taken from the original publications. † indicates approximate coordinates based on published maps or locality descriptions. For references see below.

ID	Nickname or [short name]	Locality	Reference No. in the Appendix	Coordinates
1	Rauchua Bison	W Chukotka, the mouth of the Rauchua River near Bilibino	6	69°30'N, 166°49'E
2	Yukagir Bison	N Yakutia, northern bank of Chukchalakh Lake, Yana-Indigirka Lowland	2	72°17'N, 140°54'E
3	Yuribei Mammoth	Gydan Peninsula, middle Yuribei River	17	70°18'N, 76°00'E
4	Alaskan Late Glacial mammoth*	Alaska, Cape Blossom in Kotzebue Sound, Baldwin Peninsula	3	66°53'N, 162°35'W †
5	[Reindeer]	Taimyr Peninsula, NW shore of Lake Taimyr	13	74°31'N, 100°30'E
6	Finish Creek Valley Mammoth	NE Yakutia	18	68°43'N, 161°35'E
7	Mongochen Mammoth	Gydan Peninsula, Mongocha-Yakha drainage basin	10	72°10'N, 79°35'E
8	Yukagir Mammoth	N Yakutia, Muksunuokha River	14	71°52'N, 140°34'E
9	Churapcha Rhinoceros	Central Yakutia, Churapcha settlement on the Lena-Amga interfluve	11	62°00'N, 132°25'E
10	Fishhook Mammoth	Taimyr Peninsula, the estuary of the Upper Taimyra River, Western Lake Taimyr	12	74°09'N, 99°35'E
11	Chekurovka Mammoth	N Yakutia, a tributary of Lena River near Chekurovka	16	71°00'N, 127°40'E
12	Yukon/Last Chance Creek Horse*	Yukon, Last Chance Creek near Dawson City	5	63°58'N, 139°07'W †
13	Mylakhchin Bison	NE Yakutia, middle Indigirka River	17	68°30'N, 146°40'E
14	Khalbugai Rhinoceros	N Yakutia, Khalbugai Creek, tributary of Bytantaj River, middle Yana River basin	15	67°45'N, 134°41'E †
15	Blue babe (bison)*	Alaska, Pearl Creek, a tributary of the Chatanika River	4	65°59'N, 147°19'W
16	Kolyma Rhinoceros	NE Yakutia, Malaya Filippova River, Lower Kolyma River basin	1	68°46'N, 161°38'E
17	Selerikan Horse	NE Yakutia, Balkhan Creek, Upper Indigirka River basin	17	64°40'N, 147°45'E
18	Kirgilyakh/ Dima Mammoth	NE Yakutia, Kirgilyakh Creek, upper part of Kolyma River basin	4	62°40'N, 147°59'E
19	Shandrin Mammoth	NE Yakutia, a right tributary of the lower Indigirka River	17	70°30'N, 151°00'E
20	Mammoth dung F-552	N Yakutia, Terekhtyakh River, Lower Indigirka River basin	7	68°32'N, 146°11'E
21	Yuribey/ Lyuba Baby Mammoth	Yamal Peninsula, a bank of the Yuribei River	9	68°38'N, 71°40'E
22	Vilyuy Rhinoceros	Central Yakutia, Vilyuy River, near the town of Vilyuysk	17	63°44'N, 121°37'E †
23	Berezovka Mammoth	NE Yakutia, Berezovka River, Kolyma River basin	17	67°10'N, 155°30'E
24	Chondon Rhinoceros	N Yakutia, middle Chondon River	6	70°12'N, 137°00'E
25	Mammoth dung F-3447	W Chukotka, Maly Anyui River	7	68°18'N, 161°44'E
26	[Bison]	NE Yakutia	18	68°44'N, 161°38'E
27	Drevniy Creek Mammoth	NE Yakutia	18	68°35'N, 161°45'E

**References:** 1: Boeskorov et al. (2011), 2: Boeskorov et al. (2014), 3: van Geel et al. (2011), 4: Guthrie (1990), 5: Harington (2002), 6: Kirillova et al. (2013), 7: Kirillova et al. (2016a), 8: Kirillova et al. (2016b), 9: Kosintsev et al. (2010), 10: Kosintsev et al. (2012), 11: Lazarev (1977), 12: Mol et al. (2001), 13: Mol et al. (2003), 14: Mol et al. (2006), 15: Tolmachoff (1929), 16: Tomskaya (2000), 17: Ukraintseva (1993), 18: Willerslev et al. (2014)

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**Table A2.** A list of well-preserved frozen carcasses of the Pleistocene and early-Holocene megaherbivores from which plant pollen/spores, microfossils or DNA found in the gastrointestinal tract were published. Note that some of the finds refer to coprolites. Fauna specimens are arranged by their radiocarbon age (for details see Table 1). Most carcasses were found in Siberia; those from Alaska and Yukon are indicated by an asterisk (see Table A1 for details on localities).

ID	Species	Nickname or [short name]	Pollen-spores	Macrofossils	DNA	(O) oral cavity (G) gastrointestinal (C) coprolite	References
1	<i>Bison priscus</i>	Rauchua Bison	x	x		G	19
2	<i>Bison priscus</i>	Yukagir Bison	x	x	x	G	19
3	<i>Mammuthus primigenius</i>	Yuribei Mammoth	x	x		G	11
4	<i>Mammuthus primigenius</i> *	Alaskan Late Glacial mammoth	x	x	x	C	12
5	<i>Rangifer tarandus</i>	[Reindeer]	x	x		G	18
6	<i>Mammuthus primigenius</i>	Finish Creek Valley Mammoth			x	C	18
7	<i>Mammuthus primigenius</i>	Mongochen Mammoth	x	x	x	G	13, 4, 19
8	<i>Mammuthus primigenius</i>	Yukagir Mammoth	x	x	x	G (C)	11
9	<i>Coelodonta antiquitatis</i>	Churapcha Rhinoceros	x		x	G	18
10	<i>Mammuthus primigenius</i>	Fishhook Mammoth	x	x		G	18
11	<i>Mammuthus primigenius</i>	Chekurovka Mammoth	x			G	18
12	<i>Equus lambei</i> *	Yukon/Last Chance Creek Horse		x	x	G	1, 19
13	<i>Bison priscus</i>	Mylakhchin Bison	x	x		G	7
14	<i>Coelodonta antiquitatis</i>	Khalbugai Rhinoceros	x			O	2
15	<i>Bison priscus</i> *	Blue Babe		x		G	18
16	<i>Coelodonta antiquitatis</i>	Kolyma Rhinoceros	x		x	G	8, 19
17	<i>Equus lenensis</i>	Selerikan Horse	x	x		G	17
18	<i>Mammuthus primigenius</i>	Kirgilyakh Mammoth (Dima)	x	x		G	16
19	<i>Mammuthus primigenius</i>	Shandrin Mammoth	x	x		G	15, 19
20	<i>Mammuthus primigenius</i>	Mammoth dung F-552	x	x		C	3
21	<i>Mammuthus primigenius</i>	Yuribey Baby Mammoth (Lyuba)	x	x	x	G	14, 19
22	<i>Coelodonta antiquitatis</i>	Vilyuy Rhinoceros		x		G	19
23	<i>Mammuthus primigenius</i>	Berezovka Mammoth	x	x		G	16
24	<i>Stephanorhinus kirchbergensis</i>	Chondon Rhinoceros		x		O	5
25	<i>Mammuthus primigenius</i>	Mammoth dung F-3447	x	x		C	18
26	<i>Bison priscus</i>	[Bison]			x	C	6
27	<i>Mammuthus primigenius</i>	Drevniy Creek Mammoth			x	C	9, 10

**References:** **1:** Boeskorov et al. (2011), **2:** Garut et al. (1970), **3:** van Geel et al. (2008), **4:** van Geel et al. (2011a), **5:** van Geel et al. (2011b), **6:** van Geel et al. (2014), **7:** Guthrie (1990), **8:** Harington (2002), **9:** Kirillova et al. (2013), **10:** Kirillova et al. (2015), **11:** Kirillova et al. (2016a), **12:** Kirillova et al. (2016b), **13:** Kosintsev et al. (2010), **14:** Kosintsev et al. (2012), **15:** Lazarev & Tirskaaya (1975), **16:** Mol et al. (2003), **17:** Tomskaya (2000), **18:** Ukraintseva (2013), **19:** Willerslev et al. (2014)

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**Table A3.** Most frequent palaeobotanical taxa recorded in the frozen fauna using pollen + spore analysis. Frequency refers to the number of carcasses in which the taxon was found.

Taxon	Species	Genus	Family	Frequency
<i>Artemisia</i>	.	<i>Artemisia</i>	Asteraceae	20
<i>Poaceae</i>	.	.	Poaceae	20
<i>Cyperaceae</i>	.	.	Cyperaceae	18
<i>Salix</i>	.	<i>Salix</i>	Salicaceae	17
<i>Caryophyllaceae</i>	.	.	Caryophyllaceae	17
<i>Ranunculaceae</i>	.	.	Ranunculaceae	14
<i>Rosaceae</i>	.	.	Rosaceae	12
<i>Asteraceae</i>	.	.	Asteraceae	12
<i>Brassicaceae</i>	.	.	Brassicaceae	11
<i>Chenopodiaceae/Amaranthaceae</i>	.	.	Amaranthaceae	11
<i>Apiaceae</i>	.	.	Apiaceae	11
<i>Betula</i>	.	<i>Betula</i>	Betulaceae	11
<i>Sphagnum</i>	.	<i>Sphagnum</i>	Sphagnaceae	10
<i>Larix</i>	.	<i>Larix</i>	Pinaceae	9
<i>Betula nana</i>	<i>Betula nana</i>	<i>Betula</i>	Betulaceae	9
<i>Ericaceae</i>	.	.	Ericaceae	8
<i>Alnus</i>	.	<i>Alnus</i>	Betulaceae	8
<i>Potentilla</i>	.	<i>Potentilla</i>	Rosaceae	8
<i>Valeriana capitata</i>	<i>Valeriana capitata</i>	<i>Valeriana</i>	Caprifoliaceae	8
<i>Polygonaceae</i>	.	.	Polygonaceae	8
<i>Fabaceae</i>	.	.	Fabaceae	8
<i>Picea</i>	.	<i>Picea</i>	Pinaceae	8
<i>Duschekia fruticosa</i>	<i>Duschekia fruticosa</i>	<i>Duschekia</i>	Betulaceae	8
<i>Polemonium</i>	.	<i>Polemonium</i>	Polemoniaceae	7
<i>Sanguisorba officinalis</i>	<i>Sanguisorba officinalis</i>	<i>Sanguisorba</i>	Rosaceae	7
<i>Equisetum</i>	.	<i>Equisetum</i>	Equisetaceae	7
<i>Ranunculus</i>	.	<i>Ranunculus</i>	Ranunculaceae	7
<i>Selaginella rupestris</i>	<i>Selaginella rupestris</i>	<i>Selaginella</i>	Selaginellaceae	7
<i>Polypodiaceae</i>	.	.	Polypodiaceae	7
<i>Pinus</i>	.	<i>Pinus</i>	Pinaceae	6
<i>Alnus hirsuta</i>	<i>Alnus hirsuta</i>	<i>Alnus</i>	Betulaceae	6
<i>Saxifraga</i>	.	<i>Saxifraga</i>	Saxifragaceae	6
<i>Papaver</i>	.	<i>Papaver</i>	Papaveraceae	6
<i>Pinus sibirica</i>	<i>Pinus sibirica</i>	<i>Pinus</i>	Pinaceae	6

**Table A3.** Continuation.

Taxon	Species	Genus	Family	Frequency
<i>Pinus pumila</i>	<i>Pinus pumila</i>	<i>Pinus</i>	Pinaceae	6
<i>Valeriana</i>	.	<i>Valeriana</i>	Caprifoliaceae	5
<i>Liliaceae</i>	.	.	Liliaceae	5
<i>Stellaria</i>	.	<i>Stellaria</i>	Caryophyllaceae	5
<i>Polemonium boreale</i>	<i>Polemonium boreale</i>	<i>Polemonium</i>	Polemoniaceae	5
<i>Rumex acetosa</i>	<i>Rumex acetosa</i>	<i>Rumex</i>	Polygonaceae	5
<i>Cichorioideae</i>	.	.	Asteraceae	5
<i>Lycopodium</i>	.	<i>Lycopodium</i>	Lycopodiaceae	5
<i>Plantago</i>	.	<i>Plantago</i>	Plantaginaceae	5
<i>Carex</i>	.	<i>Carex</i>	Cyperaceae	5
<i>Bistorta vivipara</i>	<i>Bistorta vivipara</i>	<i>Bistorta</i>	Polygonaceae	5
<i>Betula humilis</i>	<i>Betula humilis</i>	<i>Betula</i>	Betulaceae	5
<i>Pinus sylvestris</i>	<i>Pinus sylvestris</i>	<i>Pinus</i>	Pinaceae	5

**Table A4.** Most frequent palaeobotanical taxa recorded in the frozen fauna using macrofossil analysis. Frequency refers to the number of carcasses in which the taxon was found.

Taxon	Species	Genus	Family	Frequency
<i>Poaceae</i>	.	.	Poaceae	18
<i>Carex</i>	.	<i>Carex</i>	Cyperaceae	15
<i>Salix</i>	.	<i>Salix</i>	Salicaceae	15
<i>Cyperaceae</i>	.	.	Cyperaceae	12
<i>Betula</i>	.	<i>Betula</i>	Betulaceae	8
<i>Poa</i>	.	<i>Poa</i>	Poaceae	8
<i>Alnus</i>	.	<i>Alnus</i>	Betulaceae	7
<i>Caryophyllaceae</i>	.	.	Caryophyllaceae	7
<i>Polytrichum</i>	.	<i>Polytrichum</i>	Polytrichaceae	7
<i>Betula nana</i>	<i>Betula nana</i>	<i>Betula</i>	Betulaceae	6
<i>Festuca</i>	<i>Festuca</i>	<i>Festuca</i>	Poaceae	6
<i>Larix</i>	.	<i>Larix</i>	Pinaceae	6
<i>Sphagnum</i>	.	<i>Sphagnum</i>	Sphagnaceae	6
<i>Comarum palustre</i>	<i>Comarum palustre</i>	<i>Comarum</i>	Rosaceae	5
<i>Brassicaceae</i>	.	.	Brassicaceae	5
<i>Duschekia fruticosa</i>	<i>Duschekia fruticosa</i>	<i>Duschekia</i>	Betulaceae	5
<i>Ericaceae</i>	.	.	Ericaceae	5
<i>Eriophorum</i>	.	<i>Eriophorum</i>	Cyperaceae	5
<i>Potentilla</i>	.	<i>Potentilla</i>	Rosaceae	5

**Table A5.** Validation of the new method of the similarity-based sample assignment to vegetation type. We tested if the current vegetation plot of a given vegetation type will be most similar to this original vegetation type or another one. The values in the matrix are counts of plots originally assigned to a vegetation type (rows) that were most similar to the tested vegetation types (columns) or vegetation type groups (colours). Numbers on the diagonal indicate plots correctly assigned to the same vegetation type.

			Tested vegetation types: number of plots which were most similar to the given vegetation type																							Plots classified correctly to the original type [%]	
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23		
Original expert classification of plots	Number of plots (original assignment)		Blackish taiga	Hemiboreal forest	Taiga	Alluvial forest and scrub	Fen and swamp woodland	Bog	Open fen	Arctic or alpine deciduous scrub	Arctic or alpine heathland	Tundra grassland	<i>Betula nana</i> s.l. scrub	Tall forbs	Saline grassland	Marsh	Wet meadow	Mesic meadow	Dry meadow	Steppe scrub	Meadow-steppe	Dry steppe	Desert steppe	Semi-desert	Desert		
	1	Blackish taiga	75	59	12	1	3																			78.7	78.7
	2	Hemiboreal forest	278	8	229	12	3						3						1	1	7	11	3			82.4	86.1
	3	Taiga	204	5	65	111	4	2			10	1	6													54.4	
	4	Alluvial forest and scrub	41	3	14	1	18	2								1				2						43.9	
	5	Fen and swamp woodland	51	2	11	13	9	2	10	1		1						2								3.9	
	6	Bog	65		1	7			35	1	1	16	4													53.8	56.0
	7	Open fen	117			1	3	7	8	58	11	17	2	4			2	4								49.6	
	8	Arctic or alpine decid. scrub	42	1	1	1	1			2	20	6	2	5	1			2								47.6	79.2
	9	Arctic or alpine heathland	93		1	2		1	2	1		76	2	8												81.7	
	10	Tundra grassland	114		2	3				5	2	28	57	7	1			5				3	1			50.0	
	11	<i>Betula nana</i> s.l. scrub	54		5	7					2	8	7	25												46.3	
	12	Tall forbs	38	6	6	3	5						3		10				4							26.3	
	13	Saline grassland	212		1		1	1					3			110		13	7	53		5	7		11	51.9	51.9
	14	Marsh	217		1		19	22		1						2	132	40								60.8	60.8
	15	Wet meadow	223	1	20		12	3		2	5	1	7			2	5	152	3	5		5				68.2	64.9
	16	Mesic meadow	76		5								3			1		9	30	18		9	1			39.5	
	17	Dry meadow	88		2							1						5	3	56		21				63.6	92.4
	18	Steppe scrub	75		11								1								6	30	27			8.0	
	19	Meadow-steppe	267		20								5	1				1	3	24	1	176	36			65.9	
	20	Dry steppe	416		4		7						2							26	3	85	287	2		69.0	
	21	Desert steppe	50																			1	42	5		10.0	
	22	Semi-desert	17		1		1									1						2	2	8	1	0.0	32.6
	23	Desert	26																				6	9		42.3	