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**Palaeodistribution modelling of European vegetation types at the Last Glacial
Maximum using modern analogues from Siberia: prospects and limitations**

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Abstract

We modelled the European distribution of vegetation types at the Last Glacial Maximum (LGM) using present-day data from Siberia, a region hypothesized to be a modern analogue of European glacial climate. Distribution models were calibrated with current climate using 6274 vegetation-plot records surveyed recently in Siberia. Out of 22 initially used vegetation types, good models in terms of statistical validation and expert-based evaluation were computed for 18 types, which were then projected to European climate at the LGM. The resulting distributions were generally coincident with the reconstructions based on pollen records and dynamic vegetation models. Spatial predictions were most reliable for steppe, forest-steppe, taiga, tundra, fens and bogs in eastern and central Europe, which had LGM climate more similar to present-day Siberia. The models for western and southern Europe, regions with a lower climatic analogy, were only reliable for mires and steppe vegetation, respectively. Modelling LGM vegetation types for these wetter and warmer regions of Europe would require gathering calibration data from outside Siberia. Our approach adds a value to the reconstruction of vegetation at the LGM, which is limited by scarcity of pollen and macrofossil data, suggesting where specific habitats could have occurred. Despite the uncertainties of climatic extrapolations and the difficulty of validating the projections for specific vegetation types, the integration of palaeodistribution modelling with other approaches has a great potential for improving our understanding of biodiversity patterns during the LGM.

Keywords: Europe, Last Glacial Maximum; modern analogues; palaeoecological reconstructions; Siberia; Species Distribution Modelling

1. Introduction

The Last Glacial Maximum (LGM, ca. 26.5–19 ka BP) was the peak of the last glacial period in the Late Pleistocene when ice sheets were at their maximum extension (Clark et al., 2009). The cold and dry conditions that characterized the LGM in North America and Europe and low concentrations of atmospheric CO₂ (Petit et al., 1999; Otto-Bliesner et al., 2006) strongly restricted the distribution ranges of many species, creating a biogeographic bottleneck with fundamental impact on the present-day distribution of flora and fauna (Newnham et al., 2013; Tzedakis et al., 2013). Our knowledge about the climatic conditions and the vegetation that dominated temperate regions during the LGM in the northern hemisphere is still limited, but new data are continuously giving new insights to understand vegetation in this critical period (Binney et al., 2017).

Reconstructing palaeoclimate and palaeovegetation for the Quaternary has been traditionally approached by analyzing pollen and macrofossil records (Prentice et al., 2000; Bartlein et al., 2011; Feurdean et al., 2014). However these data are geographically sparse for the LGM period and restricted to specific sites (Binney et al., 2017). Pollen and macrofossil records are mainly informative for landscape-scale reconstructions around one site, but they are insufficient for reconstructing spatial patterns of different vegetation types across broader areas (Huntley and Allen, 2003). Low taxonomic resolution of pollen records (Klerk and Joosten, 2007) coupled with uncertainties related to large variation in pollen productivity and pollen dispersal capacity among species, makes it very difficult to reconstruct the distribution of vegetation at broad spatial scales (Gaillard et al., 2008, but see Sugita 2007).

A complement to palaeobotanical data is the use of dynamic vegetation models,

which are based on the relationships between palaeoclimatic reconstructions, biogeochemistry, hydrology and vegetation formations described through plant functional types (e.g. Allen et al., 2010). These models provide spatially-explicit information about the distribution and productivity of physiognomic vegetation types, most often across large areas such as continents and at a coarse resolution of hundreds to thousands km (Smith et al., 2001). These models are useful for inferring temporal changes in dominant ecosystems and related properties (e.g. productivity), but their applicability for understanding biogeographic patterns is limited due to the coarse nature of the vegetation types used, like biomes, formations or dominant functional types.

Another approach to reconstructing palaeoecological patterns is palaeodistribution modelling (PDM), which assumes the existence of links between species or groups of species and the environment (Svenning et al., 2011, Varela et al., 2011; Franklin et al., 2015). These methods have been proposed for hindcasting the distribution of species by combining present-day data and palaeoclimatic scenarios (Nogués-Bravo, 2009). For example, PDM have provided important insights to understanding the LGM distribution of tree species, suggesting that the general view of central Europe as a treeless landscape should be partly revised (Svenning et al., 2008). Recent modelling studies focusing on individual vegetation types also have suggested the potential of these tools for reconstructing regional habitats in the late Quaternary (Werneck et al., 2011; Potts et al., 2013; Hais et al., 2015). These models are generally calibrated with data on the distribution of vegetation or habitat types defined by species composition or dominant species (Potts et al., 2013). PDM is a promising approach for understanding past distributions of vegetation types that are defined more finely than by dominant plant

functional types or biomes. However, it is still rarely applied and needs further development at continental scales and with better spatial resolution (Franklin et al., 2015).

In this study, we use PDM to hindcast the distribution of vegetation types in Europe at the LGM using present-day vegetation data from Siberia. It has been suggested that the European LGM climate has a large overlap with the present-day climate of Siberia (Fløjgaard et al., 2009). There is also biological evidence indicating ecological similarities between present-day Siberia and European regions during the LGM (Kuneš et al., 2008; Meng 2009; Pelánková and Chytrý, 2009; Horsák et al., 2010, 2015; Magyari et al., 2014; Pavelková Řičánková et al., 2014, 2015). Although these studies suggest that, to a certain degree, present-day Siberian vegetation can be used as a model for understanding European vegetation during the LGM, the climatic analogy between the two periods and regions has not been evaluated yet. Indeed, to our knowledge this is the first attempt at applying PDM to vegetation types that could have occurred during the LGM across the whole European continent. The lack of previous studies is probably due to the difficulty of gathering occurrence data (i.e. present-day distribution of cold- and drought-adapted vegetation types) from areas with a certain similarity to the LGM climates, according to the general assumptions of PDM (Svenning et al., 2011).

We used vegetation-plot data surveyed in the field in Siberia and classified them into finely-defined vegetation types which distribution is probably driven by climate. We calibrated distribution models for these vegetation types under current climatic conditions in Siberia, and projected the models with a good performance to the climatic conditions in LGM Europe. The reliability of the models was then assessed for different European regions by reviewing the existing literature on palaeovegetation reconstructions based on

fossil data and dynamic vegetation models. By considering the uncertainties related to PDM and the assumed similarities in climate and vegetation between the two study regions and periods, we finally discuss the prospects and limitations of PDM for reconstructing European vegetation during the LGM using modern analogues from present-day Siberia.

2. Materials and methods

2.1 Study areas

Siberia occupies an area of 9141 km² in the Russian Federation, stretching from the Ural Mountains in the west to the Yablonovyi and Cherskii Range in the east, excluding the Russian Far East (Fig. 1). This region encompasses a broad range of natural conditions, comprising extensive plains, elevated plateaux as well as high mountains. The climate is extremely continental with low winter temperatures throughout the whole region and strong aridity in some areas in the south (Shahgedanova, 2002). According to climatic models (Hijmans et al., 2005), mean July temperature varies between 5 °C in the north and 21 °C in the south, while mean January temperature commonly drops below –20 °C, and in the northeast even below –35 °C. Annual precipitation for most of the region ranges between 150 mm to 700 mm, with a precipitation peak in summer.

LGM Europe corresponds to the extent of Europe during the Last Glacial Maximum (8053 km², Fig. 2), considering a decrease in the sea level of 120 m (Peltier, 1994; Yokoyama et al., 2001) and excluding the continental ice-sheet and mountain glaciers (Ehlers and Gibbard, 2004). LGM Europe was characterized by a strong thermal north-south gradient which was strongest in winter (Frenzel, 1992). Mean July temperatures

probably ranged from 0 °C in the very north and in the areas adjacent to the ice-sheets, to approximately 20 °C in southern Europe. Mean January temperatures varied between –40 °C in northern Europe and 0 °C in the Mediterranean (Frenzel, 1992; Pollard and Barron, 2003). According to the Community Climate Model System (Gent et al., 2011), annual precipitation showed a strong west-east gradient, being about 1000 mm in western Europe, 500–750 mm in central Europe and 250–500 mm in eastern Europe.

2.2 Vegetation data

Vegetation data were surveyed in the field by recording full species lists of vascular plants in relatively small areas (vegetation plots). Unlike interpreted satellite images or broad-scale vegetation maps, these data make it possible to reliably distinguish different vegetation types that are expected to be largely driven by environmental conditions, especially climate. Vegetation-plot data came from two sources: (1) the Database of Masaryk University's Vegetation Research in Siberia (Chytrý, 2012; GIVD code 00-RU-002, see www.givd.info), sampled from 2003 to 2013 and containing about 1550 vegetation-plot records with GPS coordinates from the Southern Urals, West Siberian Plain, Altai-Sayan Mountains and central Yakutia; and (2) the Database of Siberian Vegetation (Korolyuk and Zverev, 2012; GIVD code AS-RU-002) and related private databases, containing vegetation-plot records from the most temperate areas of Siberia with GPS coordinates.

The records selected from these databases, most of them sampled in plots of 100 m² in size, were classified into vegetation types based on expert knowledge and existing literature (Supplementary Appendix S3). Vegetation types represented by less than 30 plots were excluded to avoid model errors due to low sample size (Wisniewski et al., 2008). A

total of 6274 vegetation-plot records assigned to 22 vegetation types were used as occurrence records for computing the models (Fig. 1; Table 1).

2.3 Climatic analogies

To assess the extent of the climatic analogy between the two study areas, we used ArcGIS 10.2 (ESRI, Redlands, CA) to identify those areas of LGM Europe that fell within the range of present-day Siberian climate, as suggested by Fløjgaard et al. (2009). We created Individual maps (Supplementary Appendix S1) for six bioclimatic variables selected from WorldClim (see section 2.3) and then intersected them to create a synthetic map reflecting the analogy between Siberia and LGM Europe. Additionally, we tested how the calibration data fit with the most analog regions between the two studied periods. We plotted the climatic envelope of present-day Siberia and LGM Europe using annual mean temperature and annual precipitation extracted from a random selection of 10,000 points within each period; and plotted the values corresponding to the 6 274 sampling points.

2.4 Model calibration in Siberia

We computed distribution models for the 22 vegetation types using climate of present-day Siberia as provided by bioclimatic variables in WorldClim (www.worldclim.org; Hijmans et al., 2005). These variables are interpolated from average monthly climate data from weather stations for the period 1950–2000 and have a spatial resolution of 2.5 arc-minutes (. Since using correlated variables may reduce model predictive ability (Svenning et al., 2011) and confuse model interpretation (Baldwin, 2009), we screened the variables for multicollinearity by generating 10 000 random points across Siberia to extract cell values for all the variables. If for a pair of variables Pearson correlation coefficient (r) was higher than 0.7, only one of them with a supposed higher probability of causal relationship

with plant diversity was retained. At the end, six bioclimatic variables were selected (Table 2).

Vegetation records and environmental data were used to calibrate distribution models of the pre-defined vegetation types in MaxEnt V.3.3.3k (Phillips and Dudík 2008). We selected this machine-learning method because it generally performs well under different scenarios when only presence data are available and sample sizes are small (Elith et al., 2006; Wisz et al., 2008). We used the default parameterization of the “auto-feature” option in MaxEnt. This option determines the use of all feature types (mathematical transformation of the predictors) for sample sizes > 80, but only linear, quadratic and hinge features for sample sizes between 15 and 79, thus reducing model complexity (Moreno-Amat et al., 2015). The “regularization multiplier” was not modified because it is not clear whether it reduces overfitting and improves performance (Baldwin 2009). Since the occurrence records from Siberia are spatially biased towards western and southern Siberia, we corrected for this bias by manipulating the background points in MaxEnt (Radosavljevic and Anderson 2014). As recommended by Franklin (2009) and Elith et al. (2011), all the occurrence points available in the data set were used as the background points. Preliminary models computed with default background points (i.e. covering the whole study area) revealed high overfitting and much less predictive value, thus supporting this procedure as a good alternative to reduce the effect of sampling bias.

Models were evaluated using five-fold cross-validation which randomly splits the data into five equal-sized groups. In each step of the cross-validation procedure, four groups were used to build the model and the remaining one is used for model validation. Model evaluation was based on three statistical metrics following Radosavljevic and Anderson

(2014) and Muscarella et al. (2014): (1) The Area Under a ROC Curve (AUC) for assessing the probability that the model scores a presence site higher than a random site from the study area (Phillips et al., 2009); (2) AUC_{DIFF} as the difference between training and testing AUC to quantify overfitting, i.e. creating clusters around occurrence points (Baldwin, 2009); the higher is the difference, the higher overfitting and the higher loss of performance; and (3) test omission rate, a metric measuring a proportion of testing presences that fall into unsuitable area (Phillips et al., 2009) after conversion of the continuous output into binary (presence-absence) predictions using the “equal training sensitivity and specificity” threshold provided. The models were then classified as reliable (moderate or good) or not reliable (bad) according to the evaluation metrics and also the expert judgement of the authors, taking into account the land-cover map of Stolbovoi and McCallum (2002) and regional literature on plant diversity.

2.5 Model projections to LGM Europe

The models computed for each vegetation type in Siberia were projected to LGM Europe using MaxEnt. Although some palaeoecological modelling studies use a combination of projections by combining different modelling methods, we used only MaxEnt because (i) the small number of records of some vegetation types make them difficult to model with other methods (e.g. GLM), (ii) the ecological interpretation of the models for present-day Siberia and the projections for LGM Europe is better compared if they are based on the same algorithm, and (iii) the reliability of the resulting models and their inconsistencies are difficult to assess when they are based on a combination of different techniques. Only vegetation types that showed a good or very good performance in present-day Siberia were used for projections to the LGM. The same bioclimatic

variables as used for Siberia were used for LGM Europe, taken from the Community Climate System Model (CCSM4; <http://www.cesm.ucar.edu/models/ccsm4.0/>) as provided by WorldClim. We also used other climate models for the LGM Europe (e.g. MIROC), but the results did not differ in terms of spatial patterns and model parameters, therefore we present the results for CCSM4 only. Assuming that environmental conditions in some parts of LGM Europe could fall beyond the range of the values of the current climate in Siberia, MaxEnt was set to perform the “clamping” procedure which holds variables to the maximum or minimum values of the training range and removes the most clamped (non-analogous) pixels from the final predictions (Phillips et al., 2009).

3. Results

3.1 Climatic analogies

The number of climatic variables in LGM Europe that fall within the range of climatic variables in present-day Siberia was high in northern, eastern and central Europe (Fig. 2). These areas can be considered as the best climatic analogues. By contrast, lower similarity was found for western Europe, the area alongside 45 °N and the Mediterranean basin. When testing the opposite pattern, i.e. which areas of present-day Siberia cover the climatic variation of LGM Europe, we found that most of Siberia is analogue to the range of 5 or 6 variables (Supplementary Appendix S2). This suggests that the climatic variation in LGM Europe was much higher than it is in present-day Siberia.

The distribution of sampling points in the environmental space (Fig. 3) also reflects a partial analogy between the two study areas. Although some parts of LGM Europe were warmer and moister or, conversely, cooler and drier than present-day Siberia, many regions of present-day Siberia overlap with LGM Europe. Moreover, the vegetation plots

were mainly sampled in the most temperate regions of Siberia and the driest regions of LGM Europe, where the climate of the two study areas overlaps.

3.2 Models for present-day Siberia

Statistical validation suggested good model performance in most cases (Table 3). AUC ranged from 0.710 to 0.984 and overfitting rate (AUC_{DIFF}) ranged from 0.003 to 0.091, indicating that all models were characterized by a good or very good fit. However, values of omission rate, indicating the proportion of testing false negatives under a given threshold, exhibited a large variance (4–43%). The vegetation types with higher omission rates showed in general lower AUC values and higher overfitting than the rest of the models. Accordingly, the models for marshes (*e*), temperate deciduous forests (*n*) and temperate grasslands (*o–p*) were further considered as not reliable (bad) and were not used for projections to LGM Europe. The models for the other 18 vegetation types were considered reliable (7 moderate, 11 good), thus reflecting their distribution according to the current botanical knowledge in Siberia.

Variable contribution (Table 4) suggested annual mean temperature as the most relevant variable, in non-arctic regions together with precipitation seasonality. However, halophytic vegetation types were almost exclusively influenced by annual mean temperature and annual precipitation. Arctic and alpine vegetation types were modelled in northern Siberia and at high altitudes of more southerly located mountain systems, especially the Altai (Fig. 4, *a–d*). Marshes (*e*) were mainly predicted in central and eastern parts of the study area. Modelled distributions of ombrotrophic bogs (*f*) and minerotrophic fens (*g*) were similar to the arctic and alpine vegetation types although they stretched to the south. Models for peatland (*h*), dark-coniferous boreal (*i*) and *Pinus sylvestris* boreal

(j) forests assigned the highest values of suitability to the western Siberian boreal zone. By contrast, *Larix* boreal forest (k) was predicted to occur mainly in eastern Siberia and the forest-tundra zone, although it was also predicted in the Arctic tundra zone. South of the boreal forests, a mixture of hemiboreal forests (l), temperate forests (m–n), wet meadows (o) and meadow steppes (p) was predicted. Typical steppes (q), shrubby steppes (r) and halophytic vegetation (s–v) were modelled in the southernmost parts of Siberia. Typical steppes (q) and wet saline grasslands (s) were also predicted to occur in the easternmost parts of the study area.

3.3 Projections for LGM Europe

The 18 vegetation types projected to LGM Europe were in most cases hindcasted for a small fraction of the continent. Arctic and alpine heathland (Fig. 5, a) and scrub (b–c) were only predicted in the coldest regions, i.e. in the northernmost parts of the Russian Plain and in the regions immediately adjoining the eastern flank of the Scandinavian ice sheet. In contrast, the distribution of arctic or alpine tall-forb vegetation (d) was predicted in southern Europe and north of the Carpathians. Mires and fens (f–g) extended to the surrounding lowlands and also to western Europe, while peatland forest (h) was modelled as the most widespread vegetation type in central and northern Europe in a wide continuous belt along approximately 50° N parallel. Other boreal forest types (i–k) were projected to occur north and east of the Carpathians, whereas no region of Europe was climatically suitable for hemiboreal forests (l). Relatively lower quality of the Siberian model for temperate light-coniferous forest (m) was reflected also in its projection to LGM Europe, where small patches of suitable habitat were mapped throughout the continent. The distribution of steppe vegetation (q–r) was modelled for the western, central, southern

and southeastern parts of Europe, with typical steppe (*q*) attaining the widest predicted distribution. Finally, halophytic vegetation types (*s–v*) had a predicted centre of distribution in the south of the Russian Plain.

4. Discussion

4.1 LGM vegetation in eastern Europe

Our palaeovegetation models for eastern Europe at the LGM suggest a north-south gradient represented by tundra, forest-tundra, boreal forest, forest-steppe and steppe vegetation, analogous to present-day vegetation patterns in Siberia (Stolbovoi & McCallum, 2002). Above 60° N, the most widespread LGM vegetation types were related to arctic heathlands *Betula nana* scrub and deciduous scrub (Fig. 5). These patterns are in accordance with Simakova (2006), who suggested shrubby tundra interconnected with forest tundra in the Russian Plain north of 56° N during the LGM; although our models restricted tundra vegetation types to the northernmost areas. For the same regions we also predicted minerotrophic fens and to a small extent ombrotrophic bogs. Pollen records from mires are rarely dated to the LGM in northern Eurasia (Binney et al., 2017), but these vegetation types, and especially fens, are currently widely distributed in the arctic zones (Gajewski et al., 2001) suggesting that they could also occur in the arctic biomes of LGM Europe.

Between 50° and 60° N, the projections for the LGM predicted almost exclusively boreal forest ecosystems – *Pinus sylvestris* and *Larix taiga*, dark-coniferous forest and also peatland forests – gradually transitioning to tundra in the north and steppe in the south. This pattern is highly consistent with the reconstructions made for the areas north of 50° N by Granoszewski (1998), Mamakowa (2003) and Simakova (2006), who

suggested the existence of tundra-forest-steppe ecosystems with *Pinus*, *Betula* and *Picea* in central Russia, Belarus and Poland. Our models also predicted high climatic suitability for *Larix* boreal forest in the southeastern Russian Plain, suggesting the presence of open woodlands during the LGM. Although *Larix* is a poor pollen producer that may be undetected in pollen analysis (Pelánková & Chytrý, 2009), it is supposed to have occurred on the Russian Plain during the LGM (Simakova, 2006). Our results indicate that *Larix* boreal forests and *Pinus sylvestris* boreal forests may have the most common vegetation types there. Pollen data also confirm the LGM occurrence of *Larix* more to the southwest, e.g. in the Carpathians and the Pannonian Basin (Magyari et al., 2014, Jankovská and Pokorný, 2015). Nevertheless, in this case our results suggest that these occurrences had a character of temperate light-coniferous forest (predicted e.g. for some parts of Ukraine) rather than of boreal forest.

An interesting model output was the projection of dark-coniferous boreal forests associated with tall-forb vegetation in Belarus and adjacent regions. The combination of these two vegetation types suggests relatively moist conditions, which can be due to relatively high precipitation. Indeed, it has been suggested that this region contained the LGM refugium of *Picea* (Latałowa and van der Knaap, 2006, Tollefsrud et al., 2008), one of the dominant trees of dark-coniferous taiga. Rather surprising result is the predicted occurrence of peatland forest across a broad belt from the southern Urals to central Europe. Although fossil peat from the LGM is generally absent in this region and *Sphagnum* records are rare (Binney et al., 2017), *Pinus sylvestris* (*Pinus Diploxylon* type, the dominant species of peatland forests in western Siberia) is documented from the LGM in this region (Lapshina, 2010). Distribution of peatland forests can be overestimated by

the models, because they do not account for the differences in the CO₂ concentrations between the LGM and the present. Under the low-CO₂ atmosphere of the LGM (Monin et al., 2001), relatively moist sites could have been covered by more drought-adapted vegetation than would be the case under current CO₂ levels. If peatland forests occurred during the LGM in eastern and central Europe, they probably did not form deep peat layers, explaining the absence of fossil records.

The areas of Eastern Europe south of 55° N have been traditionally interpreted as a vast mammoth steppe in the LGM (e.g. Frenzel, 1992; Grichuk, 1992). Our results support this view, projecting typical and shrubby steppes in the southern part of the Russian Plain, similarly to previous reconstructions (Frenzel, 1992; Grichuk, 1992; Tarasov et al., 2000; Simakova, 2006). However, our models also predict the occurrence of steppes more restricted to the south than suggested by pollen data (Simakova, 2006), with a climatic preference of peatland forests above 47° N. We note that we could not model meadow steppes because of a poor performance of this vegetation type in models for Siberia; European meadow steppes currently occur north of typical steppes (Bohn et al. 2000-2003), thus it is probable that they were widespread at middle latitudes also in the LGM. A more northern distribution of steppes in LGM is also supported by the range of occurrence of loess (Haase et al. 2007). In the south and especially southeast of the Russian Plain, the climatic conditions of the LGM also may have been favourable for halophytic communities, which may have been supported by high evaporation and limited soil leaching under dry climate. Finally, the presence of tundra-like vegetation and especially typical steppes between 40° and 45° N agrees with fossil evidence from Bulgaria (Feurdean et al. 2014).

4.2 LGM vegetation in central Europe

Present-day ecosystems of southern Siberia have been considered similar to those occurring in central Europe during the LGM (Kuneš et al., 2008; Horsák et al., 2010, 2015; Magyari et al., 2014). Our results support that during the LGM the regions adjoining the Scandinavian ice-sheet and non-glaciated parts of the Alps and the Carpathians were suitable for treeless arctic scrub and herbaceous vegetation, including some minerotrophic fens, which may have been similar to the current fens of western Siberia (Lapshina 2010, Peterka et al., 2017). In contrast, lowlands of the southern part of central Europe, especially in the Pannonian Basin, were probably suitable for steppe vegetation.

The issue of central European Late Pleistocene vegetation has been intensively discussed in the last years, with a general trend towards the acceptance of a steppe-tundra-woodland mosaic rather than an entirely treeless landscape (e.g. Willis and van Andel, 2004; Birks and Willis, 2008). Some authors (e.g. Huntley and Birks, 1983; Grichuk, 1992; Jankovská and Pokorný, 2008; Kuneš et al., 2008) even regard the Carpathian arc as one of the most important glacial refugia of forests with *Betula*, *Pinus*, *Larix* and *Picea*, as it has been supported by charcoal and pollen records (Willis and van Andel, 2004; Magyari et al., 2014) and the occurrence of woodland species of molluscs (Juříčková et al., 2014). Our results also support this view as they revealed suitable climatic conditions for *Betula pubescens*-*Pinus sylvestris* peatland forests in the Carpathian arc. This forest type could occur on valley bottoms, but hardly on slopes where microrefugia of the other forests could have occurred. However, it is possible that also in central Europe the models overemphasized distribution of peatland forests because the differences between LGM and present CO₂ atmospheric concentrations were not accounted for.

Our results proposed very restricted distribution of shrubby tundra with *Betula nana* s.l. in central and eastern Europe. Currently this vegetation is typical of the Low Arctic (see zone E of the Arctic Vegetation Map; Walker et al. 2005), but the dwarf birches from this group also dominate mountain tundras in southern Siberia (Meusel et al. 1965; Sedel'nikov, 1988). Continuous presence of *Betula nana* throughout the LGM is reported from the Krkonoše Mountains on the Czech-Polish border (Engel et al. 2010) and it is also reported from periods before and after the LGM from the Slovak western Carpathians (Jankovská & Pokorný 2008) and Carpathian foothills in Poland (Harmala 1995). Nevertheless pollen-based models (Binney et al. 2017) suggest that tundra scrub spread only after LGM, whereas LGM tundra was dominated by herbaceous plants.

4.3 LGM vegetation in western Europe

Our results suggest that typical steppes and to a lesser extent also shrubby steppes could have been widespread in western Europe during the LGM. Similar patterns were also predicted for related functional types using dynamic vegetation models at coarse spatial resolution (Allen et al., 2010). However, the general view of the pollen-based reconstructions for the LGM in western Europe indicates a predominance of oceanic and suboceanic tundra, only towards the Alps possibly turning into steppe (Frenzel, 1992; Grichuk, 1992; Binney et al. 2017). The estimated extent of steppe versus tundra fundamentally depends on the amount of precipitation assumed by the climatic models for the LGM. Indeed, the climatic reconstructions of western Europe are generally subject to uncertainties when using dynamic vegetation models (Kageyama et al., 2008). Given the weak analogy of this region with the current climatic conditions of Siberia, where oceanic or suboceanic vegetation types are absent, the projections for steppe vegetation

in western Europe should be interpreted with caution.

The results for the LGM also suggest the occurrence of ombrotrophic bogs in western Europe, a vegetation type that depends on atmospheric water saturation in both oceanic and continental cold climates. This region is supposed to have been the main refugium of European peatlands during the LGM (MacDonald et al. 2006). Indeed, there are dated pollen sequences of peat deposits in northwestern Iberia that span the whole glacial period (Gómez-Orellana et al. 2007). Although many of these deposits have not been preserved, they are relatively common along the Atlantic coastlines of the Iberian Peninsula (Ramil-Rego, pers. com.), giving evidence for the occurrence of bogs in southwestern Europe during the LGM. These bogs were probably spatially fragmented and mixed with other vegetation types including microrefugia for temperate forests (Gómez-Orellana et al. 2013). In northwestern Europe, the small amounts of tree pollen found have always been considered to be blown from more southerly areas, but peatland forests with *Pinus sylvestris* may have existed at favourable sites (Steward and Lister 2001). This hypothesis is supported by the modeled distribution of peatland forest, predicting suitable habitats on the British Isles and in the Benelux countries (Fig. 5), which may have occurred along the margins of ice sheets.

4.4 LGM vegetation in southern Europe

Our results suggest that during the LGM large areas of southern Europe were covered by steppes (Fig. 5 q-s), especially in the central, southern and eastern parts of the Iberian Peninsula, in the northern Adriatic region and in the Balkans. This largely agrees with the traditional view of southern Europe as a territory dominated by steppes in the LGM, together with scattered trees forming open woodlands (Finlayson & Carrión 2007). The

models were also able to discriminate the central part of the Iberian Peninsula (with predominance of steppe vegetation) from the warm and suboceanic areas of northwestern Iberia, a region serving as a refuge for deciduous forests (Carrión et al. 2010). Precipitation-rich areas of both northwestern Iberia and southern mountain systems may also have supported patches of mires on elevated plateaux, although they were probably isolated in small areas from which they expanded in the late glacial (Gómez-Orellana et al. 2013). Conversely, inland halophytic vegetation may have been mingled with steppes in dry environments of the eastern parts of the Iberian and Italian peninsulas.

The existence of trees in southern Europe, supported by warm temperatures, high precipitation, absence of permafrost and topographic heterogeneity (Birks and Willis, 2008) was partially supported by the prediction of temperate light-coniferous forests in elevated and relatively humid regions of the southwestern Iberian Peninsula and southern Greece. The presence of these open (mainly pine-dominated) forests in the LGM supports the view of southern European lower mountains as forest-steppe landscapes with patches of coniferous woodlands between 400 and 800 m.a.s.l. (e.g. Bennett et al., 1991; Frenzel, 1992; Grichuk, 1992; Tzedakis et al., 2002). Our models did not suggest occurrence of tundra at high altitudes, although this vegetation type is supposed to have occurred above the forest belt in southern Europe (van der Hammen, 1971; Birks and Willis, 2008). This inconsistency suggests that the climatic envelope of the tundra vegetation types that we sampled in present-day Siberia was not represented in southern Europe during the LGM. The low degree of climatic analogy for southern Europe (Fig. 2) seems to be insufficient to extrapolate the distribution models for tundra vegetation, and

probably also for boreal coniferous forests. Moreover, it should be noted that the broad-leaved deciduous forests dominated by *Quercus*, *Carpinus* or *Fagus*, which occupied the southernmost regions of the European peninsulas at the LGM (Grichuk, 1992; Huntley and Allen, 2003), were not approached in this study, since analogous forests do not occur in Siberia.

4.5 Prospects and limitations for reconstructing European glacial vegetation using modern analogues from Siberia

This study attempted to understand the ecosystems of Europe during the LGM using palaeodistribution modelling (PDM) under the assumption of analogy in climate and vegetation. Our results indicate that the degree of climatic analogy between current Siberian and LGM European environments is high for eastern and central Europe but much lower for southern and western Europe (Fig. 2). This fact is also supported by biotic evidence of the widespread occurrence of central European glacial relict species in Siberia (Horsák et al. 2015). Similarly, the vegetation data compiled from Siberia corresponds well to the most analog climatic regions between the two study periods (Fig. 3), supporting the appropriateness of the study areas to investigate links with the LGM in Europe. While we show potential distributions of 18 vegetation types from Siberia that could have occurred in Europe during the LGM, these vegetation types had partly or entirely different species composition, though containing species groups with similar ecological requirements (Magyari et al., 2014; Horsák et al., 2015). In general, the comparison of our results with palaeoecological studies suggests reliable LGM projections for many vegetation types, but either spatially incomplete or too broad predictions for other types.

We highlight the uncertainties of PDM when projected to past scenarios that cannot be validated with occurrence data (Svenning et al. 2011). In this study, model validation using pollen and fossil record was not possible because the record for the LGM is scarce. This contrasts with other periods of the late quaternary (e.g. the middle Holocene) for which pollen records are more frequent and therefore suitable for validation (Moreno-Amat et al. 2015). Nevertheless, in many cases paleobotanical records cannot be used for inferring finely-divided vegetation types as they were described in Siberia. Uncertainty of vegetation reconstructions from pollen or macrofossil data is a well-known limitation for investigating the vegetation of the LGM (Binney et al. 2017). This limitation becomes more relevant when the vegetation types are defined more finely than through dominant plant functional types. In practice, using PDM for modelling LGM vegetation should consider similar uncertainties as those used for projecting distribution models to future climatic scenarios. Nevertheless, our study demonstrates how reconstructing vegetation in the LGM can benefit from a qualitative comparison with studies based on other approaches using pollen data and dynamic vegetation models.

We also note that present-day climatic data from Siberia suffer from inaccuracies due to very sparse network of climate stations, and a similar degree of uncertainty also exists for the climatic scenarios in the LGM (although the results for CCSM4 and MIROC-ESM were similar in this study). Due to large geographical distance and time difference of several millennia, similar vegetation types can differ in biogeographical context and species composition (Magyari et al. 2014), decreasing the degree of analogy of vegetation types subjected to similar climatic conditions. Moreover, the current climate corresponds only to a fraction of the climatic envelopes that support certain vegetation

types, making the predictions to the present and past conditions incomplete (Williams & Jackson 2007). The potential lack of analogy in vegetation also refers to other ecological features that are hardly estimated by correlative PDM. For example, Zimov et al. (1995, 2012) hypothesized that mammoth steppes may have been created and maintained by now-extinct large herbivores. Disturbances of woody plants and moss mats caused by these animals decreased soil insulation, thereby increasing thaw depth of permafrost, enhancing site productivity and supporting herbaceous growth forms.

Another limitation of PDM, as conducted here, is that the distributions of vegetation types do not depend only on temperature and precipitation but also on the concentration of atmospheric CO₂. These concentrations were much lower under full-glacial conditions (Monin et al., 2001) and we have no present analogue for such low levels. Low atmospheric CO₂ concentration required plants to open stomata for a longer period to absorb a certain amount of CO₂, resulting in higher loss of water through transpiration (Field et al. 1992). Therefore, the LGM ecosystems with the same humidity levels as current ecosystems probably supported drought-adapted vegetation. This can be the reason why models based on palaeoclimatic scenarios (e.g. Allen et al., 2010), tend to predict more forest cover than is shown by pollen-based reconstructions (e.g. Binney et al. 2017). Modelling studies showed that the pure effect of lower CO₂ leads to reduced area of forest, more open forest structure, some extension of tundra in the north and large extension of the dry open vegetation in the south (Harrison & Prentice 2003, Prentice et al. 2011). From this perspective, the real LGM distribution of forest would be less extensive than in our models, peatland forests would be reduced, tundra types would extend more to the south, and steppe with related non-forest dry types would extend more

to the north, providing a better match to the fossil record (e.g. Tzedakis et al. 2013; Binney et al. 2017).

5, Conclusion

This study is based on the assumption that several regions from current Siberia are modern analogues of climate and vegetation of Europe during the LGM. We showed that during the LGM, central and eastern Europe were the most analogue regions to present-day Siberia in terms of climatic conditions. Accordingly, the projections of vegetation types to the LGM were more reliable in these regions, providing spatially explicit models of European glacial vegetation. In contrast, we cannot provide reasonable vegetation reconstruction for the non-analogue regions of western and southern Europe, for which data from other analogue regions outside Siberia would be required; although our projections of steppes and temperate forests in these regions generally agree with previous studies (e.g. Bennett et al., 1991; Frenzel, 1992; Grichuk, 1992; Tzedakis et al., 2002). Overall, our study demonstrates how approaches using PDM and vegetation types surveyed in climatic analogue regions offer complementary information for reconstructing LGM vegetation. However, PDM has mainly been based on individual plant species or dominant growth forms at very coarse scales (e.g. Levis et al., 1999; Ray and Adams 2001; Allen et al., 2010). Although in many cases projections of vegetation types at large scales cannot be validated with palaeobotanical data, which are scarce especially for the LGM, the integration of PDM with palynological studies and dynamic vegetation models has a great potential for improving our understanding of past vegetation patterns.

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Table 1. Vegetation types and number of occurrences sampled in present-day Siberia for palaeodistribution modelling in Europe during the Last Glacial Maximum. A complete description of the vegetation types is provided in Supplementary Appendix S3.

Vegetation type	Number of occurrences
Arctic and alpine vegetation	
Arctic or alpine heathland	142
<i>Betula nana</i> s. l. scrub	81
Arctic or alpine deciduous scrub	65
Arctic or alpine tall-forb vegetation	41
Wetland and mire	
Marsh	54
Ombrotrophic bog	80
Minerotrophic fen	122
Peatland forest	114
Forest	
Dark-coniferous boreal forest	385
<i>Pinus sylvestris</i> boreal forest	203
<i>Larix</i> boreal forest	156
Hemiboreal forest	660
Temperate light-coniferous forest	330
Temperate deciduous forest	734
Grassland and scrub (except arctic and alpine)	
Wet meadow	72
Meadow steppe	774
Typical steppe	1212
Shrubby steppe	80
Saline vegetation	
Wet saline grassland	275
Dry saline grassland	294
Annual succulent halophytic vegetation	223
Perennial succulent halophytic vegetation	177

Table 2. Description of the environmental variables used for computing distribution models of vegetation types in present-day Siberia and Europe during the Last Glacial Maximum (LGM). Climatic data were collected from www.worldclim.org.

Variable	Explanation	Mean \pmSD in current Siberia	Mean \pmSD in LGM Europe
AMT	Annual mean temperature (mean of mean monthly temperatures; mean monthly temperature is the mean of maximum and minimum temperature of the given month; °C)	-7.0 ± 5.4	-2.6 ± 9.7
MDR	Mean diurnal range (mean of monthly diurnal temperature ranges; monthly diurnal range is the difference between maximum and minimum temperature of the given month; °C)	10.8 ± 1.8	10.7 ± 1.7
IT	Isothermality (proportion of mean diurnal range and annual temperature range, multiplied by 100; a quantification of how large the day-to-night temperature oscillation is in comparison with the summer-to-winter oscillation; %)	19.3 ± 3.2	27.8 ± 8.8
TS	Temperature seasonality (standard deviation of the monthly mean temperatures; °C)	156.5 ± 26.5	112.9 ± 50.8
AP	Annual precipitation (sum of the monthly precipitation values; mm)	413.4 ± 110.0	600.4 ± 313.0
PS	Precipitation seasonality (ratio of the standard deviation of the monthly total precipitation to the mean monthly total precipitation, unitless)	55.5 ± 18.8	32.2 ± 14.9

Table 3. Evaluation of distribution models computed for 22 vegetation types in present-day Siberia. The Area Under the Receiver Operating Characteristic curve (AUC), overfitting and omission rates were calculated from MaxEnt using cross-validation. Reliability reflects the final expert evaluation of the models.

Vegetation type	AUC	Overfitting	Omission rate	Reliability
(a) Arctic or alpine heathland	0.984 ± 0.002	0.003 ± 0.003	0.040 ± 0.089	good
(b) <i>Betula nana</i> s. l. scrub	0.937 ± 0.024	0.017 ± 0.030	0.143 ± 0.143	good
(c) Arctic or alpine deciduous scrub	0.929 ± 0.063	0.026 ± 0.068	0.120 ± 0.179	good
(d) Arctic or alpine tall-forb vegetation	0.912 ± 0.031	0.043 ± 0.037	0.240 ± 0.167	moderate
(e) Marsh	0.808 ± 0.084	0.057 ± 0.117	0.367 ± 0.182	bad
(f) Ombrotrophic bog	0.893 ± 0.057	0.036 ± 0.070	0.210 ± 0.198	moderate
(g) Minerotrophic fen	0.878 ± 0.033	0.030 ± 0.047	0.300 ± 0.199	moderate
(h) Peatland forest	0.843 ± 0.038	0.035 ± 0.050	0.321 ± 0.151	moderate
(i) Dark-coniferous boreal forest	0.893 ± 0.020	0.025 ± 0.026	0.238 ± 0.079	good
(j) <i>Pinus sylvestris</i> boreal forest	0.901 ± 0.043	0.025 ± 0.056	0.180 ± 0.192	good
(k) <i>Larix</i> boreal forest	0.923 ± 0.015	0.016 ± 0.020	0.211 ± 0.139	good
(l) Hemiboreal forest	0.912 ± 0.021	0.018 ± 0.027	0.198 ± 0.085	good
(m) Temperate light-coniferous forest	0.801 ± 0.008	0.051 ± 0.015	0.284 ± 0.102	moderate
(n) Temperate deciduous forest	0.803 ± 0.036	0.075 ± 0.047	0.428 ± 0.092	bad
(o) Wet meadow	0.768 ± 0.087	0.091 ± 0.108	0.287 ± 0.256	bad
(p) Meadow steppe	0.710 ± 0.059	0.060 ± 0.080	0.412 ± 0.121	bad
(q) Typical steppe	0.752 ± 0.018	0.043 ± 0.026	0.345 ± 0.083	moderate
(r) Shrubby steppe	0.889 ± 0.030	0.032 ± 0.028	0.300 ± 0.143	moderate
(s) Wet saline grassland	0.814 ± 0.039	0.028 ± 0.054	0.262 ± 0.042	good
(t) Dry saline grassland	0.893 ± 0.025	0.019 ± 0.032	0.203 ± 0.122	good
(u) Annual succulent halophytic veg	0.874 ± 0.022	0.021 ± 0.031	0.318 ± 0.112	good
(v) Perennial succulent halophytic veg	0.939 ± 0.016	0.005 ± 0.021	0.135 ± 0.126	good

Table 4. Contributions of environmental variables to MaxEnt models computed for 22 vegetation types in present-day Siberia. The values are determined by measuring the decrease in training AUC after random permutation of the variables among the training points. The three most important variables for each vegetation type are in bold. AMT: annual mean temperature; MDR: mean diurnal range; IT: isothermality; TS: temperature seasonality; AP: annual precipitation; PS: precipitation seasonality.

Vegetation type	AMT	MDR	IT	TS	AP	PS
Arctic or alpine heathland	36.1	55.9	8.0	0.0	0.0	0.0
<i>Betula nana</i> s. l. scrub	74.8	7.1	3.8	14.4	0.0	0.0
Arctic or alpine deciduous scrub	12.1	0.1	48.9	32.9	0.0	6.0
Arctic or alpine tall-forb vegetation	3.0	1.2	18.9	52.6	24.2	0.1
Marsh	13.2	4.2	1.7	29.8	5.1	46.0
Ombrotrophic bog	0.6	30.3	48.6	3.3	17.2	0.0
Minerotrophic fen	42.3	45.2	2.2	8.0	2.3	0.0
Peatland forest	41.3	5.2	0.0	1.7	0.1	51.6
Dark-coniferous boreal forest	51.7	6.9	5.3	6.7	1.5	27.9
<i>Larix</i> boreal forest	90.1	1.2	0.0	1.2	2.8	4.8
<i>Pinus sylvestris</i> boreal forest	50.0	8.8	10.0	11.0	0.0	20.1
Hemiboreal forest	17.6	2.6	4.1	25.7	42.5	7.5
Temperate light-coniferous forest	19.4	17.6	15.8	10.5	7.1	29.6
Temperate deciduous forest	10.6	15.5	0.0	51.1	6.2	16.6
Wet meadow	0.7	27.6	2.5	33.4	3.6	32.2
Meadow steppe	30.5	16.4	2.7	12.1	11.4	26.9
Typical steppe	20.5	24.7	14.3	36.4	1.5	2.6
Shrubby steppe	47.3	8.9	0.0	1.8	0.2	41.8
Wet saline grassland	21.8	1.0	2.3	20.8	44.3	9.8
Dry saline grassland	58.9	5.1	0.0	2.9	28.9	4.4
Annual succulent halophytic veg.	22.7	0.0	0.0	0.9	71.9	4.5
Perennial succulent halophytic veg.	54.1	8.9	0.0	0.0	33.3	3.7

Figure 1. Distribution of the sites surveyed in Siberia for calibrating distribution models of vegetation types under present-day climatic conditions.

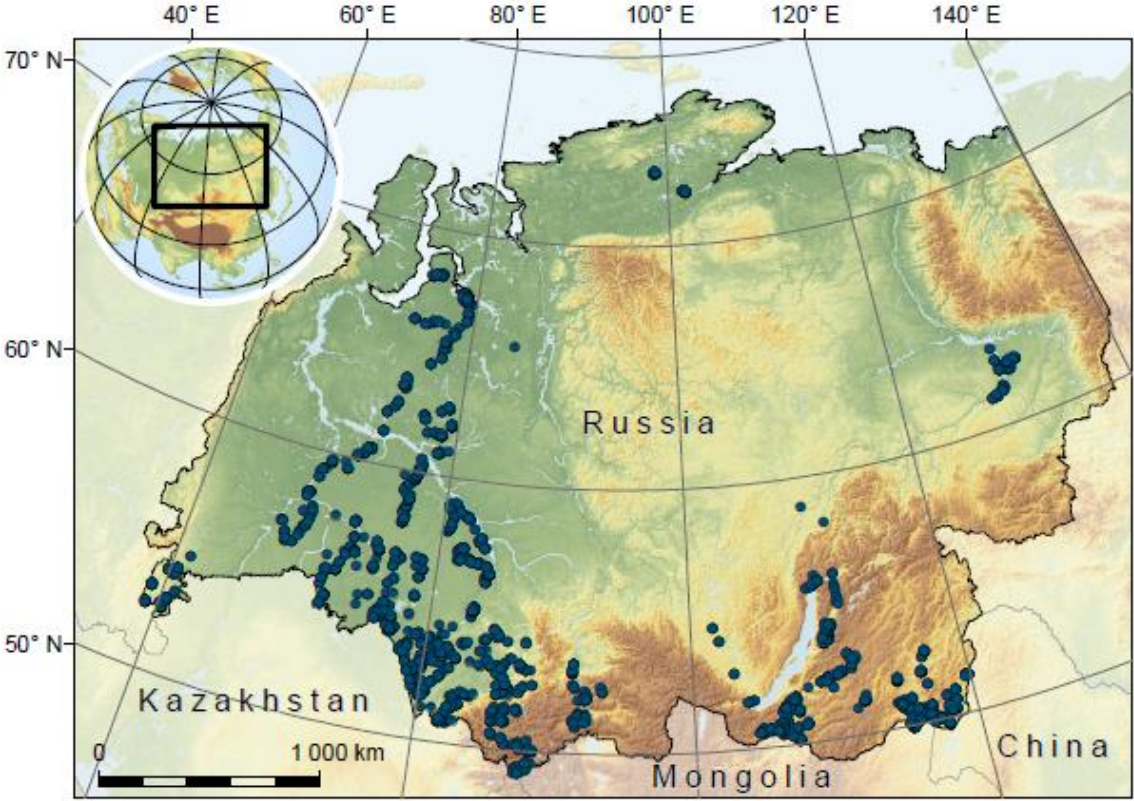


Figure 2. Climatic analogy of Europe in the Last Glacial Maximum with respect to present-day Siberia. Corresponding climatic variables were considered analogue when their values fit within the range of present-day climate in Siberia (see Supplementary Appendix S1 for individual maps of the six variables).

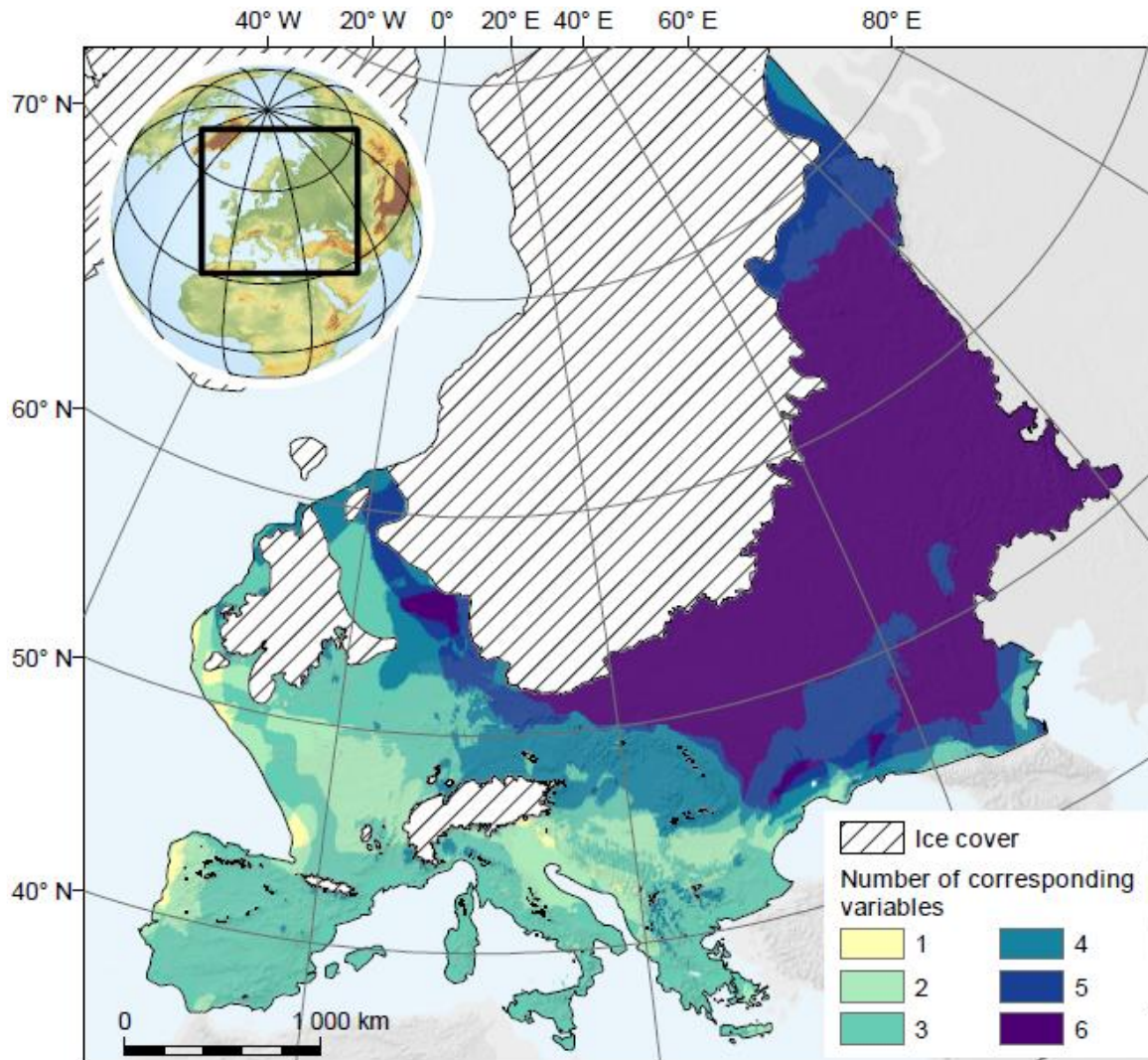


Figure 3. Climatic envelope (as a function of annual mean temperature and annual precipitation) of the vegetation plots and the study areas used for distribution modelling of vegetation types in Europe during the Last Glacial Maximum (LGM) and present-day Siberia.

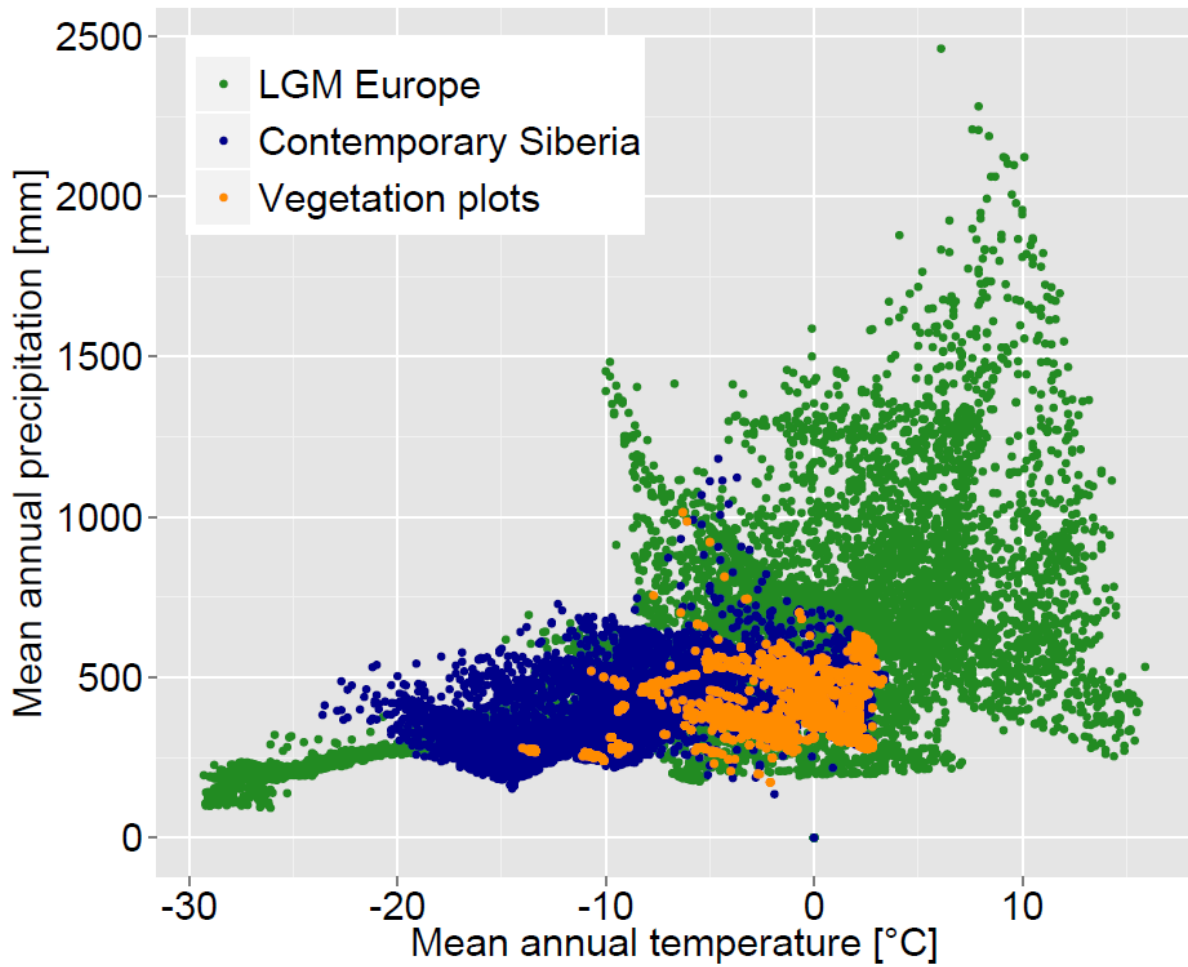


Figure 4. Spatial predictions for 22 vegetation types in Siberia, based on distribution models computed with present-day climatic data.

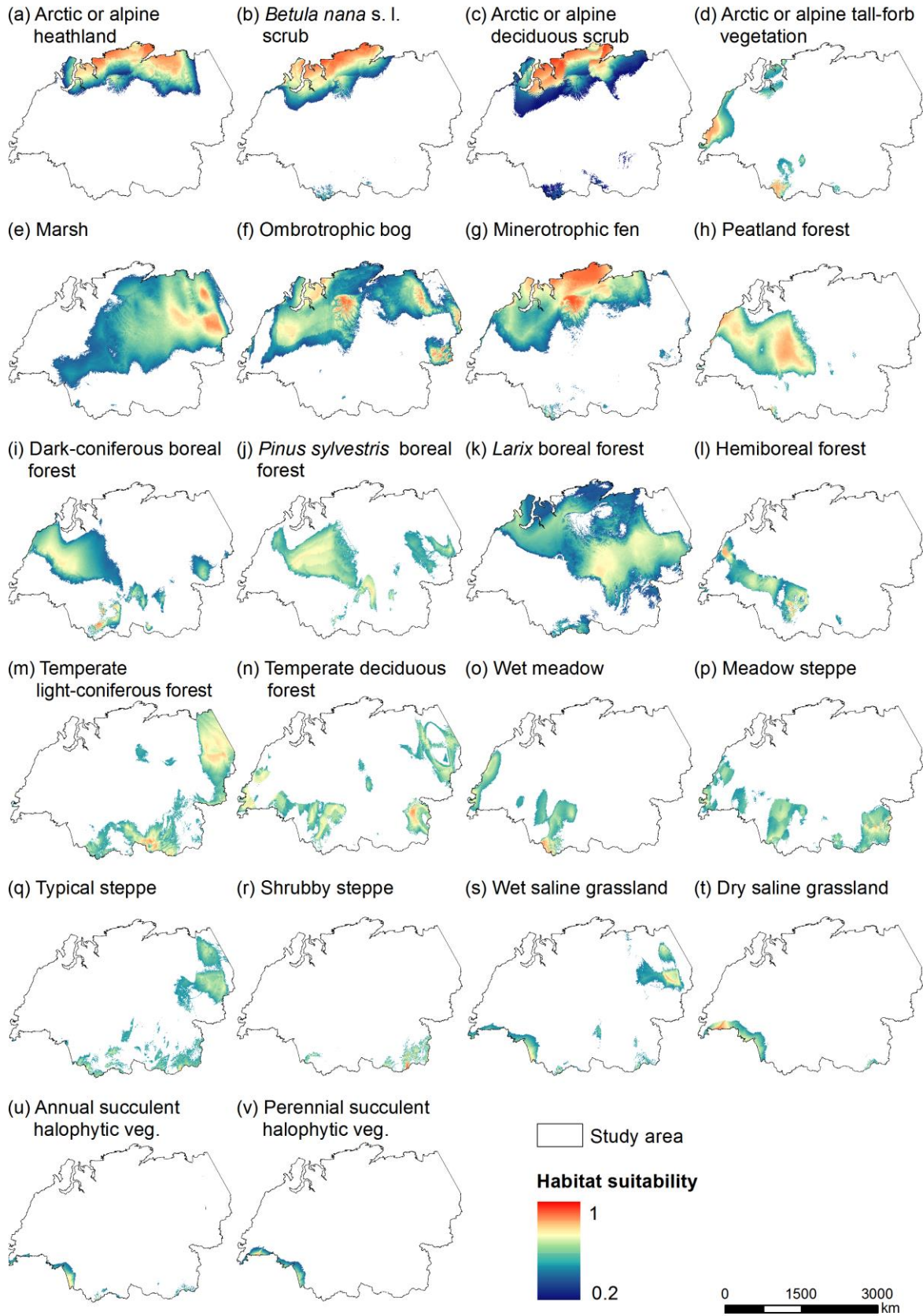
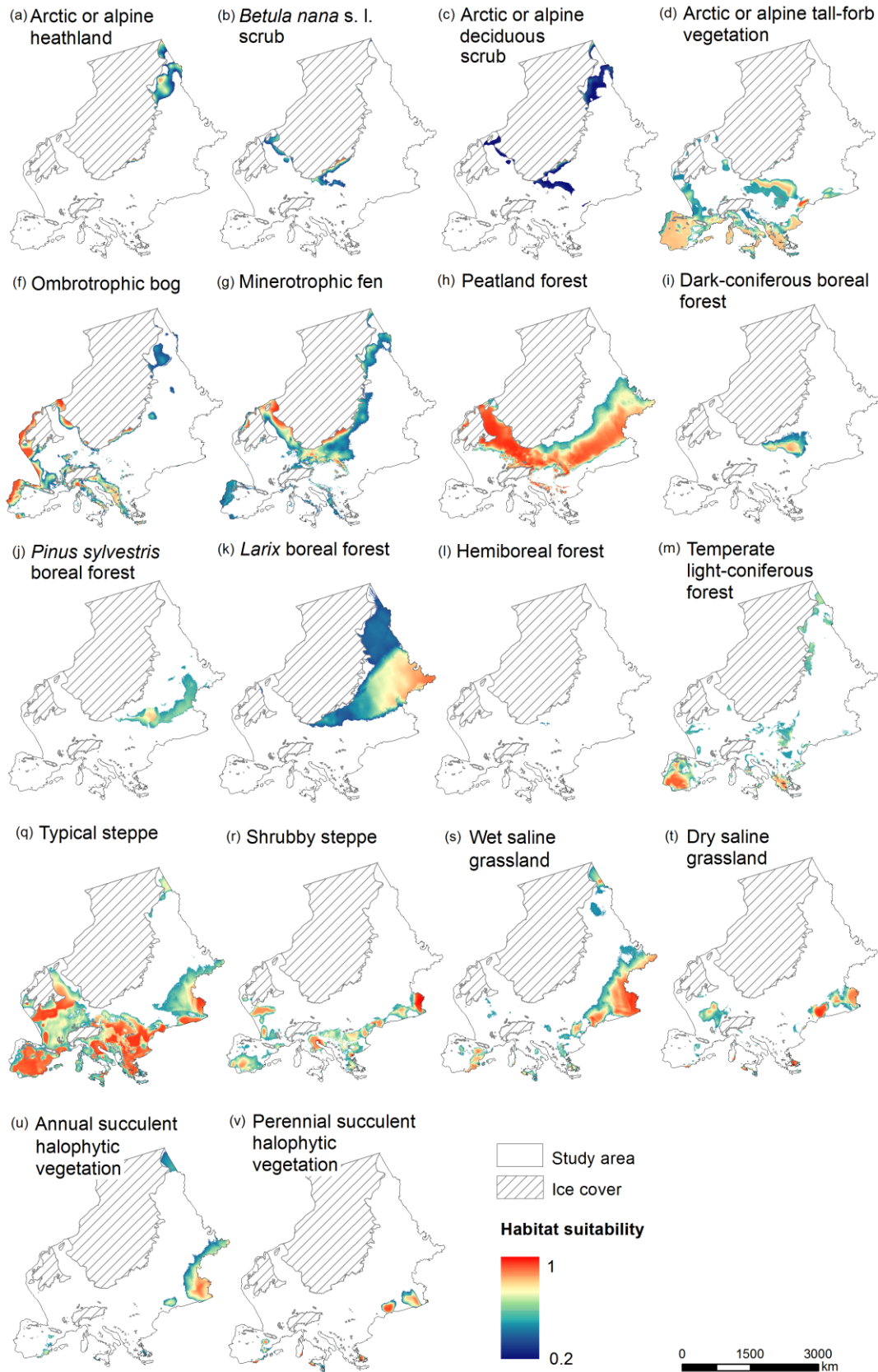


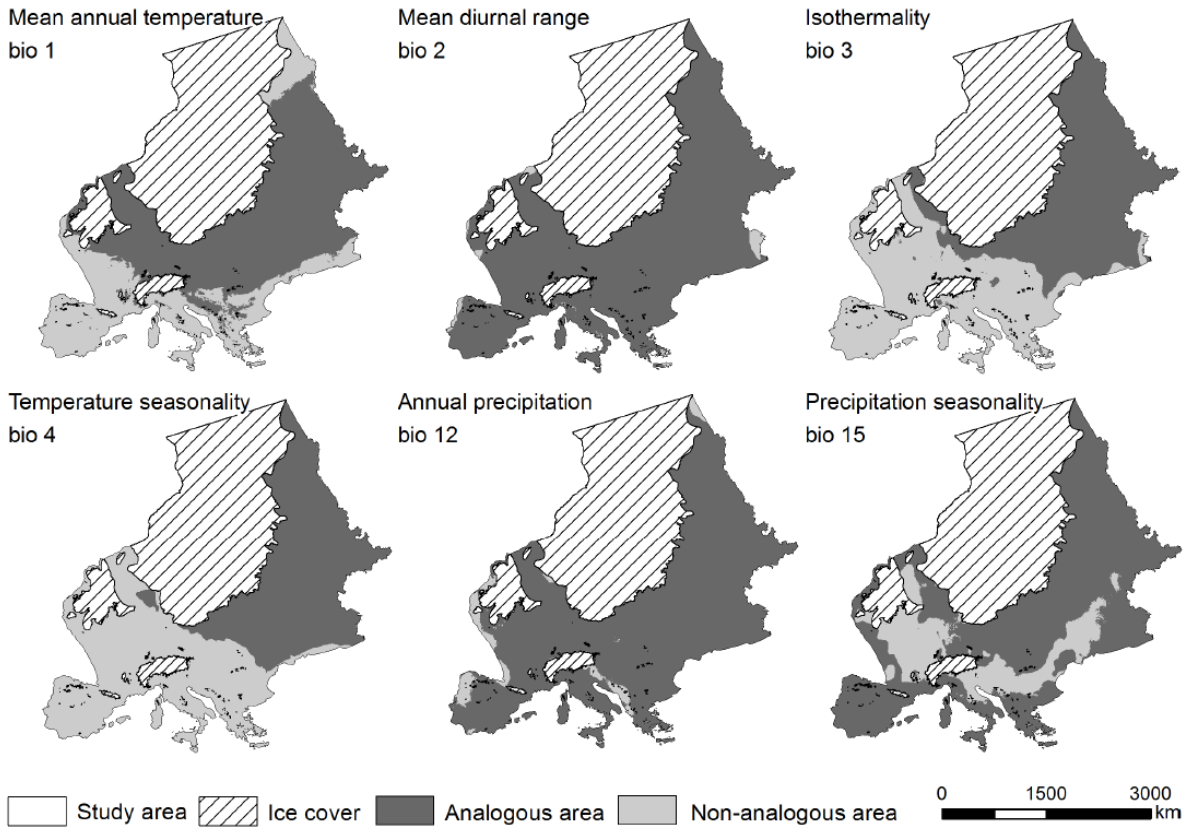
Figure 5. Spatial predictions for 18 vegetation types in Europe during the Last Glacial Maximum, projected from palaeodistribution models computed in Siberia with present-day climatic data.



Appendix A

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Figure A.1 – Areas of Europe during the Last Glacial Maximum (LGM) with climatic analogue conditions to the present-day climatic range in Siberia. Present-day and past climatic models (based on the Community Climate System Model, CCSM) were obtained from www.worldclim.org.



Appendix A

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Table A.1 – Brief characterization of the vegetation types subject to distribution modelling. Asterisks indicate the models that were evaluated as moderate or good (see Table 3) and projected to the European LGM climate. The descriptions are based on the expert knowledge of the authors and the references listed below. Species names follow Cherepanov (1995).

*Arctic or alpine heathland	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. <i>Empetrum</i> spp., <i>Vaccinium myrtillus</i> and <i>V. vitis-idaea</i>) associated with perennial herbs, graminoids, and with significant participation of bryophytes and lichens.
*<i>Betula nana</i> s. l. scrub	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 <i>Betula nana</i> , in particular <i>B. nana</i> in the Arctic tundra of northwestern Siberia, <i>B. exilis</i> in the tundra and taiga zone of northern-central and northeastern Siberia, and <i>B. rotundifolia</i> in the alpine tundra of the southern Siberian mountain systems. Associated species include various shrubs and dwarf shrubs (e.g. <i>Empetrum</i> spp., <i>Ledum palustre</i> , <i>Salix glauca</i> , <i>Vaccinium myrtillus</i> , <i>V. uliginosum</i> and <i>V. vitis-idaea</i>), graminoids, dicot herbs, bryophytes and lichens. This vegetation often occurs at topographically wetter sites and in places with a distinct snow accumulation in winter.
*Arctic or alpine deciduous scrub	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 abundance of deciduous shrubs, especially willows (<i>Salix glauca</i> , <i>S. krylovii</i> , <i>S. lanata</i> and <i>S. phylicifolia</i>), <i>Alnus fruticosa</i> and <i>Pentaphylloidesa fruticosa</i> .
*Arctic or alpine tall-forb vegetation	These high-productive tall-forb grasslands 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 <i>Aconitum septentrionale</i> , <i>Aquilegia glandulosa</i> , <i>Cirsium heterophyllum</i> , <i>Doronicum altaicum</i> , <i>Pedicularis incarnata</i> , <i>Trollius asiaticus</i> and <i>Veratrum lobelianum</i> .
Marsh	This is an azonal vegetation type occurring at topographically wet sites in the lowlands and in river valleys. The dominant species include tall wetland grasses, especially <i>Phragmites australis</i> and <i>Typha</i> spp., and tall sedges. Occurrence of bryophytes and accumulation of moss peat are insignificant in this habitats.
*Ombrotrophic bog	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 (<i>Sphagnum</i> spp.) and contain a significant amount of dwarf shrubs such as <i>Chamaedaphne calyculata</i> , <i>Ledum palustre</i> , <i>Rubus chamaemorus</i> , <i>Oxycoccus</i> spp. and <i>Vaccinium uliginosum</i>). They are either open or covered by sparse stands of <i>Pinus sylvestris</i> . In the permafrost zone of northern Siberia they often form small elevations with ice cores (palsas).
*Minerotrophic fen	This type of open mire, occurring in valleys, shallow depressions or around springs, is saturated by ground water. It is dominated by sedges (e.g. <i>Carex chordorrhiza</i> , <i>C. diandra</i> , <i>C. lasiocarpa</i> and <i>C. rostrata</i>), herbs (e.g. <i>Comarum palustre</i> and <i>Menyanthes trifoliata</i>) and mosses, although the species of genus <i>Sphagnum</i> are less abundant than in ombrotrophic bogs or even absent.

Appendix A

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<p>*Peatland forest</p>	<p>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 <i>Betula pubescens</i>, <i>Pinus sylvestris</i> and <i>Picea obovata</i>. Herb layer is rich in grasses (e.g. <i>Calamagrostis canescens</i> and <i>C. langsdorffii</i>), sedges (e.g. <i>Carex cespitosa</i> and <i>C. juncella</i>) and bryophytes including some species of <i>Sphagnum</i>.</p>
<p>*Dark-coniferous boreal forest</p>	<p>This type of boreal forest occurs in wetter habitats, either as zonal vegetation in the areas with high precipitation (e.g. on the West Siberian Plain) or as azonal vegetation on topographically wet soils on the valley bottoms or on north-facing slopes (e.g. in the mountain systems of southern Siberia). Their canopy is formed especially of <i>Abies sibirica</i>, <i>Picea obovata</i> and <i>Pinus sibirica</i>, occasionally with admixture of <i>Betula pendula</i> or <i>Populus tremula</i>. The herb layer contains abundant dwarf shrubs such as <i>Ledum palustre</i>, <i>Vaccinium myrtillus</i> and <i>V. vitis-idaea</i> and the soil is usually covered by extensive moss mats.</p>
<p>*<i>Pinus sylvestris</i> boreal forest</p>	<p>The boreal pine forest is a type of light-coniferous taiga that is most widespread in the boreal zone of western Siberia although it also occurs in eastern Siberia. In contrast to the dark-coniferous boreal forests, boreal pine 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. <i>Vaccinium vitis-idaea</i>, <i>Empetrum nigrum</i> and <i>Arctostaphylos uva-ursi</i>. Moss layer is usually well developed, with both bryophytes and lichens attaining a high cover.</p>
<p>*<i>Larix</i> boreal forest</p>	<p>The larch type of light-coniferous taiga is the most extensive vegetation type in Siberia. Whereas <i>Larix gmelinii</i> and <i>L. cajanderi</i> are dominants in most of eastern Siberia, <i>L. sibirica</i> predominates on the West Siberian Plain. Larch forests often occur on permafrost. Their herb layer contains abundant dwarf shrubs such as <i>Ledum palustre</i>, <i>Vaccinium uliginosum</i>, <i>V. vitis-idaea</i> and <i>Arctous alpina</i> together with grasses, herbs and abundant mosses and lichens.</p>
<p>*Hemiboreal forest</p>	<p>Hemiboreal forests are transitional between the boreal and temperate forests. They are composed of a mixture of coniferous and deciduous trees with both nemoral (related to temperate deciduous forest) and boreal species. They are widespread especially in the southern subtaiga and southern-taiga zone of western Siberia, but they also occur in the precipitation-rich northern ranges of the southern Siberian mountain systems such as the Altai and smaller mountain ranges north of the Altai, where they are called chervayaya (blackish) taiga. These forests are dominated by <i>Abies sibirica</i>, <i>Betula pendula</i>, <i>B. pubescens</i>, <i>Populus tremula</i>, with occasional admixture of <i>Picea obovata</i> 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.</p>
<p>*Temperate light-coniferous forest</p>	<p>These forests, dominated by <i>Pinus sylvestris</i>, <i>Larix gmelinii</i> or <i>L. sibirica</i>, are similar to the <i>Pinus sylvestris</i> and <i>Larix</i> boreal forests, but only if the composition of tree layer is considered, whereas the herb layer is quite different. This vegetation occurs especially in the mountainous southern part of Siberia, most commonly between the Altai-Sayan and Transbaikalian mountain systems, especially in continental climate of mountain valleys and basins. Unlike boreal light-coniferous taiga, these forests have a species-rich herb layer</p>

Appendix A

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	consisting of the herbs and graminoids typical of temperate forests and grasslands.
Temperate deciduous forest	This forest type forms a belt stretching approximately from the Southern Urals to the Altai Mountains, but it occurs more southerly, especially in the forest-steppe zone and partly in the subtaiga zone. To a smaller extent, it also occurs in south-eastern Siberia and as extrazonal vegetation also in dry areas of central Yakutia. The dominant species are <i>Betula pendula</i> and <i>Populus tremula</i> . Herb layer of these forests is very rich in species, composed by herbs and graminoids. Dwarf shrubs and bryophytes are much less abundant than in boreal forests.
Wet meadow	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. <i>Filipendula ulmaria</i> , <i>Galium boreale</i> , <i>Silaum silaus</i> and <i>Thalictrum simplex</i>) and graminoids (e.g. <i>Carex vulpina</i> , <i>Deschampsia cespitosa</i> and <i>Poa palustris</i>).
Meadow steppe	Meadow steppe, including also steppe meadows, is a vegetation type occupying intermediate ecological position on the moisture gradient between wet meadows and typical 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.
*Typical steppe	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 <i>Festuca valesiaca</i> , <i>Koeleria cristata</i> , <i>Stipa</i> (e.g. <i>Stipa capillata</i> , <i>S. lessingiana</i> , <i>S. krylovii</i>) and <i>Helictotrichon altaicum</i> , accompanied by sedges, non-tussocky graminoids, herbs and some low shrubs such as <i>Caragana</i> spp.
*Shrubby steppe	This vegetation type formed of drought-adapted low shrubs, especially those of genera <i>Caragana</i> and <i>Spiraea</i> , 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 edges of forest. Steppe herbs and graminoids occur below the shrub canopy.
*Wet saline grassland	These are inland meadows or meadow-like communities on saline soils, especially solonchaks, occurring in river valleys, in shallow depressions and in the surroundings of lakes. These conditions are found especially in arid and semi-arid areas of the southern West Siberian Plain, but they also occur in Yakutia and other areas. Common species include the herbs <i>Glaux maritima</i> , <i>Halerpestes salsuginosa</i> , <i>Potentilla anserina</i> , <i>Saussurea amara</i> and <i>Triglochin palustre</i> and grasses <i>Agrostis stolonifera</i> , <i>Alopecurus arundinaceus</i> and <i>Poa pratensis</i> .
*Dry saline grassland	Dry saline grasslands occur particularly on the solonetz soils in flat lowlands and on river terraces of the Siberian steppe zone. They may be waterlogged or briefly flooded in spring but dry out for the rest of the year. They contain a mixture of herbaceous halophytes such as <i>Puccinellia</i> spp. and steppe grasses and herbs.

Appendix A

Janská, V., Jiménez-Alfaro, B., Chytrý, M., Divíšek, J., Anenkhonov, O., Korolyuk, A., Lashchinskyi, N. & Culek, M. 2017. Palaeodistribution modelling of European vegetation types at the Last Glacial Maximum using modern analogues from Siberia: Prospects and limitations. *Quaternary Science Reviews* (JQSR4905).

Annual succulent halophytic vegetation	This vegetation type comprises species-poor inland saltmarshes with predominance of succulent annual halophytes of the genera <i>Salicornia</i> and <i>Suaeda</i> . They are developed in areas of dry continental climate on salt-rich sediments and in the surroundings of saline lakes in the steppe zone of southern Siberian lowlands. The habitats are waterlogged or flooded by shallow water in spring, but during summers the soil surface dries out and ground water enriched with salt rises upwards.
Perennial succulent halophytic vegetation	The vegetation of perennial succulent halophytes occurs in inland saltmarshes of the steppe zone of the southernmost part of western Siberia. They are confined to the depressions, surroundings of saline lakes and river valleys where salty ground water lies close to the surface and which are flooded in spring. Dominant species of this species-poor vegetation include <i>Halocnemum strobilaceum</i> , <i>Kalidium</i> spp., <i>Nitraria sibirica</i> and <i>Suaeda</i> spp.

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