Palaeogeography, Palaeoclimatology, Palaeoecology 438 (2015) 135–145

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

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

Modelling the Last Glacial Maximum environments for a refugium of Pleistocene biota in the Russian Altai Mountains, Siberia

Martin Hais [a], Klára Komprdová [b], Nikolai Ermakov [c], Milan Chytrý [d,*]

[a] University of South Bohemia, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic
[b] Research Centre for Toxic Compounds in the Environment, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic
[c] Central Siberian Botanical Garden, Russian Academy of Sciences, Zolotodolinskaya 101, Novosibirsk 630090, Russia
[d] Department of Botany and Zoology, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic

ARTICLE INFO

Article history:
Received 13 February 2015
Received in revised form 10 July 2015
Accepted 20 July 2015
Available online 3 August 2015

Keywords:
Climate change
Habitat distribution models
Palaeoenvironments
Pleistocene
Random Forest
Vegetation–climate relationships

ABSTRACT

Recent botanical and zoological studies have suggested that the Altai Mountains in southern Siberia are an important refugium of the last glacial biota that used to be widespread across northern Eurasia before the Pleistocene–Holocene transition. To obtain insights into the history of this relict biota, we modelled the spatial distribution of habitats during the Last Glacial Maximum (LGM) in the Russian Altai. We prepared a map of the current vegetation of this area based on the ground-truthed remote sensing data, and modelled the distribution of the current vegetation types using the Random Forest technique with climatic predictors. The models were projected onto the CCSM3 model of the LGM climate for the Russian Altai and interpreted for 72% of its area because the remaining part is supposed to have been glaciated during the LGM. The models projected LGM predominance of desert-steppe across most of the non-glaciated area of the Russian Altai, probably associated with areas of typical steppe, tundra grasslands and some other habitat types, including forest patches in stream valleys. It is likely that during the LGM, these habitats supported the cold-adapted open-landscape biota. In the Holocene, most of the previous grassland area changed into forest or forest-steppe and the Pleistocene biota retreated, with the exception of the Chuya Basin and the Ukok Plateau in the southeast, where the habitat change was very small and desert-steppe and associated vegetation types remained preserved. This refugial area is currently rich in the relict Pleistocene species. A different history was suggested for the precipitation-rich area in the northernmost Altai (north of Lake Teletskoye), where the LGM models suggested occurrence of patches of open forest of *Larix sibirica* and *Pinus sibirica* in forest-tundra and forest-steppe landscapes. These forests may have provided the LGM refugium for the temperate forest species that currently occur in this precipitation-rich area.

1. Introduction

Recent studies focusing on various plant and animal taxa have provided independent pieces of evidence that the Altai–Sayan Mountains of southern Siberia comprise a refugium preserving numerous species that during the last glacial period had been widespread over large areas of Europe and northern Asia but disappeared or strongly retreated after the Late Glacial. Palynological studies have indicated that the pollen spectra from eastern Central Europe from the last glacial period are very similar to the modern surface pollen spectra from the Altai–Sayan Mountains, suggesting a high similarity between European palaeovegetation and modern vegetation of these mountains (Kuneš et al., 2008; Magyari et al., 2014). Indeed, whole extant assemblages of snails that were typical of European Late Pleistocene loess sediments but which strongly retreated or went extinct in the Holocene were recently discovered in the Altai and the adjacent mountain ranges (Meng, 2009; Horsák et al., 2010, 2015; Hoffmann et al., 2011; Nekola et al., 2015). Furthermore, a comparison of fossil and recent mammal faunas across Eurasian regions revealed that the southeastern Altai–Sayan region experienced the lowest rate of extinction of the Pleistocene fauna and that its modern mammal fauna is most similar to the Pleistocene fauna (Pavelková Řičánková et al., 2014). This biotic evidence is supported by the results of modelling studies that indicate that over the last 42 thousand years (ka), the coarse-scale vegetation structure has been considerably more stable in this region than elsewhere in northern Eurasia (Allen et al., 2010).

Within the Russian Altai Mountains, the occurrences of relict Pleistocene species of plants, snails and mammals (Horsák et al., 2010, 2015; Pavelková Řičánková et al., 2014) are currently concentrated in their southeastern part, for which all models assume glaciation during the Last Glacial Maximum (LGM; Rudoy, 2002; Kuhle, 2004; Lehmkuhl et al., 2011; Rudoy and Rusanov, 2012; Blomdin et al., 2015). This suggest a scenario of the LGM survival of this biota in the nearby unglaciated areas and its return to the deglaciated areas during the

* Corresponding author.
E-mail addresses: martin.hais@seznam.cz (M. Hais), komprdova@recetox.muni.cz (K. Komprdová), brunnera@mail.ru (N. Ermakov), chytry@sci.muni.cz (M. Chytrý).

http://dx.doi.org/10.1016/j.palaeo.2015.07.037
0031-0182/

Late Glacial or Holocene (Agadjanian and Serdyuk, 2005; Schlütz and Lehmkuhl, 2007; Blyakharchuk et al., 2007; Tchebakova et al., 2009). An important issue in this context is the extent of the LGM glaciers in this area. Although some researchers suggested the existence of extensive ice sheets over the whole of the Russian Altai Mountains as far as their northwestern foothills (Rudoy, 2002; Rudoy and Rusanov, 2012), most Quaternary geologists and glaciologists assume that only the southeastern part of the Russian Altai was glaciated (Kuhle, 2004; Lehmkuhl et al., 2011; Blomdin et al., 2015). Also, mammal and pollen records from the sedimentary sequences in the northwestern Altai provide evidence against the existence of large glaciers in this area during the LGM (Agadjanian and Serdyuk, 2005).

To understand the history of the relict biota of the Altai–Sayan refugium and to suggest scenarios of its survival in this area, it is important to obtain insights into the environmental change that occurred between the LGM and the present. Of particular interest is the LGM distribution of habitats that could have supported the relict Pleistocene biota and the change in these habitats and their distribution between the LGM and the Holocene. Although the Altai region has been permanently inhabited by humans since at least 300 ka ago (Derevianko et al., 2005), human impact has always been too limited to cause broad-scale habitat changes. Therefore, we can safely assume that before the Russian colonisation of the Altai in the 18th century, the main driver of the broad-scale habitat change had always been the change in climate. The data on the Pleistocene biota of the Altai Mountains are scarce, restricted mainly to the Anui River valley in the northwestern Altai (Denisova Cave and some nearby sites). Pollen and vertebrate records from sedimentary sequences from this valley suggest that in the period before the LGM this area was covered by a mosaic of steppe and forest, whereas during the LGM cold steppe covered most of the area. These data provide no support for the existence of extensive areas of tundra in this region during the entire last glacial period (Agadjanian and Serdyuk, 2005). However, because fossil data on the LGM environment of the Altai Mountains are scarce and spatially restricted, the distribution and extent of different habitat types is unknown for this critical period of maximum cooling, which must have been a bottleneck for the survival of many plant and animal species. This gap can be partially overcome by habitat distribution modelling.

In this paper, we apply a modelling approach to estimate the distribution of the main habitat types in the Russian Altai Mountains during the LGM. Our investigation is premised on the recent study by Blomdin et al. (2015), indicating that only the southeastern portion of the area was glaciated. We compare the modelled distribution of the LGM habitats with the map of current habitats and use this comparison to interpret the history of the relict Pleistocene biota in this region. We define habitats as broad vegetation types because vegetation determines distributions of animal species by providing food or shelter, and different vegetation types are directly linked with the distributions of individual plant species.

Our approach involves the following steps: (1) classifying the current vegetation of the Russian Altai Mountains into broad vegetation types and mapping their distributions based on satellite images; (2) calibrating individual vegetation types using recent climatic data and bioclimatic indices; (3) developing a predictive distribution model of vegetation types based on climatic predictors; (4) applying this model to the LGM climatic scenario to obtain a projection of the distribution of vegetation types during the LGM; and (5) comparing the distributions of vegetation types between the LGM and the present.

2. Materials and methods

2.1. Study area

The study area is the Altai Republic (92 600 km^2), a part of the Russian Federation located in southern Siberia, bordering with Kazakhstan, China and Mongolia. Its population density is only 2.2 people/km^2, and the population is strongly concentrated near its northern to northwestern border. Consequently, industrial and agricultural activities are limited, and most of the area is covered by natural vegetation. The area encompasses a broad range of natural conditions within an altitudinal range of 258–4506 m (mean altitude 1676 m). The northern part is precipitation-rich and relatively warm, with annual precipitation in the foothills > 800 mm, mean July temperature about 18 °C and mean January temperature about −16 °C. The climate becomes progressively drier and cooler when moving to the high-mountain areas in the south. The intermontane basins in the southeast, such as the Chuya Basin, have a very dry continental climate with about 110 mm of annual precipitation, mean July temperature of 14 °C and mean January temperature as low as −32 °C (Modina, 1997). Distribution of natural vegetation types in the Altai is mainly driven by the climatic pattern, with human influence limited.

2.2. Vegetation map

The vegetation map of the Russian Altai Mountains was prepared using MODIS and Landsat-7 satellite data combined with ground-based vegetation observations made during the field expeditions to various parts of this region in 1985–2012, as well as with cartographic information from existing vegetation and landscape maps (Kuminova, 1960; Ogureeva, 1980; Chernykh and Samoilova, 2011)

The original map contained 17 mapping units. Of these, we excluded azonal vegetation types such as wetlands and non-vegetation features such as water bodies because they depend mainly on terrain morphology rather than climate. The resulting map contained 14 vegetation types and also glaciers. Glaciers were included into the modelling, along with vegetation types, because (1) their occurrence also depends on climate, and (2) they cover large areas in the modern Altai landscape and were much more widespread during the LGM (Blomdin et al., 2015). The following vegetation types were defined on the basis of dominant plant species or growth forms that can be recognised on satellite images and represent specific habitats with clear ecological interpretation:

1. Dark-coniferous mixed forest: co-dominated by the conifers *Abies sibirica* and *Pinus sibirica* (*P. cembra* s.l.) and broad-leaved deciduous trees *Betula pendula* and *Populus tremula*. In some places, the occurrence of broad-leaved trees is due to past disturbances in the pure coniferous taiga, and in others, the mixed forest is the climax vegetation, locally called chernevaya ('blackish') taiga.
2. Dark-coniferous forest: dominated by the conifers *Abies sibirica*, *Picea obovata* and *Pinus sibirica* (dark-coniferous taiga).
3. Birch and aspen forest: dominated by *Betula pendula* and *Populus tremula*, in some places occurring as a post-disturbance successional stage of coniferous forest, in other places representing climax vegetation of the chernevaya taiga.
4. Larch forest: open forest dominated by *Larix sibirica* (light-coniferous taiga).
5. Siberian pine forest: dominated by *Pinus sibirica*, typically occurring at high altitudes.
6. Scots pine forest: dominated by *Pinus sylvestris.*
7. Subalpine open woodland: near the timberline, dominated by *Pinus sibirica* or *Larix sibirica.*
8. Dwarf-birch tundra: *Betula rotundifolia* (*B. nana* s.l.) scrub, above the timberline or in stream valleys.
9. High-mountain tundra: usually open grassland with dwarf shrubs, above the timberline, composed of arctic-alpine and high-mountain species.
10. *Kobresia* tundra: usually closed grassland above the timberline, dominated by graminoids of the genus *Kobresia.*
11. Steppe: open to closed grassland dominated by drought-adapted graminoids.

12 Desert-steppe: open grassland with significant representation of dwarf shrubs (mainly *Artemisia* spp. and Chenopodiaceae) in the driest areas.
13 Tundra-steppe complex: a landscape mosaic of tundra and steppe vegetation types, including also grasslands consisting of a mixture of tundra and steppe species.
14 Forest-steppe: a landscape mosaic of forest and grassland patches, not at the alpine timberline.

In addition to the map with these categories, we also prepared a map with a coarser classification containing four vegetation types obtained by merging the above fourteen: forest (1–6), forest-steppe (14), forest-tundra (7–8) and grassland (9–13).

2.3. Recent climate data

Climate data used in modelling were monthly precipitation totals and monthly mean temperatures obtained from the WorldClim database (Hijmans et al., 2005; http://www.worldclim.org) and variables derived from these. The global climate model of WorldClim is generally based on data from the period 1960 to 1990, but in some areas from the period 1950 to 2000. Throughout this paper, the term 'recent' refers to these time intervals. Besides precipitation and temperature, we used various climatic indices and combinations of climatic variables to achieve better descriptions of the vegetation–climate relationships:

1 Precipitation (mm)
  1a Summer precipitation (sum of mean monthly values from April to September)
  1b Winter precipitation (sum of mean monthly values from October to March)
  1c Rainfall (sum of mean monthly precipitation for the months with mean temperature ≥0 °C)
  1d Snowfall (sum of mean monthly precipitation for the months with mean temperature <0 °C)
2 Temperature (°C)
  2a January temperatures (maximal, mean and minimal monthly values)
  2b July temperatures (maximal, mean and minimal monthly values)
3 Interactions
  3a January mean temperature × snowfall
  3b July mean temperature × rainfall

Because of autocorrelation among the monthly mean temperatures, we selected only the extremes (January and July temperatures). The WorldClim data were reprojected to the metric coordinate system (Albert-conical equal area), with the resulting spatial resolution of 920 m. The entire study area included 103 759 pixels (87 821 km^2) after excluding azonal land-cover units (wetlands and lakes).

Heat load index was computed in addition to the above-listed macroclimate data in order to characterise local topoclimate. This index represents the annual cumulative value of potential incoming solar radiation (Wh/m^2/year) depending on the aspect and slope. Its value was computed using the ArcGIS 10 software for each pixel from the digital elevation model while disregarding differences in altitude.

2.4. LGM climate data

Last Glacial Maximum (LGM) climate data were taken from the Paleoclimate Modelling Intercomparison Project Phase II (http://pmip2.lsce.ipsl.fr/). We used the CCSM3 model (Otto-Bliesner et al., 2005), which is a global model of the LGM, mid-Holocene and preindustrial climates, containing all the climatic variables that we needed for modelling the relationships between modern climate and vegetation, including the maximal and minimal monthly temperatures. The data were downscaled to obtain 920 m spatial resolution. In downscaling, we assumed that the differences between pixel values of fine- and coarse resolution data sets would be the same for recent and LGM data. The fine-resolution recent data were resampled to the same (coarse) resolution as the LGM data. This coarse grid of recent data was resampled back to the original high spatial resolution and we used the kriging method to smooth the high differences between the adjacent coarse pixel values. Next, we calculated the differences between coarse- and fine-resolution recent data, which reflected the variability in lapse rates and precipitation due to local topography. These differences were finally subtracted from the LGM climatic coarse data to obtain the downscaled high-resolution data (see http://www.worldclim.org/downscaling).

The LGM simulated surface climate was colder and drier than the preindustrial conditions. The global LGM average land cooling was 2.62 °C, and the LGM precipitation was drier by 18% (Otto-Bliesner et al., 2005). The downscaled CCSM3 data showed a similar trend for the Altai region (Fig. 1). The mean LGM cooling from recent conditions was 0.14 °C and 1.83 °C in January and July, respectively. The mean annual precipitation in the Altai decreased from recent 449 mm to 387 mm in the LGM; however, mean winter precipitation increased from 110 mm to 204 mm in the LGM. This influenced the ratio of snowfall to rainfall. Whereas snowfall makes up about 27% of annual precipitation in the recent period, it made up about 66% in the LGM. Because of its colder and drier features, the LGM climate was probably more continental, with higher diurnal and annual temperature ranges than in the recent period (Fig. 1).

2.5. Predictive vegetation modelling

The vegetation map of the Altai included up to ten-fold differences in the numbers of pixels per vegetation type. This might unduly affect the performance of the supervised classification methods and could yield predictions biased towards the categories with the high numbers of observations. This problem can be solved by modelling based on selecting equal number of pixels for each vegetation type, which was possible in our case due to the relatively uniform climatic conditions within the areas comprising each vegetation type and glaciers. We used 1000 pixels per type in the finer vegetation classification with 14 vegetation types, and 5000 pixels in the coarser classification with four types. Two versions of pixel selection were tested, the first being random (following the shapes of the real distribution; normal in our case), and the second with uniform distribution (selections of pixels with extreme and mean climatic conditions equally probable). Pixel selections were done separately for each vegetation type and glaciers. To test whether this selection represented the whole gradient of climatic conditions, we compared the overall frequency distribution and the ranges of all climatic variables compiled from each type with those obtained from a set of all pixels of the given type from the vegetation map.

The Random Forest technique (RF) (Breiman, 2001) was used for distribution modelling of the 14 finer and 4 coarser vegetation types, in each case with glaciers included as an additional category. Climatic variables, their interactions and the heat load index were used as predictors. RFs have multiple applications in ecological studies (Cutler et al., 2007), being widely used particularly for the prediction of species distributions (Iverson et al., 2008; Attorre et al., 2011; Freeman et al., 2012). This method is generally based on fewer assumptions than classical parametrical methods (e.g., GLM or discriminant analysis) and can be considered as a non-parametric type of fitting approach. It is useful especially when using a large number of correlated predictors such as climatic variables, and for the prediction of many categories (15 in our case). The RF method is based on classification and regression trees (CART; Breiman et al., 1984). CART iteratively splits the data hierarchically into increasingly homogeneous subgroups based on a criterial statistic (Gini index). However, CART results can be very unstable: a small change in the data can result in a different tree with approximately the same amount of explained variation, especially if there are many correlated predictors. This problem is solved by the use of a random forest

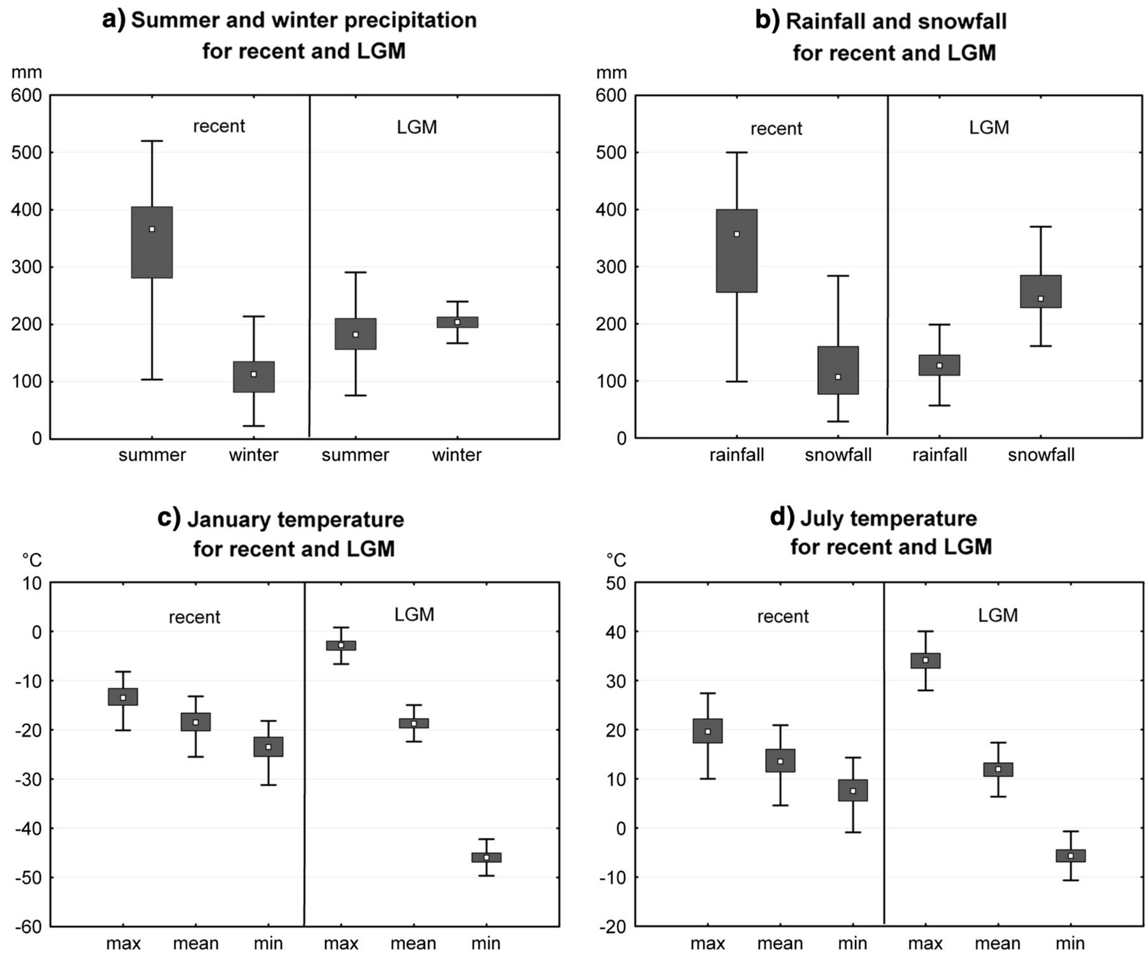

Fig. 1. A comparison of the main climatic parameters for the recent and LGM climate in the Altai.

containing many individual trees (*ntree*) instead of a single tree. Individual trees in RF are built only on a subset of observations from the entire data set, which are selected by bootstrap (random selection with replacement). Observations that are not used for growing a tree are used for estimating the overall error of this tree. The classification result is achieved by a 'majority vote' of individual trees. To avoid correlation among trees in RF, random selection of predictors (*mtry*) is used for building the trees. Various numbers of *ntree* and *mtry* were tested, and the model with the lowest classification error was chosen. Models were evaluated based on their overall accuracy (*OA*; percentage of correctly classified observations).

The RF model yields 'importance' values for individual predictors. These values can range from 0 to 100 and express the suitability of the particular predictor for the classification of areas as particular vegetation types or glaciers. Specifically, importance was calculated from the misclassification rate, which was computed by comparing classification based on random permutation of the values of each variable with non-random classification results.

The final classification of each pixel was determined by the majority vote of all trees, with the probability of voting for a given vegetation type or glacier calculated as the number of decision trees that classified the observation to that vegetation type or glacier divided by the total number of decision trees. These probabilities were used to identify the overlap between vegetation types and to establish the range of climatic conditions in which individual vegetation types or glaciers occurred with probability greater than 0.5. Pixels predicted with probability greater than 0.5 to individual vegetation types or glaciers were visualised in a contour plot defined by the two most important climatic variables. The contour plot is a projection of a three-dimensional surface onto a plane. We used a version based on spline interpolation in which the curves are approximated by a sequence of cubic polynomials (Gerald and Wheatley, 1989).

For the development of the RF models, the 'randomForest' package provided by Liaw and Wiener (2006) within the statistical software R (www.R-project.org) was used, whereas Statistica for Windows, version 12, was used to draw the contour plot.

3. Results

3.1. Vegetation distribution model for the recent climate

The Random Forest models with the lowest classification error based on testing of *mtry* and *ntree* parameters were chosen for prediction of individual vegetation types. The minimal overall classification error of RF for all tested models was achieved by using the variant with random selection of pixels and with number of predictors $mtry = 4$. These results were stable for the number of trees $ntree = 400$ for 14 vegetation types and glaciers. In the case of 4 vegetation types plus glaciers, the best model was created by using random selection of pixels (as in the previous model), with $mtry = 3$ and $ntree = 200$.

Importance values of climatic variables were similar for both models (Fig. 2), reflecting high correlations of variables within the models. Temperature had slightly more influence than precipitation. The interaction between temperature and precipitation was also an important predictor. Generally, the variables with broader ranges of values, especially summer climate characteristics as opposed to winter ones, were more

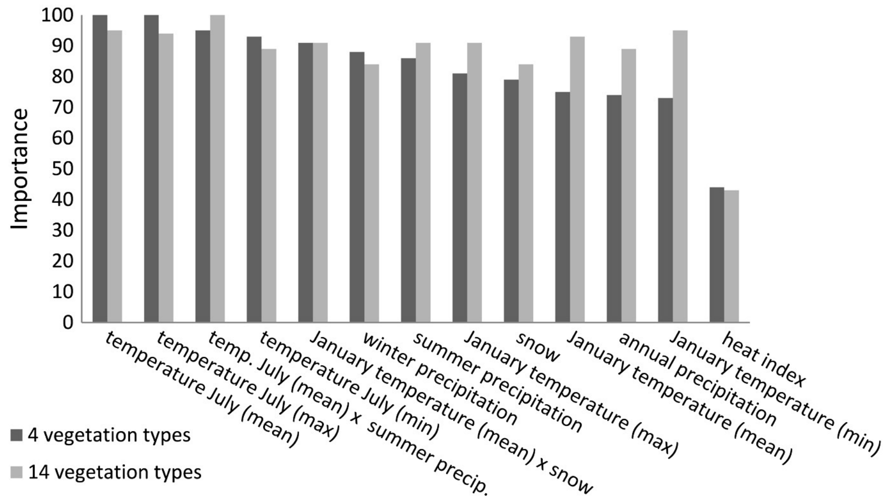

Fig. 2. The importance values of climatic variables as predictors in the RF models for vegetation types and glaciers.

important for the four vegetation types, whereas the importance values of the summer and winter variables were more balanced when considering the 14 vegetation types. The heat load index was the least important, probably because of the coarse spatial resolution of the vegetation map, which poorly captured the differences between north- and south-facing slopes. Two climatic variables (summer precipitation sum and mean July temperature) that were highly important for both models were selected to define axes for the visualisation of the relationships between climate and individual vegetation types and glaciers (Fig. 3).

For the model with 14 vegetation types, the overall accuracy was 57.7%. The best predicted vegetation types (with accuracy > 70%) were birch and aspen forest, tundra-steppe complex, *Kobresia* tundra, desert-steppe and dark-coniferous forest (Table 1). The largest overlaps were between vegetation types that belonged to the same group in the second model.

The second model, with merged vegetation types, had an overall accuracy of 70.1% (Table 2). The highest accuracy for an individual cover type was for glaciers (86.6%) followed by forest-steppe (78.1%). Considerable overlap was found between forest-steppe and forest (almost 43%) and between forest-tundra and grassland (33%). Grassland had the lowest accuracy, being classified also to other categories except forest. The reason for the low accuracy of grassland classification was probably because it occurs in the mid-range of gradient of climatic conditions found within the study area (Fig. 3).

3.2. Vegetation distribution model for the LGM

The LGM model with finer classification of vegetation types predicted only 6 of the currently occurring 14 types (Fig. 4, Table 3). Desert-steppe was modelled as the dominant LGM vegetation type in the Russian Altai, occupying 47.5% of the area, with a mean probability of occurrence of 26%. For the same area, other vegetation types with relatively high probabilities of occurrence were steppe (13%) and high-mountain tundra (10%). In the current distribution of vegetation types, the desert-steppe is rather restricted, being confined to dry areas in the southeast, namely the Chuya Basin at altitudes of 1480–2700 m, covering only 1.5 % of the Altai region. The second most common LGM vegetation type predicted by the model was the high-mountain tundra (17.9%), which tended to be associated with more precipitation-rich areas, especially in the mountain groups covered by glaciers. Subalpine open woodlands and larch forests, which currently dominate in the central part of the study area, were predicted for the LGM for the northern part, occupying areas of 3.3% and 3.0% of the Altai region, respectively. This area is currently covered mainly by

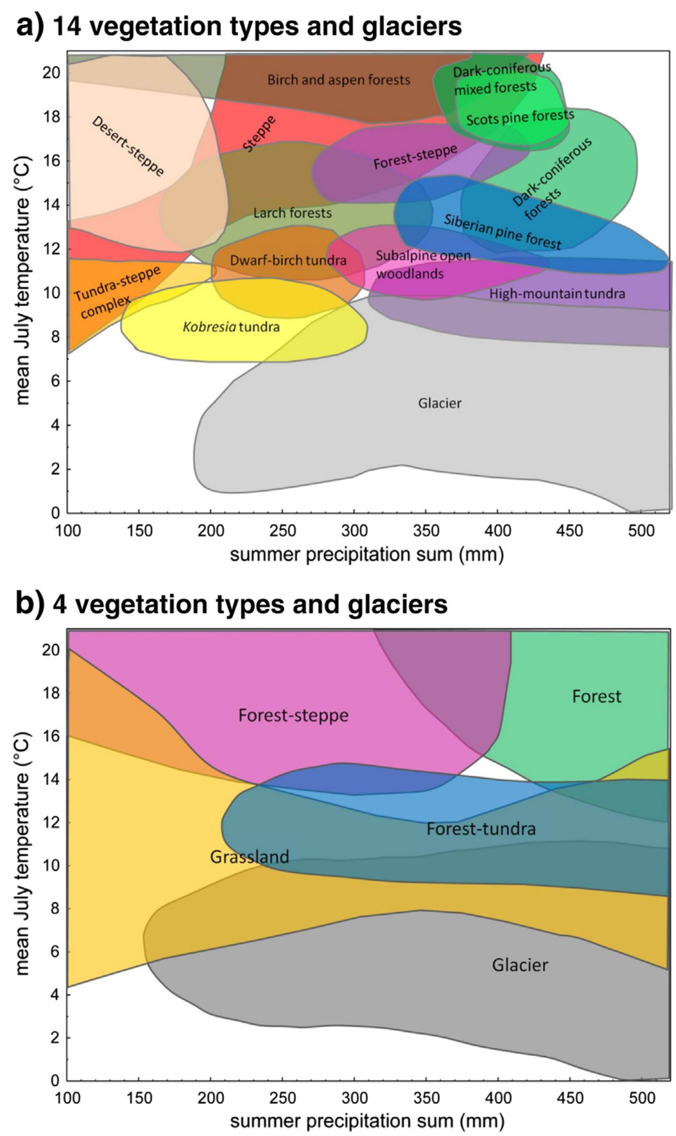

Fig. 3. Distribution of vegetation types and glaciers in the climatic space of mean July temperatures and summer precipitation sums. Areas with an occurrence probability >0.5, as identified by the RF model, are shown.

Table 1
Cross-tabulation of the observed vegetation types (finer classification into 14 vegetation types and glaciers) and those predicted by the RF model for the current vegetation of the Russian Altai. The value for each vegetation type is the percentage accounted for by it of the total number of pixels. The intensity of shading increases proportionally to the percentage value.

		predicted														
	Vegetation types	Dark-coniferous mixed forest	Dark-coniferous forest	Birch and aspen forest	Larch forest	Siberian pine forest	Scots pine forest	Subalpine open woodland	Dwarf-birch tundra	High-mountain tundra	*Kobresia* tundra	Steppe	Desert-steppe	Tundra-steppe complex	Forest-steppe	Glacier
observed	Dark-coniferous mixed forest	49.9	5.6	18.2	0	0	26.3	0	0	0	0	0	0	0	0	0
	Dark-coniferous forest	5	77.2	0.9	2.9	5.3	3.2	3.7	0	0	0	0.2	0	0	1.6	0
	Birch and aspen forest	10.5	2.4	70.4	1.7	0.1	2.8	0	0	0	0	4.8	0.6	0	6.7	0
	Larch forest	1.6	1.3	3.5	37.1	24	0.1	5.1	0.2	0.6	0	3.4	1.8	1.4	19.9	0
	Siberian pine forest	0	3.7	0.9	13.3	53.8	0	6.2	0.1	0.2	0	3.4	1.3	1.2	15.9	0
	Scots pine forest	13.2	9.2	13	0.5	0.1	61.3	0	0	0	0	0	0	0	2.7	0
	Subalpine open woodland	0	1.7	0	4.4	15.4	0	37.5	7.6	17.7	1.7	1.1	0.4	11.6	0.6	0.3
	Dwarf-birch tundra	0	0	0	0.4	0	0	3	46.7	2.7	27.8	0	0.8	14.2	0	4.4
	High-mountain tundra	0	0	0	0.4	3.1	0	13.8	7.3	50.8	6.2	0	0.1	4.6	0.2	13.5
	Kobresia tundra	0	0	0	0	0	0	0	1.2	0.2	75.7	0	0.1	17.3	0	5.5
	Steppe	0.4	0	1.1	3.7	0.7	0	0	0	0	0	48.8	18.1	13.9	13.3	0
	Desert-steppe	0	0	0	0.7	0	0	0	0	0	1.5	8.1	77.8	11.9	0	0
	Tundra-steppe complex	0	0	0	1	0	0	0	1	0	14	4.3	1.4	78.3	0	0
	Forest-steppe	0.6	0.4	11.7	14.9	13.6	0	1.6	0.2	0.4	0	13.6	2.1	1.9	39	0
	Glaciers	0	0	0	0.2	0	0	1.2	10.7	12.7	13.8	0	0	0.2	0	61.2

Table 2
Cross-tabulation of the observed vegetation types (coarser classification into 4 vegetation types and glaciers) and those predicted by the RF model for the current vegetation of the Altai. The value for each vegetation type is the percentage accounted for by it of the total number of pixels. The intensity of shading increases proportionally to the percentage value.

		predicted				
	Vegetation types	Forest	Forest-steppe	Forest-tundra	Grassland	Glacier
observed	Forest	60.3	29.1	8.6	2.1	0
	Forest-steppe	12.8	78.1	4.9	4.1	0.1
	Forest-tundra	8.7	1.7	68.3	14.9	6.5
	Grassland	0.9	7.9	17.9	57.2	16
	Glaciers	0.1	0	6.7	6.4	86.8

dark-coniferous mixed forest. The last two vegetation types predicted for the LGM were birch and aspen forest and Siberian pine forest, each occupying less than 1% of the area. The LGM refugium of the birch and aspen forest was predicted to have been located in the valleys of the Bashkaus and Chulyshman rivers south of Lake Teletskoye. The remaining part of the areas was probably covered by glaciers.

The model considering four vegetation types suggested that 80% of the non-glaciated area of the Russian Altai was covered by grasslands in the LGM (Fig. 5), whereas forest and forest-tundra covered only 10% of the area each, as opposed to their current covers of 34.2% and 19.5%, respectively. Forest-steppe covered less than 1% in the LGM landscape. Forest and associated land-cover types (forest-tundra, forest-steppe) were confined to low altitudes in the LGM.

4. Discussion

4.1. Model results and methodological issues

The models of vegetation–climate relationships developed in this study suggest that the LGM vegetation of the unglaciated part of the Russian Altai Mountains was dominated by grassland, mainly desert-steppe and to some extent also typical steppe, and in some areas, especially at higher altitudes, by vegetation corresponding to the current high-mountain tundra. Today, desert-steppe in the Russian Altai has a

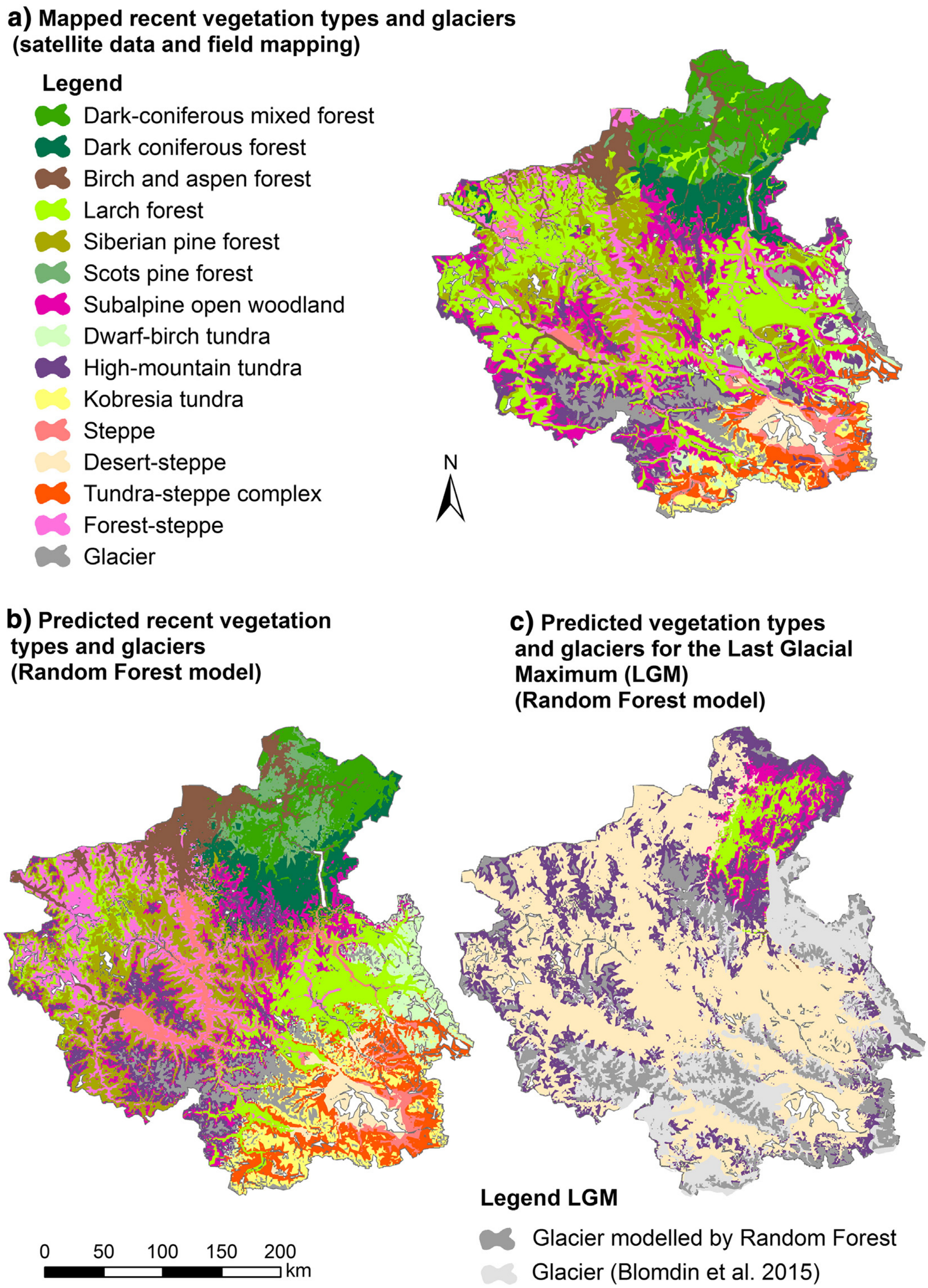

Fig. 4. Map of current vegetation (finer classification, with 14 vegetation types) of the Altai Republic (a); RF models for recent (b) and LGM (c) climates.

rather limited distribution in the southeastern part of this area, being confined to the bottom and slopes of the large intermountain Chuya Basin, which is characterised by extremely continental climate with annual precipitation below 150 mm, mean July temperatures of 14 °C and mean January temperatures of about −32 °C (Modina, 1997). Small patches of the desert-steppe can be found also on the Ukok Plateau. This vegetation type is characterised by dominance of graminoids and dwarf shrubs such as *Artemisia* and *Chenopodiaceae* (Kuminova, 1960; Ogureeva, 1980), and in the current landscape, it occurs in the neighbourhood of typical steppe, tundra-steppe and *Kobresia* tundra. Relict species of plants, snails and mammals that were typical of the Pleistocene landscapes of Europe and northern portion of Asia are currently concentrated in this area (Horsák et al., 2010, 2015; Pavelková Řičánková et al., 2014). However, snails tend to avoid dry habitats of the desert-steppe, being more common in small patches of mesic or even wet habitats such as scrub, woodland patches or fens that occur at suitable sites within the desert-steppe landscape matrix. They also occur in the high-mountain tundra, which was predicted to be found in some discontinuous, restricted areas especially at higher altitudes in the LGM model. In contrast, drier habitats of the desert-steppe are

Table 3
Percentage areas of vegetation types and glaciers in the current and modelled LGM landscape. The entire LGM glacier area is the sum of RF and Blomdin et al. (2015) model predictions, which have a 28% overlap.

	Current vegetation	RF model for the current climate	RF model projection to the LGM climate
Vegetation types			
Dark-coniferous mixed forest	8.9	6.0	
Dark-coniferous forest	5.0	5.7	
Birch and aspen forest	4.9	6.9	0.05
Larch forest	23.2	11.8	3.0
Siberian pine forest	10.5	13.4	0.004
Scots pine forest	1.3	3.3	
Subalpine open woodland	11.9	7.5	3.3
Dwarf-birch tundra	3.5	4.3	
High-mountain tundra	6.9	6.7	17.9
Kobresia tundra	2.2	4.5	
Steppe	3.0	4.4	
Desert-steppe	1.4	2.4	47.5
Tundra-steppe complex	4.3	7.2	
Forest-steppe	6.3	10.1	
Glaciers			
Glaciers (current and RF model)	5.1	4.2	12.3
Glaciers (Blomdin et al., 2015)	–	–	21.7
Total area of glaciers (Blomdin et al., 2015 combined with the RF model)	–	–	27.2
Azonal land-cover units			
Lakes and wetlands	1.5	1.5	1

suitable for several species of relict mammals, e.g., *Allactaga major*, *Equus hemionus*, *Ochotona pallasi*, *Saiga borealis* and *Vulpes corsac*. For large herbivores, low precipitation associated with these habitats can be advantageous in winter, when frozen herbs are not covered by deep snow and can be used for grazing.

The LGM vegetation models cannot be fully validated with independent data because fossil records that would enable habitat reconstruction for the LGM period in the Altai are restricted to very few sites, in particular, in the Anui valley at the northwestern edge of our study area (Agadjanian and Serdyuk, 2005). Nevertheless, in this area, our models and the fossil pollen and vertebrate data are in agreement, both suggesting dry steppe vegetation in the LGM. In contrast, our model slightly underestimated the LGM extent of glaciers, predicting they covered only 12.3% of the area, whereas the recent analysis of glacial geomorphology based on remote sensing suggests that glaciers covered 21.7% of the area (Blomdin et al., 2015). This may indicate deficiencies of the underlying climate data or of our model because the LGM predictions for glaciers were done for lower temperatures than was the range of recent temperatures used for model calibration. However, this difference could instead be due to the remote sensing analysis reflecting the total area that was occupied by glaciers at one time or another (i.e., not simultaneously), and the fact that although glaciers originate at climatically favourable sites (often at high altitudes), they can grow and travel to areas (typically valleys) where climatic conditions are not conducive to their development. For these reasons, in interpretation of the results produced by our models, we also considered the glacial extent reconstructed based on the geomorphological evidence (Blomdin et al., 2015).

One source of possible bias in the LGM models presented here is the potential existence of environments and vegetation types in the LGM that were not analogous to those of today (Williams and Jackson, 2007). First of all, the low atmospheric concentration of CO_2 during the LGM may have disadvantaged more productive, especially woody vegetation (Monin et al., 2001; Harrison and Prentice, 2003). As our models are calibrated based on the vegetation–climate relationship under the current, high CO_2 concentration, they may overestimate the distribution of woody vegetation types. Thus, the prediction of LGM forest occurrence in the northern Altai must be interpreted with caution. Second, the range of current vegetation types used to calibrate the vegetation–climate model may not have encompassed all the possible types that were present in the Russian Altai during the LGM. In particular, cold semi-deserts and deserts similar to those currently occurring in the southern half of Mongolia (Hilbig, 1995; von Wehrden and Wesche, 2009) can be considered as possible alternative LGM vegetation types in some areas where the model projected desert-steppe. However, the structures of desert-steppe, semi-desert and desert are rather similar; therefore, the mutual replacement between these types would not lead to any dramatic changes in the ecosystem properties of the Russian Altai during the LGM.

The coarse resolution of the maps used in this study does not allow modelling of small patches of azonal habitats such as riparian vegetation, which probably differed considerably from the vegetation of zonal habitats. Also, as shown by the low effect of the heat load index in our study, it does not allow modelling vegetation mosaics that reflect slope aspect or relative positions on ridges or slopes. Therefore, the maps that represent the results of our models make an impression of rather homogeneous landscapes. This would be in sharp contrast with the widespread hypothesis that the Pleistocene landscapes of northern Eurasia and North America were fine-scale habitat mosaics providing many contrasting niches for the rich Pleistocene fauna and flora (Guthrie, 2001; Markova et al., 2009). Our models indicate LGM habitat heterogeneity between stream valleys containing more mesic vegetation (some of them even having forest patches) and the areas outside the valleys, dominated by desert-steppes. However, at the coarse scale of this study, we are unable to make any conclusions about the fine-scale habitat heterogeneity that may have existed within each of the broad habitat types that the models projected onto the LGM landscape. Based on our field experience from the southeastern Russian Altai, we suggest that considerable habitat heterogeneity may have existed in this topographically complex landscape, for example between north- and south-facing slopes, wind-swept crests and wetter toe slopes and valley bottoms.

The projection of the LGM forests in the northern Altai near Lake Teletskoye is a notable exception to the general picture of open landscape projected for the other unglaciated areas of the Altai. Currently, this part of the northern Altai has the highest precipitation in the study area and it also had the highest precipitation during the LGM, though much lower than today (Otto-Bliesner et al., 2005). The LGM model projected *Larix* woodland and forest-steppe at lower altitudes of this area, subalpine open woodland of *Larix sibirica* and *Pinus sibirica* (forest-tundra) at mid-altitudes and tundra at higher altitudes. Although this model may partly over-emphasise the distribution of forest due to model calibration reflecting the current concentration of atmospheric CO_2, this projection suggests at least local occurrences of forest-steppe landscape similar to the current landscape of mid-altitudes in the central Russian Altai. This current landscape is heterogeneous, comprising a mosaic of different habitats, and harbours relict Pleistocene biota especially in southern areas where it borders high-mountain landscapes (Horsák et al., 2010, 2015; Pavelková Řičánková et al., 2014).

4.2. A scenario of the history of the relict Pleistocene biota of the Altai

Our modelling results, coupled with evidence from other studies, suggest a scenario of the history of the relict Pleistocene biota in the Altai Mountains. In the period of the last glacial predating the LGM (MIS 3), this biota may have been common in this region (Agadjanian and Serdyuk, 2005), as it was in other areas of northern Eurasia (Markova and van Kolfschoten, 2008). During the LGM, glaciers extended at higher altitudes, but a large area remained unglaciated (Blomdin et al., 2015). According to our scenario, this unglaciated area would have been covered mainly by the desert-steppe, steppe and tundra vegetation types dominated by graminoids, other herbs and dwarf shrubs. Additionally, patches of woody vegetation may have occurred in

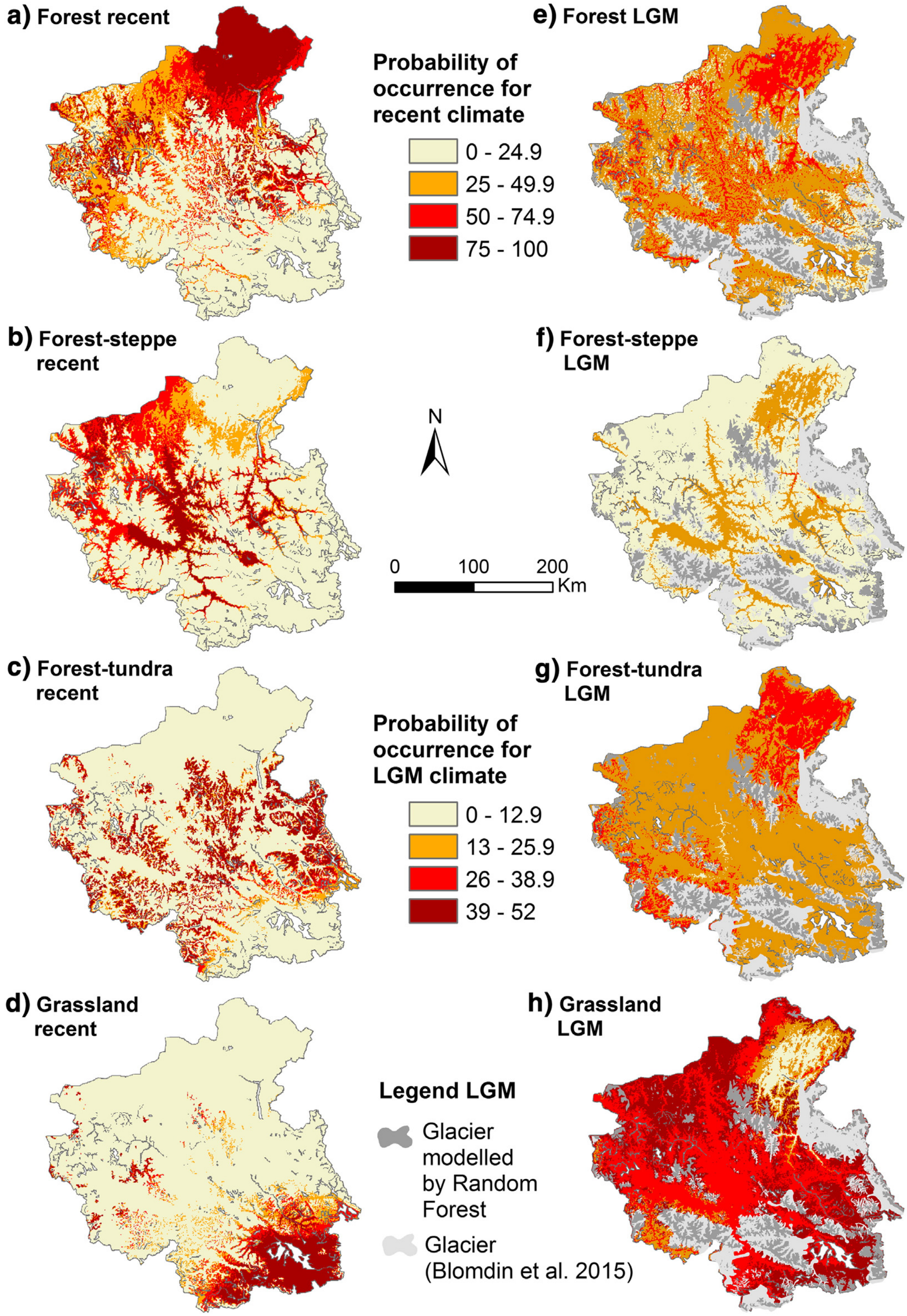

Fig. 5. Percentage probability of occurrence of the four vegetation types and glaciers in the RF models for the recent (a–d) and LGM climates (e–h).

mesoclimatically suitable habitats such as at the bottoms of stream valleys. Similar vegetation mosaics may have been widespread also in the unglaciated areas east of the Altai, in western Mongolia and Tuva. These grassland-dominated landscapes may have been heterogeneous at a fine scale, especially in areas with mountainous topography, which would have created conditions suitable for the survival of many species of the Pleistocene flora and fauna.

More sensitive species requiring mesic, more highly productive ecosystems or shelter may have survived the LGM in the northern Altai north of Lake Teletskoye, or on the western or northern mountain fringes of the Altai, which may have been covered by forests growing on permafrost during the LGM (Böhner and Lehmkuhl, 2005). Indeed, the area north of Lake Teletskoye as well as low mountain ranges adjacent to it to the north harbour several isolated occurrences of plant species typical of mesic deciduous forests, which have been traditionally considered in the Russian botanical literature as relicts of the Tertiary deciduous forests (Polozhii and Krapivkina, 1985; Ermakov, 1998). These include the broad-leaved, temperate tree *Tilia sibirica* (Khlonov, 1965; Novák et al., 2014). Although the age of these relict occurrences is uncertain and their Holocene immigration is one of the possible scenarios, the prediction of forest occurrence during the LGM in the area of their current distribution gives some support to their relict status. It needs to be kept in mind, however, that these relicts are currently confined to dark-coniferous and deciduous forests (mainly of *Abies sibiria*, *Betula pendula* and *Populus tremula*), whereas our model suggests that the forest in this area during the LGM comprised mainly *Larix sibirica* and *Pinus sibirica* woodland.

With climatic amelioration after the LGM, the grassland ecosystems were gradually overgrown by forest (Blyakharchuk et al., 2007; Blyakharchuk, 2010), forming either continuous closed forests in the more precipitation-rich areas or forest-steppe elsewhere (Kuminova, 1960). These habitats, especially the closed forests, were unsuitable for most species of the Pleistocene biota, which was predominantly adapted to grassland ecosystems (Markova and van Kolfschoten, 2008; Pavelková Řičánková et al., 2014). Nevertheless, this biota survived in the southeastern Russian Altai, especially in the Chuya Basin and on the Ukok Plateau, where these grasslands remained preserved, and in similar open landscapes of Mongolia, Kazakhstan as well as in high mountain ranges of Middle Asia. These grasslands have probably experienced very little habitat change since the LGM, although the bottoms of the basins in the southeastern Russian Altai were temporarily flooded by the ice-dammed lakes at the end of the Pleistocene (Rudoy, 2002), and mid-Holocene forest cover was probably more extensive than today (Miehe et al., 2007). Currently, the southeastern Russian Altai is an area with a high concentration of Pleistocene relict species (Horsák et al., 2010, 2015; Pavelková Řičánková et al., 2014). Our models support the hypothesis that relatively large areas of desert-steppe and similar grasslands have existed there continuously since the LGM and served as a refugium for this relict biota.

5. Conclusions

Based on the mapping of the current vegetation of the Russian Altai and on distribution modelling of vegetation types in the same area for the Last Glacial Maximum, we suggest the following:

1 The dominant LGM vegetation of the majority of the non-glaciated area of the Russian Altai was grassland, especially desert-steppe, with smaller patches of typical steppe and tundra. Woodland patches probably occurred in suitable habitats such as stream valleys. This grassland-dominated landscape supported the typical full-glacial flora and fauna.

2 In the warmer and wetter climate of the Holocene, this open grassland-dominated landscape changed into forest-steppe and forest-dominated landscape across most of the area. Large grassland areas remained preserved especially in the dry and cool areas of the southeastern Russian Altai (Chuya Basin and Ukok Plateau), which serve as a refugium with continuous existence of the relict Pleistocene biota.

3 During the LGM, larger forest areas may have existed in the northeastern Altai north of Lake Teletskoye. This area and the hilly landscapes adjacent to the north may have acted as a full-glacial refugium of some temperate forest species that currently occur in this area.

Acknowledgements

Michal Horsák, Věra Pavelková Řičánková and two anonymous referees provided valuable comments on a previous version of this paper. Frank Lehmkuhl gave us advice on the interpretation of the LGM glaciation in the Altai, Robin Blomdin provided data on the maximum glaciation extent, Jan Wild gave us advice on the downscaling of the LGM climatic data and Jonathan Rosenthal improved our English text. This study was supported by the Czech Science Foundation (project P504/11/0454); KK was also supported by the project LM2011028; NE prepared the current vegetation map with support of the Russian Science Foundation (15-14-04928). Author contributions: MC conceived the study; NE prepared the current vegetation map; MH performed GIS analyses; KK computed RF analyses; MC, MH and KK wrote the text; all authors discussed the results and their interpretations.

References

Agadjanian, A.K., Serdyuk, N.V., 2005. The history of mammalian communities and paleogeography of the Altai Mountains in the Paleolithic. Paleontol. J. 39 (Suppl. 6), S645–S821.

Allen, J.R.M., Hickler, T., Singarayer, J.S., Sykes, M.T., Valdes, P.J., Huntley, B., 2010. Last glacial vegetation of northern Eurasia. Quat. Sci. Rev. 29, 2604–2618.

Attorre, F., Alfò, M., De Sanctis, M., Francesconi, F., Valenti, R., Vitale, M., Bruno, F., 2011. Evaluating the effects of climate change on tree species abundance and distribution in the Italian Peninsula. Appl. Veg. Sci. 14, 242–255.

Blomdin, R., Heyman, J., Stroeven, A.P., Hättestrand, C., Harbor, J.M., Gribenski, N., Jansson, K.N., Petrakov, D.A., Ivanov, M.N., Alexander, O., Rudoy, A.N., Walther, M., 2015. Glacial geomorphology of the Altai and Western Sayan Mountains, Central Asia. J.Maps http://dx.doi.org/10.1080/17445647.2014.992177.

Blyakharchuk, T.A., 2010. Poslelednikovaya dinamika rastitel'nogo pokrova Zapadno-Sibirskoj ravniny i Altae-Sayanskoj gornoi oblasti (po dannym sporovo-pyl'tsevogo analiza bolotnykh i ozernykh otlozhenii) [Postglacial dynamics of plant cover of the West Siberian Plain and the Altai-Sayan mountain system (based on the data from spore-pollen analysis of mire and lake sediments)]. Tomskii gosudarstvennyi universitet, Tomsk.

Blyakharchuk, T.A., Wright, H.E., Borodavko, P.S., van der Knaap, W.O., Ammann, B., 2007. Late Glacial and Holocene vegetational history of the Altai Mountains (southwestern Tuva Republic, Siberia). Palaeogeogr. Palaeoclimatol. Palaeoecol. 245, 518–534.

Böhner, J., Lehmkuhl, F., 2005. Environmental change modelling for Central and High Asia: Pleistocene, present and future scenarios. Boreas 34, 220–231.

Breiman, L., 2001. Random forests. Mach. Learn. 45, 5–32.

Breiman, L., Friedman, J.H., Olshen, R.A., Stone, C.J., 1984. Classification and Regression Trees. Chapman and Hall, New York, US.

Chernykh, D.V., Samoilova, G.S., 2011. Landshafty Altaya (Respublika Altai i Altajskii krai). Karta – 1:500000. [Landscapes of the Altai (Altai Republic and the Altai Region). Map – 1:500000]. FGUP Novosibirskaya kartfabrika, Novosibirsk.

Cutler, D.R., Edwards, T.C., Beard, K.H., Cutler, A., Hess, K.T., Gibson, J., Lawler, J.J., 2007. Random forests for classification in ecology. Ecology 88, 2783–2792.

Derevianko, A.P., Postnov, A.V., Rybin, E.P., Kuzmin, Y.V., Keates, S.G., 2005. The Pleistocene peopling of Siberia: a review of environmental and behavioural aspects. Bull. Indo-Pac. Prehist. Assoc. 25, 57–68.

Ermakov, N.B., 1998. The Altaian relict subnemoral forest belt and the vegetation of pre-Pleistocene mountainous landscapes. Phytocoenologia 28, 31–44.

Freeman, E.A., Moisen, G.G., Frescino, T.S., 2012. Evaluating effectiveness of down-sampling for stratified designs and unbalanced prevalence in Random Forest models of tree species distributions in Nevada. Ecol. Model. 233, 1–10.

Gerald, C., Wheatley, P., 1989. Applied Numerical Analysis, fourth edition. Addison-Wesley, Reading, MA.

Guthrie, R.D., 2001. Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. Quat. Sci. Rev. 20, 549–574.

Harrison, S.P., Prentice, I.C., 2003. Climate and CO_2 controls on global vegetation distribution at the last glacial maximum: analysis based on palaeovegetation data, biome modelling and palaeoclimate simulations. Glob. Chang. Biol. 9, 983–1004.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.

Hilbig, W., 1995. The Vegetation of Mongolia. SPB Academic Publishing, Amsterdam.

Hoffmann, M.H., Meng, S., Kosachev, P.A., Terechina, T.A., Silanteva, M.M., 2011. Land snail faunas along an environmental gradient in the Altai Mountains (Russia). J. Molluscan Stud. 77, 76–86.

Horsák, M., Chytrý, M., Pokryszko, B.M., Danihelka, J., Ermakov, N., Hájek, M., Hájková, P., Kintrová, K., Kočí, M., Kubešová, S., Lustyk, P., Otýpková, Z., Pelánková, B., Valachovič, M., 2010. Habitats of relict terrestrial snails in southern Siberia: lessons for the reconstruction of palaeoenvironments of full-glacial Europe. J. Biogeogr. 37, 1450–1462.

Horsák, M., Chytrý, M., Hájková, P., Hájek, M., Danihelka, J., Horsáková, V., Ermakov, N., German, D.A., Kočí, M., Lustyk, P., Nekola, J.C., Preislerová, Z., Valachovič, M., 2015. European glacial relict snails and plants: environmental context of their modern refugial occurrence in Southern Siberia. Boreas (accepted).

Iverson, L.R., Prasad, A.M., Matthews, S.N., Peters, M., 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. For. Ecol. Manag. 254, 390–406.

Khlonov, Yu.P., 1965. Lipy i lipnyaki zapadnoi Sibiri (rasprostranenie, lesovodstvennye svoistva, tipy lesov, iskusstvennye posadki) [Limes and lime forests in Western Siberia (Distribution, forestry properties, forest types, artificial plantations)]. SO AN SSSR, Novosibirsk.

Kuhle, M., 2004. The high glacial (last Ice Age and LGM) ice cover in high and central Asia. In: Ehlers, J., Gibbard, P.L. (Eds.), Quaternary Glaciations Extent and Chronology. Part III: South America, Asia, Africa, Australasia, Antarctica. Elsevier, Amsterdam, pp. 175–199.

Kuminova, A.V., 1960. Rastitel'nyi pokrov Altaya (Plant cover of the Altai). SO AN SSSR, Novosibirsk.

Kuneš, P., Pelánková, B., Chytrý, M., Jankovská, V., Pokorný, P., Petr, L., 2008. Interpretation of the last-glacial vegetation of eastern-central Europe using modern analogues from southern Siberia. J. Biogeogr. 35, 2223–2236.

Lehmkuhl, F., Klinge, M., Stauch, G., 2011. The extent and timing of Late Pleistocene glaciations in the Altai and neighbouring mountain systems. In: Ehlers, J., Gibbard, P.L., Hughes, P.D. (Eds.), Quaternary Glaciations—Extent and Chronology. A Closer Look. Elsevier, Amsterdam, pp. 967–979.

Liaw, A., Wiener, A., 2006. The randomForest package. http://cran.r-project.org/web/packages/randomForest.pdf.

Magyari, E.K., Kuneš, P., Jakab, G., Sümegi, P., Pelánková, B., Schäbitz, F., Braun, M., Chytrý, M., 2014. Late Pleniglacial vegetation in eastern-central Europe: are there modern analogues in Siberia? Quat. Sci. Rev. 95, 60–79.

Markova, A.K., van Kolfschoten, T. (Eds.), 2008. Èvolyutsiya èkosistem Evropy pri perekhode ot pleistotsena k golotsenu (24–8 tys. l. n.). Tovarishchestvo nauchnykh izdanii KMK, Moskva.

Markova, A.K., Simakova, A.N., Puzachenko, A.Yu., 2009. Ecosystems of Eastern Europe at the time of maximum cooling of the Valdai glaciation (24–18 kyr BP) inferred from data on plant communities and mammal assemblages. Quat. Int. 201, 53–59.

Meng, S., 2009. Rezente zentralasiatische und pleistozäne mitteleuropäische Faunen mit *Vallonia tenuilabris* (A. Braun, 1843). Mollusca 27, 61–82.

Miehe, G., Schlütz, F., Miehe, S., Opgenoorth, L., Cermak, J., Samiya, R., Jäger, E.J., Wesche, K., 2007. Mountain forest islands and Holocene environmental changes in Central Asia: a case study from the southern Gobi Altay, Mongolia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 250, 150–166.

Modina, T.D., 1997. Klimaty Respubliki Altai [Climates of the Altai Republic]. Izdatel'stvo NGU, Novosibirsk.

Monin, E., Indermuhle, A., Dallenbach, A., Fluckiger, J., Stauffer, B., Stocker, T.F., Raynaud, D., Barnola, J.-M., 2001. Atmospheric CO_2 concentrations over the last glacial termination. Science 291, 112–114.

Nekola, J.C., Coles, B.F., Horsák, M., 2015. Species assignment in *Pupilla* (Gastropoda: Pulmonata: Pupillidae): integration of DNA-sequence data and conchology. J. Molluscan Stud. 81, 196–216.

Novák, J., Trotsiuk, V., Sýkora, O., Svoboda, M., Chytrý, M., 2014. Ecology of *Tilia sibirica* in a continental hemiboreal forest, southern Siberia: an analogue of a glacial refugium of broad-leaved temperate trees? The Holocene 24, 908–918.

Ogureeva, G.N., 1980. Botanicheskaya geografiya Altaya [Plant Geography of the Altai]. Nauka, Moskva.

Otto-Bliesner, B.L., Brady, E.C., Clauzet, G., Tomas, R., Levis, S., Kothavala, Z., 2005. Last Glacial Maximum and Holocene climate in CCSM3. J. Clim. 19, 2526–2544.

Pavelková Řičánková, V., Robovský, J., Riegert, J., 2014. Ecological structure of Recent and Last Glacial mammalian faunas in northern Eurasia: the case of Altai–Sayan refugium. PLOS ONE 9, e85056.

Polozhii, A.V., Krapivkina, È.D., 1985. Relikty tretichnykh shirokolistvennykh lesov vo flore Sibiri [Relicts of Tertiary Broad-Leaved Forests in the Flora of Siberia]. Izdatel'stvo Tomskogo gosudarstvennogo universiteta, Tomsk (in Russian).

Rudoy, A.N., 2002. Glacier-dammed lakes and geological work of glacial superfloods in the Late Pleistocene, Southern Siberia, Altai Mountains. Quat. Int. 87, 119–140.

Rudoy, A.N., Rusanov, G.G., 2012. Poslednee olednenie severo-zapadnogo Altaya (The last glaciation of north-western Altai Mountains). 2nd edition. Izdatel'stvo NTL, Tomsk.

Schlütz, F., Lehmkuhl, F., 2007. Climatic change in the Russian Altai, southern Siberia, based on palynological and geomorphological results, with implications for climatic teleconnections and human history since the middle Holocene. Veg. Hist. Archaeobot. 16, 101–118.

Tchebakova, N.M., Blyakharchuk, T.A., Parfenova, E.I., 2009. Reconstruction and prediction of climate and vegetation change in the Holocene in the Altai–Sayan mountains, Central Asia. Environ. Res. Lett. 4, 045025.

von Wehrden, H., Wesche, K., 2009. Plant communities of the southern Mongolian Gobi. Phytocoenologia 39, 331–376.

Williams, J.W., Jackson, S.T., 2007. Novel climates, no-analog communities, and ecological surprises. Front. Ecol. Environ. 5, 475–482.