Last glacial maximum biomes reconstructed from pollen and plant macrofossil data from northern Eurasia

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Abstract

Pollen and plant macrofossil data from northern Eurasia were used to reconstruct the vegetation of the last glacial maximum (LGM: $18,000 \pm 2000$ [14]C yr BP) using an objective quantitative method for interpreting pollen data in terms of the biomes they represent (Prentice *et al.*, 1996). The results confirm previous qualitative vegetation reconstructions at the LGM but provide a more comprehensive analysis of the data.

Tundra dominated a large area of northern Eurasia (north of 57°N) to the west, south and east of the Scandinavian ice sheet at the LGM.

Steppe-like vegetation was reconstructed in the latitudinal band from western Ukraine, where temperate deciduous forests grow today, to western Siberia, where taiga and cold deciduous forests grow today. The reconstruction shows that steppe graded into tundra in Siberia, which is not the case today.

Taiga grew on the northern coast of the Sea of Azov, about 1500 km south of its present limit in European Russia. In contrast, taiga was reconstructed only slightly south of its southern limit today in south-western Siberia.

Broadleaved trees were confined to small refuges, e.g. on the eastern coast of the Black Sea, where cool mixed forest was reconstructed from the LGM data.

Cool conifer forests in western Georgia were reconstructed as growing more than 1000 m lower than they grow today. The few scattered sites with LGM data from the Tien-Shan Mountains and from northern Mongolia yielded biome reconstructions of steppe and taiga, which are the biomes growing there today.

Keywords

Biomes, Former Soviet Union, last glacial maximum, Mongolia, plant functional types, pollen data, vegetation changes, vegetation map.

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INTRODUCTION

Data from the Former Soviet Union (FSU) and Mongolia are important to global palaeoenvironmental studies because of the broad area covered by these countries. The geographical gradients of modern vegetation and climate across this area are largely determined by: (1) distance from the Atlantic Ocean, causing a west-to-east gradient of decreasing precipitation; and (2) solar radiation, causing a south-to-north gradient of decreasing temperatures. Modelling studies have shown that the enlarged continental ice sheets in high- to mid-latitudes of the northern hemisphere during the last glacial maximum (LGM: 18,000 ^{14}C yr BP or 21,000 calendar BP) substantially altered the atmospheric circulation and the position of Westerlies in northern Eurasia (Broccoli & Manabe, 1987; COHMAP Members, 1988; Harrison *et al.*, 1992; Felzer *et al.*, 1996; Felzer *et al.*, 1998; Kutzbach *et al.*, 1998). Continental-scale syntheses of past lake-level and pollen records provide an excellent opportunity to test this hypothesis (Peterson *et al.*, 1979; Harrison *et al.*, 1996; Kutzbach *et al.*, 1998).

Qualitative reconstructions of northern Eurasian vegetation at the LGM have been presented by, e.g., Giterman *et al.* (1968), Gerasimov & Velichko (1982), Grichuk (1984), Adams *et al.* (1990) and Frenzel *et al.* (1992). Since these compilations were made, the number of radiocarbon dated pollen records has increased and new, objective methods of reconstructing vegetation from pollen and plant macrofossil data have been developed (Prentice *et al.*, 1996; Tarasov *et al.*, 1998). It is therefore appropriate to re-examine the evidence for LGM vegetation patterns.

The aims of this paper are: (1) to present a compilation of 18,000 ^{14}C yr BP pollen and plant macrofossil data from northern Eurasia; (2) to reconstruct the biomes at these sites using the pollen and macrofossil data; (3) to examine the climatic implications of the data and biome reconstructions; and (4) to discuss the palaeoclimatic significance of the reconstructed spatial distributions of biomes and the climatic mechanisms that led to the patterns. This paper complements the earlier synthesis and biomization of modern and mid-Holocene pollen and plant macrofossil data from the same region made by Tarasov *et al.* (1998).

DATA AND METHODS

Pollen data for 18,000 ^{14}C yr BP

We collected pollen and plant macrofossil records dated to 18,000 ± 2000 ^{14}C yr BP from northern Europe, central and western FSU (west of 130°E) and Mongolia from published and unpublished sources. We refer to this study region as northern Eurasia (following Tarasov *et al.*, 1998). The region can be considered a natural geographical unit because it has generally plain relief which results in broadly zonal patterns of climate and vegetation. Furthermore, the region is large enough to allow for telling comparisons between palaeo-environmental reconstructions and the results from atmospheric general circulation models. The eastern part of Russia (east of 130°E) is topographically complex and the vegetation has more affinities with that of Alaska than with the vegetation west of the Verkhoyansk Range. Biome reconstructions for the eastern part of Russia (east of 130°E) at 0, 6000 and 18,000 ^{14}C yr BP are presented by Edwards *et al.* (2000).

The LGM data set includes 39 pollen and two plant macrofossil spectra (Table 1). Only five records are from sites above 1000 m; the others are from the plains. Most of the records (32) are primary counts (Fig. 1). Prentice *et al.* (1996) suggested that priority should be given to primary pollen counts rather than digitized pollen data because minor pollen taxa (mainly herbaceous) may be of key importance for distinguishing non-arboreal biomes (e.g. tundra, steppe and desert). Tarasov *et al.* (1998) showed that reconstructions based on primary pollen data from northern Eurasia produced a better result (with 81% of the biomes correctly predicted) than digitized data (with only 69% correctly predicted). However, it was necessary to include 9 radiocarbon dated spectra digitized from published pollen and macrofossil diagrams in order to improve our coverage for specific regions (Fig. 1). Pollen and plant macrofossil spectra from northern Eurasia attributed to the last glacial maximum contain *c.* 35% less taxa than Holocene spectra (Tarasov *et al.*, 1998), reflecting the decreased diversity of the northern Eurasian flora during the maximum phase of the last glaciation, when most thermophilous plants survived in local refuges or had low pollen production (Grichuk, 1973, 1984). Pollen assemblages for 18,000 ^{14}C yr BP usually contain *c.* 10–15 terrestrial taxa and never more than 23 taxa. The paucity of taxa makes the use of digitized data for 18,000 ^{14}C yr BP less problematic.

There are only 14 records with radiocarbon dates from the interval 16,000–20,000 ^{14}C yr BP and 7 records with radiocarbon dates within 2000 years of that interval (Fig. 1, Table 1). We include 20 other records that are poorly dated, including 7 where the chronology is based on stratigraphic and/or palynological correlation because there are no radiocarbon dates, in order to improve the geographical coverage in Georgia and West Siberia. The use of pollen and stratigraphic correlation provides an adequate chronological control for sites from regions with well-developed late Pleistocene stratigraphic schemes, e.g. Georgia (Chetvertichnaya sistema Gruzii, 1982) or West Siberia (Arkhipov, 1971; Kind, 1974; Arkhipov & Volkova, 1994), or where the record can be directly correlated to a nearby radiocarbon dated site. We rejected more than 100 sites (cf. Grichuk, 1984) where the chronological control did not meet these standards. We selected the pollen or macrofossil sample closest to 18,000 ^{14}C yr BP, provided it fell within a ± 2000 yr window of the target date, rather than interpolating between pollen spectra. This is the same method used to select data for our earlier biomization (Tarasov *et al.*, 1998). Most of the late Quaternary pollen records (except discontinuous records from archaeological sites) were sampled at 25–50 cm intervals and the thickness of the samples taken for pollen analyses was up to 10 cm. Thus, an individual sample could represent up to 500–1000 years of sedimentation.

Descriptions of the modern vegetation at all the LGM sites were derived from the map of potential modern

Table 1 Characteristics of the LGM pollen and plant macrofossil sites. Macrofossil sites are indicated by #. Digitized sites are indicated by *. Dating control (DC) is a measure of the accuracy of the identification of the 18,000 ^{14}C yr BP time-slice and follows the scheme for discontinuous records given in Yu & Harrison (1995) and Tarasov et al. (1996), where 1D, 2D, 3D, 4D, 5D and 6D indicate a radiometric date within 250, 500, 750, 1000, 1500 and 2000 years, respectively, of 18,000 ^{14}C yr BP and 7 indicates that the records are poorly dated. The abbreviations for the LGM and modern biomes are given in Table 3. For mapping purposes (Figs 1 & 2) some sites (‡) that are close to one another have been displaced slightly. Corr. = Correlation.

| Site name	Country	Lat. (°N)	Long. (°E)	Elev. (m)	Sample type	No. of ^{14}C dates	^{14}C dates used to select LGM records	DC	LGM biome	Modern biome	References
Endletvatn*	Norway	69.73	19.08	35	Core	14	18,100 ± 800 (T-1775a)	1D	TUND	CLDE	Vorren, 1978
Apiancha‡	Georgia	42.97	41.25	450	Core	1	17,300 ± 500 (GIN-2565)	3D	COCO	TEDE	Tsereteli et al., 1982
Kobuleti‡	Georgia	41.90	41.77	1.5	Core	Corr.	None	7	COMX	WAMX	Kvavadze & Dzheiranashvili, 1987
Manavi*	Georgia	41.70	45.45	400	Stratigraphic section	1	20,580 ± 680 (TB-18)	7	STEP	STEP	Tumadzhanov & Gogichaishvili, 1969
Sukhumi‡	Georgia	42.92	40.93	2.7	Core	Corr.	None	7	COCO	WAMX	Kvavadze et al., 1984
Anetovka II (E-28)	Ukraine	47.65	31.10	100	Archaeological site	1	18,040 ± 150 (LE-2424)	1D	STEP	STEP	Arap et al., 1990
Korman‡	Ukraine	48.92	27.17	100	Archaeological site	4	18,000 ± 400 (GIN-719)	1D	STEP	TEDE	Pashkevich, 1977
Molodova V‡	Ukraine	48.92	27.08	100	Archaeological site	4	23,800 ± 800 (MO-11), 17,100 ± 180 (GIN-52)	3D	STEP	TEDE	Pashkevich, 1987
Alymka#	Russia	59.04	68.89	50	Stratigraphic section	1	16,770 ± 160 (SOAN-985)	5D	TUND	TAIG	Krivonogov, 1988
Ayakli-Melkoe	Russia	69.25	89.00	125	Stratigraphic section	2	19,900 ± 500 (GIN-311), 10,700 ± 200	6D	TUND	TUND	Kind, 1974
Belovo‡	Russia	53.00	83.75	n/a	Stratigraphic section	1	32,000 ± 1300 (MGU-211)	7	STEP	CLDE	Markov, 1978
Chulym‡	Russia	57.75	84.00	75	Stratigraphic section	1	21,800 ± 450 (SOAN-550)	7	TUND	TAIG	Volkova, 1980
Chumysh-Kutmanovo*‡	Russia	53.82	83.85	550	Stratigraphic section	1	24,240 ± 2700 (SOAN-31)	7	STEP	TAIG	Grichuk, 1984
Demyanskoe	Russia	59.67	69.75	65	Stratigraphic section	1	46,450 ± 450 (SOAN-2043)	7	STEP	TAIG	Bakhareva, 1983
Fabrika 1 Maya	Russia	56.37	37.19	128	Core	6	12,400 ± 160 (LU-374), 21,140 ± 590 (LU-348)	7	STEP	COMX	Semenenko et al., 1981
Igarskaya Ob	Russia	66.50	65.75	42	Stratigraphic section	1	29,500 ± 520 (SOAN-974)	7	TUND	TAIG	Lazukov & Sokolova, 1959
Isha*	Russia	52.16	87.06	400	Stratigraphic section	3	20,240 ± 740 (LG-59), 15,850 ± 680 (LG-36)	7	STEP	TAIG	Zubakov, 1972
Kalistratiha	Russia	53.50	82.25	n/a	Stratigraphic section	1	31,000 ± 800 (MGU-203)	7	STEP	CLDE	Panychev, 1979
Kolpashevo	Russia	58.25	83.00	62	Stratigraphic section	2	25,000 ± 1300(SOAN-38), 10,650 ± 90 (SOAN-323)	7	TUND	TAIG	Bukreeva & Poleshchuk, 1970
Krasnyi Yar	Russia	55.00	83.00	105	Stratigraphic section	2	23,860 ± 320 (SOAN-332)	7	STEP	CLDE	Bukreeva, 1966
Krivosheino	Russia	57.50	84.00	100	Stratigraphic section	1	38,545 ± 900 (SOAN-342)	7	STEP	TAIG	Levina, 1979
Lipovka	Russia	57.75	63.67	65	Stratigraphic section	2	30,560 ± 240 (LG-37)	7	TAIG	COCO	Volkova, 1966
Malaya Kheta	Russia	69.00	84.75	50	Stratigraphic section	2	35,500 ± 900 (GIN-258), 6800 ± 200 (GIN-25)	7	STEP	TUND	Kind, 1974
Mega‡	Russia	65.00	65.75	45	Stratigraphic section	2	21,900 ± 500 (SOAN-324), 10,650 ± 900 (SOAN-323)	7	STEP	TAIG	Lazukov & Sokolova, 1959
Nadymskaya Ob	Russia	66.33	70.75	45	Stratigraphic section	Corr.	None	7	TUND	TAIG	Kind, 1974
Prizhim‡	Russia	55.17	57.58	350	Archaeological site	3	17,070 ± 1017(IEMEZH-700), 21,085 ± 630 (IERZH-37)	4D	STEP	COMX	Smirnov et al., 1990
Puchka*#	Russia	59.70	39.33	125	Stratigraphic section	2	21,410 ± 150 (LU-18B)	7	TUND	COCO	Chebotareva & Makarycheva, 1974
Sakhta	Russia	56.92	39.58	137	Core	Corr.	None	7	TUND	COMX	Pisareva, 1971
Serpievskaya‡	Russia	55.10	57.67	350	Archaeological site	1	16,585 ± 598 (IEMEZH-722)	5D	STEP	COMX	Smirnov et al., 1990
Skorodum‡	Russia	57.83	71.13	57	Stratigraphic section	Corr.	None	7	TUND	TAIG	Volkova & Nikolaeva, 1982
Skv-469	Russia	57.25	68.17	75	Core	Corr.	None	7	TAIG	COCO	Volkova, 1970
Tugiyany‡	Russia	64.75	66.00	47	Stratigraphic section	1	26,270 ± 270 (SOAN-964)	7	TUND	TAIG	Levina, 1979
Veselo-Voznesenskoe*	Russia	47.17	38.35	38	Stratigraphic section	1	15,690 ± 330 (MGU-IOAN-58)	7	TAIG	STEP	Markov, 1976
Voronovo	Russia	56.00	84.00	62	Stratigraphic section	Corr.	None	7	STEP	TAIG	Bukreeva & Poleshchuk, 1970
Zagvozdino‡	Russia	57.92	71.02	60	Stratigraphic section	1	44,620 ± 1110 (SOAN-1894)	7	STEP	TAIG	Bakhareva, 1983
Chatyrkel'-Kokaigyr*‡	Kirghizstan	40.72	75.30	3530	Stratigraphic section	2	18,300 ± 200 (MGU-352)	2D	STEP	STEP	Shumova, 1974
Chatyrkel'-Dal'nee*‡	Kirghizstan	40.72	75.30	3530	Stratigraphic section	2	19,850 ± 400 (TA-825)	6D	DESE	STEP	Sevastyanov, 1995b
Karakul'-Aisberg	Kirghizstan	39.50	73.50	3914	Stratigraphic section	1	17,430 ± 120 (TA-1679)	3D	STEP	STEP	Sevastyanov, 1995a
Hoton-Nur	Mongolia	48.67	88.30	2083	Core	6	9070 ± 150 (TA-1419)	7	STEP	STEP	Dorofeyuk, unpublished
Kerulen*	Mongolia	47.52	111.27	900	Stratigraphic section	1	19,500 ± 340 (Vib.6)	5D	STEP	STEP	Golubeva, 1976
Tsagan-Mort-Nur	Mongolia	51.21	99.45	1539	Core	5	18,050 ± 200 (TA-1437A)	1D	TAIG	TAIG	Dorofeyuk, unpublished
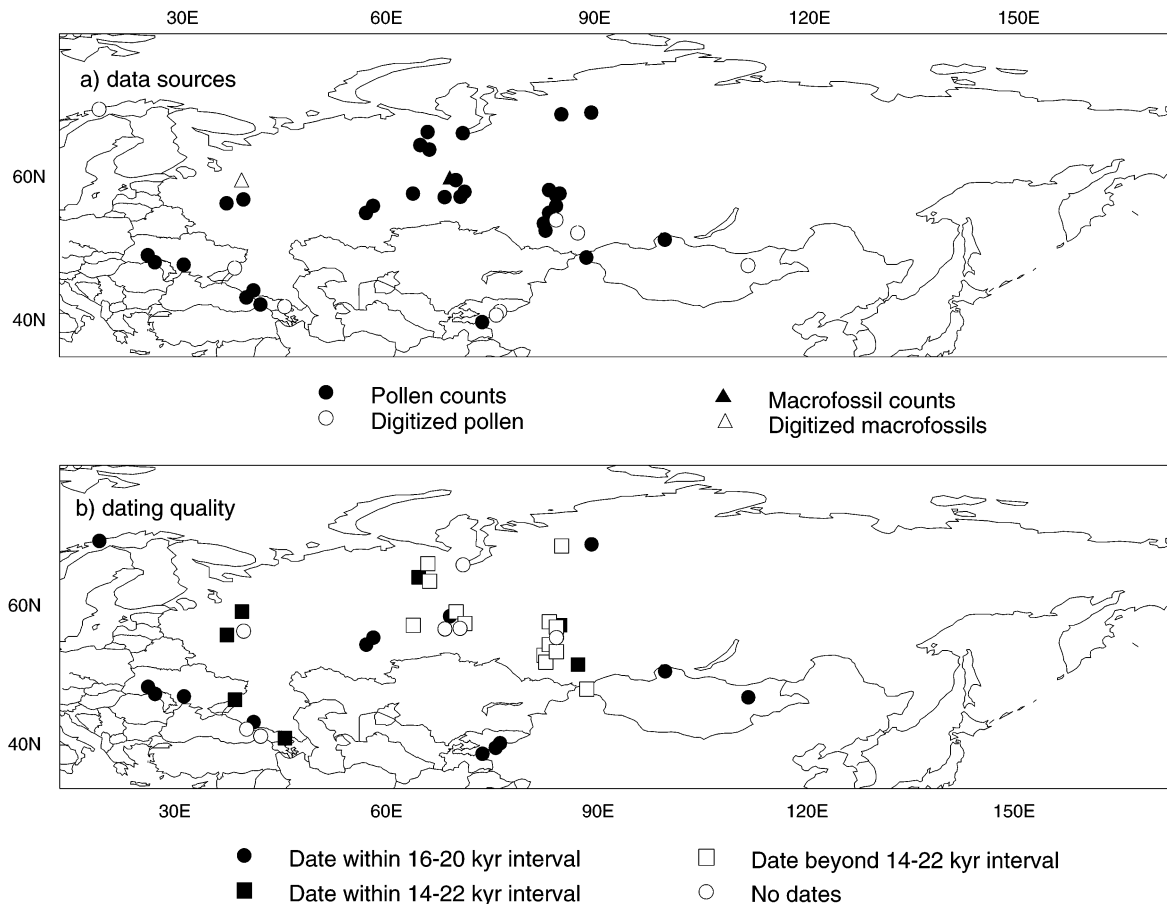
Figure I (a) Distribution of sites with LGM pollen and macrofossil data. ●, primary pollen data; ○, digitized pollen data; ▲, primary plant macrofossil data; △, digitized plant macrofossil data. (b) Dating quality for sites with LGM pollen and macrofossil data. ●, sites with radiocarbon dates within the 18,000 ± 2000 ^{14}C yr BP interval; ■, sites with radiocarbon dates within 2000 years of 16,000–20,000 ^{14}C yr BP; □, sites with radiocarbon dates more than 2000 years from 16,000 to 20,000 ^{14}C yr BP; ○, sites without radiocarbon dates.

vegetation of northern Eurasia, *Fiziko-geograficheskii atlas mira* (Gerasimov, 1964), after converting the terminology used in the atlas into the equivalent biome names (Table 1). The modern vegetation of northern Eurasia has been changed by human activity (especially in the European sector), which can affect the composition of modern surface samples and hence pollen-based biome reconstructions (Prentice *et al.*, 1996; Tarasov *et al.*, 1998), so comparison with a potential vegetation map may be more useful than comparisons based on either maps of actual vegetation or biome reconstructions based on modern surface samples.

Biomization procedure

The biomization method is described in detail by Prentice *et al.* (1996) and consists of four steps: (1) assignment of each pollen taxon to one or more PFTs according to known ecology and biogeography; (2) assignment of characteristic PFTs to biomes according to their bioclimatic range; (3) construction

of a biome-by-taxon matrix used in (4) calculation of the affinity scores for all pollen samples by a simple equation, where the score of a given biome is the sum of the square roots of the percentage (above 0.5%) of each taxon present in the biome.

The biomization method has been applied, with regional modifications, to pollen and macrofossil data from Europe (Prentice *et al.*, 1996), Africa (Jolly *et al.*, 1998), eastern North America (Williams *et al.*, 1998), China (Yu *et al.*, 1998) and northern Eurasia (Tarasov *et al.*, 1998). Tarasov *et al.* (1998) modified the biomization scheme by defining three new PFTs and modifying the taxa-PFT classification developed for Europe to take into account the ecology and geographical distribution of modern plants in northern Eurasia (Hulten & Fries, 1986; Czerepanov, 1995).

We started the present study with the same assignment of pollen taxa to PFTs and PFTs to biomes as Tarasov *et al.* (1998). Tarasov *et al.* (1998) used 94 pollen taxa, after exclusion of aquatic taxa (e.g. *Typha*, *Sparganium*), taxa represented by

Table 2 Assignment of pollen taxa from northern Eurasia to plant functional types (PFTs) used in the biomization procedure.

Abbr.	Plant functional type	Pollen taxa
aa	arctic/alpine dwarf shrub	*Alnus fruticosa*-type, *Alnus* undiff., *Betula nana*-type, *Betula* undiff., *Draba*, *Dryas*, Saxifragaceae, *Salix*, Polygonaceae
ab	arctic/boreal dwarf shrub	*Rubus chamaemorus*
bec	boreal evergreen conifer	*Picea*, *Pinus* (Haploxylon), *Abies*
bs	boreal summergreen	*Betula* (*Albae*), *Betula* undiff., *Alnus* (incl. *A. glutinosa* and *A. incana*), *Alnus* undiff., *Larix*, *Populus*, *Salix*
bts	boreal-temperate summergreen shrub	*Lonicera*
cbc	cool-boreal conifer shrub	*Pinus* (Haploxylon)
ctc	cool-temperate conifer	Abies
df	desert forb	*Artemisia*, Boraginaceae, Chenopodiaceae, *Ephedra*, *Nitraria* Polygonaceae, *Salsola*
ec	eurythermic conifer	*Juniperus*, *Pinus* (Diploxylon)
g	grass	Poaceae
h	heath	Ericales, *Rhododendron*
s	sedge	Cyperaceae
sf	steppe forb	*Allium*, Apiaceae, *Artemisia*, Asteraceae (Asteroideae), Asteraceae (Cichorioideae), Asteraceae undiff., Boraginaceae, Brassicaceae, *Cannabis*, Caryophyllaceae, Chenopodiaceae, Fabaceae, *Hippophae*, Lamiaceae, Polygonaceae, *Plantago*, Plumbaginaceae, Ranunculaceae, Rosaceae, Rubiaceae
ts	temperate summergreen	*Alnus* (incl. *A. glutinosa* and *A. incana*), *Alnus* undiff., *Acer*, *Fraxinus excelsior*-type, *Quercus* (deciduous), *Quercus* undiff., *Salix*
ts1	cool-temperate summergreen	*Carpinus*, *Corylus*, *Fagus*, *Tilia*, *Ulmus*
ts2	warm-temperate summergreen	*Castanea*, *Juglans*, *Pterocarya*
ts3	southern warm-temperate summergreen	*Zelkova*
wte	warm-temperate broadleaved evergreen	*Quercus* undiff.
wte2	warm-temperate sclerophyll shrub	*Rhus*

only one grain (e.g. *Oxalis*), exotic taxa (e.g. *Tsuga, Cedrus*), taxa restricted to local microhabitats (e.g. *Drosera, Geum*) and spores. We excluded the same taxa from the LGM samples, resulting in the use of 60 taxa (Table 2). The northern Eurasian biomes were defined as combinations of PFTs (Table 3), using the same PFT-biome classification as Tarasov *et al.* (1998). Data from Tables 2 & 3 were transformed into a biome-by-taxon matrix for the calculation of affinity scores (Prentice *et al.*, 1996). In the case of tie-breaks, biomes are assigned in the order they appear in Table 3. The same procedure was used to reconstruct biomes from macrofossil (seeds, leaves and other macro-remains) assemblages. Plant macrofossils have a more local source than pollen because of their larger size, but contamination of the macrofossil assemblages by water flow cannot be totally excluded (e.g. Krivonogov, 1988). We therefore used a threshold percentage (0.5%), as with the pollen data, to avoid possible noise due to long-distance transport of the macrofossils.

Climatic interpretation

Quantitative palaeoclimate reconstructions based on pollen and plant macrofossil records from Europe and the western FSU have been made using both statistical calibration methods (Klimanov, 1984; Huntley & Prentice, 1988, 1993; Guiot *et al.*, 1993) and modern-analogue techniques (Guiot, 1990; Cheddadi *et al.*, 1997). Peyron *et al.* (1998) developed an alternative approach based on the climatic calibration of PFTs, which are the basic units used in the BIOME1 model (Prentice *et al.*, 1992a) and in the biomization method (Prentice *et al.*, 1996). The bioclimatic limits of PFTs defined in the BIOME1 model (Prentice *et al.*, 1992a) can be used to interpret PFT and biome distributions in climatic terms. BIOME1 defines the limits of specific PFTs in terms of the mean temperature of the coldest month (MTCO), the mean temperature of the warmest month (MTWA), accumulated growing-season warmth (*GDD*) and a moisture index (α), which is the ratio of actual to equilibrium evapotranspiration. Climate reconstructions

Biome	Code	Plant functional type
tundra	TUND	aa, ab, g, h, s
cold deciduous forest	CLDE	ab, bs, cbc, ec, h
taiga	TAIG	ab, bec, bs, bts, ec, h
cold mixed forest	CLMX	bs, bts, ctc, ec, h, ts1
cool conifer forest	COCO	ab, bec, bs, bts, ctc, ec, h, ts1
temperate deciduous forest	TEDE	bs, bts, ctc, ec, h, ts, ts1, ts2
cool mixed forest	COMX	bec, bs, bts, ctc, ec, h, ts, ts1
broadleaved evergreen/warm mixed forest	WAMX	bts, ec, h, ts, ts1, ts2, ts3, wte
desert	DESE	df
steppe	STEP	g, sf

Table 3 Assignment of plant functional types (PFTs) to biomes in northern Eurasia. Abbreviations for PFTs are given in Table 2. The PFT wte2 is not used in the biomization scheme for northern Eurasia. The single taxon characteristic of this PFT never occurs in abundances greater than 0.5% in the northern Eurasian data set. In other regions wte2 contributes to the biome xerophytic woods/scrub.
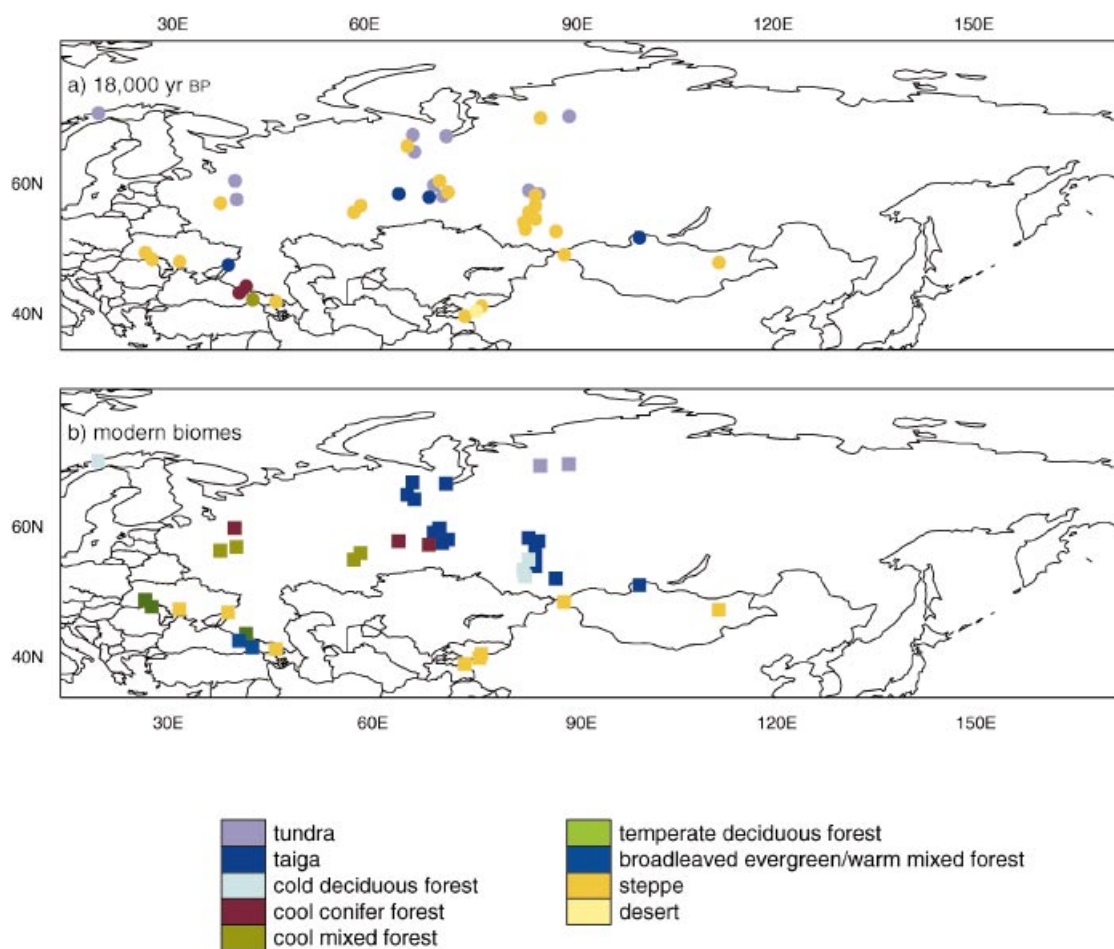
Figure 2 (a) Biomes reconstructed from LGM pollen and plant macrofossil data compared with (b) modern biomes at the same sites derived from a vegetation map (*Fiziko-geograficheskii atlas mira*; Gerasimov, 1964).

from pollen data from Europe (Guiot *et al.*, 1993; Cheddadi *et al.*, 1997) have shown that bioclimatic variables influence modern vegetation and pollen assemblages more directly than more traditional variables such as annual precipitation or mean annual temperature. This method can be used even when the plant assemblages for the LGM have no modern analogues (Prentice *et al.*, 1996; Prentice & Webb, 1998).

We use this method to make qualitative estimates of the changes in climate between the LGM and today.

RESULTS

The geographical pattern of reconstructed biomes for 18,000 ^{14}C BP (Fig. 2a) differs substantially from the

distribution of modern biomes (Fig. 2b). The main changes are:

1 The taiga belt, a characteristic feature of the northern Eurasian vegetation today, was much reduced and discontinuous at 18,000 ^{14}C yr BP Taiga-like vegetation is reconstructed at one site north of the Sea of Azov, about 1500 km south of its modern limit in eastern Europe. The data show taiga in extreme south-western Siberia just east of the Ural watershed, where cool conifer forests grow today. The absence of data from Kazakhstan precludes interpretation of the forest limits there. A single site from Mongolia demonstrates that boreal conifers were confined to the northern part of that country where they grow today.

2 Cool mixed and temperate deciduous forests were not present in the central part of the East European Plain and in the southern Urals, where they grow today. Broadleaved (ts, ts1 and ts2) taxa survived in low elevation sites near the modern coast of the Black Sea in western Georgia. The reconstructions for cool conifer and cool mixed (at the westernmost site) forests at 18,000 ^{14}C yr BP suggest a significant downslope shift of the montane coniferous forest belt dominated by *Abies* and *Picea*. These taxa grow together today above 1700–1800 m (Dolukhanov, 1989).

3 The tundra belt was expanded at 18,000 ^{14}C yr BP compared to today, extending southward to 57°N in European Russia and in western and central Siberia. Tundra was reconstructed at most sites in northern Siberia, but steppe vegetation was reconstructed at two sites. The pollen assemblages of these two sites contain pollen from typical tundra taxa such as *Betula nana*-type and Ericales, but pollen percentages for *Artemisia*, Chenopodiaceae and Poaceae are high, and therefore steppe has the highest affinity score. This reconstruction may reflect the more steppe-like composition of the tundra and/or a broad intergrading of tundra and steppe at 18,000 ^{14}C yr BP.

4 Steppe was the dominant vegetation type across northern Eurasia south of *c.* 57°N and was in direct contact with tundra to the north. Steppe occupied a much larger area in the European sector and southern Siberia and was north of its modern limit. The sparse data from the modern steppe regions in the continental interiors (the Tien-Shan Mountains, northern Mongolia) provide no evidence that 18,000 ^{14}C yr BP biomes differed from those today. Desert was reconstructed at one high-elevation site from Kirghizstan. Reconstructions from two other sites from the same area show steppe, but their second highest affinity score is desert.

DISCUSSION AND CONCLUSIONS

The biomization method that was successfully applied to Holocene pollen and macrofossil data from northern Eurasia (Prentice *et al.*, 1996; Tarasov *et al.*, 1998) has provided a reconstruction of LGM vegetation. The reconstructed spatial patterns of biomes at 18,000 ^{14}C yr BP are consistent with previous continental and regional-scale vegetation reconstructions. The most pronounced features of 18,000 ^{14}C yr BP vegetation shown in earlier reconstructions (Grichuk, 1973, 1984; Chebotareva & Makarycheva, 1974; Kind, 1974;

Gerasimov & Velichko, 1982; Adams *et al.*, 1990; Frenzel *et al.*, 1992; Arkhipov & Volkova, 1994) are: (1) the expansion of the cryoxerophilic vegetation (a combination of steppe and shrub tundra communities and associations of salty soils, with no-analogues in the modern pollen spectra from Europe and Siberia) across the northern mid-latitudes of Eurasia, and (2) the widespread distribution of *Artemisia*-grass steppe and forest-steppe (with *Larix*, *Betula* and *Pinus*) in the southern mid-latitudes of Eurasia. Our results for 18,000 ^{14}C yr BP are in good agreement with these interpretations: we reconstruct steppe at two sites and tundra at the remaining sites in northern Siberia, and an expanded area of steppe to the south of the tundra belt.

Our reconstruction of steppe vegetation in northern Siberia seems plausible on botanical grounds. Steppe–like associations grow today in the extremely continental climate (cold winter and low precipitation) of central Yakutia (Karavaev & Skryabin, 1971; Walter, 1985). Steppe communities usually occupy sunny and relatively dry slopes in the river valleys, and cold deciduous forests and extensive bogs (e.g. tundra analogues) cover watershed flat plains. Steppe elements in the modern flora of northern Eurasia are registered as far north as Wrangel Island (Walter, 1985). Although small amounts of *Artemisia* and Chenopodiaceae are registered in modern pollen samples from Russian tundra (e.g. Savvinova, 1975; Peterson, 1993) and from arctic desert (e.g. Tarasov *et al.*, 1995; Andreev *et al.*, 1997), these taxa were much more important in the fossil pollen spectra from northern Eurasia compared to today (Grichuk, 1973, 1984). Cold dry steppe intergrades today with cold but less dry tundra in the mountains of northern Mongolia (Yunatov, 1950). Modern pollen spectra from this area contain abundant *Artemisia* and Chenopodiaceae pollen and some other taxa assigned to the steppe biome (Chernova & Dirksen, 1995; Tarasov *et al.*, 1998).

Biome reconstructions for Beringia (Edwards *et al.*, 2000) indicate that tundra was the dominant vegetation type at the LGM. There is no evidence for steppe vegetation at the LGM in Beringia. This may reflect a regional difference in vegetation. However, the scheme used to allocate taxa to PFTs in Beringia is slightly different from the one used in this study, in that all of the taxa that we assigned to the steppe forb PFT are allowed to contribute to both steppe forb (and hence steppe) and arctic/alpine dwarf shrubs (and hence tundra) in Beringia. In order to demonstrate that our reconstruction of steppe is not dependent on the PFT assignment of a relatively few non-arboreal taxa, we performed a sensitivity test in which we reclassified all of our steppe forbs as both steppe forbs and arctic/alpine dwarf shrubs. The new biomization resulted in two sites from the mid-latitudes (50–60°N) of western Siberia and four sites from the European sector being reclassified as tundra. However, 16 of the 22 sites originally classified as steppe were also allocated to steppe with the new scheme, and there was no change in the biome reconstructions east of 60°E. Furthermore, the presence of arboreal pollen (chiefly *Pinus*, with some temperate and cool-temperate summergreen taxa) in the LGM spectrum of the site in eastern Georgia (Tumadzhanov & Gogichaishvili, 1969) makes the

classification of this site as tundra under the new scheme somewhat implausible. Our reconstruction of steppe therefore appears to be robust and the existence of tundra vegetation in Beringia probably reflects a spatial gradation between steppe and tundra.

Previous authors have suggested that mixed broadleaved/coniferous and coniferous forests only persisted during the LGM in isolated refuges on the northern coast of the Black Sea, and at low altitudes in the Caucasus, Carpathians, southwestern Ural and western Altay mountains. The western Caucasus and coastal zone of the Black Sea have the most favourable moisture and temperature conditions in northern Eurasia for the growth of broadleaved evergreen/warm mixed forests today (Dolukhanov, 1989), and Grichuk (1984) suggested that these areas were the most likely refuge for the warm flora during the coldest stage of the last glaciation. Our reconstructions for this region, which show a significant lowering of the montane forest belts, are consistent with this suggestion. However, our biome reconstructions (and the composition of the pollen spectra, which contain very little pollen from broadleaved temperate deciduous trees) do not confirm the location of other refugia (e.g. the southern Urals and the southern part of the Middle Russian Upland) suggested by Grichuk (1984).

Malaeva (1989) suggested forest occupied a larger area of the vast plains of northern and central Mongolia at 18,000 ^{14}C yr BP than it does today because summer temperatures were colder and hence evaporation was lower. Other authors (Giterman *et al.*, 1968; Golubeva, 1976, 1978) suggested that the climate was colder and drier than today and that trees could only have survived in refuges. Our reconstructions, though based on a limited number of sites, show vegetation similar to today and thus do not support either hypothesis.

The extension of tundra vegetation south of its present position in the regions where taiga, cold deciduous and cool conifer forests grow today can be explained by a shorter growing season and/or by colder summers than today (Prentice *et al.*, 1992a). The decrease in GDD above 5 °C per day ($GDD_5 < 350$) is sufficient to explain tundra at 18,000 ^{14}C yr BP in Norway at the Atlantic coast, where birch woodland grows today (Vorren, 1978). However, the establishment of tundra in the inner part of northern Eurasia probably requires drier conditions ($\alpha < 0.65$) than today. A northward shift of steppe in eastern Europe and western Siberia is consistent with the climate being drier at the LGM than today and having summers warm enough ($GDD_5 > 500$) to support cool grass/shrub vegetation.

The presence of taiga-like vegetation at 18,000 ^{14}C yr BP at Veselo-Voznesenskoe, north of the Sea of Azov, where the modern vegetation is steppe, indicates conditions wetter ($\alpha > 0.65$) than today. The increase in α was not necessarily associated with higher precipitation, but could be due to a decrease in summer temperature and, consequently, decreased evaporation. The fact that the 18,000 ^{14}C yr BP climate was colder than today may explain the absence of temperate deciduous (broadleaved) trees which have a GDD_5 requirement >1200. Markov (1976) suggested that the pollen from Veselo-Voznesenskoe showed that the mean annual temperature was 20 °C lower than today and annual precipitation was 375 mm, consistent with our interpretation and indicating that conditions were similar to those of the northern taiga on the Kola Peninsula today.

The presence of cool conifer and cool mixed forests in western Georgia, where the potential modern vegetation is broadleaved evergreen/warm mixed forest, suggests colder winters (MTCO < –2 °C) and conditions no drier ($\alpha > 0.75$) than today. Given the reconstructed climate changes further north, these changes were likely associated with summers that were colder than present.

The biome reconstructions indicate that the LGM vegetation in eastern Georgia, Kirghizstan and Mongolia was similar to today. Since the modern vegetation at most sites from these regions is steppe, which has a broad climatic tolerance, the similarity between the LGM and modern vegetation does not necessarily mean that the LGM climate was the same as present. However, reconstruction of steppe and cool desert vegetation at high elevations in the Tien-Shan and Mongolian Altay Mountains at 18,000 ^{14}C yr BP suggests that mountain glaciation in these regions (Bondarev, 1982; Devyatkin, 1993) was not as important as reported in earlier studies (Giterman *et al.*, 1968; Sevastyanov *et al.*, 1980).

The reconstructed patterns of vegetation and climate change can be broadly explained by changes in the global atmospheric circulation caused by the continental ice sheets. Harrison *et al.* (1996) have suggested that lake-level evidence for drier conditions in north-western Europe could be explained by the development of anticyclonic circulation over the Scandinavian ice sheet, promoting strong north-easterly and easterly flow across the southern flank of the ice sheet, and bringing very cold, dry air into the European mid-latitudes. This circulation pattern may also explain the vegetation evidence for drier and colder climate than present in Ukraine and central Russia, and the presence of forests in south-western Siberia, protected by the Urals. Peyron *et al.* (1998) show that MTCO was 25–31 °C lower than today in France and Spain at the LGM, but only 15–20 °C lower than present in the Eastern Mediterranean. Reconstructed values for α were consistently *c.* 0.4–0.7 lower than those today in western Europe.

Pollen records from Italy, Greece, Turkey and Iran are characterized by steppe vegetation at the LGM (Elenga *et al.*, 2000), while lakes in the eastern Mediterranean were higher than today (Prentice *et al.*, 1992b; Harrison *et al.*, 1996). Prentice *et al.* (1992b) showed that high lake levels could coexist with steppe vegetation, without necessitating a change in total annual rainfall, if winter precipitation increased but summer was drier and there was a general cooling and decreased evaporation. Peyron *et al.* (1998) have demonstrated that the 18,000 ^{14}C yr BP climate in the extreme south of Europe and the Near East was characterized by reduced annual precipitation (*c.* 200–500 mm less than today), but an α similar to today (*c.* 0.45–0.65). The same climate may have characterized the eastern and north-eastern coasts of the Black Sea. There, however, summer drought was not as pronounced as in the Mediterranean (because of lower summer temperatures). LGM climate conditions with α similar or slightly higher than today (even if precipitation was lower

than today) would be sufficient to explain the reconstruction of forest in western Georgia and south-western Russia.

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APPENDIX

The maps presented in our earlier publication (Tarasov *et al.*, 1998) were printed with an incorrect colour scheme and key. We therefore take the opportunity of presenting the four maps here (Fig. 3a, b, c, d) in a format identical with our map for 18,000 ^{14}C yr BP (Fig. 2).
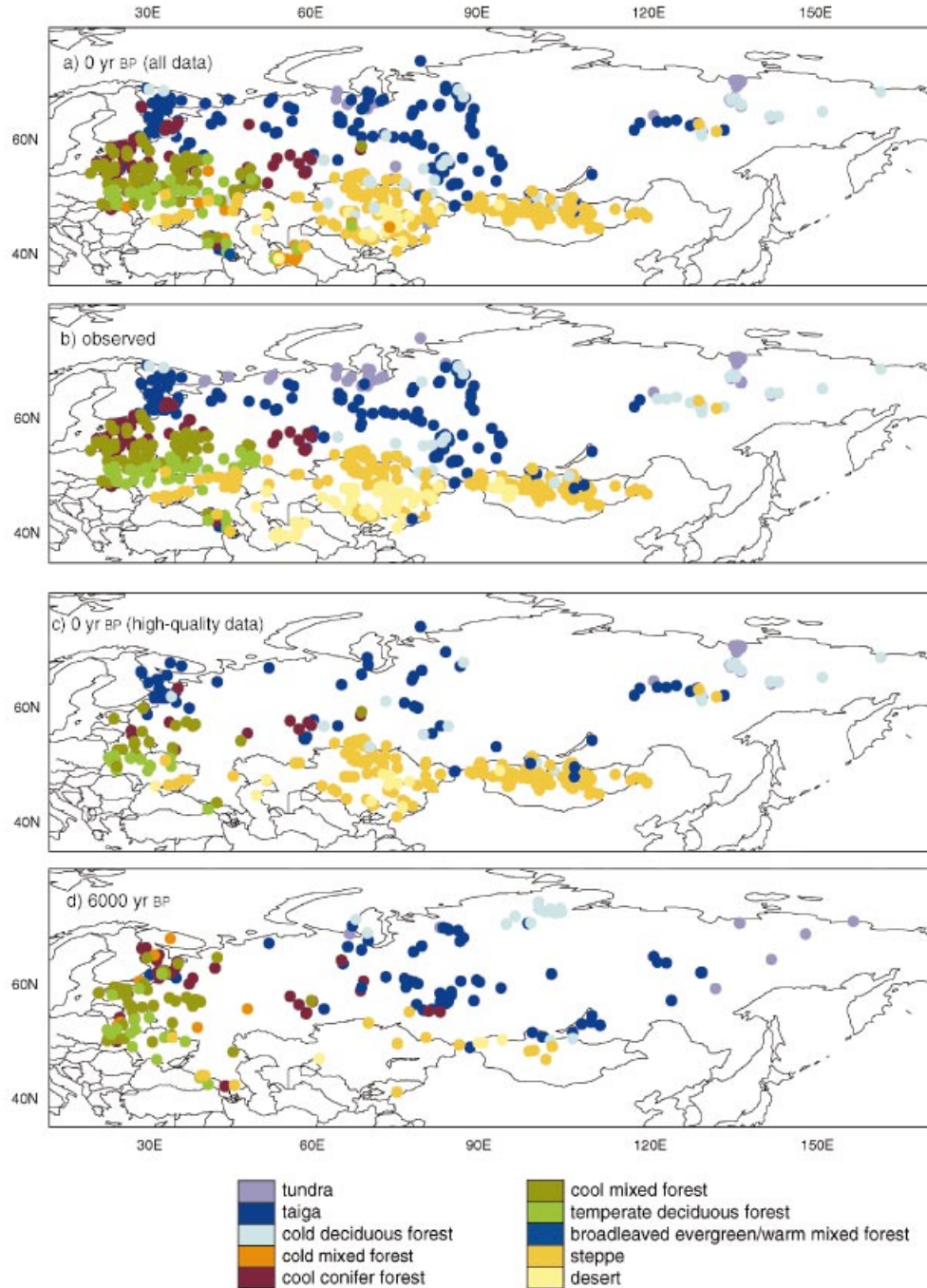

Figure 3 (a) Pollen-derived biomes at 0 ^{14}C BP (all data); (b) observed vegetation at the same sites derived from a vegetation map (*Fiziko-geograficheskii atlas mira*; Gerasimov, 1964); (c) pollen-derived biomes at 0 ^{14}C yr BP (high quality data); (d) pollen- and macrofossil-derived biomes at 6000 ^{14}C yr BP (redrawn from Tarasov *et al.*, 1998).