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Present-day and mid-Holocene biomes reconstructed from pollen and plant macrofossil data from the former Soviet Union and Mongolia

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Abstract. Fossil pollen data supplemented by tree macrofossil records were used to reconstruct the vegetation of the Former Soviet Union and Mongolia at 6000 years. Pollen spectra were assigned to biomes using the plant-functional-type method developed by Prentice *et al.* (1996). Surface pollen data and a modern vegetation map provided a test of the method. This is the first time such a broad-scale vegetation reconstruction for the greater part of northern Eurasia has been attempted with objective techniques. The new results confirm previous regional palaeoenvironmental studies of the mid-Holocene while providing a comprehensive synopsis and firmer conclusions. West of the Ural Mountains temperate deciduous forest extended both northward and southward from its modern range. The northern limits of cool mixed and cool conifer forests were also further north than present. Taiga was reduced in European Russia, but was extended into Yakutia where now there is cold deciduous forest. The northern limit of taiga was extended (as shown by increased *Picea* pollen percentages, and by tree macrofossil records north of the present-day forest limit) but tundra was still present in north-eastern Siberia. The boundary between forest and steppe in the continental interior did not shift substantially, and dry conditions similar to present existed in western Mongolia and north of the Aral Sea.

Key words. Biome, vegetation changes, vegetation maps, plant functional types, pollen taxa, Russia, Former Soviet Union, Mongolia.

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INTRODUCTION

Data from the large area of the countries of the Former Soviet Union (FSU) and Mongolia are of major importance to global palaeoenvironmental studies. The broad plains of this area support vegetation and climate distributed in a generally zonal pattern and thus provide a good opportunity for modelling and data-model comparison. Modern vegetation ranges from polar desert and tundra north of 67–70°N, through a broad (1500–2500 km) forest belt dominated by the boreal conifer species, to the steppe and deserts occupying the continental interior south of 50°N.

Studies of the vegetation history in Russia and the FSU countries, derived mainly from pollen analysis, date back almost a century (Sukachev, 1906; Dokturovskii, 1918; Dokturovskii & Kudryashov, 1923). Neishtadt (1957), Khotinskii (1977, 1984), and Peterson (1983a, 1993) compiled the available pollen data mainly from the forest zone of the USSR and demonstrated that large vegetation changes occurred during the Holocene. These changes were explained in terms of regional changes in temperature and precipitation that are related to global climate changes. However, large areas currently without forests were poorly represented in these syntheses. Peterson (1983a, 1983b) also used isopoll maps to analyse the relationships of modern-pollen spectra to present-day vegetation. His work supported the conclusions of numerous papers published in Russian showing that the spatial patterns in the modern pollen data reflect the zonal vegetation.

Recently Prentice *et al.* (1996) developed a systematic method of biome reconstruction from palaeoecological data and successfully tested it in Europe and northern Africa. This method is designed to aid in constructing global palaeovegetation maps for key times during the late Quaternary. Our study is an application of this method and is a contribution to the BIOME 6000 Project (Prentice & Webb, 1998), which was established in order to produce global palaeovegetation maps from palaeoecological data. The purpose of this study has been to reconstruct biome distributions at 6000 ^{14}C-years BP (6000 years) for the FSU and Mongolia based on expanded modern and 6000 year pollen and macrofossil data sets. The number of radiocarbon dated pollen records has increased during the last 15 years, and we compiled a 6000 year data set of 216 sites: four times more than in the most recent compilation for 6000 years by Peterson (1983a, 1993). A set of 844 surface modern pollen samples were used to check the method and to adapt it for the vegetation of northern Eurasia.

DATA AND METHODS

Area of study

Most of the data come from the western and central parts of the Former Soviet Union and Mongolia, approximating 'northern Eurasia'. This is mainly a rather flat area with a zonal pattern to the vegetation. To the east is the Russian Far East, which extends east of the political boundaries of Yakutia and Buriatia with Khabarovskii Krai, Primorskii Krai and Amurskaya Oblast, going along the mountain ranges of north-eastern and eastern Siberia from $\approx 160°$E at the north to $\approx 110°$E at the south. The political boundary generally corresponds to the natural limit of present-day Pacific monsoon activity. Data from the Russian Far East are being compiled separately within the BIOME 6000 project.

Modern pollen data

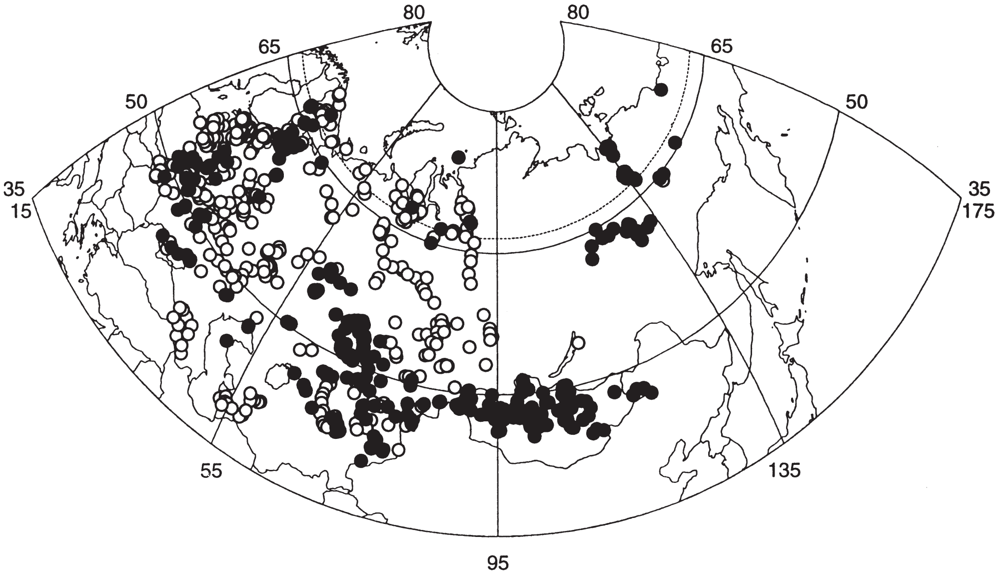
A set of 844 surface pollen spectra was compiled from published and unpublished sources (Fig. 1a). The larger part of this data set (471 samples) consists of primary pollen counts including all identified taxa. This number includes eleven samples (core tops) from Belarus (for the references see Table 1), fifty-eight from the Ukraine (Bezusko, personal communication), sixty from Karelia (Elina, 1981; Elina & Lak, 1989; Elina *et al.* 1994; 1995, 1998; Filimonova, 1985, 1995; personal communication; Filimonova & Elovicheva, 1988), sixteen from European Russia (Afanas'eva, personal communication; Gunova, 1975; Bolikhovskaya, 1990), nineteen from the Ural region (Makovskii & Panova, 1977; Panova, 1981a, 1981b, 1982, 1986, 1990, 1991; Panova & Korotkovskaya, 1990; Panova & Makovskii, 1991; Panova *et al.*, 1996, 1998), ninety-four from the Russian Arctic and Yakutia (Gitterman, 1963; Popova, 1961; Savvinova, 1975a, 1975b; Klimanov & Andreev, 1992; Tarasov *et al.*, 1995), twenty from Tuva (Dirksen, personal communication), ninety-one from Kazakhstan and Kirghizstan (Chupina, 1974; Sevastyanov *et al.*, 1980; Tarasov, 1992), and 102 from Mongolia (Mal'gina, 1971; Metel'tseva, personal communication; Sokolovskaya, personal communication).

To improve coverage over the western part of the FSU, an additional 373 modern pollen spectra were derived from published data sets of digitized pollen abundances (Peterson, 1983a, 1983b, 1993). These data were previously used in climate (Guiot *et al.*, 1993; Peterson, 1993; Cheddadi *et al.*, 1997) and biome reconstructions (Prentice *et al.*, 1996) for the European part of the FSU. The number of pollen taxa was limited to twenty-four in the digitized data sets (Peterson, 1993). We decided to use both data sets in order to see how well biomization works for each of them.

Because the pollen data came from different sources, including prior compilations, the data were carefully screened to avoid duplications. Thirty-five samples were excluded as probable duplicates, and priority was given to those with a greater number of pollen taxa, i.e. to primary pollen counts as opposed to digitized pollen data.

Pollen data for 6000 years

We compiled a set of 216 pollen spectra that date to 6000 years (±about 500 years) from different sources (Table 1). The majority are published and unpublished primary data derived from the European (EPD, Arles, France) and Global (GPD, Boulder, U.S.A.) pollen data bases (Fig. 1b). We also included thirty-six samples compiled from published pollen diagrams (Peterson, 1993) to improve the coverage, especially in the central Russian Plain and in Siberia. In each case we selected the pollen sample closest to 6000 years in the profile rather than interpolating between pollen spectra. Most of the


(a) Sites with modern pollen data

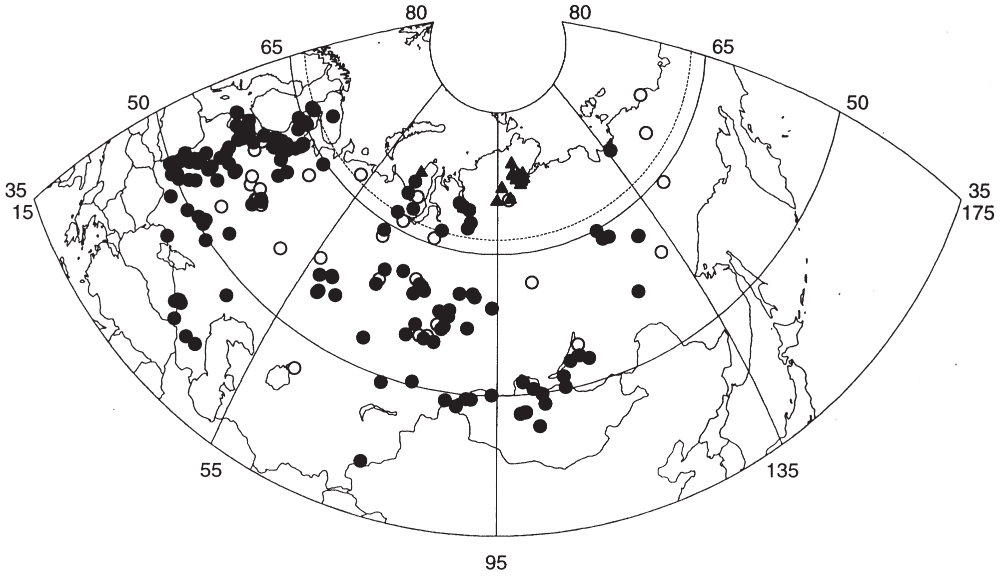

(b) Sites with 6 ka pollen and macrofossil data

FIG. 1. Distribution of sites with (a) modern pollen data and (b) 6000 year pollen and macrofossil data. Closed circles indicate recently compiled sites with primary pollen data, open circles sites with digitized pollen data from Peterson (1983a, 1983b, 1993), and closed triangles sites with plant macrofossil data (Texier *et al.*, 1997).

sites have enough radiocarbon dates to create an age model by linear interpolation between bracketing dates. Pollen-stratigraphic correlation was used to date the samples at a few sites. For duplicate data, we gave priority to the original counts rather than to digitized data, as for the set of modern data.

In order to map the changes in the forest–tundra boundary at 6000 years better, we added seventeen sites from the Russian Arctic (Table 1) with radiocarbon-dated tree macrofossils from Texier *et al.* (1997).

Biome reconstruction: the method

Prentice *et al.* (1996) developed an objective method to relate pollen taxa to plant functional types (PFTs) that

TABLE 1. Summary for sites with pollen and macrofossil data at 6000 (±500) years.

NN	Site name	Lat. (N)	Lon. (E)	Elev. (m)	No. ^{14}C dates	Source of evid.	Dat. contr.	Data base	Reference	BIOP
1	Achit-Nur 6*	49,50	90,60	1435	3	p(c)	3C	EPD	Dorofeyuk & Tarasov, personal communication	DESE
2	Achit-Nur 8	49,50	90,60	1435	4	p(c)	3D	EPD	Dorofeyuk & Tarasov, personal communication	STEP
3	Antu Sinijärv	59,13	26,33	95	7	p(c)	2C	EPD/GPD	Saarse, 1994; Saarse & Liiva (1995)	COMX
4	Arkad'evo 1745	56,50	84.00	70	1	p(c)	2D		Berezina & Liss, personal communication	TAIG
5	Baidara	68,85	66,90	12	12	p(c)	1C	EPD	Andreev & Tarasov, personal communication	TUND
6	Bezdonnoe	62,03	32,77	121	3	p(c)	2C	EPD	Elina & Filimonova (1996)	COCO
7	Boguda	63,67	123,25	119	8	p(c)	1C	EPD/GPD	Andreev & Klimanov (1989)	TAIG
8	Bol. Eravnoe	52,63	111,48	947	3	p(c)	1C		Vipper & Tarasov, personal communication	TAIG
9	Bolotnoye	51,05	24,47	184	16	p(c)	2D	EPD	Bezusko, personal communication	TEDE
10	Bolotnya	50,33	23,95	190	0	p(c)	7	EPD	Artushenko, Arap & Bezusko (1982a)	COMX
11	Bugor	60,33	90,00	80	12	p(c)	1C		Glebov& Karpenko (1989)	TAIG
12	Bugristoe	58,00	85,00	125	5	p(c)	2C		Blyakharchuk (1990)	TAIG
13	Chabada 1	61,98	129,37	290	5	p(c)	2C	EPD/GPD	Andreev & Klimanov (1989)	TAIG
14	Chabada 2	61,98	129,37	290	2	p(c)	4C	EPD/GPD	Andreev, personal communication	TAIG
15	Chany	55,00	77,50	106	4	p(c)	2D		Berdovskaya (1982)	STEP
16	Chatyrkel 1	40,72	75,30	3536	4	p(c)	1D		Sevastyanov *et al.* (1980)	STEP
17	Chechkino 2	62,25	34,07	55	3	p(c)	2C		Elina, personal communication	COCO
18	Chernikhovo	53,15	26,15	135	4	p(c)	2C	EPD	Zernitskaya (1985)	CLMX
19	Chernoe	51,37	106,57	500	4	p(c)	1C		Vipper & Tarasov, personal communication	TAIG
20	Chudesnoe	62,93	36,02	150	31	p(c)	1C		Elina (1981)	COCO
21	Chuvashi	56,33	78,82	110	5	p(c)	1D		Berezina & Liss, personal communication	TAIG
22	Daba-Nur 3	48,20	98,79	2465	2	p(c)	1C	EPD	Dorofeyuk & Tarasov, personal communication	STEP
23	Daba-Nur 8	48,20	98,79	2465	6	p(c)	1C	EPD	Dorofeyuk & Tarasov, personal communication	STEP
24	Derput	57,03	124,12	700	4	p(c)	1C	EPD/GPD	Andreev & Klimanov (1991)	TAIG
25	Dlinnoe	62,32	33,85	66	3	p(c)	1C	EPD	Filimonova & Elovicheva (1988)	COCO
26	Dolgoe 2	55,23	28,18	260	1	p(c)	3D	EPD	Zernitskaya, personal communication	COMX
27	Dood-Nur 4	51,33	99,38	1538	2	p(c)	4C	EPD	Dorofeyuk & Tarasov (1998)	TAIG
28	Dovjok	48,75	28,25	100	9	p(c)	2D	GPD	Kremenetskii (1991)	TEDE
29	Dudinka	69,45	86,22	60	4	p(c)	1C		Kind (1974)	TAIG
30	Dukhovoe	53,17	109,87	500	0	p(c)	7		Vipper & Tarasov, personal communication	TAIG
31	Dund-Nur 2*	49,50	89,79	2097	2	p(c)	4D	EPD	Dorofeyuk & Tarasov, personal communication	DESE
32	Dund-Nur 8	49,50	89,79	2097	2	p(c)	4D	EPD	Dorofeyuk & Tarasov, personal communication	STEP
33	Dzhulajsuo	64,58	30,47	247	2	p(c)	1C		Elina, personal communication	CLDE
34	Entarnoe	60,03	79,02	47	5	p(c)	2C		Arkhipov, Levina & Panychev (1980)	TAIG
35	Ezerische	55,85	30,00	165	0	p(c)	7	EPD	Bogdel' (1984)	COMX
36	Gagra	43,28	40,27	0	2	p(c)	5D	EPD	Kvavadze (1982)	TEDE
37	Gancevichi	52,73	26,50	144	1	p(c)	1D	EPD	Zernitskaya (1991)	COMX
38	Gelmazevskoye	49,67	31,83	120	7	p(c)	1C	EPD	Artushenko *et al.* (1982b)	COMX
39	Gladkoe	55,00	83,00	80	6	p(c)	1C		Firsov *et al.* (1982)	COCO
40	Glubokoe	61,07	36,05	50	1	p(c)	1D	EPD	Elina (1981)	TAIG
41	Gotnavolok	62,20	33,80	110	2	p(c)	3C	EPD	Elina & Filimonova (1996)	COMX
42	Gun-Nur	50,25	106,60	600	7	p(c)	2C	EPD	Dorofeyuk & Tarasov (1998)	CLDE
43	Hoit-Gol	50,05	94,03	925	3	p(c)	2C		Sevastyanov, Seliverstov & Chernova (1993)	DESE
44	Hoton-Nur	48,67	88,30	2083	6	p(c)	1C	EPD	Dorofeyuk & Tarasov, personal communication	TAIG

[*continued*]

TABLE 1. *Continued*

NN	Site name	Lat. (N)	Lon. (E)	Elev. (m)	No. ^{14}C dates	Source of evid.	Dat. contr.	Data base	Reference	BIOP
45	Hubsugul	50,53	100,17	1645	2	p(c)	1D	EPD	Dorofeyuk & Tarasov (1998)	TAIG
46	Hudo-Nur 3	48,13	99,53	2060	2	p(c)	4C	EPD	Dorofeyuk & Tarasov, personal communication	STEP
47	Hudo-Nur 8	48,13	99,53	2060	4	p(c)	1C	EPD	Dorofeyuk & Tarasov, personal communication	STEP
48	Igarka	67,52	86,55	60	3	p(c)	1D		Levkovskaya *et al.* (1970)	TAIG
49	Il'inskoe	60,00	38,38	130	1	p(c)	4D		Afanas'eva & Berezina, personal communication	COCO
50	Imatu	59,13	29,43	45	3	p(c)	4C	EPD/GPD	Kimmel (1995)	TEDE
51	Iosipovo	51,20	28,00	8	2	p(c)	1C	EPD	Chernavskaya & Fogel (1989)	COMX
52	Ivano-Frankovskoe	49,92	23,77	300	1	p(c)	7	EPD	Artushenko *et al.* (1982a)	COMX
53	Kalsa	58,17	27,45	38	12	p(c)	1C	EPD/GPD	Kimmel (1995)	COCO
54	Kamennyi Mokh	63,57	36,42	230	2	p(c)	4C		Elina & Yurkovskaya (1988)	COMX
55	Karakaba	49,13	86,42	2120	5	p(c)	1C		*Geoekologiya gornykh kotlovin* (1992)	STEP
56	Karas'e	53,03	70,22	435	6	p(c)	3D	EPD	Tarasov (1992)	STEP
57	Kardashinski	46,52	32,62	50	13	p(c)	1C	GPD	Kremenetskii (1991)	TEDE
58	Karginskii	70,00	83,00	85	5	p(c)	1C		Levina & Nikitin (1973)	TUND
59	Karujärv	58,38	22,20	32	10	p(c)	1C	EPD/GPG	Saarse (1994)	COMX
60	Kayakskoe	55.13	80,97	100	4	p(c)	1C		Levina *et al.* (1987)	COCO
61	Kepskoe	65,08	32,17	124	2	p(c)	1D	EPD	Elina (1981)	CLMX
62	Khoiba	60,67	89,50	57	3	p(c)	3D		Karpenko (1966)	TAIG
63	Khomin Mokh*	51,20	28,00	8	4	p(c)	1C	EPD	Chernavskaya & Fogel (1989)	TEDE
64	Khomustakh	63,82	121,62	120	9	p(c)	1C	EPD/GPD	Andreev *et al.* (1989)	TAIG
65	Kirikumäe	57,67	27,25	183	6	p(c)	1D	EPD	Saarse (1994)	COMX
66	Kojvusuo	61,80	33,48	20	2	p(c)	1C	EPD	Elina, personal communication	TEDE
67	Komaritsa	58,75	68,82	40	6	p(c)	1C		Volkov *et al.* (1973)	COCO
68	Konda	60,50	69,35	36	5	p(c)	1C		Volkova, personal communication	COCO
69	Kotokol	52,83	108,17	460	5	p(c)	1C		Khotinskii (1977)	TAIG
70	Kubenskoe	61,00	33,00	110	0	p(c)	7	EPD/GPD	Khomutova (1977)	COCO
71	Kulichkovskoe	50,33	24,12	200	0	p(c)	7	EPD	Bezusko, personal communication	COMX
72	Ladoga	61,56	31,34	5	1	p(c)	2D	EPD/GPD	Arslanov *et al.* (in press)	TAIG
73	Lagodehi	41,93	46,42	2750	0	p(c)	7	EPD	Kvavadze & Efremov (1990)	STEP
74	Ladruchie	61,00	39,00	120	1	p(c)	5D	EPD/GPD	Khomutova (1989)	COCO
75	Landshaftnoe	64,57	30,53	207	2	p(c)	2C	EPD	Elina, personal communication	COCO
76	Larino	60,52	77,68	50	9	p(c)	1C		Glebov (1988)	TAIG
77	Lebedinoe	60,50	86,67	67	4	p(c)	1D		Karpenko (1966)	TAIG
78	Liman	49,73	37,67	150	0	p(c)	7	EPD	Bezusko (1973)	TEDE
79	Lisi	41,78	44,68	676	0	p(c)	7	EPD	Kvavadze & Vekua (1989)	COCO
80	Lochinskoe	53,55	28,60	166	0	p(c)	7	EPD	Bogdel' (1984)	COMX
81	Lopatin	50,22	24,83	200	0	p(c)	7	EPD	Artushenko *et al.* (1982a)	COMX
82	Lovozero 1*	68,02	35,00	161	8	p(c)	1C	EPD	Elina *et al.* (1995)	CLDE
83	Lovozero 2	68,02	35,00	160	1	p(c)	1D	EPD	Elina *et al.* (1995)	CLMX
84	Luganskoe	43,72	40,68	2428	3	p(c)	6D	EPD	Kvavadze *et al.* (1994)	STEP
85	Lukashkin Yar	60,33	78,40	45	13	p(c)	1C		Glebov (1988)	TAIG
86	Lukashkin Yar	60,33	78,40	45	10	p(c)	1C		Glebov *et al.* (1974)	TAIG
87	Maardu	59,43	25,00	32	3	p(c)	2C	EPD/GPD	Veski (1992)	COMX

[*continued*]

TABLE 1. *Continued*

NN	Site name	Lat. (N)	Lon. (E)	Elev. (m)	No. ^{14}C dates	Source of evid.	Dat. contr.	Data base	Reference	BIOP
88	Madjagara	64,83	120,97	160	7	p(c)	3D	EPD/GPD	Andreev & Klimanov (1989)	TAIG
89	Maksimkin Yar	58,65	85,00	125	3	p(c)	1C		Blyakharchuk (1990)	TAIG
90	Mal. Kheta	69,75	84,25	42	2	p(c)	2C		Kind (1974)	TAIG
91	Mardy-Yakha	70,30	67,36	5	0	p(c)	7		Volkova, personal communication	TAIG
92	Mezhgornoe	66,37	30,70	190	1	p(c)	4C	EPD	Elina (1981)	COCO
93	Mochazhina	60,33	90,00	80	8	p(c)	1C		Glebov & Karpenko (1989)	TAIG
94	Moshkarnoe 1	62,25	34,05	58	9	p(c)	1C	EPD	Filimonova (1995)	COCO
95	Moshkarnoe 2	62,25	34,05	58	8	p(c)	1C		Filimonova (1995)	COCO
96	Moskovskiy Bobrik	50,55	34,50	135	0	p(c)	7	EPD	Artushenko (1960)	TEDE
97	Mustusuo	61,81	33,50	101	2	p(c)	4C	EPD	Elina (1981)	COCO
98	Naroch	54,00	26,00	120	2	p(c)	5C	EPD	Yakushko *et al.* (1992)	COCO
99	Nazino	60,52	77,68	45	16	p(c)	1C		Glebov (1988)	TAIG
100	Neinasuo	66,35	30,63	110	2	p(c)	4C	EPD	Elina (1981)	TAIG
101	Nenazvannoe	61,81	33,48	100	1	p(c)	4C	EPD	Elina (1981)	COCO
102	Nero 274*	57,17	39,48	93	0	p(c)	7	EPD	Gunova (1975)	COCO
103	Nero 2P	57,17	39,48	93	3	p(c)	1C	EPD	Gunova (1975)	COMX
104	Nigula	58,00	24,67	55	11	p(c)	1C	EPD/GPD	Sarv & Ilves (1976)	TEDE
105	Nikulino-1	60,50	86,67	59	4	p(c)	3D		Glebov, personal communication	TAIG
106	Nikulino-2	60,50	86,67	71	1	p(c)	4D		Glebov, personal communication	TAIG
107	Njukhchinskii Mokh	63,92	36,30	20	1	p(c)	4D	EPD	Elina (1981)	TAIG
108	Nusuo	64,57	30,83	163	1	p(c)	4C	EPD	Elina (1981)	COMX
109	Nowy Gutiski	50,27	26,83	210	0	p(c)	7	EPD	Artushenko *et al.* (1982a)	COMX
110	Nulsaveito	67,67	70,17	55	5	p(c)	1C		Panova (1990)	TAIG
111	Onego 6	61,72	34,92	33	0	p(c)	7	EPD/GPD	Khomutova (1976)	TAIG
112	Onego 8	61,72	34,92	33	0	p(c)	7	EPD/GPD	Khomutova (1976)	TAIG
113	Osoyevka	50,90	35,22	160	0	p(c)	7	EPD	Bezusko (1973)	COMX
114	Osvea	56,05	28,08	129	0	p(c)	7	EPD	Zernitskaya, personal communication	COMX
115	Ozerki	50.42	80,47	210	9	p(c)	1C	EPD	Tarasov (1992)	STEP
116	Paanajarvi	66,27	29,95	137	1	p(c)	4C		Elina *et al.* (1994)	COCO
117	Päidre	58,27	25,63	51	3	p(c)	1C	EPD/GPD	Saarse, 1994; Saarse *et al.* (1995)	COMX
118	Pashennoe	49,37	75,40	871	14	p(c)	1C	EPD	Tarasov (1992)	STEP
119	Pelisoo	58,47	22,38	33	5	p(c)	3C	EPD/GPD	Saarse (1994)	COMX
120	Peschanoe	51,98	25,48	139	0	p(c)	7	EPD	Zernitskaya (1989)	TEDE
121	Peschanoe (Ural)	56,90	60,32	310	0	p(c)	7		Panova & Korotkovskaya (1990)	COCO
122	Petrilovo	56,00	31,98	175	1	p(c)	4C	EPD/GPD	Gunova & Sirin (1995)	COMX
123	Petropavlovskii	58,33	83,00	125	4	p(c)	3D		Blyakharchuk (1990)	TAIG
124	Pit-Gorodok	59,25	93,80	45	1	p(c)	7		Kind (1974)	TAIG
125	Polonichka	50,27	24,75	200	0	p(c)	7	EPD	Artushenko *et al.* (1982a)	COMX
126	Popovschina	50,42	34,00	135	0	p(c)	7	EPD	Bezusko (1973)	TEDE
127	Ptichje	66,35	30,57	120	2	p(c)	3D	EPD	Elina (1981)	COCO
128	Punso	57,68	27,25	183	12	p(c)	1C	EPD/GPD	Saarse (1994)	COMX
129	Pur-Taz	66,70	79,73	60	5	p(c)	1C		Andreev, personal communication	TAIG

[*continued*]

TABLE 1. *Continued*

NN	Site name	Lat. (N)	Lon. (E)	Elev. (m)	No. ^{14}C dates	Source of evid.	Dat. contr.	Data base	Reference	BIOP
130	Quartzevoe	43,67	41,17	2726	1	p(c)	6D	EPD	Kvavadze & Efremov (1996)	STEP
131	Raigastvere	58,60	26,73	52	11	p(c)	1C	EPD/GPD	Pirrus, Rõuk & Liiva (1987)	COMX
132	Rittusuo	61,77	33,55	20	1	p(c)	4C		Elina, personal communication	COCO
133	Rudushskoe	56,50	27,55	150	1	p(c)	4C	EPD	Khomutova (1989)	COMX
134	Rugozero	64,08	32,63	140	2	p(c)	2C	EPD	Elina (1981)	COCO
135	S19kstrm	57,00	40,00	127	0	p(c)	7	EPD/GPD	Osipova, personal communication	COMX
136	S269saht	56,00	39,00	150	0	p(c)	7		Osipova, personal communication	COMX
137	Salekhard	66,55	66,58	5	2	p(c)	2C		Volkova, personal communication	TAIG
138	Samandon-Kazach'e	70,78	136,26	10	7	p(c)	1D	EPD/GPD	Velichko, Andreev & Klimanov (1994)	TUND
139	Sambalskoe	61,77	34,15	120	45	p(c)	1C		Elina, Arslanov & Klimanov (1996)	COMX
140	Saviku	58,42	27,24	30	6	p(c)	1C	EPD/GPD	Sarv & Ilves (1975)	COMX
141	Sebboloto	64,67	43,33	65	1	p(c)	4C		Yurkovskaya, Elina & Klimanov (1989); Yurkovskaya & Elina (1991)	COMX
142	Selyahi	51,83	23,75	154	0	p(c)	7	EPD	Zernitskaya (1991)	TEDE
143	Serny	43,67	40,48	2485	2	p(c)	5D	EPD	Kvavadze & Efremov (1995)	STEP
144	Shiret-Nur	46,53	101,82	2500	3	p(c)	3C	EPD	Dorofeyuk & Tarasov, personal communication	STEP
145	Shombashuo 1	65,12	32,98	100	2	p(c)	1C	EPD	Elina (1981)	COCO
146	Shombashuo 2	65,12	32,98	99	2	p(c)	2C		Elina, personal communication	COCO
147	Solenoe Zaimishche	47,90	46,17	−19	4	p(c)	3C		Bolikhovskaya (1990)	COMX
148	Solokiya	50,42	24,17	190	0	p(c)	7	EPD	Artushenko *et al.* (1982a)	CLDE
149	Sosvyatskoe	56,20	32,00	175	1	p(c)	4C	EPD/GP	Gunova & Sirin (1995)	COMX
150	Starniki	50,27	26,02	198	10	p(c)	1C	EPD	Bezusko, Klimanov & Shelyag-Sosenko (1988)	COMX
151	Stav	50,42	35,40	155	0	p(c)	7	EPD	Bezusko (1973)	STEP
152	Stoyanov-1	50,38	24,63	198	0	p(c)	7	EPD	Bezusko, personal communication	COMX
153	Stoyanov-2	50,38	24,63	198	8	p(c)	1C	EPD	Bezusko, Klimanov & Shelyag-Sosenko (1988)	COMX
154	Stupino	52,25	39,83	95	1	p(c)	3D	EPD	Chernavskaya, personal communication	CLMX
155	Sudoble	54,03	28,60	165	8	p(c)	1D	EPD	Bogdel' *et al.* (1983)	COMX
156	Surgut	61,23	73,33	40	5	p(c)	1C		Neishtadt (1976)	TAIG
157	Svitjaz	53,70	28,68	242	0	p(c)	7	EPD	Bogdel' (1984)	TEDE
158	Svjatoe	54,00	31,23	195	0	p(c)	7	EPD	Bogdel' (1984)	TEDE
159	Svyatoye-2	51,10	24,33	183	0	p(c)	7	EPD	Artushenko (1957)	TEDE
160	Tanino ozero	58,00	85,00	125	8	p(c)	1C		Blyakharchuk (1990)	TAIG
161	Tegul'detskii	57,00	89,00	125	3	p(c)	1D		Blyakharchuk (1990)	TAIG
162	Terkhiin-Tsagan-Nur 8	48,15	99,70	2060	8	p(c)	1C		Dorofeyuk & Tarasov, personal communication	STEP
163	Tom'	56,83	84,45	85	6	p(c)	1C		Arkhipov & Votakh (1980)	TAIG
164	Urmiin-Tsagan-Nur	48,84	102,93	1450	2	p(c)	1C		Dorofeyuk & Tarasov, personal communication	STEP
165	Ust' Mash	56,32	57,88	220	5	p(c)	1C		Panova, Makovskii & Erokhin (1996)	COCO
166	Verhi	51,85	28,80	146	2	p(c)	6D	EPD	Zernitskaya (1986)	TEDE
167	Vishnevskoe	60,50	29,52	15	1	p(c)	2D	EPD	Arslanov *et al.* (1992)	CLMX

[*continued*]

TABLE 1. *Continued*

NN	Site name	Lat. (N)	Lon. (E)	Elev. (m)	No. ^{14}C dates	Source of evid.	Dat. contr.	Data base	Reference	BIOP
168	Vodorazdel	59,38	76,90	101	17	p(c)	1C		Glebov *et al.* (1997)	TAIG
169	Võhma	59,05	27,33	46	14	p(c)	1C	EPD/GPD	Kimmel (1995)	COMX
170	Yamant-Nur	49,90	102,60	1000	1	p(c)	7	EPD	Dorofeyuk & Tarasov, personal communication	CLDE
171	Yenisei	68,17	87,15	100	6	p(c)	1D		Andreev, personal communication	TAIG
172	Zaboinoe	55,53	62,37	275	0	p(c)	7	EPD	Khomutova, personal communication	TAIG
173	Zalozci-2	49,75	25,45	320	15	p(c)	1C	EPD	Artushenko *et al.* (1982a)	COCO
174	Zamoshje	62,05	35,20	40	4	p(c)	1C		Elina, personal communication	COCO
175	Zapovednoe	65,12	32,63	110	2	p(c)	4C	EPD	Elina (1981)	COCO
176	Zarutskoe	63,90	36,25	20	5	p(c)	1C	EPD	Elina (1981)	COCO
177	Zditovo	52,60	25,55	147	1	p(c)	4C	EPD	Zernitskaya & Daineko (1986)	CLMX
178	Zuratkul'	54,90	59,27	720	0	p(c)	7		Panova (1982)	COCO
179	Aiatskoe	57,00	60,08	229	7	p(d)	1C		Petersoon (1993)	COMX
180	Aral Sea	46,67	61,50	77	0	p(d)	7		Peterson (1993)	DESE
181	B. Kuropatochya	71,07	156,50	77	4	p(d)	1C		Peterson (1993)	TUND
182	Balkashkinskii	53,03	35,37	77	2	p(d)	7		Peterson (1993)	COMX
183	Beglianskii Riam	55,50	81,57	77	0	p(d)	7		Peterson (1993)	TAIG
184	Belkachi	59,15	131,98	458	0	p(d)	7		Peterson (1993)	TUND
185	Bol. Pershino	59,35	69,00	77	2	p(d)	4C		Peterson (1993)	TAIG
186	Chunia	61,75	102,80	229	1	p(d)	4C		Peterson (1993)	TAIG
187	Davshe	54,33	110,03	458	8	p(d)	1C		Peterson (1993)	TAIG
188	Glukharinoe	66,00	69,00	77	0	p(d)	7		Peterson (1993)	TAIG
189	Iamsovei	65,67	78,25	77	0	p(d)	7		Peterson (1993)	TAIG
190	Imnatskoe	42,08	41,72	458	4	p(d)	1C		Peterson (1993)	TEDE
191	Iuribei	69,00	70,00	77	0	p(d)	7		Peterson (1993)	CLDE
192	Ivanovskoe 3	56,83	39,00	77	2	p(d)	2C		Peterson (1993)	COMX
193	Kradenoe	62,00	129,58	229	4	p(d)	1C		Peterson (1993)	TAIG
194	Lakhtinskoe	60,00	30,17	77	3	p(d)	4C		Peterson (1993)	COCO
195	Markhida	67,17	52,55	77	2	p(d)	2C		Peterson (1993)	TAIG
196	Mulianka	57,78	56,32	229	1	p(d)	5C		Peterson (1993)	COCO
197	Myksi	58,15	24,97	77	6	p(d)	1C		Peterson (1993)	COMX
198	Nizhne-Vartovsk	60,93	76,63	77	13	p(d)	1C		Peterson (1993)	TAIG
199	Orshinskii Mokh	56,95	35,95	77	3	p(d)	2C		Peterson (1993)	COMX
200	Osechenskoe	57,52	34,83	229	6	p(d)	1C		Peterson (1993)	COMX
201	Paden'ga	62,80	42,93	77	0	p(d)	7		Peterson (1993)	COCO
202	Polovetsko-Kupanskoe	57,57	37,90	77	2	p(d)	5C		Peterson (1993)	COMX
203	R. B. Romanikha	70,75	98,60	77	3	p(d)	2C		Peterson (1993)	TAIG
204	Sakhtysh 1	56,80	40,42	77	0	p(d)	7		Peterson (1993)	COMX
205	Sartynia	64,17	65,47	77	0	p(d)	7		Peterson (1993)	COCO
206	Selerikan	64,30	141,87	458	2	p(d)	2C		Peterson (1993)	TUND
207	Shuvalovskoe	60,05	30,33	77	7	p(d)	1C		Peterson (1993)	COMX

[*continued*]

TABLE 1. *Continued*

NN	Site name	Lat. (N)	Lon. (E)	Elev. (m)	No. ^{14}C dates	Source of evid.	Dat. contr.	Data base	Reference	BIOP
208	Somino	56,60	38,80	77	6	p(d)	4C		Peterson (1993)	COMX
209	Sort	68,83	148,00	0	2	p(d)	2C		Peterson (1993)	TUND
210	Tesovo-Netyl'skoe	58,92	30,90	77	6	p(d)	1C		Peterson (1993)	COMX
211	Tiuliukskoe	54,67	59,17	458	0	p(d)	7		Peterson (1993)	COCO
212	Tugiyan-Yugan	63,55	65,72	77	10	p(d)	5C		Peterson (1993)	TAIG
213	Ubinskii riam	55,32	80,00	77	0	p(d)	7		Peterson (1993)	TAIG
214	Ulanovo	55,55	48,72	77	0	p(d)	7		Peterson (1993)	CLMX
215	Vakharu	58,85	24,78	77	10	p(d)	2C		Peterson (1993)	COMX
216	Vasiugan'e I	56,87	83,08	77	1	p(d)	7		Peterson (1993)	TAIG
217	B. Balakhnia	73,25	100,72	50	1	m	3D		Texier *et al.*, (1997)	CLDE
218	B. Balakhnia (A-318)	73,30	102,63	50	1	m	1D		Texier *et al.*, (1997)	CLDE
219	B. Balakhnia-27	73,37	104,35	50	1	m	2D		Texier *et al.*, (1997)	CLDE
220	B. Balakhnia-28	73,43	100.52	50	1	m	2D		Texier *et al.*, (1997)	CLDE
221	B. Balakhnia-29	73,31	100,53	50	1	m	2D		Texier *et al.*, (1997)	CLDE
222	B. Romanikha (XX-44)	70,82	99,08	50	1	m	1D		Texier *et al.*, (1997)	CLDE
223	Karginskii	69,95	83,58	50	1	m	1D		Texier *et al.*, (1997)	TAIG
224	Khatanga	72,78	104,63	50	1	m	1D		Texier *et al.*, (1997)	CLDE
225	Kheta	70,63	94,75	50	1	m	1D		Texier *et al.*, (1997)	CLDE
226	Ladonnakh G-119	72,00	96,33	50	1	m	2D		Texier *et al.*, (1997)	CLDE
227	M. Balakhnia	72,75	103,00	50	1	m	3D		Texier *et al.*, (1997)	CLDE
228	Malaya Kheta	69,57	84,53	50	1	m	1C		Texier *et al.*, (1997)	TAIG
229	Mosun	72,78	104,22	50	1	m	3D		Texier *et al.*, (1997)	CLDE
230	Novaya-M. Balakhnia	72,55	103,50	50	1	m	1D		Texier *et al.*, (1997)	CLDE
231	Pukhuchayakha	71,43	67,96	50	1	m	3D		Texier *et al.*, (1997)	CLDE
232	Zakharova Rassokha (I-156)	72,78	101,62	50	1	m	1D		Texier *et al.*, (1997)	CLDE
233	Zap. Taimyr	74,53	100.50	50	1	m	1D		Texier *et al.*, (1997)	CLDE

1. When more than one core is available from the same site the core with better dating control has been used for mapping purposes. However, cores marked by a star are not used in Fig. 3(d).
2. Source of data is indicated by 'p(c)' for new compiled primary pollen data, by 'p(d)' for digitized pollen data and by 'm' for plant macrofossil data.
3. Dating control is a measure of the accuracy of the identification of the 6000 year time-slice and makes use of schemes for continuous (C) and discontinuous (D) records as given in Tarasov *et al.* (1996). For continuous records, a 1C in the dating control column indicates that there are two bracketing radiometric dates each within 2000 years of 6000 years BP, whereas 2C, 3C, 4C and 5C indicate two bracketing dates within 2000 and 4000; 4000 and 4000; 4000 and 6000; 6000 and 6000 years of 6000 years BP, respectively. for discontinuous records, 1D, 2D, 3D, 4D, 5D, and 6D indicate a radiometric date within 250, 500, 750, 1000, 1500 and 2000 years, respectively, of 6000 years BP. A 7 in the dating control column indicates that the records are poorly dated.
4. Data base where the pollen data are currently placed: EPD – European Pollen Data Base (Arles, France); GPD – Global Pollen Data Base (Boulder, U.S.A.).
5. BIOP – pollen-derived biomes at 6 ka, where TUND = tundra, TAIG = taiga, CLDE = cold deciduous forest, COCO = cool confier forest, CLMX = cold mixed forest, COMX = cool mixed forest, TEDE = temperate deciduous forest, STEP = steppe, and DESE = desert.

group taxa by their stature, leaf form, phenology, and bioclimatic tolerance. The method has been successfully applied to the modern and 6000-year pollen data from Europe (Prentice *et al.*, 1996), western and eastern Africa (Jolly *et al.*, 1998), eastern North America (Summers *et al.*, 1998), and China (Yu *et al.*, 1998).

The procedure for reconstructing biomes from pollen data known as 'biomization' is based on a fuzzy logic approach in which all pollen spectra are supposed to have an 'affinity' for every biome and the affinity is expressed in terms of a numerical score. The key steps are (1) assignment of each pollen taxon to one or more PFTs according to its biology; (2) assignment of characteristic PFTs to biomes according to their bioclimatic range and actual distribution; (3) construction of a biome by taxon matrix illustrating which taxa may occur in each biome; (4) calculation of the affinity scores for all pollen samples by

$$A_{ik} = \Sigma_j \delta_{ij} \sqrt{\{\max[0, (p_{jk} - \theta_j)]\}} \qquad (1)$$

where A_{ik} is the affinity of pollen sample k for biome i; summation is over all taxa j; δ_{ij} is the entry in the biome × taxon matrix for biome i and taxon j; p_{jk} are the pollen percentages, and θ_j is a threshold pollen percentage (0.5% in this paper, following Prentice *et al.* (1996)). For each pollen sample, the biome with the highest score is assigned.

Assignment of pollen taxa to plant functional types (PFTs) and PFTs to biomes

In their initial study, Prentice *et al.* (1996) used the published data set of surface pollen samples from Guiot, Harrison & Prentice (1993) to test the biomization method for the area of 'biogeographical Europe' west of 60°E. A limited number of taxa were available in this data set, and these were assigned to one or several PFTs using the PFT classification described in Prentice *et al.* (1992). The results of this study were good in terms of recovering the broad distribution of biomes. Prentice *et al.* (1996), however, noted that a restriction in the agreement between actual and reconstructed biomes may occur because many minor pollen taxa (mainly herbaceous) were not listed in their surface data set (Prentice *et al.*, 1996). This limitation could be a major problem in central Eurasia where tree-less biomes (tundra, steppe and desert) are more important than in Europe. Having a chance to use both primary pollen counts and digitised pollen percentages, we decided to start with the same assignment of pollen taxa to PFTs and PFTs to biomes as Prentice *et al.* (1996) used and then modify the assignment by paying special attention to taxa not presented in their scheme. Table 2 lists all available pollen taxa in the set of modern surface samples and shows the set of PFTs to which they were assigned. After exclusion of aquatic taxa (e.g. *Typha*, *Potamogeton*, *Sparganium*, etc.), taxa represented by only one grain (e.g. *Oxalis*), exotic taxa (e.g. *Tsuga*), and taxa restricted to local microhabitats (e.g. *Drosera*, *Scheuchzeria*, *Geum*), the remaining taxa were used in assigning biomes to the pollen samples (Table 2).

We also defined several new PFTs in an attempt to increase the number of taxa available for identification of forest biomes.

1. *Pinus pumila* (Pall.) Regel, a shrub-like form of *Pinus* subgen. *Haploxylon*, can survive under the snow cover in the cold continental climate of eastern Siberia with mean coldest-month temperature below −35 °C (*Klimaticheskii Atlas SSSR*, 1960). This taxon was assigned to a 'cool-boreal conifer' type.
2. A number of deciduous shrubs (e.g. *Lonicera*, *Sambucus*, *Viburnum*) have a range spanning the distribution of both temperate and boreal summergreen trees (Hultén & Fries, 1986). We classified these as 'boreal-temperate summergreen'.
3. *Rubus chamaemorus* L. was defined as an 'arctic-boreal dwarf shrub' since it acts both as an arctic-alpine dwarf shrub and as a common understorey or mire plant in the boreal forest (Hultén & Fries, 1986).
4. Russian studies of pollen morphology (Kupriyanova, 1965; Kupriyanova & Aleshina, 1972) demonstrated that the pollen of dwarf birch (*Betula nana* L.*, sensu lato*) and shrub alder (*Alnus fruticosa* Rupr.) can generally be distinguished from the corresponding tree forms (e.g. *Betula* sect. *Albae*, *Alnus glutinosa* (L.) Gaertner, *Alnus incana* (L.) Moench). Where these distinctions were made, we were able to assign these taxa to appropriate PFTs.

Several further modifications were made to the treatment of nonarboreal PFTs.

1. We increased the number of taxa assigned to steppe forbs and desert forbs compared to Prentice *et al.* (1996) to improve the distinction between tree and tree-less biomes and among the herbaceous biomes themselves. The same kind of empirical decisions as in Prentice *et al.* (1996) were made for the nonarboreal taxa. Most of them can appear in each biome, but certain taxa have a useful diagnostic value. For example, Rubiaceae and Caryophyllaceae have higher percentages in steppe, as do *Ephedra* in desert and Cyperaceae in tundra.
2. *Artemisia* and Chenopodiaceae were included in both steppe-forb and desert-forb PFTs because they often codominate in both the steppe and desert environments (Walter, 1985).
3. We allowed Poaceae to be characteristic in the tundra and steppe biomes where grasses grow and are a key taxon, but we excluded Poaceae from the desert biome. In Europe, Prentice *et al.* (1996) also placed this taxon in the desert biome. However, desert is only a minor biome in Europe so the accuracy of assignment to desert was not well tested.

Biomes were then characterized in terms of the newly adopted PFTs (Table 3). Data from Tables 2 and 3 provide a basis for constructing a biome-taxon matrix used for the calculation of the affinity scores. We followed Prentice *et al.* (1996) and used the universal threshold of 0.5% for pollen percentages. Biomes were identified in the order that they appear in Table 3. This order does not play any role in the choice among species-rich biomes, or biomes with well-represented indicator taxa in the pollen assemblage. The

TABLE 2. Plant functional types and the pollen taxa assigned to them.

Codes	Trees and shrubs	
bec	Boreal evergreen conifer	*Picea*
bs	Boreal summergreen	*Betula, Larix*
bec/cbc	Boreal evergreen conifer/cool-boreal conifer shrub	*Pinus (Haploxylon)*
bec/ctc	Boreal evergreen/cool-temperate conifer	*Abies*
ec	Eurythermic conifer	*Juniperus, Pinus (Diploxylon)*
bts	Boreal-temperate summergreen shrub	*Cornus, Lonicera, Sambucus, Sorbus, Viburnum*
bs/ts	Boreal/temperate summergreen	*Alnus, Populus*
bs/ts/aa	Boreal/temperate summergreen/arctic-alpine shrub	*Salix*
ts	Temperate summergreen	*Acer, Euonimus, Fraxinus excelsior*-type, *Quercus* (deciduous)
ts_1	Cool-temperate summergreen	*Carpinus, Corylus, Fagus, Frangula, Tilia, Ulmus*
ts_2	Warm-temperate summergreen	*Castanea, Juglans, Rhamnus, Vitis, Myrica*
wte	Warm-temperate broad-leaved evergreen	*Quercus* (evergreen)
wte_1	Cool-temperate broad-leaved evergreen	*Hedera*
wte_2	Warm-temperate sclerophyll shrub	*Olea*
	Others	
sf	Steppe forb	*Allium*, Apiaceae, Asteraceae (Asteroideae), Asteraceae (Cichorioideae), Brassicaceae, Campanulaceae, *Cannabis*, Caryophyllaceae, *Centaurea,* Convolvulaceae, Dipsacaceae, *Epilobium*, Euphorbiaceae, Fabaceae, *Filipendula, Galium,* Geraniaceae, *Hippophaë,* Iridaceae, Lamiaceae, *Linaria,* Liliaceae, Onagraceae, Papaveraceae, *Plantago,* Plumbaginaceae, *Potentilla,* Ranunculaceae, Rosaceae, Rubiaceae, Rutaceae, *Scabiosa, Stellera, Taraxacum*
sf/df	Steppe/desert forb	*Artemisia,* Boraginaceae, Chenopodiaceae, *Kochia*
df	Desert forb	*Ephedra, Salsola,* Tamaricaceae, Zygophyllaceae
aa	Arctic-alpine dwarf shrub	*Alnus fruticosa*-type, *Betula nana*-type, *Dryas, Gentiana, Pedicularis,* Saxifragaceae
sf/aa	Steppe/arctic-alpine forb	Scrophulariaceae, Valerianaceae
sf/df/aa	Steppe/desert/arctic-alpine forb	Polygonaceae
ab	Arctic-boreal dwarf shrub	*Rubus chamaemorus*
g	Grass	Poaceae
s	Sedge	Cyperaceae
h	Heath	*Calluna, Cassiope, Empetrum,* Ericales, *Pyrola,* Pyrolaceae

TABLE 3. FSU and Mongolian biomes and their characteristic plant functional tupes (PFTs) PFTs in parentheses are restricted to part of their biome. Abbreviations for PFTs as in Table 2.

Tundra	aa, (ab), g, s, (h)
Cold deciduous forest	bs, (cbc), ec, (ab), (h)
Taiga	bs, bec,(bts), ec, (ab), (h)
Cold mixed forest	bs, ctc, ec, (bts), (ts_1), (h)
Cool conifer forest	bs, bec, ctc, ec, (bts), (ts_1), (ab), (h)
Temperate deciduous forest	bs, (ctc), ec, bts, ts, ts_1, (ts_2), (wte_1), (h)
Cool mixed forest	bs, bec, (ctc), ec, bts, ts, ts_1, (h)
Warm mixed forest	ec, (bts), ts, ts_1, ts_2, wte
Xerophytic woods/scrub	ec, wte, wte_2
Desert	df
Steppe	sf, g

order becomes important when biomes are represented by only a few broadly distributed taxa (e.g. cold deciduous or cold mixed forest) where some biomes are distinguished only by the absence of one or more of these taxa.

Extension of the method to plant macrofossil data

A similar biomization procedure was applied to the radiocarbon-dated plant macrofossils, which are mainly woody remains from the now tree-less Arctic region. We assume that the presence even of a single tree stump, bark fragment, cone or needle at sites north of the present-day tree line indicates a shift in the forest boundary and can therefore help to define the boundary between tundra and forest. In cases when only a single arboreal macrofossil was recorded we took it as 100%. If more than one arboreal taxon was identified then each was assigned an equal proportion. The order of biomes, as discussed before, play

TABLE 4. Simplified vegetation types used in the *Fiziko-Geograficheskii Atlas Mira* (1964) and their allocation to the biomes used by Prentice *et al.* (1992)

Biome name	Vegetation type
Tundra	Arctic tundra
	Moss-lichen, dwarf shrub and sedge tundra
	Mountain arctic and subarctic tundra
Cold deciduous forest	Larch taiga-like forest
	Birch and larch-birch thin forest (forest-tundra)
	Pinus pumila shrubby weeds
	Poplar-birch and pine forests of western Siberia
	Pine-birch forests of Kazakhstan and Mongolia
Taiga	"Dark" conifer (taiga) forest with *Picea, Abies* and *Pinus sibirica*
	Pine and pine-larch forests (with *Pinus sibirica*)
	Spruce-birch and spruce-larch thin forests (forest-tundra)
Cool conifer forest	"Dark" conifer (taiga) forest (southern part)
	Mixed broad-leaved-"dark" conifer forest (northern part)
Cool mixed forest	Mixed broad-leaved-"dark" conifer forest (southern part)
	Pine-broad-leaved forest (northern part)
Temperate deciduous forest	Deciduous broad-leaved forest
	Pine-broad-leaved forest (southern part)
Broad-leaved evergreen/warm mixed forest	Broad-leaved forest with subtropical elements (western Caucasus)
Steppe	Meadow-steppe and steppe-meadows (forest-steppe)
	Graminoid (typical) steppe
	Alpine and subalpine meadow
	Artemisia–graminoid desertic steppe (semidesert)
	Mountain and submountain steppe
Desert	*Artemisia*, chenopod and ephemeral-wormwood shrub deserts
	Haloxylon persicum and *H. ammodendron* tree-shrub and shrub desert
	High-altitude *Artemisia* and dwarf shrub desert

a key role for the biomization of tree macrofossil data. Thus the presence of only a temperate summergreen tree (e.g. *Betula* or *Larix*) gives priority to the cold deciduous forest biome, but the presence of a boreal conifer as well (e.g. *Picea*) results in assignment to the taiga biome. This simple diagnostic approach based on limited data works well for regions where the forest vegetation is characterized by only a few species, belonging to one or two PFTs.

Testing the method with modern pollen data

Vegetation descriptions for the modern pollen samples with primary counts were obtained from site descriptions and were derived from vegetation maps of the USSR and Mongolia (*Fiziko-Geograficheskii Atlas Mira*, 1964) for the other sites.

Biome reconstructions based on the modern pollen samples were then compared with vegetation assignments on a site-by-site basis. The names of the vegetation types in the Russian botanical literature are different from the biome names used in this paper, but it was easy to assign these vegetation types to biomes (Table 4). The only problem was to identify the cold mixed forest biome as shown by Prentice *et al.* (1992) in the discontinuous belt along the forest-steppe transition east of the Urals, where there are in fact woodlands with *Pinus*, *Populus* and *Betula*. This vegetation type occupies a relatively small area in northern Eurasia and has no well-represented indicative taxa to separate it from cold deciduous forests. In the map of present vegetation at the sampling sites (Fig. 3b) and in Table 4 we have simply assigned this vegetation type to cold deciduous forest.

RESULTS

Mapped patterns in the pollen data

Figure 2 indicates some of the geographical patterns in pollen abundance that provide the basis for reconstructed biome distributions and their changes from 6000 years to present. The present-day pollen abundances (Fig. 2a) show strong geographical patterns that clearly reflect the zonal vegetation pattern. *Picea* is strongly represented throughout the modern taiga (including high-elevation sites in the central Asian mountains). Cool-temperate summergreen and temperate summergreen taxa are confined to the western part and are abundant in the deciduous forest zone (including the belt of deciduous forest that lies between the taiga and the steppe). The cool-temperate taxa extend further north, with moderate abundances also in the cool mixed forest zone. *Artemisia* and Chenopodiaceae have high abundances in the steppe and desert zones of south-eastern Europe and central Asia as well as in the steppe-like vegetation of interior Yakutia. Poaceae have high pollen abundances primarily in the steppes but also in the Arctic tundra. Moderate and variable abundances of Poaceae also appear throughout the European part, probably mainly as a result of human impact in agricultural areas.

Broadly similar patterns are observed for 6000 years (Fig. 2b) but with certain important differences. *Picea* shows

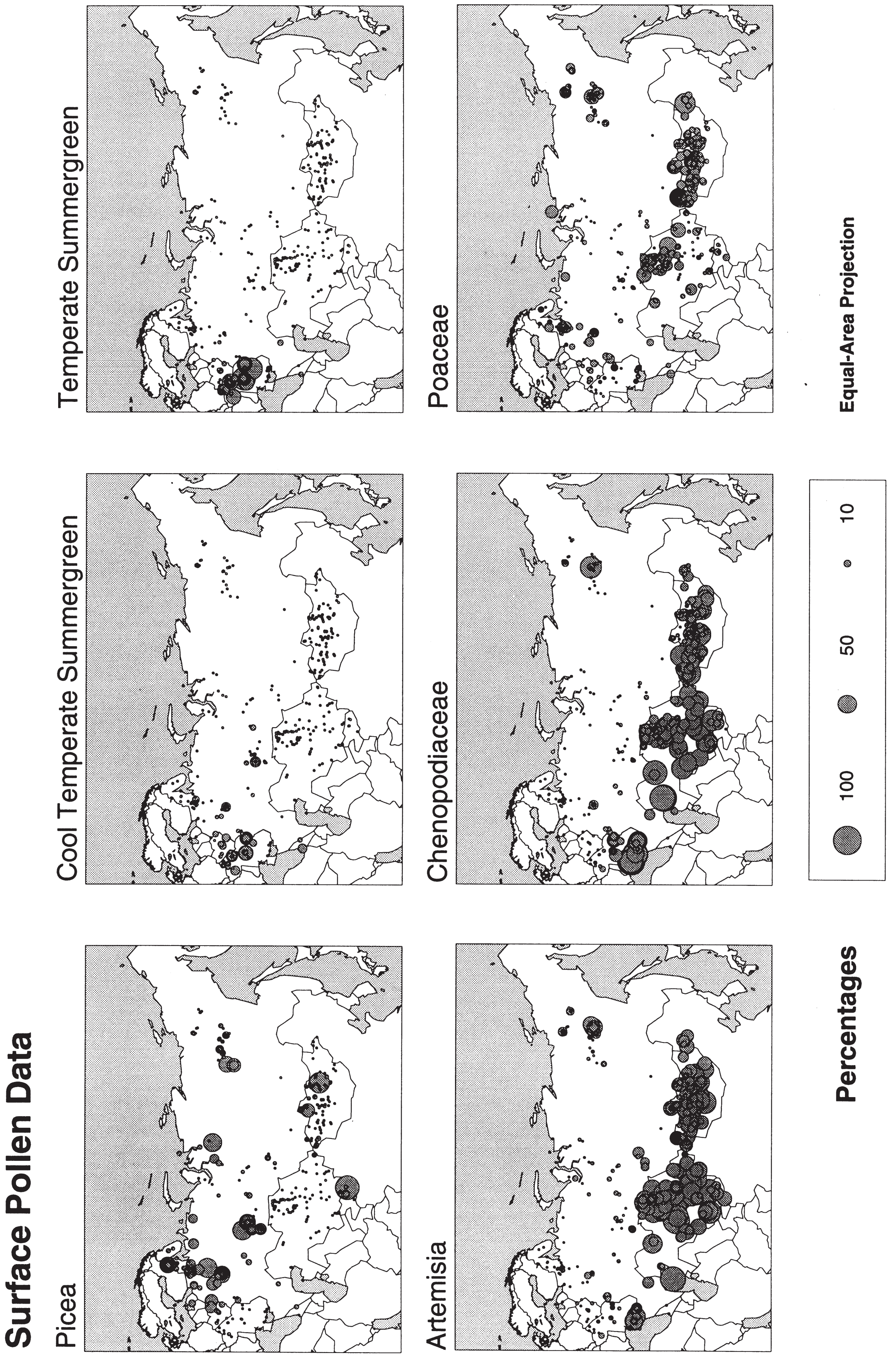

Surface Pollen Data
Picea
Cool Temperate Summergreen
Temperate Summergreen
Artemisia
Chenopodiaceae
Poaceae
Percentages
100
50
10
Equal-Area Projection

FIG. 2.

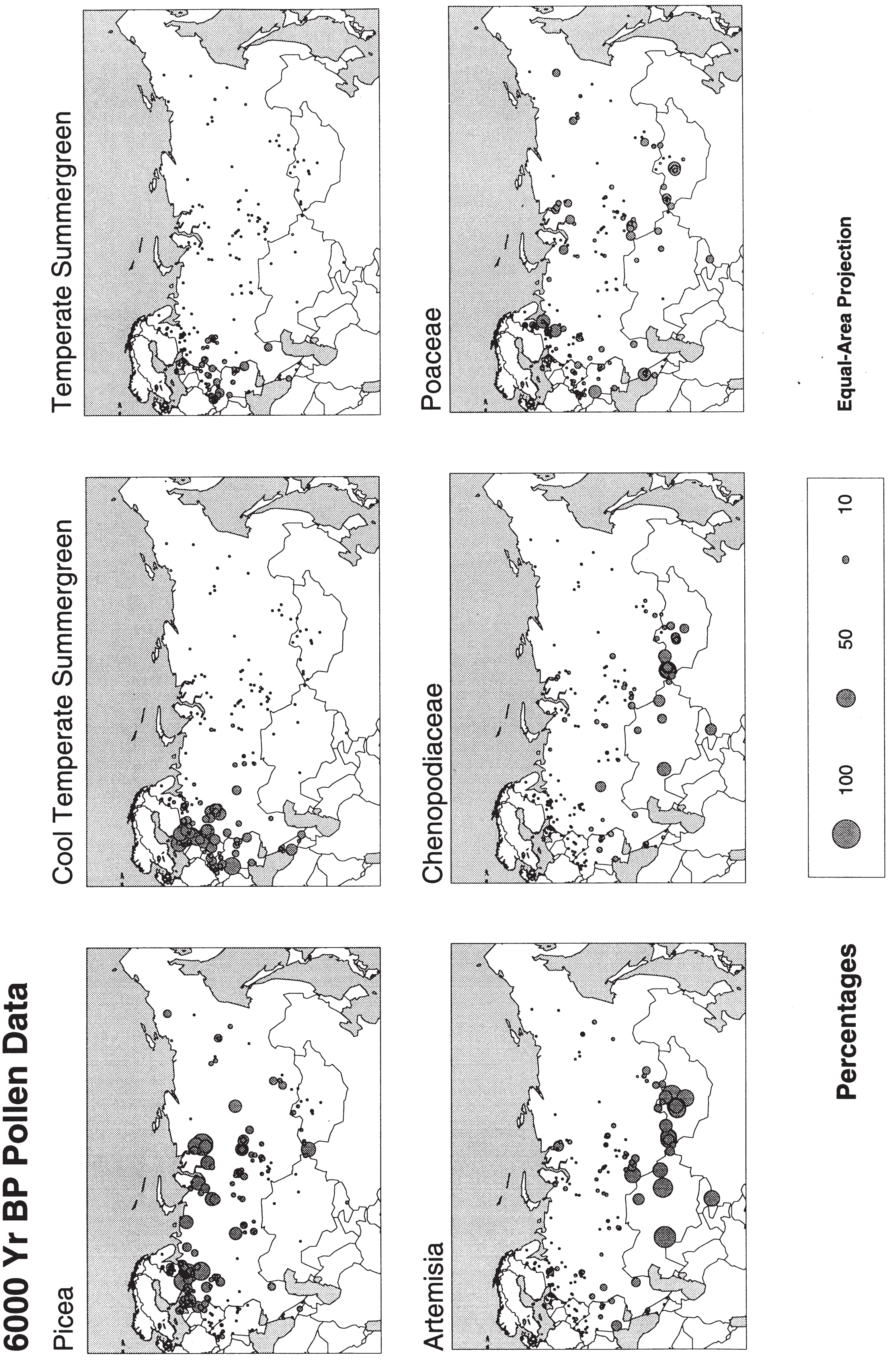


FIG. 2. Mapped total abundances of selected taxa or PFTs: (a) in modern pollen samples, (b) in 6000 year pollen samples.

TABLE 5. Numerical comparison for each site between biomes derived from modern surface samples (indexed by a "p") for which primary pollen data was available and observed biomes (indexed by an "a"). (TUND = tundra, TAIG = taiga, CLDE-cold deciduous forest, COCO = cool conifer forest, COMX = cool mixed forest, TEDE = temperate deciduous forest, STEP = steppe, DESE = desert).

	DESE$_p$	STEP$_p$	TEDE$_p$	COMX$_p$	COCO$_p$	CLDE$_p$	TAIG$_p$	TUND$_p$
DESE$_a$	**10**	25	0	0	0	0	0	0
STEP$_a$	1	**170**	0	0	0	1	5	0
TEDE$_a$	0	0	**32**	0	0	0	0	0
COMX$_a$	0	0	0	**14**	0	0	0	0
COCO$_a$	0	0	0	0	**17**	0	5	0
CLDE$_a$	0	3	0	0	0	**37**	23	2
TAIG$_a$	0	0	0	0	2	7	**70**	0
TUND$_a$	0	2	0	0	0	6	5	**34**

TABLE 6. Numerical comparison for each site between biomes derived from modern surface samples (indexed by a "p") for which digitised pollen data was available and observed biomes (indexed by an "a"). (TUND = tundra, TAIG = taiga, CLDE = cold deciduous forest, COCO = cool conifer forest, CLMX = cold mixed forest, COMX = cool mixed forest, TEDE = temperate deciduous forest, WAMX = warm mixed forest, STEP = steppe, DESE = desert).

	DESE$_p$	STEP$_p$	WAMX$_p$	TEDE$_p$	COMX$_p$	CLMX$_p$	COCO$_p$	CLDE$_p$	TAIG$_p$	TUND$_p$
DESE$_a$	**9**	9	0	4	0	12	0	3	0	0
STEP$_a$	0	**19**	2	1	4	2	2	4	1	2
TEDE$_a$	0	0	0	**20**	13	2	5	0	2	0
COMX$_a$	0	0	0	1	**56**	3	2	2	2	0
COCO$_a$	0	0	0	0	0	0	**45**	0	12	0
CLDE$_a$	0	0	0	0	0	0	0	**10**	4	2
TAIG$_a$	0	0	0	0	1	0	2	3	**91**	0
TUND$_a$	0	0	0	0	0	0	0	0	12	**9**

a slight increase in pollen abundances and areal extent in the far north (at least in the western half of the region), and is somewhat more abundant in the eastern interior of Siberia. Cool-temperate summergreen taxa also show a distinct northward expansion in eastern Europe, while pollen of both cool-temperate and temperate summergreen taxa also were found at locations further south than present in what is now the steppe zone. *Artemisia* and Chenopodiaceae show little change between 6000 years and present except for generally lower than present abundances in the steppe zone of eastern Europe.

Comparison of actual and reconstructed biomes for the present

The results of this comparison are shown separately for the raw (Table 5) and digitized (Table 6) pollen data sets. The results show that 81% of the biomes are correctly predicted in reconstructions based on primary pollen data as opposed to only 69% correctly predicted using digitized data. The contrast is even more pronounced in the reconstruction of tree-less biomes: the percentages of sites correctly identified are 29% *v.* 24% for desert, 97% *v.* 51% for steppe, and 72% *v.* 43% for tundra.

Maps of pollen-derived biomes were produced for all of the available modern pollen samples (Fig. 3a) and separately for the data set, which includes samples with primary counts and forty-seven digitized samples (Peterson, 1993) in which dwarf shrub- and tree-forms of *Betula* and *Alnus* were separated (Fig. 3c). The comparison of the observed and reconstructed vegetation shows the following.

1. The tree-less biomes (e.g. desert, steppe and tundra) are reconstructed well. Few samples in these regions are classified as being from forest biomes. The use of additional nonarboreal taxa with positive indicator value contributed to this success. Often, however, steppe was reconstructed where the vegetation map shows desert. This discrepancy occurs systematically when the modern surface samples were collected in large river valleys (e.g. Volga, Ural, Amu-Darya) or close to fresh-water lakes (e.g. Balkhash, Chatyrkel). River samples yield the same type of bias in the tundra where forest biomes (e.g. taiga or cold deciduous forest) are reconstructed. These discrepancies, which reflect the growth of trees in protected microhabitats, show that the biomization method works well for reconstructing the local vegetation, when its pollen dominates in a surface sample. No problem will arise when fossil pollen samples are

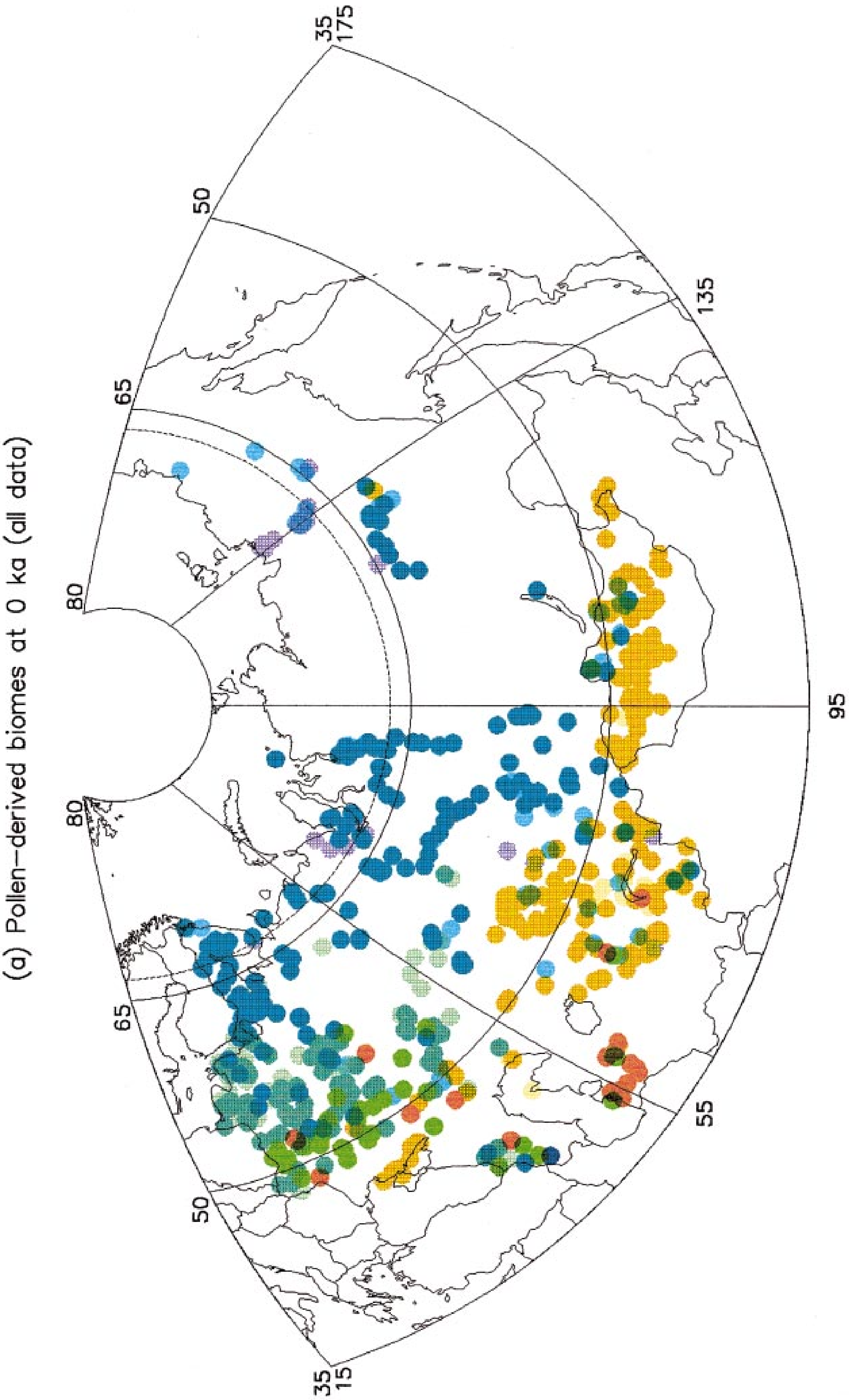

(a) Pollen–derived biomes at 0 ka (all data)

FIG. 3.

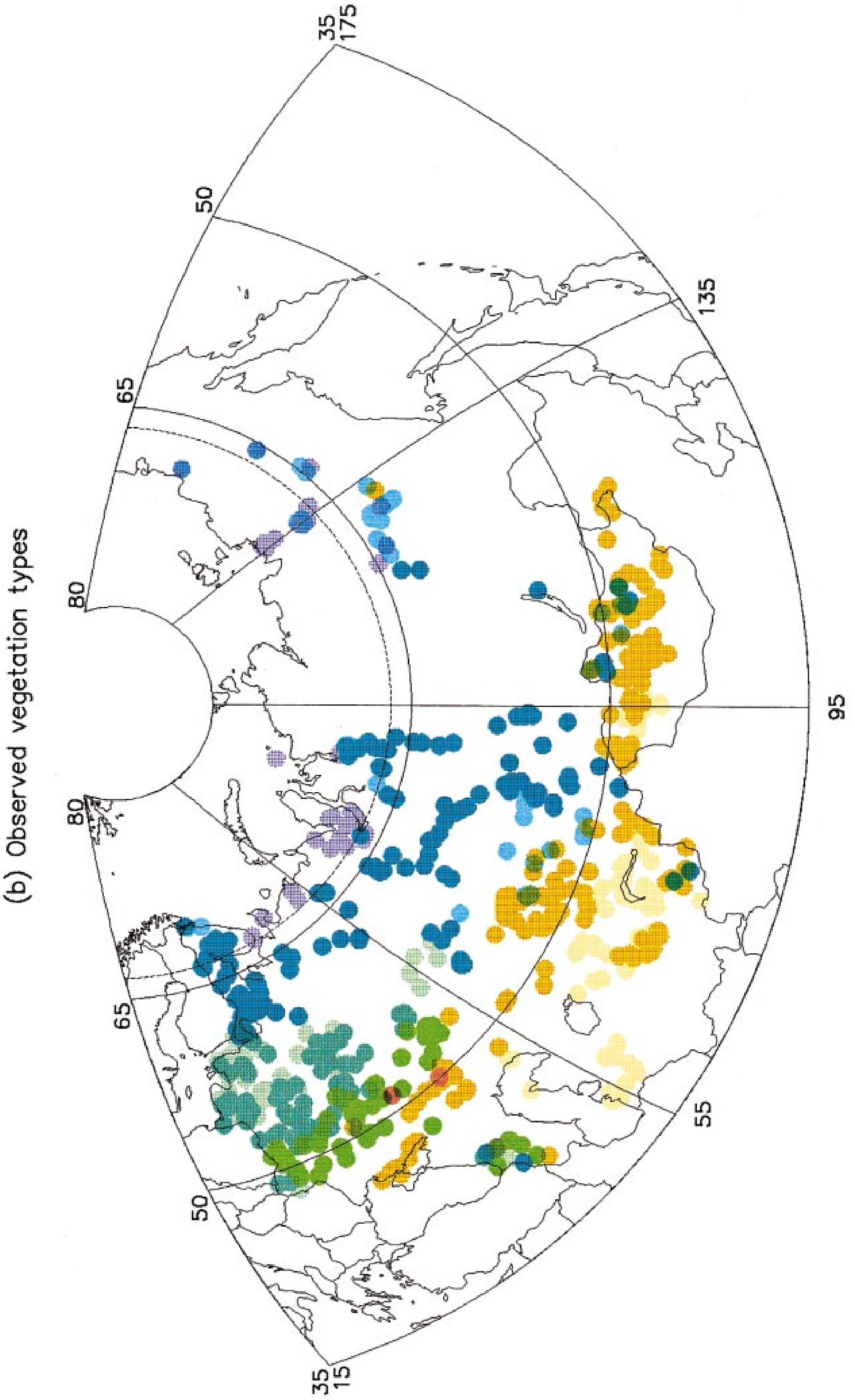
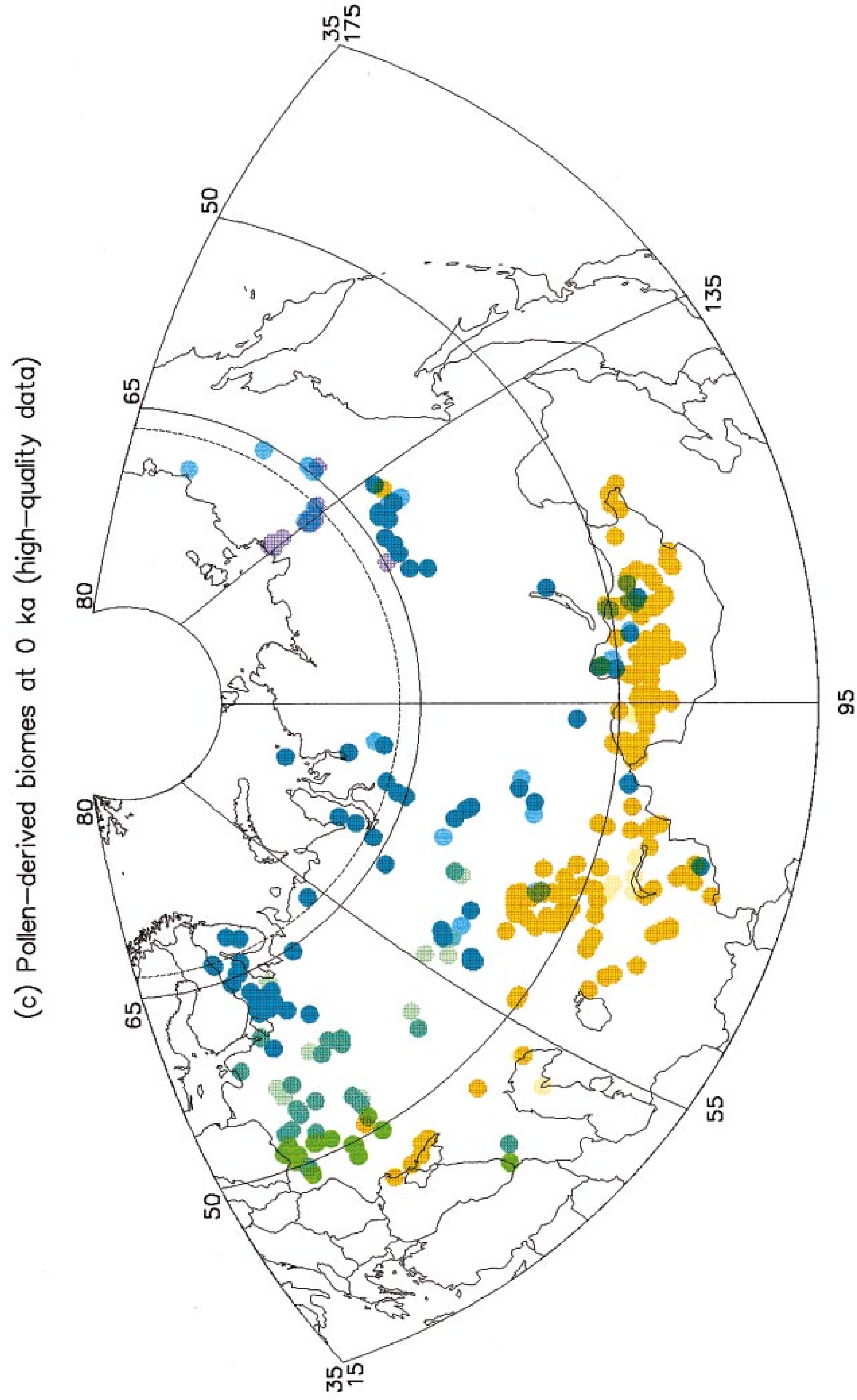

(b) Observed vegetation types

FIG. 3.



(c) Pollen-derived biomes at 0 ka (high-quality data)

FIG. 3.

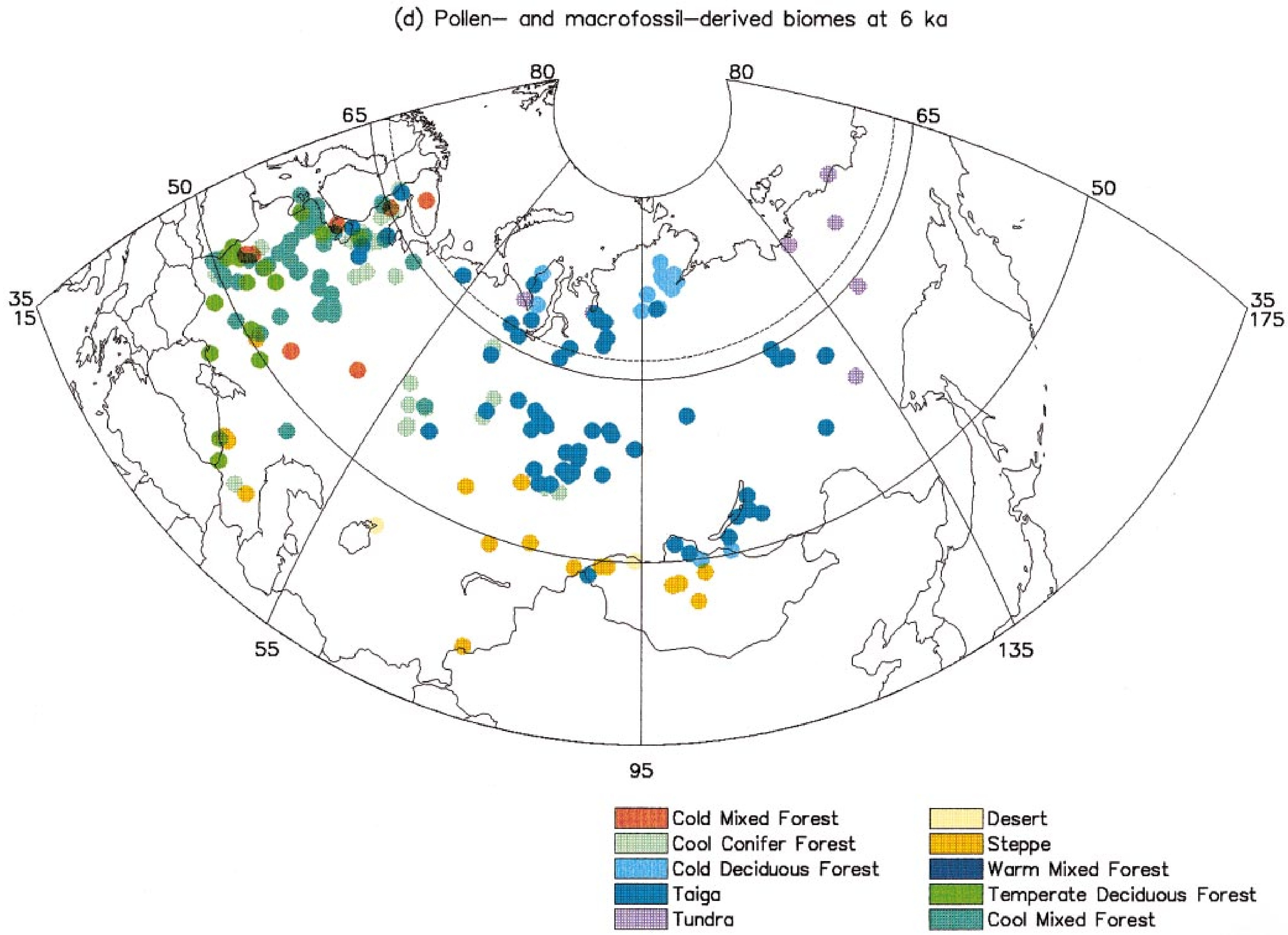


FIG. 3. Distribution of (a) pollen-derived biomes at present, (b) present vegetation types at the sampling sites, (c) pollen-derived biomes at present based only on sites for which high-quality data was available, and (d) pollen- and macrofossil-derived biomes at 6000 years.

derived from lakes or mires whose pollen source area is regional rather than local.

2. Among the forest biomes, temperate deciduous and cool conifer forests are well reconstructed. Cool mixed forests are sometimes shown in the place of temperate deciduous forests because of the presence of *Picea* pollen in the spectra, partly due to widespread planting. The same problem was mentioned by Prentice *et al.* (1996) as a weakness of the biomization method when applied to surface samples in Europe.
3. Cold mixed forest was incorrectly reconstructed in a few places, especially pollen samples subject to long-distance pollen transport (e.g. from the Caucasus to the Karakumy desert over the Caspian Sea).
4. The absence of key taxa led to reconstruction of taiga in place of cool conifer forest at some locations along the southern limit of the taiga belt.
5. The map (Fig. 3a) and Tables 5 and 6 show that the method has a limitation for pollen samples collected in areas with sparse or no vegetation (e.g. the central part of the hot sandy desert, or the polar desert of the Arctic islands). When the pollen production of local plants is extremely low, long distance transport (mostly from forested areas) dominates, leading to incorrect biome assignments. This is not likely to cause problems in reconstructing vegetation from fossil pollen spectra, however, because nonvegetated environments do not generally provide conditions for continuous sedimentation.

Biome reconstructions for 6000 years

Figure 3 confirms the impression from the pollen abundance maps (Fig. 2) that the biome distribution at 6000 years (Fig. 3d) differed substantially from both the actual modern biome distribution (Fig. 3b) and the biome distribution as reconstructed from surface samples (Fig. 3c). The 6000 year biome distributions look even more coherent than the patterns seen in surface pollen data, because the 6000 year data are more homogeneous (the fossil pollen data being all from peat and lake sediments), and because human impact on the mid-Holocene vegetation was minimal. The available 6000 year pollen sites from the Arctic are rather sparse; however, the inclusion of tree macrofossil records increases confidence in the reconstructed tree-line changes because the macrofossils are not subject to long-distance transport beyond the forest limit.

The main features revealed by comparison of Fig. 3(d) with Fig. 3(b) and (c).

1. At 6000 years the temperate deciduous forest belt extended both northward and southward from its modern position. The southward extension occurred along the river valleys as far as the northern Black Sea in the area currently dominated by steppe. The northward extension was less pronounced. However, individual 6000 year samples record temperate deciduous forest close to the Gulf of Finland and Lake Ladoga, near the modern boundary between taiga and cool conifer forests. The northern limit of cool mixed forests was also shifted correspondingly northwards.
2. Taiga was apparently reduced in overall area at 6000 years, mainly because cool conifer forests extended northwards far into what is now the broad taiga belt of European Russia. Cool conifer forests also occurred further north and east than present in the Ural Mountains and western Siberia. Cold mixed forest was present instead of taiga in the extreme north-west of the region (northern Karelia and Kola). However, taiga had attained its modern range in the continental interior (central and southern Siberia and northern Mongolia). One site in western Mongolia shows taiga where there is steppe today, and taiga was present at some sites in central Yakutia where now there is cold deciduous forest.
3. The northern forest limit was extended poleward at 6000 years. This is shown most clearly by tree macrofossil data from sites in the Yamal and Taymyr peninsulas, several hundred km north of the modern forest limit, and by increased *Picea* pollen percentages along the Arctic coast from the White Sea to Taymyr. The limited data available from eastern Siberia, however, indicate that tundra was present at 6000 years in coastal locations, just as it is today.
4. Apart from the slight encroachment of temperate deciduous forest in the west, the steppe biome is shown occupying essentially the same area at 6000 years as today. There is not enough data to locate the boundary between steppe and desert. The available data however, show that arid conditions similar to present were found north of the Aral Sea and in western Mongolia.

DISCUSSION

Our results for 6000 years are in good agreement with previous studies of Holocene vegetation changes of northern Eurasia (e.g. Khotinskii, 1984).

The extension of temperate deciduous forests at 6000 years north of their present position, as far as the eastern Baltic, implies both warmer summers (or at least a longer growing season), and warmer winters, than today. The occurrence of temperate deciduous forests at scattered sites across the south-eastern Baltic region may imply conditions drier than present, analogous to the modern forest-steppe border region.

Warmer summers during the mid-Holocene have previously been inferred from many pollen sites across the northern and central part of the East-European Plain (Klimanov, 1978, 1987, 1989; Bezusko & Klimanov, 1987; Bezusko *et al.*, 1988; Bolikhovskaya *et al.*, 1988; Elovicheva *et al.*, 1988). The largest inferred July temperature increase (3–4 °C above the modern value) was reconstructed for the high latitudes north of 60°N; the increase declines almost to zero south of 50°N (Klimanov, 1978). According to constrained analogue climate reconstructions for Europe at 6000 years (Cheddadi *et al.*, 1997), winter temperatures were also significantly (up to 2–3 °C) warmer than present in the northern part of the Russian Plain. Summer warming in mid-to high latitudes at 6000 years is expected as a direct effect of higher-than-present summer insolation caused by changes in the Earth's orbital geometry (Berger & Loutre, 1991). The summer insolation anomalies were greater in the high latitudes (where total annual insolation was also higher than present), but other (indirect) mechanisms are required to explain winter temperatures higher than present.

Conditions drier than present in the band south and south-east of the Baltic Sea were previously reconstructed from lake-status data (Harrison *et al.*, 1996). Such conditions may reflect an increased incidence of blocking anticyclones centred on the Baltic. (Harrison *et al.*, 1996) By contrast, the annual water balance (precipitation minus evapotranspiration) reconstructed from pollen and lake-level data was 50–150 mm greater than present across most of the rest of the European part of the FSU (Cheddadi *et al.*, 1997). The southward shift of temperate deciduous trees to the northern coast of the Black Sea, indicates conditions clearly wetter than present. Pollen records from the southern East-European Plain suggest that patchy forests dominated by broad-leaved deciduous species and *Pinus* were common in the valleys of the Dniper, Don, Dnestr (Khotinskii, 1984; Kremenetskii, 1991) and Volga (Bolikhovskaya, 1990). However, the adjacent plains were covered by steppe and meadow-steppe vegetation as they are today. According to pollen-based climate reconstructions, the mean July temperature in the lowland north of the Black Sea was similar to present while the annual precipitation was 50–100 mm higher (Kremenetskii, 1991).

The northward extension of forests in northern Russia at 6000 years implies warmer summers and/or longer growing seasons than present. The warming was most pronounced in European Russia, where tundra was probably absent at 6000 years (Khotinskii, 1984) and open boreal forests dominated by spruce and birch extended northwards to the Barents Sea (Bolikhovskaya *et al.*, 1988). In western Siberia the taiga and cold deciduous forests extended 100–150 km into the modern tundra area (Khotinskii, 1984) or up to 500 km further north on the Yamal and Taymyr peninsulas (Nikol'skaya & Cherkasova, 1982; Nikol'skaya, 1982; Vasil'chuk *et al.*, 1983; Volkova *et al.*, 1989; MacDonald *et al.* submitted). However, forest vegetation in the far north may have been represented by individual trees or small forest patches (forest tundra), rather than continuous zonal taiga or cold deciduous forests. On the Yamal Peninsula, pollen-based temperatures reconstructions for 5750 years BP (Nikol'skaya *et al.*, 1989) were 2–3 °C greater in July and 2 °C greater in January than today, and annual precipitation was 100 mm more than present.

Qualitatively similar changes have been reconstructed further east near the Laptev Sea coast (Nikol'skaya *et al.*, 1989). However, the mid-Holocene climate change there was not strong enough for a northward shift of the forest to be detectable in the biome map. Khotinskii (1984) suggested that the northward extension of forest in this region at 6000 years was less than 100 km, suggesting a more modest temperature increase than occurred further west.

A greater extension of *Picea* at 6000 years compared to present was noted from pollen records in central and southern Yakutia (Khotinskii, 1977; Andreev *et al.*, 1989; Andreev & Klimanov, 1991). The presence of boreal evergreen conifers in the area that is now dominated by cold deciduous forests indicates that mid-Holocene winters were warmer than present also in this region. Pollen-based reconstructions for central Yakutia in fact suggest both that July and January temperatures were 2 °C higher, and that precipitation was slightly higher, than today during mid-Holocene time (Andreev *et al.*, 1989).

The pollen record provides no evidence that steppe occupied a larger area at 6000 years than now (Khotinskii, 1984). Lake-status data from Kazakhstan and Mongolia (Harrison *et al.*, 1996) even indicate slightly wetter conditions than present during the mid-Holocene, and suggest that the direct drying effect of higher 6000 years summer insolation on evapotranspiration was compensated by atmospheric circulation-induced changes in precipitation. However, small forest patches with boreal and eurythermic conifers that grow today in the Asian steppe were apparently less widely distributed in Kazakhstan and Mongolia at 6000 years. This change could indicate that conditions in the interior were drier at 6000 years than today. Tarasov *et al.* (1997) analysing the well-dated pollen record from Ozerki (Tarasov, 1992; Kremenetskii *et al.*, 1994), eastern Kazakhstan, concluded that either warmer (and drier) summers or colder winters could explain the absence of conifers during the early to mid-Holocene. At the same time boreal summergreen taxa (e.g. *Betula, Salix*) grew continuously at Ozerki. Evergreen conifers have similar moisture requirements to boreal summergreen trees, but cannot tolerate an absolute minimum temperature below −60 °C (Prentice *et al.*, 1992). Given that at 6000 years winter insolation was 9.6% less than at present at 50°N (Berger & Loutre, 1991) and that the absolute minimum temperature recorded today in Kazakhstan is −52 °C (Klimaticheskii Atlas SSSR, 1960), it is possible that colder than present winters could have been a limiting factor for the evergreen conifers in the cold continental climate of central Asia. Cold winters at 6000 years are to be expected in low to mid-latitudes, which experienced the largest negative insolation anomalies, in contrast with high latitudes where winter temperatures are more strongly controlled by atmospheric circulation patterns.

In conclusion, the results of biomization show a strong, coherent spatial pattern to the way that the 6000 year vegetation differed from today. These changes can be broadly explained by orbitally induced changes in insolation, and can be further used for comparisons with climate model simulations. We have been able to obtain a good data coverage for much of the FSU and Mongolia, but some regions are still poorly represented. For example, more data are needed for the high Arctic and for the southern forest limit, in order to determine more exactly the boundaries among forest, tundra and steppe at 6000 years. More data are also needed to reconstruct vegetation changes in the mountain regions, since the available data do not provide clear evidence for shifts in the elevation and in the composition of mountain forests, although such shifts are likely to have occurred.

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