



Late Quaternary biomes of Canada and the eastern United States

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Abstract

Pollen data have been used to construct biome maps for today, 6000 ¹⁴C yr BP and 18,000 ¹⁴C yr BP for Canada and the eastern United States.

The inferred modern biome distributions agree well with independent reconstructions of North American vegetation prior to European settlement. Some discrepancies between the pollen data and the modern potential vegetation are caused by post-settlement clearing of the landscape and the consequent increase of herbaceous types in the recent pollen record.

Biome distributions at 6000 ¹⁴C yr BP reflected the warmer and drier conditions then prevalent in the continental interior, but the overall position of biomes was similar to that of today. The boreal treeline in North America was not significantly north of its present position, in contrast to the 100–200 km shift reported for Siberia. At the last glacial maximum (18,000 ¹⁴C yr BP), steppe and tundra were prevalent in the Midwest and north-western Canada, and coniferous forests and woodlands grew in eastern North America. The open vegetation at 18,000 ¹⁴C yr BP was probably due to drier conditions and/or lower concentrations of atmospheric CO₂.

The composition and physical structure of biomes is not constant over time. Mid-Holocene biomes were similar in structure to those of today, but shifts in the relative importance of individual plant functional types are large enough that the physical properties of biomes, such as albedo, canopy conductance and surface roughness, are likely to have varied even during the Holocene. Last glacial maximum biomes were structurally different from their modern counterparts. The biome maps therefore may obscure significant vegetational changes in space and time during the late Quaternary.

The difference between the highest and next highest affinity scores for each sample measures how strongly affinity scores discriminate among biomes. For many biomes, the difference is not large, and affinity score ties are not uncommon, highlighting the importance of tie-break procedures when using the biomization method.

Keywords

Pollen data, plant functional types, biomes, vegetation changes, eastern North America, Canada, mid-Holocene, last glacial maximum.

INTRODUCTION

BIOME 6000 was formed to produce biome maps for key time periods using a uniform procedure and based upon quality-controlled data, with the intent of testing climate and vegetation model results with the maps (Prentice & Webb,

1998). The biomization method (Prentice *et al.*, 1996) is based upon the observation that on subcontinental scales, vegetation assemblages in similar climates generally have a similar structure and will include similar physiological responses, even if they are composed of different species. Biomes are accordingly defined as assemblages of plant functional types (which should be roughly the same around the world) rather than assemblages of species (which will vary by region). This is similar to the approach taken by most biome models (e.g. Prentice *et al.*, 1992; Haxeltine & Prentice, 1996). The focus

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Table 1 Summary of surface pollen data set by sample type and biome. Biomes are those selected by the biomization method.

Reconstructed biome	Pollen sample type						Total
	Lake	Bog	River/estuary	Moss polster	Soil	Unknown	
desert	28	2	3	2	1	0	36
xerophytic woods/scrub	1	0	0	1	1	0	3
cold deciduous forest	0	0	0	0	1	0	1
tundra	71	12	0	68	0	0	151
broadleaved evergreen/warm mixed forest	50	19	1	68	3	0	141
steppe	58	18	2	21	21	3	123
open conifer woodland	6	27	20	16	3	10	82
temperate deciduous forest	237	40	1	9	3	4	294
taiga	314	101	0	135	1	6	557
cold mixed forest	0	0	0	0	0	0	0
cool conifer forest	34	49	1	41	4	0	129
cool mixed forest	668	144	1	45	1	5	864
Total	1467	412	29	406	39	28	2381

in BIOME 6000 was on 6000 ¹⁴C yr BP and 18,000 ¹⁴C yr BP because of much prior model experimentation and data compilation, and because the climatic boundary conditions contrast so markedly between these times. At 6000 ¹⁴C yr BP, the orbital conditions differed from today but other boundary conditions were similar, whereas orbital conditions at the last glacial maximum (LGM) were similar to today but ice sheet extent and CO₂ were different (Joussaume & Taylor, 1995; Kutzbach *et al.*, 1998).

An alternative use for data-derived palaeovegetation maps is to constrain the land surface conditions for palaeoclimate simulations. The need for such maps has been underscored by modelling experiments that indicate that biogeophysical interactions between vegetation and the atmosphere can have significant effects upon regional climates. Positive feedbacks associated with a simulated northward movement of the boreal treeline enhanced the orbital-induced mid-Holocene warming of the high northern latitudes (Foley *et al.*, 1994; TEMPO, 1996). A series of experiments have shown that the choice of initial vegetation conditions for the northern African region in the mid-Holocene in the model strongly influences monsoonal strength, and in part determines the final vegetation patterns (Claussen, 1994; Kutzbach *et al.*, 1996; Claussen & Gayler, 1997; Claussen, 1998). The dot maps presented here are not suitable for input into general circulation models, but future refinements of the BIOME 6000 palaeovegetation maps may include spatially interpolating the data to produce gridded vegetation maps. The production of gridded biome maps has already been achieved regionally (Williams, 2000).

Our paper uses the biomization method to reconstruct biomes from fossil pollen data for eastern North America and western Canada at 6000 ¹⁴C yr BP and 18,000 ¹⁴C yr BP. Our study uses more taxa than Williams *et al.* (1998) used in estimating biomes in eastern North America for 6000 ¹⁴C yr BP and augments the most recent compilation of pollen sites for 6000 and 18,000 ¹⁴C yr BP for Canada and eastern North America (Webb *et al.*, 1993; Ritchie & Harrison, 1993). We first validate the results of the biomization method against a composite map of the modern potential vegetation, derived from Olson *et al.* (1984), Küchler (1964) and Webb & Bernabo

(1977), and then apply the method to reconstruct past biome distributions. In addition to reconstructing past biome distributions, we explore whether biomes change in structure over time and whether such changes were large enough to have affected physical attributes of biomes such as annual and seasonal albedo, canopy conductance and surface roughness.

DATA AND METHODS

Modern pollen data

We selected 2381 surface samples (Table 1) from a pollen database housed at Brown University (Delcourt *et al.*, 1984; Avizinis & Webb, 1985) to reconstruct the modern vegetation of North America east of 105°W. Duplicate samples from a site were averaged together because individual samples may be noisier than a single composite. We did not use pollen samples that had been obtained directly from the atmosphere, or from snowbanks or pitcher plants, and we eliminated samples for which non-arboreal pollen had not been counted. We checked to see whether including other samples not directly collected from lakes or bogs (e.g. from moss polsters) led to a significant bias in biome choice, and finding none, retained the samples for this study.

Pollen data for 6000 and 18,000 ¹⁴C yr BP

We used 485 fossil pollen sites for 6000 ¹⁴C yr BP and 24 fossil pollen sites for 18,000 ¹⁴C yr BP. Most of the pollen data were available as raw pollen counts (96%) from the North American Pollen Database (NAPD) and the Base de données polliniques et macrofossiles du Québec (P. J. H. Richard, pers. comm.), but we supplemented these data where necessary with data digitized from published pollen diagrams (49%). Most of the sites used here are listed in Webb *et al.* (1993) and Ritchie & Harrison (1993), but the chronologies from Webb *et al.* (1993) for 15 sites have been modified (Williams, 2000). Information about the 209 sites not listed in, or with chronologies modified from, these earlier studies are given in Table 2. Digitization was

Table 2 Sites used in this study not reported in either Webb *et al.* (1993) or Ritchie & Harrison (1993), or reported in Webb *et al.* (1993) but used here with a revised chronology (†). Sites for which we used digitized data are marked by an asterisk (*). Site elevations were obtained from the original publication or from the ETOPO5 digital elevation data set (National Geophysical Data Center, 1988). Dating control (DC) codes are based on the COHMAP dating control scheme (Webb, 1985; Yu & Harrison 1995). For sites with continuous sedimentation (indicated by a C after the numeric code), the dating control is based on bracketing dates where 1 indicates that both dates are within 2000 years of the selected interval, 2 indicates one date within 2000 years and the other within 4000 years, 3 indicates both within 4000 years, 4 indicates one date within 4000 years and the other within 6000 years, 5 indicates both dates within 6000 years, 6 indicates one date within 6000 years and the other within 8000 years, and 7 indicates bracketing dates more than 8000 years from the selected interval. For sites with discontinuous sedimentation (indicated by D after the numeric code), 1 indicates a date within 250 years of the selected interval, 2 a date within 500 years, 3 a date within 750 years, 4 a date within 1000 years, 5 a date within 1500 years, 6 a date within 2000 years, and 7 a date more than 2000 years from the selected interval. We assigned a dating control of 7 to data from digitized pollen diagrams with a time scale but no reported radiocarbon dates and to sites with bracketing stratigraphic (i.e. non-radiometric) dates. For e.g. the 6000 ¹⁴C yr BP interval at Allenberg Bog (‡) is constrained by the *Tsuga* decline at c. 4700 yr BP and *Pinus* peak dated to 8700 yr BP from Protection Bog (Williams, 2000).

Site	Site name	Lat. (°N)	Long. (°W)	Elev. (m)	Sample type	Record length (kyr)	No. of ¹⁴ C dates	DC at 6000 ¹⁴ C yr BP	DC at 18,000 ¹⁴ C yr BP	Database	References
1	Alenberg Bog†	42.25	78.88	494	bog	0–10.5	0†	7C	n/a	NAPD	Miller, 1973
2	Almora Lake	46.21	95.29	437	lake	3.5–11.5	0	7C	n/a	NAPD	Digerfeldt <i>et al.</i> , 1992
3	Andy Lake	64.65	128.08	1360	lake	0–11.5	4	1C	n/a	NAPD	Szeicz <i>et al.</i> , 1995
4	Axe Lake	45.38	79.50	323	lake	0–10	3	1C	n/a	NAPD	J. H. McAndrews, unpublished
5	Baie du Diana	60.78	69.83	50	lake	0.5–6.5	1	6C	n/a	NAPD	Richard, 1977
6	Barchampe Lake	30.62	83.25	43	lake	0–7.5	2	4C	n/a	NAPD	Watts <i>et al.</i> , 1996
7	Barry Lake	44.30	77.92	167	lake	0–10.5	1	4C	n/a	NAPD	McAndrews, 1984
8	Baseball Bog	47.23	79.78	292	bog	0–10.5	2	4C	n/a	NAPD	J. H. McAndrews, unpublished
9	Basswood Road Lake/Splan Pond†	45.26	67.33	106	lake	0–12.5	5	2C	n/a	NAPD	Mott, 1975
10	Bear Bog	47.18	80.16	304	bog	3.5–10	2	2C	n/a	NAPD	Gordon & McAndrews, 1992
11	Bear Cove Bog 1*	50.88	128.00	30	bog	0–10	1	6C	n/a		Hebda, 1983
12	Bear Cove Bog 2*	50.88	128.00	30	bog	0–14	3	6C	n/a		Hebda, 1983
13	Beckman Lake	45.42	93.18	278	lake	0–10.5	0	7C	n/a	NAPD	Keen & Shane, 1990
14	Bell's Lake	65.02	127.48	580	lake	0–11.5	5	2C	n/a	NAPD	Szeicz <i>et al.</i> , 1995
15	Belmont Bog†	42.25	77.92	497	bog	0–11	5	3C	n/a	NAPD	Spear & Miller, 1976
16	Bishops Falls	48.94	55.51	75	lake	0–10.5	1	6C	n/a	NAPD	Blake, 1983
17	Bluffers Pingo*	69.65	132.22	0	lake	2–10.5	0	7C	n/a		Spear, 1993
18	Bob Black Pond	34.32	84.87	285	lake	12.5–24	1	n/a	7D	NAPD	Watts, 1970
19	Bride	47.33	74.50	425	lake	0–8.5	3	2C	n/a	BDPMQ	P. J. H. Richard, unpublished
20	Brisay 2	54.36	70.36	595	lake	0–6	2	1D	n/a	NAPD	Richard <i>et al.</i> , 1982
21	Browns Pond	38.15	79.62	620	lake	0–17.5	7	6C	n/a	NAPD	Kneller & Peteet, 1993
22	Buck Lake	27.23	81.33	45	lake	0–8.5	1	6C	n/a	NAPD	W. A. Watts, unpublished
23	Candelabra Lake	61.68	130.65	1040	lake	0–10.5	11	1C	n/a	NAPD	Cwynar & Spear, 1995
24	Caribou Bog	45.93	68.77	37	bog	0–9.5	6	1C	n/a	NAPD	Gajewski, 1987
25	Cedar Bog Lake	45.41	93.20	275	lake	0–11	2	1C	n/a	NAPD	Cushing, 1967
26	Chapman Lake*	64.87	138.25	1463	lake	0–14	3	6C	n/a		Terasmae & Hughes, 1966
27	Cheyenne Bottoms	38.47	98.67	547	bog	0–29.5	5	2C	7C	NAPD	Fredlund, 1995
28	Chilhil Lake*	50.65	121.80	915	lake	0–8	3	1C	n/a		Mathewes & King, 1989
29	Clear Lake, Iowa	43.15	93.35	374	lake	0–13	9	1C	n/a	NAPD	Baker <i>et al.</i> , 1992
30	Clear Pond, South Carolina	33.80	78.95	10	lake	0–20.5	9	1C	1C	NAPD	Hussey, 1993
31	Clo	48.50	79.35	280	lake	0–8.5	3	2C	n/a	BDPMQ	Richard, 1980
32	Colville Lake*	67.10	125.78	275	lake	0–7	7	1C	n/a		Nichols, 1974
33	Comb Lake	49.69	57.71	678	lake	0–8	1	6C	n/a	NAPD	Lowdon & Blake, 1979
34	Compass Pond	50.03	56.2	236	lake	0–13.5	6	1C	n/a	NAPD	Dyer, 1986
35	Cottonwood Lake	44.84	99.91	549	lake	0–12.5	10	3C	n/a	NAPD	Barnosky <i>et al.</i> , 1987
36	Couchepaganiche-centre	48.36	71.85	191	lake	0–8.5	4	1D	n/a	BDPMQ	P. J. H. Richard, unpublished
37	Cranberry Lake	44.10	78.10	170	lake	0–10	6	1C	n/a	NAPD	J. H. McAndrews, unpublished
38	Cristal Lake	52.12	90.08	355	lake	0–7	2	6C	n/a	NAPD	Björck, 1985
39	Crowfoot Lake	51.65	116.42	1940	lake	0–12	7	2C	n/a	NAPD	Osborn <i>et al.</i> , 1995
40	Cummins Pond	48.41	89.35	229	lake	4–9.5	4	1D	n/a	NAPD	Julig <i>et al.</i> , 1990
41	Decoy Lake	43.23	80.37	260	lake	0–11.5	5	2C	n/a	NAPD	Szeicz & MacDonald, 1991
42	Delorme 1	54.42	69.92	513	lake	0.5–5.5	3	3D	n/a	NAPD	Richard <i>et al.</i> , 1982
43	Desautels	49.46	73.25	480	lake	0–9.5	5	1C	n/a	BDPMQ	P. J. H. Richard, unpublished
44	East Twin Lake, Ohio	41.20	81.33	322	lake	0–13	19	2C	n/a	NAPD	Shane & Anderson, 1993
45	Fairfax Lake*	52.97	116.57	1400	lake	0–11.5	1	6C	n/a		Schweger <i>et al.</i> , 1981
46	Fawn Lake, Ontario	45.42	79.38	333	lake	0–10	3	1C	n/a	NAPD	J. H. McAndrews, unpublished
47	Ferme des Picard	45.27	72.61	227	bog	0–11	5	2C	n/a	BDPMQ	P. J. H. Richard, unpublished
48	Fishblue Lake*	49.98	121.48	332	lake	0–10.5	1	6C	n/a		Mathewes & King, 1989
49	Forêt de Beauséjour	46.65	71.17	120	bog	0–8.5	2	1D	n/a	BDPMQ	Chabot & Ménard, 1978
50	Fresh Pond	41.16	71.58	28	lake	0–13	5	2C	n/a	NAPD	Dunwiddie, 1990
51	Fudger Lake	40.10	83.53	320	lake	0–14.5	1	5C	n/a	NAPD	Shane & Anderson, 1993

Table 2 *continued*

Site	Site name	Lat. (°N)	Long. (°W)	Elev. (m)	Sample type	Record length (kyr)	No. of ¹⁴ C dates	DC at 6000 ¹⁴ C yr BP	DC at 18,000 ¹⁴ C yr BP	Database	References
52	Furnival Lake	48.21	84.93	440	lake	0–8	2	1D	n/a	NAPD	J. H. McAndrews, unpublished
53	Gass Lake†	44.05	87.73	211	lake	0–12	3	3C	n/a	NAPD	Webb, 1983
54	Gause Bog	30.79	96.72	113	bog	4–10	0	7C	n/a	NAPD	Bryant, 1977
55	Georgian Bay, Lake Huron [1]	44.74	80.86	176	lake	0–11.5	0	7C	n/a	NAPD	J. H. McAndrews, unpublished
56	Georgian Bay, Lake Huron [2]	45.17	81.32	176	lake	0.5–12	0	7C	n/a	NAPD	J. H. McAndrews, unpublished
57	Gill Lake*	65.62	139.75	1143	lake	0–12.5	1	7C	n/a		Terasmae & Hughes, 1966
58	Gould Pond†	44.98	69.32	89	lake	0–13.5	7	1C	n/a	NAPD	Jacobson <i>et al.</i> , 1987
59	Green Point Pond	49.67	57.95	2	lake	0–9.5	1	6C	n/a	NAPD	J. H. McAndrews, unpublished
60	Hail Lake	60.03	129.02	690	lake	0–10	7	2C	n/a	NAPD	Cwynar & Spear, 1995
61	Hams Lake	43.24	80.41	301	lake	0–11.5	20	1D	n/a	NAPD	Bennett, 1987
62	Harris Lake*	49.58	109.83	1310	lake	0–9	4	2C	n/a		Sauchyn & Sauchyn, 1991
63	Hershop Bog	29.58	97.61	124	bog	0.5–12	3	1D	n/a	NAPD	Larson <i>et al.</i> , 1972
64	Houghton Bog†	42.54	78.67	428	bog	0–12.5	1	5C	n/a	NAPD	Miller, 1973
65	Ile aux Chats	45.51	73.76	23	forest hollow	0–7.5	3	1C	n/a	BDPMQ	P. J. H. Richard, unpublished
66	Inglesby Lake	44.48	77.05	167	lake	0.5–10.5	2	4C	n/a	NAPD	Fritz <i>et al.</i> , 1987
67	Iola Bog	44.50	89.12	258	lake	0–10	0	7C	n/a	NAPD	Schweger, 1969
68	Irvin Lake	47.14	93.64	478	lake	0–10.5	5	1D	n/a	NAPD	Alwin, 1982
69	Jackson Pond†	37.45	85.72	212	lake	0–20	6	5C	2C	NAPD	Wilkins, 1985; Wilkins <i>et al.</i> , 1991
70	Jim Lakes Basin*	47.53	113.90	1888	lake	0–11	0	7C	n/a		Gerloff <i>et al.</i> , 1995
71	Joes Pond	48.24	58.24	100	lake	0–13.5	3	3C	n/a	NAPD	Anderson & Lewis, 1992
72	Keele Lake	64.17	127.62	1150	lake	0–12	6	1D	n/a	NAPD	Szeicz <i>et al.</i> , 1995
73	Kellners Lake	44.24	87.85	261	lake	0–11	4	4C	n/a	NAPD	Goodwin, 1976
74	Kellys Hollow	45.30	90.35	470	bog	0–10.5	2	2C	n/a	NAPD	Heide, 1984
75	Kelowna Bog*	49.93	119.38	405	bog	0–8.5	2	3C	n/a		Alley, 1976
76	Kennys Pond	47.59	52.71	70	lake	0–8.5	3	1D	n/a	NAPD	Blake, 1983
77	Lac à Euloge	49.24	65.37	83	lake	0–10	7	2C	n/a	BDPMQ	Marcoux & Richard, 1995
78	Lac à la Fourche	47.61	70.62	305	lake	0–9.5	1	6C	n/a	NAPD	Labelle & Richard, 1981
79	Lac à la Fourche Four	47.98	69.21	160	lake	0–9.5	4	2C	n/a	BDPMQ	Richard <i>et al.</i> , 1992
80	Lac à la Main	47.70	70.62	730	lake	0–9	6	1C	n/a	BDPMQ	Bussièrès, 1992
81	Lac à la Tortue†	45.55	73.32	137	lake	0–9	3	2C	n/a	NAPD	Gauthier, 1981
82	Lac à Robin	48.05	65.27	50	lake	0.5–9.5	4	1C	n/a	NAPD	Jetté & Richard, 1992
83	Lac Bastien	46.40	78.92	305	lake	0–9.5	5	1C	n/a	NAPD	Bennett, 1987
84	Lac Boucané	47.46	69.45	500	lake	5–9	3	1C	n/a	NAPD	Lortie & Richard, 1986
85	Lac Bromont	45.27	72.67	135	lake	0–14	9	2C	n/a	BDPMQ	P. J. H. Richard, unpublished
86	Lac Caribou	48.20	64.94	116	lake	0–9.5	5	1D	n/a	NAPD	Jetté & Richard, 1992
87	Lac Dolbeau	48.80	65.95	975	lake	0–11.5	7	2C	n/a	BDPMQ	P. J. H. Richard, unpublished
88	Lac du Diable	48.91	66.12	494	lake	0–10.5	4	2C	n/a	NAPD	Richard & Labelle, 1989
89	Lac Ebron	49.04	65.88	530	lake	0–9	5	1D	n/a	BDPMQ	P. J. H. Richard, unpublished
90	Lac Flévy	48.22	71.22	381	lake	0–10.5	3	4C	n/a	BDPMQ	P. J. H. Richard, unpublished
91	Lac Harriman	48.24	65.84	65	lake	0–11.5	1	7C	n/a	NAPD	Jetté & Richard, 1992
92	Lac J'arrive	49.25	65.38	56	lake	0–15	6	2C	n/a	BDPMQ	Marcoux & Richard, 1995
93	Lac Joncas	47.26	71.18	780	lake	0–8.5	4	4C	n/a	BDPMQ	P. J. H. Richard, unpublished
94	Lac Lavoie -latérale	48.44	67.26	305	lake	0–9	5	2C	n/a	BDPMQ	P. J. H. Richard, unpublished
95	Lac Madeleine	47.67	70.72	800	lake	0–7.5	4	1C	n/a	BDPMQ	Bussièrès, 1992
96	Lac Neume cgc-27	47.59	77.11	382	lake	0–8.5	5	2C	n/a	BDPMQ	P. J. H. Richard, unpublished
97	Lac Ouellet	47.53	68.94	300	lake	0–10.5	3	1C	n/a	NAPD	Richard <i>et al.</i> , 1992
98	Lac Perdu (Ruisseau Castor)	49.17	66.32	152	lake	0–14	11	1D	n/a	BDPMQ	P. J. H. Richard, unpublished
99	Lac Pluvieux	47.84	69.35	180	lake	0–6.5	1	6C	n/a	NAPD	Richard <i>et al.</i> , 1992
100	Lac Poulin	46.83	71.50	384	lake	0–8.5	3	1D	n/a	BDPMQ	P. J. H. Richard, unpublished
101	Lac Sheldrake 3	56.88	76.39	180	lake	0–6	3	1D	n/a	BDPMQ	P. J. H. Richard, unpublished
102	Lac Spearman cgc-41	46.54	78.50	374	lake	0–9.5	5	1D	n/a	BDPMQ	P. J. H. Richard, unpublished
103	Lac Triangle	48.71	65.42	465	lake	0–9.5	6	1C	n/a	BDPMQ	P. J. H. Richard, unpublished
104	Ladd Lake	41.42	84.75	249	lake	0–13.5	5	4C	n/a	NAPD	Shane & Anderson, 1993
105	Lake Ann	45.42	93.69	291	lake	1–10.5	2	1C	n/a	NAPD	Keen & Shane, 1990
106	Lake BI2	57.12	76.38	210	lake	0–7	4	1C	n/a	NAPD	Gajewski & Garralla, 1992
107	Lake Carlson	44.82	93.16	254	lake	0–12	0	7C	n/a	NAPD	Wright <i>et al.</i> , 1963
108	Lake CH2	49.68	74.58	830	lake	0–8	6	1C	n/a	NAPD	Garralla & Gajewski, 1992
109	Lake EC1	56.28	75.10	250	lake	0–6.5	4	1D	n/a	NAPD	Gajewski <i>et al.</i> , 1993
110	Lake Erie	41.92	82.76	168	lake	0–13	3	1D	n/a	NAPD	Lewis & Anderson, 1989
111	Lake GB2	56.10	75.28	300	lake	0–6.5	4	1D	n/a	NAPD	Gajewski <i>et al.</i> , 1993
112	Lake LB1	57.92	75.62	200	lake	0–6	4	1D	n/a	NAPD	Gajewski <i>et al.</i> , 1993
113	Lake LR1	58.58	75.25	170	lake	0–6.5	4	1C	n/a	NAPD	Gajewski <i>et al.</i> , 1993
114	Lake LR3	58.58	75.25	160	lake	0–5.5	3	3D	n/a	NAPD	Gajewski & Garralla, 1992

Table 2 continued

Site	Site name	Lat. (°N)	Long. (°W)	Elev. (m)	Sample type	Record length (kyr)	No. of ¹⁴ C dates	DC at 6000 ¹⁴ C yr BP	DC at 18,000 ¹⁴ C yr BP	Database	References
115	Lake LT1	58.14	75.15	150	lake	0–6	4	1D	n/a	NAPD	Gajewski & Garralla, 1992
116	Lake Mendota†	43.10	89.42	257	lake	0–10.5	5	1C	n/a	NAPD	Winkler <i>et al.</i> , 1986
117	Lake Minnie	47.24	95.01	429	lake	0–11.5	2	3C	n/a	NAPD	Almendinger, 1992
118	Lake O'Hara	51.36	116.35	2015	lake	0.5–10.5	1	6C	n/a	NAPD	Reasoner & Hickman, 1989
119	Lake Ontario, Mississauga Basin	43.56	78.15	75	lake	0–12	0	7C	n/a	NAPD	McAndrews, 1973
120	Lake Ontario, Rochester Basin	43.51	76.90	75	lake	0–12	0	7C	n/a	NAPD	McAndrews, 1972
121	Lake QC	46.83	80.70	333	lake	0–11	3	2C	n/a	NAPD	McAndrews & Campbell, 1993
122	Lake RS29	73.13	95.28	180	lake	0.5–10	7	1C	n/a	NAPD	Gajewski, 1995
123	Lake RS36	72.58	95.07	160	lake	0.5–8.5	9	1D	n/a	NAPD	Gajewski, 1995
124	Lake Wabamun*	53.57	114.45	725	lake	0–9.5	9	1C	n/a	n/a	Hickman <i>et al.</i> , 1984
125	Langdale Pond	30.64	83.19	58	lake	0–8	1	4C	n/a	NAPD	Watts <i>et al.</i> , 1996
126	L'Anse aux Meadows Road Cut Bog	51.60	55.53	–48	bog	0–6.5	2	2C	n/a	NAPD	Davis, 1984
127	Large Tea Field 1	45.12	74.21	51	bog	0–11	4	2C	n/a	BDPMQ	Laframboise, 1987
128	Leading Ticks	49.47	55.47	105	lake	0–12.5	5	1D	n/a	NAPD	Blake, 1983
129	LG-4-83-06 m	54.08	72.94	365	lake	0–6.5	5	1C	n/a	BDPMQ	P. J. H. Richard, unpublished
130	LG-4-83-1P	54.04	72.87	470	lake	0–6	4	1D	n/a	BDPMQ	P. J. H. Richard, unpublished
131	LG-4-83-6P	54.08	72.94	365	lake	0–6.5	7	1C	n/a	BDPMQ	P. J. H. Richard, unpublished
132	Little Round Lake	44.80	76.68	206	lake	0–11	1	7C	n/a	NAPD	Lowdon & Blake, 1968
133	Lofty Lake*	54.73	112.48	625	lake	0–11.5	5	1C	n/a	n/a	Lichti-Federovich, 1970
134	Loon Pond†	45.03	68.20	110	lake	0–12	8	2C	n/a	NAPD	G. L. Jacobson Jr, unpublished
135	Louise Pond	53.42	131.75	650	lake	0–10	5	1D	n/a	NAPD	Pellatt & Mathewes, 1994
136	Maligne Lake	52.73	117.63	1690	lake	0–8	1	6C	n/a	NAPD	Kearney & Luckman, 1987
137	Mansell Pond	45.04	68.73	58	lake	0–9	18	1C	n/a	NAPD	Almquist-Jacobson & Sanger, 1995
138	Maria Lake	68.27	133.47	105	lake	0–12.5	7	2C	n/a	NAPD	Ritchie, 1977
139	Mariana Lake*	55.95	112.17	690	lake	0–11.5	6	1C	n/a	n/a	Hutton <i>et al.</i> , 1994
140	Marion Lake, British Columbia	49.33	123.00	305	lake	0–13	7	1C	n/a	NAPD	Mathewes, 1973
141	McCarston's Lake	45.05	80.09	433	lake	0–9	2	4C	n/a	NAPD	J. H. McAndrews, unpublished
142	McMaster Lake	64.13	110.58	480	lake	0–8	0	7C	n/a	NAPD	Moser & MacDonald, 1990
143	Mermaid Bog	46.25	63.02	15	bog	0–9.5	1	4C	n/a	NAPD	Anderson, 1980
144	Moon Lake	46.86	98.16	444	lake	0–12	13	1C	n/a	NAPD	Laird <i>et al.</i> , 1996
145	Mordsgger Lake	51.38	94.25	400	lake	0–9.5	2	1D	n/a	NAPD	McAndrews, 1986
146	Mt. Hayes*	54.05	130.08	30	bog	0–8.5	1	6C	n/a	n/a	Banner <i>et al.</i> , 1983
147	No Bottom Pond	41.28	70.21	6	lake	0–14	6	6C	n/a	NAPD	Dunwiddie, 1990
148	Nutt Lake	45.22	79.45	305	lake	0–10	20	1C	n/a	NAPD	Bennett, 1987
149	Oliver Pond	48.42	89.32	250	lake	0–10.5	2	2C	n/a	NAPD	Julig <i>et al.</i> , 1990
150	Opabin Lake	51.34	116.31	2280	lake	0.5–8.5	1	6C	n/a	NAPD	Reasoner & Hickman, 1989
151	Parc de Frontenac	45.97	71.15	329	bog	0–11	7	1D	n/a	BDPMQ	P. J. H. Richard, unpublished
152	Pass Lake	48.56	88.74	250	lake	0–10	3	1C	n/a	NAPD	McAndrews, 1986
153	Patschke Bog	30.37	97.12	142	bog	0–17.5	4	5C	n/a	NAPD	Camper, 1991
154	Paynter Marsh	44.10	78.34	188	bog	0–11.5	4	1C	n/a	NAPD	Yu <i>et al.</i> , 1996
155	Peggy Lake	49.48	92.00	470	lake	0–9	2	1C	n/a	NAPD	J. H. McAndrews, unpublished
156	Phair Lake*	36.83	121.87	715	lake	0–6.5	3	1C	n/a	n/a	Mathewes & King, 1989
157	Pinecrest Lake	50.50	121.50	320	lake	0–11	1	6C	n/a	NAPD	Mathewes & Rouse, 1975
158	Porqui Pond	44.17	79.77	188	lake	0–13.5	3	1C	n/a	NAPD	J. H. McAndrews, unpublished
159	Portage Marsh	41.58	87.22	189	bog	1–11	3	4C	n/a	NAPD	Singer <i>et al.</i> , 1996
160	Powers Fort Swale	36.60	90.58	91	lake	0–18	18	n/a	3D	NAPD	Royall, 1988
161	Protection Bog†	42.62	78.47	430	bog	0–9	3	2C	n/a	NAPD	Miller, 1973
162	Prudent	48.30	72.04	315	lake	0–9	2	3C	n/a	BDPMQ	P. J. H. Richard, unpublished
163	Quarles Pond	38.00	79.07	500	lake	0–12.5	0	7C	n/a	NAPD	Craig, 1969
164	Queens Lake	64.12	110.57	480	lake	0–8	5	1C	n/a	NAPD	Moser & MacDonald, 1990
165	Quillin Site	41.00	81.97	305	bog	4–13.5	9	2C	n/a	NAPD	Shane, 1987
166	R Lake, Ontario	54.31	84.56	147	lake	0–7	2	2C	n/a	NAPD	McAndrews <i>et al.</i> , 1982
167	Radtke Lake†	43.40	88.10	274	lake	0–12	4	2C	n/a	NAPD	Webb, 1983
168	Reidel Lake	46.21	95.28	443	lake	0–11.5	7	2C	n/a	NAPD	Almquist-Jacobson <i>et al.</i> , 1992
169	Rice Lake, Minnesota	46.92	95.58	443	lake	0–7	0	7D	n/a	NAPD	McAndrews, 1969
170	Rice Lake, North Dakota	48.01	101.53	620	lake	0–9.5	10	1C	n/a	NAPD	E. C. Grimm, unpublished
171	Roberts Creek	42.99	91.50	308	lake	0–12.5	23	1C	n/a	NAPD	Chumbley <i>et al.</i> , 1990
172	Robinson's Pond	48.26	58.80	32	lake	0–14	2	4C	n/a	NAPD	J. H. McAndrews, unpublished
173	Ross Pond	43.92	69.41	37	lake	0–12	6	7C	n/a	NAPD	Kellogg, 1991
174	Sarnia Elk Site Section	42.98	82.32	185	section	0–5.5	2	3D	n/a	NAPD	J. H. McAndrews, unpublished
175	SC1 Pond	54.42	131.91	550	lake	0–7	3	1D	n/a	NAPD	Pellatt & Mathewes, 1997
176	Shangri-La Bog	53.27	132.41	595	bog	0.25–7	1	6C	n/a	NAPD	Pellatt & Mathewes, 1997
177	Sheelar Lake†	29.52	82.00	51	lake	0–24	7	4C	2C	NAPD	Watts & Stuiver, 1980

Table 2 continued

Site	Site name	Lat. (°N)	Long. (°W)	Elev. (m)	Sample type	Record length (kyr)	No. of ¹⁴ C dates	DC at 6000 ¹⁴ C yr BP	DC at 18,000 ¹⁴ C yr BP	Database	References
178	Sinkhole Pond†	43.97	70.35	95	lake	0–12.5	5	4C	n/a	NAPD	G. L. Jacobson Jr, unpublished
179	Sleet Lake	69.28	133.58	n/a	lake	0–12	5	1C	n/a	NAPD	Spear, 1993
180	Small Tea Field 1	45.13	74.29	50	bog	0–9.5	4	1D	n/a	BDPMQ	Laframboise, 1987
181	Smallboy Lake*	53.58	115.33	762	lake	0–8	5	1C	n/a		Vance <i>et al.</i> , 1983
182	South Soefje Bog	29.60	97.52	97	bog	0–8	0	7C	n/a	NAPD	Bryant, 1977
183	Spiritwood Lake	47.07	98.59	437	lake	0–10.5	2	3C	n/a	NAPD	J. H. McAndrews, unpublished
184	Spruce Pond	41.24	74.20	223	lake	0–12.5	9	1C	n/a	NAPD	Maenza-Gmelch, 1997a
185	Stone Lake Tamarack Swamp	44.89	93.69	288	bog	0–11	0	7C	n/a	NAPD	Swain, 1979
186	Sud du Lac du Noyer	46.79	72.84	270	lake	0.5–10	5	2C	n/a	NAPD	Richard, 1977
187	Sugarloaf Pond†	47.62	52.67	100	lake	0–9.5	3	4C	n/a	NAPD	MacPherson, 1982
188	Surprise Lake	49.33	122.75	540	lake	0–8	5	2C	n/a	NAPD	Mathews, 1973
189	Sutherland Pond	41.39	74.04	380	lake	0–12.5	10	2C	n/a	NAPD	Maenza-Gmelch, 1997b
190	Tassiujak	58.64	70.12	150	bog	0–6	3	1D	n/a	BDPMQ	P. J. H. Richard, unpublished
191	Taupawshas Bog	41.27	70.06	14	bog	0–10.5	3	3C	n/a	NAPD	Dunwiddie, 1989
192	Third Lake	48.11	92.02	446	lake	0–10	0	7C	n/a	NAPD	Swain, 1979
193	Three Pines Bog	47.00	80.12	294	bog	0–6.5	2	2C	n/a	NAPD	Gordon, 1990
194	Toboggan Lake	50.77	114.60	1480	lake	0–10.5	5	1D	n/a	NAPD	MacDonald <i>et al.</i> , 1987
195	Touquin Pass*	52.73	118.35	1935	bog	0–9.5	2	6C	n/a		Kearney & Luckman, 1983
196	Tourbière aux Orignaux	48.85	64.33	326	bog	0–7	2	2C	n/a	BDPMQ	P. J. H. Richard, unpublished
197	Tourbière de Lanoraie Coteau Jaune	45.96	73.34	18	bog	1–6.5	5	1C	n/a	NAPD	Comtois, 1982
198	Twin Lakes, British Columbia	50.75	116.33	1100	lake	0–7	1	6D	n/a	NAPD	Hazell, 1979
199	Upper Elk Valley Bog A*	50.38	114.93	1586	bog	0–10.5	2	6C	n/a		Fergusson & Hills, 1983
200	Upper Graven Lake	46.18	95.31	446	lake	0–11	4	2C	n/a	NAPD	Almquist-Jacobson <i>et al.</i> , 1992
201	Upper Mallot Lake	47.31	84.26	422	lake	0–10.5	3	1C	n/a	NAPD	McAndrews & Campbell, 1993
202	Wapizagonke	46.73	73.03	230	bog	1–9.5	2	1D	n/a	NAPD	Richard, 1977
203	Watchtower Basin	52.80	117.83	2142	lake	0–7	2	1D	n/a	NAPD	Luckman & Kearney, 1986
204	Waterdevil Lake*	59.77	134.93	875	lake	0–10.5	13	1C	n/a		Spear & Cwynar, 1997
205	Waubashene Nipissing Transgression Site	44.78	79.68	190	section	6–6.5	8	1D	n/a	NAPD	J. H. McAndrews, unpublished
206	Weslemkoon Lake	45.03	77.43	316	lake	0–7	3	1C	n/a	NAPD	Julig <i>et al.</i> , 1990
207	Wilcox Pass	52.24	117.22	2355	bog	0–11	2	7C	n/a	NAPD	Beaudoin & King, 1990
208	Wylde Bog	43.90	80.40	484	bog	0–12.5	2	1C	n/a	NAPD	J. H. McAndrews, unpublished
209	Wylde Lake	43.91	80.40	484	lake	0–12.5	3	1C	n/a	NAPD	J. H. McAndrews, unpublished

performed only for pollen sites in western Canada, a region sparsely represented in the NAPD. A test digitization of seven pollen diagrams for which raw counts were available indicated that the digitization added an error of 10% to the pollen percentages. Although raw counts are preferred, the digitizing error is acceptable for the broad biome-scale reconstructions performed here, and in other regions the application of the biomization method to digitized data has resulted in reasonable biome reconstructions (e.g. Prentice *et al.*, 1996; Tarasov *et al.*, 1998; Yu *et al.*, 1998).

Four sites with pollen stratigraphies that extend to the LGM have been added to the data sets (Table 2). At Clear Pond, South Carolina (Hussey, 1993), there are bracketing radiocarbon dates of 16,240 ¹⁴C yr BP and 18,180 ¹⁴C yr BP. The 18,000 ¹⁴C yr BP horizon at Powers Fort Swale, Missouri, was determined by linearly extrapolating below the basal ¹⁴C date of 17,370 ¹⁴C yr BP. The LGM at Bob Black Pond, Georgia (Watts, 1970), and Cheyenne Bottoms, Kansas (Fredlund, 1995), is poorly dated. Bob Black Pond has one radiocarbon date of 22,900 ¹⁴C yr BP, which has been supplemented by correlating the *Pinus* decline (c. 13,500 ¹⁴C yr BP) with the better dated and adjacent Quicksand Pond.

Cheyenne Bottoms has bracketing radiocarbon dates of 9690 and 24,470 ¹⁴C yr BP, but these are bulk sediment dates from the Great Plains which often are too old (E. C. Grimm, pers. comm.).

Biomization procedure

The biomization method (Prentice *et al.*, 1996) has five key steps: (1) biomes are defined as global assemblages of plant functional types (PFTs); (2) the plant taxa for a region are grouped into these PFTs; (3) for each pollen sample, affinity scores are calculated for all biomes; (4) the highest-scoring biome(s) is (are) chosen; and (5) if necessary, ties among affinity scores are resolved. Williams *et al.* (1998) describe the initial application of the biomization method to eastern North American pollen data. The assignment of PFTs (defined in Table 3) to biomes here (Table 4) follows Prentice *et al.* (1996) with five exceptions:

- Temperate summergreens were split into intermediate (ts2) and warm (ts3) variants to distinguish between the climatic tolerances of several taxa. A similar subdivision was made for temperate summergreens in China (Yu *et al.*, 2000).

Table 3 Assignments of pollen taxa from Canada and eastern North America to the plant functional types (PFTs) used in the biomization procedure.

Abbr.	Plant functional type	Pollen taxa
aa	arctic/alpine shrub or herb	<i>Alnus</i> , Apiaceae, <i>Betula</i> , Brassicaceae, Caryophyllaceae, Fabaceae, <i>Oxyria</i> , Ranunculaceae, <i>Salix</i> , Saxifragaceae
bec	boreal evergreen conifer	<i>Abies</i> , <i>Picea</i>
bs	boreal summergreen	<i>Alnus</i> , <i>Betula</i> , <i>Corylus</i> , <i>Larix/Pseudotsuga</i> , Myricaceae, <i>Populus</i> , <i>Salix</i>
ctc	cool-temperate conifer	<i>Abies</i> , <i>Larix/Pseudotsuga</i> , <i>Picea</i> , <i>Pinus strobus</i> , <i>Tsuga</i>
df	desert forb	Apiaceae, Asteraceae, <i>Ambrosia</i> , Brassicaceae, Caryophyllaceae, Chenopodiaceae/Amaranthaceae, <i>Ephedra</i> , <i>Euphorbia</i> , Fabaceae, Ranunculaceae, <i>Sphaeralcea</i>
ec	eurythermic conifer	Cupressaceae/Taxaceae, <i>Pinus</i> undiff.
g	grass	Poaceae
h	heath	Ericales
s	sedge	Cyperaceae
sf	steppe forb	Apiaceae, Asteraceae, <i>Ambrosia</i> , <i>Artemisia</i> , Brassicaceae, Caryophyllaceae, Chenopodiaceae/Amaranthaceae, <i>Sarcobatus vermicularis</i> , <i>Ephedra</i> , <i>Euphorbia</i> , Fabaceae, Ranunculaceae, Saxifragaceae, <i>Sphaeralcea</i>
ts	temperate summergreen	<i>Acer</i> , <i>Alnus</i> , Aquifoliaceae, <i>Carya</i> , <i>Ceanothus</i> , <i>Clethra</i> , <i>Fraxinus</i> , Myricaceae, <i>Ostrya/Carpinus</i> , <i>Populus</i> , <i>Quercus</i> , <i>Salix</i> , <i>Ulmus</i>
ts1	cool-temperate summergreen	<i>Betula</i> , <i>Corylus</i> , <i>Fagus</i> , <i>Larix/Pseudotsuga</i> , <i>Tilia</i>
ts2	intermediate-temperate summergreen	<i>Castanea</i> , <i>Celtis</i> , <i>Cephalanthus</i> , Fabaceae, <i>Juglans</i> , <i>Nyssa</i> , <i>Platanus</i>
ts3	warm-temperate summergreen	<i>Celtis</i> , <i>Cephalanthus</i> , <i>Liquidambar</i> , <i>Nyssa</i>
wtc	warm-temperate conifer	<i>Taxodium</i>
wte	warm-temperate broadleaved evergreen	Aquifoliaceae, <i>Quercus</i>
wte1	cool-temperate broadleaved evergreen	Aquifoliaceae
wte2	warm-temperate sclerophyll shrub	<i>Ceanothus</i> , <i>Quercus</i>

Table 4 Assignment of plant functional types (PFTs) to biomes in Canada and the eastern United States.

Biome	Code	Plant functional types
desert	DESE	df, g
xerophytic woods/scrub	XERO	ec, wte, wte2
cold deciduous forest	CLDE	bs, ec, h
tundra	TUND	aa, g, h, s
broadleaved evergreen/warm mixed forest	WAMX	ec, h, ts, ts3, wtc, wte, wte1
steppe	STEP	g, s, sf
open conifer woodland	OC	ec, sf
temperate deciduous forest	TEDE	bs, ec, h, ts, ts1, ts2, wte1
taiga	TAIG	bs, bsc, ec, h
cold mixed forest	CLMX	bs, ctc, ec, h, ts1
cool conifer forest	COCO	bs, bec, ctc, ec, h, ts1
cool mixed forest	COMX	bs, bec, ctc, ec, h, ts, ts1

- The functional type warm-temperate conifer (wtc) was created as a climatic equivalent to warm-temperate broadleaved evergreen (wte) to reflect the presence of *Pinus* in the south-eastern United States.
- Cool-temperate conifers (ctc) were deleted from temperate deciduous forest because in North America (unlike Europe) cool-temperate conifers, such as *Tsuga*, *Abies*, *Pinus strobus* and *Picea*, are only minor constituents of the temperate deciduous forest.
- The sedge PFT was added to steppe. Although Cyperaceae is not characteristic of steppe in most regions of the world, it is present in the Great Plains in moist or sandy soils (Mohlenbrock, 1976; McGregor *et al.*, 1977; Johnson & Nichols, 1982).
- A new biome, open conifer woodland, was created (Table 4). Open conifer woodland is not a major assem-

blage in Canada or the eastern United States today, but is common in the western United States (Thompson & Anderson, 2000) and is included here for consistency.

These changes allow for slight compositional differences between North America and Eurasia and are consistent with the decisions made for the western United States and Alaska (Thompson & Anderson, 2000; Edwards *et al.*, 2000). We started with the 70 most important pollen taxa for North America given by the NAPD and removed redundant categories and taxa which had extremely low abundances (<1% across all pollen samples for today, 6000 ¹⁴C yr BP and 18,000 ¹⁴C yr BP). If a taxon ever had an abundance greater than 1% in a pollen sample, it was retained in all samples. We expanded the taxon list of Williams *et al.* (1998) from 23 to 50 taxa (Table 3). The additional pollen taxa were assigned to PFTs. An atlas showing the distributions of modern plant species

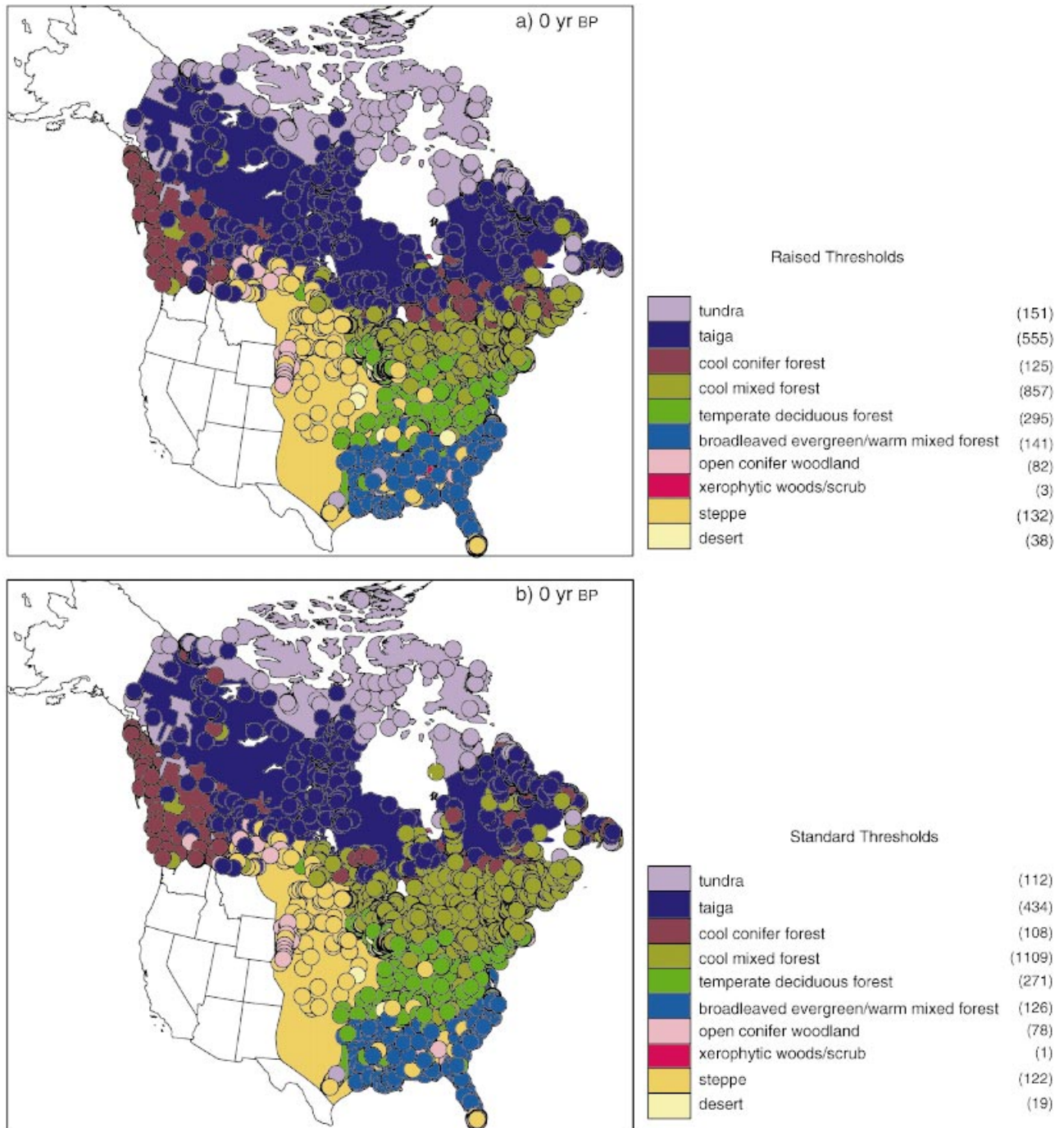


Figure 1 Maps of modern biomes as inferred from surface pollen samples. Pollen samples are represented as dots colour-coded by biome. The number of sites assigned to each biome is listed for each figure. A map of modern potential vegetation (derived from K uchler, 1964; Bernabo & Webb 1977; Olsen *et al.*, 1984) underlies the pollen dots. The map in (a) was produced using thresholds of *Pinus* 5%, *Quercus* 2.5% and all other taxa 1%. The map in (b) was produced using a threshold of 0.5% for all taxa. Note that samples assigned to cold deciduous forest using raised (2 samples) or standard (1 sample) thresholds are not shown on these maps. There are no samples assigned to cold deciduous forest with either raised or standard thresholds.

in climate and geographical space (Thompson *et al.*, 1999a, b) aided this assignment. Most of the additional taxa were derived from a splitting of the prairie forbs category used in Williams *et al.* (1998) into its constituent herbaceous types

(*Ambrosia*, *Apiaceae*, *Artemisia*, *Asteraceae*, *Brassicaceae*, *Caryophyllaceae*, *Chenopodiaceae/Amaranthaceae*, *Ephedra*, *Euphorbiaceae*, *Fabaceae*, *Ranunculaceae*, *Sarcobatus*, *Saxifragaceae* and *Sphaeralcea*).

The taxonomic resolution of individual pollen samples varies: identifications may have been made to species in some studies (e.g. *Pinus strobus*), to genus level in others (e.g. *Pinus* or *Ambrosia*) and only to family level in others (e.g. Asteraceae). Our scheme for allocating taxa to PFTs allows for varying taxonomic resolution by including both the general categories and the subcategories, which will have more general and more specific PFT assignments, respectively. Thus, when *Pinus strobus* is identified, it is classified as a cool-temperate conifer and contributes only to the cool temperate biomes of which it is characteristic. In contrast, undifferentiated *Pinus* is a eurythermic conifer and can contribute to a wide range of forests. Similarly, Asteraceae is both a steppe and desert forb whereas *Artemisia* (if distinguished) is only assigned to the steppe forb category. This approach preserves the highest level of taxonomic resolution possible in order to maximize the amount of information that can be extracted from a heterogeneous data set.

Following Williams *et al.* (1998), we raise the thresholds for several taxa that are generally over-represented in the pollen record in order to reduce the chance of misassignments by the biomization method. The thresholds used here to produce biome maps for Canada and the eastern United States (Figs 1a, 2a, 3a) are *Pinus* 5%, *Quercus* 2.5%, and 1% for the rest. However, because this technique is not followed by other BIOME 6000 workers, we also present a set of biome maps (Figs 1b, 2b, 3b) that adheres to the standard practice of setting all thresholds equal to 0.5% (Prentice *et al.*, 1996). In the rest of the paper these variants are referred to as 'raised thresholds' and 'standard thresholds', respectively.

The tie-break procedure for both sets of maps varies slightly from that of Prentice *et al.* (1996), who decided that when affinity score ties occur between two biomes whose taxon lists are subsets/supersets of one another, the subset biome wins the tie. We extend the tie-break method of Prentice *et al.* (1996) to situations when biomes are not subsets of one another by ranking biomes according to the summed abundances of their taxa, averaged over all pollen samples for a given time period (Williams *et al.*, 1998). Biomes are assigned in the order they appear in Table 4. The Prentice *et al.* (1996) tie-break method favours the biome with fewer taxa; the Williams *et al.* (1998) tie-break method favours the biome with fewer and/or rarer taxa.

As a supplement to the biome maps, we have mapped the difference between the highest affinity score and the next highest for all time periods (Fig. 4). This difference provides a measure of how strongly the pollen data supports a biome choice. We have grouped affinity score differences into four categories: tied ($\Delta_{\text{aff}} = 0$), weakly differentiated ($0 < \Delta_{\text{aff}} < 1$), moderately differentiated ($1 \leq \Delta_{\text{aff}} < 4$) and strongly differentiated ($\Delta_{\text{aff}} \geq 4$). The median PFT abundance for each biome (Fig. 5) provides a measure of biome structure, which may change over time. The abundance of a PFT is the summed abundances of all its constituent taxa. In cases where a taxon could potentially belong to multiple PFTs (Table 3), we determined the most likely PFT for each individual sample by consideration of the biome to which the sample had been assigned. For example, *Abies* could potentially be

allocated to both boreal evergreen conifer (bec) and cool-temperate conifer (ctc). However, in a sample which has already been assigned on the basis of its assemblage of taxa to taiga, it is reasonable to assume that the *Abies* pollen present is from a boreal evergreen conifer species.

To assess the accuracy of the biome reconstructions for 0 ¹⁴C yr BP, a map of modern potential vegetation was compiled from Bernabo & Webb (1977), Küchler (1964) and Olson *et al.* (1984). (Potential vegetation is defined as the vegetation that was present prior to European settlement and would likely be present today in the absence of human activity.) The map by Olson *et al.* (1984) includes changes in land use, and so was used only for Canada, where the position of the major biomes have remained relatively unchanged by human intervention. The Bernabo & Webb (1977) potential vegetation map was used for the United States, which has experienced a much heavier degree of land-use change. The Bernabo & Webb (1977) map adapts the vegetation formation classification of Küchler (1964) into a smaller number of biomes consistent with the classification of Olson *et al.* (1984).

The simple kappa statistic (Cohen, 1960) is used to measure the degree of agreement between the pollen-derived and potential modern biome maps. The kappa statistic varies between -1 and 1, with 1 indicating perfect agreement, -1 perfect disagreement, and 0 the amount of agreement that would be expected due to chance (Cohen, 1960; Monserud & Leemans, 1992). Monserud (1990) proposed that kappa values <0.4 indicates poor or very poor, 0.4–0.55 fair, 0.55–0.7 good, 0.7–0.85 very good, and >0.85 excellent agreement between maps.

RESULTS

Modern Biomes

The biome distribution inferred from the modern pollen data, using raised thresholds, is in good agreement with the map of potential vegetation (Fig. 1a, Table 5). In eastern North America, the broadleaved evergreen/warm mixed forest in the south-east gives way to temperate deciduous forest, which in turn is succeeded by cool mixed forest and a thin strip of cool conifer forest. To the west, the grasslands of the Midwest replace the temperate forest biomes, and are replaced further north by taiga and tundra, which stretch unbroken across Canada. The taiga includes the structurally distinct southern closed boreal forest and northern open boreal forest (La Roi, 1967; Richard, 1995), which share the same PFTs. The west coast of Canada is occupied by cool conifer forest. Open conifer woodland is assigned to sites in eastern Colorado and at the north-west limit of the steppe. Secondary features of the vegetation, such as the extension of cool mixed forest along the Appalachians and the occasional presence of coastal tundra in northern regions, are also represented clearly by the pollen data.

The biome assignments for some of the pollen samples differ from the underlying biome on the potential vegetation map. Eastern Colorado contains shortgrass prairie, not open

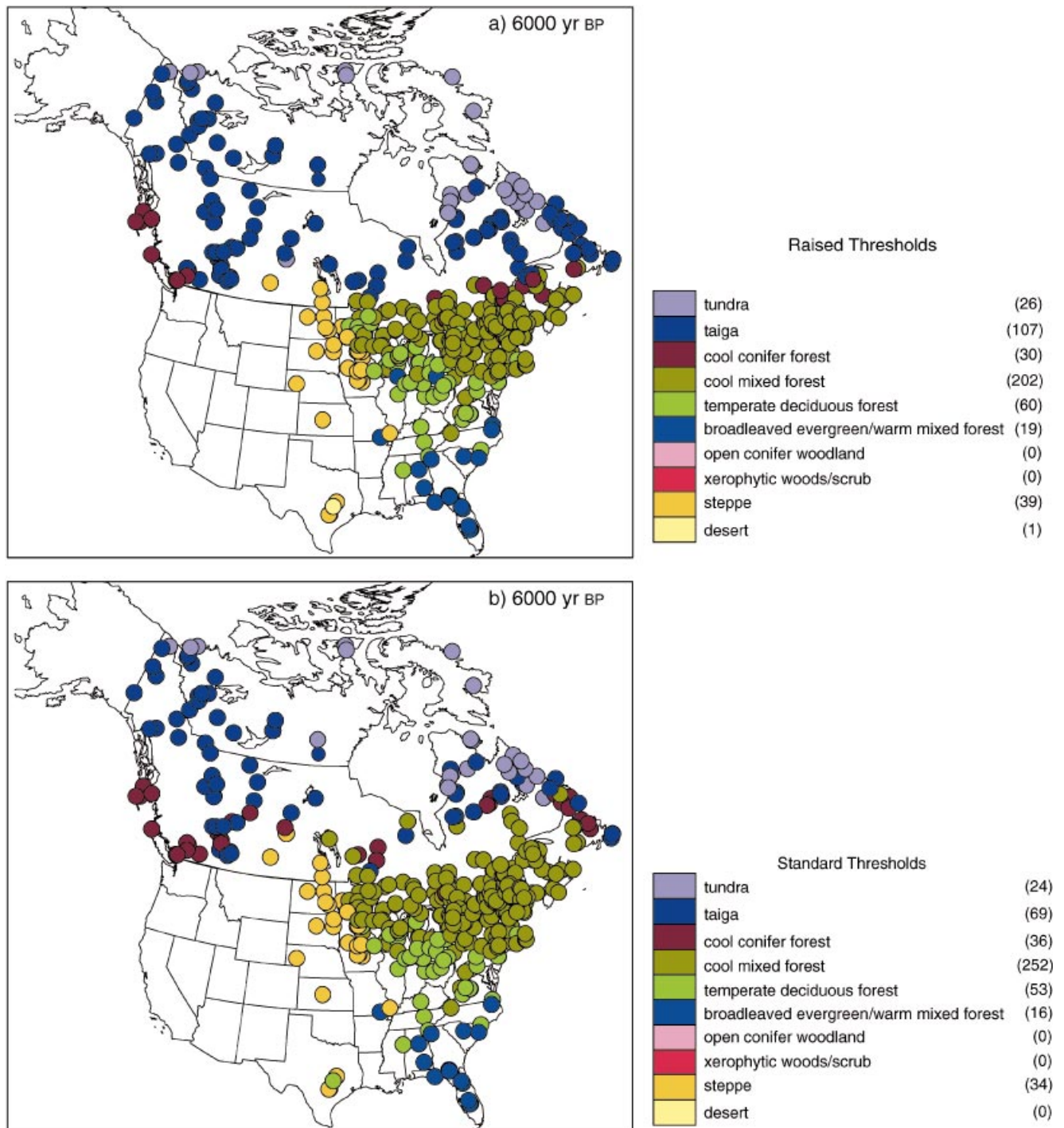


Figure 2 Biome maps for 6000 ^{14}C yr BP using (a) raised thresholds and (b) standard thresholds.

conifer woodland, so the inferred presence of open conifer woodland likely reflects the long-distance dispersal of pine pollen from the Front Range and foothills, 100–200 km to the west. In the south-eastern United States, a number of sites are assigned to non-forest biomes (steppe, desert and tundra) and open conifer woodland, in a region generally

considered to support broadleaved evergreen/warm mixed forest. The assignment of pollen sites in the south-east to non-forest biomes reflects the extent to which modern actual vegetation departs from the potential. Removing *Ambrosia* and *Poaceae* (taxa that thrive in areas of human disturbance) decreases the number of non-forested sites in the south-east

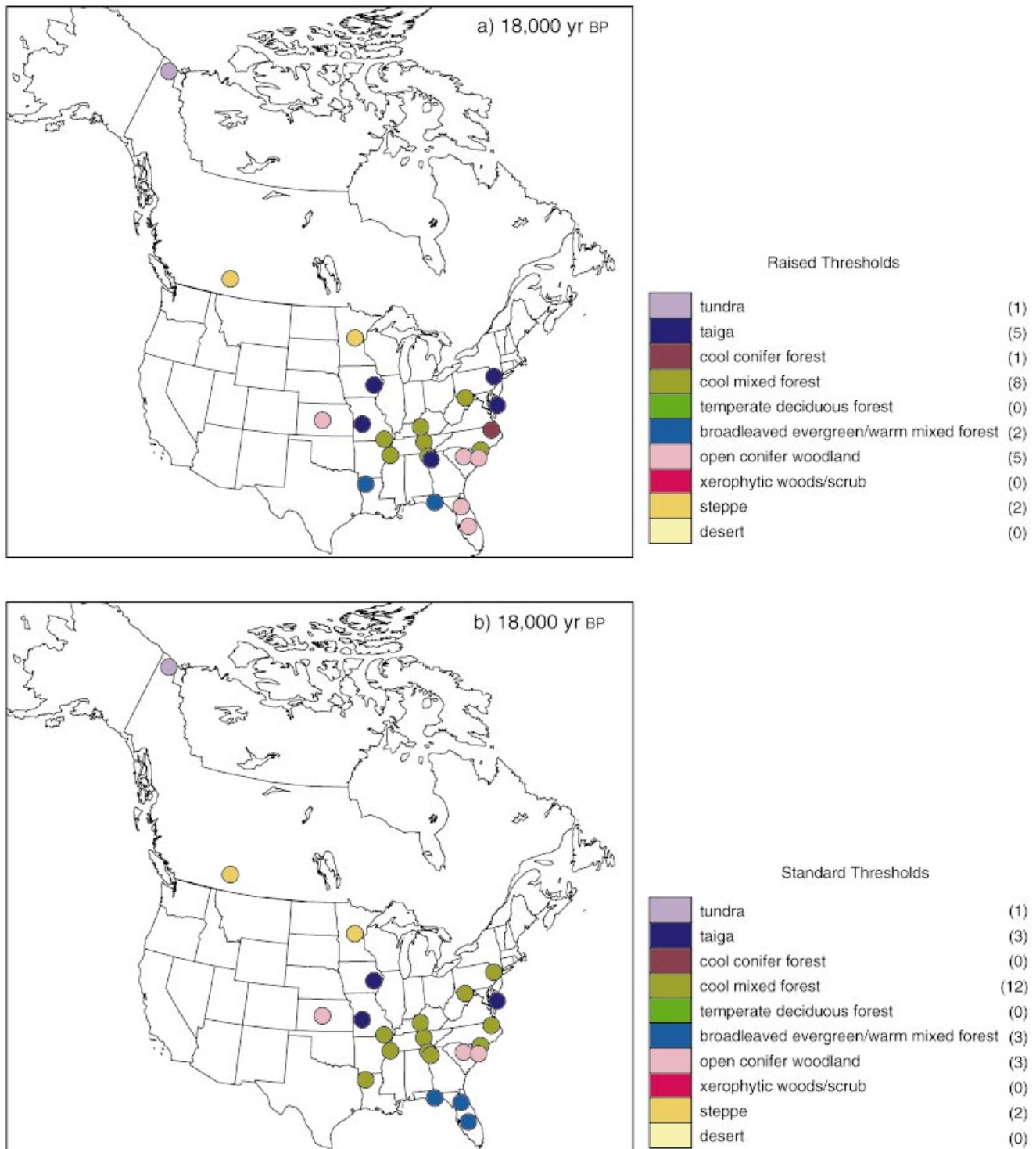


Figure 3 Biome maps for 18,000 ^{14}C yr BP using (a) raised thresholds and (b) standard thresholds.

from 36 to 6, but also results in a poorer representation of the extent of steppe and tundra in the west and north. The primary aim of this exercise is to reconstruct past biomes, so we included *Ambrosia* and *Poaceae* in our standard reconstruction and accept the discrepancies in the modern recon-

struction caused by human disturbance of the landscape. The assignment of pollen samples to desert occurs because most of the eastern forb taxa also occur in the deserts of the south-western United States, and the taxa that distinguish desert from steppe in the west are not present in our study

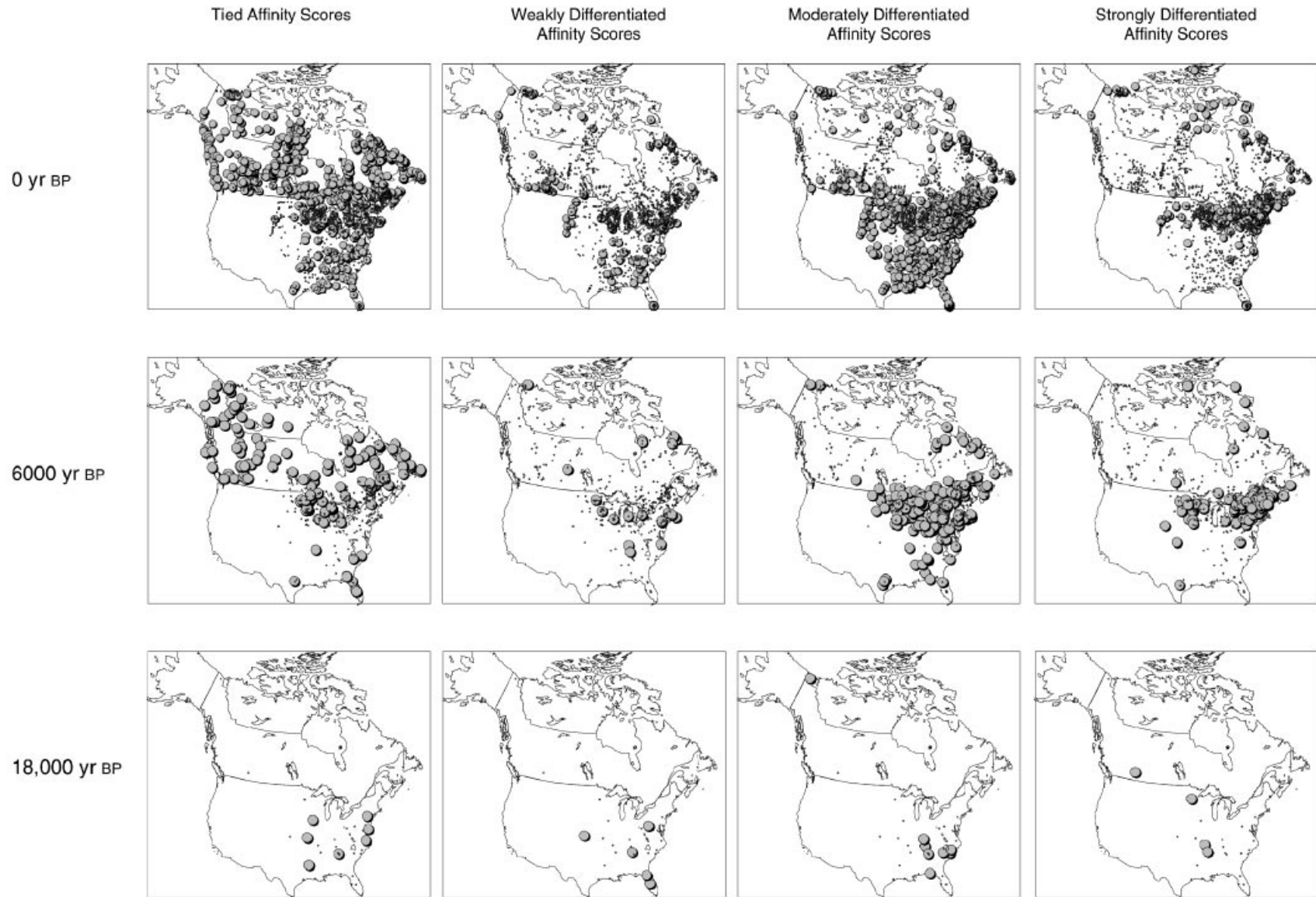


Figure 4 Site maps grouped by the difference between the highest and runner-up affinity scores. The rows represent 0, 6000, and 18,000 ^{14}C yr BP, each column shows the sites for which affinity scores are, respectively, tied ($\Delta_{\text{aff}} = 0$), weakly differentiated ($0 < \Delta_{\text{aff}} < 1$), moderately differentiated ($1 \leq \Delta_{\text{aff}} < 4$), or strongly differentiated ($\Delta_{\text{aff}} \geq 4$).

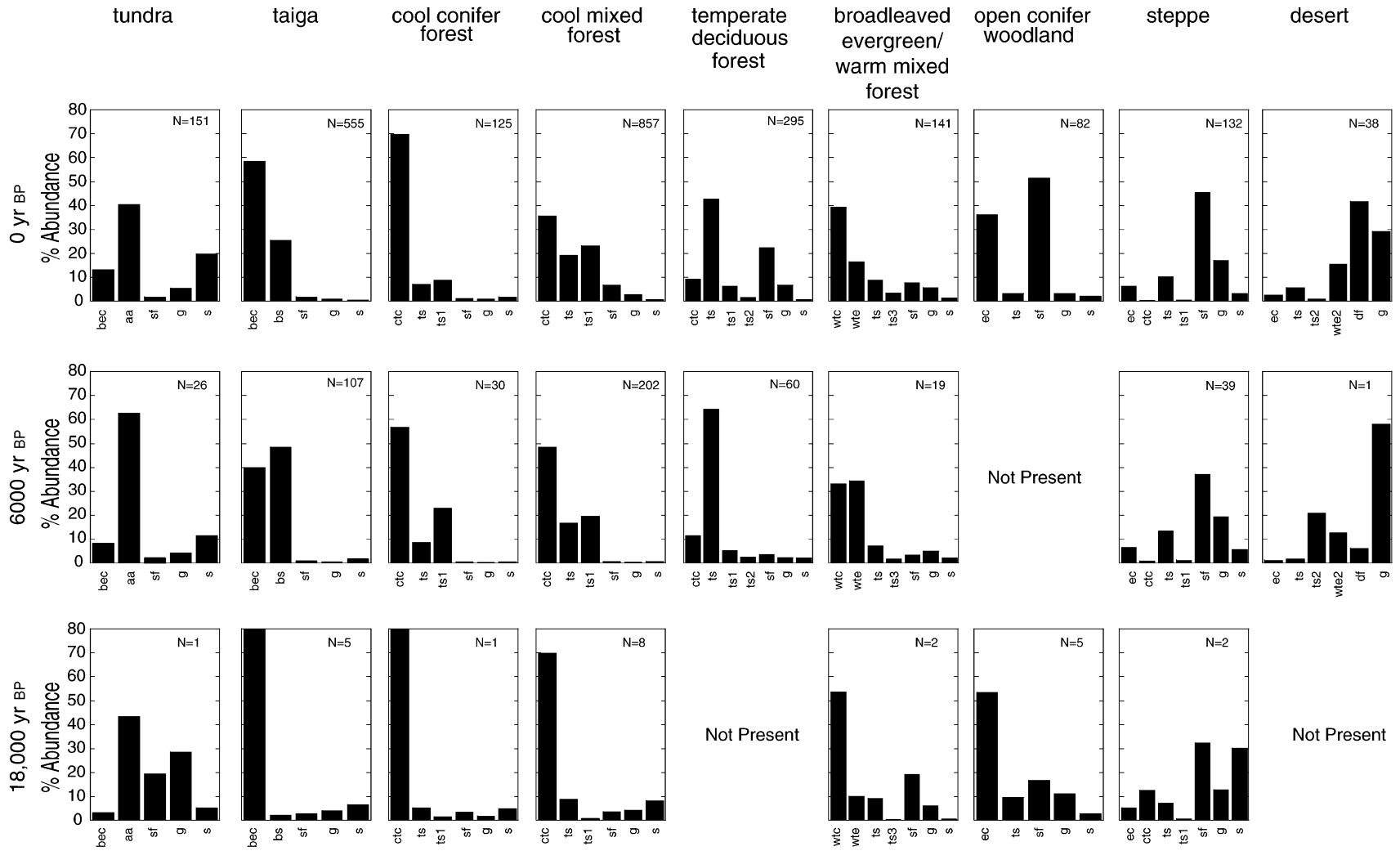


Figure 5 Bar graphs showing the median abundances of the major plant functional types for each biome at 0, 6000, and 18,000 ^{14}C yr BP. The number of sites (N) assigned to a biome is in the upper right-hand corner of each graph. Biomes which have no sites assigned to them for a period are marked as Not Present. The PFTs are abbreviated as follows: aa = arctic/alpine shrub or herb, bec = boreal evergreen conifer, bs = boreal summergreen, ctc = cool-temperate conifer, df = desert forb, ec = eurythermic conifer, g = grass, s = sedge, sf = steppe forb, ts = temperate summergreen, ts1 = cool-temperate summergreen, ts2 = intermediate-temperate summergreen, ts3 = warm-temperate summergreen, wtc = warm-temperate conifer, wte = warm-temperate broadleaved evergreen and wte2 = warm-temperate sclerophyll shrub.

Table 5 Comparison of the pollen-derived biomes using raised thresholds (Fig. 1a) and standard thresholds (Fig. 1b), and the modern vegetation map (Küchler, 1964; Bernabo & Webb, 1977; Olson *et al.*, 1984) using the simple kappa statistic. The figures given under Number of samples do not correspond exactly to the figures given in Fig. 1a because there is no information about potential vegetation for a small number of sites. The kappa statistic could not be calculated for some biomes because these biomes are not distinguished in the observed vegetation data set.

	Raised thresholds (Fig. 1a)	Standard thresholds (Fig. 1b)	Number of samples
Overall kappa	0.59	0.58	2229
Standard deviation	0.01	0.01	—
desert	n/a	n/a	38
xerophytic woods/scrub	n/a	n/a	3
cold deciduous forest	n/a	n/a	0
tundra	0.64	0.68	83
broadleaved evergreen/warm mixed forest	0.64	0.66	140
steppe	0.43	0.46	132
open conifer woodland	n/a	n/a	78
temperate deciduous forest	0.53	0.54	290
taiga	0.62	0.61	514
cool conifer forest	0.25	0.26	102
cool mixed forest	0.56	0.51	849

area. Eastern sites assigned to desert by the biomization method should be considered as steppe.

When a standard threshold of 0.5% is applied to the pollen data (Fig. 1b), results are similar for most regions (Table 5) but are noticeably poorer for eastern Canada. The eastern cool conifer forest becomes highly under-represented and sites are assigned to cool mixed forest as far north as James Bay—a northward extent not supported by observations of the modern taiga (Rowe, 1972; Olson *et al.*, 1984). In climatic terms, this misclassification would be equivalent to a warming of several degrees. In the boreal regions, the biomization method is highly sensitive to minor abundances of temperate pollen taxa for which increased thresholds are an effective filter (compare Figs 1a & 1b). Long-distance transport of pollen from temperate trees may explain why surface pollen samples from the taiga frequently have minor abundances (<1%) of temperate tree pollen. Low pollen counts may be a factor, but the majority of the sites affected (91 out of 161) have counts of 400 or greater. Even with raised thresholds, four pollen samples collected from the midst of the taiga are assigned to cool mixed forest (Fig. 1a) because each site has a single temperate pollen type (*Ostrya/Carpinus*, *Carya*, *Ulmus* or *Fraxinus*) in minor abundance (<2%).

Mid-Holocene biomes

The spatial distribution of biomes at 6000 ¹⁴C yr BP (Figs 2a & 2b) was similar to today, but moderate changes occurred in some regions. The steppe–forest boundary at 6000 ¹⁴C yr BP was 100–300 km eastward of its present position in Wisconsin and Minnesota, but was close to its present-day position in Canada and the central and southern Great Plains. The location of the northern treeline in Quebec and north-western Canada at 6000 ¹⁴C yr BP does not significantly differ from today, but the data coverage is insufficient to determine its location in the Keewatin District. The northern limit of cool mixed forest was further north than today, displacing cool conifer forest and taiga, whereas the southern limit of cool mixed forest was further north around the Great Lakes and slightly

further south along the eastern seaboard. The transition between the temperate deciduous and warm mixed forests was similar to today along the East Coast but was 100–150 km south of its current location further west. Only one fossil pollen site in the south-eastern United States was assigned to steppe, supporting the conclusion that the assignment of pollen assemblages to non-forested biomes in the south-east today (Fig. 1) is mainly due to human disturbance. Old Field, Missouri (37.12°N, 89.83°W; King & Allen, 1977), the one exception, is a local wet meadow today, and at 6000 ¹⁴C yr BP contains 68% Poaceae pollen, so its assignment to steppe may reflect the local vegetation more than the regional setting.

The biomes assigned to four sites appear anomalous: tundra for Lake A in central Saskatchewan (Mott, 1973), and broadleaved evergreen/warm mixed forest for Cupola Pond (36.80°N, 91.10°W; Smith, 1984), Volo Bog (42.35°N, 88.18°W; King, 1981) and Lake Erie (41.92°N, 82.76°W; Lewis & Anderson, 1989). The tundra site is more likely steppe or boreal woodland: it contains 34% *Artemisia*, 20% *Betula*, 12% *Pinus* and 9% *Alnus*, but the *Betula* and *Alnus* pollen (which can occur in the arctic/alpine shrub or herb PFT) favour the assignment of tundra over steppe. The three broadleaved evergreen/warm mixed forest sites all have tied affinity scores (Fig. 4) and are chosen by the tie-break procedure: their pollen taxa are mostly temperate deciduous forest generalists, dominated by *Quercus* (>40%), and are not diagnostic of either the temperate deciduous or broadleaved evergreen/warm mixed forests. These sites are more likely to have been in temperate deciduous forest.

Last glacial maximum biomes

The Laurentide Ice Sheet was fringed by tundra in north-western Canada and by steppe in southern Canada and the central United States (Figs 3a & 3b). In the eastern United States, a north-to-south zonation of forests and woodlands existed with taiga farthest north, cool conifer forest and cool mixed forest in the centre, and open conifer woodland and warm mixed forest in the south. Overpeck *et al.* (1992)

placed temperate deciduous forest in the south-eastern United States where we infer open conifer woodland and broadleaved evergreen/warm mixed forest. The sites assigned to open conifer woodland contain mostly *Pinus* and herbaceous pollen, with the extremes ranging from 90% *Pinus* and 7% herbaceous pollen at White Pond (34.17°N, 80.78°W; Watts, 1980), to 53% *Pinus* and 25% herbaceous types at Clear Pond (33.80°N, 78.95°W; Hussey, 1993). All of the sites classified as open conifer woodland lack diagnostic boreal taxa such as *Picea* or *Abies*. Lake Tulane in southern Florida (27.58°N, 81.50°W; Watts & Hansen, 1988; Grimm *et al.*, 1993) has a mix of *Pinus*, *Quercus*, Poaceae and *Ambrosia*, and probably represented an oak savannah (Grimm *et al.*, 1993) or oak scrub vegetation (Watts, 1975). Of the two sites classified as broadleaved evergreen/warm mixed forest in Fig. 3a, Camel Lake (30.27°N, 85.02°W; Watts *et al.*, 1992) has 83% *Pinus* and a small amount of *Taxodium* indicating that broadleaved evergreen/warm mixed forest is a reasonable choice, whereas Rayburn's Dome (32.47°N, 93.17°W; Kolb & Fredlund, 1981), containing 29% *Ambrosia*, 15% *Quercus*, 11% *Pinus* and 10% Cupressaceae/Taxaceae, is more likely an oak savannah.

Affinity difference maps

The difference between the highest and next highest affinity score is most commonly either moderate or zero. Strongly differentiated scores and weakly differentiated scores are uncommon (Fig. 4). The distribution of affinity score differences between the four categories is similar in the modern, 6000 and 18,000 ¹⁴C yr BP cases. The magnitude of affinity score differences depends on which biome is being considered, and largely reflects the degree of overlap between the pollen taxa characteristic of each biome. In our data set, the taxon lists of taiga, cool conifer forest, desert and xerophytic woods/scrub are entirely duplicated in the taxon list of another biome. These four biomes will always have affinity scores tied with another biome and their selection must be determined by a tie-break procedure. Tied affinity scores are also obtained for other biomes, particularly for sites assigned to broadleaved evergreen/warm mixed and temperate deciduous forests. Weakly differentiated affinity scores occur most often for pollen samples assigned to open conifer woodland, broadleaved evergreen/warm mixed forest or tundra. Moderately differentiated affinity scores occur across all six biomes. Sites assigned to the cool mixed forest contain most of the strongly differentiated affinity scores, and those assigned to tundra and steppe have nearly all of the rest. Most of the mid-Holocene and LGM sites with anomalous biome assignments (Figs 2 & 3) have either tied or weakly differentiated affinity scores.

Abundance shifts within biomes

The PFT composition of biomes at 6000 ¹⁴C yr BP is similar to those of today but, even so, differences do exist. These differences are greatest in the taiga and broadleaved evergreen/warm mixed forests, which today are dominated by

conifers but in the mid-Holocene had roughly equal abundances of coniferous (*Picea*, *Pinus* and *Abies*) and broadleaved tree/shrub pollen (*Alnus* and *Betula*). For the cool mixed forest, cool conifer forest, tundra and steppe, the most abundant PFT today is also the most abundant at 6000 ¹⁴C yr BP, but its relative abundance (relative to the other PFTs) differs between today and the mid-Holocene. In particular, shrub pollen (*Alnus*, *Betula* and *Salix*) was relatively more abundant in the 6000 ¹⁴C yr BP tundra and conifer pollen is much more prevalent in the modern cool conifer forest. The cool mixed, temperate deciduous and broadleaved evergreen/warm mixed forests all have higher abundances of herbaceous types today, again reflecting a human disturbance signal in modern samples. Despite these abundance shifts, biomes remain recognizable between 6000 ¹⁴C yr BP and today.

In contrast, LGM biomes strongly differ in composition from Holocene biomes. Forest biomes at 18,000 ¹⁴C yr BP contain at least 50% coniferous pollen and have little deciduous broadleaved pollen. LGM forest biomes contain more coniferous and herbaceous pollen types than their Holocene counterparts, and the open conifer woodland biome, not present at 6000 ¹⁴C yr BP, is a major component of the 18,000 ¹⁴C yr BP landscape. Differences among the taiga, cool conifer forest and cool mixed forest are subtle at the LGM, and these biomes are most similar in composition to the modern cool conifer forest. The sole site assigned to tundra at the LGM has relatively high Poaceae and steppe forb abundances compared to the Holocene tundra, whereas the two steppe sites have a large amount of Cyperaceae pollen.

DISCUSSION AND CONCLUSIONS

The biomization method

The standard biomization procedure uses a fixed (0.5%) pollen threshold (Prentice *et al.*, 1996; other papers in this issue) for consistency among regions and to reduce the amount of subjectivity in the method. We selectively raised pollen thresholds for our study region because of the improved representation of present and past biomes that results. Some pollen taxa are known to be over-represented in the pollen record (Faegri *et al.*, 1989; Webb *et al.*, 1981), so setting one threshold common to all taxa will not screen out all false presences. The biomization method clearly is sensitive in boreal regions to slight changes in thresholds. The thresholds used here are not large (only 5% for *Pinus*, 2.5% for *Quercus* and 1% for all other types) but they improve a number of the biome assignments for boreal sites (Figs 1a & 1b). Biomes in other regions contain uniquely characteristic plant taxa, but the taiga and cool conifer forest are only distinguished from cool mixed forest by the absence of temperate taxa. Therefore, if temperate taxa are not screened out by thresholds, the biomization procedure will erroneously select cool mixed forest over taiga and cool conifer forest. These thresholds, selected by examination of the modern data set, should be reasonable for biome reconstructions from fossil pollen data because the underlying taxonomic attributes which cause the over- and under-representation

of plant taxa in pollen records (pollen morphology, plant height and number of pollen grains produced per individual) are conservative on millennial time scales, and the differences among taxa are larger than intra-taxon variation.

The large number of tied affinity scores in Fig. 4 is one of the most striking features of the affinity difference maps. Ties do not necessarily indicate dubious biome choices because tied affinity scores are inevitable when the taxon list of one biome is a subset of the other. However, tied scores indicate that the choice of biome is easily perturbed by small fluctuations in pollen abundances; for example, the difference between 1% and 1.1% *Ulmus* could be enough to sway the biome assignment from taiga to cool mixed forest. Thus, for the boreal regions, careful selection of thresholds is particularly important, for they become the key filters of noise for the biomization algorithm. For ties that occur between non-subset biomes, we have chosen to favour the biome that contains fewer and/or rarer taxa, the logic being that it is the absence of the more abundant taxa that is more significant than the absence of the rarer taxa (Williams *et al.*, 1998). What is remarkable is how well the tie-break procedure works, assigning the vast majority of tied samples to the correct biome. Nevertheless, the tie-break procedure is not perfect and in particular tends to wrongly assign steppe sites to desert for today and to favour the broadleaved evergreen/warm mixed forest over the temperate deciduous forest at 6000 and 18,000 ¹⁴C yr BP.

Biome distributions at 6000 and 18,000 ¹⁴C yr BP

The biome distributions reconstructed for the past from the fossil pollen evidence in this study compare favourably with other pollen-based reconstructions of vegetation (Jacobson *et al.*, 1987; Webb, 1987; Overpeck *et al.*, 1992; Richard, 1995; Vance *et al.*, 1995) and are consistent with the plant macrofossil evidence (Jackson *et al.*, 1997). The northward extension of the cool mixed forest at 6000 ¹⁴C yr BP was largely due to a northward migration of *Pinus strobus* (Richard, 1995), and the eastward extension of steppe in Minnesota matches previous reconstructions of prairie forb types showing eastward migrations of Cyperaceae and prairie forb taxa (Jacobson *et al.*, 1987; Webb, 1987). In central Canada, Vance *et al.* (1995) report a northward shift of steppe which is difficult to see in the biome map here. A key site is Lofty Lake (54.73°N, 112.48°W; Lichti-Federovich, 1970), which here is classified as taiga, but, with 22% herbaceous pollen, may more appropriately be considered a boreal parkland (Vance *et al.*, 1995). The biome distributions at 6000 and 18,000 ¹⁴C yr BP inferred using the modern analogue technique (Overpeck *et al.*, 1992) are very similar to those shown here. One discrepancy occurs at 18,000 ¹⁴C yr BP in the south-eastern United States, where modern analogues assigned temperate deciduous forest to the pollen samples. Our biomization procedure, however, assigns open conifer woodland, a biome not considered by Overpeck *et al.* (1992). This biome fits well with the high abundances of *Pinus* and herbaceous pollen types found in this region. Our reconstruction of taiga south of the Laurentide Ice Sheet and

a conifer-dominated cool mixed forest south of the taiga is supported by the macrofossil record (Jackson *et al.*, 1997), which shows a presence of boreal and cool-temperate conifers (*Pinus banksiana*, *P. resinosa*, *Abies*, *Larix laricina* and *Picea*) and the exclusion of other types.

The differences in biome distributions and PFT abundances between today and 6000 ¹⁴C yr BP (Figs 1, 2 & 5) are not major enough to argue for a massive reorganization and relocation of biomes between these two times. The greater eastward extent and the greater northward extent of several forest biomes in the Great Lakes region (Figs 1 & 2) is presumably due to the warmer summers and lower precipitation occurring as a result of increased summer insolation (COHMAP, 1988; Webb *et al.*, 1993). The PFT composition of mid-Holocene biomes is recognizably similar to those of their modern counterparts, but variations in PFT abundances reflect structural shifts occurring during the Holocene. For example, the higher abundance of boreal summergreen pollen in the mid-Holocene taiga reflects the fact that the northern part of the taiga at 6000 ¹⁴C yr BP was denser than today with a layer of *Alnus* and *Betula* shrubs beneath a *Picea* canopy (Richard, 1995). Payette (1992) has shown that increased fire frequencies in the late Holocene led to the replacement of *Alnus* and *Betula* with a *Picea*-lichen woodland. Herbaceous pollen types are less abundant in the mid-Holocene forests than today (Fig. 5), because the modern samples are affected by human disturbance and/or the mid-Holocene forests were more closed than at present.

According to our reconstructions, the position of the northern treeline differs little between today and 6000 ¹⁴C yr BP. Recent simulations posit that an albedo feedback caused by the migration of dark boreal conifers over a light, snow-covered tundra, amplified the warming effect of increased summer insolation in the high latitudes (Foley *et al.*, 1994; TEMPO, 1996). The treeline shifted north by 100–200 km in Europe and central Siberia (Prentice *et al.*, 1996; Tarasov *et al.*, 1998) with a smaller movement in North America of 0–100 km (TEMPO, 1996). Our reconstruction of the tundra/taiga boundary at 6000 ¹⁴C yr BP (Fig. 2a) shows it at or slightly south of its present location in eastern Canada (Richard, 1995), and little changed in north-west Canada. The placement of treeline in the Canadian interior is not well constrained by the available data, but previous authors have suggested that treeline was north of its present position (Ritchie, 1987; Vance *et al.*, 1995). The pollen evidence at Long Lake, the northernmost site directly west of Hudson Bay, is evenly balanced between tundra and taiga, causing the biome choice to switch with small changes in thresholds. This site was originally interpreted to be boreal forest (Kay, 1979), but given the high amounts of Cyperaceae pollen (>50%) and presence of *Alnus* (5%) and *Betula* (8%) it can be interpreted as representing a wooded tundra near treeline. Thus the simulations of relatively small shifts in the North American treeline at 6000 ¹⁴C yr BP (TEMPO, 1996) are supported by the data available, but the treeline in Quebec appears to have been slightly south of its present position, opposite to that simulated. Remnants of the Laurentide Ice Sheet remained in northern Quebec at

6000 ^{14}C yr BP (Richard, 1995), which may have cooled this region and delayed the general trend of high-latitude warming and vegetation response.

According to the biome reconstructions, western Canada was covered by tundra in the north-west and by steppe in areas south of the ice sheet during the LGM; eastern North America was covered by a succession (from north to south) from boreal to more temperate forests. However, the PFT abundances of LGM biomes were apparently quite different from today (Fig. 5). Although there are only a few sites with LGM data, the dominant PFTs in the LGM tundra (found in north-western Canada) appear to have been grasses and steppe forbs, and the Midwestern steppe at the LGM has much more sedge pollen than it does today (Jacobson *et al.*, 1987). The tundra and steppe may therefore have been more similar to one another at the LGM than at present. The LGM forests were dominated by conifers, were more open and were structurally much less distinct from one another than they are today. Boreal conifers were dominant across the ice-free portion of eastern North America, regardless of the biome assignment. Taiga and cool mixed forest both have >70% conifer pollen (mostly *Picea*, *Pinus* and *Abies*) and differ mainly in the amount of pollen from temperate summergreen trees: none in the taiga sites and *c.* 7% in the cool mixed forest sites. The fact that temperate summergreen pollen is found only in southern samples, and then only in small amounts, suggests that these taxa grew in the south either in low abundance or in isolated microhabitats (Davis, 1976; Delcourt & Delcourt, 1977; Watts & Stuiver, 1980; Davis, 1981; Davis, 1983; Ritchie, 1987). The presence of herbaceous pollen in all forest biomes, along with the presence of open conifer woodland forests in the southeast (Watts, 1980; Grimm *et al.*, 1993), suggests that the LGM forests were relatively open compared to their modern counterparts. This openness may indicate drier conditions, or may have been caused by lower water use efficiencies for C_3 plants resulting from low atmospheric CO_2 concentrations at the LGM (Barnola *et al.*, 1987; Bazzaz, 1990).

Implications of changes in plant functional type abundances over time

The changes in the PFT composition of biomes over time imply corresponding differences in the physical attributes of a biome. The co-dominance of boreal conifers and summergreens at 6000 ^{14}C yr BP, for example, implies that seasonal variations in albedo over the taiga were larger than today. Similarly, the wintertime albedo and year-round surface roughness of the LGM forests would have been affected by their greater openness. A standard assumption of land surface models is that the physical attributes associated with modern biomes may be applied to biomes in the past (e.g. Kutzbach *et al.*, 1996). Our results suggest this is an oversimplification, but whether these differences were large enough to have affected past climates is unknown. One alternative to reconstructing vegetation properties at the level of biomes would be to create transfer functions between PFT abundances and physical properties such as albedo, surface

roughness and canopy conductance for modern pollen samples and apply these to fossil pollen samples.

Plants respond individualistically to climate change (Gleason, 1926; Davis, 1983; Jacobson *et al.*, 1987; Huntley, 1988; Webb, 1988), so biomes should not be expected to remain constant in their floristic composition. Our study shows that, furthermore, biomes do not maintain constant proportions of their PFTs, and hence are not structurally uniform over time. The LGM biomes structurally do not much resemble their Holocene counterparts (Fig. 5). The Holocene biome closest in structure to the LGM forests is the cool conifer forest, a relatively minor component of the modern vegetation in eastern North America. Structural differences among LGM forests are much subtler than differences between forest types during the Holocene. The key concern here becomes whether structural or climatic considerations are central to defining a biome. Structurally, using a median 7% pollen abundance from temperate summergreen trees to distinguish between two biomes may seem arbitrary, but climatically the albeit minor presence of pollen from temperate summergreen trees indicates mild winter temperatures and a lengthy growing season (Prentice *et al.*, 1992), whereas its absence strongly suggests conditions too harsh for temperate taxa to survive. Therefore, these biome maps are good representations of past vegetation-climate zones, but LGM biomes should not be considered structurally analogous to their modern counterparts.

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