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Pollen-based biome reconstruction for southern Europe and Africa 18,000 yr BP

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Abstract

Pollen data from 18,000 ^{14}C yr BP were compiled in order to reconstruct biome distributions at the last glacial maximum in southern Europe and Africa. Biome reconstructions were made using the objective biomization method applied to pollen counts using a complete list of dryland taxa wherever possible. Consistent and major differences from present-day biomes are shown.

Forest and xerophytic woods/scrub were replaced by steppe, both in the Mediterranean region and in southern Africa, except in south-western Cape Province where fynbos (xerophytic scrub) persisted.

Sites in the tropical highlands, characterized today by evergreen forest, were dominated by steppe and/or xerophytic vegetation (cf. today's Ericaceous belt and Afroalpine grassland) at the last glacial maximum.

Available data from the tropical lowlands are sparse but suggest that the modern tropical rain forest was largely replaced by tropical seasonal forest while the modern seasonal or dry forests were encroached on by savanna or steppe. Montane forest elements descended to lower elevations than today.

Keywords

Pollen data, plant functional types, biomes, vegetation changes, Europe, Africa, last glacial maximum.

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INTRODUCTION

Comparisons using data models for key periods in the past are required in order to evaluate the realism of climate model simulations (COHMAP, 1988; Wright *et al.*, 1993). Global vegetation models (Prentice *et al.*, 1992a; Foley *et al.*, 1996; Haxeltine & Prentice, 1996) provide a way to translate the outputs from atmospheric general circulation models into maps of potential vegetation distribution for specified periods (e.g. Prentice *et al.*, 1993; Claussen & Esch, 1994; Texier *et al.*, 1997; Harrison *et al.*, 1998; Joussaume *et al.*, 1999). In order to make data-model comparisons in a direct sense, the palaeodata have to be compiled in a global data set in a uniform manner, comparable with the output of vegetation models, using an objective method to express the pollen and plant macrofossil data in terms of biomes (Prentice *et al.*, 1996; Prentice & Webb, 1998).

The biomization method (Prentice *et al.*, 1996; Prentice & Webb, 1998) is an objective method based on assigning taxa to one or more plant functional types (PFTs). The method was first developed for Europe, then tested and applied to 6000 ^{14}C yr BP data sets in the former Soviet Union (Tarasov *et al.*, 1998), China (Yu *et al.*, 1998), and the Arabian peninsula and Africa (Jolly *et al.*, 1998a). This paper applies the PFT schemes developed by Prentice *et al.* (1996), Peyron *et al.* (1998) and Jolly *et al.* (1998a) to data from the entire Euro-African continental area under the very different conditions of the last glacial maximum (LGM). The area considered corresponds approximately to about half of the IGBP-PAGES PEP III transect (Gasse, 1997) and thus provides baseline information for the higher time-resolution studies planned for PEP III. We do not consider northern Europe in this paper. The single available pollen site for the LGM north of the Scandinavian ice sheet is included in the assessment of Tarasov *et al.* (2000), along with other data from northern Eurasia, with which this site has greater floristic affinity.

DATA AND METHODS

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

The LGM pollen data set comprises 24 pollen records from Africa and 18 records from Europe (Table 1). For all sites, the sample nearest 18,000 ^{14}C yr BP was estimated by interpolation between two ^{14}C dates. Since ice sheets and periglacial landscapes covered a large part of northern and central Europe, the pollen data set only contains sites from the southern part of Europe, plus data from Anatolia, Syria and Iran, i.e. the data set covers the region around the north and east of the Mediterranean Sea. Fifteen pollen spectra from this region dated 18,000 ± 2000 ^{14}C yr BP were compiled by Peyron *et al.* (1998). We have added a further three sites: Banyoles (Spain), Sogût Golû and Karamik Batagligi (Anatolia). We are not aware of any LGM terrestrial pollen records from northern Africa, and only one (Tibesti, Chad) is available from the entire Sahara/Sahel region. The remaining African sites lie between 10°N and 32°S: Ngamakala in Congo; Bosumtwi in Ghana; Barombi Mbo in Cameroon; Cherangani Hill, Sacred, Rutundu and Naivasha Lakes in Kenya; Ahakagyezi and Muchoya in Uganda; Rusaka and Kashiru in Burundi; Kamiranzovu in Rwanda; Ishiba Ngandu in Zambia; two records from Lake Tanganyika; five records from South Africa and Namibia (Wonderkrater, Sossus Vlei, Equus, Elim and Cornelia); and two (Torotofotsy, Tritrivakely) from Madagascar.

Most of these pollen records have been published and raw data are available from the APD (African Pollen Database) or from the EPD (European Pollen Database). Except for 8 digitized sites (Table 1), all the pollen records are primary counts. Primary pollen counts can give better results than digitized pollen data, since minor herbaceous pollen taxa (often omitted or indistinct in published records, especially older publications) may be of importance for the correct definition of treeless biomes (Prentice *et al.*, 1996; Tarasov *et al.*, 1998). We therefore used the primary pollen data whenever possible. We have not used pollen data from marine cores. Marine pollen cores can potentially contain pollen from a much larger area than cores from terrestrial sites, and thus may conflate signals from several different biomes. The biome reconstructions from marine cores may therefore not be strictly comparable to those obtained from terrestrial pollen records.

Pollen percentages were calculated on the basis of the total pollen minus the pollen of (1) aquatic taxa, such as *Nymphaea*, *Laurembergia* and *Polygonum*, (2) exotic taxa such as *Eucalyptus* and *Mangifera indica*, (3) taxa inflated by human impact in the modern data set (e.g. *Cerealia*), and (4) non-excluded taxa present only once with one pollen grain. Spores were also excluded from the percentage calculations. Cyperaceae is treated differently at different sites. In Europe, Cyperaceae can occur as 'upland' species characteristic of tundra. Although Cyperaceae occur in semiarid biomes (such as steppe) in Africa, more generally, this taxon occurs in high abundance only in wetland environments where it represents a local signal. We therefore included Cyperaceae in the pollen sum for European sites but excluded it from the pollen sum for African sites. The total number of non-excluded taxa in the 18,000 ^{14}C yr BP samples was less than that for the 6000 ^{14}C yr BP samples. There are 48 taxa for Europe and 114 taxa for Africa at 18000 ^{14}C yr BP. The African tropical flora is especially poorly represented in pollen records at the LGM, as pointed out by Hamilton (1982), and in both Europe and Africa the LGM was characterized by low abundances and diversity of trees. The low taxonomic richness could also be explained by the smaller number of sites recording the LGM (i.e. only 10–15% of the number of sites recording 6000 ^{14}C yr BP).

Biomization procedure

The biomization procedure translates pollen and plant macrofossil spectra into biome assignments. The concept and the different steps of this method were fully described in Prentice *et al.* (1996) and Prentice & Webb (1998). First, all identified taxa are assigned to one or more plant functional types (PFTs) based on their basic biology and bioclimatic

Table 1 Characteristics of the 18,000 ^{14}C yr BP pollen sites from Europe and Africa. Latitude and longitude are expressed by the standard convention, with + for °N or °E, and – for °S or °W, respectively. 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 dates within 4000 years, 4 indicates one date within 4000 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 a 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. The source of most of the LGM pollen data is either the European Pollen Database (EPD) or the African Pollen Database (APD); 8 pollen spectra are digitized (D).

Site name	Lat. (°)	Long. (°)	Elev. (m)	DC	Source	References
La Grande Pile	47.73	6.50	330	6D	EPD	de Beaulieu & Reille, 1992
Les Echets	45.67	4.89	267	1D	EPD	de Beaulieu & Reille, 1984
Le Bouchet	44.89	3.67	1200	5D	EPD	Reille & de Beaulieu, 1988
Biscaye	43.27	−0.17	410	7D	EPD	Reille & Andrieu, 1995
Lourdes	43.17	−0.17	430	3D	EPD	Reille & Andrieu, 1995
Ajo	43.05	−6.15	1570	7D	EPD	Watts, 1986; Allen *et al.*, 1996
Banyoles	42.13	2.75	173	1C	EPD	Perez-Obiol & Julia, 1994
Castiglione	41.89	12.75	44	7D	D	Follieri *et al.*, 1988
Tenaghi Philippon	41.17	24.30	50	2D	D	Wijmstra, 1969
Monticchio	40.94	15.60	530	2D	EPD	Watts, 1985
Khimaditis	40.61	21.58	560	7D	EPD	Bottema, unpublished
Ioannina	39.76	20.73	469	7C	EPD	Van Zeist & Bottema, 1982
Xinias	39.05	22.26	500	7D	EPD	Bottema, 1979
Karamik Batagligi	38.42	30.80	1000	7D	EPD	Van Zeist *et al.*, 1975
Sögüt Gölü	37.05	29.88	1400	7D	EPD	Van Zeist *et al.*, 1975
Padul	37.00	−3.67	785	2D	EPD	Pons & Reille, 1988
Ghab	35.68	35.30	300	7C	EPD	Niklewski & Van Zeist, 1970
Zeribar	35.53	46.11	1300	7D	EPD	Van Zeist & Bottema, 1977
Tibesti	21.00	18.50	1800	7D	APD	Maley, 1981, 1989
Bosumtwi	6.53	−1.33	100	2C	APD	Maley & Livingstone, 1983; Talbot *et al.*, 1984
Barombi Mbo	4.67	9.40	300	2C	APD	Maley & Brénac, 1987; Brénac, 1988
Cherangani Hill	1.00	35.47	2900	4D	D	Coetzee, 1967
Sacred Lake	0.03	37.47	2400	7C	D	Coetzee, 1967
Rutundu	−0.17	37.32	3140	7D	D	Coetzee, 1967
Naivasha	−0.75	36.33	1890	4C	D	Maitima, 1991
Ahakagyezi	−1.11	29.90	1830	4C	APD	Taylor, 1990
Muchoya	−1.28	29.80	2260	1D	APD	Taylor, 1990
Kamiranzovu	−2.33	29.00	1950	4C	APD	Hamilton, 1982
Rusaka	−3.43	29.62	2070	7D	APD	Bonnefille *et al.*, 1995
Kashiru	−3.47	29.57	2240	2C	APD	Bonnefille & Riollet, 1988
Ngamakala	−4.07	15.38	400	4C	APD	Elenga *et al.*, 1994
Tanganyika Sd-24	−4.97	29.37	773	5D	APD	Vincens, 1993
Tanganyika Mpu-12	−8.50	30.62	773	1D	APD	Vincens, 1989, 1991
Ishiba	−11.21	31.74	1500	7D	D	Livingstone, 1971
Torotorofotsy	−19.00	48.50	956	7C	APD	Straka, 1993
Tritrivakely	−19.78	46.92	1778	1C	APD	Gasse *et al.*, 1994; Van Campo, unpublished
Wonderkrater	−24.43	28.75	1100	2C	APD	Scott, 1982
Sossus Vlei	−25.30	15.51	750	7D	D	Van Zinderen Bakker, 1983
Equus Cave	−27.85	24.37	1250	4C	APD	Scott, 1987
Elim	−28.49	28.42	1890	5D	APD	Scott, 1989
Cornelia	−28.50	28.42	1800	4C	APD	Scott, 1986, 1989a
Pakhuis	−32.06	19.04	600	1C	APD	Scott, 1994

ranges (Tables 2 and 3). Affinity scores are then calculated between each pollen spectrum and each biome, based on the pollen taxa abundances and the list of PFTs allowed to occur in each biome (Tables 4 and 5). If a taxon is assigned to more than one PFT (for example PFT_a and PFT_b), its percentage is taken into account for the calculation of the affinity scores for all the biomes including PFT_a and/or PFT_b. The name of the biome having the highest affinity score is finally assigned

Table 2 Assignment of pollen taxa to the plant functional types (PFTs) used in the biomization procedure for Europe.

Abbr.	Plant functional type	Pollen taxa
aa	arctic/alpine dwarf shrub	*Alnus*, *Betula*, *Empetrum*, *Dryas*, *Rhododendron*, *Salix*, *Saxifraga*, *Vaccinium*
bec	boreal evergreen conifer	*Abies*, *Picea*
bs	boreal summergreen	*Betula*, *Alnus*, *Salix*
ctc	cool-temperate conifer	*Abies*
ctc1	intermediate-temperate conifer	*Cedrus*
df	desert forb/shrub	*Ephedra*
ec	eurythermic conifer	*Juniperus*, *Pinus* subgen. Diploxylon
g	grass	Poaceae
h	heath	Ericaceae, *Calluna*
sf	steppe forb/shrub	*Artemisia*, Apiaceae, *Armeria*, Asteraceae, Brassicaceae, Campanulaceae, Caryophyllaceae, *Centaurea*, Chenopodiaceae, Dipsacaceae, *Ephedra fragilis*, Fabaceae, *Helianthemum*, *Hippophae*, *Plantago*, *Polygonum*, Rosaceae, Rubiaceae, *Rumex*, *Sanguisorba*, *Thalictrum*
ts	temperate summergreen	*Alnus*, *Fraxinus excelsior*, *Populus*, *Quercus* (deciduous), *Salix*
ts1	cool-temperate summergreen	*Carpinus*, *Corylus*, *Fagus*, *Tilia*, *Ulmus*
ts2	warm-temperate summergreen	*Ostrya*
wte	warm-temperate broadleaved evergreen	*Quercus* (evergreen)
wte1	cool-temperate broadleaved evergreen	*Buxus*, *Hedera*, *Ilex*
wte2	warm-temperate sclerophyll shrub	*Olea*, *Phillyrea*, *Pistacea*

Table 3 Assignment of pollen taxa to the plant functional types (PFTs) used in the biomization procedure for Africa.

Abbr.	Plant functional type	Pollen taxa
df	desert forb/shrub	Amaranthaceae, *Artemisia*, Chenopodiaceae, Geraniaceae, Liguliflorae, Tubuliflorae
g	grass	Poaceae
sf	steppe forb/shrub	*Acacia*, Acanthaceae, *Achyranthes aspera*, *Alchemilla*, Amaranthaceae, *Anthrocaryon klaineana*, *Artemisia*, *Centaurea perrottetii*, Chenopodiaceae, Geraniaceae, *Gunnera*, *Indigofera*, Liguliflorae, Ranunculaceae, *Teclea*, Tiliaceae, Tubuliflorae, Umbelliferae, Vernonieae
Te1	wet-tropical evergreen tree	*Aeschynomene baumii*, *Alchornea*, *Bridelia*, *Calpocalyx*, *Canthium*, Celastraceae, *Cleistanthus*, Combretaceae/Melastomataceae, *Drypetes*, *Ekebergia*, *Ficus*, *Hymenostagia pellegrini*, *Irvingia gabonensis*, *Landolphia*, Leguminosae, *Lophira*, *Macaranga*, Moraceae, Papilionoideae, *Pausinystalia macroceras*, *Piptadeniastrum*, Sapotaceae, *Strombosia grandifolia*, *Syzygium*, *Uapaca*, Urticaceae
Te2	dry-tropical evergreen tree	*Aeschynomene baumii, Alchornea, Bridelia, Canthium,* Celastraceae*, Cleistanthus*, Combretaceae/ Melastomataceae, *Drypetes*, *Ekebergia*, *Ficus*, *Hymenostagia pellegrini*, *Landolphia*, Leguminosae, *Lophira*, *Macaranga*, Moraceae, Papilionoideae, Sapotaceae, *Syzygium*, *Trichilia emetica*, *Uapaca*, Urticaceae
Tr1	wet-tropical raingreen tree	*Acalypha*, *Allophyllus*, *Anthocleista*, *Anthostema senegalensis*, *Baikaeia*, *Blighia*, *Bridelia*, *Canthium*, Celastraceae, *Celtis*, *Chaectacme*, *Chlorophora*, *Cleistanthus*, Combretaceae/ Melastomataceae*,* Connaraceae, *Dracaena steudneri*, *Drypetes*, *Ekebergia*, *Ficus*, *Guibourtia demeusii*, *Hallea rubrostipulata*, *Hymenocardia*, *Isoberlinia*, *Isoglossa*, Leguminosae, Moraceae, *Mussaenda*, Ochnaceae, *Olea capensis*, Papilionoideae, Sapotaceae, *Symphonia globulifera*, *Syzygium*, *Teclea*, *Tetrorchidium*, *Trema*, *Trichilia emetica*, *Uapaca*, Urticaceae
Tr2	dry-tropical raingreen tree	*Acacia*, *Acalypha*, Acanthaceae, *Achyranthes aspera*, *Allophylus*, Amaranthaceae, *Anthospermum*, *Anthostema senegalensis*, *Anthrocaryon klaineana*, *Baikaeia*, *Brachystegia*, *Bridelia*, Campanulaceae, *Canthium*, *Cardiospermum halicacabum*, Caryophyllaceae, Celastraceae, *Celtis*, *Chlorophora*, *Cleistanthus*, *Clematis*, *Cola gigantea*, Combretaceae/Melastomataceae, Connaraceae, *Dialium guineense*, *Dombeya*, *Dracaena steudneri*, *Drypetes*, *Ekebergia*, *Euphorbia hirta*, *Ficus*, *Hallea rubrostipulata*, *Holoptelea grandis*, *Hymenocardia*, *Hypoestes*, *Ilex aquifolium*, *Isoberlinia*, *Julbernardia*, *Justicia striata*, Labiateae, *Mimusops*, Moraceae, *Mussaenda*, Papilionoideae, *Paullinia pinnata*, *Rhynchosia*, Rubiaceae, Sapotaceae, *Teclea*, *Tetrorchidium*, Tiliaceae, *Trema*, *Trichilia emetica*, *Uapaca*, Urticaceae
Tr3	tropical raingreen tree/savanna	*Acacia*, *Acalypha*, Acanthaceae, *Achyranthes aspera*, *Ajuga*, *Allophylus*, Amaranthaceae, *Anthospermum*, *Anthrocaryon klaineana*, *Baikaeia*, *Brachystegia*, Campanulaceae, *Clematis*, Combretaceae/Melastomataceae, *Detarium*, *Dombeya*, *Hallea rubrostipulata*, *Indigofera*, *Isoglossa*, *Justicia*, Labiateae, *Mimusops*, *Paullinia pinnata*, *Rhynchosia*, Sapotaceae, *Teclea*, Tiliaceae, *Trema*, *Uapaca*, Umbelliferae, Vernonieae
tss	temperate sclerophyll/succulent	*Acacia*, Acanthaceae, *Alchemilla*, *Anthospermum*, *Anthrocaryon klaineana*, Campanulaceae, *Dombeya*, Ericaceae, *Euphorbia hirta*, *Gunnera*, *Juniperus procera*, *Myrica*, *Protea*, *Stoebe*, Umbelliferae
Txws	tropical xerophytic woods/scrub	*Acacia*, Acanthaceae, *Achyranthes aspera*, Amaranthaceae*, Anthrocaryon klaineana*, Campanulaceae, Combretaceae/Melastomataceae, *Indigofera*, Tiliaceae, Tubuliflorae, Umbelliferae
wte	warm-temperate evergreen tree	*Acalypha*, *Afrocrania*, *Ajuga*, *Alchornea*, *Allophylus*, *Anthocleista*, *Antrocaryon klaineana*, *Blighia*, *Bridelia*, *Byttneria*, *Cadia*, *Canthium*, Celastraceae, *Celtis*, *Chlorophora*, Combretaceae/ Melastomataceae, *Dombeya*, *Drypetes*, *Ekebergia*, *Hagenia abyssinca*, *Ilex*, *Juniperus procera*, *Lophira*, *Macaranga*, Moraceae, *Mussaenda*, *Myrica*, *Olea capensis*, Papilionoideae, *Podocarpus*, Sapotaceae, Syzygium, *Tetrorchidium*, *Trema*, *Uapaca*, Urticaceae

Table 4 Assignment of plant functional types (PFTs) to European biomes. PFT abbreviations are given in Table 2.

Biome	Code	Plant functional types
cold deciduous forest	CLDE	bs, h
taiga	TAIG	bec, bs, ec, h
cold mixed forest	CLMX	bs, ctc, ctc1, ec, h, ts1
cool conifer forest	COCO	bec, bs, ctc, ec, h, ts1
temperate deciduous forest	TEDE	bs, ctc, ctc1, ec, h, ts, ts1, ts2, wte1
cool mixed forest	COMX	bec, bs, ctc, ec, h, ts, ts1
broadleaved evergreen/warm mixed forest	WAMX	ec, h, ts, ts1, ts2, wte, wte1
tundra	TUND	aa, g, h
xerophytic woods/scrub	XERO	ec, wte, wte2
steppe	STEP	g, sf
desert	DESE	df

Table 5 Assignment of plant functional types (PFTs) to African biomes. PFT abbreviations are given in Table 3.

Biome	Code	Plant functional types
desert	DESE	df
tropical rain forest	TRFO	Te1, Te2
tropical seasonal forest	TSFO	Te2, Tr1
tropical dry forest	TDFO	Tr2
xerophytic woods/scrub	XERO	g, tss, Txws
steppe	STEP	g, sf
savanna	SAVA	g, Tr3
broadleaved evergreen/warm mixed forest	WAMX	wte

to the pollen spectrum. In the case of tie-breaks, biomes are assigned in the order they appear in Table 4 (for Europe) and Table 5 (for Africa). It can also be instructive to examine which biome(s) have the next highest affinity score (Table 6).

There is as yet no unique and global biomization scheme. We therefore used the published regional biomization schemes for Europe and for Africa. For Europe, we apply the PFT assignments and biome definitions used previously by Prentice *et al.* (1996; Tables 1 & 2) and Peyron *et al.* (1998; Tables 2 & 3). Biome reconstructions in Africa used the scheme from Jolly *et al.* (1998a; Tables 2 & 3). The validation procedure for the biomization in Africa has shown that steppe, xerophytic woods/scrub, savanna, broadleaved evergreen/warm mixed forest, and even tropical rain forest and tropical seasonal forest (despite a very large pollen production difference between entomophilous and anemophilous species) are predicted with high confidence (Jolly *et al.*, 1998a).

Some taxa (such as *Artemisia*) are not assigned to PFTs in exactly the same ways in the two regions. A sensitivity test to examine the consequence of applying the alternative scheme in the overlapping areas (for example around the Mediterranean Sea) shows that there are some major differences in terms of affinity scores. The reconstructed biome results are, however, very similar. This study demonstrates the necessity to use a universal and global biomization scheme in order to use pollen-based biome reconstructions for model comparison at a global scale.

RESULTS

The LGM biome reconstructions (Fig. 1b) shows a remarkably homogeneous pattern that is significantly different from present-day biomes (Fig. 1a).

Last glacial maximum biomes of Europe

Steppe (i.e. grassland or shrubland) is reconstructed as the dominant vegetation for all the sites in southern Europe and around the Mediterranean basin. There is some evidence for the persistence of trees locally (*Quercus*, *Pinus* or *Cedrus*) near Mediterranean sites (Wright, 1976), probably representing a savanna-like structure that can be found in arid parts of Spain today. Certain Italian pollen diagrams (e.g. Monticchio: Watts, 1985; Castiglione: Follieri *et al.*, 1988) in addition to the usual high percentages of *Artemisia*, Poaceae and Chenopodiaceae, also have a significant presence of *Pinus* and *Juniperus*. Pollen diagrams from Greece are similar in this respect (Wijmstra, 1969; Bottema, 1979; Van Zeist & Bottema, 1982). At Castiglione, the pollen diagram also shows expansion phases of Ranunculaceae, Compositae and Caryophyllaceae, while *Ephedra* is continuously present, implying arid conditions throughout the glacial period. The pollen diagram from Ghab in Syria also shows steppe vegetation but trees, especially *Quercus* and *Cedrus*, reach relatively high percentages (Niklewski & Van Zeist, 1970). It seems likely that steppe vegetation predominated across this broad region, especially

Table 6 Affinity scores of samples for different biomes (biome codes are given in Tables 4 & 5). The best and the second-best biome affinity score are shown in bold and italics, respectively.

Site	TRFO	TSFO	TDFO	WAMX	XERO	SAVA	STEP	DESE	TUND	CLDE	TAIG	CLMX	COCO	COMX	TEDE
La Grande Pile	—	—	—	0.9	0.0	—	**25.4**	1.4	*9.5*	1.8	1.8	1.8	1.8	1.8	1.8
Les Echets	—	—	—	0.4	0.0	—	**21.8**	0.8	*8.1*	2.5	2.9	2.9	2.9	2.9	2.9
Le Bouchet	—	—	—	0.0	0.0	—	**23.6**	2.4	*6.7*	0.3	0.3	0.3	0.3	0.3	0.3
Biscaye	—	—	—	0.3	0.3	—	**22.6**	1.0	*7.8*	0.0	0.3	0.3	0.3	0.3	0.3
Lourdes	—	—	—	0.8	0.8	—	**20.3**	0.4	*8.7*	0.2	1.0	1.0	1.0	1.0	1.0
Ajo	—	—	—	1.8	0.4	—	**20.5**	4.1	*7.6*	1.6	2.0	2.0	2.0	3.4	3.4
Banyoles	—	—	—	*4.1*	*4.1*	—	**18.1**	1.3	3.9	0.0	*4.1*	*4.1*	*4.1*	*4.1*	*4.1*
Castiglione	—	—	—	4.1	2.7	—	**24.8**	3.6	*4.3*	0.7	3.4	3.4	3.4	4.1	4.1
Tenaghi Philippon	—	—	—	5.3	5.3	—	**18.4**	1.1	*7.7*	1.6	6.9	6.9	6.9	6.9	6.9
Monticchio	—	—	—	6.8	6.2	—	**17.0**	3.5	5.9	0.5	6.8	6.9	6.9	*7.3*	*7.3*
Khimaditis	—	—	—	6.8	2.8	—	**18.0**	4.4	*7.8*	1.0	4.8	4.8	4.8	7.3	*7.8*
Ioannina	—	—	—	5.8	2.5	—	**20.7**	3.0	7.0	0.8	3.8	4.1	4.1	*7.1*	*7.1*
Xinias	—	—	—	5.3	3.8	—	**20.5**	4.6	6.1	1.3	5.4	5.4	5.4	*6.9*	*6.9*
Karamik Batagligi	—	—	—	4.2	2.7	—	**17.0**	3.0	4.0	0.8	3.9	7.6	3.9	5.4	*9.2*
Sögüt Gölü	—	—	—	6.3	2.1	—	**20.3**	3.5	3.0	0.0	2.1	2.9	2.1	6.3	*7.1*
Padul	—	—	—	6.5	4.1	—	**18.2**	3.1	5.6	1.5	5.6	5.6	5.6	*7.7*	*7.7*
Ghab	—	—	—	7.4	1.7	—	**19.3**	4.9	4.0	0.6	2.1	3.2	2.1	7.2	*8.3*
Zeribar	—	—	—	1.1	0.0	—	**19.7**	*5.7*	4.8	0.0	0.0	0.0	0.0	1.1	1.1
Tibesti	0.0	0.0	0.0	0.0	*10.0*	*10.0*	**10.0**	0.0	—	—	—	—	—	—	—
Bosumtwi	1.8	2.0	2.0	2.0	*10.1*	*10.1*	**10.7**	1.3	—	—	—	—	—	—	—
Barombi Mbo	7.7	**21.5**	9.8	*16.8*	5.5	7.3	6.6	1.1	—	—	—	—	—	—	—
Cherangani Hill	0.0	0.0	3.1	2.6	*14.3*	13.2	**19.6**	6.4	—	—	—	—	—	—	—
Sacred Lake	2.7	2.7	4.9	10.7	**16.5**	8.2	*11.9*	4.8	—	—	—	—	—	—	—
Rutundu	0.0	0.0	3.8	7.1	**15.6**	11.8	*13.6*	6.3	—	—	—	—	—	—	—
Naivasha	0.0	1.9	3.6	6.8	*12.7*	*12.7*	**12.7**	2.5	—	—	—	—	—	—	—
Ahakagyezi	1.2	1.8	2.9	2.9	**16.3**	12.2	*15.3*	0.6	—	—	—	—	—	—	—
Muchoya	0.0	2.2	3.6	8.4	**19.5**	10.2	*13.3*	3.6	—	—	—	—	—	—	—
Kamiranzovu	4.3	5.4	3.7	*9.7*	**12.6**	7.4	7.2	0.0	—	—	—	—	—	—	—
Rusaka	0.0	0.0	1.7	1.2	**14.2**	11.0	*13.2*	2.6	—	—	—	—	—	—	—
Kashiru	4.9	5.3	1.5	7.9	**16.1**	9.7	*14.3*	3.1	—	—	—	—	—	—	—
Ngamakala	*21.8*	**25.5**	16.6	19.2	3.2	11.5	1.3	0.0	—	—	—	—	—	—	—
Tanganyika Sd-24	2.1	3.5	4.5	7.6	**12.7**	*10.8*	8.9	1.2	—	—	—	—	—	—	—
Tanganyika Mpu-12	2.6	5.0	6.3	8.7	**14.5**	*10.9*	9.2	3.9	—	—	—	—	—	—	—
Ishiba	2.0	2.6	6.2	9.4	**16.1**	*14.2*	12.2	2.8	—	—	—	—	—	—	—
Torotofotsy	1.5	6.9	*11.2*	**20.8**	10.0	9.1	5.9	3.7	—	—	—	—	—	—	—
Tritrivakely	1.8	4.8	10.2	*15.3*	**20.7**	13.4	9.7	2.6	—	—	—	—	—	—	—
Wonderkrater	0.0	1.9	2.6	5.4	9.3	10.9	**18.0**	*13.3*	—	—	—	—	—	—	—
Sossus Vlei	1.7	1.7	2.8	1.7	*20.1*	16.3	**20.2**	15.7	—	—	—	—	—	—	—
Equus Cave	0.0	0.0	3.6	0.0	*15.3*	**16.8**	*15.3*	2.9	—	—	—	—	—	—	—
Elim	0.0	0.0	0.0	1.5	*12.6*	*12.6*	**14.1**	5.1	—	—	—	—	—	—	—
Cornelia	0.0	0.0	0.0	0.8	*13.6*	13.3	**17.3**	7.0	—	—	—	—	—	—	—
Pakhuis	0.6	0.0	2.1	5.7	**22.2**	13.0	*16.8*	6.9	—	—	—	—	—	—	—

the lowlands of Italy and Greece, but that suitable habitats for the persistence of tree taxa existed at moderate elevations in nearby mountains (Tzedakis, 1993, 1994). This additional information is reflected in affinity scores for temperate deciduous or cool mixed forest biomes, which quite closely approach the scores for steppe (Table 6).

The situation was very different at Zeribar, in the mountains of western Iran (Van Zeist & Bottema, 1977), where the pollen diagram suggests a more arid steppe vegetation with high percentages of Chenopodiaceae, *Artemisia* and Umbelliferae, while Poaceae pollen values were low. Scattered stands of trees (*Acer* and *Pistacia*) were present in the Zeribar area before *c*. 22,000 ^{14}C yr BP, but trees disappeared from the pollen record after this. A comparison of the Zeribar pollen record with the Xinias, Tenaghi Philippon, Sögüt Gölü and Ghab sites indicates that the climate of continental western Iran must have been more adverse for tree growth than areas nearer the Mediterranean coast.

The pollen spectrum from the low elevation site of Banyoles in northern Spain (Perez-Obiol & Julia, 1994) is marked by the dominance of *Artemisia* and Poaceae and low percentages of tree pollen. Lake Ajo (Watts, 1986), at higher altitude, has similar pollen spectra. Padul in southern Spain (Pons & Reille, 1988) however, shows high percentages of both steppe

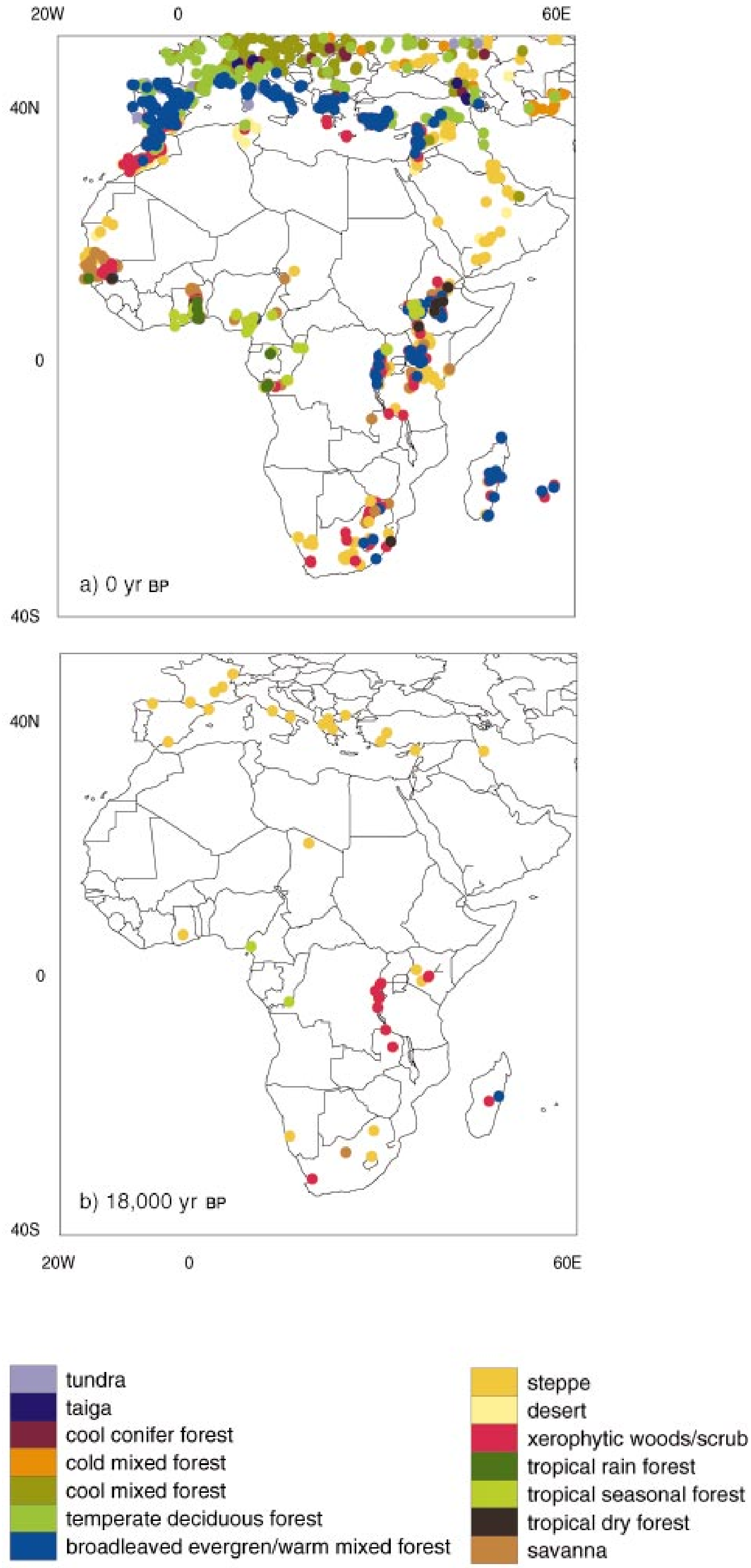

Figure 1 (a) Pollen-derived biomes at 0 ^{14}C yr BP (from Prentice *et al*., 1996; Jolly *et al*., 1998a); (b) pollen-derived biomes at 18,000 ^{14}C yr BP.

taxa and *Pinus*. Pollen records from the Pyrenean piedmont (Biscaye and Lourdes: Reille & Andrieu, 1995) show a long phase dominated by Poaceae, while initially higher percentages of *Pinus* are attributed to long distance transport. Sites north of the Alps also indicate steppe vegetation but with no indication of trees nearby and with some tundra-like features. At La Grande Pile (de Beaulieu & Reille, 1992), most of the arboreal taxa (except *Betula*) disappear during the LGM. At Le Bouchet in the Massif Central, the relative frequencies of (presumably long distance transport) *Pinus* reached their maximum during the LGM, while the herbaceous assemblage was reduced essentially to Poaceae, *Artemisia*, Chenopodiaceae and *Thalictrum*, probably reflecting extreme cold. The different floristic affinities of these northern samples are indicated by the fact that tundra has the second highest affinity score (Table 6).

Last glacial maximum biomes of Africa

Open grassland landscapes extended further south than today, occupying areas now covered by tropical rain and tropical seasonal forests, e.g. around Lake Bosumtwi. The biome reconstruction classified this site as steppe. The pollen indicate that the modern vegetation at mid-altitude (tropical seasonal forest) was locally replaced at 18,000 ^{14}C yr BP by cool herbaceous formations including *Olea capensis* (Maley & Livingstone, 1983; Talbot *et al.*, 1984). This interpretation is supported by the affinity scores (Table 6): the values for steppe, xerophytic woods/scrub and savanna are very close. Thus, the vegetation around this site was probably a mosaic composed of forest patches and grass, i.e. perhaps a dry savanna rather than a pure grassland, but nevertheless a much drier type of vegetation than occurs in the region today.

In western-central Africa, the biome reconstruction shows predominantly tropical seasonal forest. Tropical rain forest was reduced while more extensive open landscapes with montane evergreen taxa such as *Podocarpus*, *Olea capensis* and *Ilex mitis* occurred (Maley & Brénac, 1987; Brénac, 1988; Maley, 1989, 1991; Elenga *et al.*, 1991; Giresse *et al.*, 1994). Palynological investigations from several marine cores near the coast of western equatorial Africa (e.g. Caratini & Giresse, 1979; Bengo & Maley, 1991; Lézine & Vergnaud-Grazzini, 1993; Frédoux, 1994; Marret, 1994; Dupont, 1995; Jahns, 1996) likewise show a decrease of the rain forest taxa and an increase of Poaceae and *Podocarpus*. Thus, the lowland tropical rain forests in Africa appear to have been encroached on from above by montane evergreen taxa and laterally by savanna or grassland elements, as first suggested by Hamilton (1976).

In East Africa, the predominant biome was xerophytic woods/scrub. The data suggest that treeline on the East African mountains was depressed by *c.* 900–1100 m following the estimates of Coetzee (1967) and Hamilton (1982). Jolly *et al.* (1997) suggested that during this period the interlacustrine highlands of Burundi, Rwanda and western Uganda may have been dominated by xerophytic (ericaceous) woods/scrub and grassland (steppe), but with some upper montane forest elements (Hamilton, 1982; Marchant *et al.*, 1997). In the Tanganyika basin (*c.* 700–800 m), open herbaceous vegetation (steppe, with Poaceae and Cyperaceae) was present while trees were less dense than in the modern woodlands (tropical dry forest or savanna; Vincens, 1991). Ericaceous trees were probably present there while the low percentages of *Podocarpus* may have been blown in from further away. The Zambezian tree taxa present are thought to be of local origin. These results (Vincens, 1991) are concordant with those previously obtained from the higher-elevation site of Ishiba Ngandu (Livingstone, 1971). Thus, this region may in fact have been characterized by a vegetation type intermediate between xerophytic woods/scrub and steppe but with some tropical dry forest or savanna elements at lower elevations.

Similar changes have been reconstructed further east, at Mount Kenya (Sacred Lake and Rutundu), where the modern broadleaved evergreen/warm mixed (montane) forest was replaced by xerophytic woods/scrub. This inference is supported by the high incidence of *Artemisia* in the pollen spectra from Sacred Lake (Coetzee, 1967). However, reconstructions from the other two sites from the same area show steppe (Naivasha and Cherangani Hills).

In Madagascar, broadleaved evergreen/warm mixed (equivalent to tropical montane) forest was present at relatively low altitudes (900–1000 m). Thus, it appears that conifers moved down from mountains and were more widely distributed at the LGM than today (Straka, 1993).

In southern Africa, the reconstructed biome distribution shows non-forested biomes (especially steppe) as the dominant vegetation type, between *c.* 24°S and 28°S. According to Scott (1982, 1984, 1989a, b) and Scott & Vogel (1983), pollen records have high percentages of grasses and other non-arboreal pollen types, such as *Artemisia*, *Stoebe*, *Cliffortia* and *Anthospermum*, implying the presence of an open grassveld (i.e. steppe) subsisting under cool-temperate conditions. At Pakhuis, in south-west South Africa, the result is xerophytic woods/scrub, in agreement with the interpretation of Scott (1994). This implies that fynbos (South African Mediteranean-type xerophytic scrub) persisted throughout the glacial period on the Cederberg as suggested by Meadows & Sugden (1990) and recently confirmed both by wood charcoal assemblages (Cartwright & Parkington, 1997) and pollen data (Meadows & Baxter, in press).

DISCUSSION AND CONCLUSIONS

The biomization method

This study suggests that assigning pollen spectra to a single biome is an important restriction of the biomization method. In particular, the assignment of many disparate vegetation types to steppe conceals much useful information about the affinities of the vegetation. For example, the tundra plant types are more important (affinity scores higher than 5) at the sites located to the west of 30°E. A similar situation is the assignment of large parts of the northern high latitudes at the last glacial maximum to tundra, when the tundra vegetation indicated by the pollen records is clearly very different from the modern tundra (Edwards *et al.*, 2000). Examination of affinity scores for runner-up biomes provides additional information about the composition of the vegetation, suggesting that future developments might include (1) further subdivision of these broad treeless vegetation classes and/or (2) explicit procedures to make use of the richer numerical information contained in the aggregate scores for PFTs (e.g. Guiot *et al.*, 1996), or in the spectrum of affinity scores across all biomes. This limitation of the method is also a limitation of some biome models (e.g. BIOME 1: Prentice *et al.*, 1992a), which predict a single biome at each location. This problem could also be overcome using the numerical information on primary production of different PFTs that is calculated by the more complex biogeography models (e.g. BIOME3: Haxeltine & Prentice, 1996; CARAIB: Warnant *et al.*, 1994; François *et al.*, 1999) or by dynamic global vegetation models (Foley *et al.*, 1996). These limitations are emphasized at the LGM when forests were reduced in many areas, while greatly expanded regions were occupied by treeless biomes conventionally labelled as tundra, desert or steppe.

Vegetation and climate of southern Europe and Africa at the last glacial maximum

The prevalence of steppe vegetation around the Mediterranean (Fig. 1) indicates that the availability of water for plants was less than today, i.e. conditions were more arid than present. However, palaeohydrological records from the eastern Mediterranean (e.g. Ioannina and Zeribar) and from the Arabian peninsula indicate higher lake-levels than present (Street-Perrott & Roberts, 1983; Harrison & Digerfelt, 1993). Prentice *et al.* (1992b) simulated both the water budget and the vegetation at Lake Ioannina under various scenarios, and found that steppe vegetation could coexist with high lake levels, but only if a cold, wet winter was combined with a dry summer. Increased precipitation and decreased evaporation in winter produce high lake levels through increased runoff, which does not contribute to summer soil moisture. In addition, very cold winters would exclude the Mediterranean evergreen trees and shrubs that characterize the region today. These results are confirmed by two recent studies, from Vico Maar (Francis *et al.*, 1993; Leroy, 1994) and Lake Albano (Lowe *et al.*, 1996) which show steppe vegetation. The pollen counts from these sites are not yet available but will be included in future updates of the BIOME 6000 maps.

In Africa, our reconstructions show coherent spatial patterns and indicate large changes between the glacial and Holocene vegetation. Our reconstructions generally support previous interpretations inferring a major reduction of tropical rain forest and a lowering of vegetation zones in the mountains of southern, eastern and central Africa (e.g. Van Zinderen Bakker & Clark, 1962; Scott, 1982; Bonnefille & Riollet, 1988; Maley, 1991; Street-Perrott & Perrott, 1993; Elenga *et al.*, 1994; Jolly *et al.*, 1998b). Although low atmospheric CO_2 concentration could potentially contribute to the lowering of the upper montane treeline (Jolly & Haxeltine, 1997; Street-Perrott *et al.*, 1997), the biomization scheme does not reconstruct an LGM steppe which is very different from the present-day Afroalpine steppe in terms of its strong component of C_4 grasses. In the future, the use of phytoliths may give us the opportunity to estimate the ratio of C_3/C_4 grasses, and thus an excellent control of the herbaceous functional types occurring in such a biome. The low atmospheric CO_2 concentration is not a likely explanation for the descent of relatively cold-tolerant trees such as *Olea capensis* and *Ilex mitis* into regions where the modern tree flora is tropical. Estimates of the temperature change required to produce the observed vegetation shifts are as large as −8 °C (Coetzee, 1967), with smaller estimates (*c.* −4 °C) when the possible effects of low precipitation are taken into account (Bonnefille *et al.*, 1990, 1992; Chalié, 1992; Vincens *et al.*, 1993). Lake-level records indicate widespread aridity except at the highest elevations where the effects of reduced evaporation might be decisive (Street-Perrott *et al.*, 1989; Farrera *et al.*, 1999). Low CO_2 could also contribute to the effective aridity of lowland vegetation, although to an extent that has not yet been quantified (Jolly & Haxeltine, 1997). A fuller understanding of the environmental changes that brought about these major biome shifts will require modelling not only the climate changes themselves but also the complex responses of vegetation to the joint effects of changes in temperature, precipitation and CO_2. The palaeobiome data are a benchmark against which the realism of such simulations can be measured (Pinot *et al.*, 1999).

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BIOSKETCH

The European Pollen Database (EPD) and the African Pollen Database (APD) were established in late 1990 and in 1996, respectively, in co-ordination with a similar effort in North America. The aim of these databases is to give free access, after an exhaustive checking by the community of palynologists, to the primary pollen data and to associated metadata (coordinates, chronology, site description, etc.) for the existing Quaternary sites in Europe and Africa. The two pollen databases are lead by an executive committee consisting of J.-L. de Beaulieu, B. Huntley and A. Lotter for the EPD and R. Bonnefille, A. M. Lézine, A. Sowunmi and L. Scott for the APD. More information about the EPD and APD can be accessed via http://medias.meteo.fr/paleo/epd.html and http://medias.meteo.fr/apd/, respectively; the raw pollen counts of the sites will be in the public domain in early 2001.