

Palaeovegetation in China during the late Quaternary: Biome reconstructions based on a global scheme of plant functional types

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ARTICLE INFO

Article history:

Received 31 July 2009

Received in revised form 4 February 2010

Accepted 6 February 2010

Available online 11 February 2010

Keywords:

Biome
Biomization
China
Last glacial maximum
Mid-Holocene
Plant functional types (PFTs)
Pollen
Vegetation shift

ABSTRACT

Two previous reconstructions of palaeovegetation across the whole of China were performed using a simple classification of plant functional types (PFTs). Now a more explicit, global PFT classification scheme has been developed, and a substantial number of additional pollen records have become available. Here we apply the global scheme of PFTs to a comprehensive set of pollen records available from China to test the applicability of the global scheme of PFTs in China, and to obtain a well-founded reconstruction of changing palaeovegetation patterns. A total of 806 pollen surface samples, 188 mid-Holocene (MH, 6000 ¹⁴C yr BP) and 50 last glacial maximum (LGM, 18,000 ¹⁴C yr BP) pollen records were used to reconstruct vegetation patterns in China, based on a new global classification system of PFTs and a standard numerical technique for biome assignment (biomization). The biome reconstruction based on pollen surface samples showed convincing agreement with present potential natural vegetation. Coherent patterns of change in biome distribution between MH, LGM and present are observed. In the MH, cold and cool-temperate evergreen needleleaf forests and mixed forests, temperate deciduous broadleaf forest, and warm-temperate evergreen broadleaf and mixed forest in eastern China were shifted northward by 200–500 km. Cold-deciduous forest in northeastern China was replaced by cold evergreen needleleaf forest while in central northern China, cold-deciduous forest was present at some sites now occupied by temperate grassland and desert. The forest–grassland boundary was 200–300 km west of its present position. Temperate xerophytic shrubland, temperate grassland and desert covered a large area on the Tibetan Plateau, but the area of tundra was reduced. Treeline was 300–500 m higher than present in Tibet. These changes imply generally warmer winters, longer growing seasons and more precipitation during the MH. Westward shifts of the forest–shrubland–grassland and grassland–desert boundaries imply greater moisture availability in the MH, consistent with a stronger summer monsoon. During the LGM, in contrast, cold-deciduous forest, cool-temperate evergreen needleleaf forest, cool mixed forests, warm-temperate evergreen broadleaf and mixed forest in eastern China were displaced to the south by 300–1000 km, while temperate deciduous broadleaf forest, pure warm-temperate evergreen forest, tropical semi-evergreen and evergreen broadleaf forests were restricted or absent from the mainland of southern China, implying colder winters than present. Strong shifts of temperate xerophytic shrubland, temperate grassland and desert to the south and east in northern and western China and on the Tibetan Plateau imply drier conditions than present.

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1. Introduction

Large-scale palaeovegetation reconstruction benefits not only the better understanding of vegetation change in the past and for the

future, but also the evaluation of model experiments in order to better investigate the dynamics and interactions of past climate and vegetation changes, and the responses of climate to external forcing (CLIMAP Project Members, 1981; COHMAP Members, 1988; Wright et al., 1993; Prentice and Webb, 1998; Prentice et al., 2000). Since the 1980s, palaeo-scientists have made major efforts to reconstruct the continental and global vegetation patterns in the late Quaternary, based on data syntheses. The Cooperative Holocene Mapping Project (COHMAP Members, 1988; Wright et al., 1993) was the first attempt in 1980s to summarize the palaeovegetation data in the forms of regional syntheses. In the 1990s, the Global Palaeovegetation Mapping Project (BIOME 6000) attempted to create fully-documented pollen and plant macrofossil data sets for 6000 ± 500 ¹⁴C yr BP (mid-

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Holocene, MH) and $18,000 \pm 2000$ ^{14}C yr BP (last glacial maximum, LGM), and to reconstruct global maps of vegetation for these time periods (Prentice and Webb, 1998; Prentice et al., 2000), using a standard technique called biomization (Prentice et al., 1996).

The geographic patterns of MH and LGM palaeovegetation of the northern continents and Africa were established by applying the biomization method (Prentice and Webb, 1998; Prentice et al., 2000) to pollen or plant macrofossil records for Europe, Africa and the Arabian Peninsula, North America, Alaska and western Beringia, the Former Soviet Union and Mongolia, China, and Japan (see the two Special Features in the *Journal of Biogeography* in 1998 and 2000, respectively). New reconstructions in the Southeast Asia and the Pacific region (Pickett et al., 2004), Latin America (Marchant et al., 2009), and Indian Subcontinent (Sutra et al., in preparation) have helped to fill the remaining gaps, especially in the southern Hemisphere. There are also regional and local case studies based on pollen and plant macrofossil records that have used the biomization technique, e.g. for palaeobiome distribution in Colombia (Marchant et al., 2001, 2002), Holocene vegetation in Mexico (Ortega-Rosas et al., 2008), modern and late Quaternary disturbed vegetation in Japan (Gotanda et al., 2008), and vegetation in the Mediterranean–Black Sea Corridor since the LGM (Cordova et al., 2009).

China covers about 1/10 of the world's land area and possesses climate regimes ranging from perennial snow cover on the high western mountains to extreme aridity in the northwestern lowlands, and from cold climates in the northeast to warm and humid tropical climates along the southeastern coast (Zhang, 1991). The dynamics of the East Asian summer and winter monsoons, and the high uplift of the Tibetan Plateau, contribute to producing a remarkably diverse set of bioclimate and ecosystems, ranging from boreal coniferous forest in the northeast to tropical rain forest in the south, and from temperate grassland in the northern-central region to deserts in the west and tundra and alpine vegetation on the Tibetan plateau (ECVC, 1980). Pollen-based reconstructions of late Quaternary vegetation and climate have been performed by applying various data and document syntheses across the whole country and in some large regions for the Holocene (e.g. Shi et al., 1993; Ren and Beug, 2002; Feng et al., 2006) and for the last 20,000 years (An et al., 1990), in addition to a great many site-based palaeovegetation studies. Biomization was applied to reconstruct vegetation patterns across China initially based on a limited set of digitized pollen data for the MH (Yu et al., 1998) and later using additional raw pollen counts for numerous sites at MH and LGM (Yu et al., 2000). Modern reconstruction based on surface pollen samples in both studies showed good agreement between reconstructed biomes and present vegetation, both geographically and in terms of elevation gradients in mountain regions (Yu et al., 1998, 2000).

These earlier pollen-based biome reconstructions used a simple classification of plant functional types (PFTs) related to the set of PFTs used in the BIOME1 model (Prentice et al., 1992a). More recently, a more explicit, global PFT classification scheme has been developed (Harrison et al., 2009). Further, a substantial number of additional pollen records have become available in electronic form since the previous biomization studies (Yu et al., 1998, 2000). In this study, we apply the global scheme of PFTs to a comprehensive set of surface, MH and LGM pollen records from China. The modern vegetation is reconstructed from surface pollen samples in order to test the applicability of the global scheme of PFTs in China, and to demonstrate a good empirical relationship between modern vegetation and surface pollen. Then the same procedure is applied to the MH and LGM in order to obtain a well-founded reconstruction of changing palaeovegetation patterns.

2. Data and methods

2.1. Pollen data for modern, MH and LGM

The modern pollen data set comprises a total of 840 samples. We used the set of 658 raw pollen counts (Yu et al., 2000), supplemented

by 41 digitized pollen records from diagrams (Yu et al., 1998), 100 raw pollen counts from the Tibetan Plateau (Yu et al., 2001a) and 41 additional raw pollen counts compiled from published and unpublished sources (Fig. 1a, see also Appendix A). The surface samples include soil samples (518), moss polsters (80), dust trap samples (81), grab samples of surface sediments (94), sediment core tops (26), and digitized samples of unspecified provenance (41). Some modern pollen samples were excluded from further analysis because of contamination, very low pollen counts, or very small numbers of reported taxa (10 samples) or because of heavy anthropogenic influence (21 samples). Three of the digitized samples used by Yu et al. (2000) were removed and replaced by full pollen counts (Miaoershan, Nanshan and Xingou). Thus, 806 pollen surface samples were finally used (Fig. 1a).

The pollen data set for the MH (6 ka BP) consists of 192 samples. In addition to the 118 raw pollen counts and 39 digitized records used by Yu et al. (2000), we compiled 35 pollen records from published and unpublished sources (Fig. 1b, see also Appendix B). Four MH samples were excluded from analysis because of either low pollen counts (Baiyangdian, Dalainuoer, and Dundee) or strong anthropogenic influence (HF). Thus, 188 MH pollen samples were used in the biomization procedure (Fig. 1b).

The pollen data set for the LGM (18 ka BP) consists of 52 samples. Most of them (37) were derived from Yu et al. (2000). A further 10 digitized records were obtained from terrestrial units within marine cores from the Chinese continental shelf (Harrison et al., 2001). Raw pollen counts were compiled from five new sites (Fig. 1c, see also Appendix B). Two LGM samples (Haerbin and Niuquanzi) were excluded from further analysis because they had low pollen counts. Thus, 50 LGM samples were used in the biomization procedure (Fig. 1c).

2.2. Biomization procedure

The method of pollen-based biome assignment (biomization) begins with a quantitative assemblage of pollen or plant macrofossil taxa and ends with an assignment of the biome most likely to have produced that assemblage (Prentice et al., 1996; Prentice and Webb, 1998). The method has five steps: (1) each pollen taxon is assigned to one or more PFTs (PFT vs. taxon matrix), on the basis of the biology and biogeography of the plant species it includes; (2) biomes are defined in terms of their characteristic PFTs (biome vs. PFT matrix); (3) the two matrices are multiplied to produce a taxon vs. biome matrix, indicating which pollen taxa may occur in which biome; (4) affinity scores for each biome are then calculated for all pollen samples. A threshold pollen percentage (0.5%) is generally defined in order to reduce the noise due to occasional pollen grains derived from long-distance transport or contamination; (5) each pollen sample is assigned to the biome having the highest affinity score, subject to a tie-breaking rule that favours the less PFT-rich biome in the case where the affinity score for two or more biomes is equal. We used this standard procedure to reconstruct the biomes from the pollen data of China. Further details on this method can be found in Prentice et al. (1996) and Prentice and Webb (1998).

2.3. PFT classification

The PFT classification is a central concept for assigning pollen taxa to biomes. PFTs are defined on the basis of traits referring to species morphology, physiology, life history, and bioclimatic tolerances (Duckworth et al., 2000). The previous assignments of pollen taxa to PFTs by Yu et al. (1998, 2000) were based on a minor extension of the very simple implicit PFT classification of Prentice et al. (1992a). Here, we use a new global PFT classification defined explicitly in terms of four traits: life form, leaf form, phenology and bioclimatic tolerances (principally related to cold-tolerance mechanisms in woody plants), on the basis of current understanding of their significance in terms of adaptation to the physical environment (Harrison et al., 2009).

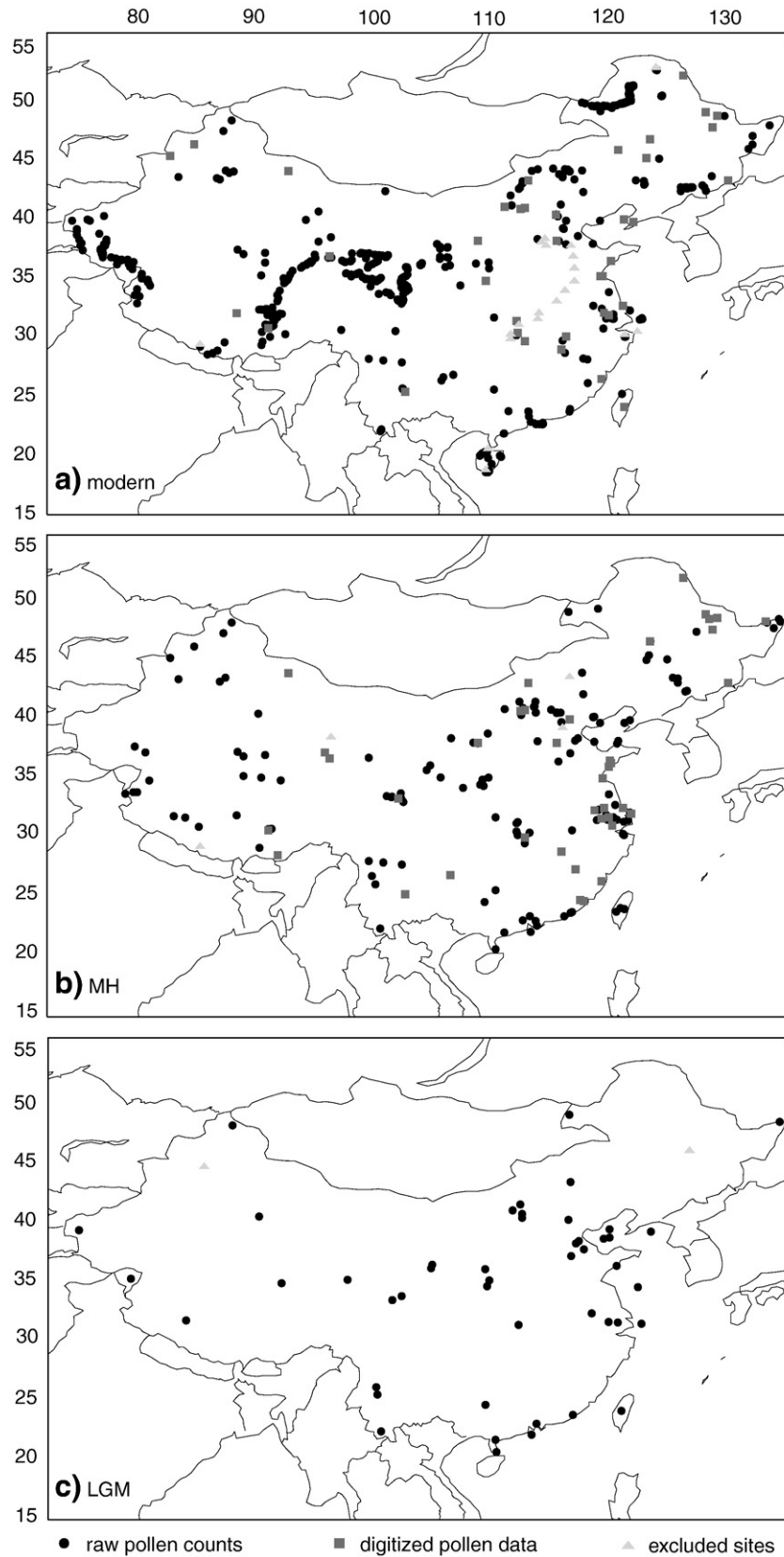


Fig. 1. Site maps of available Chinese pollen data for (a) modern, (b) MH and (c) LGM. Black dots represent sites for which raw pollen counts were available; gray squares represent sites for which digitized pollen data were used; light gray triangles represent sites (all are raw pollen counts) which were excluded from the analysis.

Life form: This category broadly follows Raunkiaer's scheme which has strong geographic patterns and can be related to bioclimate, with some amendments and simplification of nomenclature. Twenty-four

life forms are recognized: tree, tuft tree, tuft fern, tree treelet, low and high shrub, erect dwarf-shrub, prostrate dwarf-shrub, cushion shrub, liana or vine, succulent (stem and leaf), mangrove, wood parasite,

epiphyte, climber, forb, rosette or cushion-forb, halophyte, hydrophyte, aquatic, graminoid (grass, sedge, and rush), geophyte, bryophyte, fern or fern ally, and root parasite.

Leaf form: This is only applied to tree and shrub life forms. Four leaf forms of needle-leaved, broad-leaved, small-leaved (leaf area 20–2000 mm²) and micro-leaved (<20 mm²) are distinguished. Broad-leaved plants are further classified into types with sclerophyll versus malacophyll leaves.

Leaf phenology: This separates evergreen from deciduous trees and shrubs. The deciduous plants are further subdivided according to whether leaves are normally shed in response to cold or to drought.

Bioclimatic tolerances: The final level of classification is based on cold-tolerance and/or drought-tolerance limits. The principal cold-tolerance categories applied to trees and shrubs are tropical, warm-temperate, temperate, cool-temperate, boreal, and Arctic. These terms are used in a strictly bioclimatic sense, without geographic connotations. Temperate deciduous broad-leaved trees are further subdivided into spring-frost tolerant, avoiding, and intolerant types. Some plants with an exceptionally broad range of temperature tolerance (e.g. some *Pinus* species) are termed “eurythermic”. Three broad categories with respect to drought-tolerance (drought-adapted, drought-tolerant and drought-intolerant) are also recognized. Within the intermediate class of drought-tolerant plants, we distinguish two classes (mesic and xeric) of deciduous trees and shrubs.

Ecophysiological and bioclimatic foundations of the PFT classification have been summarized in Harrison et al. (2009). The PFTs are named here by four-part codes (Harrison et al., in preparation) reflecting the four classification levels in the order bioclimatic tolerance, phenology, leaf form, and life form. Thus, for example, “boreal evergreen needle-leaved trees” are bo.e.n.t; “eurythermic mesic drought-deciduous malacophyll low or high shrub” is eu-m.dd.mb.lhs. The PFT scheme recognizes 99 PFTs worldwide, including 25 arboreal PFTs, 37 shrub PFTs, 10 other kinds of woody plants, and 27 non-woody PFTs (Harrison et al., in preparation). Seventy-six of these 99 PFTs occur in China (Table 1).

Pollen taxa were allocated to one or more of the PFTs (Table 1), on the basis of information about the life form, leaf form, phenology and bioclimatic tolerances of constituent species derived from a variety of sources including floras and plant atlases (e.g. ECFC, 1959–1999; ECVC, 1980; IBCAS, 1987; Wu et al., 1992; Hou, 1998). Some taxa were excluded from the biomization procedure and are therefore not allocated to PFTs. These include specifically agricultural pollen taxa (e.g. *Oryza* and *Oryza sativa*), taxa known to be recent human introductions to China (e.g. *Eucalyptus* and *Opuntia*), pollen (and spores) of pre-Quaternary plants that represent redeposition (e.g. *Tricolporopollenites*). Algae (e.g. *Concentricystes*, *Mongeotia*, *Pediastrum*, *Spirogyra*, *Zygnema*, *Zygnemataceae*, and *Hystrichosphaera*), fungi, and indeterminate spores (e.g. monoletes and triletes) are frequently included in pollen counts or on pollen diagrams from China, but are not used in the biomization procedure.

Some of the PFTs are characteristic of highly localized or azonal vegetation types, e.g. aquatic, halophyte, hydrophyte, and mangrove. Some PFTs are constituents of several different broad-scale vegetation types, but are too widely distributed to have diagnostic value within the biomization procedure. Drought-intolerant forbs, drought-intolerant climbers, and drought-intolerant lianas or vines, for example, are present in several biomes but never become the predominant or characteristic PFT within any biome. Similarly, ferns never appear to characterize a unique biome. PFTs with characteristic of highly localized vegetation types, and PFTs that lack diagnostic value are therefore not used in the final version of the biomization procedure. A total of 53 PFTs were found to have diagnostic value and were therefore used in the biomization procedure (Table 1).

2.4. Biome classification

There is no standard global classification of biomes. The set of biomes used within the BIOME 6000 project, including the Chinese

biomizations (Yu et al., 1998, 2000), was initially based on the 17 biomes recognized by the BIOME1 biogeography model (Prentice et al., 1992a). The BIOME1 model distinguishes several kinds of mid- and high-latitude forests, but has less discrimination in respect to subtropical and tropical forests and non-arboreal vegetation types. Modifications were at first made to this initial scheme in an *ad hoc* fashion based on regional considerations. Recent developments within the Pan-Arctic Initiative (PAIN: Bigelow et al., 2003; Kaplan et al., 2003) have led to an improved classification of tundra vegetation types and this scheme, as well as improvements in the classification of subtropical vegetation, has been adopted in the BIOME4 biogeography model (Kaplan, 2001; Kaplan et al., 2003). In this paper, we use the nomenclature used in BIOME4 for tundra, high-latitude (boreal) and mid-latitude (temperate) forests, and combine information from the ECVC (1980) vegetation classification of China with aspects of the classification used in BIOME1 for other types of vegetation.

We recognize a total of 19 biomes (Table 2). Five different cold (boreal) and cool-temperate forest biomes were recognized by Yu et al. (1998, 2000). These biomes are distributed in relatively small areas in the higher mountains in northeastern China, northwestern China, central China and the northern and eastern Tibetan Plateau (ECVC, 1980). The zonal distribution of these biomes in China are confined to the Daxingan Mountains of northeasternmost China and several other mountain ranges including the Changbai Mountains in northeastern China, approximately 40–54°N, 120–135°E (ECVC, 1980).

Warm-temperate evergreen and mixed forests, by contrast, cover about one-fourth of the whole area of China and are mainly distributed in the subtropical part from ca. 31–32°N to the Tropic of Cancer (ECVC, 1980). The compilers of the Vegetation of China (ECVC, 1980) divided the warm-temperate (= subtropical) forests into four types: warm-temperate mixed evergreen and deciduous broadleaf forest (evergreen trees mixed with temperate deciduous trees), warm-temperate evergreen broadleaf/warm mixed forest (evergreen trees mixed with warm-temperate deciduous trees), warm-temperate evergreen broadleaf forest, and warm-temperate evergreen sclerophyll broadleaf forest. These four forest types are mainly differentiated at the species level, rather than at the genus level to which most pollen identification is possible. As a result, we were only able to distinguish two types, warm-temperate evergreen broadleaf and mixed forest (equivalent to warm-temperate mixed evergreen and deciduous broadleaf forest plus warm-temperate evergreen broadleaf/warm mixed forest) and warm-temperate evergreen broadleaf forest (equivalent to warm-temperate evergreen broadleaf forest plus warm-temperate evergreen sclerophyll broadleaf forest).

Temperate xerophytic shrubland was distinguished from temperate grassland and from desert in this study. Warm-temperate xerophytic woodland/scrub, which was recognized but never reconstructed in previous biomizations for China (Yu et al., 1998, 2000), was not distinguished in this biomization. This biome is confined to hot and dry river valleys in southwestern China and the coastal area of southern China and western Hainan Island (ECVC, 1980); there are not enough modern surface samples to characterize this biome and there is no evidence suggesting that it was any more widely distributed at MH or LGM. The temperate xerophytic shrubland, by contrast, is distributed widely in northern China, western China and the Tibetan Plateau (ECVC, 1980); previously, this biome was classified as steppe or desert (Yu et al., 1998, 2000). We reserve “steppe” here for temperate grassland, or grass–shrub mixtures.

We follow the PAIN project (Bigelow et al., 2003) and the BIOME4 model (Kaplan, 2001; Kaplan et al., 2003) in distinguishing five tundra biomes: cushion-forb tundra, graminoid and forb tundra, prostrate dwarf-shrub tundra, erect dwarf-shrub tundra, and low and high shrub tundra. These five biomes are found in the Tibetan Plateau and also in high mountains in central and northwestern China (ECVC, 1980). All PFTs were assigned to above mentioned 19 biomes used in the biomization procedure (Table 2).

Table 1

Assignments of pollen taxa from China to plant functional types (PFTs). PFTs with (*) were not used in the final biomization procedure.

PFT code	PFT name	Pollen taxa
bo.e.n.t	Boreal evergreen needle-leaved tree	<i>Abies</i> , <i>Juniperus</i> , <i>Picea</i> , <i>Picea jezoensis</i> , <i>Pinus</i> (Haploxyton), <i>Pinus pumila</i> , <i>Sabina</i>
c-te.e.n.t	Cool-temperate evergreen needle-leaved tree	<i>Abies</i> , <i>Keteleeria</i> , <i>Picea</i> , <i>Picea schrenkiana</i> , <i>Pinus koraiensis</i> , <i>Pinus pumila</i> , <i>Pinus sylvestris</i> var. <i>mongolica</i> , <i>Sabina</i> , Taxaceae,
te.e.n.t	Temperate evergreen needle-leaved tree	<i>Taxus</i> , <i>Tsuga</i>
wt.e.n.t	Warm-temperate evergreen needle-leaved tree	<i>Pinus tabulaeformis</i> , <i>Picea</i> + <i>Larix</i> + <i>Abies</i>
eu.e.n.t	Eurythermic evergreen needle-leaved tree	<i>Cedrus</i> , <i>Cryptomeria</i> , <i>Cunninghamia</i> , <i>Cupressus</i> , <i>Dacrydium</i> , <i>Keteleeria</i> , <i>Pinus massoniana</i> , <i>Podocarpus</i> , Taxaceae, Taxodiaceae, <i>Taxus</i> , <i>Tsuga</i>
bo.cd.n.t	Boreal cold-deciduous needle-leaved tree	Cupressaceae, Pinaceae, <i>Pinus</i> , <i>Pinus</i> (Diploxyton)
wt.d.n.t	Warm-temperate deciduous needle-leaved tree	<i>Larix</i>
wt.e.sb.t	Warm-temperate evergreen sclerophyll broad-leaved tree	<i>Glyptostrobus</i> , <i>Pseudolarix</i> , Taxodiaceae, <i>Taxodium</i>
wt.e.mb.t	Warm-temperate evergreen malacophyll broad-leaved tree	Buxaceae, <i>Castanopsis</i> , <i>Cyclobalanopsis</i> , Euphorbiaceae, <i>Flacourtia</i> , Flacourtiaceae, <i>Ilex</i> , Lauraceae, Leguminosae, <i>Lithocarpus</i> , Myrtaceae, <i>Olea</i> , Oleaceae, <i>Pasania</i> , <i>Quercus</i> , <i>Quercus</i> (evergreen), Rhamnaceae, Rutaceae, <i>Ziziphus</i>
tr.e.sb.t	Tropical evergreen sclerophyll broad-leaved tree	<i>Acalypha</i> , <i>Adina</i> , <i>Adinandra</i> , <i>Alchornea</i> , <i>Altingia</i> , <i>Altingiaceae</i> , Anacardiaceae, <i>Antidesma</i> , Apocynaceae, Araliaceae, <i>Ardisia</i> , <i>Bauhinia</i> , Bignoniaceae, Boraginaceae, <i>Camellia</i> , Capparidaceae, <i>Castanopsis</i> , Celastraceae, <i>Clerodendrum</i> , <i>Clethra</i> , <i>Cyclobalanopsis</i> , <i>Cyclobalanopsis glauca</i> , <i>Dalbergia</i> , <i>Dendropanax</i> , <i>Diospyros</i> , <i>Distylium</i> , Ebenaceae, Elaeagnaceae, <i>Elaeocarpus</i> , <i>Engelhardtia</i> , <i>Euonymus</i> , Euphorbiaceae, <i>Eurya</i> , <i>Evodia</i> , <i>Excoecaria</i> , <i>Ficus</i> , <i>Fortunella</i> , <i>Garcinia</i> , Gesneriaceae, <i>Girroniera</i> , <i>Glochidion</i> , Hamamelidaceae, Icacinaceae, <i>Ilex</i> , <i>Lagerstroemia</i> , Lauraceae, Leguminosae, <i>Ligustrum</i> , <i>Lithocarpus</i> , Lythraceae, <i>Macaranga</i> , <i>Magnolia</i> , Magnoliaceae, <i>Mallotus</i> , <i>Mallotus paniculatus</i> , Malvaceae, <i>Manglietia</i> , <i>Michelia</i> , <i>Microtropis</i> , Moraceae, <i>Myrica</i> , Myricaceae, Myrsinaceae, <i>Myrsine</i> , Myrtaceae, <i>Neolitsea</i> , <i>Nothocarpus</i> , <i>Nothopanax</i> , Olacaceae, <i>Ola</i> , <i>Olea</i> , Oleaceae, <i>Osmanthus</i> , <i>Pasania</i> , <i>Phoebe</i> , <i>Photinia</i> , <i>Phyllanthus</i> , <i>Pistacia</i> , <i>Prunus</i> , <i>Pyrus</i> , <i>Quercus</i> , <i>Quercus</i> (evergreen), <i>Quercus glauca</i> , Rhamnaceae, <i>Rhamnus</i> , Rubiaceae, Rutaceae, Sabiaceae, Sapindaceae, <i>Sapindus</i> , <i>Schefflera</i> , <i>Schima</i> , Scrophulariaceae, Solanaceae, <i>Styrax</i> , <i>Sycopsis</i> , Symplocaraceae, <i>Symplocos</i> , <i>Syzygium</i> , Theaceae, Thymelaeaceae, <i>Tricalysia</i> , Trochodendraceae, <i>Trochodendron</i> , Verbenaceae, <i>Wendlandia</i> , <i>Wikstroemia</i> , <i>Xylosma</i> , <i>Ziziphus</i>
tr.e.mb.t	Tropical evergreen malacophyll broad-leaved tree	Anacardiaceae, <i>Antidesma</i> , <i>Artocarpus</i> , <i>Caesalpinia</i> , <i>Canarium</i> , Combretaceae, <i>Elaeocarpus</i> , Euphorbiaceae, <i>Girroniera</i> , <i>Heritiera</i> , Lauraceae, Leguminosae, Melastomataceae, Myrtaceae, Oleaceae, Papilionaceae, Proteaceae, Rutaceae, <i>Schefflera</i> , Verbenaceae, <i>Vitex</i> , <i>Wendlandia</i>
bo.cd.mb.t	Boreal cold-deciduous malacophyll broad-leaved tree	<i>Adina</i> , <i>Adinandra</i> , <i>Aglaia</i> , <i>Aleurites</i> , <i>Allophylus</i> , <i>Altingia</i> , <i>Altingiaceae</i> , Anacardiaceae, Annonaceae, <i>Antidesma</i> , <i>Aphanamixis</i> , Apocynaceae, Araliaceae, <i>Artocarpus</i> , <i>Averrhoa</i> , <i>Bauhinia</i> , Bignoniaceae, Boraginaceae, Buxaceae, <i>Canthium</i> , <i>Cassia</i> , Celastraceae, <i>Cleistocalyx operulatus</i> , Combretaceae, <i>Decaspermum</i> , <i>Dodonaea</i> , <i>Elaeocarpus</i> , <i>Eugenia</i> , Euphorbiaceae, <i>Fagraea</i> , <i>Ficus</i> , <i>Flacourtia</i> , Flacourtiaceae, <i>Garcinia</i> , <i>Girroniera</i> , <i>Guttiferae</i> , <i>Helicia</i> , <i>Heritiera</i> , <i>Homalium</i> , Icacinaceae, <i>Kleinhovia</i> , Lauraceae, Leguminosae, <i>Lithocarpus</i> , Lythraceae, <i>Macaranga</i> , <i>Malaria</i> , <i>Mallotus</i> , Malvaceae, <i>Melanolepis</i> , Melastomataceae, Mimosaceae, Moraceae, Myristicaceae, Myrsinaceae, Myrtaceae, <i>Neolitsea</i> , Nyctaginaceae, Olacaceae, <i>Ola</i> , <i>Olea</i> , Oleaceae, Papilionaceae, <i>Pasania</i> , Pittosporaceae, <i>Platanus</i> , Proteaceae, <i>Psidium</i> , <i>Pterolobium</i> , <i>Randia</i> , <i>Reevesia</i> , Rubiaceae, Rutaceae, Sabiaceae, Sapindaceae, <i>Sapium</i> , Sapotaceae, <i>Schefflera</i> , Scrophulariaceae, <i>Sterculia</i> , <i>Syzygium</i> , <i>Terminalia</i> , Thymelaeaceae, Tiliaceae, Ulmaceae, <i>Ulmus</i> , Verbenaceae, <i>Vitex</i> , <i>Wendlandia</i>
te-ft.cd.mb.t	Temperate (spring-frost tolerant) cold-deciduous malacophyll broad-leaved tree	<i>Alnus</i> , <i>Betula</i> , <i>Betula alba-sinensis</i> , <i>Betula costata</i> , <i>Betula davurica</i> , <i>Betula fruticosa</i> , <i>Betula gmelinii</i> , <i>Betula middendorffii</i> , <i>Betula nana</i> , <i>Betula ovaliflora</i> , <i>Betula platyphylla</i> , Betulaceae, <i>Betula</i> -type, <i>Maackia</i> , <i>Populus</i> , <i>Salix</i>
te-fa.cd.mb.t	Temperate (spring-frost avoiding) cold-deciduous malacophyll broad-leaved tree	<i>Acer</i> , <i>Aceraceae</i> , <i>Alnus</i> , <i>Betula</i> , <i>Betula alba-sinensis</i> , <i>Betula davurica</i> , <i>Betula fruticosa</i> , <i>Betula gmelinii</i> , <i>Betula middendorffii</i> , <i>Betula ovaliflora</i> , <i>Betula platyphylla</i> , Betulaceae, <i>Betula</i> -type, <i>Corylus</i> , <i>Fraxinus</i> , <i>Fraxinus mandshurica</i> , Leguminosae, <i>Lonicera</i> , <i>Maackia</i> , Papilionaceae, <i>Populus</i> , <i>Pyrus</i> , <i>Quercus</i> , <i>Quercus</i> (deciduous), <i>Quercus liaotungensis</i> , <i>Quercus mongolica</i> , Rosaceae, <i>Salix</i> , <i>Tilia</i> , Tiliaceae, Ulmaceae, <i>Ulmus</i> , <i>Xanthoceras</i>
te-fi.cd.mb.t	Temperate (spring-frost intolerant) cold-deciduous malacophyll broad-leaved tree	<i>Acalypha</i> , <i>Acanthopanax</i> , <i>Aesculus</i> , <i>Ailanthus</i> , Anacardiaceae, <i>Aralia</i> , Araliaceae, <i>Carpinus</i> , Celastraceae, <i>Celtis</i> , Cornaceae, <i>Cornus</i> , <i>Cotinus</i> , <i>Crataegus</i> , <i>Diospyros</i> , Ebenaceae, Euphorbiaceae, <i>Evodia</i> , <i>Ginkgo</i> , <i>Gleditsia</i> , <i>Hypericum</i> , <i>Kalopanax</i> , Labiatae, Leguminosae, <i>Magnolia</i> , Magnoliaceae, <i>Morus</i> , Oleaceae, Papilionaceae, <i>Phellodendron</i> , <i>Phellodendron amurense</i> , <i>Platanus</i> , <i>Prunus</i> , <i>Quercus</i> , <i>Quercus</i> (deciduous), <i>Quercus variabilis</i> , <i>Quercus dendata</i> , Rhamnaceae, <i>Rhamnus</i> , <i>Rhus</i> , Rosaceae, Rutaceae, <i>Salix</i> , <i>Sambucus</i> , Scrophulariaceae, <i>Sorbus</i> , <i>Syringa</i> , <i>Toxicodendron</i> , Ulmaceae, <i>Ulmus</i> , <i>Zelkova</i> , Verbenaceae, <i>Vitex</i> , <i>Ziziphus</i>
wt.cd.mb.t	Warm-temperate cold-deciduous malacophyll broad-leaved tree	<i>Acer</i> , <i>Aceraceae</i> , <i>Alangium</i> , Betulaceae, Bignoniaceae, <i>Broussonetia</i> , Caprifoliaceae, <i>Carpinus</i> , <i>Carya</i> , <i>Castanea</i> , <i>Castanea</i> -type, <i>Celtis</i> , <i>Cladrastis</i> , Elaeagnaceae, <i>Euonymus</i> , <i>Fagus</i> , <i>Fagus longipetiolata</i> , <i>Fagus lucida</i> , <i>Fraxinus</i> , <i>Ginkgo</i> , Hamamelidaceae, <i>Idesia</i> , Juglandaceae, <i>Juglans</i> , <i>Juglans cathayensis</i> , <i>Kalopanax</i> , <i>Koelreuteria</i> , <i>Lagerstroemia</i> , Leguminosae, <i>Liquidambar</i> , <i>Liquidambar formosana</i> , <i>Lonicera</i> , Lythraceae, <i>Melia</i> , <i>Melia azedarach</i> , Meliaceae, <i>Meliosma</i> , Moraceae, <i>Morus</i> , <i>Ostrya</i> , Papilionaceae, <i>Phyllanthus</i> , <i>Pistacia</i> , <i>Populus</i> , <i>Pterocarya</i> , <i>Pyrus</i> , <i>Quercus</i> , <i>Quercus</i> (deciduous), <i>Quercus variabilis</i> , <i>Quercus dendata</i> , Rosaceae, Sabiaceae, <i>Salix</i> , <i>Sambucus</i> , <i>Syringa</i> , <i>Tilia</i> , Tiliaceae, Ulmaceae, <i>Ulmus</i> , <i>Zelkova</i> , <i>Zelkova sinica</i>
tr-m.dd.mb.t	Tropical mesic drought-deciduous malacophyll broad-leaved tree	<i>Acacia</i> , <i>Adina</i> , <i>Alangium</i> , <i>Albizia</i> , <i>Alnus</i> , Boraginaceae, <i>Broussonetia</i> , Caprifoliaceae, <i>Carya</i> , <i>Celtis</i> , <i>Cladrastis</i> , Cornaceae, <i>Cornus</i> , <i>Corylopsis</i> , <i>Cyclocarya</i> , Euphorbiaceae, <i>Euphoria</i> , Flacourtiaceae, Hamamelidaceae, <i>Hamamelis</i> , <i>Idesia</i> , Juglandaceae, <i>Juglans</i> , <i>Juglans cathayensis</i> , <i>Kalopanax</i> , <i>Koelreuteria</i> , <i>Lagerstroemia</i> , Lauraceae, Leguminosae, <i>Liquidambar</i> , <i>Liriodendron</i> , Lythraceae, <i>Magnolia</i> , Magnoliaceae, <i>Melia</i> , Meliaceae, <i>Meliosma</i> , <i>Microtropis</i> , <i>Mimosa</i> , Mimosaceae, Moraceae, <i>Morus</i> , <i>Myrica</i> , Myricaceae, <i>Nyssa</i> , <i>Phellodendron</i> , <i>Phyllanthus</i> , <i>Pistacia</i> , <i>Platycarya</i> , <i>Prunus</i> , <i>Pterocarya</i> , Rhamnaceae, <i>Rhamnus</i> , <i>Rhus</i> , Rosaceae, <i>Sambucus</i> , <i>Sapium</i> , <i>Sinojackia xylocarpa</i> , <i>Styrax</i> , Thymelaeaceae, <i>Toxicodendron</i> , <i>Trema</i> , <i>Ulmus</i> , Urticaceae, Verbenaceae, <i>Vitex</i> , <i>Wikstroemia</i> , <i>Zelkova</i> , <i>Ziziphus</i>
tr-x.dd.mb.t	Tropical xeric drought-deciduous malacophyll broad-leaved tree	<i>Acacia</i> , <i>Albizia</i> , Anacardiaceae, Annonaceae, Betulaceae, Bombacaceae, <i>Bombax</i> , <i>Caesalpinia</i> , Celastraceae, <i>Chukrasia</i> , Combretaceae, Euphorbiaceae, <i>Hainania</i> , <i>Lannea</i> , Leguminosae, Lythraceae, <i>Mallotus</i> , Melastomataceae, Meliaceae, <i>Mimosa</i> , Mimosaceae, Oleaceae, Papilionaceae, Rubiaceae, Sapindaceae, Tiliaceae, Ulmaceae, <i>Ulmus</i>
ml.t	Micro-leaved tree	<i>Acacia</i> , <i>Albizia</i> , Anacardiaceae, Annonaceae, Capparidaceae, <i>Cassia</i> , Celastraceae, Combretaceae, <i>Dalbergia</i> , <i>Dodonaea</i> , Euphorbiaceae, <i>Flacourtia</i> , Flacourtiaceae, <i>Helicteres</i> , Icacinaceae, <i>Lannea</i> , Leguminosae, Lythraceae, <i>Mallotus</i> , Melastomataceae, Mimosaceae, Papilionaceae, <i>Randia</i> , Rubiaceae, Sapindaceae, <i>Terminalia</i> , Tiliaceae, <i>Wendlandia</i> , <i>Ziziphus</i>
		<i>Casuarina</i>

Table 1 (continued)

PFT code	PFT name	Pollen taxa
slt	Small-leaved tree	<i>Acacia</i> , <i>Albizia</i> , <i>Elaeagnaceae</i> , <i>Elaeagnus</i> , <i>Leguminosae</i> , <i>Mimosa</i> , <i>Mimosaceae</i> , <i>Papilionaceae</i> , <i>Tamaricaceae</i> , <i>Tamarix</i> , <i>Ziziphus</i> , <i>Zygophyllaceae</i> , <i>Zygophyllum</i>
tut	Tuft tree	<i>Cycas</i> , <i>Palmae</i> , <i>Phoenix</i> , <i>Trachycarpus</i>
ar.e.n.lhs	Arctic evergreen needle-leaved low or high shrub	<i>Pinus pumila</i>
wt.e.n.lhs*	Warm-temperate evergreen needle-leaved low or high shrub	<i>Dacrydium</i> , <i>Podocarpus</i> , <i>Taxaceae</i> , <i>Taxus</i>
eu.e.n.lhs*	Eurythermic evergreen needle-leaved low or high shrub	<i>Cupressaceae</i> , <i>Pinaceae</i>
ft.ml.lhs	Frost-tolerant micro-leaved low or high shrub	<i>Anabasis</i> , <i>Ephedra</i> , <i>Ephedra monosperma</i> , <i>Ephedra sinica</i> , <i>Ephedraceae</i> , <i>Myricaria</i> , <i>Reaumuria</i> , <i>Reaumuria soongorica</i> , <i>Tamaricaceae</i> , <i>Tamarix</i> , <i>Tamarix chinensis</i>
dt.sl.lhs	Drought-tolerant small-leaved low or high shrub	<i>Acacia</i> , <i>Alhagi</i> , <i>Artemisia-type</i> , <i>Atraphaxis</i> , <i>Calligonum</i> , <i>Caragana</i> , <i>Ceratoides</i> , <i>Chenopodiaceae</i> , <i>Chenopodium</i> , <i>Elaeagnaceae</i> , <i>Elaeagnus</i> , <i>Hippophae</i> , <i>Kalidium</i> , <i>Leguminosae</i> , <i>Lycium</i> , <i>Mimosaceae</i> , <i>Nitraria</i> , <i>Papilionaceae</i> , <i>Salsola</i> , <i>Solanaceae</i> , <i>Sympegma</i> , <i>Zygophyllaceae</i> , <i>Zygophyllum</i>
di.sl.lhs	Drought-intolerant small-leaved low or high shrub	<i>Empetrum</i> , <i>Ericaceae</i>
wt.e.sb.lhs	Warm-temperate evergreen sclerophyll broad-leaved low or high shrub	<i>Buxaceae</i> , <i>Cyclobalanopsis</i> , <i>Euphorbiaceae</i> , <i>Flacourtia</i> , <i>Flacourtiaceae</i> , <i>Ilex</i> , <i>Olea</i> , <i>Oleaceae</i> , <i>Quercus</i> , <i>Quercus</i> (evergreen), <i>Rhamnaceae</i> , <i>Ziziphus</i>
ar.e.mb.lhs	Arctic evergreen malacophyll broad-leaved low or high shrub	<i>Empetrum</i> , <i>Ledum</i> , <i>Ledum palustre</i>
bo.e.mb.lhs	Boreal evergreen malacophyll broad-leaved low or high shrub	<i>Ericaceae</i> , <i>Ledum</i> , <i>Ledum palustre</i> , <i>Rhododendron</i> , <i>Rhododendron parvifolium</i> , <i>Vaccinium</i>
wt.e.mb.lhs	Warm-temperate evergreen malacophyll broad-leaved low or high shrub	<i>Acalypha</i> , <i>Acanthaceae</i> , <i>Adina</i> , <i>Adinandra</i> , <i>Alchornea</i> , <i>Anacardiaceae</i> , <i>Antidesma</i> , <i>Apocynaceae</i> , <i>Araliaceae</i> , <i>Ardisia</i> , <i>Bauhinia</i> , <i>Berberidaceae</i> , <i>Boraginaceae</i> , <i>Camellia</i> , <i>Capparidaceae</i> , <i>Capparis</i> , <i>Caprifoliaceae</i> , <i>Castanopsis</i> , <i>Celastraceae</i> , <i>Chloranthus</i> , <i>Clerodendrum</i> , <i>Clethra</i> , <i>Cyclobalanopsis</i> , <i>Damnacanthus</i> , <i>Daphne</i> , <i>Dendropanax</i> , <i>Diospyros</i> , <i>Distylium</i> , <i>Ebenaceae</i> , <i>Elaeagnaceae</i> , <i>Elaeagnus</i> , <i>Engelhardtia</i> , <i>Ericaceae</i> , <i>Euonymus</i> , <i>Euphorbiaceae</i> , <i>Eurya</i> , <i>Evodia</i> , <i>Fortunella</i> , <i>Garcinia</i> , <i>Gesneriaceae</i> , <i>Girardinia</i> , <i>Hamamelidaceae</i> , <i>Helicteres</i> , <i>Icacinaceae</i> , <i>Ilex</i> , <i>Illicium</i> , <i>Itea</i> , <i>Jasminum</i> , <i>Justicia</i> , <i>Lauraceae</i> , <i>Leguminosae</i> , <i>Ligustrum</i> , <i>Lithocarpus</i> , <i>Lonicera</i> , <i>Lythraceae</i> , <i>Macaranga</i> , <i>Maesa</i> , <i>Magnoliaceae</i> , <i>Mallotus</i> , <i>Malvaceae</i> , <i>Michelia</i> , <i>Microtropis</i> , <i>Moraceae</i> , <i>Myrica</i> , <i>Myricaceae</i> , <i>Myrsinaceae</i> , <i>Myrsine</i> , <i>Myrtaceae</i> , <i>Neolitsea</i> , <i>Nerium</i> , <i>Nothopanax</i> , <i>Olacaceae</i> , <i>Olax</i> , <i>Olea</i> , <i>Oleaceae</i> , <i>Osmanthus</i> , <i>Photinia</i> , <i>Phyllanthus</i> , <i>Pistacia</i> , <i>Prunus</i> , <i>Quercus</i> , <i>Quercus</i> (evergreen), <i>Rhamnaceae</i> , <i>Rhamnus</i> , <i>Rhododendron</i> , <i>Rubiaceae</i> , <i>Rutaceae</i> , <i>Sabiaceae</i> , <i>Sapindaceae</i> , <i>Schefflera</i> , <i>Scrophulariaceae</i> , <i>Solanaceae</i> , <i>Styrax</i> , <i>Sycopsis</i> , <i>Symplocaceae</i> , <i>Symplocos</i> , <i>Syzygium</i> , <i>Theaceae</i> , <i>Thymelaeaceae</i> , <i>Tricalysia</i> , <i>Trochodendraceae</i> , <i>Trochodendron</i> , <i>Vaccinium</i> , <i>Verbenaceae</i> , <i>Viburnum</i> , <i>Wendlandia</i> , <i>Wikstroemia</i> , <i>Xylosma</i> , <i>Zanthoxylum</i> , <i>Ziziphus</i>
tr.e.mb.lhs	Tropical evergreen malacophyll broad-leaved low or high shrub	<i>Adina</i> , <i>Adinandra</i> , <i>Aglaia</i> , <i>Allomorpha</i> , <i>Allophylus</i> , <i>Annonaceae</i> , <i>Antidesma</i> , <i>Aphanamixis</i> , <i>Apocynaceae</i> , <i>Araliaceae</i> , <i>Bauhinia</i> , <i>Boraginaceae</i> , <i>Buxaceae</i> , <i>Canthium</i> , <i>Cassia</i> , <i>Celastraceae</i> , <i>Decaspermum</i> , <i>Dodonaea</i> , <i>Eugenia</i> , <i>Fagraea</i> , <i>Flacourtiaceae</i> , <i>Garcinia</i> , <i>Girardinia</i> , <i>Guttiferae</i> , <i>Helicia</i> , <i>Helicteres</i> , <i>Homalium</i> , <i>Icacinaceae</i> , <i>Justicia</i> , <i>Lardizabalaceae</i> , <i>Lauraceae</i> , <i>Lawsonia</i> , <i>Leguminosae</i> , <i>Lythraceae</i> , <i>Macaranga</i> , <i>Mallotus</i> , <i>Malvaceae</i> , <i>Melanolepis</i> , <i>Melastomataceae</i> , <i>Mimosaceae</i> , <i>Moraceae</i> , <i>Myristicaceae</i> , <i>Myrsinaceae</i> , <i>Myrtaceae</i> , <i>Nerium</i> , <i>Nyctaginaceae</i> , <i>Olea</i> , <i>Oleaceae</i> , <i>Papilionaceae</i> , <i>Piper</i> , <i>Piperaceae</i> , <i>Pittosporaceae</i> , <i>Proteaceae</i> , <i>Psidium</i> , <i>Pterolobium</i> , <i>Randia</i> , <i>Ricinus</i> , <i>Rubiaceae</i> , <i>Sabiaceae</i> , <i>Sapindaceae</i> , <i>Sapium</i> , <i>Sapotaceae</i> , <i>Scrophulariaceae</i> , <i>Syzygium</i> , <i>Verbenaceae</i> , <i>Vitex</i> , <i>Wendlandia</i> , <i>Hydrangea</i> , <i>Viburnum</i>
ar.cd.mb.lhs	Arctic cold-deciduous malacophyll broad-leaved low or high shrub	<i>Alnus</i> , <i>Betula</i> , <i>Betulaceae</i> , <i>Betula-type</i> , <i>Ericaceae</i> , <i>Rhododendron</i> , <i>Salix</i> , <i>Viburnum</i>
bo.cd.mb.lhs	Boreal cold-deciduous malacophyll broad-leaved low or high shrub	<i>Alnus</i> , <i>Betula</i> , <i>Betulaceae</i> , <i>Betula-type</i> , <i>Ericaceae</i> , <i>Rhododendron</i> , <i>Salix</i> , <i>Viburnum</i>
te.cd.mb.lhs	Temperate cold-deciduous malacophyll broad-leaved low or high shrub	<i>Acalypha</i> , <i>Acanthopanax</i> , <i>Acer</i> , <i>Aceraceae</i> , <i>Alangium</i> , <i>Alnus</i> , <i>Anacardiaceae</i> , <i>Araliaceae</i> , <i>Berberidaceae</i> , <i>Berberis</i> , <i>Betula</i> , <i>Betulaceae</i> , <i>Betula-type</i> , <i>Bignoniaceae</i> , <i>Caprifoliaceae</i> , <i>Caragana</i> , <i>Carpinus</i> , <i>Celastraceae</i> , <i>Celtis</i> , <i>Cornaceae</i> , <i>Cornus</i> , <i>Corylus</i> , <i>Cotinus</i> , <i>Cotoneaster</i> , <i>Crataegus</i> , <i>Deutzia</i> , <i>Diospyros</i> , <i>Ebenaceae</i> , <i>Elaeagnaceae</i> , <i>Elaeagnus</i> , <i>Ericaceae</i> , <i>Euonymus</i> , <i>Euphorbiaceae</i> , <i>Evodia</i> , <i>Forsythia</i> , <i>Fraxinus</i> , <i>Gleditsia</i> , <i>Glochidion</i> , <i>Hamamelidaceae</i> , <i>Helwingia</i> , <i>Hippophae</i> , <i>Hydrangea</i> , <i>Hypericum</i> , <i>Ilex</i> , <i>Koelreuteria</i> , <i>Labiatae</i> , <i>Lagerstroemia</i> , <i>Leguminosae</i> , <i>Lespedeza</i> , <i>Lonicera</i> , <i>Lycium</i> , <i>Lythraceae</i> , <i>Maackia</i> , <i>Malvaceae</i> , <i>Melia</i> , <i>Meliaceae</i> , <i>Meliosma</i> , <i>Moraceae</i> , <i>Morus</i> , <i>Oleaceae</i> , <i>Ostryopsis</i> , <i>Papilionaceae</i> , <i>Philadelphus</i> , <i>Phyllanthus</i> , <i>Pistacia</i> , <i>Polemoniaceae</i> , <i>Prunus</i> , <i>Quercus</i> , <i>Quercus</i> (deciduous), <i>Rhamnaceae</i> , <i>Rhamnus</i> , <i>Rhododendron</i> , <i>Rhus</i> , <i>Rosa</i> , <i>Rosaceae</i> , <i>Rubus</i> , <i>Rutaceae</i> , <i>Sabiaceae</i> , <i>Salix</i> , <i>Sambucus</i> , <i>Scrophulariaceae</i> , <i>Solanaceae</i> , <i>Sorbus</i> , <i>Spiraea</i> , <i>Spiraea blumei</i> , <i>Syringa</i> , <i>Tilia</i> , <i>Tiliaceae</i> , <i>Toxicodendron</i> , <i>Ulmaceae</i> , <i>Ulmus</i> , <i>Vaccinium</i> , <i>Vaccinium uliginosum</i> , <i>Valeriana</i> , <i>Valerianaceae</i> , <i>Verbenaceae</i> , <i>Viburnum</i> , <i>Violaceae</i> , <i>Vitex</i> , <i>Wikstroemia</i> , <i>Xanthoceras</i> , <i>Zanthoxylum</i> , <i>Zelkova</i> , <i>Ziziphus</i>
wt.cd.mb.lhs	Warm-temperate cold-deciduous malacophyll broad-leaved low or high shrub	<i>Acacia</i> , <i>Adina</i> , <i>Alangium</i> , <i>Albizia</i> , <i>Berberidaceae</i> , <i>Berberis</i> , <i>Boraginaceae</i> , <i>Bredia</i> , <i>Caprifoliaceae</i> , <i>Celtis</i> , <i>Cornaceae</i> , <i>Cornus</i> , <i>Corylopsis</i> , <i>Desmodium</i> , <i>Euphorbiaceae</i> , <i>Fontanesia</i> , <i>Hamamelidaceae</i> , <i>Hamamelis</i> , <i>Hypericum</i> , <i>Koelreuteria</i> , <i>Lagerstroemia</i> , <i>Lauraceae</i> , <i>Leguminosae</i> , <i>Linaceae</i> , <i>Lonicera</i> , <i>Lythraceae</i> , <i>Melia</i> , <i>Meliaceae</i> , <i>Meliosma</i> , <i>Mimosa</i> , <i>Mimosaceae</i> , <i>Moraceae</i> , <i>Morus</i> , <i>Photinia</i> , <i>Phyllanthus</i> , <i>Pistacia</i> , <i>Prunus</i> , <i>Rhamnaceae</i> , <i>Rhamnus</i> , <i>Rhus</i> , <i>Ricinus</i> , <i>Rosaceae</i> , <i>Rubus</i> , <i>Sambucus</i> , <i>Sapium</i> , <i>Schisandra</i> , <i>Spiraea</i> , <i>Styrax</i> , <i>Thymelaeaceae</i> , <i>Toxicodendron</i> , <i>Trema</i> , <i>Ulmus</i> , <i>Urticaceae</i> , <i>Verbenaceae</i> , <i>Violaceae</i> , <i>Vitex</i> , <i>Wikstroemia</i> , <i>Zanthoxylum</i> , <i>Zelkova</i> , <i>Ziziphus</i>
eu-m.dd.mb.lhs*	Eurythermic mesic drought-deciduous malacophyll low or high shrub	<i>Albizia</i> , <i>Allophylus</i> , <i>Anacardiaceae</i> , <i>Artemisia</i> , <i>Artemisia-type</i> , <i>Caesalpinia</i> , <i>Capparidaceae</i> , <i>Caprifoliaceae</i> , <i>Compositae</i> , <i>Euphorbia</i> , <i>Euphorbiaceae</i> , <i>Labiatae</i> , <i>Malvaceae</i> , <i>Rhamnaceae</i> , <i>Rhamnus</i> , <i>Rubiaceae</i> , <i>Rutaceae</i>
eu-x.dd.mb.lhs	Eurythermic xeric drought-deciduous malacophyll low or high shrub	<i>Acacia</i> , <i>Acanthaceae</i> , <i>Anacardiaceae</i> , <i>Artemisia</i> , <i>Artemisia-type</i> , <i>Calligonum</i> , <i>Capparidaceae</i> , <i>Capparis</i> , <i>Compositae</i> , <i>Cruciferae</i> , <i>Euphorbia</i> , <i>Euphorbiaceae</i> , <i>Leguminosae</i> , <i>Papilionaceae</i> , <i>Polygonaceae</i> , <i>Rhamnaceae</i> , <i>Rubiaceae</i> , <i>Rutaceae</i> , <i>Solanaceae</i> , <i>Solanum</i> , <i>Ziziphus</i>
ar.e.mb.eds	Arctic evergreen malacophyll broad-leaved erect dwarf-shrub	<i>Berberidaceae</i> , <i>Empetrum</i> , <i>Salix</i> , <i>Vaccinium</i>
ar.cd.mb.eds	Arctic cold-deciduous malacophyll broad-leaved erect dwarf-shrub	<i>Betula</i> , <i>Betula ermanii</i> , <i>Betula fruticosa</i> , <i>Betula middendorffii</i> , <i>Betula ovaliflora</i> , <i>Betulaceae</i> , <i>Betula-type</i> , <i>Caragana</i> , <i>Hippophae</i> , <i>Rhododendron</i> , <i>Rosa</i> , <i>Rosaceae</i> , <i>Salix</i>
ar.e.n.pds	Arctic evergreen need-leaved prostrate dwarf-shrub	<i>Juniperus</i> , <i>Sabina</i>
ar.e.mb.pds	Arctic evergreen malacophyll broad-leaved prostrate dwarf shrub	<i>Rosaceae</i> , <i>Salix</i>

(continued on next page)

Table 1 (continued)

PFT code	PFT name	Pollen taxa
ar.cd.mb.pds	Arctic cold-deciduous malacophyll broad-leaved prostrate dwarf shrub	<i>Betula nana</i> , <i>Ceratoides</i> , <i>Rhododendron</i> , <i>Rosa</i> , Rosaceae, <i>Salix</i> , <i>Vaccinium</i>
cs	Cushion shrub	<i>Ceratoides</i> , <i>Nanophyton</i>
wt-dt.lv*	Warm-temperate drought-tolerant liana or vine	<i>Dalbergia</i>
tr-dt.lv	Tropical drought-tolerant liana or vine	<i>Caesalpinia</i> , <i>Dalbergia</i> , Euphorbiaceae, <i>Ficus</i> , <i>Piper</i> , Piperaceae, Rubiaceae, Rutaceae, Vitaceae
te-di.lv*	Temperate drought-intolerant liana or vine	<i>Actinidia</i> , <i>Aeschynanthus</i> , <i>Alyxia</i> , <i>Anodendron</i> , Bignoniaceae, Capparidaceae, <i>Capparis</i> , Celastraceae, <i>Celastrus</i> , <i>Clematis</i> , <i>Cocculus</i> , Compositae, <i>Erycibe</i> , <i>Hedera</i> , Lardizabalaceae, Leguminosae, <i>Lonicera</i> , Menispermaceae, Oleaceae, Papilionaceae, Ranunculaceae, Rhamnaceae, <i>Rhynchosia</i> , Rosaceae, Sabiaceae, <i>Sageretia</i> , <i>Schisandra</i> , <i>Thalictrum</i> , Vitaceae, <i>Vitis</i> , <i>Zanthoxylum</i>
tr-di.lv	Tropical drought-intolerant liana or vine	Acanthaceae, <i>Actinidia</i> , <i>Aeschynanthus</i> , <i>Alyxia</i> , Annonaceae, <i>Anodendron</i> , Apocynaceae, <i>Bauhinia</i> , Bignoniaceae, <i>Bowringia</i> , <i>Calamus</i> , Capparidaceae, Celastraceae, <i>Celastrus</i> , <i>Cocculus</i> , Combretaceae, Convolvulaceae, <i>Erycibe</i> , <i>Ficus</i> , <i>Hedera</i> , Icacinaceae, Lardizabalaceae, Leguminosae, <i>Mappianthus</i> , Melastomataceae, Menispermaceae, Moraceae, Myrsinaceae, Nyctaginaceae, Olacaceae, <i>Olex</i> , Oleaceae, <i>Pachygone</i> , Palmae, Papilionaceae, Pittosporaceae, <i>Pterolobium</i> , Ranunculaceae, Sabiaceae, <i>Schefflera</i> , <i>Stephania</i> , <i>Tristellateia</i> , <i>Ventilago</i> , Verbenaceae
man*	Mangrove	<i>Avicennia</i> , <i>Bruguiera</i> , <i>Ceriops</i> , Euphorbiaceae, <i>Excoecaria</i> , <i>Excoecaria allogacha</i> , <i>Kandelia</i> , Myrsinaceae, <i>Rhizophora</i> , Rhizophoraceae, Rubiaceae, <i>Sonneratia</i>
wpa*	Woody parasite	<i>Elytranthe</i> , Loranthaceae
te-di.c*	Temperate drought-intolerant climber	<i>Actinostemma</i> , Amaranthaceae, Araliaceae, Campanulaceae, <i>Citrullus</i> , <i>Clematis</i> , Convolvulaceae, <i>Convolvulus</i> , Cucurbitaceae, <i>Cuscuta</i> , <i>Galium</i> , <i>Glycine</i> , <i>Humulus</i> , <i>Lathyrus</i> , <i>Lathyrus davidii</i> , Leguminosae, Liliaceae, <i>Mimosa</i> , Mimosaceae, Papilionaceae, Polemoniaceae, Polygonaceae, Rubiaceae, Solanaceae, <i>Solanum</i> , <i>Valeriana</i> , Valerianaceae, <i>Vicia</i> , <i>Vigna</i>
tr-di.c*	Tropical drought-intolerant climber	Acanthaceae, <i>Actinostemma</i> , Amaranthaceae, Araceae, Araliaceae, Campanulaceae, Convolvulaceae, <i>Convolvulus</i> , Cucurbitaceae, <i>Cuscuta</i> , <i>Galium</i> , <i>Glycine</i> , <i>Lathyrus</i> , Lauraceae, Leguminosae, Liliaceae, <i>Mimosa</i> , Mimosaceae, Papilionaceae, <i>Rhynchosia</i> , Rubiaceae, Sapindaceae, Solanaceae, <i>Solanum</i> , <i>Vicia</i> , <i>Vigna</i>
ar.fb	Arctic forb	<i>Achillea</i> , <i>Androsace</i> , <i>Anemone</i> , <i>Arenaria</i> , <i>Artemisia</i> , <i>Artemisia</i> -type, <i>Biebersteinia</i> , Campanulaceae, Caryophyllaceae, <i>Centaurea</i> , <i>Cerastium</i> , Compositae, <i>Corydalis</i> , Cruciferae, <i>Dianthus</i> , <i>Gentiana</i> , Gentianaceae, Geraniaceae, <i>Geranium</i> , <i>Impatiens</i> , Iridaceae, <i>Iris</i> , Labiatae, Leguminosae, <i>Liguliflorae</i> , <i>Liquiliflora</i> , <i>Lysimachia</i> , <i>Lythrum</i> , <i>Monotropa</i> , <i>Onobrychis</i> , <i>Orostachys</i> , <i>Oxytropis</i> , Papaveraceae, Papilionaceae, <i>Pedicularis</i> , <i>Pertya</i> , Polemoniaceae, <i>Polemonium</i> , Polygonaceae, <i>Polygonum</i> , <i>Potentilla</i> , <i>Primula</i> , Primulaceae, <i>Pulsatilla</i> , <i>Pyrola</i> , Ranunculaceae, <i>Rhodiola</i> , <i>Saussurea</i> , <i>Saxifraga</i> , Saxifragaceae, <i>Scrophularia</i> , Scrophulariaceae, <i>Sedum</i> , <i>Sibbaldia</i> , <i>Stelleria</i> , <i>Thalictrum</i> , <i>Tubuliflorae</i> , Umbelliferae, <i>Verbasicum</i> , <i>Veronica</i>
bo-di.fb*	Boreal drought-intolerant forb	Caryophyllaceae, <i>Plantago</i> , Plantagonaceae
te-di.fb*	Temperate drought-intolerant forb	<i>Acalypha</i> , <i>Aconitum</i> , <i>Aeschynomene</i> , Amaranthaceae, <i>Amaranthus</i> , <i>Ambrosia</i> , <i>Androsace</i> , <i>Anemone</i> , <i>Aquilegia</i> , Araceae, <i>Arachis</i> , Araliaceae, <i>Arctium</i> , <i>Arisaema</i> , <i>Artemisia</i> , <i>Artemisia argyi</i> , <i>Artemisia</i> -type, <i>Asperula</i> , <i>Aster</i> , <i>Astragalus</i> , <i>Atractylis</i> , <i>Atractylodes</i> , Berberidaceae, <i>Bidens</i> , <i>Biebersteinia</i> , <i>Bumias</i> , <i>Caltha</i> , Campanulaceae, <i>Cannabis</i> , Caprifoliaceae, Caryophyllaceae, <i>Cassia</i> , <i>Castilleja</i> , <i>Caulophyllum</i> , <i>Caulophyllum robustum</i> , <i>Centaurea</i> , <i>Cerastium</i> , <i>Chamaenerion</i> , <i>Chelidonium</i> , Chenopodiaceae, <i>Chenopodium</i> , <i>Chloranthus</i> , <i>Chrysanthemum</i> , <i>Cimicifuga</i> , <i>Circaea</i> , <i>Cirsium</i> , <i>Clematis</i> , Commelinaceae, Compositae, Convolvulaceae, <i>Convolvulus</i> , Cornaceae, <i>Corydalis</i> , <i>Crepis</i> , Cruciferae, <i>Dianthus</i> , <i>Dipsacaceae</i> , <i>Dipsacus</i> , <i>Drosera</i> , <i>Droseraceae</i> , <i>Epilobium</i> , <i>Eriophostylis</i> , <i>Euphorbia</i> , Euphorbiaceae, <i>Fagopyrum</i> , <i>Filipendula</i> , <i>Gentiana</i> , Gentianaceae, Geraniaceae, <i>Gerbera</i> , <i>Geum</i> , <i>Glycine</i> , Haloragidaceae, <i>Hemerocallis</i> , <i>Hypericum</i> , <i>Impatiens</i> , Iridaceae, <i>Iris</i> , <i>Ixeris</i> , <i>Kochia</i> , Labiatae, <i>Lamium</i> , Leguminosae, <i>Leonurus</i> , <i>Lespedeza</i> , <i>Liguliflorae</i> , Liliaceae, <i>Lilium</i> , Linaceae, <i>Liquiliflora</i> , <i>Lithospermum</i> , <i>Lotus</i> , Lythraceae, <i>Lythrum</i> , <i>Macleaya</i> , <i>Malva</i> , Malvaceae, <i>Mazus</i> , <i>Medicago</i> , <i>Melilotus</i> , <i>Mercurialis</i> , <i>Mimosa</i> , Mimosaceae, <i>Monotropa</i> , <i>Oenothera</i> , <i>Oenotheraceae</i> , Onagraceae, <i>Onobrychis</i> , Orchidaceae, <i>Origanum</i> , <i>Oxalis</i> , <i>Oxytropis</i> , Papaveraceae, Papilionaceae, <i>Patrinia</i> , <i>Pedicularis</i> , <i>Persicaria</i> , <i>Phlomis</i> , <i>Phtheirospermum</i> , <i>Plantago</i> , Plantagonaceae, <i>Platycodon</i> , Polemoniaceae, <i>Polemonium</i> , <i>Polygala</i> , Polygonaceae, <i>Polygonatum</i> , <i>Polygonum</i> , <i>Polygonum amphibium</i> , <i>Polygonum convolvulus</i> , <i>Portulaca</i> , <i>Potentilla</i> , <i>Primula</i> , Primulaceae, <i>Pyrola</i> , Ranunculaceae, <i>Ranunculus</i> , <i>Reseda</i> , <i>Resedaceae</i> , <i>Rheum</i> , <i>Rhynchosia</i> , <i>Ricinus</i> , <i>Rubia</i> , Rubiaceae, <i>Rumex</i> , <i>Sanguisorba</i> , <i>Saururus</i> , <i>Saussurea</i> , <i>Saxifraga</i> , Saxifragaceae, <i>Scabiosa</i> , <i>Scrophularia</i> , Scrophulariaceae, <i>Serratula</i> , Solanaceae, <i>Solanum</i> , <i>Solidago</i> , <i>Stellera</i> , <i>Suaeda</i> , <i>Symphytum</i> , <i>Taraxacum</i> , <i>Thalictrum</i> , Thymelaeaceae, <i>Tribulus</i> , <i>Trollius</i> , Umbelliferae, <i>Urtica</i> , Urticaceae, <i>Utricularia</i> , <i>Valeriana</i> , Valerianaceae, Verbenaceae, <i>Viola</i> , Violaceae, <i>Xanthium</i> , <i>Youngia</i> , <i>Zinnia</i> , <i>Zygophyllaceae</i>
wt-di.fb*	Warm-temperate drought-intolerant forb	<i>Acalypha</i> , <i>Aconitum</i> , <i>Aeschynomene</i> , <i>Alternanthera</i> , Amaranthaceae, <i>Amaranthus</i> , Araceae, Araliaceae, <i>Arisaema</i> , <i>Artemisia</i> , <i>Artemisia</i> -type, <i>Aster</i> , <i>Astragalus</i> , <i>Atractylis</i> , <i>Atractylodes</i> , Berberidaceae, <i>Bidens</i> , <i>Bredia</i> , Campanulaceae, Caprifoliaceae, Caryophyllaceae, <i>Cassia</i> , <i>Chamaenerion</i> , Chenopodiaceae, <i>Chenopodium</i> , <i>Chloranthus</i> , <i>Chrysanthemum</i> , <i>Circaea</i> , <i>Cirsium</i> , <i>Clematis</i> , <i>Clerodendrum</i> , Commelinaceae, Compositae, <i>Convolvulus</i> , Cornaceae, <i>Corydalis</i> , <i>Crepis</i> , Cruciferae, <i>Desmodium</i> , <i>Dianthus</i> , Dipsacaceae, <i>Dipsacus</i> , <i>Drosera</i> , <i>Droseraceae</i> , <i>Epilobium</i> , <i>Euphorbia</i> , Euphorbiaceae, <i>Gentiana</i> , Gentianaceae, Geraniaceae, <i>Gerbera</i> , Gesneriaceae, <i>Glycine</i> , Haloragidaceae, <i>Hemerocallis</i> , <i>Impatiens</i> , Iridaceae, <i>Iris</i> , <i>Ixeris</i> , Labiatae, <i>Laggyra</i> , <i>Lamium</i> , Leguminosae, <i>Leonurus</i> , <i>Lespedeza</i> , <i>Liguliflorae</i> , Liliaceae, <i>Lilium</i> , Linaceae, <i>Lobelia</i> , Lobeliaceae, <i>Lotus</i> , Lythraceae, <i>Lythrum</i> , <i>Macleaya</i> , <i>Malva</i> , Malvaceae, <i>Mazus</i> , <i>Medicago</i> , <i>Melilotus</i> , <i>Mercurialis</i> , <i>Mimosa</i> , Mimosaceae, <i>Oenothera</i> , <i>Oenotheraceae</i> , Onagraceae, Orchidaceae, <i>Oxalis</i> , Papaveraceae, Papilionaceae, <i>Paraphlomis</i> , <i>Patrinia</i> , <i>Pedicularis</i> , <i>Phlomis</i> , <i>Phtheirospermum</i> , <i>Plantago</i> , Plantagonaceae, <i>Platycodon</i> , <i>Polygala</i> , Polygonaceae, <i>Polygonatum</i> , <i>Polygonum</i> , <i>Portulaca</i> , <i>Potentilla</i> , <i>Primula</i> , Primulaceae, <i>Pyrola</i> , Ranunculaceae, <i>Ranunculus</i> , <i>Rheum</i> , <i>Rhynchosia</i> , <i>Rubia</i> , Rubiaceae, <i>Rumex</i> , <i>Sanguisorba</i> , <i>Saururus</i> , <i>Saussurea</i> , <i>Saxifraga</i> , Saxifragaceae, <i>Scrophularia</i> , Solanaceae, <i>Solanum</i> , <i>Solidago</i> , <i>Stellera</i> , <i>Suaeda</i> , <i>Taraxacum</i> , <i>Thalictrum</i> , Umbelliferae, Urticaceae, <i>Utricularia</i> , Verbenaceae, <i>Vigna</i> , <i>Viola</i> , Violaceae, <i>Xanthium</i> , <i>Youngia</i>
tr-di.fb*	Tropical drought-intolerant forb	<i>Acalypha</i> , Acanthaceae, <i>Aeschynomene</i> , Aizoaceae, <i>Alternanthera</i> , Amaranthaceae, <i>Amaranthus</i> , <i>Anagallis</i> , Apocynaceae, Araceae, Araliaceae, <i>Arisaema</i> , <i>Artemisia</i> , <i>Artemisia argyi</i> , <i>Artemisia</i> -type, <i>Aster</i> , <i>Asyneuma</i> , Berberidaceae, <i>Bidens</i> , Bignoniaceae, Campanulaceae, Capparidaceae, Caryophyllaceae, <i>Cassia</i> , Chenopodiaceae, <i>Chenopodium</i> , <i>Chingiacanthus</i> , <i>Chloranthus</i> , <i>Chrysanthemum</i> , <i>Cirsium</i> , <i>Clematis</i> , Commelinaceae, Compositae, Convolvulaceae, Cornaceae, <i>Corydalis</i> , <i>Crepis</i> , Cruciferae, <i>Desmodium</i> , <i>Dianthus</i> , <i>Drosera</i> , <i>Droseraceae</i> , <i>Euphorbia</i> , Euphorbiaceae, <i>Gentiana</i> , Gentianaceae, Geraniaceae, <i>Gerbera</i> , Gesneriaceae, <i>Glycine</i> , Haloragidaceae, Icacinaceae, <i>Impatiens</i> , Iridaceae, <i>Iris</i> , <i>Ixeris</i> , Labiatae, <i>Justicia</i> , Labiatae, Leguminosae, <i>Lespedeza</i> , <i>Liguliflorae</i> , Liliaceae, <i>Lilium</i> , <i>Lobelia</i> , Lobeliaceae, Lythraceae, <i>Lythrum</i> , <i>Macleaya</i> , Malvaceae, <i>Mazus</i> , Melastomataceae, <i>Melilotus</i> , <i>Mercurialis</i> , Moraceae, <i>Oenothera</i> , <i>Oenotheraceae</i> , Onagraceae, Orchidaceae, <i>Oxalis</i> , Papilionaceae, <i>Paraphlomis</i> , <i>Patrinia</i> , <i>Phlomis</i> , <i>Phtheirospermum</i> , <i>Phyllanthus</i> , <i>Piper</i> , Piperaceae, <i>Plantago</i> , Plantagonaceae, <i>Platycodon</i> , <i>Polygala</i> , Polygonaceae, <i>Polygonatum</i> , <i>Polygonum</i> , <i>Portulaca</i> , <i>Potentilla</i> , <i>Primula</i> , Primulaceae, <i>Proboscidea</i> , Proteaceae, Ranunculaceae, <i>Ranunculus</i> , <i>Rubia</i> , Rubiaceae, <i>Rumex</i> ,

Table 1 (continued)

PFT code	PFT name	Pollen taxa
te-dt.fb	Temperate drought-tolerant forb	<i>Saussurea</i> , <i>Saxifraga</i> , Saxifragaceae, <i>Scrophularia</i> , Scrophulariaceae, Solanaceae, <i>Solanum</i> , <i>Taraxacum</i> , <i>Thalictrum</i> , Tiliaceae, Umbelliferae, Urticaceae, <i>Utricularia</i> , Verbenaceae, <i>Veronica</i> , <i>Vigna</i> , <i>Viola</i> , Violaceae, <i>Xanthium</i> , <i>Youngia</i> , <i>Achillea</i> , <i>Aconitum</i> , <i>Agriophyllum</i> , <i>Ajania</i> , Amaranthaceae, <i>Ambrosia</i> , <i>Arabis</i> , <i>Arenaria</i> , <i>Artemisia</i> , <i>Artemisia anethifolia</i> , <i>Artemisia desertorum</i> , <i>Artemisia frigida</i> , <i>Artemisia</i> -type, <i>Aster</i> , <i>Astragalus</i> , <i>Attractylis</i> , <i>Attractylodes</i> , <i>Atriplex</i> , <i>Bidens</i> , Boraginaceae, <i>Brachyactis</i> , Campanulaceae, Caryophyllaceae, <i>Centaurea</i> , Compositae, <i>Crepis</i> , Cruciferae, <i>Daphne</i> , <i>Dianthus</i> , Euphorbiaceae, <i>Filifolium</i> , <i>Filifolium sibiricum</i> , <i>Filipendula</i> , <i>Gentiana</i> , <i>Gentianaceae</i> , Geraniaceae, <i>Geranium</i> , <i>Gerbera</i> , <i>Glycine</i> , <i>Hemerocallis</i> , <i>Hypecoum</i> , Iridaceae, <i>Iris</i> , <i>Ixeris</i> , <i>Kalidium</i> , Labiatae, Leguminosae, <i>Lespedeza</i> , <i>Liguliflora</i> , Linaceae, <i>Liquiliflora</i> , <i>Lithospermum</i> , <i>Lysinachia</i> , <i>Macleaya</i> , <i>Medicago</i> , <i>Onobrychis</i> , <i>Orobanche</i> , <i>Oxytropis</i> , Papaveraceae, Papilionaceae, <i>Paraphlomis</i> , <i>Patrinia</i> , <i>Pertya</i> , Polemoniaceae, <i>Polemonium</i> , Polygonaceae, <i>Polygonum</i> , <i>Portulaca</i> , <i>Potentilla</i> , <i>Primula</i> , Primulaceae, <i>Pulsatilla</i> , <i>Rheum</i> , Rosaceae, <i>Rumex</i> , Rutaceae, <i>Salsola</i> , <i>Saussurea</i> , <i>Saxifraga</i> , Saxifragaceae, <i>Scrophularia</i> , Scrophulariaceae, <i>Serratula</i> , Solanaceae, <i>Solidago</i> , <i>Stellera</i> , <i>Suaeda</i> , <i>Thalictrum</i> , <i>Thellungiella</i> , <i>Tribulus</i> , <i>Tubuliflora</i> , Umbelliferae, Urticaceae, <i>Verbascum</i> , <i>Veronica</i> , <i>Viola</i> , Violaceae, <i>Xanthium</i> , <i>Zinnia</i> , Zygophyllaceae, <i>Zygophyllum</i>
eu-dt.fb	Eurythermic drought-tolerant forb	<i>Allium</i> , <i>Allomorpha</i> , Amaryllidaceae, <i>Atriplex</i> , <i>Barleria</i> , <i>Boerhavia</i> , Chenopodiaceae, <i>Chenopodium</i> , Nyctaginaceae
rcfb	Rosette or cushion-forb	<i>Arenaria</i> , Caryophyllaceae, <i>Christolea</i> , Compositae, Leguminosae, <i>Oxytropis</i> , Papaveraceae, Papilionaceae, <i>Rhodiola</i> , <i>Saussurea</i> , <i>Saxifraga</i> , Saxifragaceae
hal	Halophyte	Chenopodiaceae, <i>Chenopodium</i> , <i>Salsola</i> , <i>Suaeda</i> , <i>Thellungiella</i>
hyd*	Hydrophyte	<i>Acorus</i> , <i>Caltha</i> , Haloragidaceae, Onagraceae, <i>Phragmites</i> , Ranunculaceae, <i>Ranunculus</i> , <i>Saururus</i> , <i>Scheuchzeria</i> , Sparganiaceae, <i>Sparganium</i> , Thelypteridaceae, <i>Thelypteris</i> , <i>Thelypteris palustris</i> , <i>Triglochin</i> , <i>Trollius</i>
aq*	Aquatic	<i>Acorus</i> , <i>Alisma</i> , Alismataceae, Araceae, <i>Ceratopteris</i> , <i>Drosera</i> , Droseraceae, Equisetaceae, <i>Equisetum</i> , <i>Equisetum heleocharis</i> , <i>Hydrocharis</i> , Hydrocharitaceae, Isoetaceae, <i>Isoetes</i> , <i>Lemma</i> , <i>Menyanthes</i> , <i>Myriophyllum</i> , <i>Nelumbo</i> , <i>Nuphar</i> , <i>Nymphaea</i> , <i>Nymphaeaceae</i> , <i>Nymphoides</i> , Parkeriaceae, <i>Phragmites</i> , <i>Potamogeton</i> , <i>Potamogetonaceae</i> , Ranunculaceae, <i>Ranunculus</i> , <i>Sagittaria</i> , <i>Salvinia</i> , Salviniaceae, Sparganiaceae, <i>Sparganium</i> , <i>Trapa</i> , <i>Typha</i> , Typhaceae, <i>Utricularia</i>
g	Grass graminoid	Gramineae, <i>Hierochloa</i> , Poaceae, <i>Stipa</i>
s	Sedge graminoid	<i>Carex</i> , Cyperaceae, <i>Cyperus</i> , <i>Dichostylis</i> , <i>Eriophorum</i> , <i>Eriophostylis</i> , <i>Scirpus</i>
r*	Rush graminoid	Juncaceae
geo*	Geophyte	<i>Allium</i> , Amaryllidaceae, Araceae, <i>Arisaema</i> , Convolvulaceae, Cyperaceae, <i>Liliaceae</i> , <i>Lilium</i> , Orchidaceae, <i>Polygonatum</i>
ssuc	Stem succulent	Cactaceae, <i>Euphorbia</i> , Euphorbiaceae
lsuc	Leaf succulent	Aizoaceae, <i>Bryophyllum</i> , Chenopodiaceae, <i>Chenopodium</i> , Crassulaceae, <i>Kalidium</i> , <i>Orostachys</i> , <i>Portulaca</i> , <i>Rhodiola</i> , <i>Sedum</i>
ar.f*	Arctic fern or fern ally	<i>Athyrium</i> , Botrychiaceae, <i>Botrychium</i> , <i>Cystopteris</i> , <i>Lunathyrium</i> , <i>Woodsia</i> , Woodsiaceae
eu.f*	Eurythermic fern or fern ally	Adiantaceae, <i>Adiantum</i> , <i>Aleuritopteris</i> , <i>Allantadia</i> , <i>Asplenium</i> , Athyriaceae, <i>Athyrium</i> , Botrychiaceae, <i>Botrychium</i> , <i>Botrychium lunaria</i> , <i>Coniogramme</i> , <i>Cystopteris</i> , <i>Davallia</i> , <i>Davalliaceae</i> , <i>Dennstaedtia</i> , <i>Dennstaedtiaceae</i> , <i>Dryopteridaceae</i> , <i>Dryopteris</i> , Equisetaceae, <i>Equisetum</i> , <i>Equisetum heleocharis</i> , Filicales, <i>Gonocormus</i> , <i>Gymnopteris</i> , Hymenophyllaceae, <i>Hymenophyllum</i> , <i>Lepidogrammitis</i> , <i>Lepisorus</i> , Lycopodiaceae, <i>Lycopodium</i> , <i>Lycopodium fordii</i> , Lygodiaceae, <i>Lygodium</i> , <i>Lygodium flexuosum</i> , <i>Lygodium japonicum</i> , <i>Lygodium microphyllum</i> , <i>Lygodium microstachyum</i> , Ophioglossaceae, <i>Ophioglossum</i> , <i>Osmunda</i> , Polypodiaceae, <i>Polypodium</i> , <i>Polystichum</i> , Pteridaceae, <i>Pteridium</i> , Pteridophyta, <i>Pteris</i> , <i>Pteris maclurei</i> , <i>Pyrrosia</i> , <i>Salvinia</i> , Salviniaceae, <i>Selaginella</i> , <i>Selaginella sanguinolenta</i> , <i>Selaginella sinensis</i> , Selaginellaceae, Sinopteridaceae, <i>Sinopteris</i> , Thelypteridaceae, <i>Thelypteris</i> , <i>Thelypteris palustris</i> , <i>Woodsia</i> , Woodsiaceae
tr.f*	Tropical fern or fern ally	<i>Acrostichum</i> , <i>Allantadia</i> , Angiopteridaceae, <i>Angiopteris</i> , <i>Antrophyum</i> , <i>Araiostegia</i> , <i>Araiostegia yunnanensis</i> , <i>Arthromeris lehmannii</i> , <i>Belvisia</i> , Botrychiaceae, <i>Botrychium</i> , <i>Ceratopteris</i> , <i>Cibotium</i> , <i>Cibotium barometz</i> , <i>Ctenitis</i> , <i>Cyclosorus</i> , <i>Dicranopteris</i> , <i>Diplazium</i> , <i>Diploplerygium</i> , <i>Drynaria</i> , <i>Gleichenia</i> , <i>Gleicheniaceae</i> , <i>Helminthostachys</i> , <i>Hicriopteris</i> , <i>Histiopteris</i> , Isoetaceae, <i>Isoetes</i> , <i>Lemmaphyllum</i> , <i>Leptogramma</i> , <i>Lindsaea</i> , <i>Loxogramme chinensis</i> , Lygodiaceae, <i>Lygodium</i> , <i>Lygodium flexuosum</i> , <i>Lygodium japonicum</i> , <i>Lygodium microphyllum</i> , <i>Microlepia</i> , <i>Microlepia caudifolia</i> , <i>Monachosorum</i> , <i>Onychium</i> , <i>Ophioderma pendula</i> , <i>Osmunda vachellii</i> , <i>Parathelypteris</i> , Parkeriaceae, <i>Pellaea</i> , <i>Plagiogyria</i> , <i>Plagiogyriaceae</i> , <i>Pseudocyclosorus</i> , <i>Psilotum</i> , Pteridaceae, <i>Pteris</i> , <i>Pteris hainanensis</i> , <i>Pteris subsimplex</i> , <i>Saxiglossum angustissimum</i> , <i>Schizaea</i> , <i>Schizaeaceae</i> , <i>Selaginella bodinerei</i> , <i>Selaginella heterostachys</i> , <i>Selaginella labordei</i> , <i>Selaginella moellendorffii</i> , <i>Vittaria</i> , Vittariaceae
tf	Tree fern	<i>Cyathea</i> , Cyatheaceae
epi*	Epiphyte	Orchidaceae
spa*	Root parasite	Lauraceae, Loranthaceae, <i>Monotropa</i> , <i>Orobanche</i>
m*	Bog moss	Bryaceae, Bryophyta, Dicranaceae, <i>Rhacomitrium</i> , <i>Sphagnum</i>

Table 2

Assignment of plant functional types (PFTs) to biomes used in the biomization procedure in China. The PFT codes are given in Table 1.

Biome name	Code	PFTs
Cold-deciduous forest	CLDE	bo.cd.n.t, eu.e.n.t, bo.cd.mb.t, bo.e.mb.lhs, bo.cd.mb.lhs
Cold evergreen needleleaf forest	CLEG	bo.cd.n.t, bo.e.n.t, eu.e.n.t, bo.cd.mb.t, bo.e.mb.lhs, bo.cd.mb.lhs
Cool-temperate evergreen needleleaf and mixed forest	CLMX	bo.cd.n.t, c-te.e.n.t, eu.e.n.t, bo.cd.mb.t, bo.e.mb.lhs, bo.cd.mb.lhs
Cool evergreen needleleaf forest	COEG	bo.cd.n.t, c-te.e.n.t, eu.e.n.t, bo.cd.mb.t, te-ft.cd.mb.t, bo.e.mb.lhs, bo.cd.mb.lhs
Cool mixed forest	COMX	bo.cd.n.t, c-te.e.n.t, eu.e.n.t, te-ft.cd.mb.t, te-fa.cd.mb.t, bo.e.mb.lhs, te.cd.mb.lhs
Temperate deciduous broadleaf forest	TEDE	te.e.n.t, eu.e.n.t, te-fa.cd.mb.t, te-fi.cd.mb.t, bo.cd.mb.t, te.cd.mb.lhs
Warm-temperate evergreen broadleaf and mixed forest	WTEM	wt.e.n.t, wt.d.n.t, eu.e.n.t, wt.e.sb.t, wt.e.mb.t, wt.cd.mb.t, wt.e.sb.lhs, wt.e.mb.lhs, wt.cd.mb.lhs
Warm-temperate evergreen broadleaf forest	WTEG	wt.e.n.t, eu.e.n.t, wt.e.sb.t, wt.e.mb.t, wt.e.sb.lhs, wt.e.mb.lhs, tf
Tropical semi-evergreen broadleaf forest	TRSE	tr.e.mb.t, tr-m.dd.mb.t, wt.e.n.t, wt.d.n.t, wt.e.sb.t, wt.e.mb.t, tr.e.mb.lhs, tf, tr-dt.lv
Tropical evergreen broadleaf forest	TREG	tr.e.mb.t, tr.e.sb.t, tut, wt.e.n.t, wt.d.n.t, wt.e.sb.t, wt.e.mb.t, tr.e.mb.lhs, tf, tr-dt.lv
Tropical deciduous broadleaf forest and woodland	TRDE	tr-x.dd.mb.t, tr-m.dd.mb.t, g
Temperate xerophytic shrubland	TEXE	ml.t, sl.t, dt.sl.lhs, te-dt.fb, g
Temperate grassland	TEGR	di.sl.lhs, te-dt.fb, eu-dt.fb, g, s
Desert	DESE	ft.ml.lhs, dt.sl.lhs, eu-x.dd.mb.lhs, cs, hal, lsuc, ssuc, g
Cushion-forb tundra	CUSH	rcfb, ar.fb, g
Graminoid and forb tundra	DRYT	ar.fb, g, s
Prostrate dwarf-shrub tundra	PROS	ar.e.mb.pds, ar.cd.mb.pds, ar.fb, g
Erect dwarf-shrub tundra	DWAR	ar.e.mb.pds, ar.cd.mb.pds, ar.e.mb.eds, ar.cd.mb.eds, g, s
Low and high shrub tundra	SHRU	ar.e.n.lhs, ar.e.mb.lhs, ar.cd.mb.lhs, ar.e.mb.eds, ar.cd.mb.eds, ar.e.n.pds, ar.e.mb.pds, ar.cd.mb.pds, g, s

The observed modern biomes were obtained by combining information derived from field observations of vegetation, or from the digitized vegetation map of China at 1:4 million scale (Hou et al., 1982) in cases where there were no field observations. For sites from regions mapped as agricultural vegetation, the modern biome was assessed from its potential zonal vegetation type based on field observations at surrounding sites.

3. Results

3.1. Modern biome reconstruction

The biomes reconstructed from a set of 806 surface pollen samples spanning all biomes and regions of China (Fig. 2a) showed good agreement with observed natural vegetation types (Fig. 2b), both geographically and in terms of the altitudinal gradients in mountain regions (Fig. 3). A numerical comparison across all samples indicated 77.4% agreement between the modern vegetation types and reconstructed present-day biomes (Fig. 2a, b). Our results are based on more surface pollen samples than previous work, discriminate a wider range of biomes, and show a better statistical agreement than was achieved in this earlier work.

Cold-deciduous forest (CLDE), dominated by boreal summergreen trees, occurs naturally in northeasternmost China (mainly in the Daxingan Mountains), but does not occupy large areas and generally occurs in a mosaic with cold evergreen needleleaf forest (CLEG) (ECVC, 1980). These two biomes were reconstructed correctly in 60–80% of cases, but seven samples from CLDE were reconstructed as CLEG, probably due to the mosaic-like distribution of CLDE and CLEG in northernmost China (Table 3). A further seven samples of CLDE were mis-assigned to cool evergreen needleleaf forest (COEG) or cool mixed forest (COMX). Two samples from temperate xerophytic shrubland were reconstructed as CLDE. Two CLEG samples were mis-assigned to prostrate dwarf-shrub tundra (PROS) and COEG, respectively. Four samples from COEG, COMX and temperate grassland were incorrectly assigned to CLEG (Table 3).

Cool-temperate evergreen needleleaf and mixed forest (CLMX) exists south of the area of CLDE and CLEG in northeastern China, but only in very small areas. No pollen surface sample was available from this biome, and none was identified in the biomization procedure. Cool evergreen needleleaf forest (COEG) is mainly distributed in the Daxingan Mountains, moister regions on the Inner Mongolian Plateau in northeastern China, in the high mountains around the northern and eastern periphery of the Tibetan Plateau, and in the Tianshan and Altai Mountains in northwestern China (ECVC, 1980). Eighteen surface samples from this biome were correctly identified; two COEG samples were mis-assigned to shrubland and tundra, respectively. Eleven samples from the cool mixed forest and one sample from warm-temperate evergreen broadleaf and mixed forest were confused with COEG. Eight samples from temperate grassland, four samples from temperate xerophytic shrubland and three samples from erect dwarf-shrub tundra were mis-assigned to COEG (Table 3), probably reflecting long-distance transport of tree pollen to areas near the forest border. Cool mixed forest (COMX) is distributed in the Daxingan and Changbai Mountains of northeastern China, the eastern slope of the Tibetan Plateau, and some high mountains in the central and eastern China (ECVC, 1980). Seventy samples were correctly assigned to this biome (73%). Thirteen samples from the temperate and warm-temperate forests, temperate grassland, shrubland and tundra were also assigned to this biome. Four COMX samples were mis-assigned to temperate deciduous forest, and eight to non-forest biomes (Table 3).

Temperate deciduous broadleaf forest (TEDE) is the potential natural vegetation in areas of eastern central and northeastern China where there is strong human disturbance and most of the potential area of TEDE is now farmland (ECVC, 1980). Nevertheless, twenty-seven surface samples were correctly assigned to TEDE. Thirteen TEDE

samples were mis-assigned to non-forest, as might be expected given the prevalence of agriculture in the region and other anthropogenic impacts on the remaining forest. Two samples derived from warm-temperate mixed forest were incorrectly assigned to TEDE (Table 3). A number of samples from ca 31°N are derived from deciduous and evergreen mixed forests in which temperate deciduous trees form the upper canopy layer (ECVC, 1980). In this study, we do not recognize this vegetation type as a separate biome but have considered these forests to be a subset of TEDE and the samples indeed were reconstructed as TEDE (Fig. 2a).

Warm-temperate evergreen broadleaf and mixed forest (WTEM), in which warm-temperate evergreen trees are dominant but mixed with temperate and warm-temperate deciduous trees, occurs over large areas, including southern and southwestern China (from ca. 31 to 32°N latitude to the Tropic of Cancer), the northern part of Taiwan and at moderate elevations on the eastern part of the southern slope of the Tibetan Plateau (ECVC, 1980). This forest type, together with pure warm-temperate evergreen forest, covers about a quarter of the land area of China (ECVC, 1980). WTEM was correctly reconstructed at 94% of the sites from this biome (133 correct identifications). A small number of WTEM high-elevation samples were assigned to other biomes (Fig. 2a). A few samples from other biomes, notably tropical semi-evergreen broadleaf forest, were incorrectly assigned to WTEM (Table 3). Pure warm-temperate evergreen broadleaf forest (WTEG) occurs in areas with monsoonal summer rainfall around the Tropic of Cancer in southern mainland China and southern Taiwan (ECVC, 1980). This biome was identified correctly in eight samples. Two samples from this biome were incorrectly assigned to tropical semi-evergreen broadleaf forest (Table 3).

Tropical semi-evergreen broadleaf forest (TRSE) occurs in disjunct areas: southernmost Taiwan, Hainan Island, along the southeastern coast of mainland China and small areas of southern Yunnan and Guangxi Provinces (ECVC, 1980). The eight surface pollen samples in the data set from this biome were all incorrectly assigned to WTEM (Fig. 2a, Table 3). However, six of these samples were taken from sites where the regional TRSE vegetation has been degraded to shrublands or dry scrub (Yu et al., 2000). Thus, it is not surprising that we fail to reconstruct TRSE at those sites. One sample from tropical evergreen broadleaf forest however was incorrectly assigned to TRSE (Table 3). Tropical evergreen broadleaf forest (TREG) occurs only in the southeasternmost part of the Chinese mainland, southern Taiwan and central Hainan (ECVC, 1980). There are three surface pollen samples in the data set; two were assigned correctly. The other sample was mis-assigned to WTEM (Table 3). Tropical deciduous broadleaf forest and woodland (TRDE) occurs in disjunct coastal areas on the tropical mainland of China, Hainan and the islands of the South China Sea (ECVC, 1980). We have no surface pollen samples from this biome. One sample from warm-temperate evergreen broadleaf and mixed forest was incorrectly reconstructed as TRDE (Table 3).

Temperate xerophytic shrubland (TEXE) occurs at the ecotone between cool-temperate forests and temperate grassland, and between temperate forests and desert in northern China (ECVC, 1980). Seventy-seven surface pollen samples (78%) were correctly assigned to this biome. Twenty samples from temperate grassland, desert and tundra were mis-assigned to TEXE while 12 TEXE samples were mis-assigned to these biomes (Table 3). Temperate grassland (TEGR) occurs today in northern China and some areas of central China, and is the characteristic vegetation in the semi-arid regions between forest and desert in the east, and between tundra and desert in the west. Temperate grassland also occurs in the Tianshan Mountains and on the southern slope of the Altai Mountains in northwestern China (ECVC, 1980). We obtained a good agreement between the observed and reconstructed biomes, with 148 samples correctly assigned (Table 3), and a good geographic patterning (Fig. 2a). However, there is still some confusion with other non-forest biomes; 17 TEGR samples were mis-assigned to other non-forest biomes and 14 samples from other non-forest biomes were

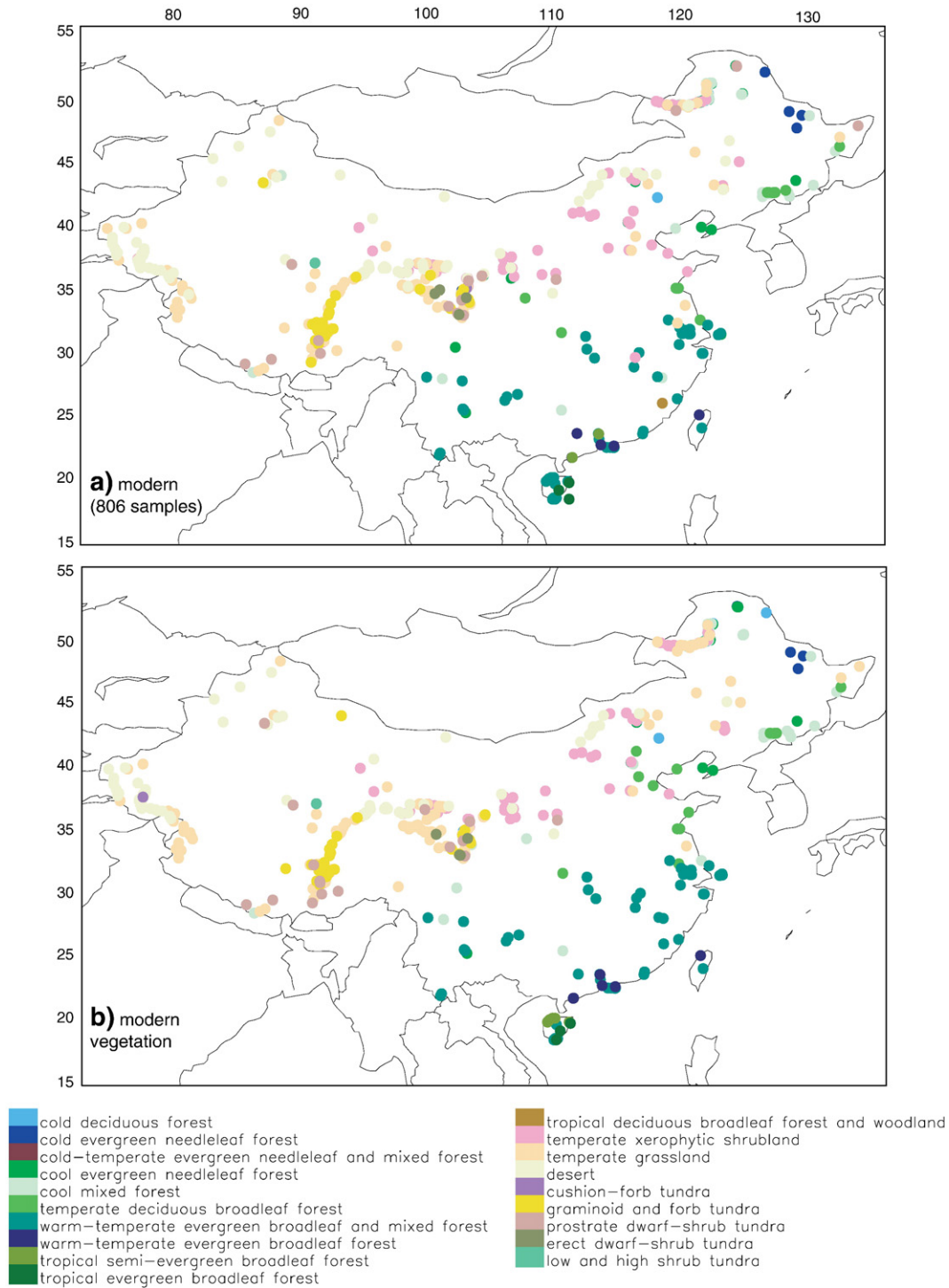


Fig. 2. Biomes reconstructed across all 806 surface pollen samples (a). Present-day vegetation patterns of China (b) were obtained from the digitized vegetation map of China at 1:4 million scale (Hou et al., 1982) with additional information on the observed modern vegetation types provided by the pollen data contributors.

assigned to TEGR (Table 3). Desert (DESE) is found in the temperate areas from central northern China to northwestern and western China (ECVC, 1980). This biome was correctly reconstructed from surface pollen at 72 sites (94%). Four tundra samples were mis-assigned to desert (Table 3).

The most widely distributed tundra biomes in China are the graminoid and forb tundra (DRYT) and prostrate dwarf-shrub tundra (PROS), mainly in the Tibetan Plateau and a few high mountains in central and northwestern China (ECVC, 1980). Other tundra types, the cushion-forb tundra (CUSH), erect dwarf-shrub tundra (DWAR) and

low and high shrub tundra (SHRU) only occupy small areas on the Tibetan Plateau (ECVC, 1980). The geographic patterns of tundra biomes reconstructed from pollen data (Fig. 2a) are in good agreement with the observed patterns (Fig. 2b), and each type is generally correctly identified (Table 3).

The reconstructed biome distribution along the altitudinal gradients in seven high regions of mountain and plateau (Fig. 3) are reasonable. The Daxingan Mountains are located in northeastern China, where grassland and shrubland occur at lower elevations and forests at higher elevations. The reconstructions show temperate xerophytic shrubland

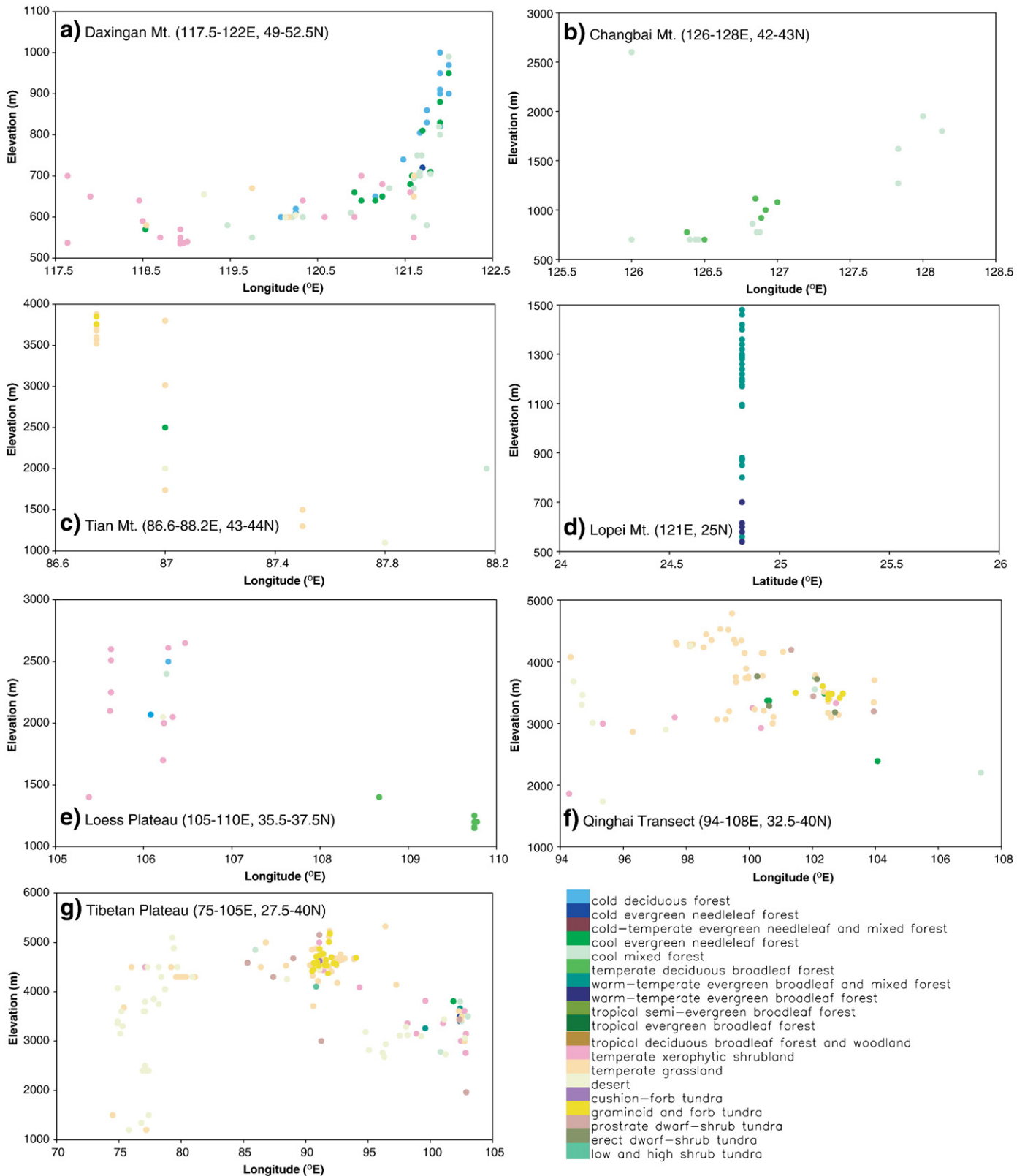


Fig. 3. Surface pollen-based biomes along altitudinal gradients in the mountain ranges: (a) Daxingan Mountains, (b) Changbai Mountains, (c) Tianshan Mountains, (d) Lopei Mountains, (e) Loess Plateau, (f) Qinghai Transect, and (g) Tibetan Plateau.

and temperate grassland around 500–700 m, cool mixed forest from 600 to 800 m and cool evergreen needleleaf forest and cold-deciduous forest from 650 to 1000 m (Fig. 3a). In the Changbai Mountains in northeastern China, the reconstructions show temperate deciduous forest associated with cool mixed forest below 1200 m, but only cool

mixed forest above 1500 m (Fig. 3b). The Tianshan Mountains in northwestern China have desert below 2000 m, temperate grassland from about 2000 to 4000 m, deciduous and evergreen needleleaf forests between 2000 and 2500 m, and graminoid and forb tundra above 3700 m (Fig. 3c). There are no high mountains in southern China. In the

Table 3 Comparison between observed modern vegetation types and biomes reconstructed using the 806 surface pollen samples from China. The biome codes are given in Table 2.

Observed biomes	Reconstructed biomes																	Total	% correct predictions			
	CLDE	CLEG	CLMX	COEG	COMX	TEDE	WTEM	WTEG	TRSE	TREG	TRDE	TEXE	STEP	DESE	CUSH	DRYT	PROS			DWAR	SHRU	
CLDE	18	7		2	5												1			32	56	
CLEG		10		1																	12	83
CLMX																					0	–
COEG		1		18								1	2				1				21	86
COMX		2		11	70	4						4	2			1					95	74
TEDE				1	1	27						9	3				1				41	66
WTEM				1	1	2	133	1		1	1	1									141	94
WTEG							1	8	2												11	73
TRSE							8			2											3	67
TREG							1														0	–
TRDE																					3	67
TEXE	2			4	3							77	7	4	1						98	79
STEP		1		8	6						14	148	10			4	2	1			194	76
DESE					1						1	2	72								76	95
CUSH											1	1	1		1	2					5	20
DRYT											1	8	3		26	2					40	65
PROS											3	3	3	1	4	4	10				21	48
DWAR				3	1													3			7	43
SHRU																			1	1	1	100
Total	20	21	0	48	88	33	143	9	2	3	1	112	174	90	2	37	18	4	1	1	806	

moderately high mountains of Taiwan (Lopei Mountains), warm-temperate evergreen forest occurs below 700 m and warm-temperate mixed forest between 800 and 1500 m (Fig. 3d). The Loess Plateau in central China lies in a transitional vegetation zone between forest and temperate grassland. Temperate xerophytic shrubland is mostly found at elevations from 1500 to 2700 m and temperate deciduous forest in a few low-elevation sites, around 1200 m (Fig. 3e). Cold-deciduous forest and cool mixed forest are found above 2000 m (Fig. 3e). The Qinghai Transect in the northern slope of the Tibetan Plateau has temperate grassland, shrubland and dry tundra (graminoid and forb) from 3000 to 5000 m with a few needleleaf and deciduous forests less than 3500 m (Fig. 3f). The geographic patterns of reconstructed biomes on the Tibetan Plateau are more complex than in other mountain regions because of the greater climatic diversity of Tibet (Fig. 3g). The biomes between 74 and 82°E are mostly temperate grassland and desert from 1000 m to 5000 m (Fig. 3g). From 85 to 95°E, graminoid and forb tundra and prostrate dwarf-shrub tundra occurred at elevations from 4200 to 5500 m (Fig. 3g). The shrubland, desert, cool mixed forest and evergreen needleleaf forest, however, occupied the eastern part of the plateau between 95 and 103°E in longitudes from 2800 to 4000 m (Fig. 3g).

3.2. Biome reconstruction for MH

The application of the same biomization procedure to the MH data set showed coherent patterns of changes in biome distribution (Fig. 4a). The distribution of cold forests in northeastern China was very different in the MH (Fig. 4a) compared to today (Fig. 2). Cold-deciduous forest was not present in the region. The single CLDE in the modern vegetation was reconstructed as COMX in MH. COMX and CLMX replaced CLEG in northeastern China in the MH and only one site of CLEG was found in far northeastern China (Fig. 4a). Two sites of CLDE and two sites of CLMX in central northern China and northwestern China occurred in the semi-arid and arid environments (Fig. 4a), where grassland, desert or xerophytic shrubland occur in the modern vegetation (Fig. 2a, b). The 6 ka reconstruction suggests that the cold and cool-temperate deciduous and mixed forests were shifted northward in northeastern China (ca. 3–5° in latitude) and shifted westward (ca. 2–3° in longitude) in central northern China during the MH.

Cool evergreen needleleaf forest and cool mixed forest in the MH occupied some sites where CLEG and grassland occur at present in northeastern China (Fig. 4a). Several sites of COEG at present also have been occupied by the COMX and TEDE in the MH along the border between China and Korea (Fig. 4a). Some, though by no means all, of the sites in central and southern China, which are cool-temperate forests today (Fig. 2a, b), were assigned to WTEM and TEDE in the MH (Fig. 4a). Thus the data show that cool-temperate forests were also shifted northward (1–2° in latitude) during the MH, although the latitudinal shift appears to have been less than shown by cold forests.

The northern limit of temperate deciduous forest in eastern China was ca 5°N of its modern position in the MH (Fig. 4a). Several sites in northeastern China which lie in COMX today were reconstructed as TEDE in the MH (Fig. 4a). The southern limit of TEDE in eastern and central China was shifted to the north in MH. A few sites in the modern grassland region (Fig. 2a, b) were assigned to TEDE in the MH (Fig. 4a), suggesting somewhat moister conditions prevailed.

Subtropical China was characterized by warm-temperate evergreen broadleaf and mixed forest in the MH (Fig. 4a). Two sites around 34–35°N (Lianyungang and Qingfeng), which lie in the temperate deciduous forest belt at present, were reconstructed as WTEM in the MH. This indicates a moderate northward shift (ca. 2° in latitude) of the northern limit of this biome. Several sites along the Tropic of Cancer that lie within WTEG today were reconstructed as WTEM during the MH (Fig. 4a). This indicates that the southern limit of WTEM may have been further south than today during the MH.

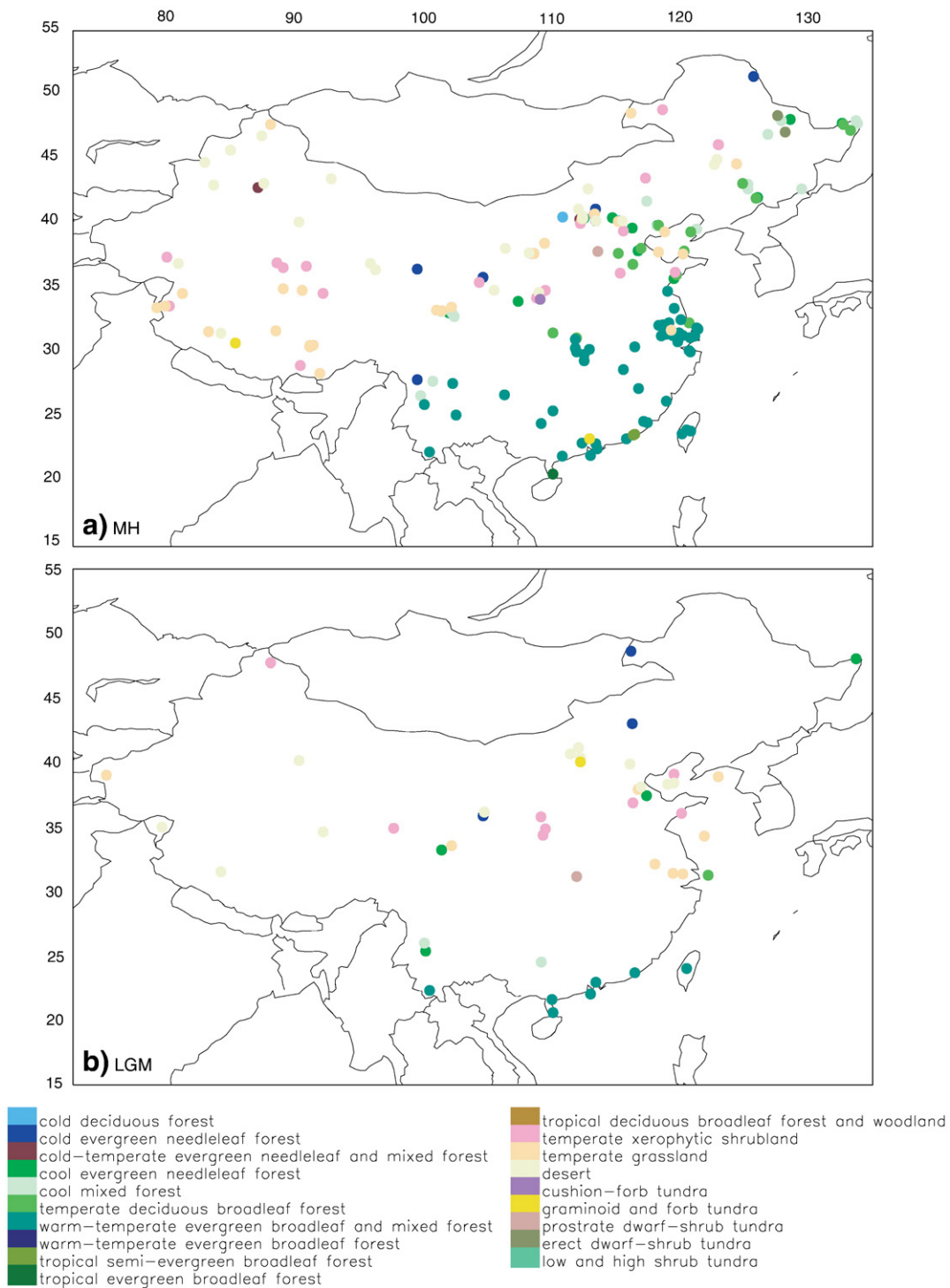


Fig. 4. Biomes in the MH (a) and at the LGM (b) reconstructed from pollen records in China.

There are no sites assigned to WTEG in MH. This may reflect the fact that there is a large sampling gap in central-eastern China (Fig. 4a). The extent of tropical forests appears to have been even more restricted in the MH than today. TRSE did apparently expand north along the southeastern coast at the MH (Fig. 4a) but any inference from this should be viewed with caution, because there is only one site showing this change, and given that some tropical forest samples were misclassified as WTEM in the modern vegetation reconstruction (Fig. 2, Table 3).

TEXE showed no large changes in northern China, but in northeastern China TEXE replaced temperate grassland or desert. A few sites in eastern China (the Shandong Peninsula) were also reconstructed as TEXE. However, TEXE on the Tibetan Plateau in the MH occupied some sites where tundra or desert is found today (Fig. 4a). Otherwise, the geographic patterns of temperate grassland and desert in northern China in the MH did not change much (Fig. 4a) compared to present (Fig. 2a), but some temperate grassland and desert locations showed forest or shrubland in MH (Fig. 4a). On the Tibetan Plateau, however,

most of the PROS and DRYT sites were occupied by temperate grassland and TEXE in the MH (Fig. 4a). Only six tundra sites were reconstructed in the MH on the Tibetan Plateau (Fig. 4a). Comparison of tundra distribution on the Tibetan Plateau between 6000 years ago and present indicates a reduced area in the MH.

There are insufficient samples to document changes in vegetation belts along altitudinal transects in the MH. However, reconstructions at a few sites (Qinghai Lake, Nabahai, Wasong, Luoqu, Hongyuan and RM-F) on the eastern and southeastern slope of the Tibetan Plateau suggest that cold and cool-temperate forests occurred at ca. 3200–3500 m, indicating that the treeline was ca. 300–500 m higher than today.

3.3. Biome reconstruction for LGM

The reconstruction of LGM biomes using the same biomization procedure also showed relatively coherent patterns of biome distribution in China although the number of sites is limited (Fig. 4b). CLEG is present in northern China at the LGM with a southward shift of the southernmost margin of ca. 3° in latitude compared to today. One site of COEG was found about 33°N in latitude in eastern China, 3–4° further south than this vegetation occurs today. COMX occurred in southern China. TEDE was not represented at any of the sites in eastern mainland China, although it is present at a single site (31.2°N) on the exposed continental shelf. WTEM was restricted to the coastal area of mainland southern China, indicating a southward shift of the northern margin of this biome of 10° latitude compared to today. WTEG and tropical biomes were not found at any of the sites. TEXE, temperate grassland and desert occurred significantly further east than today, occupying most of the region dominated by TEDE at present. TEXE, temperate grassland and (most importantly) desert were found on the Tibetan Plateau; no tundra was identified there, but tundra was found at two sites in central China (Fig. 4b).

4. Discussion

4.1. Pollen data

This study is based on pollen records from an older version of the Chinese Pollen Database (CPD), supplemented by new data assembled by the first author for this study. Data quality of both pollen records and radiocarbon dating were generally well controlled, but some problems still exist in the CPD. More pollen data have been recently published, or will be published, and new data collection is still desirable for some regions. Since the present biomization study we have further updated the data set, which now includes more than 2300 surface pollen samples and more than 350 fossil records. Vegetation changes are being reconstructed at 500–1000 year intervals from the LGM onwards, in order to evaluate space–time patterns of past vegetation and climate.

4.2. PFTs

We adopted a PFT scheme based on principles discussed by Harrison et al. (in preparation, 2009) thus making the classification explicit (in terms of plant characteristics) and globally consistent. Nevertheless, many of the 53 PFTs used in this biomization are broadly equivalent to the PFTs used in the earlier biomization by Yu et al. (2000). For example the PFT called here “boreal evergreen needle-leaved tree (bo.e.n.t)” is equivalent to the PFT called “bec” by Yu et al. (2000). Similarly, the PFT called here “boreal cold-deciduous malacophyll broad-leaved tree (bo.cd.mb.t)” is equivalent to the PFT called “boreal summergreen (bs)” by Yu et al. (2000). Some of the PFTs used by Yu et al. (2000) represent an amalgamation of two (or more) PFTs in the current scheme. For example, the PFT “warm-temperate broad-leaved evergreen (wte)” used by Yu et al. (2000) represents four

PFTs: “warm-temperate evergreen sclerophyll broad-leaved tree (wt.e.sb.t)”, “warm-temperate evergreen malacophyll broad-leaved tree (wt.e.mb.t)”, “warm-temperate evergreen sclerophyll broad-leaved low and high shrub (wt.e.sb.lhs)”, and “warm-temperate evergreen malacophyll broad-leaved low and high shrub (wt.e.mb.lhs)” in this study. Some PFTs represented in the current scheme were not used in the previous biomization by Yu et al. (2000). Stem succulents and leaf succulents were not recognized as PFTs by Yu et al. (2000), for example, but are characteristic of desert vegetation and are used in the current study. Other PFTs, including most of the low and high shrub, dwarf-shrub and liana/vine PFTs used in the current biomization were subsumed under tree PFTs in Yu et al. (2000). Similarly, the climber PFTs used in this study were included in forbs by Yu et al. (2000).

The successful reconstruction of Chinese biomes today, in MH and at LGM based on pollen data and the biomization technique suggests that the new global scheme of PFTs provides a useful basis for vegetation classification and mapping. The new PFT scheme appears to provide a more robust way of distinguishing non-forest biomes than previous schemes. Yu et al. (1998) – working with restricted list of taxa – distinguished deserts from steppe partly on the basis of defining *Artemisia* as characteristic of steppe and *Chenopodiaceae* of desert, which is somewhat artificial although it does reflect a trend in their abundance. Yu et al. (2000) used a larger set of taxa to differentiate desert and steppe by classifying the taxa as typical steppe forb/shrub (e.g. *Artemisia*, *Ajania*, *Filifolium*, and *Iris*), and as typical desert forb/shrub (e.g. *Chenopodiaceae*, *Alhagi*, *Ephedra*, *Nitraria*, *Tamarix*, and *Zygophyllum*). In this study, the PFT classification for shrubland, grassland and desert is more explicit and quite different from Yu et al. (1998, 2000). We used the small-leaved trees and micro-leaved trees to separate shrubland from grassland and desert, and small-leaved shrubs, micro-leaved shrubs, xeric shrubs and succulents to separate desert from shrubland and grassland (Table 2). The five tundra biomes were also successfully distinguished, mainly by the erect dwarf-shrubs and prostrate dwarf-shrubs (Table 2).

However, our results show that some issues could be usefully re-examined in future applications of the global scheme. For example, ecologists generally subdivide the evergreen broadleaf forests of subtropical China into four vegetation zones (from north to south): the warm-temperate evergreen and deciduous mixed forest, which is an ecotone between the temperate deciduous forest and the warm-temperate evergreen forest; northern evergreen and mixed forest; middle evergreen and mixed forest; and southern evergreen forest, which is a transitional type from subtropical to tropical vegetation (ECVC, 1980). These subzones correspond to four major forest types: the warm-temperate evergreen and deciduous (temperate) broadleaf mixed forest, warm-temperate evergreen broadleaf and mixed forest, warm-temperate pure evergreen broadleaf forest, and warm-temperate sclerophyll evergreen broadleaf forest (ECVC, 1980). We were unable to differentiate these four zones on the basis of the pollen data using the current PFT scheme. Many of the taxa (e.g. *Castanopsis*, *Cyclobalanopsis*, *Lithocarpus*, and *Schima*) as characteristic of the warm-temperate broadleaf and mixed forests have leaves that are physically intermediate between malacophyll and sclerophyll (i.e. coriaceous leaves). This intermediate category does not exist in the current PFT scheme, and as a result we allocated these taxa either to malacophyll (*Schima*) or to both malacophyll and sclerophyll (*Castanopsis*, *Cyclobalanopsis*, and *Lithocarpus*) PFTs with a consequent loss of discriminatory power. It is possible that a better discrimination of subtropical biomes could be achieved by recognizing coriaceous-leaved trees (and also coriaceous-leaved shrubs) as separate PFTs.

The assignment of taxa to PFTs is in principle unique because it is based on the biological characteristics of the taxa and their bioclimatic ranges. The definition of biomes in terms of PFTs, however, is not unique. We tried initially to define biomes on the basis of all the PFTs present. Thus, forest biomes were defined using not only tree PFTs but also the shrubs, lianas/vines, forbs, graminoids and ferns PFTs that

characterize the understory. The reconstructed biomes and patterns were not realistic, largely because secondary PFTs in the forest understory had too much influence in the biomization procedure. Some pollen sites in the temperate broadleaf forest biome, for example, include significant amounts of pollen from taxa (such as *Compositae*, *Chenopodiaceae* and *Artemisia*) which also exist in shrubland, grassland and desert biomes. If the temperate forb PFT is used to define the temperate forest biome, these forest sites would be mis-assigned to non-forest. Therefore, in the end only the dominant tree PFTs and some of the more highly characteristic elements of the secondary PFTs were used to define forest biomes (Table 2).

4.3. Biomes

The biome classification used is globally applicable and allows straightforward comparison of biome reconstructions among regions and continents. It could be improved, however, e.g. to allow greater discrimination within the warm-temperate forest, grassland and desert biomes.

4.4. Biome reconstructions

The maps of observed and reconstructed biomes (Fig. 2a, b) show a high level of similarity, and numerical comparisons at individual sites suggest that it is possible to reconstruct most biomes accurately (Table 3). Our analyses suggest that non-forest biomes are as easily distinguished from one another as forest biomes using the current methodology. Thus 79% of all forest-derived samples are correctly assigned and 76% of all non-forest samples. These results are not materially affected by the limited use of digitized samples (38 samples) in the modern data set.

Mis-allocations of samples derived from forest biomes appear to be due to a small number of readily-identifiable causes. Some regions are characterized by mosaic-like arrangements of one or more biomes, each of which occupies relatively small, disjunct areas. The distribution of CLDE and CLEG in northernmost China provides an example of this mosaic-like distribution. In such regions, it is possible that our observed biome assignment (which is derived from a relatively coarse-scale mapping of Chinese vegetation) may not accurately represent the vegetation at a specific site. We do not believe that this is the explanation in the present case, however, because although some CLDE samples are incorrectly attributed to CLEG in the biomization procedure, no CLEG samples are incorrectly attributed to CLDE (Table 3). Rather we suggest that in areas characterized by mosaic-like mixtures of biomes, pollen transport results in some blurring of the signal at sites close to the margin of the different biomes. A similar explanation likely holds for the misattributions of tropical forest types (TREG, TRSE) to warm-temperate forests (WTEM), since the tropical forest types have disjunct distributions and are confined to relatively small areas in close proximity to the more extensive warm-temperate forests, and the forests are around some sites are degraded.

In mountain regions, there is a tendency for samples to be allocated to forest biomes which occur at lower elevations than the sample site. This phenomenon of upward transport of pollen to higher elevations in mountain regions has been noted in the previous biomization of data from China (Yu et al., 2000) and was convincingly demonstrated as the major cause of mis-allocations of samples in Japan (Takahara et al., 2000).

Long-distance transport of arboreal pollen into non-forested regions has been widely recognized as a cause for the mis-allocation of samples from tundra, desert and grassland regions to forest and/or woodland biomes in previous biomizations (e.g. Edwards et al., 2000; Tarasov et al., 2000; Yu et al., 2000). Of the 65 samples from tundra, desert and grassland in the modern Chinese data set that are incorrectly assigned, 34% are attributed to shrubland or forest biomes (Table 3) as a result of long-distance pollen transport. The fact remains that this does not

seem to be the biggest cause of the mis-assignment of samples from these biomes. Rather, most (66%) of the mis-assigned samples are mis-assigned to other non-forest biomes.

In general our analyses of the biomization of modern samples from China suggest that the current scheme is likely to yield reasonably good reconstructions of the broad-scale patterns of palaeovegetation, and particularly large-scale shifts in biomes in non-mountainous regions (Fig. 4). This work has the advantage of making the palaeovegetation patterns clearer than previous ones (e.g. Yu et al., 1998, 2000), although the changes of vegetation in MH and at the LGM are similar to Yu et al. (2000). Some misclassifications of modern biomes should be carefully treated when exploring the past vegetation changes. For example, the mis-assignments of tropical forests to warm-temperate forests might affect the explanation of southward expansion of warm-temperate forests in MH (Fig. 4a) and the interpretation of past climate changes (see Section 4.5).

4.5. Implication of palaeoclimates

The forest zonation from boreal deciduous forests to tropical rain forests in eastern China parallels the north–south gradients of temperature and precipitation (ECVC, 1980). Winter temperatures are decisive in determining the global distribution of major woody plant types (Prentice et al., 1992a). The significant northward shifts of the cold and cool-temperate evergreen needleleaf and mixed forests, temperate deciduous forest, warm-temperate evergreen broadleaf and mixed forest in eastern China, and the disappearance of cold-deciduous forests in northeastern and central China in the MH (Fig. 4a), imply that winters were warmer than today. The southward expansion of warm-temperate evergreen broadleaf and mixed forest into regions characterized today by tropical forests implies likely colder winter conditions. Thus, in northern China the vegetation changes imply warmer conditions while in southern China they suggest a slight cooling. The reduction in the area of tundra on the Tibetan Plateau suggests a larger accumulated temperature sum during the growing season than today.

The seasonal and spatial patterns of temperature changes implied by our reconstructions are consistent with previous vegetation-based estimates of the mid-Holocene climate (Shi et al., 1993; Yu et al., 2000). However, some aspects of these patterns are difficult to explain. The increase in the accumulated temperature sum during the growing season, implied by the reduction in tundra area, is consistent with increased insolation during the summer half-year due to orbital changes (Berger, 1978). Similarly, the southward expansion of warm-temperate forests is consistent with the orbitally-induced reduction in winter insolation. However, the winter warming indicated by the northward migration of temperate, cool and cold forests is opposite to what is expected from direct radiative forcing. Yu et al. (2000) suggested that this indicates that winter temperature changes were mediated by changes in atmospheric circulation. The nature and cause of such circulation changes is unresolved. Neither atmosphere-only climate models (Harrison et al., 1998) nor coupled ocean–atmosphere models (Braconnot et al., 2004) produce winter warming in central and northern eastern China. Vegetation-feedback has been shown to offset orbitally-induced changes in insolation and produce winter warming in northern Africa (Broström et al., 1998; Kutzbach et al., 2001). Whether observed MH vegetation changes in China were sufficiently large to have a similar impact on winter climates needs to be investigated.

The longitudinal transition from forests to grassland and desert in northern China is controlled by moisture availability. The westward shifts of the forest–shrubland–grassland and grassland–desert boundaries imply increased moisture availability in the MH compared to today. However, a few sites in central-eastern China of temperate xerophytic shrubland, temperate grassland and desert occupied a small part of the temperate deciduous forest in the MH (Fig. 4a), indicating a drier local habitat.

The expansion of the summer monsoon, implied by the westward shifts in the forest–shrubland–grassland and grassland–desert boundaries, has been inferred from several other lines of evidence. The reduction in loess accumulation rates and the increased tendency towards soil formation on the Chinese Loess Plateau during the MH (Sun et al., 2000), for example, has been attributed to increased monsoonal precipitation (An et al., 2000). Similarly, lake-level records from China (Yu et al., 2001a) show conditions considerably wetter than today on the Tibetan Plateau, over much of western China, as well as at the modern northern limit of the temperate deciduous forest (35–40°N). The lake-level data are consistent with the reconstructed expansion of grassland and shrubland at the expense of dry tundra on the Tibetan Plateau. Furthermore, increased moisture in the latitude band between 35 and 40°N in eastern China may well have contributed to the observed MH expansion of the temperate deciduous forest, which is believed to be partially limited by drought today as a result of high precipitation seasonality (Zhang and Yang, 1993). The expansion of the monsoon into western China implied by the lake-level data appears to be very much larger than the change implied by the vegetation. The reason for this difference between the two environmental indicators is unclear. The lake-level data suggest that the MH was somewhat drier than today in southeastern China. Our data provide no evidence of drier conditions in the southeast, but this probably reflects the fact that the vegetation of this region is more sensitive to changes in winter temperature than to the moderate decreases in precipitation indicated by the lakes.

In contrast to the comparatively modest changes in vegetation patterns in the MH, the reconstructed LGM vegetation patterns are radically different from today. Tropical forests were apparently absent from the mainland of southern China, or at least sufficiently restricted not to be identifiable at any of the available sampling sites. Warm-temperate evergreen and mixed forest was confined to the southernmost part of eastern China. The northern boundary of this biome appears to have been at least 6° south of its modern position (Fig. 4b). The near-disappearance of tropical forests and the restricted distribution of the warm-temperate forests imply minimum temperatures considerably colder than today in southern China. The replacement of tropical forests by warm-temperate forests may imply a reduction of the mean temperature of the coldest month (MTCO) by as much as 10 °C in southern China (see e.g. Farrera et al., 1999). Colder conditions are also implied by the fact that northern forests, specifically cold temperate and cool-temperate forests, are registered at sites far south of their modern location. There are too few sites from northern China to be sure whether these forests occurred as continuous belts (similar to today) or whether the northern forests were not only displaced southward but reduced in extent and fragmented. The existence of generally colder conditions across China is supported by records of the increased extent of permafrost and the expansion of mountain glaciers in western China and Tibet (Wang and Jiao, 1989; Han et al., 1993; Shi et al., 1998).

The most striking difference between the modern and LGM vegetation patterns is the apparent absence or strong restriction of temperate deciduous forests in eastern China and the significant expansion of non-forest biomes to occupy the mid-latitudes of eastern China and much of the exposed continental shelf. Temperate deciduous forest, which today occupies the zone between ca 32 and 45°N in eastern China, was reconstructed at only a single site (East China Sea Ch1 core) on the exposed continental shelf at ca 31°N. Lack of data from the zone between 25 and 30°N makes it difficult to be certain that the temperate forests were not displaced far south of their modern position, in response to the cooling shown by the displacement of other kinds of forests. However, the widespread occurrence of non-forest biomes in eastern China indicates that the colder conditions were accompanied by a greatly increased in aridity; this suggests an alternative explanation for the apparent absence of the temperate forests. Increased aridity in the mid-latitudes of central and

eastern China is supported by evidence for widespread loess deposition (Liu et al., 1986; Kohfeld and Harrison, 2003), and increased export of Asian dust to Greenland (Biscaye et al., 1997).

Our LGM data set includes more sites than were available to Yu et al. (2000) but nevertheless the reconstructed LGM vegetation patterns (Fig. 4b) are similar to those shown by Yu et al. (2000). The encroachment of non-forest biomes on the present area of temperate forests in eastern China is a conspicuous feature of the LGM vegetation as presented by Yu et al. (2000) and here. Although the available data are still geographically sparse (so that, for example, the existence of pockets of temperate forest in unsampled areas of eastern China remains a possibility), the overall tendency is unambiguous and differs sharply from earlier maps of the LGM vegetation of China in which temperate forests were shown occupying large unbroken areas of eastern China extending across the exposed continental shelf to the Japanese islands (see e.g. CLIMAP, 1981; Adams et al., 1990; Crowley, 1995; Adams and Faure, 1998). These earlier reconstructions were based on extrapolation from an even more limited amount of data or, in the case of the Adams et al. (1990) and Adams and Faure (1998) reconstructions, on combining a very little pollen information with indirect inferences about the vegetation based on non-biological proxies. It is not surprising that more extensive data compilations show different patterns. However, these differences could have serious consequences. The absence of a continuous temperate forest zone suggested by our reconstruction, for example, argues against the idea put forward by Qian and Ricklefs (2000) (on the basis of the CLIMAP (1981) vegetation map) that the species-rich character of the Asian temperate flora was a result of increased speciation through mixing of forest populations during glacial intervals (Harrison et al., 2001). Similarly, the replacement of temperate forests by non-forest biomes in our reconstruction implies that estimates of LGM terrestrial carbon storage (e.g. Adams et al., 1990; van Campo et al., 1993; Crowley, 1995; Peng et al., 1995; Adams and Faure, 1998) based on earlier reconstructions need to be revised. There are only four sites from the Tibetan Plateau at the LGM. Nevertheless, three of these sites show desert conditions at the LGM (Fig. 4b), rather than grassland or tundra which is more characteristic of the vegetation on the Plateau today (Fig. 2). These data seem to suggest that conditions were drier than today, a view put forward by previous studies of the vegetation of the region (e.g. Kong et al., 1996). However, geomorphic and biostratigraphic data from the Tibetan Plateau suggest that the lakes were higher at the LGM than today (Yu et al., 2001b) implying less arid conditions. The co-existence of drought-tolerant vegetation and high lake levels is theoretically possible, given a markedly seasonal precipitation and temperature regime (see e.g. Prentice et al., 1992b). However, given the difficulties in distinguishing reliably between different kinds of non-forest vegetation using the biomization technique, and the fact that we have no modern reconstruction from two of the LGM sites and so cannot be sure how far the LGM signal reflects a real change in vegetation, it seems unnecessary to invoke a fundamental change in the climate of the Tibetan Plateau to explain our vegetation reconstructions.

Acknowledgements

This study was supported through grants from the National Natural Science Foundation of China (NSFC 30590383 and 39700018), German Research Foundation (DFG SPP 1266), Alfried Krupp von Bohlen und Halbach-Stiftung, Max Planck Society (MPG), Max Planck Institute for Biogeochemistry (MPI-BGC) and the China Scholarship Council (CSC). We thank many palynologists and ecologists for providing the Chinese pollen data: Yong-Li Cai, Xudong Chen, Huiyou Han, Cixuan Huang, Manhong Ke, Zhaochen Kong, Baosheng Li, Pingri Li, Rongquan Li, Shengfeng Li, Wenyi Li, Pingmei Liew, Guangxiu Liu, Junfeng Liu, Qingsi Liu, Kam-Biu Liu, Weili Qiu, Guoyu Ren, Changqing Song, Xiangjun Sun, Lingyu Tang, E. Van Campo, Manhua Wang, Qizhong Wen, Yumei Xia,

Jiasheng Xu, Qinghai Xu, Shun Yan, Xiangdong Yang, Ji Zhao, Zhuo Zheng, and Cheng Zhu. Special thanks to Yong-Li Cai (Department of Geography, East China Normal University, Shanghai), Cixuan Huang (Institute of Geography, Chinese Academy of Sciences (CAS), Beijing), Zhaochen Kong (Institute of Botany, CAS, Beijing), Pingri Li (Institute of Geography, Guangdong Academy of Sciences, Guangzhou), Junfeng Liu (Department of Geography, Xianyang Teachers College, Xianyang), Manhua Wang (Department of Geography, Yantai Normal College, Yantai), Qizhong Wen (Guangzhou Institute of Geochemistry, CAS, Guangzhou), Yumei Xia (Changchun Institute of Geography, CAS, Changchun), and Qinghai Xu (College of Resource and Environment, Hebei Normal University, Shijiazhuang) for providing new pollen records.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2010.02.008.

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