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Quantifying modern biomes based on surface pollen data in China

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ABSTRACT

Large-scale surface pollen records and reconstructions of modern biomes are a necessary prerequisite for the understanding of past vegetation and climate changes, especially in large countries such as China which is subject to a variety of climatic regimes and has experienced long-term intensive anthropogenic disturbances. An updated surface pollen data set consisting of 2324 samples and 737 taxa is used to reconstruct biome distribution in China according to a newly established and well-tested global classification of plant functional types, based on the regional assessment of pollen taxa and the quantitative pollen-biome assignment method of biomization. Nineteen reconstructed types of biome present a reasonable reflection of the latitudinal and altitudinal distributions of modern vegetation in China. Incorrect assignment has previously occurred in some biomes, for example among the cold and cool temperate coniferous forests and mixed forest, among warm-temperate evergreen forest, mixed forest and tropical forests, and among temperate shrubland, grassland, desert and tundra biomes. Mega-biomes, grouped for the same bioclimatic zones, result in a better reconstruction than the nineteen separate biome types. The correct assignments increased from 68.8% to 80.6%. However, comparison of pollen-based biome reconstructions to climate-driven vegetation simulations performed using the global vegetation model BIOME4 indicates a low correlation rate (only 24.8%), suggesting that more needs to be done to combine palaeoenvironmental data with model simulations of past vegetation changes. The misassignment of surface pollen to modern biomes usually occurs in areas which have similar bioclimatic features and vegetation types and for biomes which share the same plant functional types. These mis-matches often occur in mountainous regions where transitional vegetation zones occur on hill slopes at mid-altitudes. Our new modern biome reconstruction for China is more robust and reliable; however continued analysis of pollen records is required in the remote areas of western China and the Tibetan Plateau, as well as in regions of central and eastern China which have suffered from high levels of anthropogenic activity. This type of anthropogenic biome reconstruction presents a new challenge.

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1. Introduction

Modern pollen assemblages, related to the current distribution of vegetation, land use and climate, provide a framework for inferring spatial and temporal variations in palaeovegetation and palaeoclimate from fossil pollen records (e.g. Overpeck et al., 1985; Prentice, 1985; Gajewski et al., 2002; Whitmore et al., 2005; Watrin et al., 2007). Modern pollen records, especially across broad regions, are therefore very useful for evaluating current pollen-vegetation relationships and for calibrating reconstructions of past vegetation and climate. In local and regional studies, modern pollen are closely related not only to vegetation and climate, but also to anthropogenically induced land use (e.g. Gaillard et al., 1994, 2008; Hjelle, 1999; Broström et al., 2004;

Court-Picon et al., 2006). However, at extra-regional and continental scales, analysis of the distribution of modern pollen taxa is more focused on vegetation-pollen-climate relationships (e.g., Anderson et al., 1991; Gajewski et al., 2002; Whitmore et al., 2005; Watrin et al., 2007; Minckley et al., 2008), on pollen-vegetation relationships (e.g. Newsome, 1999; Markgraf et al., 2002; Ma et al., 2008) and on pollen-climate relationships (e.g. Seppä et al., 2004; Finsinger et al., 2007). These studies are all based on statistical approaches used to investigate pollen distributions and to reconstruct past changes in vegetation and climate. Less attention is paid to the impact of large-scale land use change on modern pollen spectra (Liu et al., 2006, 2008).

The quantitative reconstruction of the large-scale geographical distribution of vegetation from pollen data using the concept of plant functional types (PFTs) is a commonly accepted method called 'biomization' (Prentice et al., 1996; Prentice and Webb, 1998). Continental and modern global biomes that can be used to compare and validate past vegetation changes during the mid-Holocene and at

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the last glacial maximum have been reconstructed from modern pollen records worldwide (see [Prentice et al., 2000](#), and papers from two Special Features of *Journal of Biogeography* in 1998 and 2000, for the northern Hemisphere and Africa). Modern pollen-based large-scale biome reconstructions have recently been extensively compared to natural vegetation in, for example, SE Asia, Australia and the Pacific ([Pickett et al., 2004](#)), Africa ([Vincens et al., 2006](#); [Lebamba et al., 2009](#)), Latin America ([Marchant et al., 2009](#)) and Indian Continental (Sutra et al., unpublished). However these comparisons used potential modern biomes, i.e. by assigning vegetation types based on field observations and from various vegetation maps of natural biomes (all cultivated vegetation types were assigned to potential natural biomes in the same bioclimatic zones) in order to compare to the reconstructed biomes. Whilst modern pollen samples are normally taken from areas subject to minimal amounts of disturbance by human activity, this does not discount any influence from vegetation change and the impact of human activity in the past. Conversely, the biomization method can be used to reconstruct modern disturbed vegetation in highly disturbed regions such as Japan ([Gotanda et al., 2008](#)). This provides a method for investigating the impact of humans on vegetation during the late Holocene in Japan ([Gotanda et al., 2008](#)) and in other regions such as China, where there has been long-term human activity and historical land use changes.

Understanding the environmental history of China during the Quaternary has been of special interest to Earth System scientists. This is not only due to its large area, the diverse vegetation and broad climate regimes, but also due to the long history of human activities in China, including irrigated agriculture and forest clearance, in addition to the current environmental problems ([Liu and Diamond, 2005](#)). Addressing these problems requires a quantitative understanding of past environmental change and climate variability. A study of modern pollen, climate and vegetation is therefore a fundamental requirement for investigating these issues.

Studies of surface pollen at local and regional scales in China date back to the 1960s, but more comprehensive and quantitative research has only been conducted during the last decade. The Tibetan Plateau ([Cour et al., 1999](#); [Yu et al., 2001](#); [Li et al., 2005](#); [Shen et al., 2006, 2008](#); [Herzschuh, 2007](#); [Lu et al., 2008](#)), the arid and semi-arid areas of northern and western China ([Liu et al., 2006, 2008](#); [Li et al., 2007](#); [Xu et al., 2007, 2009](#)), and areas of eastern China which have been highly disturbed by human activity ([Zheng et al., 2007](#)), are three major target regions for modern pollen studies. On a national level, the only studies which have been reported are those of arboreal pollen–vegetation relationships ([Yu et al., 2004](#)) and the biome reconstructions ([Yu et al., 1998, 2000](#); [Ni et al., 2010](#)) using the biomization technique ([Prentice et al., 1996, 2000](#); [Prentice and Webb, 1998](#)). Quantifying and reconstructing China's modern biomes from pollen data has been the basis for past biome reconstructions ([Yu et al., 2000](#); [Ni et al., 2010](#)). However, the limited number of pollen records and the uneven distribution of sampling sites in previous studies (the maximum is 806 samples only) has restricted the accurate interpolation of modern biomes to past vegetation and climate, as well as limited our understanding of biome boundaries. Disturbed modern vegetation types were treated as potential natural biomes, leading to inaccurate comparisons between reconstructed and observed modern biomes ([Ni et al., 2010](#)).

In this paper we use an extensive collection of new modern pollen records to quantitatively reconstruct modern biomes using the biomization method. We use a new global scheme of PFTs ([Harrison et al., 2010, in preparation](#)) that has been proven in China ([Ni et al., 2010](#)), and also conduct a more precise assignment of pollen taxa to PFTs based on newly published floras and online resources. The aims of this work are (1) to investigate the spatial variation of modern pollen–vegetation relationships in China, (2) to compare surface pollen-based biome reconstructions with modern vegetation including natural, potential and simulated biomes, and (3) to more precisely

reconstruct modern biome distribution in order to better calibrate past vegetation changes.

2. Data and methods

2.1. Modern pollen data

The modern pollen data set comprises 2324 samples including 1770 raw pollen counts and 554 digitized ones ([Fig. 1](#), Appendices A and B). Of them, 802 samples (764 raw and 38 digitized) were taken from previous publications of Chinese pollen biomization ([Yu et al., 1998, 2000](#); [Ni et al., 2010](#)). Another 437 raw pollen samples were downloaded from the Eastern Asia Surface Pollen Dataset (<http://eapd.sysu.edu.cn/2/eapd.html>). The remaining 569 raw samples were obtained from recent publications and unpublished resources. 516 digitized samples were hand-measured from pollen diagrams published largely between 2000 and 2008. Modern pollen samples were taken from a variety of deposition types, including soil surface (1589), moss polster (295), lake sediment surface (220), sediment core or profile tops (100), dust flux (80), marine sediment surface (19), and snow, ice and glacier (21). More detailed site information can be found in Appendix A.

The new expanded surface pollen data set has nearly three times the number of pollen samples than the previous one ([Ni et al., 2010](#)). Whilst geographical gaps in pollen sampling still exist, especially in the northern and northwestern desert areas, non-settlement areas of the Tibetan Plateau, mountainous regions of middle-southern China and some highly populated areas of eastern China, the current data set is the most updated version available. It comprises 181 more pollen taxa and 34 more taxon combinations compared to the previous data set.

2.2. Biomization procedure

The biomization procedure requires a list of pollen taxa, and the classifications of PFTs and biomes. In total we obtained 737 pollen taxa (species, genera and families) from the surface pollen dataset ([Table 1](#)). We cross-checked and standardized the different nomenclature used by various authors according to the *Floras of China* ([ECFC, 1959–2002](#)), and *Dictionaries of Families and Genera of Chinese Seed Plants* ([Hou, 1998](#)) and *Ferns* ([Wu et al., 1992](#)). The classification of PFTs in China adopted a newly established global scheme for PFTs ([Harrison et al., 2010, in preparation](#)) based on four principles: bioclimatic control (e.g. tropical, warm-temperate, temperate, boreal and arctic), phenology (e.g. evergreen or deciduous), leaf form (e.g. needle-leaved, broad-leaved, small-leaved and micro-leaved) and life form (e.g. tree, shrub, liana or vine, forb, climber, and fern). This scheme has been tested in a previous biomization of China based on limited surface pollen samples and fossil pollen records ([Ni et al., 2010](#)). The eurythermic mesic and xeric drought-deciduous malacophyll low or high shrubs were modified to tropical ones because in China taxa from these two PFTs are restricted in tropical zones. Two additional PFTs, the warm-temperate drought-intolerant liana or vine, and climber were added. In total, 78 PFTs were used to establish the modern biomization of China ([Table 1](#)).

The recent biomization of China ([Ni et al., 2010](#)) used a total of 19 biomes, including 11 forest biomes, one shrubland, one grassland, one desert and five tundra biomes ([Tables 2 and 3](#)), and was based on the previous biome classifications of the world ([Prentice et al., 1992](#); [Kaplan, 2001](#); [Kaplan et al., 2003](#)) and of China ([Yu et al., 1998, 2000](#)). This type of biome scheme has its disadvantages, for example having overly complex biomes in cold- and cool-temperate zones and too few biomes in the warm-temperate (subtropical) zones ([Ni et al., 2010](#)). However, to date it is so far the best biome classification for palaeovegetation study in China and is comparable with the world biome system. Therefore we use this scheme in this study. Further

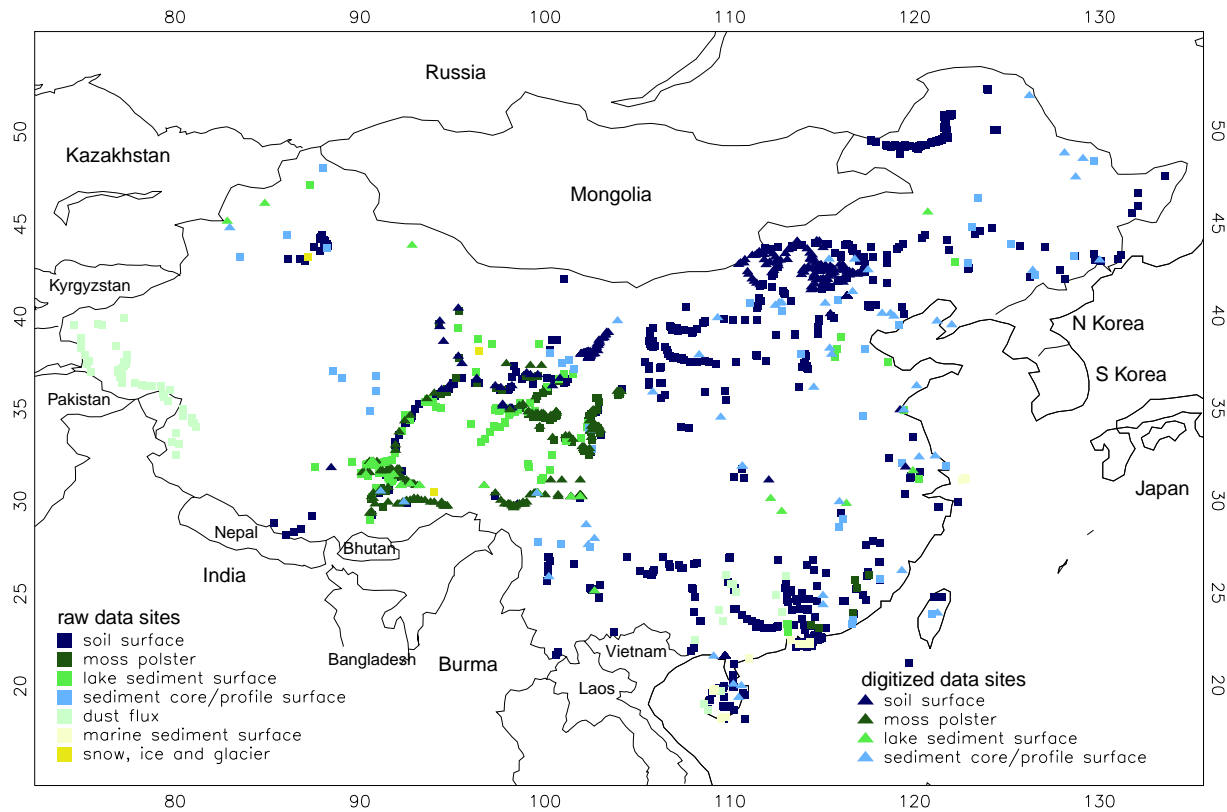


Fig. 1. Location of modern pollen samples.

details for this system are given in Table 2 based on the vegetation of China (ECVC, 1980) and the Vegetation Atlas of China (EBVAC, 2001).

We applied the standard biomization technique by following five steps (Prentice et al., 1996; Prentice and Webb, 1998):

- (1) 737 pollen taxa were assigned to one or more of 78 PFTs (Table 1). The assignment was greatly improved in comparison to previous works (Yu et al., 1998, 2000; Ni et al., 2010) mostly due to the recent availability and correction of various floras and plant atlases (e.g. ECFC, 1959–2002; Wu et al., 1992; Hou, 1998; Fu et al., 1999–2009; Wu et al., 1994–2009). Of these, the assignments of 142 pollen taxa to PFTs were modified in relation to a change in PFT name, the update of various floras and the description of new PFTs mentioned previously. The improvement of such assignments include, for example, changing *Ajanina* from “te-dt.fb” to “cs” and “rcf”, adding “wt.cd.mb.t” to *Fagus*, adding “dt.sl.lhs” and “te-dt.fb” to *Kochia*, Malvaceae changing from “e” to “cd” in warm-temperate zones and to “dd” in tropical zones, adding “wt.e.mb.t” and “wt.e.mb.lhs” to *Randia*, and adding “tr.e.mb.t” to *Sapindus* (see Table 1 for more details). Some taxa were excluded from the biomization procedure and were not allocated to any PFTs as per Ni et al. (2010), including algae (e.g. *Concentricystes*, *Mongeotia*, *Pediastrum*, *Spirogyra*, *Zygnema*, *Zygnemataceae*, and *Hystriochosphaera*), fungi and indeterminate spores (e.g. monoletes and triletes).
- (2) Key PFTs which characterize the composition and structure of certain biomes and determine their spatial distribution were used to define 19 biomes (Table 3). 25 PFTs such as the warm-temperate and eurythermic evergreen needle-leaved low and high shrubs, mangrove, most of liana or vines, climbers, forbs, and ferns, as well as the woody parasite, root parasite, hydrophyte, aquatic, geophyte, epiphyte, and moss, were not

used to define biomes because of their relative unimportance in characterizing zonal vegetation (Table 3).

- (3) The two previously discussed matrices, the pollen taxa vs. PFTs and PFTs vs. biomes, were multiplied to produce a pollen taxa vs. biomes matrix that directly links pollen taxa to biome types.
- (4) The affinity scores for each biome were then calculated for all pollen samples using a summarizing equation $A_{ik} = \sum_j \delta_{ij} \sqrt{\{\max[0, (p_{jk} - \theta_j)]\}}$. Where A_{ik} is the affinity of pollen sample k for biome i ; summation is over all taxa j ; δ_{ij} is the entry (0 or 1) in the biome vs. taxon matrix for biome i and taxon j ; p_{jk} are the pollen percentages; and θ_j is a threshold pollen percentage, here defined as 0.5%, to reduce noise resulting from occasional pollen grains derived from long-distance transport or contamination. Taxon with low pollen percentage less than 0.5% was excluded from the affinity score calculation (for more details, see Prentice et al., 1996; Prentice and Webb, 1998).
- (5) Finally the biome of each pollen sample with the highest affinity score was assigned, subject to a rule that the least PFT-rich biome takes priority where the affinity scores for two or more biomes are equal.

The five-step biomization procedure was performed using Biomise 3 software (Ben Smith, Lund University). Four data files are prepared prior to running the software: a file containing pollen data with information on site-name, longitude, latitude and altitude; a nomenclature file which enables pollen taxa to be recognized and files of pollen taxa vs. PFTs and of PFTs vs. biomes.

2.3. Modern vegetation data

Information on modern vegetation distribution is required to compare with the reconstructed biome data. We relied on field observations (vegetation type and/or species compositions) recorded

Table 1

The assignment of modern pollen taxa to plant functional types (PFTs). PFTs marked 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>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>Abies fargesii</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> , <i>Taxus</i> , <i>Tsuga</i>
te.e.n.t	Temperate evergreen needle-leaved tree	No taxa
wt.e.n.t	Warm-temperate evergreen needle-leaved tree	<i>Cathaya</i> , <i>Cedrus</i> , <i>Cryptomeria</i> , <i>Cunninghamia</i> , <i>Cupressus</i> , <i>Dacrydium</i> , <i>Keteleeria</i> , <i>Podocarpus</i> , <i>Podocarpus macrophyllus</i> , <i>Sequoia</i> , <i>Taxodiaceae</i> , <i>Taxus</i> , <i>Tsuga</i>
eu.e.n.t	Eurythermic evergreen needle-leaved tree	Cupressaceae, Pinaceae, <i>Pinus</i> , <i>Pinus</i> (Diploxyton)
bo.d.n.t	Boreal deciduous needle-leaved tree	<i>Larix</i>
wt.d.n.t	Warm-temperate deciduous needle-leaved tree	<i>Pseudolarix</i> , <i>Taxodiaceae</i> , <i>Taxodium</i>
wt.e.sb.t	Warm-temperate evergreen sclerophyll broad-leaved tree	Aquifoliaceae, Buxaceae, <i>Buxus</i> , <i>Castanopsis</i> , Euphorbiaceae, Fagaceae, <i>Flacourtia</i> , <i>Flacourtiaceae</i> , <i>Ilex</i> , Lauraceae, Leguminosae, <i>Lithocarpus</i> , Myrtaceae, <i>Olea</i> , Oleaceae, <i>Quercus</i> , <i>Quercus</i> (evergreen), Rhamnaceae, Rutaceae, <i>Ziziphus</i>
wt.e.mb.t	Warm-temperate evergreen malacophyll broad-leaved tree	<i>Acacia</i> , <i>Acronychia</i> , <i>Adinandra</i> , Alangiaceae, <i>Altingia</i> , Anacardiaceae, Apocynaceae, Aquifoliaceae, Araliaceae, <i>Ardisia</i> , Bignoniaceae, <i>Bischofia</i> , Boraginaceae, <i>Bridelia</i> , <i>Camellia</i> , Capparidaceae, <i>Castanopsis</i> , Celastraceae, <i>Citrus</i> , <i>Clerodendrum</i> , <i>Clethra</i> , <i>Croton</i> , <i>Cyclobalanopsis</i> , <i>Dalbergia</i> , <i>Daphniphyllum</i> , <i>Dendropanax</i> , <i>Diospyros</i> , <i>Diplospora</i> , <i>Distylium</i> , Ebenaceae, Elaeagnaceae, Elaeocarpaceae, Elaeocarpaceae, <i>Elaeocarpaceae</i> , <i>Euonymus</i> , Euphorbiaceae, <i>Eurya</i> , <i>Exbucklandia</i> , <i>Excoecaria</i> , Fagaceae, <i>Ficus</i> , <i>Garcinia</i> , <i>Gardenia</i> , <i>Glochidion</i> , <i>Gordonia</i> , Guttiferae, Hamamelidaceae, <i>Ilex</i> , <i>Illicium</i> , <i>Lagerstroemia</i> , Lauraceae, Leguminosae, <i>Ligustrum</i> , <i>Lithocarpus</i> , <i>Loropetalum</i> , Lythraceae, <i>Magnolia</i> , Magnoliaceae, <i>Mallotus</i> , <i>Manglietia</i> , Melastomataceae, <i>Michelia</i> , <i>Microtropis</i> , Moraceae, <i>Myrica</i> , <i>Myrica rubra</i> , Myrsinaceae, <i>Myrsine</i> , Myrtaceae, Olacaceae, <i>Olea</i> , Oleaceae, <i>Ormosia</i> , <i>Osmanthus</i> , Pentaphragaceae, <i>Photinia</i> , <i>Phyllanthus</i> , <i>Pistacia</i> , <i>Prunus</i> , <i>Quercus</i> , <i>Quercus</i> (evergreen), <i>Quercus semicarpifolia</i> , <i>Randia</i> , Rhamnaceae, <i>Rhamnus</i> , Rubiaceae, Rutaceae, Sabiaceae, Sapindaceae, <i>Sapindus</i> , <i>Schefflera</i> , <i>Schima</i> , Scrophulariaceae, Simaroubaceae, Solanaceae, Sterculiaceae, <i>Styracaceae</i> , <i>Styrax</i> , <i>Sycopsis</i> , <i>Symplocaceae</i> , <i>Symplocos</i> , <i>Syzygium</i> , Theaceae, Thymelaeaceae, <i>Trochodendron</i> , Verbenaceae, <i>Wendlandia</i> , <i>Wikstroemia</i> , <i>Ziziphus</i>
tr.e.sb.t	Tropical evergreen sclerophyll broad-leaved tree	<i>Artocarpus</i> , <i>Caesalpinia</i> , <i>Canarium</i> , Combretaceae, Elaeocarpaceae, <i>Elaeocarpus</i> , Euphorbiaceae, Lauraceae, Leguminosae, Myrtaceae, Oleaceae, Papilionaceae, Rutaceae
tr.e.mb.t	Tropical evergreen malacophyll broad-leaved tree	<i>Acacia</i> , <i>Acronychia</i> , <i>Adinandra</i> , <i>Aglaia</i> , <i>Ailanthus</i> , Alangiaceae, <i>Allophylus</i> , <i>Altingia</i> , Anacardiaceae, Annonaceae, <i>Antidesma</i> , <i>Aphanamixis</i> , Apocynaceae, Araliaceae, <i>Artocarpus</i> , Bignoniaceae, <i>Bischofia</i> , Boraginaceae, <i>Bridelia</i> , Buxaceae, <i>Canthium</i> , <i>Carallia</i> , <i>Casearia</i> , <i>Cassia</i> , Celastraceae, <i>Cephalomappa</i> , <i>Claoxylon</i> , Combretaceae, <i>Croton</i> , <i>Crypteronia</i> , <i>Decaspermum</i> , <i>Dendropanax</i> , <i>Dimocarpus confinis</i> , <i>Diplospora</i> , <i>Dodonaea</i> , Elaeocarpaceae, <i>Elaeocarpus</i> , <i>Endospermum</i> , <i>Epiprinus</i> , <i>Eucalyptus</i> , Euphorbiaceae, <i>Eurya</i> , <i>Exbucklandia</i> , <i>Ficus</i> , <i>Flacourtia</i> , <i>Flacourtiaceae</i> , <i>Garcinia</i> , <i>Gardenia</i> , <i>Gironiera</i> , <i>Glochidion</i> , <i>Gordonia</i> , Guttiferae, <i>Helicia</i> , <i>Heritiera</i> , <i>Heteropanax</i> , <i>Homalium</i> , <i>Homonoia</i> , <i>Hopea</i> , Icacinaceae, <i>Kleinhovia</i> , Lauraceae, Leguminosae, <i>Lithocarpus</i> , Lythraceae, <i>Macaranga</i> , <i>Malania</i> , <i>Mallotus</i> , Melastomataceae, <i>Microdesmis</i> , Mimosaceae, Moraceae, Myricaceae, Myrsinaceae, Myrtaceae, <i>Myrtus</i> , <i>Neonuclea</i> , <i>Nephelium</i> , Nyctaginaceae, Olacaceae, <i>Olea</i> , Oleaceae, <i>Ormosia</i> , Pandanaceae, <i>Pandanus tectorius</i> , Papilionaceae, Pentaphragaceae, <i>Phyllanthus</i> , <i>Platea</i> , Proteaceae, <i>Pterolobium</i> , <i>Randia</i> , <i>Randia merrillii</i> , <i>Rhodoleia</i> , <i>Rhodomyrtus</i> , Rubiaceae, Rutaceae, Sabiaceae, Sapindaceae, <i>Sapindus</i> , Sapotaceae, <i>Schefflera</i> , <i>Schoepfia</i> , Scrophulariaceae, Simaroubaceae, <i>Sterculia</i> , Sterculiaceae, <i>Styracaceae</i> , <i>Syzygium</i> , <i>Tamarindus</i> , <i>Terminalia</i> , Thymelaeaceae, Tiliaceae, Ulmaceae, <i>Ulmus</i> , <i>Vatica</i> , Verbenaceae, <i>Vitex</i> , <i>Wendlandia</i>
bo.cd.mb.t	Boreal cold-deciduous malacophyll broad-leaved tree	<i>Alnus</i> , <i>Betula</i> , <i>Betula albo-sinensis</i> , <i>Betula costata</i> , <i>Betula dahurica</i> , <i>Betula middendorffii</i> , <i>Betula platyphylla</i> , Betulaceae, <i>Populus</i> , Salicaceae, <i>Salix</i>
te-ft.cd.mb.t	Temperate (spring-frost tolerant) cold-deciduous malacophyll broad-leaved tree	<i>Acer</i> , Aceraceae, <i>Alnus</i> , <i>Betula</i> , <i>Betula albo-sinensis</i> , <i>Betula dahurica</i> , <i>Betula middendorffii</i> , <i>Betula platyphylla</i> , Betulaceae, <i>Corylus</i> , Fagaceae, <i>Fraxinus</i> , <i>Fraxinus mandshurica</i> , Leguminosae, Papilionaceae, <i>Populus</i> , <i>Quercus</i> , <i>Quercus</i> (deciduous), Rosaceae, Salicaceae, <i>Salix</i> , <i>Tilia</i> , Tiliaceae, <i>Toona sinensis</i> , Ulmaceae, <i>Ulmus 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, Fagaceae, <i>Ginkgo</i> , <i>Gleditsia</i> , Guttiferae, Leguminosae, <i>Magnolia</i> , Magnoliaceae, <i>Morus</i> , Oleaceae, Papilionaceae, <i>Platanus</i> , <i>Prunus</i> , <i>Quercus</i> , <i>Quercus</i> (deciduous), Rhamnaceae, <i>Rhamnus</i> , <i>Rhus</i> , Rosaceae, Rutaceae, Salicaceae, <i>Salix</i> , <i>Sambucus</i> , Scrophulariaceae, <i>Sorbus</i> , <i>Syringa</i> , <i>Toxicodendron</i> , Ulmaceae, <i>Ulmus</i> , Verbenaceae, <i>Vitex</i> , <i>Ziziphus</i>
te-fa.cd.mb.t	Temperate (spring-frost avoiding) cold-deciduous malacophyll broad-leaved tree	<i>Acer</i> , Aceraceae, Bignoniaceae, <i>Broussonetia</i> , Caprifoliaceae, <i>Carpinus</i> , <i>Carya</i> , <i>Castanea</i> , <i>Celtis</i> , Elaeagnaceae, Eucommiaceae, <i>Euonymus</i> , <i>Euptelea</i> , Fagaceae, <i>Fagus</i> , <i>Fraxinus</i> , <i>Ginkgo</i> , Hamamelidaceae, <i>Idesia</i> , Juglandaceae, <i>Juglans</i> , <i>Koelreuteria</i> , <i>Lagerstroemia</i> , Leguminosae, <i>Liquidambar</i> , <i>Liquidambar formosana</i> , Lythraceae, <i>Melia</i> , Meliaceae, <i>Meliosma</i> , Moraceae, <i>Morus</i> , <i>Ostrya</i> , Papilionaceae, <i>Phyllanthus</i> , <i>Pistacia</i> , <i>Platycarya</i> , <i>Platycarya strobilacea</i> , <i>Populus</i> , <i>Pterocarya</i> , <i>Pteroceltis</i> , <i>Quercus</i> , <i>Quercus</i> (deciduous), Rosaceae, Sabiaceae, Salicaceae, <i>Salix</i> , <i>Sambucus</i> , Simaroubaceae, <i>Tilia</i> , Tiliaceae, Ulmaceae, <i>Zelkova</i>
wt.cd.mb.t	Warm-temperate cold-deciduous malacophyll broad-leaved tree	Aceraceae, <i>Adina</i> , <i>Aesculus</i> , <i>Aesculus wilsonii</i> , <i>Ailanthus</i> , <i>Albizia</i> , <i>Alchornea</i> , <i>Alnus</i> , Anacardiaceae, Araliaceae, Betulaceae, Boraginaceae, <i>Broussonetia</i> , Caprifoliaceae, <i>Carya</i> , <i>Celtis</i> , Cornaceae, <i>Cornus</i> , <i>Corylopsis</i> , <i>Crataegus</i> , <i>Cyclocarya</i> , <i>Engelhardtia</i> , Eucommiaceae, Euphorbiaceae, <i>Euptelea</i> , <i>Fagus</i> , <i>Flacourtiaceae</i> , <i>Gleditsia</i> , Hamamelidaceae, <i>Hamamelis</i> , <i>Idesia</i> , Juglandaceae, <i>Juglans</i> , Juglandaceae, <i>Juglans</i> , <i>Koelreuteria</i> , <i>Lagerstroemia</i> , Lauraceae, Leguminosae, <i>Liquidambar</i> , <i>Liriodendron</i> , Lythraceae, <i>Magnolia</i> , Magnoliaceae, Malvaceae, <i>Melia</i> , Meliaceae, <i>Meliosma</i> , <i>Mimosa</i> , Mimosaceae, Moraceae, <i>Morus</i> , <i>Myrica</i> , <i>Nyssa</i> , <i>Phyllanthus</i> , <i>Pistacia</i> , <i>Platanus</i> , <i>Platycarya</i> , <i>Platycarya strobilacea</i> , <i>Prunus</i> , <i>Pterocarya</i> , <i>Pteroceltis</i> , Rhamnaceae, <i>Rhamnus</i> , <i>Rhoiptelea</i> , <i>Rhus</i> , Rosaceae, <i>Sambucus</i> , <i>Sapium</i> , <i>Schoepfia</i> , Simaroubaceae, <i>Sorbus</i> , Sterculiaceae, <i>Styracaceae</i> , <i>Styrax</i> , Thymelaeaceae, <i>Toxicodendron</i> , <i>Toxicodendron succedaneum</i> , Urticaceae, Verbenaceae, <i>Vitex</i> , <i>Wikstroemia</i> , <i>Zelkova</i> , <i>Ziziphus</i>
tr-m.dd.mb.t	Tropical mesic drought-deciduous malacophyll broad-leaved tree	<i>Albizia</i> , Anacardiaceae, Bombacaceae, <i>Caesalpinia</i> , Celastraceae, <i>Chukrasia</i> , Combretaceae, <i>Engelhardtia</i> , Euphorbiaceae, <i>Flacourtiaceae</i> , <i>Hainania</i> , <i>Lannea</i> , Leguminosae, Malvaceae, <i>Meliaceae</i> , <i>Microcos</i> , <i>Mimosa</i> , Mimosaceae, Oleaceae, Papilionaceae, Rubiaceae, Sapindaceae, <i>Sapium</i> , <i>Spondias</i> , <i>Styracaceae</i> , Tiliaceae, <i>Trema</i> , Ulmaceae, <i>Ulmus</i>
tr-x.dd.mb.t	Tropical xeric drought-deciduous malacophyll broad-leaved tree	<i>Acacia</i> , Bombacaceae, Capparidaceae, <i>Cassia</i> , <i>Dalbergia</i> , <i>Dodonaea</i> , Euphorbiaceae, <i>Flacourtia</i> , <i>Flacourtiaceae</i> , Leguminosae, Mimosaceae, Papilionaceae, <i>Randia</i> , Rubiaceae, <i>Terminalia</i> , Tiliaceae, <i>Wendlandia</i> , <i>Ziziphus</i>
ml.t	Micro-leaved tree	<i>Casuarina</i>
sl.t	Small-leaved tree	Elaeagnaceae, <i>Elaeagnus</i> , Leguminosae, <i>Mimosa</i> , Mimosaceae, Papilionaceae, Tamaricaceae, <i>Tamarix</i> , <i>Ziziphus</i> , Zygothylaceae, <i>Zygothylum</i>

(continued on next page)

Table 1 (continued)

PFT code	PFT name	Pollen taxa
tu.t	Tuft tree	<i>Areca</i> , <i>Cocos</i> , <i>Cycas</i> , <i>Palmae</i> , <i>Phoenix</i> , <i>Trachycarpus</i>
ar.e.n.lhs	Arctic evergreen needle-leaved low and high shrub	<i>Pinus pumila</i>
wt.e.n.lhs*	Warm-temperate evergreen needle-leaved low and high shrub	<i>Dacrydium</i> , <i>Podocarpus</i> , <i>Taxus</i>
eu.e.n.lhs*	Eurythermic evergreen needle-leaved low and high shrub	Cupressaceae, Pinaceae
ft.ml.lhs	Frost-tolerant micro-leaved low and high shrub	<i>Ephedra</i> , <i>Ephedra distachya</i> , <i>Ephedra equisetina</i> , Ephedraceae, <i>Myricaria</i> , <i>Reaumuria</i> , Tamaricaceae, <i>Tamarix</i>
dt.sl.lhs	Drought-tolerant small-leaved low and high shrub	<i>Alhagi</i> , <i>Calligonum</i> , <i>Caragana</i> , <i>Ceratoides</i> , Chenopodiaceae, <i>Chenopodium</i> , Elaeagnaceae, <i>Elaeagnus</i> , <i>Euphorbia</i> , Euphorbiaceae, <i>Hippophae</i> , <i>Kochia</i> , Leguminosae, Mimosaceae, <i>Nitraria</i> , Papilionaceae, <i>Potania</i> , <i>Reaumuria</i> , <i>Salsola</i> , Solanaceae, <i>Tetraena</i> , <i>Thymus</i> , Zygophyllaceae, <i>Zygophyllum</i>
di.sl.lhs	Drought-intolerant small-leaved low and high shrub	<i>Empetrum</i> , Ericaceae
wt.e.sb.lhs	Warm-temperate evergreen sclerophyll broad-leaved low and high shrub	Aquifoliaceae, Buxaceae, <i>Buxus</i> , Euphorbiaceae, Fagaceae, <i>Flacourtia</i> , Flacourtiaceae, <i>Ilex</i> , <i>Olea</i> , Oleaceae, <i>Quercus</i> , <i>Quercus</i> (evergreen), Rhamnaceae, <i>Ziziphus</i>
ar.e.mb.lhs	Arctic evergreen malacophyll broad-leaved low and high shrub	<i>Empetrum</i> , <i>Ledum</i> , <i>Ledum palustre</i>
bo.e.mb.lhs	Boreal evergreen malacophyll broad-leaved low and high shrub	Ericaceae, <i>Ledum</i> , <i>Ledum palustre</i> , <i>Oxycoccus</i> , <i>Rhododendron</i> , <i>Ribes</i> , <i>Vaccinium</i> , <i>Vaccinium uliginosum</i>
wt.e.mb.lhs	Warm-temperate evergreen malacophyll broad-leaved low and high shrub	<i>Acacia</i> , <i>Adinandra</i> , Anacardiaceae, Apocynaceae, <i>Aporusa</i> , Aquifoliaceae, Araliaceae, <i>Ardisia</i> , Asclepiadaceae, Berberidaceae, Bignoniaceae, Boraginaceae, <i>Bridelia</i> , <i>Cajanus</i> , <i>Camellia</i> , Capparidaceae, <i>Capparis</i> , Caprifoliaceae, <i>Castanopsis</i> , Celastraceae, <i>Citrus</i> , <i>Clerodendrum</i> , <i>Clethra</i> , Cornaceae, <i>Croton</i> , <i>Damnacanthus</i> , <i>Daphne</i> , <i>Daphniphyllum</i> , <i>Dendropanax</i> , <i>Diospyros</i> , <i>Diplospora</i> , <i>Distylium</i> , Ebenaceae, Elaeagnaceae, <i>Elaeagnus</i> , Elaeocarpaceae, Ericaceae, <i>Euonymus</i> , Euphorbiaceae, <i>Eurya</i> , <i>Excoecaria</i> , Fagaceae, <i>Ficus</i> , <i>Garcinia</i> , <i>Gardenia</i> , <i>Glochidion</i> , Guttiferae, Hamamelidaceae, <i>Ilex</i> , <i>Illicium</i> , <i>Itea</i> , <i>Jasminum</i> , Lauraceae, Leguminosae, <i>Ligustrum</i> , <i>Lonicera</i> , <i>Loropetalum</i> , <i>Lycium</i> , Lythraceae, <i>Maesa</i> , Magnoliaceae, <i>Mallotus</i> , Melastomataceae, <i>Michelia</i> , <i>Microtropis</i> , Moraceae, <i>Myrica</i> , Myrsinaceae, <i>Myrsine</i> , Myrtaceae, <i>Nandina</i> , <i>Nerium</i> , Olacaceae, <i>Olea</i> , Oleaceae, <i>Osmanthus</i> , <i>Photinia</i> , <i>Phyllanthus</i> , <i>Pistacia</i> , <i>Prunus</i> , <i>Pterolobium</i> , <i>Quercus</i> , <i>Quercus</i> (evergreen), <i>Randia</i> , Rhamnaceae, <i>Rhamnus</i> , <i>Rhaphiolepis</i> , <i>Rhododendron</i> , <i>Rhododendron fargesii</i> , Rubiaceae, Rutaceae, Sabiaceae, Sapindaceae, <i>Schefflera</i> , Scrophulariaceae, Simaroubaceae, <i>Skimmia</i> , Solanaceae, Sterculiaceae, Styracaceae, <i>Styrax</i> , <i>Sycopsis</i> , Symplocaceae, <i>Symplocos</i> , <i>Syzygium</i> , Theaceae, Thymelaeaceae, <i>Trochodendron</i> , <i>Vaccinium</i> , Verbenaceae, <i>Viburnum</i> , <i>Wendlandia</i> , <i>Wikstroemia</i> , <i>Zanthoxylum</i> , <i>Ziziphus</i>
tr.e.mb.lhs	Tropical evergreen malacophyll broad-leaved low and high shrub	<i>Acacia</i> , <i>Adinandra</i> , <i>Aglaia</i> , <i>Allomorphia</i> , <i>Allophylus</i> , Annonaceae, <i>Antidesma</i> , <i>Aphanamixis</i> , Apocynaceae, <i>Aporusa</i> , Araliaceae, Asclepiadaceae, Bignoniaceae, Boraginaceae, <i>Bridelia</i> , Buxaceae, <i>Canthium</i> , <i>Casearia</i> , <i>Cassia</i> , Celastraceae, <i>Claoxylon</i> , Combretaceae, <i>Croton</i> , <i>Decaspermum</i> , <i>Dendropanax</i> , <i>Diplospora</i> , <i>Dodonaea</i> , Elaeocarpaceae, <i>Epiprinus</i> , <i>Eucalyptus</i> , <i>Eurya</i> , <i>Ficus</i> , Flacourtiaceae, <i>Garcinia</i> , <i>Gardenia</i> , <i>Gironniera</i> , <i>Glochidion</i> , Guttiferae, <i>Hedyotis</i> , <i>Helicteres</i> , <i>Heteropanax</i> , <i>Homalium</i> , <i>Homonioia</i> , Icacinaceae, <i>Lardizabalaceae</i> , Lauraceae, Leguminosae, Lythraceae, <i>Macaranga</i> , <i>Mallotus</i> , Melastomataceae, <i>Microdesmis</i> , Mimosaceae, Moraceae, <i>Morinda</i> , Myrsinaceae, Myrsinaceae, Myrtaceae, <i>Myrtus</i> , <i>Neonauclea</i> , <i>Nerium</i> , Nyctaginaceae, <i>Olea</i> , Oleaceae, Pandanaceae, Papilionaceae, <i>Phyllanthus</i> , <i>Piper</i> , Piperaceae, Proteaceae, <i>Pterolobium</i> , <i>Randia</i> , <i>Rhaphiolepis</i> , <i>Rhodoleia</i> , <i>Rhodomyrtus</i> , <i>Ricinus</i> , Rubiaceae, Sabiaceae, Sapindaceae, Sapotaceae, <i>Sauropus</i> , <i>Schizomussaenda</i> , <i>Schoepfia</i> , Scrophulariaceae, Simaroubaceae, <i>Skimmia</i> , Sterculiaceae, Styracaceae, <i>Syzygium</i> , Verbenaceae, <i>Vitex</i> , <i>Wendlandia</i>
ar.cd.mb.lhs	Arctic cold-deciduous malacophyll broad-leaved low and high shrub	<i>Hydrangea</i> , <i>Oxytropis</i> , <i>Spiraea</i> , <i>Viburnum</i>
bo.cd.mb.lhs	Boreal cold-deciduous malacophyll broad-leaved low and high shrub	<i>Alnus</i> , <i>Betula</i> , Betulaceae, Ericaceae, Guttiferae, <i>Hypericum</i> , <i>Oxytropis</i> , <i>Rhododendron</i> , <i>Ribes</i> , Salicaceae, <i>Salix</i> , <i>Viburnum</i>
te.cd.mb.lhs	Temperate cold-deciduous malacophyll broad-leaved low and high shrub	<i>Abelia</i> , <i>Acalypha</i> , <i>Acer</i> , Aceraceae, <i>Alnus</i> , Anacardiaceae, <i>Aralia</i> , Araliaceae, Asclepiadaceae, Berberidaceae, <i>Berberis</i> , <i>Betula</i> , Betulaceae, Bignoniaceae, <i>Broussonetia</i> , Caprifoliaceae, <i>Caragana</i> , Celastraceae, <i>Celtis</i> , Cornaceae, <i>Cornus</i> , <i>Corylus</i> , <i>Cotinus</i> , <i>Cotoneaster</i> , <i>Crataegus</i> , <i>Daphne</i> , <i>Diospyros</i> , Ebenaceae, Elaeagnaceae, <i>Elaeagnus</i> , Ericaceae, <i>Euonymus</i> , Euphorbiaceae, <i>Euptelea</i> , Fagaceae, <i>Fontanesia</i> , <i>Gleditsia</i> , <i>Glochidion</i> , Guttiferae, Hamamelidaceae, <i>Helwingia</i> , <i>Hippophae</i> , <i>Hydrangea</i> , <i>Hypericum</i> , <i>Ilex</i> , <i>Koeleruteria</i> , Labiatae, <i>Lagerstroemia</i> , Leguminosae, <i>Lespedeza</i> , <i>Ligustrum</i> , <i>Lonicera</i> , <i>Lycium</i> , Lythraceae, Malvaceae, <i>Melia</i> , Meliaceae, <i>Meliosma</i> , Moraceae, <i>Morus</i> , Oleaceae, <i>Ostryopsis</i> , <i>Oxytropis</i> , Papilionaceae, <i>Phyllanthus</i> , <i>Pistacia</i> , <i>Prunus</i> , <i>Quercus</i> , <i>Quercus</i> (deciduous), Rhamnaceae, <i>Rhamnus</i> , <i>Rhododendron</i> , <i>Rhus</i> , <i>Ribes</i> , <i>Rosa</i> , Rosaceae, <i>Rubus</i> , Rutaceae, Sabiaceae, Salicaceae, <i>Salix</i> , <i>Sambucus</i> , Scrophulariaceae, Solanaceae, <i>Sorbaria</i> , <i>Sorbus</i> , <i>Spiraea</i> , <i>Syringa</i> , Tiliaceae, <i>Toxicodendron</i> , Ulmaceae, <i>Vaccinium</i> , Verbenaceae, <i>Viburnum</i> , Violaceae, <i>Vitex</i> , <i>Vitex negundo</i> var. <i>heterophylla</i> , <i>Weigela</i> , <i>Wikstroemia</i> , <i>Zanthoxylum</i> , <i>Zelkova</i> , <i>Ziziphus</i>
wt.cd.mb.lhs	Warm-temperate cold-deciduous malacophyll broad-leaved low and high shrub	<i>Abelia</i> , <i>Acalypha</i> , Acanthaceae, <i>Adina</i> , <i>Albizia</i> , <i>Alchornea</i> , Anacardiaceae, <i>Aralia</i> , Araliaceae, Asclepiadaceae, Berberidaceae, <i>Berberis</i> , Boraginaceae, <i>Bredia</i> , <i>Broussonetia</i> , Caprifoliaceae, <i>Celtis</i> , Cornaceae, <i>Cornus</i> , <i>Corylopsis</i> , <i>Daphne</i> , <i>Desmodium</i> , Euphorbiaceae, <i>Euptelea</i> , <i>Fontanesia</i> , <i>Gleditsia</i> , Guttiferae, Hamamelidaceae, <i>Hamamelis</i> , <i>Helwingia</i> , <i>Hydrangea</i> , <i>Hypericum</i> , <i>Koeleruteria</i> , <i>Lagerstroemia</i> , Lauraceae, Leguminosae, <i>Lespedeza</i> , Linaceae, <i>Lonicera</i> , Lythraceae, Malvaceae, <i>Melia</i> , Meliaceae, <i>Meliosma</i> , <i>Mimosa</i> , Mimosaceae, Moraceae, <i>Morus</i> , <i>Photinia</i> , <i>Phyllanthus</i> , <i>Pistacia</i> , <i>Prunus</i> , Rhamnaceae, <i>Rhamnus</i> , <i>Rhus</i> , <i>Ricinus</i> , Rosaceae, <i>Rubus</i> , <i>Sambucus</i> , <i>Sapium</i> , <i>Schisandra</i> , <i>Schoepfia</i> , Simaroubaceae, <i>Sorbaria</i> , <i>Sorbus</i> , <i>Spiraea</i> , Sterculiaceae, Styracaceae, <i>Styrax</i> , Thymelaeaceae, <i>Toxicodendron</i> , Urticaceae, Verbenaceae, Violaceae, <i>Vitex</i> , <i>Weigela</i> , <i>Wikstroemia</i> , <i>Zanthoxylum</i> , <i>Zelkova</i> , <i>Ziziphus</i>
tr-m.dd.mb.lhs	Tropical mesic drought-deciduous malacophyll low and high shrub	<i>Acalypha</i> , Acanthaceae, <i>Albizia</i> , <i>Alliophylus</i> , Anacardiaceae, <i>Artemisia</i> , Asteroideae, <i>Caesalpinia</i> , Capparidaceae, Caprifoliaceae, Compositae, <i>Euphorbia</i> , Euphorbiaceae, Flacourtiaceae, <i>Helicteres</i> , Labiatae, Malvaceae, <i>Microcos</i> , <i>Mussaenda</i> , Rhamnaceae, <i>Rhamnus</i> , Rubiaceae, Rutaceae, <i>Sapium</i> , Simaroubaceae, Styracaceae, <i>Trema</i>
tr-x.dd.mb.lhs	Tropical xeric drought-deciduous malacophyll low and high shrub	<i>Acacia</i> , <i>Artemisia</i> , Asteroideae, <i>Calligonum</i> , Capparidaceae, <i>Capparis</i> , Compositae, Cruciferae, <i>Euphorbia</i> , Euphorbiaceae, <i>Flacourtia</i> , Flacourtiaceae, Leguminosae, Papilionaceae, Plumbaginaceae, Polygonaceae, Rhamnaceae, Rubiaceae, Rutaceae, Simaroubaceae, Solanaceae, <i>Solanum</i> , <i>Ziziphus</i>
ar.e.mb.eds	Arctic evergreen malacophyll broad-leaved erect dwarf shrub	Berberidaceae, <i>Empetrum</i> , <i>Vaccinium</i> , <i>Vaccinium uliginosum</i>

Table 1 (continued)

PFT code	PFT name	Pollen taxa
ar.cd.mb.eds	Arctic cold-deciduous malacophyll broad-leaved erect dwarf shrub	<i>Betula</i> , <i>Betula middendorffii</i> , Betulaceae, <i>Caragana</i> , <i>Hippophae</i> , <i>Rhododendron</i> , <i>Rosa</i> , Rosaceae
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>Oxycoccus</i> , Rosaceae
ar.cd.mb.pds	Arctic cold-deciduous malacophyll broad-leaved prostrate dwarf shrub	<i>Betula</i> , Betulaceae, <i>Ceratoides</i> , <i>Rhododendron</i> , <i>Rosa</i> , Rosaceae, Salicaceae, <i>Salix</i>
cs	Cushion shrub	<i>Ajania</i> , <i>Ceratoides</i> , <i>Nanophyton</i> , <i>Oxytropis</i> , <i>Oxytropis aciphylla</i> , Plumbaginaceae, <i>Salsola</i>
wt-dt.lv*	Warm-temperate drought-tolerant liana or vine	<i>Dalbergia</i>
tr-dt.lv	Tropical drought-tolerant liana or vine	<i>Acacia</i> , <i>Albizia</i> , Asclepiadaceae, <i>Bowringia</i> , <i>Caesalpinia</i> , <i>Calamus</i> , Capparidaceae, <i>Capparis</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> , Asteroideae, Bignoniaceae, Capparidaceae, Celastraceae, <i>Celastrus</i> , <i>Cocculus</i> , Compositae, <i>Hedera</i> , Lardizabalaceae, Leguminosae, <i>Lonicera</i> , Menispermaceae, Oleaceae, Papilionaceae, Ranunculaceae, Rhamnaceae, Rosaceae, <i>Rubus</i> , <i>Sabia</i> , Sabiaceae, <i>Schisandra</i> , Vitaceae, <i>Vitis</i> , <i>Zanthoxylum</i>
wt-di.lv*	Warm-temperate drought-intolerant liana or vine	<i>Actinidia</i> , <i>Aeschynanthus</i> , <i>Alyxia</i> , <i>Anodendron</i> , Apocynaceae, Bignoniaceae, <i>Broussonetia</i> , Capparidaceae, Celastraceae, <i>Celastrus</i> , <i>Cocculus</i> , <i>Hedera</i> , Lardizabalaceae, Leguminosae, <i>Lonicera</i> , Menispermaceae, Myrsinaceae, Oleaceae, Papilionaceae, <i>Porana</i> , Ranunculaceae, <i>Rubus</i> , <i>Sabia</i> , Sabiaceae
tr-di.lv*	Tropical drought-intolerant liana or vine	Acanthaceae, <i>Actinidia</i> , <i>Aeschynanthus</i> , <i>Aganosma</i> , <i>Alyxia</i> , Annonaceae, <i>Anodendron</i> , Apocynaceae, Asclepiadaceae, Bignoniaceae, <i>Aralia</i> , Celastraceae, <i>Celastrus</i> , <i>Cocculus</i> , Combretaceae, <i>Convolvulus</i> , Cucurbitaceae, <i>Hedera</i> , <i>Hedyotis</i> , Icacinaceae, Lardizabalaceae, Leguminosae, <i>Mallotus</i> , <i>Mappianthus</i> , Melastomataceae, Menispermaceae, <i>Merremia</i> , Moraceae, <i>Morinda</i> , <i>Mussaenda</i> , Myrsinaceae, Nyctaginaceae, Olacaceae, Oleaceae, <i>Pachygone</i> , Palmae, Pandanaceae, Papilionaceae, <i>Porana</i> , <i>Pterolobium</i> , Ranunculaceae, <i>Rhynchosia</i> , <i>Rubus</i> , <i>Sabia</i> , Sabiaceae, <i>Schefflera</i> , <i>Schisandra</i> , <i>Schizomussaenda</i> , Simaroubaceae, <i>Stephania</i> , Sterculiaceae, <i>Tristellateia</i> , Verbenaceae
man*	Mangrove	Acanthaceae, <i>Acanthus ilicifolius</i> , <i>Aegiceras</i> , <i>Aegiceras corniculatum</i> , <i>Avicennia marina</i> , Bignoniaceae, <i>Bruguiera</i> , <i>Bruguiera gymnorhiza</i> , <i>Ceriops</i> , Euphorbiaceae, <i>Excoecaria</i> , <i>Excoecaria agallocha</i> , <i>Kandelia</i> , <i>Kandelia candel</i> , <i>Lumnitzera racemosa</i> , Myrsinaceae, <i>Rhizophora</i> , <i>Rhizophora apiculata</i> , <i>Rhizophora stylosa</i> , Rhizophoraceae, Rubiaceae
wpa*	Woody parasite	<i>Arceuthobium</i> , <i>Elytranthe</i> , Loranthaceae, <i>Loranthus</i>
te-di.c*	Temperate drought-intolerant climber	Amaranthaceae, Araliaceae, Campanulaceae, Cannabaceae, <i>Clematis</i> , Convolvulaceae, <i>Convolvulus</i> , Cucurbitaceae, <i>Cuscuta</i> , <i>Galium</i> , <i>Humulus</i> , Leguminosae, Liliaceae, <i>Mimosa</i> , Mimosaceae, Papilionaceae, Polygonaceae, <i>Rubia</i> , Rubiaceae, Solanaceae, <i>Solanum</i> , <i>Trichosanthes</i> , <i>Valeriana</i> , Valerianaceae, <i>Vigna</i>
wt-di.c*	Warm-temperate drought-intolerant climber	Acanthaceae, Araliaceae, Araceae, Araliaceae, Asclepiadaceae, Campanulaceae, Convolvulaceae, <i>Convolvulus</i> , Cucurbitaceae, <i>Galium</i> , <i>Lathyrus</i> , Lauraceae, Leguminosae, Liliaceae, <i>Merremia</i> , <i>Mimosa</i> , Mimosaceae, Papilionaceae, <i>Rubia</i> , Rubiaceae, Sapindaceae, Solanaceae, <i>Solanum</i> , <i>Trichosanthes</i> , <i>Vigna</i>
tr-di.c*	Tropical drought-intolerant climber	Acanthaceae, Araliaceae, Araceae, Araliaceae, Asclepiadaceae, Campanulaceae, Convolvulaceae, <i>Convolvulus</i> , Cucurbitaceae, <i>Galium</i> , <i>Lathyrus</i> , Lauraceae, Leguminosae, Liliaceae, <i>Merremia</i> , <i>Mimosa</i> , Mimosaceae, Papilionaceae, <i>Rubia</i> , Rubiaceae, Sapindaceae, Solanaceae, <i>Solanum</i> , <i>Trichosanthes</i> , <i>Vigna</i>
ar.fb	Arctic forb	<i>Androsace</i> , <i>Anemone</i> , <i>Arabis</i> , <i>Arenaria</i> , <i>Artemisia</i> , <i>Aster</i> , Asteroideae, <i>Astragalus</i> , <i>Bupleurum</i> , <i>Campanula</i> , Campanulaceae, <i>Carduoideae</i> , Caryophyllaceae, <i>Centaurea</i> , <i>Cerastium</i> , Compositae, <i>Corydalis</i> , <i>Cruciferae</i> , <i>Dianthus</i> , Dipsacaceae, <i>Dipsacus</i> , <i>Gentiana</i> , Gentianaceae, Geraniaceae, <i>Hypocoum</i> , <i>Impatiens</i> , <i>Incarvillea</i> , Iridaceae, <i>Iris</i> , Labiatae, <i>Lamium</i> , Leguminosae, Liguliflorae, Liliaceae, <i>Liquiliflora</i> , <i>Lysimachia</i> , <i>Lythrum</i> , <i>Mazus</i> , <i>Morina</i> , <i>Onobrychis</i> , <i>Orostachys</i> , <i>Oxytropis</i> , Papaveraceae, Papilionaceae, <i>Parnassia</i> , <i>Pedicularis</i> , Plumbaginaceae, <i>Polemonium</i> , Polygonaceae, <i>Polygonum</i> , <i>Potentilla</i> , <i>Primula</i> , Primulaceae, <i>Pulsatilla</i> , <i>Pyrola</i> , Pyrolaceae, Ranunculaceae, <i>Rhodiola</i> , <i>Saussurea</i> , <i>Saxifraga</i> , Saxifragaceae, Scrophulariaceae, <i>Sedum</i> , <i>Serratula</i> , <i>Sibbaldia</i> , <i>Souliea</i> , <i>Thalictrum</i> , Umbelliferae, <i>Verbascum</i> , <i>Veronica</i>
bo-di.fb*	Boreal drought-intolerant forb	<i>Aconitum</i> , Caryophyllaceae, <i>Centaurea</i> , <i>Epilobium</i> , <i>Euphorbia</i> , Euphorbiaceae, <i>Filipendula</i> , <i>Hypocoum</i> , <i>Lathyrus</i> , <i>Melilotus</i> , <i>Onobrychis</i> , <i>Pedicularis</i> , Plantaginaceae, <i>Plantago</i> , <i>Platycodon</i> , <i>Pyrola</i> , Pyrolaceae, Scrophulariaceae
te-di.fb*	Temperate drought-intolerant forb	<i>Acalypha</i> , <i>Aconitum</i> , Araliaceae, <i>Amaranthus</i> , <i>Ambrosia</i> , <i>Androsace</i> , <i>Anemone</i> , <i>Anthemis</i> , <i>Aquilegia</i> , <i>Arabis</i> , Araceae, <i>Aralia</i> , Araliaceae, <i>Arctium</i> , <i>Arisaema</i> , <i>Artemisia</i> , Asclepiadaceae, <i>Asperula</i> , <i>Aster</i> , Asteroideae, <i>Astragalus</i> , <i>Atractylodes</i> , Berberidaceae, Boraginaceae, <i>Bupleurum</i> , <i>Caltha</i> , <i>Campanula</i> , Campanulaceae, Cannabaceae, Caprifoliaceae, <i>Carduoideae</i> , Caryophyllaceae, <i>Cassia</i> , <i>Centaurea</i> , <i>Cerastium</i> , <i>Chamaenerion</i> , <i>Chamaenerion angustifolium</i> , <i>Chelidonium</i> , Chenopodiaceae, <i>Chenopodium</i> , <i>Chloranthus</i> , <i>Chrysanthemum</i> , <i>Chrysosplenium</i> , <i>Cichorium</i> , <i>Circaea</i> , <i>Cirsium</i> , <i>Clematis</i> , Commelinaceae, Compositae, Convolvulaceae, <i>Convolvulus</i> , Cornaceae, <i>Corydalis</i> , <i>Cruciferae</i> , <i>Dianthus</i> , Dipsacaceae, <i>Dipsacus</i> , Droseraceae, <i>Elsholtzia</i> , <i>Epilobium</i> , <i>Euphorbia</i> , Euphorbiaceae, <i>Filipendula</i> , <i>Fragaria</i> , <i>Galium</i> , <i>Gentiana</i> , Gentianaceae, Geraniaceae, <i>Geranium</i> , <i>Glycyrrhiza</i> , <i>Guttiferae</i> , <i>Hedysarum</i> , <i>Hemerocallis</i> , <i>Hypericum</i> , <i>Impatiens</i> , Iridaceae, <i>Iris</i> , <i>Ixeris</i> , <i>Kochia</i> , Labiatae, <i>Lamium</i> , <i>Lathyrus</i> , Leguminosae, <i>Lespedeza</i> , <i>Ligularia</i> , Liguliflorae, Liliaceae, <i>Lilium</i> , Linaceae, <i>Linum</i> , <i>Liquiliflora</i> , <i>Lysimachia</i> , Lythraceae, <i>Lythrum</i> , <i>Macleaya</i> , Malvaceae, <i>Mazus</i> , <i>Medicago</i> , <i>Melilotus</i> , <i>Mimosa</i> , Mimosaceae, <i>Morina</i> , Onagraceae, <i>Onobrychis</i> , <i>Origanum</i> , <i>Oxalis</i> , <i>Oxytropis</i> , <i>Papaver</i> , Papaveraceae, Papilionaceae, <i>Parnassia</i> , <i>Pedicularis</i> , <i>Phlomis</i> , Plantaginaceae, <i>Plantago</i> , <i>Platycodon</i> , <i>Polemonium</i> , <i>Polygala</i> , Polygonaceae, <i>Polygonum</i> , <i>Polygonum bistorta</i> , <i>Polygonum viviparum</i> , <i>Potentilla</i> , <i>Primula</i> , Primulaceae, <i>Pulsatilla</i> , <i>Pyrola</i> , Pyrolaceae, Ranunculaceae, <i>Ranunculus</i> , <i>Rheum</i> , <i>Ricinus</i> , <i>Rubia</i> , Rubiaceae, <i>Rumex</i> , <i>Sanguisorba</i> , Saururaceae, <i>Saururus</i> , <i>Saussurea</i> , <i>Saxifraga</i> , Saxifragaceae, <i>Scabiosa</i> , Scrophulariaceae, <i>Serratula</i> , Solanaceae, <i>Solanum</i> , <i>Stellera</i> , <i>Taraxacum</i> , <i>Thalictrum</i> , Thymelaeaceae, <i>Tribulus</i> , <i>Trollius</i> , Umbelliferae, <i>Urtica</i> , Urticaceae, <i>Valeriana</i> , Valerianaceae, Verbenaceae, <i>Veronica</i> , <i>Viola</i> , Violaceae, <i>Xanthium</i> , Zygophyllaceae
wt-di.fb*	Warm-temperate drought-intolerant forb	<i>Acalypha</i> , Acanthaceae, <i>Aconitum</i> , <i>Alocasia</i> , Araliaceae, <i>Amaranthus</i> , Apocynaceae, <i>Arabis</i> , Araceae, Araliaceae, <i>Arisaema</i> , <i>Artemisia</i> , Asclepiadaceae, <i>Aster</i> , Asteroideae, <i>Astragalus</i> , <i>Atractylodes</i> , Boraginaceae, <i>Bredia</i> , <i>Bupleurum</i> , <i>Campanula</i> , Campanulaceae, Caprifoliaceae, Caryophyllaceae, <i>Cassia</i> , <i>Chamaenerion</i> , <i>Chelidonium</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> , <i>Corydalis</i> , <i>Cruciferae</i> , <i>Desmodium</i> , <i>Dianthus</i> , Dipsacaceae, <i>Dipsacus</i> , Droseraceae, <i>Elsholtzia</i> , <i>Eomecon</i> , <i>Epilobium</i> , <i>Euphorbia</i> , Euphorbiaceae, <i>Fragaria</i> , <i>Galium</i> , <i>Gentiana</i> , Gentianaceae, Geraniaceae, <i>Geranium</i> , Gesneriaceae, <i>Glycyrrhiza</i> , <i>Guttiferae</i> , <i>Hedyotis</i> , <i>Hemerocallis</i> , <i>Hypericum</i> , <i>Impatiens</i> , Iridaceae, <i>Iris</i> , <i>Ixeris</i> , Labiatae, <i>Lamium</i> , <i>Lathyrus</i> , Leguminosae, <i>Lespedeza</i> , <i>Ligularia</i> , Liguliflorae, Liliaceae, <i>Lilium</i> , Linaceae, <i>Lobelia</i> , <i>Lysimachia</i> , Lythraceae, <i>Lythrum</i> , Malvaceae, <i>Mazus</i> , <i>Medicago</i> , Melastomataceae, <i>Melilotus</i> , <i>Mercurialis</i> , <i>Mimosa</i> , Mimosaceae, <i>Morina</i> ,

(continued on next page)

Table 1 (continued)

PFT code	PFT name	Pollen taxa
tr-di.fb*	Tropical drought-intolerant forb	Onagraceae, <i>Ophiorrhiza</i> , Oxalis, Papaveraceae, Papilionaceae, <i>Parnassia</i> , <i>Pedicularis</i> , <i>Phlomis</i> , Plantaginaceae, <i>Plantago</i> , <i>Platycodon</i> , <i>Polygala</i> , Polygonaceae, <i>Polygonum</i> , <i>Potentilla</i> , <i>Primula</i> , Primulaceae, <i>Pyrola</i> , Pyrolaceae, Ranunculaceae, <i>Ranunculus</i> , <i>Rheum</i> , <i>Rostellularia</i> , <i>Rubia</i> , Rubiaceae, <i>Rumex</i> , <i>Sanguisorba</i> , Saururaceae, <i>Saururus</i> , <i>Saussurea</i> , <i>Saxifraga</i> , Saxifragaceae, Scrophulariaceae, <i>Sesamum</i> , Solanaceae, <i>Solanum</i> , <i>Stellera</i> , <i>Taraxacum</i> , <i>Thalictrum</i> , Tropaeolaceae, Umbelliferae, <i>Urtica</i> , Urticaceae, <i>Valeriana</i> , Valerianaceae, Verbenaceae, <i>Vigna</i> , <i>Viola</i> , Violaceae, <i>Xanthium</i>
te-dt.fb	Temperate drought-tolerant forb	<i>Acalypha</i> , Acanthaceae, Aizoaceae, <i>Alocasia</i> , Amaranthaceae, <i>Amaranthus</i> , <i>Anagallis</i> , Apocynaceae, Araceae, Araliaceae, <i>Argemone</i> , <i>Argostemma</i> , <i>Arisaema</i> , <i>Artemisia</i> , Asclepiadaceae, <i>Aster</i> , Asteroideae, Berberidaceae, Boraginaceae, 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, <i>Convolvulus</i> , <i>Corydalis</i> , Cruciferae, <i>Desmodium</i> , <i>Dianthus</i> , Droseraceae, <i>Eranthemum</i> , <i>Euphorbia</i> , Euphorbiaceae, <i>Galium</i> , <i>Gentiana</i> , Gentianaceae, Geraniaceae, <i>Geranium</i> , Gesneriaceae, <i>Hedyotis</i> , <i>Hemiphragma</i> , <i>Impatiens</i> , Iridaceae, <i>Iris</i> , <i>Ixeris</i> , <i>Justicia</i> , Labiatae, <i>Lathyrus</i> , Leguminosae, Liguliflorae, Liliaceae, <i>Lilium</i> , <i>Lobelia</i> , Lythraceae, Malvaceae, Melastomataceae, <i>Melilotus</i> , <i>Mercurialis</i> , Moraceae, Onagraceae, <i>Ophiorrhiza</i> , <i>Oxalis</i> , Papilionaceae, <i>Phlomis</i> , <i>Phyllanthus</i> , <i>Piper</i> , Piperaceae, Plantaginaceae, <i>Plantago</i> , <i>Platycodon</i> , <i>Polygala</i> , Polygonaceae, <i>Polygonum</i> , <i>Potentilla</i> , <i>Primula</i> , Primulaceae, Proteaceae, Ranunculaceae, <i>Ranunculus</i> , <i>Reseda</i> , <i>Rostellularia</i> , <i>Rubia</i> , Rubiaceae, <i>Rumex</i> , <i>Rungia</i> , <i>Saussurea</i> , <i>Saxifraga</i> , Saxifragaceae, Scrophulariaceae, <i>Sesamum</i> , Solanaceae, <i>Solanum</i> , <i>Taraxacum</i> , <i>Thalictrum</i> , Tiliaceae, Umbelliferae, Urticaceae, Verbenaceae, <i>Veronica</i> , <i>Vigna</i> , <i>Viola</i> , Violaceae
eu-dt.fb rc.fb	Eurythermic drought-tolerant forb Rosette or cushion forb	<i>Aconitum</i> , Amaranthaceae, <i>Ambrosia</i> , <i>Androsace</i> , <i>Anthemis</i> , <i>Arabis</i> , <i>Arenaria</i> , <i>Artemisia</i> , <i>Aster</i> , Asteroideae, <i>Astragalus</i> , <i>Attractylodes</i> , <i>Atriplex</i> , Bignoniaceae, Boraginaceae, Campanulaceae, Carduioideae, Caryophyllaceae, <i>Centaurea</i> , <i>Cerastium</i> , <i>Cichorium</i> , <i>Cirsium</i> , Compositae, Convolvulaceae, Cruciferae, <i>Dianthus</i> , Dipsacaceae, <i>Echium</i> , <i>Filifolium</i> , <i>Filipendula</i> , <i>Gentiana</i> , Gentianaceae, Geraniaceae, <i>Hedysarum</i> , <i>Hemerocallis</i> , <i>Hypecoum</i> , <i>Incarvillea</i> , Iridaceae, <i>Iris</i> , <i>Ixeris</i> , <i>Kochia</i> , Labiatae, Leguminosae, <i>Lespedeza</i> , Liguliflorae, Liliaceae, <i>Lilium</i> , Linaceae, <i>Liquiliflora</i> , <i>Medicago</i> , <i>Onobrychis</i> , <i>Orobanchae</i> , <i>Oxytropis</i> , <i>Papaver</i> , Papaveraceae, Papilionaceae, <i>Peganum</i> , <i>Phlomis</i> , Plumbaginaceae, <i>Polemonium</i> , Polygonaceae, <i>Polygonum</i> , <i>Potentilla</i> , <i>Primula</i> , Primulaceae, <i>Pulsatilla</i> , Rosaceae, Rutaceae, <i>Salsola</i> , <i>Saussurea</i> , <i>Saxifraga</i> , Saxifragaceae, Scrophulariaceae, <i>Serratula</i> , <i>Sibbaldia</i> , Solanaceae, <i>Sophora alopecuroides</i> , <i>Stellera</i> , <i>Thalictrum</i> , <i>Thellungiella</i> , <i>Thymus</i> , <i>Tribulus</i> , Umbelliferae, <i>Verbascum</i> , <i>Veronica</i> , <i>Viola</i> , Violaceae, <i>Xanthium</i> , Zygophyllaceae, <i>Zygophyllum</i>
eu-dt.fb rc.fb	Eurythermic drought-tolerant forb Rosette or cushion forb	<i>Allium</i> , Amaryllidaceae, <i>Atriplex</i> , Chenopodiaceae, <i>Chenopodium</i> , <i>Limonium</i> , Nyctaginaceae, Plumbaginaceae, <i>Ajania</i> , <i>Androsace</i> , <i>Arenaria</i> , Asteroideae, Caryophyllaceae, <i>Cerastium</i> , Compositae, Dipsacaceae, <i>Gentiana</i> , Gentianaceae, Geraniaceae, Leguminosae, <i>Mazus</i> , <i>Oxytropis</i> , Papaveraceae, Papilionaceae, Plumbaginaceae, <i>Rhodiola</i> , <i>Saussurea</i> , <i>Saxifraga</i> , Saxifragaceae
ha	Halophyte	Chenopodiaceae, <i>Chenopodium</i> , <i>Salsola</i> , <i>Thellungiella</i>
hy*	Hydrophyte	<i>Acorus</i> , <i>Caltha</i> , Haloragidaceae, Onagraceae, <i>Phragmites</i> , Ranunculaceae, <i>Ranunculus</i> , Saururaceae, <i>Saururus</i> , Sparganiaceae, <i>Sparganium</i> , Thelypteridaceae, <i>Thelypteris</i> , <i>Trollius</i>
aq*	Aquatic	<i>Acorus</i> , <i>Alisma</i> , Alismataceae, Araceae, <i>Butomus</i> , <i>Ceratopteris</i> , Droseraceae, <i>Equisetum</i> , <i>Equisetum heleocharis</i> , Haloragidaceae, Hydrocharitaceae, <i>Menyanthes</i> , <i>Myriophyllum</i> , <i>Nelumbo</i> , <i>Nuphar</i> , Nymphaeaceae, <i>Nymphoides</i> , Parkeriaceae, <i>Phragmites</i> , Polygonum, <i>Potamogeton</i> , <i>Potamogetonaceae</i> , Ranunculaceae, <i>Ranunculus</i> , <i>Salvinia</i> , Sparganiaceae, <i>Sparganium</i> , <i>Typha</i> , Typhaceae
g	Grass	Gramineae, <i>Oryza sativa</i> , <i>Stipa</i>
s	Sedge	<i>Carex</i> , Cyperaceae, <i>Cyperus</i> , <i>Scirpus</i>
r*	Rush	Juncaceae
geo*	Geophyte	<i>Allium</i> , Amaryllidaceae, Araceae, <i>Arisaema</i> , Convolvulaceae, Cyperaceae, Iridaceae, <i>Iris</i> , Liliaceae, <i>Lilium</i>
ssuc	Stem succulent	Cactaceae, <i>Chrysosplenium</i> , <i>Euphorbia</i> , Euphorbiaceae
lsuc	Leaf succulent	Aizoaceae, Chenopodiaceae, <i>Chenopodium</i> , Crassulaceae, <i>Orostachys</i> , <i>Rhodiola</i> , <i>Sedum</i>
ar.f*	Arctic fern or fern ally	<i>Athyrium</i> , <i>Botrychium</i> , <i>Lunathyrium</i> , Lycopodiaceae, <i>Lycopodium</i>
eu.f*	Eurythermic fern or fern ally	Adiantaceae, <i>Adiantum</i> , Athyriaceae, <i>Athyrium</i> , <i>Botrychium</i> , <i>Coniogramme</i> , <i>Davallia</i> , Davalliaceae, <i>Dennstaedtia</i> , <i>Dennstaedtiaceae</i> , Dryopteridaceae, <i>Dryopteris</i> , <i>Equisetum</i> , <i>Equisetum heleocharis</i> , Filicales, <i>Gymnopteris</i> , Hemionitidaceae, Hymenophyllaceae, <i>Hymenophyllum</i> , <i>Lepisorus</i> , Lycopodiaceae, <i>Lycopodium</i> , <i>Lycopodium serratum</i> , Lygodiaceae, <i>Lygodium</i> , <i>Onychium</i> , <i>Ophioglossum</i> , <i>Osmunda</i> , Osmundaceae, Polypodiaceae, <i>Polypodium</i> , Pteridaceae, <i>Pteridium</i> , <i>Pteris</i> , <i>Pyrrhosia</i> , <i>Salvinia</i> , <i>Selaginella</i> , <i>Selaginella sinensis</i> , Sinopteridaceae, <i>Sinopteris</i> , Thelypteridaceae, <i>Thelypteris</i>
tr.f*	Tropical fern or fern ally	Angiopteridaceae, <i>Angiopteris</i> , <i>Antrophyum</i> , <i>Bauhinia</i> , <i>Botrychium</i> , <i>Ceratopteris</i> , <i>Cibotium</i> , <i>Cibotium barometz</i> , <i>Dicranopteris</i> , <i>Gleichenia</i> , Gleicheniaceae, Hemionitidaceae, <i>Hicriopteris</i> , <i>Histiopteris</i> , <i>Lindsaea</i> , Lycopodiaceae, <i>Lycopodium</i> , Lygodiaceae, <i>Lygodium</i> , <i>Microlepia</i> , Osmundaceae, <i>Parathelypteris</i> , Parkeriaceae, <i>Pellaea</i> , <i>Phymatosorus</i> , <i>Plagiogyria</i> , Plagiogyriaceae, Pteridaceae, <i>Pteris</i> , <i>Schizaea</i> , <i>Vittaria</i>
tf	Tree fern	<i>Alsophila</i> , Cyatheaceae
epl*	Epiphyte	No taxa
rps*	Root parasite	<i>Cuscuta</i> , Lauraceae, Loranthaceae, <i>Monotropa</i> , <i>Orobanchae</i>
m*	Moss	<i>Sphagnum</i>

while collecting pollen samples. In sites where modern vegetation information was not available, it was simply recorded (e.g. only forest, grassland, or shrubland, without any species composition), or where vegetation data were ambiguous, information derived from the digitized vegetation map of China at 1:1 million scale (EBVAC, 2001) was used to define the biomes in conjunction with observed vegetation records from surrounding sites. Wherever agricultural vegetation has been mapped onto a site or the mapped vegetation is considered to be incorrect, we have usually used the potential natural vegetation based on bioclimatic information and the observed vegetation from surrounding sites. The observed “real” modern

biomes were then assigned (Fig. 2a; Appendix A) according to the observed and mapped vegetation types as well as the principle vegetation of China (ECVC, 1980; EBVAC, 2001) and biome characteristics (Table 2).

The surface pollen assemblages not only reflect the natural vegetation but also vegetation affected by human activity and land use. Therefore the pollen-based reconstruction of modern biomes incorporates information on anthropogenic biomes. The observed biomes also reflect information from natural and disturbed vegetation. Comparison between the observed and reconstructed biomes therefore implies a level of disturbance by human activity. However

Table 2
Characteristics of Chinese biomes.

Biome	Structure	Dominant PFT(s)	Characteristic taxa	Terminology used in the Chinese literature for equivalents	Distribution in China
Cold deciduous forest	More or less open canopy forest, medium to tall cold-deciduous malacophyll broad-leaved trees, with a rich understory of shrubs, forbs and mosses in moist habitats or a depauperate understory of shrubs and lichens in dry habitats	Boreal deciduous needle-leaved trees, boreal cold-deciduous malacophyll broad-leaved trees	<i>Larix, Betula</i>	Cold-temperate deciduous needle-leaved forest	northern Daxingan Mountains, Tianshan and Altai Mountains and subalpine regions around the southeastern Tibetan Plateau
Cold evergreen needle-leaved forest	Closed canopy forest of evergreen needle-leaved trees with a rich understory of shrubs, forbs and mosses	Boreal evergreen needle-leaved trees	<i>Abies sibirica, A. fabri, Picea obovata, P. purpurea</i>	Cold-temperate evergreen needle-leaved forest; taiga	Daxingan and Changbai Mountains; Wutai, Yan, Luliang and Taihang Mountains; Qinling and Daba Mountains; Altai, Tianshan, Qilian, Helan and Yin Mountains; and eastern and southern slopes of the Tibetan Plateau, 1100–4300 m
Cool-temperate evergreen needle-leaved and mixed forest	Closed to open canopy forest of evergreen needle-leaved trees and deciduous broad-leaved trees	Cool-temperate evergreen needle-leaved trees, boreal cold-deciduous malacophyll broad-leaved trees	<i>Pinus sylvestris</i> var. <i>mongolica, Betula, Populus</i>	Cold mixed forest	High mountains in northeastern, western and southwestern China
Cool evergreen needle-leaved forest	Closed to open canopy forest of evergreen needle-leaved trees	Boreal and cold-temperate evergreen needle-leaved trees	<i>Abies nephrolepis, Picea jezoensis, P. schrenkiana, Pinus, Sabina</i>	Cool conifer forest	Daxingan Mountains, Altai Mountains, eastern high slope of the Tibetan Plateau
Cool mixed forest	Closed to open canopy forest with evergreen needle-leaved trees and deciduous broad-leaved trees	Boreal and cold-temperate evergreen needle-leaved trees, temperate spring-frost tolerant cold-deciduous malacophyll broad-leaved trees	<i>Pinus koraiensis, Larix, Abies, Picea, Betula, Tilia, Fraxinus, Acer</i> (northeast China); <i>Tsuga, Abies, Picea, Acer, Betula, Pinus</i> (high mountains in southwest China)	Cool-temperate mixed conifer broad-leaved forest	Changbai, Xiaoxingan and Zhangguangcai Mountains; high mountains in southwestern China and southern Tibetan Plateau
Temperate deciduous broad-leaved forest	More or less open canopy forest (ground cover between 40 and 70%) of deciduous broad-leaved trees	Temperate spring-frost avoiding and intolerant cold-deciduous malacophyll broad-leaved trees, sometimes with temperate evergreen needle-leaved trees and eurythermic evergreen needle-leaved trees	<i>Quercus, Castanea, Acer, Alnus, Ulmus, Populus, Pinus tabbulaeformis, Pinus densiflora, Platycladus</i>		northern, central, northwestern and southwestern China
Warm-temperate evergreen broad-leaved and mixed forest	Closed canopy forest of tall malacophyll and sclerophyll broad-leaved trees, with deciduous broad-leaved trees, and deciduous and evergreen needle-leaved trees	Warm-temperate evergreen malacophyll and sclerophyll broad-leaved trees, temperate spring-frost intolerant cold-deciduous malacophyll broad-leaved trees, warm-temperate evergreen and deciduous needle-leaved trees	<i>Castanopsis, Lithocarpus, Cyclobalanopsis, Schima, Machilus, Cinnamomum, Phoebe, Quercus, Liquidamber, Platycarya, Fagus, Metasequoia, Glyptostrobus, Pseudolarix, Taxodium, Pinus</i> (<i>massoniana, yunnanensis, khaya, griffithii</i>), <i>Keteleeria, Cupressus, Cunninghamia</i>	Northern and central subtropical evergreen broad-leaved forest, typical evergreen broad-leaved forest	southern China (northern to central subtropical region)
Warm-temperate evergreen broad-leaved forest	Closed canopy forest of tall warm-temperate evergreen malacophyll and sclerophyll broad-leaved trees in the first layer, with sparse warm-temperate deciduous broad-leaved trees in the second and third layers	Warm-temperate evergreen malacophyll and sclerophyll broad-leaved trees	<i>Castanopsis, Cryptocarya, Elaeocarpus, Engelhardtia, Schima, Syzygium, Lauraceae, Fagaceae, evergreen Quercus</i> (<i>aquifolioides, pannosa, gilliana, spinosa, senescens, spathulata</i>)	Monsoon evergreen broad-leaved forest, montane and river valley sclerophyll evergreen broad-leaved forest	southern China (southern subtropical region); high mountains and dry river valley of southwestern China and southeastern Tibetan Plateau
Tropical semi-evergreen broad-leaved forest	Closed canopy forest dominated by tropical mesic drought-deciduous broad-leaved trees with more or less tropical evergreen malacophyll broad-leaved trees; some proportion of the canopy leaves fall in the dry season	Tropical mesic drought-deciduous malacophyll broad-leaved trees, tropical evergreen malacophyll broad-leaved trees, tropical evergreen malacophyll low to high shrubs, drought-tolerant lianas and vines	<i>Ficus, Gironniera, Syzygium, Steculia, Vatica, Parashorea, Burretiodendron</i>	Semi-evergreen seasonal forest; tropical seasonal forest	southern China (south of the Tropic of Cancer) and southern slope of Himalayan Ranges
Tropical evergreen broad-leaved forest	Closed canopy forest with tall tropical evergreen broad-leaved malacophyll	Tropical evergreen sclerophyll and malacophyll broad-leaved trees, tropical	<i>Myristica, Vatica, Hopea, Dipterocarpus, Terminalia, Pomelia</i>	Tropical rainforest	southernmost mainland of China, southern Taiwan Island and Hainan Island

(continued on next page)

Table 2 (continued)

Biome	Structure	Dominant PFT(s)	Characteristic taxa	Terminology used in the Chinese literature for equivalents	Distribution in China
Tropical deciduous broad-leaved forest and woodland	and sclerophyll trees, shrubs, lianas and vines Open canopy forest dominated by medium tropical xeric drought-deciduous trees with sparse shrubs and herbs; most or all the canopy leaves fall in the dry season (5–7 months)	evergreen malacophyll low to high shrubs, drought intolerant lianas and vines Tropical xeric drought-deciduous malacophyll broad-leaved trees, eurythemic mesic drought-deciduous malacophyll low or high shrubs	<i>Bombax</i> , <i>Albizia</i> , <i>Terminalia</i> , <i>Lannea</i>	Seasonal deciduous forest	hot and dry river vallies in southern Yunnan Province, and western Hainan Island
Temperate xerophytic shrubland	Sparse to open, clumped or un-clumped vegetation dominated by small-leaved and micro-leaved small trees and shrubs	Small-leaved and micro-leaved trees and low/high shrubs, temperate drought-tolerant forbs	<i>Artemisia</i> , <i>Ephedra</i> , <i>Chenopodiaceae</i> , <i>Caragana</i>	Forested dry steppe	northern to western China
Temperate grassland	Dense to sparse treeless vegetation dominated by graminoids and forbs with few shrubs	Graminoids, temperate forbs and shrubs	<i>Stipa</i> , <i>Leymus</i> , <i>Festuca</i> , <i>Cleistogens</i> , <i>Agropyron</i> , <i>Artemisia</i>	Typical (dry) steppe, meadow steppe, desert steppe	northern and western China, including the Tibetan Plateau
Desert	Bare ground with sparse grasses and shrubs	Graminoids, temperate drought-tolerant shrubs	<i>Haloxylon</i> , <i>Ephedra</i> , <i>Zygophyllum</i> , <i>Nitraria</i> , <i>Caragana</i> , <i>Calligonum</i> , <i>Reaumuria</i> , <i>Salsola</i> , <i>Sympegma</i> , <i>Artemisia</i> , <i>Ajania</i> , <i>Papaver</i> , <i>Oxytropis</i> , <i>Draba</i> , <i>Saussurea</i> , <i>Caryophyllaceae</i> , <i>Saxifragaceae</i> , <i>Rhodiola</i> , <i>Carex</i>	Little tree desert, shrub desert, semi-shrub desert	western China, including the Tibetan Plateau
Cushion-forb tundra	Discontinuous treeless vegetation characterised by rosette or cushion forbs, grasses, mosses and lichens	Rosette or cushion forbs, graminoids	<i>Kobresia</i> , <i>Stipa</i> , <i>Carex</i> , <i>Polygonum</i> , <i>Gentiana</i> , <i>Festuca</i> , <i>Artemisia</i>	High mountain tundra	Changbai Mountains, Tianshan and Qilian Mountains, eastern Tibetan Plateau, Yulong Mountains
Graminoid and forb tundra	Treeless and predominantly herbaceous vegetation dominated by alpine forbs, graminoids, and lichens	Alpine forbs, graminoids	<i>Dryas</i> , <i>Vaccinium</i> , <i>Rhododendron xanthastephonum</i> , <i>Salix rotundifolia</i> , <i>Pedicularis</i> , <i>Arenaria</i> , <i>Thylacospermum</i> , <i>Androsace</i> , <i>Potentilla</i> , <i>Sibbaldianthe</i> , <i>Acantholimon</i> , <i>Oxytropis</i> , <i>Astragalus</i> , <i>Ceratoides</i>	High-cold meadow, high-cold steppe	Tibetan Plateau and its periphery, Qilian, Tianshan, Parmir, Taibai and Xiaowutai Mountains
Prostrate dwarf-shrub tundra	Treeless vegetation dominated by prostrate dwarf shrubs, graminoids, arctic forbs, true mosses and lichens	Alpine prostrate dwarf shrubs, graminoids, arctic forbs	<i>Sabina</i> , <i>Juniperus</i> , <i>Dasiphora</i> , <i>Empetrum</i> , <i>Vaccinium</i>	High mountain dwarf vegetation, high-cold desert	Changbai Mountains, Qilian Mountain, Tibetan Plateau, Tianshan Mountains
Erect dwarf-shrub tundra	Treeless vegetation dominated by erect dwarf shrubs, with grasses, true mosses and lichens	Erect dwarf shrubs, graminoids		High-cold shrubland (evergreen conifer shrub)	Altai and Tianshan Mountains, Changbai Mountains, Tibetan Plateau and high mountains around its periphery
Low and high shrub tundra	Treeless vegetation dominated by deciduous or evergreen low or high shrubs, sometimes with tussock-forming graminoids and true mosses, bog mosses, and lichens	Deciduous or evergreen low or high shrubs, graminoids	<i>Rhododendron capitatum</i> , <i>Betula rotundifolia</i> , <i>Salix oritrepha</i> , <i>S. cupularis</i> , <i>Hippophae</i> , <i>Spiraea</i>	High-cold shrubland, evergreen sclerophyll shrubland, deciduous broad-leaved shrubland	Tianshan, Altai and Qilian Mountains, Changbai Mountains, eastern Tibetan Plateau, high mountains in southwestern China, Taibai Mountains, Yushan Mountains

Please note that a vegetation type may be assigned to different biomes because it is distributed in broad altitudinal range (e.g. *Pinus*, *Picea* and *Abies* forests) and/or broad horizontal belt (e.g. many kinds of steppes, deserts and shrublands), but here it is only assigned to one biome due to insufficient information in the digitized vegetation map.

past vegetation reconstructed from pollen is usually expressed as potential natural biomes. Human disturbed biomes are concealed from the reconstruction. Therefore more information about the modern potential natural biomes (and also the anthropogenic biomes) is needed in order to better reconstruct biomes from pollen records.

For this purpose we used the potential natural biomes predicted by the BIOME4 global vegetation model with coupled biogeographical and biogeochemical processes (Kaplan, 2001; Kaplan et al., 2003). The model is driven by gridded monthly mean temperature, precipitation, cloudiness and minimum temperature, soil properties and a fixed CO₂ concentration of 360 ppm. The original climate data was derived from averaged long-term observations at 1814 weather stations between 1971 and 2000 (China Meteorological Administration, unpublished). The data was interpolated into 10 km grid cells by the thin plate

smoothing spline surface fitting technique (Hutchinson, 2006) on the basis of the STRM digital elevation model (Farr et al., 2007). The soil water holding capacity and percolation rate compiled by Kaplan (2001) were derived from a global digital soil map of the Food and Agriculture Organization (FAO) of the United Nations.

The model originally predicted 26 biomes in China, of which 19 appeared in surface pollen sampling sites (modeling grids), but such 19 simulated biomes do not match exactly with the 19 biomes used for biomization (Tables 2 and 3). The biomes used for biomization are derived to a great extent from BIOME4 model (Ni et al., 2010), so that we combined or separated some biomes from BIOME4 simulation to match the 19 biomes used for biomization based on their consistent definitions. On the other hand, some simulated biomes are distributed in fewer sites, for example the temperate conifer forest, evergreen and

Table 3
Defining biomes of China using key plant functional types (PFTs).

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

deciduous taiga, and tropical savanna which can be assigned to close biomes with larger distributions. The simulated temperate deciduous forest and temperate conifer forest were combined to form a biome of temperate deciduous broad-leaved forest that in definition match the same biome represented in the pollen samples. The simulated warm-temperate mixed forest was separated by its latitudinal range into warm-temperate evergreen broad-leaved and mixed forest ($>24^{\circ}\text{N}$), and warm-temperate evergreen broad-leaved forest ($<24^{\circ}\text{N}$). Evergreen taiga/montane forest was combined with cold evergreen needle-leaved forest, deciduous taiga/montane forest with cold-deciduous forest, and tropical savanna with tropical deciduous broad-leaved forest. Other simulated biomes are the same as for the biomization used (Tables 2 and 3).

3. Results and discussion

3.1. Zonal biome reconstruction

Pollen-based reconstruction shows a relatively clear spatial distribution of modern biomes throughout China (Fig. 2b). Site by site comparison with the vegetation observations (Fig. 2a) indicated a 68.8% agreement (Table 4), implying that the application of the biomization method to Chinese surface pollen records was successful.

3.1.1. Biome distribution and comparison

Cold-deciduous forest (CLDE) was only correctly reconstructed in 15 samples (26.8%; Table 4) in mountainous areas of northeastern and northwestern China and in subalpine regions of southeastern Tibet (Fig. 2b). Other sites were wrongly assigned to cold evergreen needle-leaved forest (CLEG), cool evergreen needle-leaved forest (COEG), and cool mixed forest (COMX) within similar areas as CLDE, and also to prostrate dwarf-shrub tundra (PROS) in northeastern China (Fig. 2b). Six COMX sites were incorrectly assigned to CLDE. The reconstructed CLDE also occurred in subtropical areas as a result of seven samples from warm-temperate evergreen broad-leaved and mixed forest (WTEM) in mountains being wrongly identified as CLDE (Fig. 2b and Table 4).

Samples correctly reconstructed as CLEG (57.4%) mainly originate from the same mountainous areas as CLDE (Fig. 2b), which are geographically coincident with the actual vegetation (Fig. 2a). CLEG was also wrongly assigned to COMX and temperate xerophytic shrubland (TEXE), whilst COEG, COMX and temperate grassland (TEGR) were incorrectly identified as CLEG (Table 4).

There are only three samples of cold-temperate evergreen needle-leaved and mixed forest (CLMX) which often coexists with CLDE and CLEG and occupies very small areas in northeastern China (Table 2). The biome was not correctly reconstructed (Table 4).

Modern biomes of COEG and COMX occur together in both northeastern China, on the eastern and northern Tibetan Plateau and in the high mountains in central and eastern China (Table 2). They were largely correctly reconstructed (64.4% and 65%, respectively; Table 4). COEG and COMX were incorrectly assigned in a few sites to CLEG, COMX, TEXE and TEGR, while some of CLDE, COMX and TEGR were wrongly identified as COEG and COMX (Table 4). Furthermore COMX was wrongly assigned to PROS in 17 sites and as temperate deciduous broad-leaved forest (TEDE) in seven sites (Fig. 2b and Table 4).

The incorrect assignment of cold- and cool-temperate forests results mainly from the fact that these biomes contain the same widespread needle-leaved pollen taxa (*Abies*, *Picea*, *Pinus* and *Tsuga*) and therefore the same key PFTs. Incorrect identification of forest biomes and some treeless biomes of grassland, shrubland and tundra are the likely result of two factors: the local existence of conifer trees in small patches and/or the long-distance transportation of conifer tree pollen from forested areas, and the share in forest and non-forest biomes of the same pollen taxa but assigned to different shrub PFTs used to differentiate different biomes. For example, *Betula* and *Salix* were assigned to boreal cold-deciduous malacophyll broad-leaved low and high shrub, and *Rhododendra* and *Ledum* to boreal evergreen malacophyll broad-leaved low and high shrub (Table 1), which were used to define several cold-temperate forests (Table 3). However *Rhododendra* and *Ledum* were also assigned to arctic evergreen malacophyll broad-leaved low and high shrub, and *Betula* and *Rhododendra* to arctic cold-deciduous malacophyll broad-leaved erect and prostrate dwarf shrubs (Table 1), which were used to define tundra biomes (Table 3). These led likely to wrong assignment between cold-temperate forests and tundra biomes.

64.2% of samples of TEDE, which is widely distributed in northern, central, northwestern and southwestern China (Table 2), were correctly identified (Table 4 and Fig. 2b). Eight samples of TEDE were incorrectly assigned as cold-temperate forests, and seven COMX sites were wrongly identified as TEDE, in the Changbai Mountains where deciduous broad-leaved forest grows in mosaic patches with evergreen conifer and mixed forests (Table 2). 22 sites of TEDE were incorrectly classified as non-forest biomes (TEXE, TEGR and PROS).

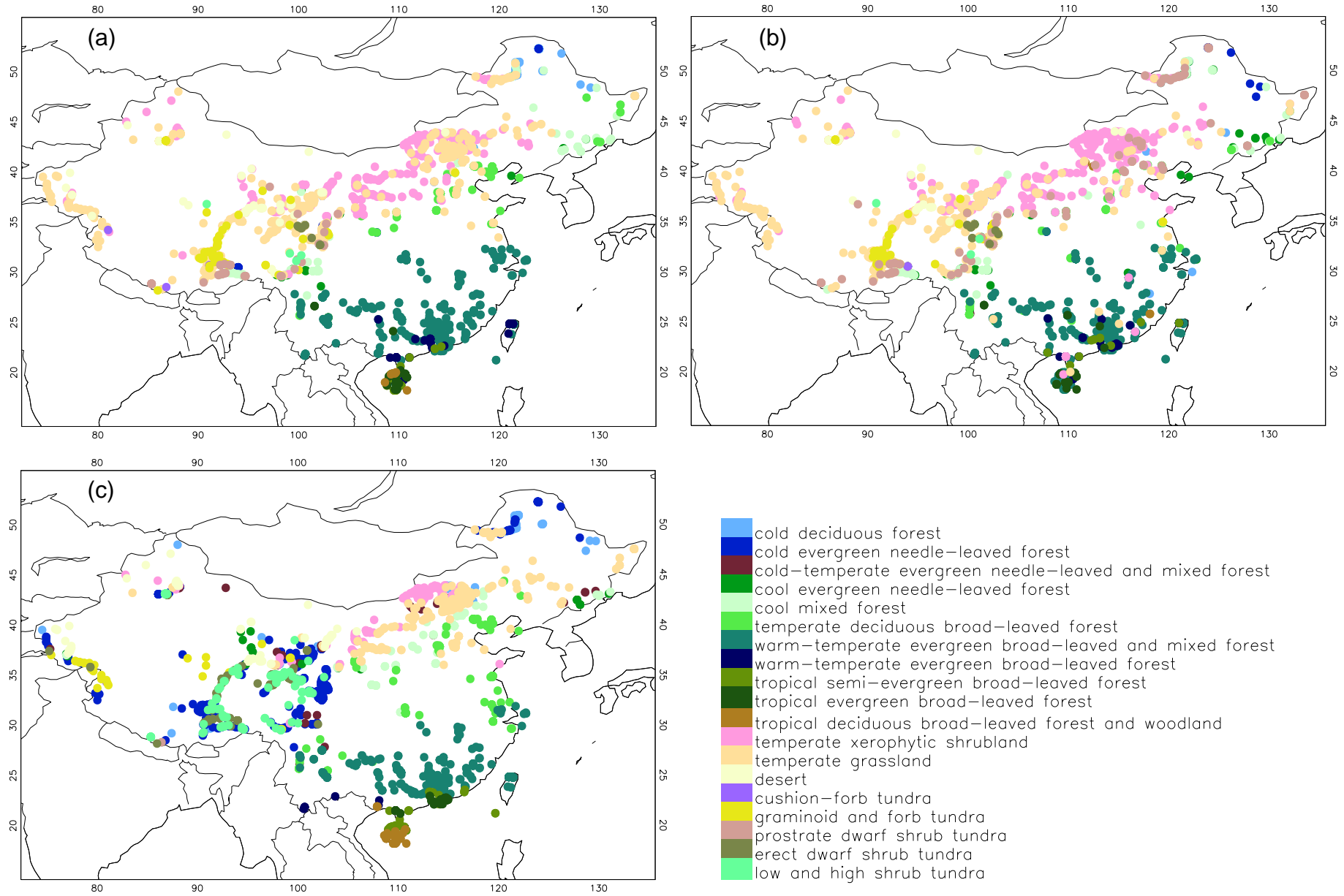


Fig. 2. The observed modern biomes (a) based on field observations and vegetation map of China, the reconstructed biomes (b) based on modern surface pollen, and the potential biome (c) predicted by BIOME4 model.

Table 4
Comparison between observed and reconstructed modern biomes in China. The biome codes are given in Table 3.

Observed versus reconstructed biomes	Mega-biomes	CLDE	CLEG	CLMX	COFG	COMX	TEDE	WTEM	WTEG	TRSE	TREG	TRDE	TEXE	TEGR	DESE	CUSH	DRYT	PROS	DWAR	SHRU	Observed
CLDE	BOFO	15	9	10	11	1							2					8			56
CLEG		3	27	1	5						1		6	2	1	1					47
CLMX														1				2			3
COFG	CTFO	1	4	47	6	2	1	2					7	4			1				73
COMX		6	8	21	132	7							8	4				17			203
TEDE	TEFO		2	4	4	61	1	1			1		14	4				4			95
WTEM	WTFO	7		3	1	17	448	17	4	5	2	2	2	4				4			512
WTEG							37	24	7	7			7								75
TRSE	TRFO						16	1	6	6	1			1							30
TREG		1					11		4	15	1										32
TRDE							6						1								8
TEXE	GRSH	3	6	2	5	2		4	328	18	3	4	328	18	3		1	4			365
TEGR								4	144	404	5	4	5	19	18		12	31	1	1	643
DESE													5	2			1	1			44
CUSH													1	2			1	1			4
DRYT													1	32			35	2	2		72
PROS													2	6			3	32			50
DWAR														2				5			8
SHRU														2							8
Reconstructed		36	56	2	102	185	91	524	42	21	27	12	527	504	27	1	53	103	8	3	2324

BOFO: boreal forest; CTFO: cool-temperate forest; TEFO: temperate forest; WTFO: warm-temperate forest; TRFO: tropical forest; GRSH: grassland and dry shrubland; DESE: desert; and ALTU: alpine tundra.

The incorrect assignment of 17 WTEM samples leads to a slight southern expansion of this forest (Fig. 2b).

WTEM and the pure warm-temperate evergreen broad-leaved forest (WTEG) are mainly distributed in the wide subtropical regions of southern China (Table 2). Compared to other forest biomes, the reconstruction of WTEM was the most accurate (87.5%) which fits well with our field observations (Fig. 2a and b). However there remain 17 sites which were incorrectly assigned to WTEG and a further 17 sites which were assigned to TEDE whilst some other sites were assigned to forest and non-forest biomes (Table 4). The WTEG biome is mostly distributed in areas between WTEM and tropical vegetation, but also often occurs in the WTEM area (Fig. 2a and Table 2). In comparison, WTEG was less well reconstructed (32%) than WTEM and it has been wrongly assigned to WTEM (Table 4) because they share the same evergreen woody PFTs (Table 3).

Tropical semi-evergreen broad-leaved forest (TRSE), tropical evergreen broad-leaved forest (TREG) and tropical deciduous broad-leaved forest and woodland (TRDE) occur in the southernmost mainland of China, Hainan Island and Taiwan (Table 2). These biomes were not always correctly reconstructed, and were often confused with each other and with the warm-temperate forests (Table 4). There was no assignment of TRDE which was wrongly assigned to WTEM and from temperate shrubland and grassland (Table 4).

TEXE and TEGR coexist in the same arid and semi-arid areas of northern and northwestern China and on the Tibetan Plateau (Fig. 2a and Table 2). The pollen samples (accounting for 43% of the surface sites) were quite well reconstructed at 90% and 63% for TEXE and TEGR, respectively (Fig. 2b and Table 4), but they were often confused with each other and were also wrongly identified as cold-temperate forests, desert and tundra biomes, particularly the graminoid and forb tundra (DRYT) and PROS, and vice versa (Table 4).

The correctly reconstructed desert biome (DESE), occupying approximately 20% of the whole country and stretching from central northern to western China (ECVC, 1980), was found to be 40.9% (Fig. 2b) as some samples on the Tibetan Plateau were incorrectly assigned to the TEGR, TEXE and tundra biomes. Eight samples from TEXE and TEGR were also wrongly identified as DESE (Table 4).

Modern pollen samples assigned to tundra biomes are largely distributed on the Tibetan Plateau (Fig. 2a). Only four samples of cushion-forb tundra (CUSH) were reconstructed. Four other tundra biomes: DRYT, PROS, erect dwarf-shrub tundra (DWAR) and SHRU were all only partially reconstructed (Table 4). However DRYT was often confused with TEGR, whereas TEGR, CLDE and COMX were all wrongly identified as PROS (Table 4). The tundra biomes of DRYT and PROS occur in the Daxingan and Changbai Mountains and on the Inner Mongolian and Loess Plateaus (Fig. 2b) which should mainly consist of TEGR and cold/cool-temperate forests (Fig. 2a).

3.1.2. Factors affecting biome assignment and reconstruction

Map and data comparisons indicated that there is good agreement between the observed and reconstructed modern Chinese biomes, but incorrect assignments have occurred in some instances. Previous pollen-based biome reconstructions in China encountered similar problems. These include the incorrect assignment of cold- and cool-temperate forests, tropical and warm-temperate forests, and steppe, desert and tundra biomes (Yu et al., 1998, 2000; Ni et al., 2010). The same problems also exist in central and northern Eurasia (Tarasov et al., 1998) where tundra and forest biomes (taiga or cold deciduous forest) and desert and steppe biomes were mistaken for each other, especially in large river valleys and lakes. Taiga and cool conifer forests and cold and cool mixed forests and temperate deciduous forest were wrongly assigned in some places (Tarasov et al., 1998). These issues were also encountered in other European surface samples and are viewed as a weakness of the biomization method (Prentice et al., 1996).

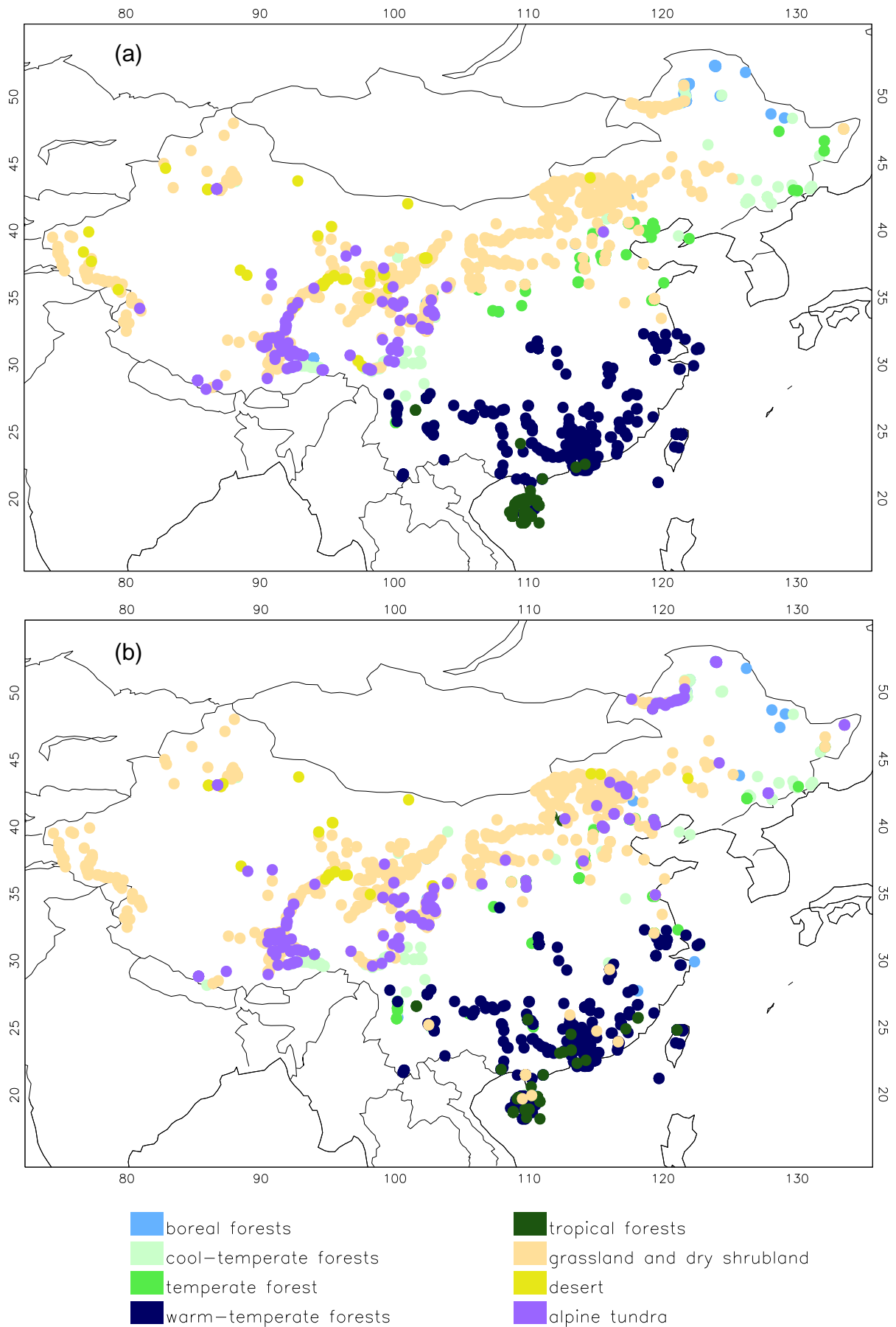


Fig. 3. Observed (a) and reconstructed (b) modern mega-biomes.

There are several factors which account for the incorrect assignment of modern biomes in China. The principal reason is that biomes within the same or neighboring bioclimatic zones (e.g. cold-temperate and cool-temperate, and warm-temperate and tropical zones) are defined by the same combination of PFTs which are clearly not distinguishable for each biome during biomization. Another factor to consider is the long-distance transportation of pollen grains from forests to shrubland, steppe and desert, and vice versa, and from low to high altitudes. This was confirmed in previous reconstructions from China and Eurasia (Tarasov et al., 1998; Yu et al., 1998, 2000; Ni et al., 2010). In addition, pollen production, representation and dispersion affect the agreement between pollen and vegetation at local and regional scales (e.g. Prentice, 1985). Quantitative vegetation reconstruction based on pollen data should take these factors into account, e.g. by using model REVEALS and LOVE (Sugita, 2007a,b).

Pollen identification is also a key problem which is difficult to resolve. The assignment from pollen taxa to PFTs (and then to biomes) at family and genus levels rather than at species level reduced the amount of ecological information available for biome assignment. For example, the genus *Pinus* is found in various forest vegetation zones in eastern China and in mountainous regions. *Pinus sylvestris* var. *mongolica* is an indicator of cold mixed forest, whilst *Pinus koraiensis* is found in cool mixed forests, *Pinus tabulaeformis* in temperate deciduous forests, *Pinus massoniana* in warm-temperate forests, and *Pinus yunnanensis* is an indicator of tropical forest (ECVC, 1980). The difficulty in identifying these species within pollen records makes it almost impossible to distinguish biomes based on the *Pinus* genus.

It is also likely that anthropogenic modification of pollen assemblages has affected the assignment of pollen to biome, by the plantation of coniferous trees (e.g. *Pinus* and *Cunninghamia*) in many forest areas of eastern China, and agricultural activities across the whole country. The under-representation of some pollen taxa is an unresolved palynological problem for vegetation reconstruction. Problems with modern vegetation observation and mapping also influence the comparison of biomes.

3.2. Biome reconstruction and simulation

Comparing the observed (Fig. 2a) and reconstructed biomes (Fig. 2b) with the vegetation model-simulated biome data (Fig. 2c) indicates low correlations of 28.4% and 24.8%, respectively (data not shown). Instances of incorrect identification occurred in all biomes, especially the cool-temperate forests, warm-temperate forests, temperate grassland and shrubland, and tundra biomes. This reveals a large discrepancy between the 'real' and potential vegetation.

The global vegetation models of the BIOME family have been successfully used in modern, past and future simulations of large-scale vegetation (Prentice et al., 1992, 2007; Kaplan, 2001; Kaplan et al., 2003). BIOME3 does a good job of predicting the biomes in China (Ni et al., 2000). The BIOME4 model developed from the BIOME3 also does a reasonable job of simulating the pattern of Chinese biomes (Ni, unpublished data). However the model simulation is performed on

the basis of grid cells. The dominant biome for each grid cell of $10 \times 10 \text{ km}^2$ was simulated, but as the pollen-based reconstruction is site-specific the larger grid cell area does not accurately reflect the dominant biome. This is one of the main reasons for the discrepancy between the reconstructed and simulated biomes. Vegetation models also have their shortcomings in simulating global and regional vegetation (e.g. Kaplan, 2001; Prentice et al., 2007). Vegetation simulation in China has similar problems (e.g. Ni et al., 2000) which impact upon comparisons between reconstructed and simulated biomes. Biases in climate and soil data furthermore reduce the accuracy of biome simulation. The considerable problems associated with biome assignment from vegetation types and the disadvantages of biomization described previously should be carefully considered prior to combining palaeo-environmental data with model outputs for modern pollen assemblages. The anthropogenic biome impact on biomes also needs to be assessed and involved in vegetation modeling and in the pollen biomization procedure.

3.3. Mega-biome comparison

Biomes which have similar bioclimatic controls and share the same PFTs were often confused with each other (Fig. 2a and b). This makes direct comparisons between biomes somewhat ambiguous. We have therefore grouped biomes that occur within the same bioclimatic zone into mega-biomes. This reclassification results in a more accurate spatial pattern between biomes (Fig. 3). Boreal forest (BOFO) occupied the coldest northeastern and northwestern areas of China and southeast Tibet (Fig. 3a; some sites in the northwest and Tibet were concealed by the altitudinal distribution of other sites), was correctly allocated in more than 50% of places (Fig. 3b and Table 5). Cool-temperate forest (CTFO) was correctly reconstructed in northern China and on the southeast Tibetan Plateau (75%). Temperate forest (TEFO) was distributed across the central and northern regions of China, whilst the warm-temperate forest mega-biome (WTFO) was correctly assigned in 90% of areas and occurs in subtropical southern China (Fig. 3 and Table 5). However tropical forest (TRFO) distributed in the southernmost Chinese mainland and in Taiwan and Hainan (Fig. 3a and b) was only correctly assigned in 50% of cases. The grassland and dry shrubland mega-biome (GRSH) in northern and western China (Fig. 3a) has a correlation factor of 89% (Table 5). However this value decreases in subtropical China (Fig. 3b) as a result of anthropogenic activity. The desert biome remains the same as previously described, but a poor correlation is clear between GRSH and tundra (Table 5). All tundra biomes (CUSH, DRYT, PROS DWAR and SHRU) were grouped into one mega-biome of alpine tundra (ALTU). Its modern distribution occurs mostly on the Tibetan Plateau and in the high mountains of northern and western China (Fig. 3a), however there were also a number of incorrect assignments in the eastern part of northern China (Fig. 3b) with a correlation of 60% (Table 5). Overall, the regrouping of the observed and reconstructed biomes (Fig. 3) shows greater agreement (80.6%) than the non-grouped biomes (Fig. 2).

Table 5
Comparison between observed and reconstructed modern mega-biomes in China.

Observed versus reconstructed biomes	BOFO	CTFO	TEFO	WTFO	TRFO	GRSH	DESE	ALTU	Observed
Boreal forest (BOFO)	54	27		1	1	11	1	11	106
Cool-temperate forest (CTFO)	19	206	8	2		23		18	276
Temperate forest (TEFO)	2	8	61	1	1	18		4	95
Warm-temperate forest (WTFO)	9	4	17	526	18	13			587
Tropical forest (TRFO)	1	1		34	32	2			70
Grassland and dry shrubland (GRSH)	9	32	5	2	8	894	8	50	1008
Desert (DESE)						24	18	2	44
Alpine tundra (ALTU)		9				46		83	138
Reconstructed	94	287	91	566	60	1031	27	168	2324

3.4. Altitudinal biome distribution

Whilst all of the previously described biomes and mega-biomes have marked zonal distribution changes, altitudinal changes are often not clearly highlighted (Figs. 2 and 3). Therefore the biome distributions within six mountainous regions were also separately mapped (Fig. 4). In the Daxingan Mountains of northeast China, the vertical distribution of observed biomes from lower to higher

elevations is TEXE, TEGR, COMX and then CLDE (Fig. 4a). A number of samples of TEGR were wrongly assigned as PROS and some of CLDE were wrongly assigned as COEG and COMX. There are overlaps between the different biome boundaries and also altitudinal biome change is not obvious because of the relatively low altitudes (Fig. 4a).

The Tianshan Mountains in northwestern China has different vegetation patterns on the northern (alpine and subalpine meadow, montane conifer forest, steppe and shrubland, and desert) and

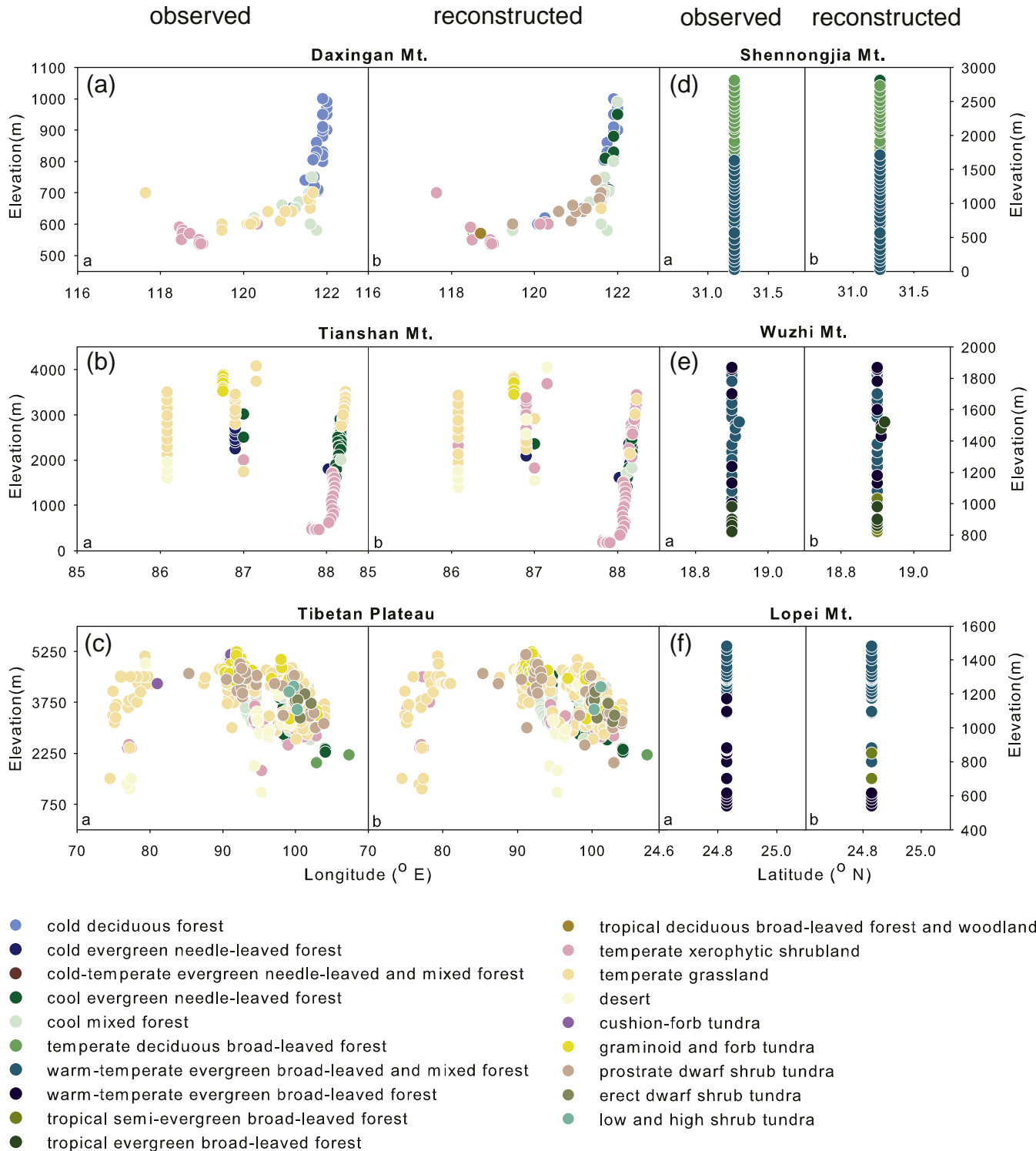


Fig. 4. Altitudinal distributions of observed and reconstructed biomes in six high mountain ranges: (a) Daxingan Mt.; (b) Tianshan Mt.; (c) Tibetan Plateau; (d) Shennongjia Mt.; (e) Wuzhi Mt.; and (f) Lopei Mt.

southern slopes (steppe and sparse succulent vegetation). Pollen data from the northern slopes indicate a gradient change between several biomes: shrubland and desert in the low elevations, needle-leaved forests at mid-elevations, and steppe (meadow) mixed with small amounts of tundra at higher elevations. The reconstructed TEXE biome covers a large altitudinal range in the Tianshan Mountains (Fig. 4b). An incorrect assignment of xerophytic shrubland at high elevations is due to the transport of shrub pollen from the lowland deserts to the upland regions.

The Tibetan Plateau has extremely complex vegetation patterns as shown in Fig. 2. There is a general trend from subalpine coniferous forest and shrubland in the southeast, to alpine meadow and alpine steppe in the central region, and to alpine desert in the northwest (ECVC, 1980). A total of 616 samples from the Tibetan Plateau produced 11 biomes, which show a good gradient change that is comparable with our observations (Fig. 4c).

The reconstructed biomes for the northern subtropical mountains of Shennongjia are also in good agreement with our observations: WTEM occurs at low elevations and TEDE at higher elevations (Fig. 4d). There are no high mountains in tropical China, however the mid-high mountain ranges of Wuzhi on Hainan Island contain TRSE and TREG at elevations of <1000 m, WTEG between 1000 and 1900 m, and WTEM between 1800 and 2000 m (Fig. 4e). Three TREG sites were incorrectly identified as WTEM, whilst there was confusion between WTEG and WTEM at several sites (Fig. 4e). In the Lopei Mountains of Taiwan the reconstructed biomes show that WTEG occurs below 1200 m and WTEM above 1200 m except where some of the WTEG samples have been wrongly identified as TRSE and WTEM (Fig. 4f).

4. Conclusions and perspectives

- (1) The surface pollen data set is more extensive, both in terms of geographical coverage and pollen samples and taxa included, than previous data sets used in the biomization (Yu et al., 1998, 2000; Ni et al., 2010) thus making our modern pollen-based biome reconstruction more robust.

Whilst 554 digitized pollen samples have incomplete pollen assemblages (reduced or combined) and less accurate pollen records, this has not affected the final pollen-biome assignments because all digitized samples included key pollen taxa that characterize the biomes through the assignment of PFTs. In addition, there are still geographical gaps in the collection of surface pollen samples, for example in the central and northwestern Tibetan Plateau, the desert regions of Tarim Basin in southern Xinjiang Autonomous Region, on Alashan Plateau in western Inner Mongolia, the mountainous regions of eastern China and parts of eastern China which have been highly affected by human activity (Fig. 1). In these regions there has either been no surface pollen sampling or no collection of existing samples. More extensive sample collections are therefore required in these areas. Complete pollen assemblages and records with raw data are always desirable.

- (2) The globally tested, robust biomization technique has been improved in this study by the assignment of pollen-PFTs and the classification of biomes. This has made the modern pollen-based biome reconstruction more reliable.

The biomization method has been broadly tested for modern and past biome reconstructions on continental and regional scales (Prentice and Webb, 1998; Prentice et al., 2000). The newly established global PFT scheme has reasonable plant traits-based ecophysiological and bioclimatic foundations (Harrison et al., 2010), and has been successfully used in pollen-based reconstruction of present and past vegetation (Ni et al., 2010). The assignment of pollen taxa to PFTs has been updated and calibrated based on the recent availability of

updated Chinese floras. Biomes have been defined in detail based on regional vegetation information and can also be compared to global biome classifications. Our biome reconstruction based on this updated biomization method is therefore more reliable.

We adopted the standard biomization technique, i.e., only assignments from pollen taxa to PFTs and from PFTs to biomes were used and other rules in the biomization procedure (Prentice et al., 1996; Prentice and Webb, 1998) were not changed. Regional alterations such as pollen percentage thresholds and weighting for some key taxa should be taken into account in further research.

- (3) Multiple comparisons between biome reconstructions, observed biomes, observed potential biomes, and biome simulations provide insights into quantitative modern pollen-vegetation relationships. This benefits past vegetation simulations and efforts to combine modelling and palaeo-environmental data as well as multi-proxy biome reconstructions.

The reconstructed biomes were compared with modern vegetation information obtained from direct field observations, the natural and agricultural vegetation patterns from digitized atlases, and the vegetation model-simulated biomes. Whilst there is good correlation between the biome reconstruction and biomes derived from other sources, there is a low correlation rate between reconstructed and simulated biomes. This will hopefully lead to new research comparing pollen data with models in the future resulting in more realistic past vegetation modeling.

- (4) The human impact on modern surface pollen assemblages was only considered in parts of this study. Whilst not considered in this study, the large-scale reconstruction of anthropogenic biomes based on modern pollen records presents a challenge for future pollen research.

More than 75% of the ice-free land on Earth has been altered by human activity, which has modified global patterns of biodiversity and ecosystem processes (Ellis and Ramankutty, 2008). The anthropogenic biome has therefore become an important research target for Earth System Science, especially given current global change (Alessa and Chapin, 2008). The study of regional-scale climate-human-environmental interactions is essential for fully understanding global environmental changes, both at present and in the past and future, and anthropogenically impacted large-scale pollen studies could play a key role.

However we must pay more attention to the careful treatment of human-disturbed surface pollen samples when apply them to reconstruct biomes and past climates. Some of highly modified samples that might result in misunderstanding and confusion of local vegetation and climate may be excluded from pollen dataset.

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