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1 **Holocene warming and evergreen/deciduous forest replacement across**
2 **eastern China**

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25 **ABSTRACT**

26 Combined variations of insolation and ice sheet led to major global climatic and ecosystem changes
27 between the Last Glacial Maximum (LGM) and the Holocene. However, little is known about effects
28 of these changes on the alternating dominance of deciduous and evergreen vegetation in East Asia,
29 particularly in the regions now dominated by evergreen broadleaved forest (EBLF) that forms a vast
30 ecotonal zone between tropical and temperate belts. In this study, we have used two representative
31 records in center of the EBLF distribution, associated with broader regional pollen data from eastern
32 China, to reconstruct spatiotemporal biome changes over the last 22 ka. The results showed a
33 dominance of deciduous broadleaved forest at the LGM in most mountainous regions of the subtropical
34 zone, and the EBLF began to migrate and expand into the low latitude subtropical areas during the last
35 deglaciation, particularly at ca.11.3 ka after the Younger Dryas. However, major biome replacement
36 from deciduous to evergreen forest across eastern China did not occur until 8.1 ka, indicating an earlier
37 forest replacement at sites in low latitude regions as compared to sites located further north or at higher
38 mountains. Our evidence agrees well with quantitative climate reconstruction and simulations at local
39 and regional scales, showing that forest transformed when thermal conditions reached relevant
40 thresholds. Both simulated and reconstructed paleotemperatures are consistent with the early-to-
41 middle Holocene being a key period when climatic thresholds (particularly winter and/or annual
42 temperatures) gradually approached then exceeded bioclimatic constraints on EBLF recolonization.
43 By contrast, the precipitation in most part of mountainous subtropical southeast China may not be a
44 key constraint for evergreen/deciduous forest transformation since the last deglaciation. During the
45 late Holocene, the reconstructed biome has shifted unstably, probably due to interactive effects of
46 several regional-scale factors, including seasonal climate biases and major fluctuations in effective

47 moisture associated with weakening of summer monsoon before the enhanced human interventions of
48 the last 3000 years.

49 **Keywords:** Evergreen broadleaved forest; Deglaciation; Holocene; Biome change; Transient
50 simulation; Climate threshold.

51

52 **1. Introduction**

53 In East Asia, evergreen broadleaved forest (EBLF), also known as laurophyllous forest, is currently
54 the most widespread vegetation type in the subtropical zone, extending from $\sim 22^\circ$ N, near the Tropic
55 of Cancer, to the Yangtze River basin at $31\text{--}33^\circ$ N in China and $33\text{--}35^\circ$ N in southern Japan (Wu, 1980;
56 Fang et al., 2011). During the Last Glacial Maximum (LGM), the mean surface temperature of
57 mainland China and adjacent areas is estimated to have been $2\text{--}8^\circ\text{C}$ colder than today (Jiang et al.,
58 2011; Tian and Jiang, 2016). Simulated and reconstructed biome distribution patterns during the LGM
59 indicate a large-scale southward shift of temperate deciduous forests (DBLF) in regions where EBLF
60 dominates today, followed by a gradual recolonization by continental evergreen biomes during
61 postglacial global warming (Yu et al., 2000; Kageyama et al., 2012; Ni et al., 2014). However, little is
62 known about the high-resolution temporal changes in forest transformation from deciduous to
63 evergreen vegetation and the threshold climatic conditions required for forest replacement across the
64 Asia since the last deglaciation. Important questions remain regarding the timing of the onset,
65 dynamics, and causes of this large biome transformation over the subtropical belt in East Asia (Zhao
66 et al., 2009; Li et al., 2019).

67 As yet, there are few well-dated, high-resolution fossil records dating back to the LGM from
68 subtropical regions (Zheng et al., 2016), which severely hinders reconstruction of the nature of spatial
69 vegetation shifts and their relationships with past climate change. Moreover, the modeled cold-tolerant
70 DBLF biome in southern China is poorly represented as a vegetation type in the LGM fossil pollen
71 record, casting doubt on the accuracy of reconstructed vegetation, both spatially and temporally (Yu
72 et al., 2000; Harrison et al., 2001). Therefore, we here have used two representative pollen records,
73 together with other regional pollen and biomarker data, to reconstruct past biome changes, focusing
74 on the EBLF's migration history in subtropical Asia. The two high-resolution records are located in a
75 sensitive montane forest zone in central subtropical regions, where current climatic conditions are near
76 the temperature thresholds for shifts between evergreen and deciduous forest. As temperatures
77 constrain plant photosynthetic efficiency physiologically (Bai et al., 2010; Song et al., 2016), and thus
78 are key controls of biome change between EBLF and DBLF, we quantitatively reconstructed
79 paleotemperatures using pollen and biomarker data and linked them to local and regional climate
80 simulations by a transient model. The results indicate dramatic biome and climate changes during the
81 last 22 ka in subtropical Asia, and past temperature thresholds for forest transformation under deglacial
82 warming from the LGM to the Holocene. The study has important implications for the projection of
83 future forest migration in Asia under global warming.

84

85 **2. Materials and Methods**

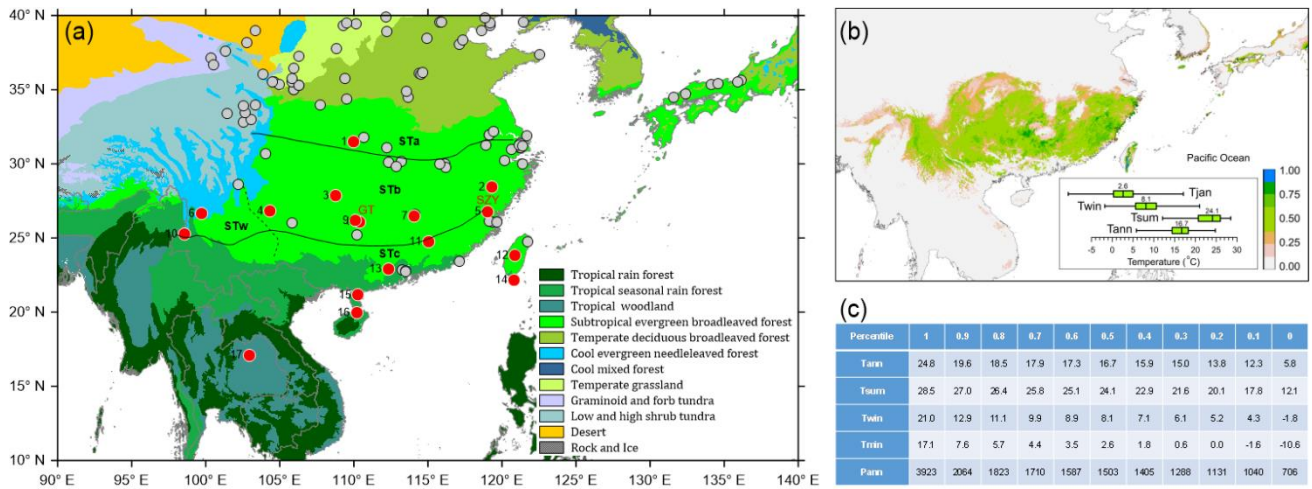
86 *2.1. Regional setting and materials*

87 Vegetation in the subtropical zone of China is composed mainly of EBLF that can be divided into
88 two main components: humid forest in southeastern China and semi-humid mountainous forest in
89 southwestern China, the southeast margin of the Tibetan Plateau (Wu, 1980). The eastern subtropical
90 humid EBLF region generally includes three subzones: a northern subtropical evergreen and
91 deciduous broadleaved forest zone (STa), middle subtropical zone (STb) and southern subtropical
92 zone (STc). The northern boundary of the subtropical zone is near a geographical line joining
93 Qinling mountain ranges and Huaihe River, and the northern subzone (STa) is dominated by
94 deciduous oak forest mixed with evergreen broadleaved trees. The STa subzone has also been
95 assigned to an independent vegetation ecotone (evergreen-deciduous broadleaved forest) of the
96 warm-temperate zone, dominated by deciduous trees (Fang et al., 2002). However, the large lowland
97 river plains of this subzone are cultivated with rice and aquatic plants. The middle subzone (STb),
98 restricted to the area between the Yangtze River and Nanling mountain ranges, is characteristically
99 covered by EBLF dominated by evergreen genera such as *Cyclobalanopsis*, *Castanopsis*,
100 *Lithocarpus*, *Schima*, *Machilus*, *Phoebe*, *Altingia*, *Elaeocarpus* and *Eurya*. The southern subzone
101 (STc) hosts monsoonal humid evergreen forest characterized by genera from families including
102 Fagaceae, Lauraceae, Theaceae, Myrtaceae, Meliaceae, Moraceae, Myrsinaceae, Rubiaceae and
103 Hamamelidaceae. In the west, there is a semi-humid subzone (STw), typically comprising alpine
104 EBLF characterized by montane sclerophilous *Quercus* (Sect. *Heterobalanus*), subalpine
105 *Cyclobalanopsis* and pine forests (Wu, 1980). The distribution of EBLF in the subtropical East Asia
106 is strongly influenced by monsoon climate circulation. The mean annual temperature of the EBLF
107 distribution area is usually between 16 and 22°C, with a relatively warm winter generally higher than

108 0°C (Song, 1999). Annual precipitation generally exceeds 1100 mm (Fang and Yoda, 1991), and the
109 relative humidity is about 75-80% on average.

110 We reconstructed past vegetation changes during the transition from the LGM, at around 22 ka, to
111 the Holocene. For this, we used two high-resolution pollen records, based on cores from the sites of
112 Gutian (GT) and Shuizhuyang (SZY) in the middle subtropical EBLF subzone (STb), together with
113 other pollen data from sites across the zone (Fig. 1a, Table 1). The GT site is in the hinterland of the
114 Yuecheng Mountains in the west Nanling Ranges, southern China (110.366°E, 26.084°N; 1677 m
115 asl). This is in the southern part of the central subtropical zone, which is strongly influenced by the
116 monsoon climate system. The local mean annual temperature is about 14-15°C, and the coldest mean
117 temperature (January) is only 1-2°C at an altitude of about 1000 m. The annual precipitation, of
118 1200-1600 mm, is concentrated between the end of March and July. Lithologically, the GT core
119 comprises a thin sand layer interbedded with gravel at the base, grey silty clay at 140-194 cm depth,
120 dark clay with a high plant debris content at 22-140 cm, and brown root-rich gyttja in the upper 0-22
121 cm layer. The SZY core was collected from a mountain peat bog in Jiufeng Mountains, southeastern
122 China (119.034°E, 26.777°N; 1007 m asl) (Yue et al., 2012). The site is in the mid-subtropical zone,
123 with an annual mean temperature and precipitation of about 15°C and 1400-1800 mm, respectively.
124 Zonal vegetation types at the GT and SZY sites are evergreen broadleaved and evergreen/deciduous
125 mixed forest, respectively. Each site is in a summit wetland of a mountainous area, with a local
126 landscape mainly covered by shrubs and grasses of various families, including Ericaceae, Theaceae,
127 Saxifragaceae, Clethraceae, Rosaceae, Symplocaceae, Poaceae, Cyperaceae, and Asteraceae.

128



129 **Fig. 1. Locations of the examined pollen records across East Asia, present-day biome map and simulated EBLF**
 130 **distribution.** (a) Vegetation map showing the modern biomes in eastern Asia, in which the subtropical evergreen
 131 broadleaved forest (EBLF) zone is divided into northern (STa), middle (STb), southern (STc) and western (STw)
 132 (Wu, 1980). The dots are locations of the examined pollen records from eastern China (108 sites in total), and those in red
 133 (1-17) were used for EBLF data integrations (Table 1). (b) The potential distribution of EBLF today as simulated by the
 134 Species Distribution Model (SDM). The most important bioclimatic thresholds are indicated using quartile values (25%,
 135 50% and 75% in green boxes). (c) Percentiles for the five key climatic variables characterizing the EBLF distribution in
 136 southern China, based on 500 random grids of digital georeferenced data: annual precipitation (Pann) and mean
 137 temperatures of the coldest month (Tjan), winter (Twin), summer (Tsum), and year (Tann).

138
 139
 140 **Table 1.** Locations of 14 subtropical (1-14) and 3 tropical pollen records (15-17) for the regional EBLF integration study,
 141 selected from 108 examined sites across East Asia.

No.	Core (site name)	Location	Elevation (m)	Type of archive* and age range (ka BP)	Reference
1	DJH (Dajiuhu)	110.001°E, 31.484°N	1751	P (0-42)	Li et al., 2013
2	LTJ (Lantianyan)	119.310°E, 28.430°N	902	L (1-8)	Ma et al., 2016
3	JLC (Fanjingshan)	108.775°E, 27.847°N	2200	P (0-10)	Gao et al., 2019
4	NT (Nantun)	104.340°E, 26.810°N	2203	L (1-22)	This paper

5	SZY (Shuizhuyang)	119.034°E, 26.777°N	1007	P (0-50)	This paper
6	TCK1 (Tengchong)	99.716°E, 26.641°N	3898	L (0-22)	Xiao et al., 2014
7	JXA (Jiangxi'ao)	114.092°E, 26.470°N	1650	P (0-11)	This paper
8	GT (Gutian)	110.366°E, 26.084°N	1677	P (0-21)	This paper
9	DP (Daping)	110.117°E, 26.167°N	1620	P (0-15)	Zhong et al., 2015
10	TCQH (Tengchong)	98.553°E, 25.261°N	1885	L (0-18)	Zhang et al., 2020
11	DH (Dahu)	115.033°E, 24.750°N	200	L (0-18)	Xiao et al., 2007
12	TS (Toushe)	120.883°E, 23.817°N	650	L, P (1-73)	Liew et al., 2006
13	GY (Gaoyao)	112.333°E, 22.901°N	16	P (0-6)	Peng et al., 2015
14	DY (Dongyuan)	120.833°E, 22.167°N	330	L (0-22)	Lee and Liew, 2010
15	HML (Huguangyan)	110.283°E, 21.153°N	87	L (0-20)	Sheng et al., 2017
16	SC (Shuangchi)	110.183°E, 19.951°E	90	L (0-8)	Zheng et al., 2003
17	NPK2 (Nong Pa Kho)	102.933°E, 17.102°N	180	L (0-36)	Penny et al., 2001

142 *Type of archive: P=peat; L=lacustrine

143 The chronology for the GT core was based on 10 AMS ¹⁴C dates ([Fig. 2, Table 2](#)). For the SZY
144 core, new ¹⁴C dates were obtained and additional pollen analyses carried out to improve the temporal
145 resolution, especially for the late glacial and deglacial intervals. To incorporate age uncertainties
146 associated with the resolution of pollen sampling, Bayesian estimation was applied to age model
147 outputs using the Bchron package in R statistical software ([Parmell et al., 2008](#)). This provided
148 probability distribution over the mean age of transitions between successive sampling levels. All ¹⁴C
149 dates were calibrated to calendar years using IntCal13 ([Reimer et al., 2013](#)). Median values were
150 used for interpolation at different sample depths, except for the transition from the last glacial to the
151 Holocene in the SZY core, where 90% quantiles were assumed between the two dating points.

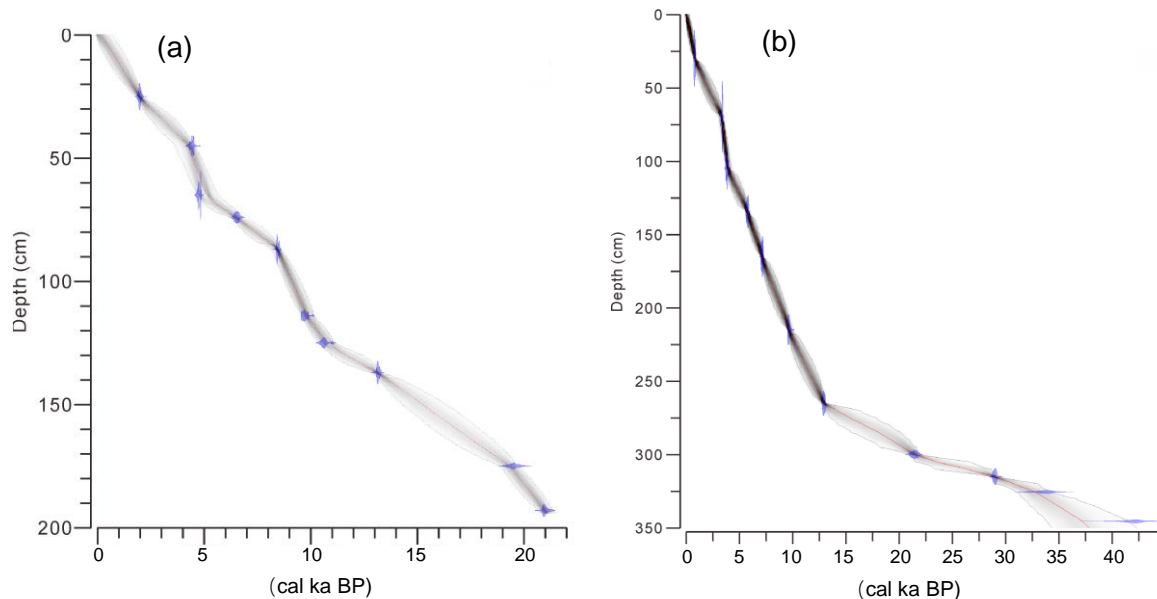


Fig. 2. Age-depth model of the GT (a) and SZY (b) cores.

152

153

154 **Table 2.** AMS ^{14}C dates and calibrated ages for the GT and SZY cores

Core	Depth (cm)	Laboratory* Number	Dated material	Radiocarbon age (a BP)	Calibrated age (cal. a BP)
GT	25	Beta-440773	Bulk sediment	2030 ± 30	1907-2090
	45	Poz-84956	Pollen	3970 ± 40	4299-4522
	64	XA 6643	Bulk sediment	4233 ± 28	4662-4850
	74	Poz-84957	Pollen	5740 ± 70	6384-6695
	87	Beta-326017	Bulk sediment	7600 ± 40	8390-8534
	114	XA 6639	Bulk sediment	8738 ± 43	9568-9891
	125	Poz-84958	Pollen	9390 ± 70	10422-10984
	137	Beta-326015	Bulk sediment	11210 ± 60	13025-13237
	175.5	Poz-84960	Pollen	16170 ± 140	19148-19861
	192	XA 6638	Bulk sediment	17395 ± 66	20813-21181
SZY	30	Beta-440771	Pollen	890 ± 30	738-903
	70	Beta-324767	Bulk organic matter	3170 ± 30	3347-3447
	105	GZ 4920	Bulk organic matter	3555 ± 35	3729-3953
	134.5	Poz-84961	Pollen	5020 ± 40	5661-5888
	165	GZ 4922	Bulk organic matter	6230 ± 35	7023-7245
	215	GZ 4921	Bulk organic matter	8690 ± 45	9553-9814
	245	Beta-324765	Bulk organic matter	9240 ± 40	10240-10440
	265	GZ 4860	Bulk sediment	11000 ± 60	12747-13016
	277.5	Beta-469574	pollen	24700 ± 100	28470-28980
	284.5	Beta-469575	pollen	22400 ± 90	26371-27076
	290	Beta-324768	Wood fragment	8430 ± 40	9410-9529
	300	Poz-84966	Pollen	17700 ± 120	21075-21742
	315	GZ 4923	Bulk sediment	24770 ± 110	28620-29004
	325.5	Poz-84968	Pollen	29320 ± 610	31791-34435
	333	Beta-324766	Wood fragment	21880 ± 100	25883-26352
345.5	Poz-84969	Pollen	37900 ± 1100	40117-43875	

*Beta, Beta Analytic Inc.; Poz, Poznan Radiocarbon Laboratory; XA, Xi'an Institute of Earth and Environment, Chinese Academy of Sciences; GZ, Guangzhou Institute of Geochemistry, Chinese Academy of Sciences

155 Following a preliminary examination of a broader fossil pollen dataset (Cao et al., 2013; Penny et
156 al., 2001; Zheng et al., 2016), we selected records from sites in relatively closed basins (upland lakes
157 or marshes) within the subtropical zone with a reliable age model for comprehensive regional
158 analysis. Pollen records from of alluvial, deltaic and river-fed lacustrine sedimentary materials were
159 excluded due to the uncertainty of pollen sources transported by rivers. Thus, only 14 well-dated
160 pollen records (Table 1) were used for regional data integration. Of the selected records, pollen
161 analysis from GT, SZY, JXA, NT and DJH cores were conducted by our laboratory (Yue et al.,
162 2012; Li et al., 2013; Han et al., 2016).

163 2.2. Methods

164 We analyzed pollen in samples from several cores collected from the subtropical zone after
165 preparation following standard techniques (Faegri and Iversen, 1989) with minor amendments. Each
166 sample consisted of 2–3 g of sediment and after chemical treatment approximately 500 pollen grains
167 were counted and classified in most samples. The pollen total used for percentage calculations was
168 based on the total number of pollen grains counted, excluding aquatic pollen and spores, and
169 percentages of pteridophyte and fungal spores were based on total counts of palynomorphs. Pollen
170 taxa were grouped by ecological affinity and distribution of parent plants. Pollen groups classified by
171 plant ecological affinity were used to summarize structural-functional changes in the vegetation, with
172 no pollen taxon assigned to more than one group. We summed relative values for the following
173 groups: cold-tolerant conifers, temperate deciduous broadleaved trees, subtropical evergreen

174 broadleaved trees, eurythermic and subtropical warm conifers, forbs, and wetland plants. For
175 comparative study of regional variation trend, the percentages of arboreal pollen group of evergreen
176 broadleaved trees (EBT) in the selected lacustrine pollen records were standardized by rescaling to
177 values from 0 to 1, and the tropical records (from three sites) and subtropical records (from 14 sites)
178 were separately combined. The EBT pollen data from temperate zone were not used for synthetic
179 analysis because the dominant component is always deciduous taxa rather than evergreen.

180 To illustrate spatiotemporal vegetation changes in the study area, we used biomes that are
181 geographically and climatically distributed in broad physiognomic zones. Pollen-based biome
182 reconstruction has been successfully performed by applying the biomization technique to various plant
183 functional type (PFT) schemes (Yu et al., 2000; Chen et al., 2010). A recently described scheme for
184 converting pollen taxa to biomes, with some modifications to the PFTs to suit the particular subtropical
185 situations in China (Ni et al., 2014) and adjacent islands (Lee and Liew, 2010; Gotanda et al., 2002)
186 was applied to the GT, SZY and other records. Essentially, we applied a biome PFT taxon matrix
187 previously developed for East Asia (Ni et al., 2014), apart from the exclusion of some PFTs from high-
188 latitude Arctic and boreal zones, such as Arctic shrub, boreal summergreen, and conifers PFTs. The
189 biome taxa matrix was then simplified to focus on the subtropical region that includes locations of the
190 fossil pollen sites. In total, 136 pollen taxa were assigned to 18 PFTs (Table 3). The defined
191 composition of each biome in terms of PFTs is given in Table 4, and 9 biomes from the study area was
192 used. In accordance with previous modifications of the subtropical zone biome, ts2 (a PFT
193 characterized by *Alnus* and *Fagus*) as proposed by Yu et al. (2000) was assigned exclusively to the
194 DBLF biome. The alpine shrub-land biome (ALSH) (Lee and Liew, 2010), characterized by

195 subtropical mountain vegetation, was also included. The results of biome reconstruction for modern
 196 pollen spectra indicate that most samples are correctly assigned. The improved result of biome
 197 reconstruction has good correspondence with the present-day vegetation distribution across eastern
 198 China (Fig. 3), and some exceptions from the northern subzones of subtropical regions show a
 199 dominance of DBLF and CLMX biomes caused by temperature gradients in mountainous regions
 200 (samples below 800 m were deleted due to strong human disturbance). We used the difference in biome
 201 scores between EBLF and DBLF (E-T) to evaluate the biome shifts.

202 **Table 3.** Assignment of pollen taxa from southern China to plant functional types (PFTs) for biomization.

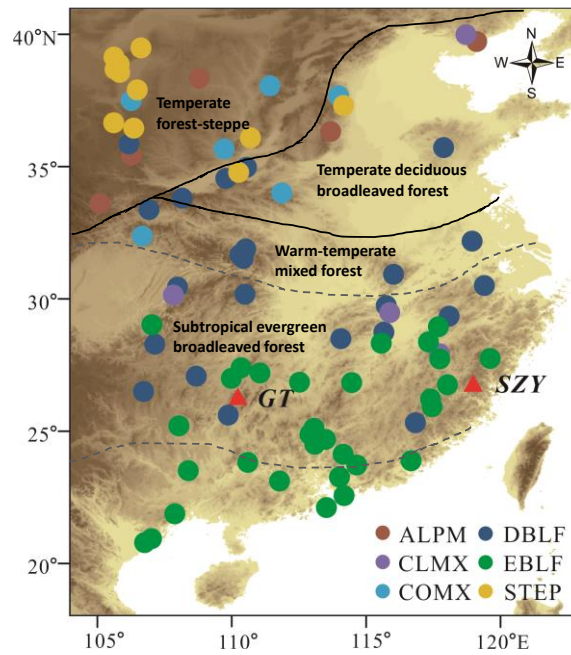
Code	PFT	Pollen taxa
bec	Boreal evergreen conifer	<i>Abies, Picea, Pinus</i> (Haploxyton)
ctc	Cool-temperate conifer	<i>Abies, Tsuga</i>
ec	Eurythermic or heliophilous conifer	Cupressaceae, <i>Pinus</i>
ts	Temperate summergreen	<i>Acer</i> , Araliaceae, <i>Betula, Buxus, Carpinus, Cornus, Corylus, Euphorbia, Fraxinus, Galium, Quercus</i> (deciduous), Rhamnaceae, <i>Rhus</i> , Rosaceae, Rubiaceae, Rutaceae, <i>Salix, Sambucus, Spiraea, Tilia, Viburnum</i>
ts1	Intermediate-temperate summergreen	<i>Alnus</i> , Caprifoliaceae, <i>Carpinus, Carya, Celtis, Fagus</i> , Hamamelidaceae, <i>Hedera, Juglans, Liquidambar</i> , Mimosaceae, <i>Myrica, Nyssa, Pterocarya</i> , Thymelaeaceae, <i>Ulmus-Zelkova</i> , Urticaceae, <i>Vitis</i>
ts2	Warm-temperate summergreen	Ebenaceae, Elaeagnaceae, <i>Engelhardtia, Platycarya, Pterocarya, Rhus</i>
wtc	Subtropical evergreen conifer	<i>Cephalotaxaceae, Dacrydium, Keteleeria, Podocarpus</i> , Taxodiaceae
wte	Subtropical broadleaved evergreen	<i>Altingia</i> , Anacardiaceae, <i>Antidesma, Aporosa</i> , Araliaceae, Berberidaceae, <i>Breynia, Buxus, Camellia, Castanopsis-Lithocarpus</i> , Celastraceae, <i>Claoxylon</i> , Cucurbitaceae, <i>Cyclobalanopsis, Elaeocarpus, Engelhardtia, Eriobotrya</i> , Euphorbiaceae, <i>Eurya</i> , Fabaceae, Gesneriaceae, Hamamelidaceae, Lauraceae, <i>Mallotus</i> , Malvaceae, Melastomataceae, Meliaceae, Mimosaceae, Moraceae, Myrtaceae, Oleaceae, Papilionaceae, <i>Phyllanthus, Polygala</i> , Proteaceae, <i>Pterospermum, Reevesia</i> , Rhamnaceae, Rubiaceae, Rutaceae, Sapindaceae, Solanaceae, <i>Symplocos, Ternstroemia, Tetracentron</i> , Theaceae
sse	Southern subtropical evergreen	Apocynaceae, <i>Castanopsis-Lithocarpus</i> , Celastraceae, Cucurbitaceae, Euphorbiaceae, <i>Exoecaria</i> , Fabaceae, <i>Flacourtia</i> , Hamameliaceae, Loranthaceae, Lythraceae, <i>Mallotus</i> , Malvaceae, Meliaceae, <i>Nyssa</i> , Papilionaceae, Sapindaceae, <i>Symplocos, Tilia</i> , Vitaceae
te	Tropical evergreen	Anacardiaceae, <i>Antidesma</i> , Apocynaceae, <i>Aporosa</i> , Araceae, Araliaceae, Berberidaceae, <i>Camelia, Claoxylon, Eurya, Ficus</i> , Lauraceae,

		<i>Macaranga</i> , Melastomataceae, Mimosaceae, Moraceae, Myrtaceae, Olacaceae, Oleaceae, <i>Phylanthus</i> , Proteaceae, <i>Pterospermum</i> , Solanaceae, Verbenaceae
tr	Tropical raingreen	Apocynaceae, <i>Aphanamixis</i> , <i>Celtis</i> , <i>Dalbergia</i> , Euphorbiaceae, <i>Exoecaria</i> , Fabaceae, Flacourtiaceae, Lythraceae, <i>Mallotus</i> , Malvaceae, Meliaceae, Myrsinaceae, <i>Nyssa</i> , Papilionaceae, Sapotaceae, <i>Tilia</i>
suf	Subtropical forb/shrub	Apiaceae, Araceae, Asteraceae (spiny), Campanulaceae, Solanaceae, Convolvulaceae, <i>Ilex</i> , Fabaceae, <i>Symplocos</i> , Verbenaceae
sf	Steppe forb/shrub	Amaranthaceae-Chenopodiaceae, Apiaceae, <i>Artemisia</i> , Asteraceae, <i>Astragalus</i> , Brassicaceae, Campanulaceae, Cannabaceae, Caryophyllaceae, Convolvulaceae, Elaeagnaceae, <i>Euphorbia</i> , Fabaceae, <i>Gentiana</i> , Labiatae, Liliaceae, Onagraceae, <i>Plantago</i> , <i>Polygonum</i> , Primulaceae, Ranunculaceae, Rosaceae, <i>Rumex</i> , Rutaceae, <i>Thalictrum</i> , <i>Verbascum</i> , <i>Xanthium</i> , <i>Zanthoxylum</i>
af	Alpine forb/shrub	Apiaceae, <i>Artemisia</i> , Asteraceae, Boraginaceae, Brassicaceae, Caryophyllaceae, Crassulaceae, Fabaceae, <i>Gentiana</i> , Geraniaceae, Gesneriaceae, <i>Impatiens</i> , Labiatae, Onagraceae, Papaveraceae, Papilionaceae, <i>Pedicularis</i> , <i>Plantago</i> , <i>Polygala</i> , <i>Polygonum</i> , <i>Potentilla</i> , Primulaceae, Ranunculaceae, Rosaceae, <i>Sanguisorba</i> , <i>Thalictrum</i> , <i>Verbascum</i> , <i>Viburnum</i>
h	Heath	Ericaceae, <i>Rhododendron</i>
g	Grass	Poaceae
s	Sedge	Cyperaceae

203 **Table 4.** Assignments of plant functional types to biomes.

Code	Biome	Plant functional type (PFT)*
ALSM	Alpine shrub-land, meadow/tundra	af, g, h, s
CLMX	Cold mixed forest	ctc, ec, ts1
COMX	Cool mixed forest	bec, ctc, ec, h, ts
DBLF	Temperate deciduous broadleaved forest	ctc, ec, h, ts, ts1, ts2
EBLF	Subtropical evergreen broadleaved forest	ec,te, tr, ts2, wtc, wte
STEP	steppe	g, sf
TDFO	Tropical dry forest/savanna	g, tr
TRFO	Tropical rainforest	te, sse, suf
TSFO	Tropical seasonal forest	tr, suf, wtc

* PFT codes: bec, boreal evergreen conifer; ctc, cool-temperate conifer; ec, eurythermic or heliophilous conifer; ts, temperate summergreen; ts1, intermediate-temperate summergreen; ts2, warm-temperate summergreen; wtc, subtropical evergreen conifer; wte, subtropical broadleaved evergreen; sse, southern subtropical evergreen; te, tropical evergreen; tr, tropical raingreen; suf, subtropical shrub/forb; sf, steppe forb/shrub; af, alpine forb/shrub; h, heath; g, grass; and s, sedge.

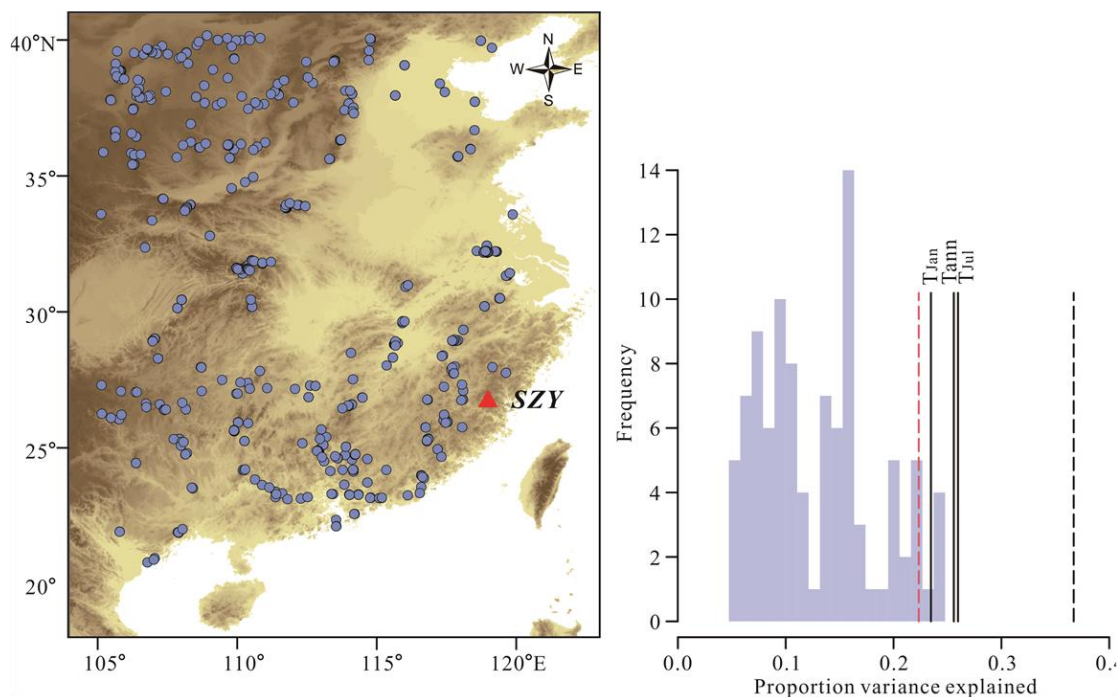


204
 205 **Fig. 3. Predicted biomes for modern pollen surface samples from latitudes of 20°N to 40°N in eastern China. Some**

206 samples from the north and northwestern subzones of subtropical regions show a dominance of DBLF and CLMX
 207 biomes caused by vertical temperature lapse rate in mountainous localities.

208 We applied the transfer function method to reconstruct the paleoclimate quantitatively from the
 209 SZY pollen record, using the Locally-Weighted Weighted-Averaging (LWWA) model (Juggins and
 210 Telford, 2012; Juggins and Birks, 2012). Modern pollen data were extracted from the recently
 211 updated Eastern Asia Pollen Dataset (EAPD) (Zheng et al., 2014; Zheng and Huang, 2022), with the
 212 addition of some recently completed samples. An area in mainland China between 20°-40° N latitude
 213 and 105°-120° E longitude around the research site (SZY) was selected (Fig. 4). We screened the
 214 modern samples and excluded those that had clearly been disturbed by human activities, leaving 683
 215 surface samples for use in the calculations. The climate at each modern site was interpolated from
 216 modern climatic data of 756 meteorological stations in the years of 1981-2010 in China
 217 (<http://data.cma.cn>). The thin plate spline regression was applied in the interpolation process for each
 218 modern pollen site. The robustness of the transfer function model was assessed by calculating the

219 root mean square error of prediction (RMSEP) and coefficient of determination (R²) between
220 measured and predicted values. The R software package (Juggins, 2017) was used to calculate the
221 pollen-climate model.



222
223 **Fig. 4. Modern pollen samples (left; gray circles) and a significance test for the pollen-based climate**
224 **reconstructions (right).** The red triangle indicates the location of the SZY core. Gray bars indicate the proportion of
225 variance, and the red dotted line indicates the proportion of variance below which 95% of the random data-trained
226 calibration functions can be explained.

227 We use the branched glycerol dialkyl glycerol tetraether (brGDGT) as an independent method to
228 quantify past temperature changes (Wang, et al., 2017). Samples for biomarker analysis were taken
229 from the same core (SZY) of pollen analysis, which was measured using high-performance liquid
230 chromatography/atmospheric pressure chemical ionization-mass spectrometry. GDGTs were
231 detected by using the selected ion monitoring (SIM) mode, following the methods described by
232 Schouten et al. (2007). The quantification of GDGTs was achieved by integration of the peak area of

233 [M+H]⁺ ion traces of branched GDGTs. Replicate HPLC/APCI-MS analysis of more than 10
234 samples showed the reproducibility of MBT^{*}(Methylation index of Branched Tetraethers), which
235 was used for calculating the annual mean temperature with the equations given by [Weijers et al.](#)
236 [\(2007\)](#) and [Peterse et al. \(2012\)](#).

237 For climate simulation, we use the TRACE21 model at the T31 spatial resolution (3.75°x3.75°),
238 which is the first state-of-the-art transient simulation of global climate change over the last 21 ka
239 ([Liu et al., 2009; 2012](#)). We selected an area covering 22°-27° N to 105°-120° E to represent
240 subtropical southern China to compare results of the simulations with corresponding proxies. The
241 simulated local climate variables of the studied sites were extracted directly from the corresponding
242 spatial grids simulated by TRACE21 model ([Liu et al., 2009](#)). Six climatic variables are analyzed:
243 annual mean precipitation and mean temperature, mean winter (December-February) and summer
244 (June-August) temperatures, and indices of temperature and precipitation seasonality (corresponding
245 to WorldClim bioclimatic variables 4 and 15) ([Hijmans et al., 2005](#)). These variables were chosen
246 because they provided the maximal explanatory power of potential predictors, although some co-
247 linearity was still present, especially for winter temperature and temperature seasonality.

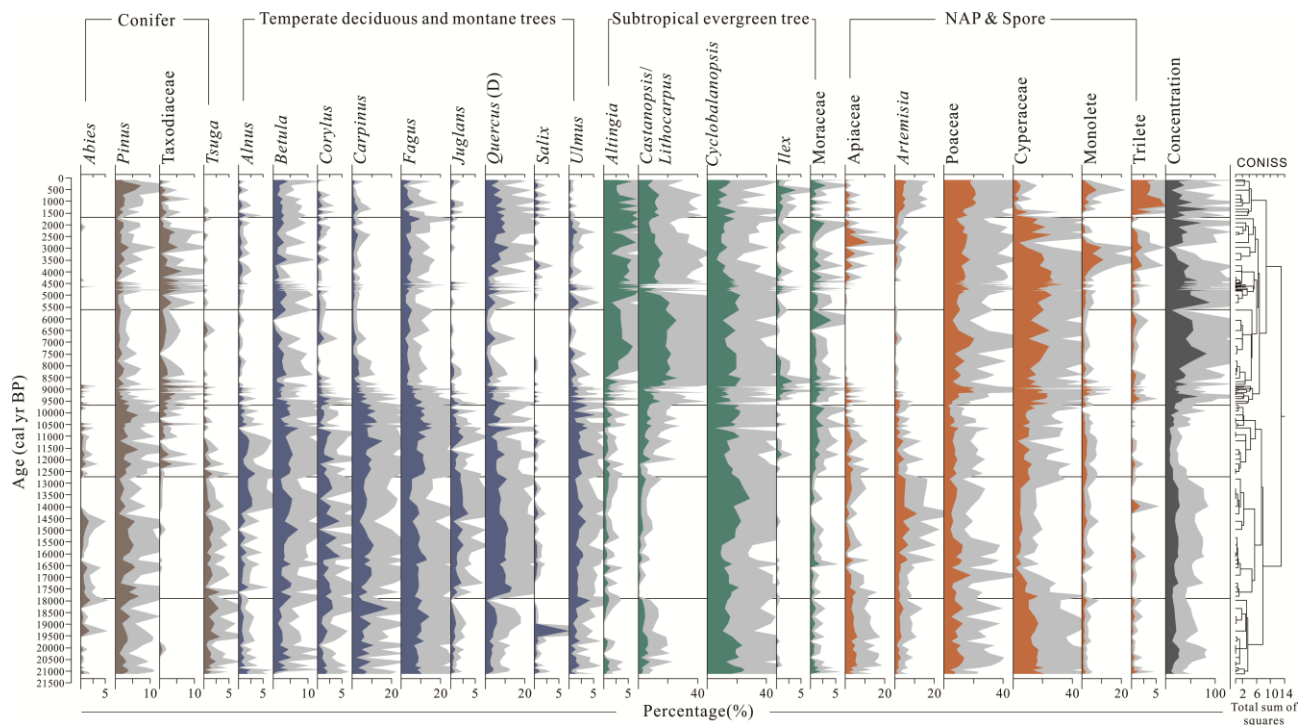
248

249 **3. Results and discussion**

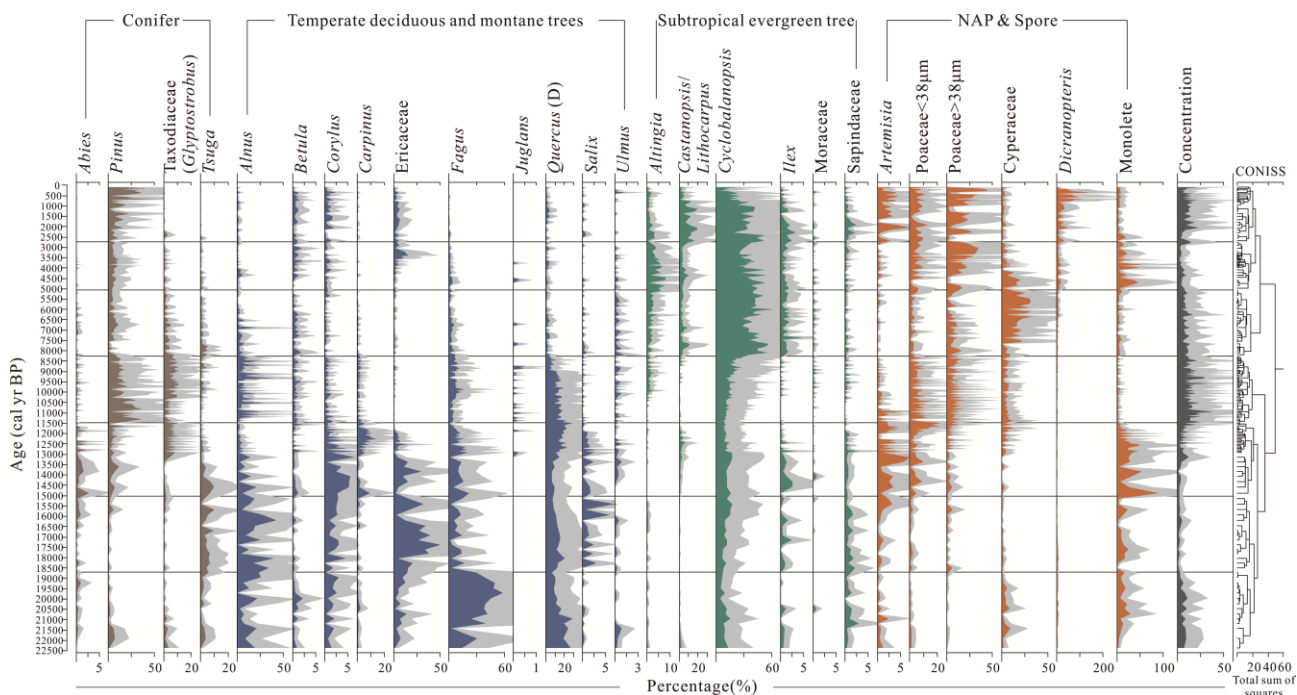
250 *3.1. Pollen records and biome reconstructions*

251 We regard results from the two high-resolution pollen records as representative of vegetation
252 changes in the middle subtropical zone during the last glacial-interglacial transition. Both records

253 indicate a substantial change in distribution of the subtropical ecosystem from the LGM at 22 ka BP
 254 to the Holocene. The pollen at the LGM at sites of the two records was dominated by cold-tolerant,
 255 temperate broadleaved forest taxa (*Fagus*, *Carpinus*, *Betula*, *Corylus*, *Juglans* and deciduous
 256 *Quercus*), mixed with cold-tolerant alpine conifer taxa (*Tsuga* and *Abies*), indicating that temperatures
 257 were much lower than today (Figs. 5 and 6). During the Bölling/Alleröd (B/A) warm period (15.5-13
 258 ka BP), there was an early increase in pollen of the evergreen forest tree genus *Cyclobalanopsis*.
 259 However, the taxa *Castanopsis/Lithocarpus* and *Altingia* increased significantly and reached dominant
 260 percentages until the middle Holocene at both sites. Among the non-arboreal pollen (NAP) taxa,
 261 Poaceae was the most abundant, and tended to increase, reaching maximum percentages in the late
 262 Holocene. Cyperaceae, a wetland plant, began to increase at ca.12 ka and peaked in the mid-Holocene,
 263 positively correlating with pollen taxa of evergreen broadleaved trees.



264
 265 **Fig. 5. Detailed pollen diagram of selected taxa from the GT core.** Percentages were calculated from the sum of all
 266 pollen grains counted. The unity of pollen concentration is the count number per gram ($\times 10^4$).



267

268

Fig. 6. Detailed pollen diagram of selected taxa from the SZY core. Percentages were calculated from the sum of all

269

pollen grains counted. The unity of pollen concentration is the count number per gram ($\times 10^4$).

270

We used pollen groups classified by plant ecological affinity to synthesize the taxonomic pollen

271

data (Fig. 7), and reconstructed biomes using the biomization technique (Yu, et al., 2000) based on its

272

successful application with modern pollen samples (Fig. 3). Arboreal taxa of the two pollen records

273

indicated the dominance of temperate deciduous broadleaved trees (DBT), corresponding to the DBLF

274

biome, during the glacial and early Holocene periods. Such temperate deciduous forest vegetation

275

indicates glacial climatic conditions different from those of today in the subtropical zone. During the

276

Bölling/Alleröd (B/A) warm period (16-13 ka), there was a moderate increase in pollen group of

277

evergreen broadleaved trees (EBT). The primary increase in evergreen broadleaved tree (EBT) during

278

the B/A was more pronounced at SZY than GT, reflecting the difference in sites' elevation (1007 and

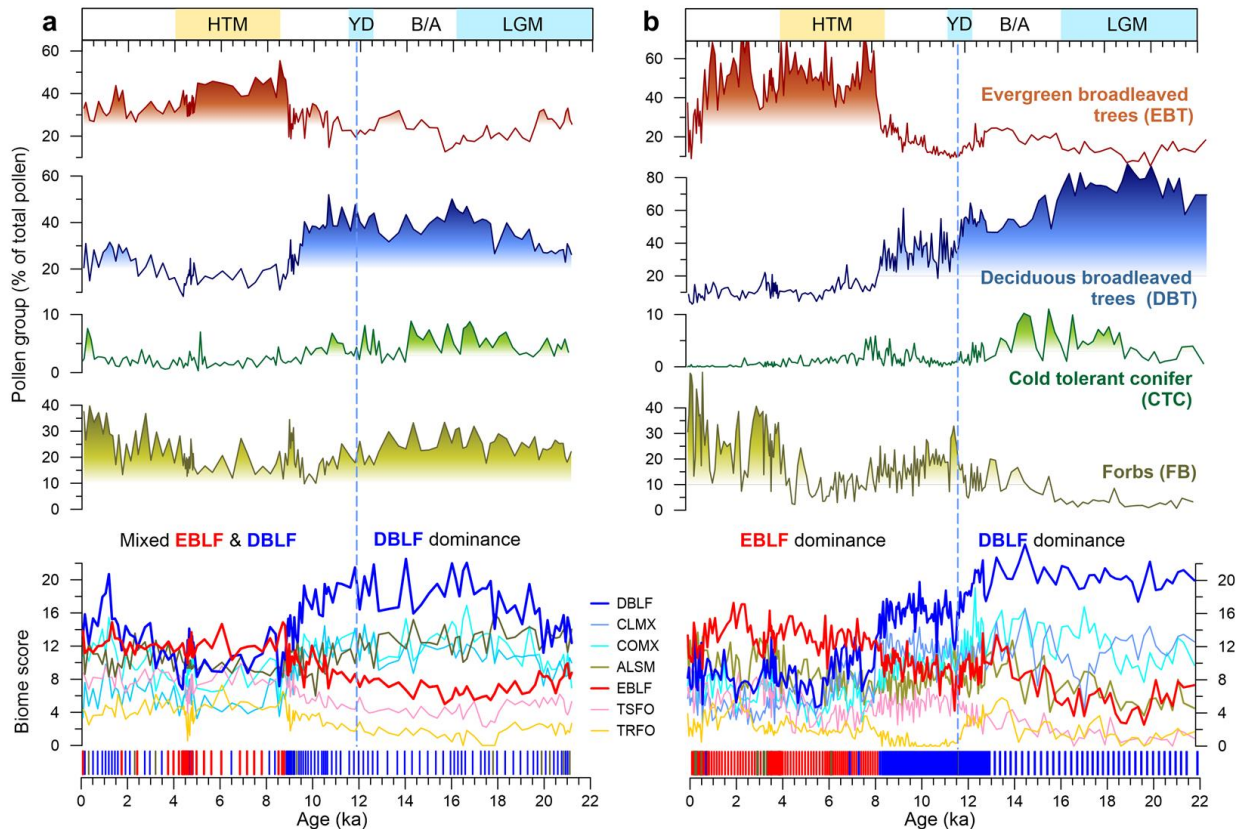
279

1677 m asl, respectively). The biomization result shows that the evergreen forest biome (EBLF) during

280

the last glacial and early deglacial periods did not exceed those of temperate deciduous broadleaved

281 forest (DBLF). The primary increase in broadleaf evergreen forest components since the last
282 deglaciation was interrupted during the cold Younger Dryas (YD). Such an abrupt change was also
283 marked by increases in forbs and sedges, reflecting drier condition on land and locally shallowing lake
284 waters. After the YD, EBT forest group slowly increased again from about 11.3 ka, and biome change
285 from DBLF to EBLF occurred at 8.7 ka in GT and 8.1 ka at SZY (Fig. 7), reflecting a time difference
286 between latitudinal locations. In particular, the reconstructed biome changes during the mid-Holocene
287 showed that the decrease in DBLF was more significant than the increase in EBLF. There was also
288 only a marginal dominance of EBLF or a mixed EBLF and DBLF biome at sites characterized by
289 relatively high elevation and low air temperature, such as GT (1677 m asl), during the middle to late
290 Holocene. This elevational effect suggests that deglacial migration of vegetation occurred not only
291 along a north-south latitudinal transect but also along an elevational gradient. Over the last 4,000 years,
292 EBLF decreased relative to DBLF, indicating that the forest type was more consistent with the
293 evergreen/deciduous mixed forest since then. In addition, the abundance of non-arboreal taxa (forbs)
294 increased progressively in both records, suggesting a drying trend that probably had interactive effects
295 with anthropogenic influences, at least within the last 2 ka (Ma et al., 2018).

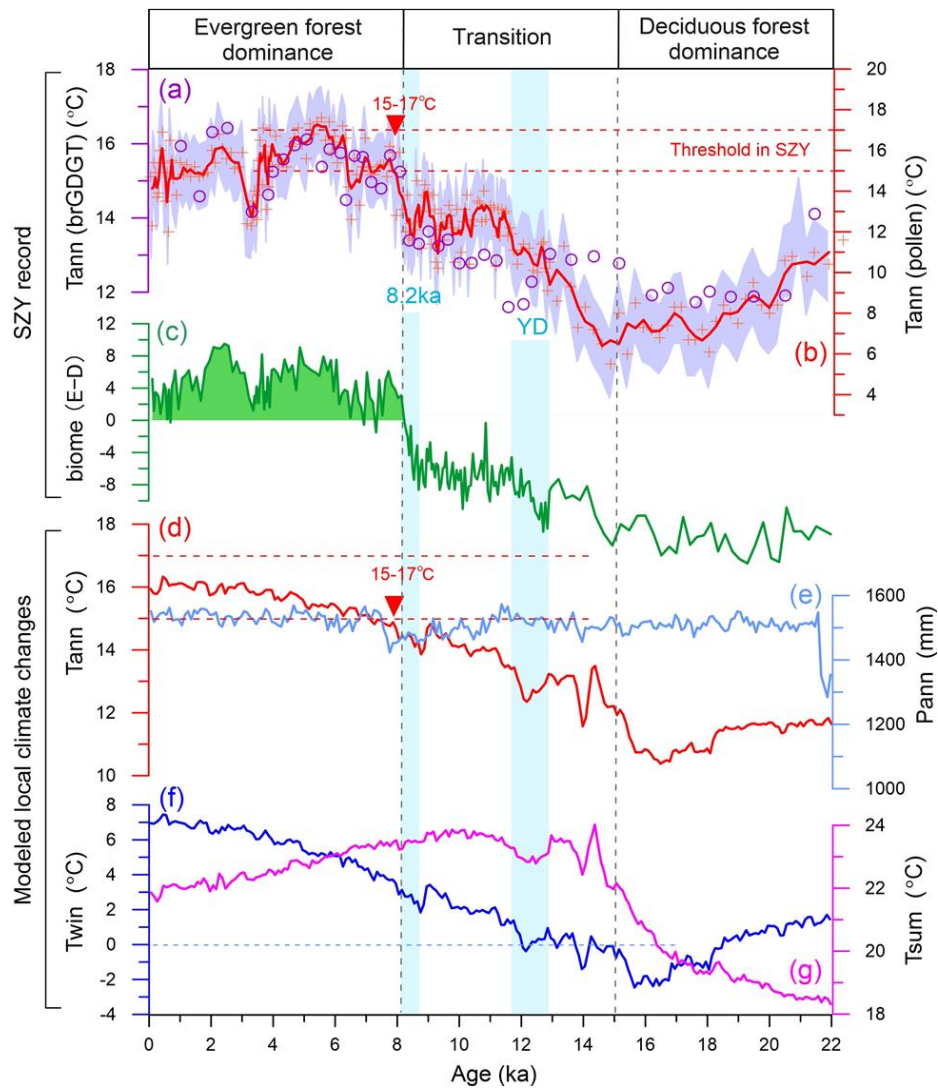


296
 297 **Fig. 7. Pollen groups and reconstructed biomes for the last 22 ka based on the GT (a) and SZY (b) cores from the**
 298 **middle subtropical zone.** Percentages (of total pollen grains) counted of the following four pollen groups are shown:
 299 evergreen broadleaved trees, deciduous broadleaved trees, cold-tolerant conifers and terrestrial forbs. The biomes shown
 300 in the lower panels are temperate deciduous broadleaved forest (DBLF), cold mixed forest (CLMX), cool mixed forest
 301 (COMX), alpine shrub and meadow/tundra (ALSM), subtropical evergreen broadleaved forest (EBLF), tropical seasonal
 302 forest (TSFO) and tropical rainforest (TRFO) (Table 3).

303 3.2. Quantitative climate reconstruction and comparison with simulation result

304 We applied a quantitative method to reconstruct the paleoclimate from the SZY pollen record. The
 305 mean annual temperature (Tann), which may strongly influence regional forest distributions, passed
 306 the significance test for the reconstruction (Fig. 4). We selected annual mean temperature as the
 307 representative parameter to explore the vegetation-climate relationship. The result shows that the

308 estimated Tann from the SZY fossil pollen record was lowest (about 8°C) during the LGM, and it
309 increased to 15–17°C during the mid-Holocene, with an amplitude in variation of up to ~8°C
310 between the glacial and postglacial periods (Fig. 8). The reconstructed temperatures below 12°C
311 during the glacial period from 22 ka to 15 ka are consistent with conditions suitable for the deciduous
312 forest biome, but far from the threshold temperatures required by evergreen forest. This quantitative
313 estimate falls within the framework of previously simulated temperature using climate models,
314 showing that in subtropical areas annual climatic conditions for deciduous forest expansion during
315 the LGM could include annual temperatures as low as 11°C (Ju et al., 2007; Tian and Jiang, 2016).
316 According to the reconstruction there was a temperature rise at 15 ka, corresponding with the B/A
317 warming. However, after the YD the rate of warming in the SZY locality slowed, with fluctuations,
318 and only increased rapidly to near the EBLF threshold temperature (>15°C) after the 8.2 ka event.
319 The perfect match of quantitative climate data with biome changes revealed that the temperature
320 threshold leading to EBLF as the dominant forest was about 15–17°C in the mountains of the middle
321 subtropical zone. It should be noted that both the SZY and GT sites are on summits of subtropical
322 mountains, which may receive pollen carried by upward wind from nearby lower forest belts.



323

324 **Fig. 8. Reconstructed and modeled temperatures compared with biome changes in the SZY record.** (a) brGDGT-
 325 based mean annual temperature reconstruction (Wang et al., 2017) (purple circles) coupled with (b) pollen-based annual
 326 temperature reconstruction (red line of smoothed data over the grey error range), showing local temperature threshold
 327 range for EBLF (red dotted line). (c) Biome changes as indicated by the difference between evergreen and deciduous
 328 biome scores (EBLF-DBLF). Climate simulation by transient model extracted from the grid point at SZY locality: (d)
 329 annual mean temperature (Tann) and (e) annual precipitation (mm). (f) Winter (Twin) and (g) summer (Tsum)
 330 temperatures.

331 To validate the pollen-based temperature proxy, we performed a parallel reconstruction of air

332 temperature from the same core (SZY) using brGDGT (Wang et al., 2017), as an independent
333 climate reconstruction method. The brGDGT-based Tann indicated a rapid increase 13°C to >15°C at
334 ~8.1 ka, which is largely consistent with the pollen-based climate reconstruction. Similar degrees of
335 variation and thresholds apply to the two temperature proxies, particularly for the key timing of the
336 YD event and the substantial forest transformation starting at ~8.1 ka, despite some differences
337 between absolute values of the LGM derived by the two methods. Overall, there is strong agreement
338 between forest transitions and quantitative climate changes derived from pollen and other biomarkers
339 in the same sediment material (SZY), both long-term (orbital scale) and short-term (rapid shifts, e.g.,
340 in the YD event), indicating sensitive response to climate change (Fig. 3). Since about 8.1 ka, the
341 reconstructed annual temperature derived from both pollen and branched glycerol dialkyl glycerol
342 tetraethers (brGDGT, see below) remained consistently high in the mid- to late Holocene (15–18°C),
343 since about 8.1 ka, with only a clear cooling event at about 3.5 ka.

344 We used transient simulation, generated with TRACE21 (Liu et al., 2009), to assess the seasonal
345 and annual climatic changes in the study area during the last 21 ka. The modeled climate data
346 corresponding to the geographical location of the SZY study site were extracted, and systematically
347 corrected according to the present-day local climate observations. The results show that modelled
348 mean annual and winter temperatures, characterized by progressive increase towards the late
349 Holocene, were crucial for changes in forest components (Fig. 8). The simulated mean annual
350 temperature (Tann) threshold for local EBLF as the dominant forest was higher than 15°C, in good
351 agreement with the pollen- and brGDGT-based climate reconstructions. In terms of seasonal climate,
352 a threshold simulated winter temperature of about 4°C for EBLF expansion in subtropical

353 mountainous areas was obtained. The simulation indicates that precipitation may not be a key factor
354 for the focal forest transformations, because it remained similar during the covered period, with
355 annual rainfall consistently exceeding 1000 mm since the LGM (Fig. 8e). In summary, the model-
356 proxy comparison revealed good consistency for the climate thresholds for local forest
357 transformation from DBLF to EBLF, except for a few differences in the late Holocene.

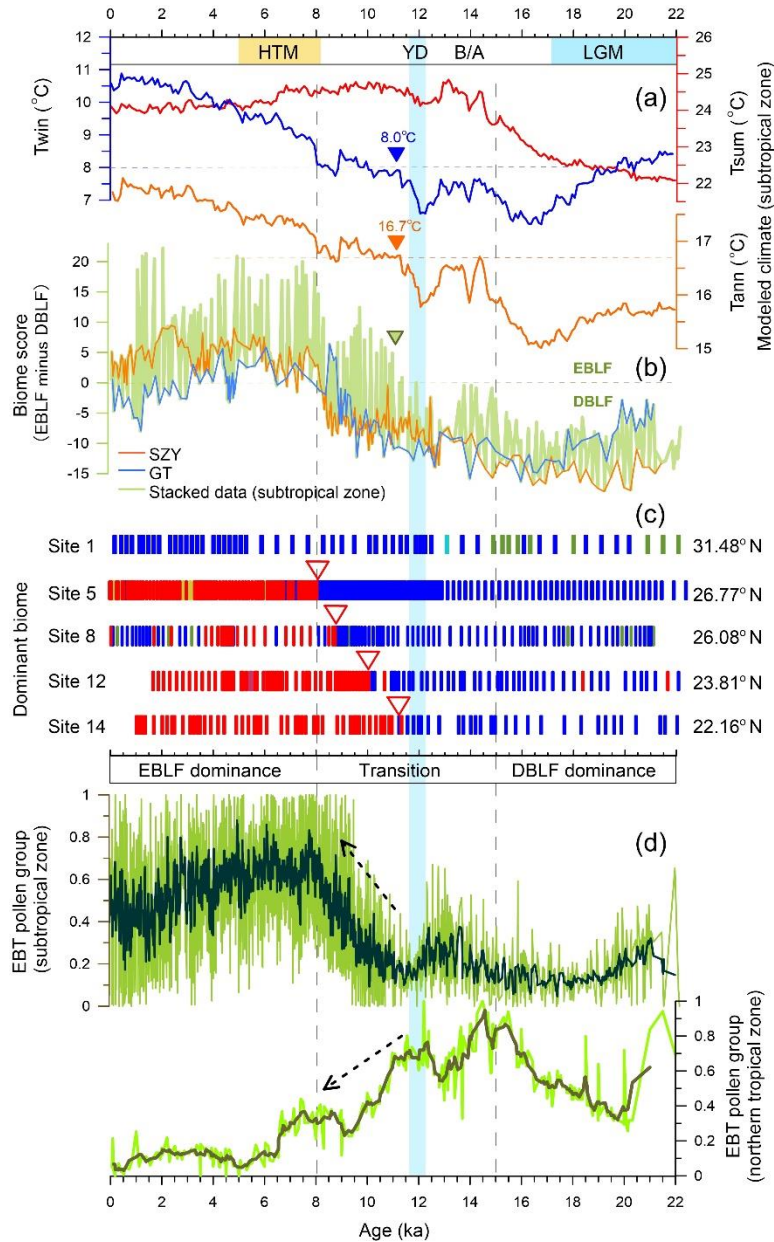
358 *3.3. Evergreen/deciduous forest alternation since the last glacial maximum across eastern China*

359 Three distinct evolutionary stages of vegetation change over the subtropical zone could be identified
360 (Fig. 8). During the LGM (stage I), the dominant biome was DBLF, with negative score values of
361 biome difference between EBLF and DBLF (E-D) ranging from -15 to -5. During stage II (from 15 to
362 8.1 ka), this score gradually increased from -10 to +10, most strongly between 11.3 and 8.1 ka. This
363 indicates a transition period characterized by an increase in the evergreen biome to an extent equal to
364 or greater than that of the deciduous biome. However, the score only rose from -10 to 0 in the SZY
365 and GT records, due to their locations in mountainous areas at altitudes higher than 1000 m. During
366 stage III (after 8.1 ka), substantial evergreen forest recolonization occurred, with E-D scores rising up
367 to +5 to +20. Integration of pollen records from the subtropical region consistently shows that the two
368 abrupt global cooling events (i.e., the YD and 8.2 ka event) had major impacts on the regional
369 vegetation and Asian climate system (Wang et al., 2001; Cheng et al., 2020). Our data from across the
370 subtropical region indicate a period of maximum EBLF dominance between 8 and 5 ka, corresponding
371 to the Holocene Thermal Maximum (HTM). The late Holocene records from the study sites show a
372 decline of EBLF or an unstable fluctuation with complex changes in the local ecosystems, such as a

373 decline in wetlands, colonization by terrestrial forbs instead of forest trees, and expansion of secondary
374 forest with abundant pioneer ferns (Figs. 5 and 6).

375 Previously compiled vegetation proxy data suggest that the modern forest distribution in
376 southeastern China does not differ greatly from that of the LGM, and that forest cover has changed
377 little (mostly between 5%) during the last 22 ka (Tian et al., 2016). However, our pollen data and
378 biome reconstruction, which distinguish between deciduous and evergreen forests, suggest a
379 fundamental change in forest type occurred during the last glacial cycle. In this study, we compiled
380 data on pollen groups composed of representative evergreen broadleaved trees from multiple records
381 across the subtropical zone (Fig. 9). The results indicate that an initial increase in EBT during the B/A
382 warming coincided with a peak period in the tropical zone, and hence an early northward expansion
383 of evergreen forests. However, since the YD event, the decline of EBT in the tropics indicates an
384 opposite trend to that of the subtropical zone. Such contrasting trends in EBT between the tropical and
385 subtropical zones since the end of YD can be interpreted as a northward biome migration. The timing
386 of EBLF biome transformation at four locations from 22° N to 27° N latitude shows a successive
387 northward shift, with dates at 11.2, 10.2, 8.7, and 8.1 ka (Fig. 9c), strongly suggesting a time-
388 transgressive pattern. That is, vegetation response to Holocene warming apparently occurred earlier in
389 the southern subzone than in the middle and northern subzones. The results also indicate that the
390 latitudinal limit of the evergreen forest was south of site DJH, located at the northern subtropical
391 boundary (31.5° N latitude and 1751 m asl). Site DJH was not dominated by EBLF during the mid-
392 Holocene, and it is still not dominated by EBLF today, which is not surprising as the current annual
393 temperature (Tann) is about 7–8°C at an elevation of 1700 m, far below the climatic range for EBLF

394 dominance. The findings suggest that the EBLF's northward migration during the HTM only reached
 395 the mountainous regions south of 31° N.

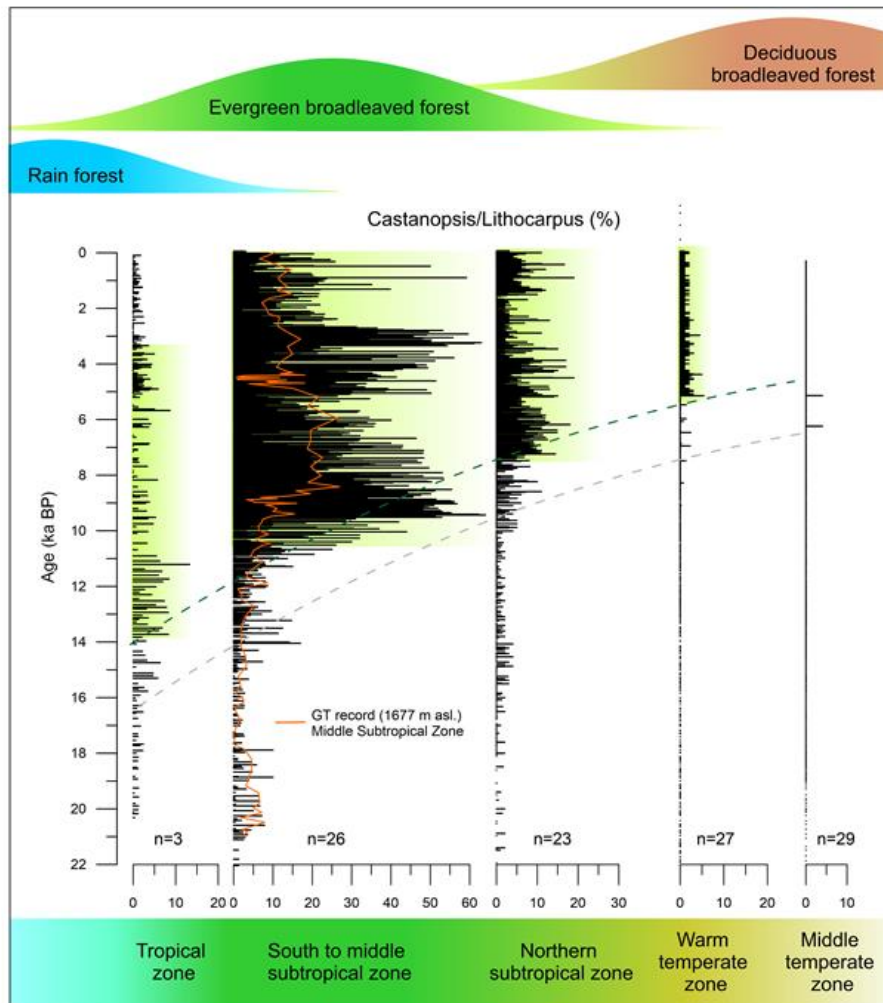


396
 397 **Fig. 9. Relationship between biome and climate changes in the subtropical zone.** (a) Winter (blue), summer (red) and
 398 annual mean (orange) temperatures for the subtropical zone simulated by TRACE21. (b) Stacked data of regional biome
 399 changes showing differences between evergreen and deciduous biome scores (light green), where SZY and GT mountain
 400 records are indicated in particular. (c) Dominant biome comparison among sites 1 (DJH), 4 (SZY), 7 (GT), 11 (TS) and

401 12 (DY) (see the legend for biomes in Fig. 7). (d) Combined pollen data of the evergreen broadleaved tree (EBT) in the
402 subtropical and tropical zones of the Northern Hemisphere (5-point moving average in brown) (pollen data from each
403 record are standardized to 0-1 values).

404

405 In order to reconstruct the regional shifts of EBLF across eastern China and better understand its
406 spatiotemporal changes, we selected a key pollen taxon *Castanopsis/Lithocarpus* which is dominant
407 in evergreen broad-leaved forest for data integration of different climate zones. The taxon of *Quercus*
408 was not used because of the great uncertainty in the identification of pollen taxa at the genus level
409 between evergreen-type and deciduous-type. A total of 108 records from the pollen database in eastern
410 China (Cao et al., 2013; Zheng et al., 2016) have been examined. The data integration results of
411 different climate zones in eastern China (longitude and latitude ranges from 100 to 125°E and from 18
412 to 40°N) show the increases in *Castanopsis/Lithocarpus* (equivalent to EBLF) since the last
413 deglaciation represent a significant time-transgressive forest response from south to north. The
414 proportion of evergreen forest elements decreased obviously in the northern subtropical subzone, and
415 almost disappeared northward in the temperate zone (Fig. 10). It is clear that the EBLF distribution
416 was restricted to the south of northern subtropical boundary even during the HTM. Besides, the EBLF
417 expansion along altitudinal gradients in mountain ranges of the middle subtropical zone (e.g. GT record
418 at 1677m asl.) also lagged behind those in the southern subtropical lowland regions and/or coastal
419 plains.



420

421 **Fig. 10. Synthetic changes of the dominant pollen type of *Castanopsis/Lithocarpus*, a representative taxon in**

422 **evergreen broadleaved forest, in different climate zones across eastern China over the last 22 ka.** The number of

423 records (n) used in each climate zone is shown. The dotted line indicates the early forest response to climate warming and

424 a time-transgressive pattern across eastern China. The orange line is the record from GT mountain peatland at 1677m.

425

426 The large-scale biome shifts across eight degrees of latitude, from 22 to 30°N, and the high temporal

427 precision of the fossil record, enabled us to estimate the forest migration rate. Our results indicate that

428 a fundamental biome upheaval began as early as 11.2 ka, initially in the southern subtropical subzone

429 (south of ~22°N). General recolonization of evergreen forests in the middle subtropical mountains

430 (around 24-28°N) then accelerated during the mid-Holocene (8-6 ka), until the modern northern
431 subtropical boundary was reached at around 6-5 ka. According to the relationship between migration
432 distance and time, the average migration rate was about 155km/ka northward during the transition
433 period from early to middle Holocene.

434

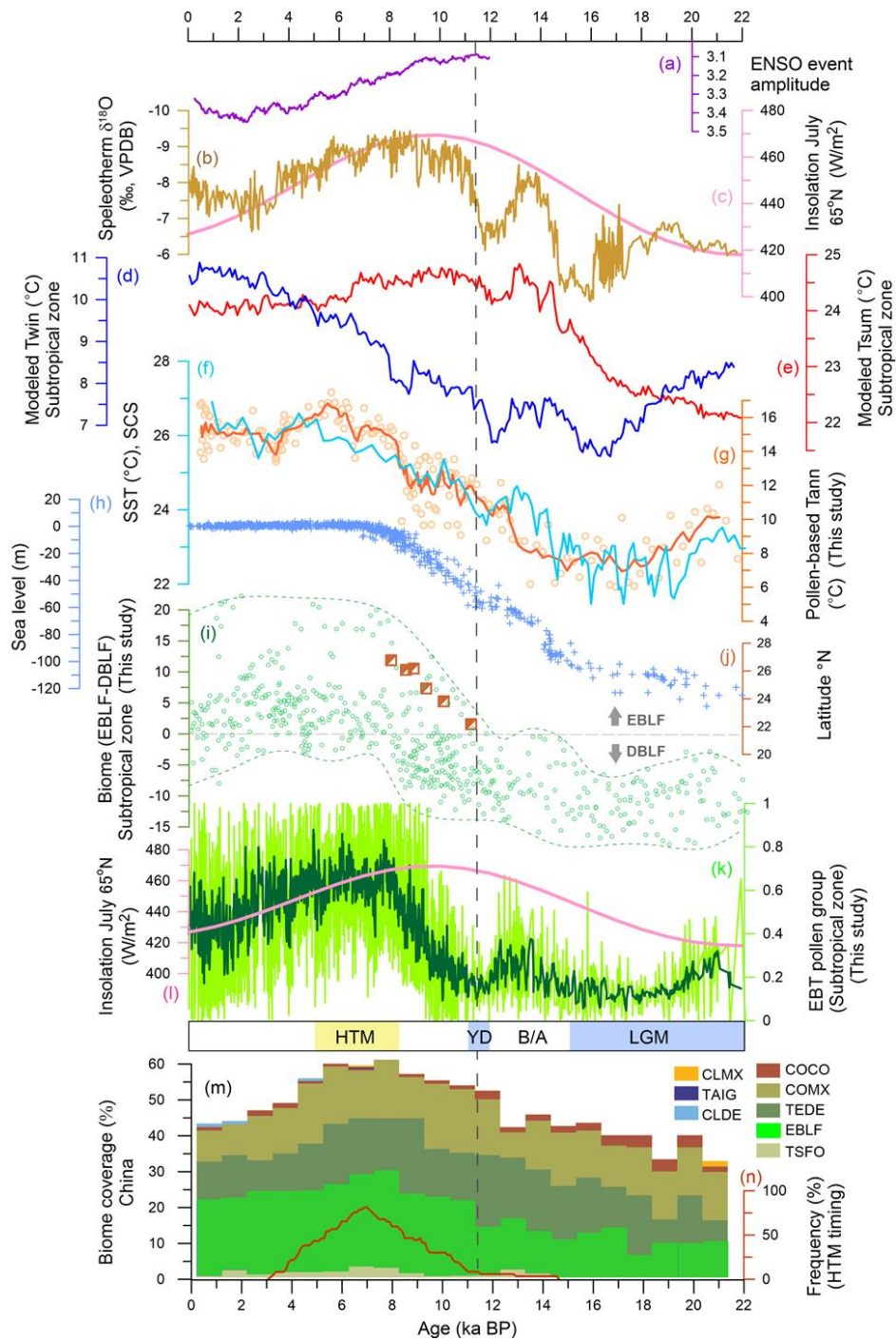
435 *3.4. Regional climate changes and thresholds leading to EBLF expansion*

436 The general patterns of deglacial warming observed in the climate simulations may help to improve
437 understanding of the forcing and dynamic mechanisms involved in spatial migration history of EBLF.
438 For each individual locality, the EBLF variation in many records shows a rapid change in forest
439 replacement within a relatively narrow time span, suggesting that climatic thresholds may play a key
440 role in forest transformation. Among the bioclimates required for EBLF growth, temperatures are the
441 most important determinants for its boundaries in China (Fang and Yoda, 1991; Hu et al., 2014).
442 Annual and winter temperatures from the transient model over the subtropical zone show consistent
443 variation with integrated subtropical biome changes between deciduous and evergreen broadleaved
444 forests. There was a moderate increase in the modeled temperatures, particularly in summer, during
445 the B/A warming. This resulted in a limited increase in EBLF, mainly in the southeastern and low-
446 altitude parts of the subtropical area near the west Pacific Ocean, such as the Chinese coastal regions
447 and islands (e.g., sites 11 and 12 in Fig. 9c). However, both simulated and proxy climate variables for
448 the mountainous localities in the central subtropical zone (e.g., SZY record) indicate that temperatures
449 remained below the thresholds for evergreen forest transformation during the early deglacial warming

450 (B/A). Thus, dominance of the deciduous forest biome persisted there. Soon after the YD cooling,
451 simulated temperatures for the subtropical area reached regional mean thresholds of ca.16.7°C (Tann)
452 and 8.0 °C (Twin) (Fig. 9d). Such average climate thresholds for EBLF dominance during the
453 Holocene in subtropical China are highly consistent with current optimum climate conditions for EBLF
454 simulated using the Species Distribution model (Hijmans et al., 2016), with median percentiles of
455 16.7°C and 8.1°C for Tann and Twin, respectively (Fig. 1c). Our results are also consistent with
456 meteorological data delineating the modern EBLF distribution in the subtropical mountains (Liu et al.,
457 2010). It should be noted that in the vertical and northern boundary areas of the subtropical region, the
458 temperature thresholds for EBLF transformation are slightly lower than the regional averages. For
459 example, records for mountainous parts such as the SZY site (altitude, 1007 m) indicate that the Tann
460 and Twin thresholds are 15 and 4 °C, respectively, and these areas cover roughly 10–30% of the
461 modern EBLF distribution. During the transition period of the early Holocene, the warming reached
462 the thresholds for EBLF dominance earlier in the south than in the north. Such time difference in
463 temperature rises to the threshold along latitude and vertical gradients since the LGM are reflected in
464 delayed biome changes northward. During the early Holocene, temperatures in subtropical Asia
465 gradually increased to levels near the EBLF thresholds. However, temperatures in a large area to the
466 northern boundary of the zone may have still been below the thresholds, resulting in a north-south
467 temperature gradient, and thus there was an earlier forest response at sites along low latitudes as
468 compared to sites located further north. Similar time-transgressive patterns have already been observed
469 in proxy records of the East Asian monsoon region (An et al., 2000; Zhou et al., 2016; Ren and Yi,
470 2019).

471

472 Low winter and/or minimum temperatures compared with summer, linked with the length of the
473 growing season, were likely important constraints on the rate of EBLF migration during this period. A
474 vegetation shift from the early to mid-Holocene triggered by the winter warming effect on vegetation
475 has been corroborated by sensitivity experiments involving rainfall and thermal forcing with a land-
476 vegetation model (Cheng et al., 2021). As well as temperature, mountainous topography in the study
477 area may have also played a role, as a geographic barrier hindering northward biome migration (Xu et
478 al., 2015). Notably, records for site TCK1, at 3898 m asl, indicate that the major forest biome change
479 in the southwestern plateau of China occurred at ~6 ka (Xiao et al., 2014), more than 2,000 years later
480 than at a similar latitude in southeastern China. This may have been a consequence of the temperature
481 lapse rate along the altitudinal gradient, so both latitude and altitude may have geographically
482 influenced temperature gradients and constrained the vegetation belts (Cheng et al., 2018).



483

484 **Fig. 11. Comparison of proxy records, simulations and paleoclimate forcings. (a)** Mean amplitude of 500-year
 485 overlapping windows for ENSO events exceeding 3 k (in °C) (Clement et al., 2000). **(b)** Speleothem oxygen isotopic
 486 records from the Hulu and Dongge caves (Wang et al., 2001; Dykoski et al., 2005). **(c)** July insolation at 65°N latitude.
 487 **(d)** and **(e)** TRACE21 winter (blue) and summer (red) temperatures for the subtropical zone; **(f)** Alkenone-sea surface
 488 temperature estimates for the northern South China Sea (He et al., 2008). **(g)** Pollen-based temperature reconstruction

489 (Tann) from the SZY record (the orange line shows the five-point averages). **(h)** Ice-volume equivalent sea level estimate
490 ([Lambeck et al., 2014](#)). **(i)** Stacked data of the biome scores (EBLF-DBLF) for the subtropical zone. **(j)** Timing and
491 latitude positions for the EBLF as a dominant forest from record sites 4, 7, 8, 10, 11, 12 ([Table 1](#)). **(k)** Standardized
492 values of pollen group of evergreen broadleaved taxa (EBT) in the subtropical zone; **(l)** July insolation at 65°N latitude.
493 **(m)** Proportion of biome coverages in China at 1000-yr resolution ([Li et al., 2019](#)). **(n)** Frequency variation of the HTM
494 interval indicated by pollen data in China ([Jiang et al., 2019](#)).

495 Our solid evidence of the subtropical biome shift during the last glacial-interglacial transition
496 enables better understanding of the sensitivity and potential mechanism of vegetation response to
497 global climate change. The observed onset of primary increases in evergreen arboreal elements
498 coincides with the B/A warming during the early deglaciation. The initial gradual increase in EBLF
499 biome coincided with the main phase of deglaciation occurred from ~16.5 ka to ~8.2 ka BP at an
500 average rate of sea-level rise of 12 m·ka⁻¹ inferred by [Lambeck et al., 2014](#) since about 16 ka ([Fig.11](#)).
501 Effects of changes in land-sea configuration associated with sea-level changes also suggest that
502 internal variability in the climate system linked with global energy fluxes on millennial time scales
503 play important roles in radiative imbalances ([Baggenstos et al., 2019](#)), and hence both temperature and
504 vegetation. In addition, coupled trends between temperatures reconstructed from a middle subtropical
505 record and surface temperatures of the northern South China Sea ([He et al., 2008](#)) imply a close land-
506 sea relationship and the importance of tropical ocean circulation ([DiNezio and Tierney, 2013](#)). Our
507 data reveal that the EBLF distribution peaked in a Holocene interval between 8.1 and 5 ka, associated
508 with the maximum forest coverage in China ([Li et al., 2019](#)). Such interval of forest expansion indicates
509 the warmest condition, which is consistent with the HTM, traditionally thought to have occurred during

510 the mid-Holocene in Asia (Shi et al., 1993; Jiang et al., 2019).

511 Our analysis shows a time-transgressive pattern of forest replacement from south to north,
512 consistent with the assumption that there was an expansion and/or northward retreat of the Holocene
513 Optimum (Ren and Yi, 2019). Similarly, monsoon precipitation previously reconstructed from pollen
514 data also shows a time-transgressive pattern of maximum precipitation, with earlier occurrence in the
515 southern area and later in the northern area (Zhou et al., 2022). They suggested that the monthly
516 insolation changes force regional climate in different parts of the monsoonal China through a shift in
517 the Western Pacific Subtropical High. In northern China, there was also a delayed ecosystem (tree
518 cover) response to changes of monsoon intensity which was likely caused by winter warming and the
519 subsequent feedback effects on soil moisture (Cheng et al., 2021). In this study, we suggest that
520 temperature change (particularly winter warming) was crucial for the EBLF expansion. Apparently,
521 rainfall in the subtropical mountainous areas of southeast China during the last glacial cycle remained
522 relatively high due to the orographic effects, indicating that precipitation changes may not be a key
523 factor for the EBLF/DBLF alternation. Moreover, simulated variations in precipitation and
524 temperature were not coupled during the early to mid-Holocene.

525 , implying a gradual weakening of the temperature gradient between high and low latitudes. This
526 may have been related to airflows linked to the Hadley circulation and changes in position of the
527 Intertropical Convergence Zone (ITCZ) (Reimi et al., 2016). Such evidence of time-transgressive The
528 EBLF biome and climate variation trends during the mid- to late Holocene indicated by proxy records
529 showed a pattern of temperature decline or unstable fluctuations, conflicting with modeled indications
530 of sustained warming (Fig. 9a). This contradiction between the reconstructed cooling (or unstable

531 variation) and simulated progressive warming has been attributed to biases in the seasonality of the
532 proxy reconstruction and climate sensitivity of models (Liu et al., 2015). Moreover, we found that the
533 pollen assemblages indicating cooler conditions in the late Holocene were complex and differed from
534 those from the last glacial period, as the evergreen forest components were not simply replaced by the
535 deciduous components. Instead, grassland and secondary plant elements such as Poaceae, *Pinus*, and
536 *Alnus* gradually increased. Some studies suggest that there was a decline in effective moisture in
537 southern Asia resulted from the weakened summer monsoon and decreased precipitation since the
538 middle Holocene (Li et al., 2020). In the meanwhile, the mean El Niño Southern Oscillation (ENSO)
539 amplitude significantly increased (Clement et al., 2000), leading to frequent floods and droughts in
540 China. Further, numerous proxy studies have indicated that a major loss of plant biodiversity, spread
541 of rice cultivation and increasing frequency of fires in southern China occurred 2000-3000 years ago
542 (Kaplan et al., 2011; Ma et al., 2020; Xu et al., 2021). Therefore, we suggest that combinations of
543 factors, such as the weakening Asian summer monsoon, reduced precipitation and effective moisture,
544 increased amplitude of ENSO events and associated changes in the western Pacific subtropical high,
545 as well as fire frequencies associated with anthropogenic disturbances, may have affected the regional
546 climate and thus EBLF/DBLF forest transformation from the mid- to late Holocene.

547

548 **4. Conclusion**

549 Although the EBLF components began to increase in low latitude regions during the deglaciation,
550 biome change from deciduous to evergreen forest in the southern subtropical zone did not begin until

551 11.3 ka, after the Younger Dryas when regional annual and winter temperatures reached the zonal
552 average thresholds of $\sim 16.7^{\circ}\text{C}$ and $\sim 8.0^{\circ}\text{C}$, respectively. These values are highly consistent with the
553 simulated results for current EBLF distribution. Both modeled and proxy data are consistent with the
554 early Holocene being a key period when climatic thresholds (particularly winter and annual
555 temperatures) approached then exceeded bioclimatic constraints for EBLF expansion. The EBLF
556 biome recolonized the entire subtropical landscape including northern and mountainous areas during
557 8-5 ka, when regional air temperature (T_{ann}) was higher than 15°C , indicating a warmest climate
558 interval in accordance with the age of HTM commonly defined by multi-proxy records in China. Our
559 integrated data indicate a time transgressive pattern that an earlier forest replacement at sites in low
560 latitude regions as compared to sites located further north or at higher elevation in the subtropical zone
561 of east China. This study highlights the greater importance of postglacial warming than rainfall
562 changes for the EBLF recolonization across southeast China. However, the environment factors
563 causing forest changes in the latter half of the Holocene were more complex. The sensitivity of forest
564 responses to complex seasonal and abrupt climate changes (such as ENSO events), as well as
565 increasing human activities during the late Holocene, may lead to the pollen-based climate
566 reconstruction different from the model results. Our study provides new quantitative information
567 regarding past biome and climate changes, as well as thresholds for forest transformation, that enhance
568 understanding of long-term vegetation dynamics in the ecologically sensitive region between
569 temperate and tropical bioclimatic zones. The observed amplitude of subtropical ecosystem changes
570 during the postglacial warming may also serve as an analog for projections of forest responses to the
571 increasing greenhouse conditions expected under future climate scenarios.

572

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579

580 **CRedit authorship contribution statement**

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582 draft, Writing – review & editing, Funding acquisition. **Cong Chen:** Investigation, Methodology, Data
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592

593 **Declaration of Competing Interest**

594 The authors declare that they have no known competing financial interests or personal relationships
595 that could have appeared to influence the work reported in this paper.

596

597 **Data availability**

598 Data of biome and climate reconstructions can be found in the Supplementary data. Modern pollen
599 dataset from EAPD for climate reconstruction is shared at <https://doi.org/10.5281/zenodo.6918393>.

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