



1 **Pollen-based quantitative land-cover reconstruction for northern Asia during**
2 **the last 40 ka**

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14

15 **ABSTRACT**

16 We collected the available relative pollen productivity (RPP) estimates for 27 major
17 pollen taxa from Eurasia and applied them to estimate plant abundances during the
18 last 40 cal. ka BP (calibrated thousand-year before the present) using pollen counts
19 from 203 fossil pollen records in northern Asia (north of 40°N). These pollen records
20 were organised into 42 site groups; and regional mean plant abundances were
21 calculated using the REVEALS (Regional Estimates of Vegetation Abundance from
22 Large Sites) model. Time-series clustering, constrained hierarchical clustering, and
23 detrended canonical correspondence analysis were performed to investigate the
24 regional pattern, time, and strength of vegetation changes, respectively.
25 Reconstructed regional land cover for each site group is generally consistent with *in*
26 *situ* modern vegetation in that vegetation changes within the regions are
27 characterized by minor changes in the abundance of major taxa rather than by



28 invasions of new taxa, particularly during the Holocene. We argue that pollen-based
29 REVEALS estimates of plant abundances should be a more reliable reflection of the
30 vegetation as pollen may overestimate the turnover, particularly when a high pollen
31 producer invades areas dominated by low pollen producers. Comparisons with
32 vegetation-independent climate records show that climate change is the primary
33 factor driving land-cover changes at broad spatial and temporal scales. Vegetation
34 changes in certain regions or periods, however, could not be explained by direct
35 climate change, for example inland Siberia, where a sharp increase in evergreen
36 conifer tree abundance occurred at ca. 7~8 cal. ka BP despite an unchanging climate,
37 potentially reflecting their response to complex climate-permafrost-fire-vegetation
38 interactions and thus a possible lagged climate response.

39 *Keywords:* boreal forests, China, Holocene, late Quaternary, pollen productivity,
40 quantitative reconstruction, Siberia, vegetation

41 **1 Introduction**

42 High northern latitudes such as northern Asia experience above-average temperature
43 increases in times of past and recent global warming (Serreze et al., 2000; IPCC,
44 2007), known as polar amplification (Miller et al., 2010). Temperature rise is
45 expected to promote vegetation change as the vegetation composition in these areas
46 is assumed to be controlled mainly by temperature (Li J. et al., 2017; Tian et al.,
47 2018). However, a more complex response can occur mainly because vegetation is
48 not linearly related to temperature change (e.g. due to resilience, stable states or
49 time-lagged responses; Soja et al., 2007; Herzsuh et al., 2016) and/or vegetation is
50 only indirectly limited by temperature and other temperature-related environmental
51 drivers such as permafrost conditions are more influential (Tchebakova et al., 2005).

52 Such complex relationships between temperature and vegetation may help explain
53 several contradictory findings of recent ecological change in northern Asia. For
54 example, simulations of vegetation change in response to a warmer and drier climate
55 indicate that steppe should expand in the present forest–steppe ecotone of south



56 Siberia (Tchebakova et al., 2009) but, contrarily, pine forest in south Siberia
57 increased during the past 74 years, probably because the warming temperature was
58 mediated by improved local moisture conditions (Shestakova et al., 2017). In another
59 example, evergreen conifers, which are assumed to be more susceptible to frost
60 damage than *Larix*, expanded their distribution by 10% during a period with cooler
61 winters from 2001 to 2012, while the distribution of *Larix* forests decreased by 40%
62 on the West Siberia Plain as revealed by a remote sensing study (He et al., 2017).
63 Additionally, some field studies and dynamic vegetation models infer a rapid
64 response of the treeline to warming in northern Siberia (e.g., Moiseev, 2002; Soja et
65 al., 2007; Kirdyanov et al., 2012), but combined model- and field-based
66 investigations of larch stands in north-central Siberia reveal only a densification of
67 tree-stands, not an areal expansion (Kruse et al., 2016; Wieczorek et al., 2017).

68 These findings on recent vegetation dynamics that contradict a straightforward
69 vegetation-temperature relationship may be better understood in the context of
70 vegetation change over longer time-scales. Synthesizing multi-record pollen data is
71 the most suitable approach to investigate quantitatively the past vegetation change at
72 broad spatial and long temporal scales. Broad spatial scale pollen-based land-cover
73 reconstructions have been made for Europe (e.g. Mazier et al., 2012; Nielsen et al.,
74 2012; Trondman et al., 2015) and temperate China (Li, 2016) for the Holocene.
75 However, vegetation change studies in northern Asia are restricted to biome
76 reconstructions (Tarasov et al., 1998, 2000; Bigelow et al., 2003; Binney et al. 2017;
77 Tian et al., 2018), which do not reflect compositional change. Syntheses of pure
78 pollen percentage data are not appropriate due to differences in pollen productivity,
79 which may result in an overestimation of the strength of vegetation changes (Wang
80 and Herzschuh, 2011). This might be particularly severe when strong pollen
81 producers such as pine (Mazier et al., 2012) invade areas dominated by low pollen
82 producers such as larch (Niemeyer et al, 2015). Marquer et al. (2014, 2017) also
83 demonstrated the strength of pollen-based REVEALS estimates of plant abundance
84 in studies of Holocene vegetation change and plant diversity indexes in Europe.



85 Accordingly, syntheses of quantitative plant cover derived from the application of
86 RPP to multiple pollen records (Trondman et al., 2015; Li, 2016) should be a better
87 way to investigate Late Glacial and Holocene vegetation change in northern Asia.

88 In this study, we employ the taxonomically harmonized and temporally standardized
89 fossil pollen datasets available from eastern continental Asia (Cao et al., 2013, 2015)
90 and Siberia (Tian et al., 2018) covering the last 40 cal. ka BP (henceforth abbreviated
91 ka). We compile all the available RPP estimates from Eurasia and use the mean of
92 estimates for each taxon. Finally, we quantitatively reconstruct plant cover using the
93 REVEALS model (Sugita, 2007) for 27 major taxa at 18 key time slices. Our aims
94 are to (1) reveal the nature, strength, and timing of vegetation change in northern
95 Asia and its regional peculiarities; and 2) discuss the driving factors of vegetation
96 change.

97 **2 Data and methods**

98 *2.1. Fossil pollen data process*

99 The fossil pollen records were obtained from the extended version of the fossil
100 pollen dataset for eastern continental Asia containing 297 records (Cao et al., 2013,
101 2015) and the fossil pollen dataset for Siberia with 171 records (Tian et al., 2017).
102 For the 468 pollen records, pollen names were harmonized and age-depth models
103 were re-established using the same procedures (further details are described in Cao
104 et al., 2013). We selected 203 pollen records from lacustrine sediments (110 sites)
105 and peat (93 sites) north of 40°N, with chronologies based on ≥ 3 dates and < 500
106 year/sample temporal resolution generally, following previous studies (Mazier et al.,
107 2012; Nielsen et al., 2012; Fyfe et al., 2013; Trondman et al., 2015). Out of the 203
108 pollen records, 170 sites (83 from lakes, 87 from bogs) have original pollen counts,
109 while in the other 33 sites only pollen percentages are available. Due to overall low
110 site density, we decided to include these data. The original pollen counts were back
111 calculated from percentages using the terrestrial pollen sum indicated in the original
112 publications. Detailed information (including data quality, chronology reliability and



113 data source) of the selected sites is presented in Appendix 1.

114 Table 1 Selected time windows.

115

Time window (cal a BP)	Abbreviated name
-60~100	0 ka
100~350	0.2 ka
350~700	0.5 ka
700~1200	1 ka
1700~2200	2 ka
2700~3200	3 ka
3700~4200	4 ka
4700~5200	5 ka
5700~6200	6 ka
6700~7200	7 ka
7700~8200	8 ka
8700~9200	9 ka
9700~10200	10 ka
10500~11500	11 ka
11500~12500	12 ka
13500~14500	14 ka
19000~23000	21 ka
23000~27000	25 ka
36000~44000	40 ka

116

117 We selected 18 key time slices for reconstruction (Table 1) to capture the general
118 temporal patterns of vegetation change during the last 40 ka, i.e. 40, 25, 21, 18, 14,
119 and 12 ka during the late Pleistocene and 1000-year resolution (i.e. 500-year time
120 windows around each millennium, e.g. 0.7-1.2 ka, 1.7-2 ka, etc.) during the
121 Holocene. For the 0 ka time slice, the ca. 150-year time window (<0.1 ka) was set to
122 represent the modern vegetation. Since few pollen records have available samples at
123 the 0 ka time slice, the 0.2 and 0.5 ka time slices were added with 250-year or
124 350-year time windows (0.1~0.35 ka and 0.35~0. ka, respectively) to represent the
125 recent vegetation pattern, following the strategy and time windows implemented in
126 Europe (Mazier et al., 2012; Trondman et al., 2015). For the last glacial period, even
127 broader time windows were chosen to offset the sparsely available samples (Table 1).
128 Pollen counts of all available samples within one time window were summed up to



129 represent the total pollen count for each time slice. In this study, we selected 27
 130 major pollen taxa that form dominant components in both modern vegetation
 131 communities and the fossil pollen spectra with available PPE values and reconstruct
 132 their abundances in the past vegetation (Table 2).

133 Table 2 Fall speed of pollen grains (FS) and the means of the relative pollen productivity (RPP)
 134 estimates with their standard error (SE). Plant-functional type (PFT) assignment according to
 135 previous biome reconstructions (Tarasov et al., 1998, 2000; Bigelow et al., 2003; Ni et al., 2010).

136

PFT	PFT description	pollen type	FS (m/s)	PPE (SE)
I	evergreen conifer tree	<i>Pinus</i>	0.031 ¹	9.629 (0.075)
I	evergreen conifer tree	<i>Picea</i>	0.056 ¹	2.546 (0.041)
I	evergreen conifer tree	<i>Abies</i>	0.120 ¹	6.875 (1.442)
II	deciduous conifer tree	<i>Larix</i>	0.126 ¹	3.642 (0.125)
III	boreal deciduous tree	<i>Betula_tree</i>	0.024 ¹	8.106 (0.125)
III	boreal deciduous tree	<i>Alnus_tree</i>	0.021 ¹	9.856 (0.092)
III	boreal deciduous tree	<i>Corylus</i>	0.025 ²	1.637 (0.065)
IV	temperature deciduous tree	<i>Quercus</i>	0.035 ¹	6.119 (0.050)
IV	temperature deciduous tree	<i>Fraxinus</i>	0.022 ¹	2.046 (0.105)
IV	temperature deciduous tree	<i>Juglans</i>	0.037 ³	4.893 (0.221)
IV	temperature deciduous tree	<i>Carpinus</i>	0.042 ¹	5.908 (0.285)
IV	temperature deciduous tree	<i>Tilia</i>	0.032 ²	1.055 (0.066)
IV	temperature deciduous tree	<i>Ulmus</i>	0.032 ²	6.449 (0.684)
V	boreal shrub	<i>Betula_shrub</i>	0.024 ¹	1.600 (0.132)
V	boreal shrub	<i>Alnus_shrub</i>	0.021 ¹	6.420 (0.420)
V	boreal shrub	<i>Salix</i>	0.034 ²	1.209 (0.039)
V	boreal shrub	Ericaceae	0.034 ⁴	0.200 (0.029)
VI	arid-tolerant shrub and herb	<i>Ephedra</i>	0.015 ⁸	0.960 (0.140)
VI	arid-tolerant shrub and herb	<i>Artemisia</i>	0.014 ⁶	9.072 (0.176)
VI	arid-tolerant shrub and herb	Chenopodiaceae	0.019 ⁶	5.440 (0.460)
VII	steppe and forb tundra	Poaceae	0.035 ⁴	1.000 (0.000)
VII	steppe and forb tundra	Cyperaceae	0.035 ⁵	0.757 (0.044)
VII	steppe and forb tundra	Asteraceae	0.051 ⁷	0.465 (0.066)
VII	steppe and forb tundra	<i>Thalictrum</i>	0.007 ⁸	3.855 (0.258)
VII	steppe and forb tundra	Ranunculaceae	0.014 ⁹	2.900 (0.363)
VII	steppe and forb tundra	Caryophyllaceae	0.028 ⁹	0.600 (0.050)
VII	steppe and forb tundra	Brassicaceae	0.002 ³	4.185 (0.188)

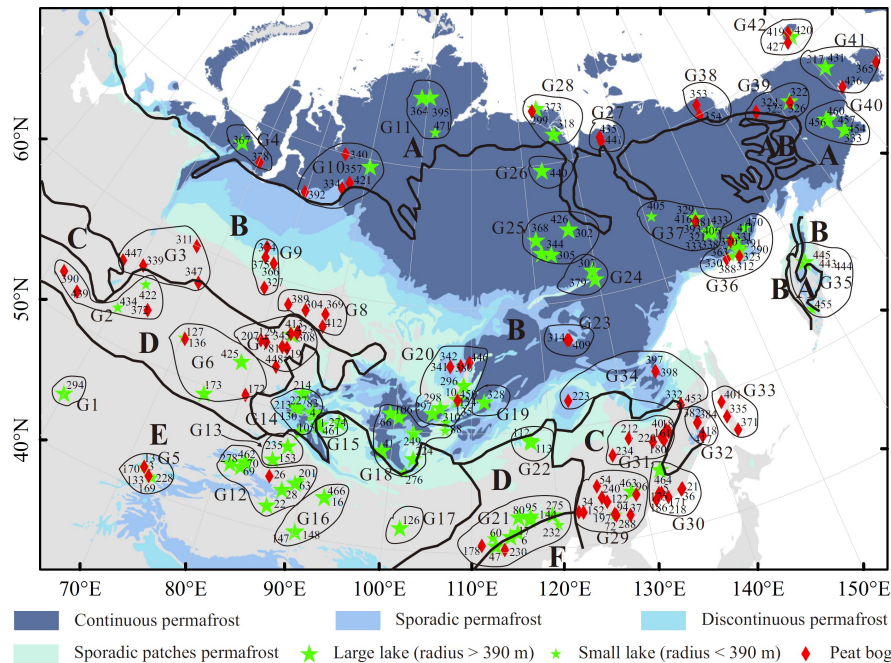
137 ¹ Eisenhut (1961); ² Gregory (1973); ³ Li et al. (2017); ⁴ Broström et al. (2004); ⁵ Sugita et al.
 138 (1999); ⁶ Abraham and Kozáková (2012); ⁷ Broström et al. (2002); ⁸ Xu et al. (2014); ⁹ Bunting
 139 et al. (2013).



140 *2.2 The REVEALS model setting*

141 The REVEALS model requires parameter inputs including sediment basin radius (m),
142 fall speed of pollen grain (FS, m/s), and PPE with standard error (SE; Sugita, 2007).
143 The areas of the 110 lakes were obtained from descriptions in original publications
144 and validated by measurements on Google Earth. Their basin radii were
145 back-calculated from their areas assuming a circular shape. There are 83 large lakes
146 (radius >390 m; following Sugita, 2007) in our dataset with a fairly even distribution
147 across the study area (Fig. 1), which helps ensure the reliability of the regional
148 vegetation estimations (Sugita, 2007; Mazier et al., 2012). Only 18 bogs have
149 published descriptions about their size and it is infeasible to measure them on
150 Google Earth because of indefinite boundaries, hence an identical radius of 100 m
151 was set for all bogs.

152 We collected available RPP estimates for the 27 selected pollen taxa from 20 studies
153 in Eurasia (Appendix 2). We calculated the mean PPE from all available PPE values,
154 but excluded records with $PPE \leq SE$ (Mazier et al., 2012). For simplification, we did
155 not evaluate the values and further selected RPP values following consistent criteria
156 as was done in Europe (Mazier et al., 2012). We used instead the original values
157 from the studies included in Mazier et al. (2012) and added new RPP values from
158 Europe published since the synthesis of Mazier et al. (2012). SE of the mean PPE
159 was estimated using the delta method (Stuart and Ord, 1994). Fall speeds for each of
160 the 27 pollen taxa were retrieved from previous studies (see Table 2).



161

162 **Fig. 1.** Distribution of the 203 fossil pollen sites and the 42 site groups together with the modern
 163 vegetation zones and permafrost extent in northern Asia. The vegetation-zone map modified
 164 from Tseplyayev (1961), Dulamsuren et al. (2005), and Hou (2001) includes: A: tundra, B: taiga
 165 forest, C: temperate mixed conifer-deciduous broadleaved forest, D: temperate steppe, E:
 166 semi-desert and desert; F: warm-temperate deciduous forest.

167 The REVEALS model generally performs best with pollen records from large lakes,
 168 although multiple pollen records from small lakes and bogs (at least two sites) can
 169 also produce reliable results where large lakes are absent (Sugita, 2007; Trondman et
 170 al., 2016). Here, due to the sparse distribution of available sites, we divided the 203
 171 sites into 42 site groups, based on criteria of geographic location, vegetation type
 172 (vegetation zone map modified from Tseplyayev, 1961; Dulamsuren et al., 2005;
 173 Hou, 2001), climate (based on modern precipitation and temperature contours), and
 174 permafrost (Brown, 1997) following the strategy of Li (2016) to ensure the
 175 reliability of REVEALS estimates of plant cover, each group includes at least one
 176 large lake or two small sites (small lakes or bogs; Fig. 1; Appendix 1).



177 The REVEALS model was run with a mean wind speed set to 3 m/s and neutral
178 atmospheric conditions following e.g. Trondman et al. (2015), and the maximum
179 distance of regional vegetation Z_{max} was set to 100 km. The lake and bog sites were
180 reconstructed using the models of pollen dispersal and deposition for lakes (Sugita,
181 1993) and bogs (Prentice, 1985), respectively in REVEALS version 5.0 (Sugita,
182 unpublished). The mean estimate of plant abundances from lakes and bogs was
183 calculated for each of the 42 site-groups, which includes both sediment types (using
184 the computer program `bog.lake.data.fusion`, Sugita, unpublished). Finally, the 27
185 taxa were assigned to seven plant functional types (PFT; Table 1) following the PFT
186 definitions for China and Siberia (Tarasov et al. 1998, 2000; Bigelow et al. 2003; Ni
187 et al., 2010; Tian et al., 2017), with the restriction that each pollen taxon is attributed
188 to only one PFT according to the strategy of Li (2016) (Table 2).

189 *2.2 Numerical analyses of reconstruction*

190 The abundance variations of the seven PFTs during the Holocene (time slices
191 between 12 and 1 ka) from 34 site-groups were used in a clustering analysis. Eight
192 site groups had to be excluded from the analysis due to poor coverage of time slices
193 (G1, G5, G17, G19, G27, G42). For site-groups with <3 missing time slices during
194 the Holocene (G3, G16, G26, G32, G33, G35, G38, G39, G41), linear interpolation
195 was employed to estimate the PFT abundances for the missing time slices.
196 Time-series clustering for the three-way dataset was performed to generate a
197 distance matrix among the site-groups using the `tsclust` function in the `dtwclust`
198 package (Sarda-Espinosa, 2018) in R 3.4.1 (R Core Team, 2017). The distance
199 matrix was employed in hierarchical clustering (using the `hclust` function in R) to
200 cluster the site-groups. Constrained hierarchical clustering (using `chclust` function in
201 `rioja` package version 0.9-15.1; Juggins, 2018) together with the broken-stick model
202 were used to determine the timing of primary vegetation changes in each site-group.
203 The amount of PFT compositional change (turnover) through time during the
204 Holocene was estimated by detrended canonical correspondence analysis (DCCA)

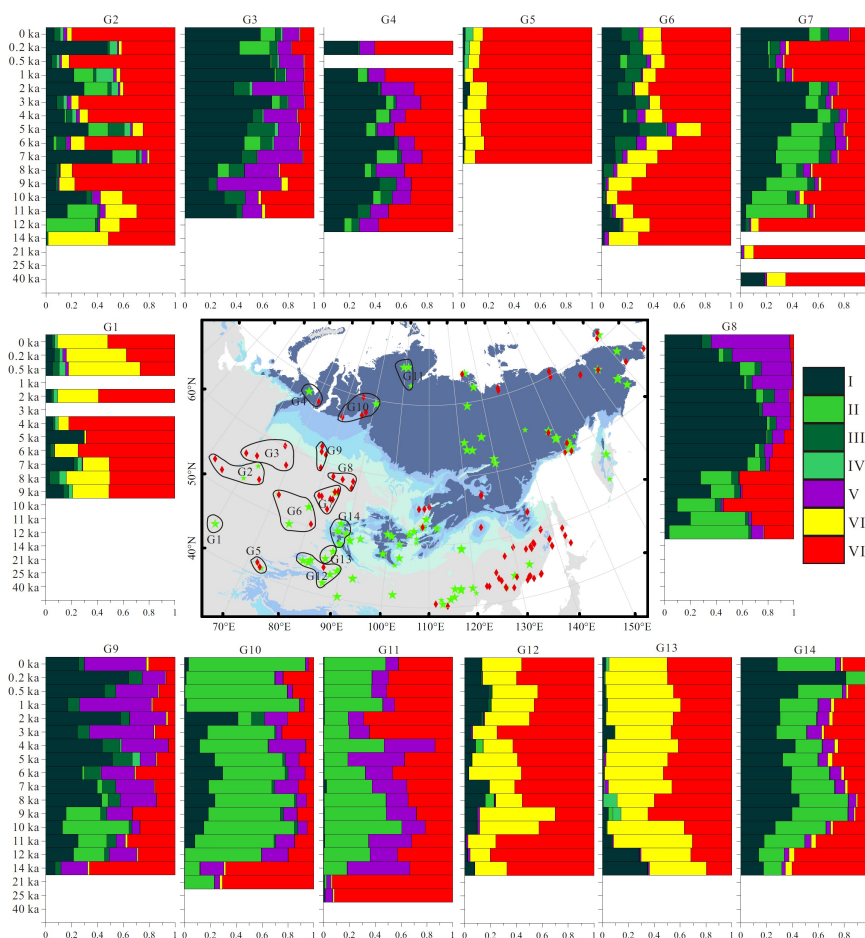


205 for each site-group (ter Braak, 1986) using CANOCO 4.5 (ter Braak and Šmilauer,
206 2002).

207 **3. Results**

208 *Large-scale pattern*

209 On a glacial-interglacial scale, marked temporal changes in the occurrence and
210 abundance of PFTs are revealed, in particular the high cover of tree PFTs during the
211 Holocene as opposed to the widespread open landscape during the glacial period. In
212 contrast, vegetation changes in northern Asia within the Holocene are rather minor
213 with only slight changes in PFT abundances. Cluster analyses of grouped vegetation
214 records from the Holocene find five clusters. Their spatial distribution is largely
215 consistent with the distribution of modern vegetation types as characterized by
216 certain PFTs. (1) Records from the forest-steppe ecotone (e.g. G12, G21) in
217 north-central China and the Tianshan Mts. (the mentioned geographic locations are
218 indicated in Appendix 3) have high tree PFTs during the middle Holocene. (2) Areas
219 in southern and south-western Siberia and north-eastern China were covered by
220 cool-temperate mixed forest or light taiga with a high diversity of trees throughout
221 the Holocene (e.g. G2, G7, G14, G29). (3) The West Siberian Plain and south-eastern
222 Siberia that are presently covered by open dark taiga forests (e.g. G8, G9, G33) had
223 an even higher abundance of evergreen conifer trees during the middle Holocene
224 than at present. (4) *Larix* formed light taiga forests in central Yakutia throughout the
225 Holocene (e.g. G25, G26). (5) Northern Siberia, which is presently covered by
226 tundra formed by boreal shrubs and herbs, had a higher share of tree PFTs during the
227 middle Holocene (e.g. G28, G39; Fig. 2).



228

229 Fig. 2. Temporal changes of plant functional type (PFT) cover in proportion for 42 site groups.
 230 PFT I: evergreen conifer tree; PFT II: deciduous conifer tree; PFT III: boreal deciduous tree; PFT
 231 IV: temperate deciduous tree; PFT V: boreal shrub; PFT VI: arid-tolerant shrub and herb; and
 232 PFT VII: steppe and tundra forb.

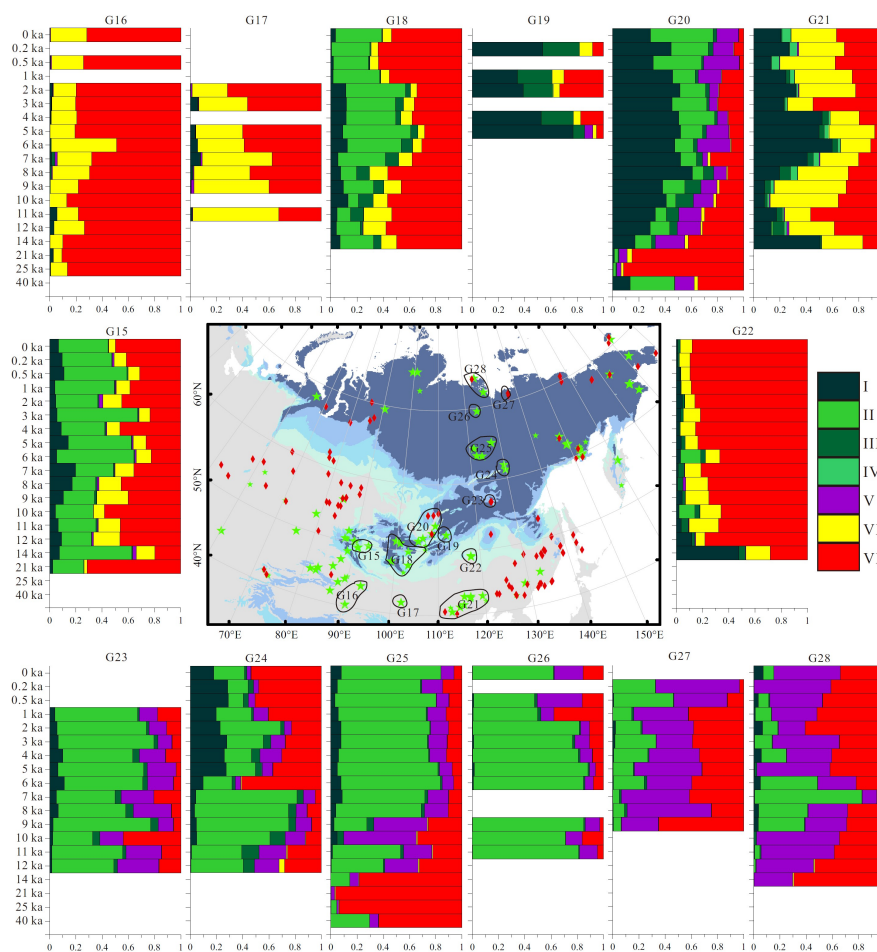
233 The turnover in PFT composition is <0.7 SD units in almost all site-groups, except
 234 G8 (0.88 SD), G9 (0.73 SD), and G24 (0.76 SD), indicating only slight vegetation
 235 change during the Holocene. The three site-groups with higher turnover show a
 236 distinct transition from light taiga to dark taiga in the middle Holocene (at ca. 8 ka).
 237 This result is consistent with the finding that PFT abundance from 16 site groups
 238 show no significant temporal clusters. The primary vegetation changes (i.e. all



239 significant splits or, if no significant split occurs in a record, the first insignificant
240 split) occur during different intervals in each site-group. Overall, the early Holocene
241 (including 11.5, 10.5, and 9.5 ka time-slices) has the highest frequency of primary
242 vegetation changes. Records from the south-eastern coastal part of the study area are
243 characterized by relatively many early-Holocene splits (e.g. G29, G30, G32, G33,
244 G34, G36, G37). There are 16 site groups whose primary vegetation changes during
245 the middle Holocene (including 8.5, 7.5, 6.5, and 5.5 ka time-slices), and most of
246 them are from inland areas such as the West Siberian Plain, central Yakutia, and
247 northern Mongolia. Only seven site groups have late-Holocene primary vegetation
248 changes (Fig. 3).

249 *Warm temperate forest margin zone in vicinity of Tianshan Mts. and north-central*
250 *China (G6, G12, G13, G16, G21, G22)*

251 Six site-groups from the warm temperate forest-steppe transition zone (G6, G21,
252 G22) and from the lowlands adjacent to mountainous forest in arid central Asia (G12,
253 G13, G16) are clustered together (Fig. 3). Our results indicate that these areas, which
254 are now dominated by arid-tolerant shrub and steppe species, had more arboreal
255 species, mainly evergreen conifer tree taxa, in the middle Holocene (Fig. 2). For
256 example, north-central China (G21) has a marked mid-Holocene maximum in forest
257 cover (7–4 ka; mean 51%). However, certain peculiarities are noted: open landscape
258 is reconstructed between 14 and 7 ka in northern Kazakhstan (G6), followed by an
259 abundance of evergreen conifer trees and an increase in boreal deciduous trees that
260 maintain high values (mean 30%) after 7 ka. In the eastern branch of the Tianshan
261 Mts. (G12), evergreen conifer trees are highly abundant from 10 to 7 ka and after 2
262 ka, while low abundance occurs from 14 to 11 ka and from 6 to 3 ka. In the Gobi
263 desert near the Tianshan Mts. (G16) there was an even higher abundance of
264 arid-tolerant species with no notable temporal trend in abundance of arboreal species.
265 We assume that the high arboreal cover at site-groups G13 and G22 at 14 and 12 ka
266 originates from riverine transport and therefore exclude them from further analyses.

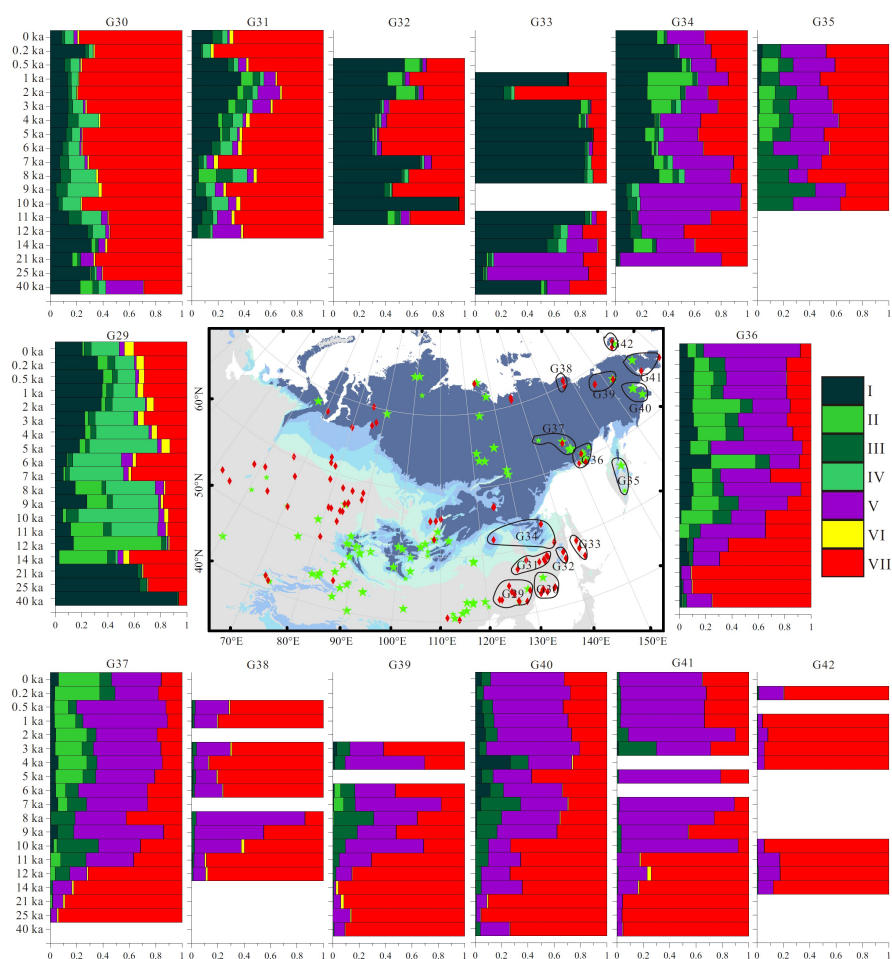


267

268 Fig. 2. Continued.

269 *Cool-temperate mixed forest and taiga forest in southern and southwestern Siberia*
 270 *and north-eastern China (G2, G7, G14, G15, G18, G29, G30, G31)*

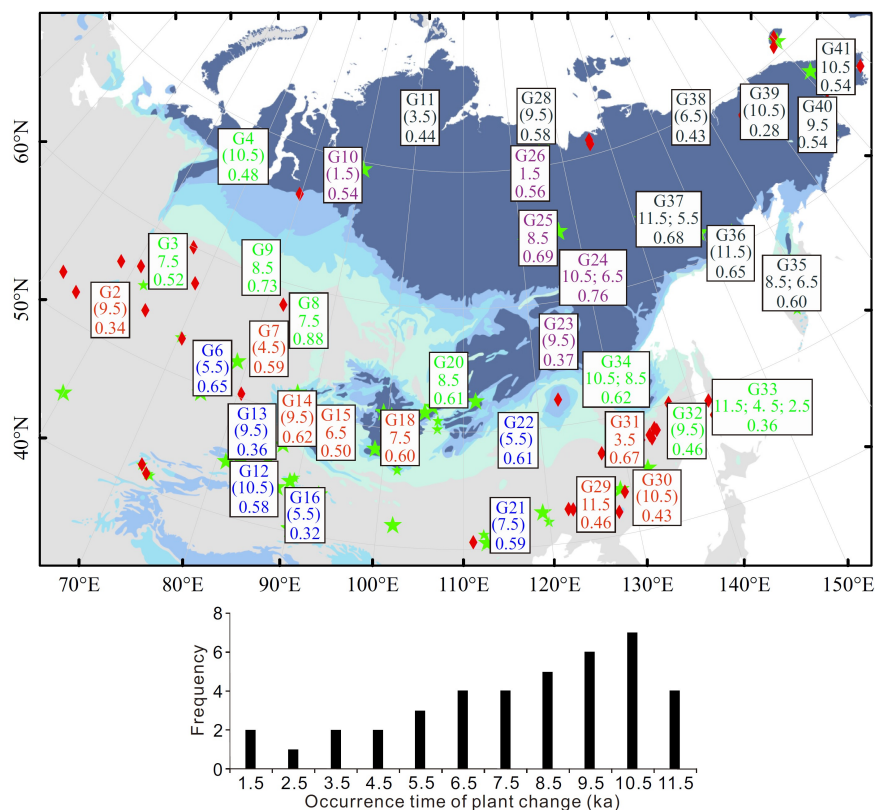
271 Eight site-groups located in (or near) the temperate mixed conifer-deciduous
 272 broadleaved forest zone (G2, G29, G30, G31) and taiga-steppe transition zone (G7,
 273 G14, G15, G18) show similar PFT compositions and temporal evolutions. At these
 274 sites, evergreen conifer tree is the dominant PFT intermixed with other arboreal
 275 PFTs, such as deciduous conifers (*Larix*) in the Altai Mts. and northern Mongolia,
 276 and/or temperate deciduous trees in northeastern China.



277

278 Fig. 2. Continued.

279 Evergreen conifer tree is the dominant PFT at 40, 25, and 21 ka in the southern part
 280 of north-eastern China (G29), *Larix* then becomes the dominant taxa at 14 and 12 ka,
 281 and temperate deciduous trees increase thereafter and maintain high cover between
 282 11 and 3 ka. After 2 ka, evergreen conifer trees increase to 32% on average while
 283 temperate deciduous trees decrease to 18% on average. While arboreal abundance is
 284 lower in the northern part of northeastern China (G30, G31) than in the southern part
 285 (G29), it shows a similar temporal pattern.



286

287 Fig. 3. Clustering results of the 34 site groups represented by the colour of the boxes, with
 288 age of primary vegetation changes (middle row of each box; data in brackets means the
 289 hierarchical clustering failed the broken-stick testing) and the compositional change (turnover;
 290 lower row) during the Holocene. A summary of the frequency of when the changes occurred is
 291 provided below the map.

292 Open landscape is revealed for the southern Ural region (G2) with high abundances
 293 of herbaceous species at 14 ka. The cover of *Larix* and evergreen conifer trees
 294 increases after 12 ka and maintains high values thereafter with no notable temporal
 295 trend.

296 In the taiga-steppe transition zone, *Larix* is the dominant arboreal taxon, particularly
 297 in the northern Altai Mts. and northern Mongolia (G15, G18). Open landscapes are
 298 inferred at 40, 21, and 12 ka on the southern West Siberian Plain (G7); cover of



299 *Larix* increases at 11 ka, and evergreen conifer trees increase from 9 ka and become
300 the dominant forest taxon after 4 ka. The temporal pattern of evergreen conifer trees
301 in the Altai Mts. (G14) is similar to the southern West Siberian Plain, although *Larix*
302 maintains high abundances into the late Holocene. Relative to the Altai Mts., the
303 abundance of evergreen conifer trees for all time windows are lower in the area north
304 of the Altai Mts. and in northern Mongolia (G15, G18), but their temporal change
305 patterns are consistent with those of the Altai Mts. (G14).

306 *Dark taiga forest in western and southeastern Siberia (G3, G4, G8, G9, G20, G32,*
307 *G33, G34)*

308 Site-groups with dark taiga forest from western Siberia (G3, G4, G8, G9), the Baikal
309 region (G20), and south-eastern Siberia (G32, G33, G34) form one cluster sharing
310 similar PFT compositions dominated by evergreen conifer trees, with *Larix* and
311 boreal broadleaved shrubs as the common woody taxa during the Holocene.

312 On the West Siberian Plain (G8, G9), high cover of *Larix* is reconstructed during the
313 early Holocene as well as high woody cover since the middle Holocene formed by
314 evergreen conifer trees and boreal shrubs. In the Ural region (G3, G4), evergreen
315 conifer trees dominate the arboreal species throughout the Holocene. The absence of
316 *Larix* in the early Holocene in this Ural region is a notable difference to the West
317 Siberian Plain.

318 In the Baikal region (G20), relatively closed landscape is revealed at 40 ka; openness
319 then increases to >95% at 25 and 21 ka. Since 14 ka, woody cover increases as
320 shown by a notable rise in evergreen conifer trees from 14 to 8 ka and by increases
321 of *Larix* after 7 ka.

322 In south-eastern Siberia (G32, G34), arboreal abundance is high in the early and late
323 Holocene, but low in the middle Holocene. South of Sakhalin Island (G33), closed
324 landscape is revealed between 40 and 1 ka with >80% woody cover. Evergreen
325 conifer tree PFT has lower cover than boreal shrub PFT at 25 and 21 ka, but
326 increases in abundance around 14 ka rising to 83% on average between 11 and 3 ka,



327 and reduces thereafter.

328 *Light taiga forest in north-western Siberia and central Yakutia (G10, G23, G24, G25,*
329 *G26)*

330 Plant composition of this cluster is dominated by *Larix* with high arboreal cover
331 during the Holocene. Evergreen conifer trees are present at ca. 15% cover between
332 11 and 2 ka, with high arboreal values (mean 73%) during the Holocene in
333 northwestern Siberia (G10). In central Yakutia (G23, G24, G25), evergreen conifer
334 trees increase markedly from ca. 8 ka, 6 ka and 7 ka, respectively and maintain high
335 cover thereafter, with ca. 60% arboreal cover throughout the Holocene. Evergreen
336 conifer trees are almost absent in the taiga-tundra ecotone (G26).

337 *Tundra on the Taymyr Peninsula and taiga-tundra ecotone in northeastern Siberia*
338 *(G11, G28, G35, G36, G37, G38, G39, G40, G41)*

339 Plant compositions of this cluster are characterized by high abundances of boreal
340 shrubs and tundra forbs. *Larix* is the only tree species on the Taymyr Peninsula (G11)
341 and its abundance increases from 18% at 14 ka to 60% at 10 ka, and then decreases
342 to 18% at 5 ka. The landscape of the north Siberian coast (G28) is dominated by
343 shrub tundra from 14 ka to 10 ka, then *Larix* increases sharply and maintains high
344 values between 9 and 6 ka. After 5 ka, *Larix* reduces, and shrub tundra becomes the
345 dominant landscape again.

346 In north-eastern Siberia, arboreal cover shows a decreasing trend from southerly site
347 groups (G35, G36, G37) to northerly ones (G40, G38, G39, G41) following the
348 increasing latitude. In the Olsky District, temporal patterns of vegetation changes in
349 G37 are consistent with G36, with stable vegetation during the Holocene and
350 increases in evergreen conifer tree abundance from ca. 9 ka. Arboreal composition
351 on the southern Kamchatka Peninsula (G35) is dominated by boreal deciduous trees
352 during the first stage of the Holocene, followed by rising abundances of *Larix* and
353 evergreen conifer trees from 5 ka.

354 In northeastern Siberia (G40, G38, G39, G41), the landscape is dominated by forb



355 tundra with sparse shrubs between 40 and 21 ka; the cover of shrubs increases at 14
356 ka and arboreal cover (dominated by boreal deciduous trees) increases in the early
357 Holocene (11 or 10 ka). Shrubs maintain a high abundance throughout the Holocene,
358 while trees peak between 10 and 2 ka generally.

359 [Fig. 2](#)

360 [Fig. 3](#)

361 **4. Discussion**

362 *4.1 Land-cover changes and potential biases*

363 The overall patterns of pollen-based REVEALS estimates of land cover are generally
364 consistent with previous vegetation reconstructions. Although only a few site-groups
365 cover the period from 40 to 21 ka, a consistent vegetation signal indicates that
366 relatively closed landscapes occurred in south-eastern Siberia, north-eastern China,
367 and the Baikal region (Fig. 2), while most of Siberia was rather open, particularly
368 around 21 ka (Fig. 2). These findings are consistent with previous pollen-based
369 (Tarasov et al., 1998, 2000; Bigelow et al., 2003; Binney et al. 2017; Tian et al.,
370 2018) and model-estimated biome reconstructions (Tian et al., 2018). During the late
371 Pleistocene (40, 25, 21, 14 ka), steppe PFT abundance was high in central Yakutia
372 and north-eastern Siberia (e.g. G25, G36, G37, G39, G40, G41), which may reflect
373 the expansion of tundra-steppe, consistent with results from ancient sediment DNA
374 (Jørgensen et al., 2012). The tundra-steppe was replaced by light taiga in southern
375 Siberia and by tundra in northern Siberia at the beginning of Holocene or the last
376 deglaciation, which is consistent with ancient DNA results (Willerslev et al., 2014).

377 During the Holocene, reconstructed regional land cover for each site-group is
378 generally consistent with *in situ* modern vegetation. The slight vegetation changes
379 are represented by changes of PFT abundance rather than by changes in
380 presence/absence. Minor changes are also indicated in the cluster analysis, which
381 shows that plant compositions and their temporal patterns are consistent among the



382 site-groups within the same modern vegetation zone (Fig. 3). PFT datasets from 16
383 site groups fail the broken-stick test for clustering analysis, and most of the
384 remaining site-groups have only one significant vegetation change, further
385 supporting the case that only slight changes occurred during the Holocene in
386 northern Asia. In addition, the low total amount of PFT change (turnover) over the
387 Holocene for most site groups supports the view of slight temporal changes in land
388 cover.

389 Vegetation turnover on the Tibetan Plateau inferred from pollen percentages is
390 documented to overestimate the strength of vegetation changes (Wang and
391 Herzschuh, 2011). This matches with our results. In central Yakutia, the pollen
392 percentage data indicate a strong vegetation change during the middle Holocene,
393 represented by a sharp increase of *Pinus* pollen, but the strength of the vegetation
394 change is overestimated because of the high PPE of *Pinus*. The PPE-corrected
395 arboreal abundances in central Yakutia after ca. 7 ka with ca. 70% *Larix* and ca. 10%
396 *Pinus* are consistent with modern light taiga (Katamura et al., 2009). Furthermore,
397 the absence of *Pinus* macrofossils in central Yakutia throughout the Holocene
398 (Binney et al., 2009) also suggests a restricted distribution of *Pinus*, possibly to
399 sandy places such as river banks (Isaev et al., 2010).

400 Pollen-based turnover estimates from southern Norway range between 0.84 to 1.3
401 SD (mean 1.02 SD) for ten Holocene pollen spectra (Birks, 2007), and from northern
402 Europe between 0.01 (recent) to 0.99 (start of the Holocene) SD for three sites (N
403 Sweden, NW and SE Finland) (Marquer et al., 2014). Moreover, the
404 REVEALS-based turnover estimates (0.3-1) for northern Europe are significantly
405 higher than the pollen-based one (0.2-0.8) from 11 ka to 5.5 ka BP. The same is true
406 for all other regions studied by Marquer et al. (2014) in northwestern Europe, and
407 the turnover estimates (pollen- and REVEALS-based) are generally higher at lower
408 latitudes from southern Sweden down to Switzerland and eastwards to Britain and
409 Ireland. These European values are higher than our REVEALS-based turnover
410 estimates (from 0.37 to 0.88 SD, mean 0.66 SD; G3, G8, G9, G23, G24, G25, G36,



411 G37) from a similar latitudinal range (Fig. 3). Aside from the methodological aspects,
412 the lower turnover in northern Asia may, at least partly, originate from differences in
413 the environmental history between northern Europe compared with northern Asia, i.e.
414 glaciation followed by postglacial invasion vs. non-glaciated areas with trees in
415 refugia, respectively, and a maritime climate with temperature-limited vegetation
416 distribution vs. a continental climate with temperature- and moisture-limited
417 vegetation.

418 We consider the REVEALS-based regional vegetation-cover estimations in this
419 study as generally reliable thanks to the thorough selection of records with high
420 quality pollen data reliable chronologies. In addition, the landscape reconstructions
421 are generally consistent with previous syntheses of past vegetation change (e.g. Tian
422 et al., 2018) and known global climate trends (Marcott et al., 2013), plus the
423 clustering results of PFT abundance are consistent with modern spatial vegetation
424 patterns. That said, this study faced two major methodological challenges, discussed
425 below, that may reduce the reliability of the obtained quantitative land-cover
426 reconstructions, i.e. 1) the low number of RPP estimates and their origin and 2)
427 restrictions with respect to the number, distribution, and type of available sites.

428 (1) Twenty RPP sets were used which mostly originate from Europe and
429 temperate northern China (the typical steppe in north-central China,
430 Xilinhaote, Xu et al., 2014; and the temperate coniferous and broadleaved
431 mixed forest in north-eastern China, Changbai Mt.; Li et al., 2015), but also
432 included RPP records from the taiga-tundra ecotone in arctic Siberia
433 (Niemeyer et al., 2015). We assume that the compiled RPP sets can be used
434 to extract major broad-scale and long-term vegetation patterns because the
435 regional differences among RPP estimates within one taxon are small
436 compared to the large between-taxa differences in RPP estimates. Also, the
437 mean values of available RPPs that were used in the REVEALS modelling
438 (Table 2) and the calculated PPEs are broadly consistent with those obtained
439 from Europe (Mazier et al., 2012). In addition, although there is no PPE



440 records from the core of the Siberia taiga forest, available studies on modern
441 pollen composition confirm the trends in the applied RPP for major taxa in
442 terms of pollen under- or over-representation of vegetation abundance. For
443 example, modern pollen investigation in north-eastern Siberia revealed that
444 pollen records from northern *Larix* forest often have less than 13% *Larix*
445 pollen confirming the low pollen productivity of *Larix* relative to
446 over-represented pollen taxa such as *Betula* and *Alnus* (Pisaric et al., 2001,
447 Klemm et al., 2016). Similarly, a study on modern pollen in southern Siberia
448 (transitional area of steppe and taiga) finds that *Artemisia*, *Betula*, and *Pinus*
449 are high pollen producers compared to *Larix* (Pelánková et al., 2008). Also,
450 despite *Larix* being the most common tree in taiga forest in north-central
451 Mongolia, the pollen abundance of *Larix* is generally lower than 3% (Ma et
452 al., 2008), implying its low pollen productivity.

453 (2) In this study, we attempt to reconstruct past landscape changes at a regional
454 scale. Pollen signals from large lakes are assumed to reflect regional
455 vegetation patterns (e.g. Sugita et al., 2010; Trondman et al., 2015). If large
456 lakes are absent in a region, multiple small-sized sites can also be used,
457 although error estimates are usually large (Sugita, 2007; Mazier et al., 2012;
458 Trondman et al., 2016). In our study, 70% of the time slices for the 42 site
459 groups include pollen data from large lakes (i.e. radii >390m), which
460 supports the reliability of REVEALS estimates (Table 3). However, sites are
461 unevenly distributed and occasionally sites from different areas were
462 combined into one group (G2, G6, G34), which might produce a different
463 vegetation-change signal because of the broad distribution of these sites.
464 Finally, pollen signals from certain sites and during certain periods may be of
465 riverine rather than aerial origin violating the assumption of the
466 REVEALS-model that pollen is transported by wind.

467



468 Table 3 Number of pollen records from large lakes (with ≥ 390 m radius; represented by L), small lakes (with < 390 m radius; represented by S), and bogs (B) for
 469 each site group used to run REVEALS for each time slice. For example, site group G6 has 2 large lake records, 1 small lake record and 2 bog records at 4 ka
 470 (represented by 2L1S2B).

Group	0 ka	0.2 ka	0.5 ka	1 ka	2 ka	3 ka	4 ka	5 ka	6 ka	7 ka	8 ka	9 ka	10 ka	11 ka	12 ka	14 ka	21 ka	25 ka	40 ka
G1	1L	1L	1L	-	1L	1L	1L	1L	1L	1L	1L	1L	-	-	-	-	-	-	-
G2	6B	1S6B	1S6B	1S6B	1S4B	2S6B	2S6B	1S4B	2S2B	1S	2S	2S	1S2B	1S2B	1S2B	2B	-	-	-
G3	4B	4B	8B	8B	8B	8B	8B	8B	8B	6B	6B	4B	4B	4B	-	-	-	-	-
G4	-	1L	-	1L	1L	1L	1L	1L	1L	1L2B	1L2B	1L	1L	1L	1L	-	-	-	-
G5	4S4B	4S4B	4S4B	4S4B	1S4B	1S4B	1S4B	1S2B	1S2B	1S2B	-	-	-	-	-	-	-	-	-
G6	2L1S2B	1L1S2B	2L1S4B	2L1S4B	2L1S2B	2L1S2B	2L1S2B	1S	1L1S	1L2B	1L2B	1L2B	2B	2B	2B	2B	-	-	-
G7	4B	10B	12B	12B	1L12B	1L12B	1L10B	1L10B	1L10B	6B	6B	8B	8B	1L6B	2B	2B	-	-	2B
G8	2B	2B	4B	4B	2B	4B	6B	8B	8B	8B	8B	4B	4B	4B	2B	-	-	-	-
G9	4B	4B	6B	6B	4B	6B	6B	2B	6B	4B	4B	8B	8B	8B	4B	2B	-	-	-
G10	1L	1L	1L	1L	2B	1L2B	1L4B	1L6B	1L8B	1L6B	1L6B	1L6B	1L4B	1L2B	1L	1L	1L	-	-
G11	2L1S	2L1S	2L1S	2L1S	1L1S	2L1S	1L1S	1L1S	2L1S	2L1S	2L	2L	1L	1L	2L	1L	1L	1L	-
G12	6L1S2B	5L1S2B	5L1S2B	6L1S2B	5L1S2B	3L1S2B	5L1S2B	4L1S2B	4L2B	4L2B	5L2B	4L	4L	3L	4L	1L	-	-	-
G13	1L	1L	1L	2L	2L	2L	2L	2L	2L	2L	2L	2L	1L	1L	1L	1L	-	-	-
G14	4L	4L	4L	4L1S	5L1S	5L2S	5L1S	4L1S	3L1S	4L2S	4L2S	4L2S	3L1S	4L2S	4L1S	3L2S	-	-	-
G15	1L	2L	2L	2L	2L	3L	3L	3L	3L	2L	2L	3L	1L	3L	3L	2L	1L	-	-
G16	1L	-	2L	-	2L	2L	2L	1L	1L	2L	2L	2L	2L	2L	3L	1L	2L	3L	-
G17	-	-	-	-	1L	1L	-	1L	1L	1L	1L	1L	-	1L	-	-	-	-	-
G18	2L2S	3L1S	2L2S	4L2S	2L1S	4L1S	5L1S	4L1S	4L1S	4L	5L	4L1S	2L1S	3L1S	4L	2L	-	-	-
G19	-	1L	-	1L	1L	1L	1L	1L	-	-	-	-	-	-	-	-	-	-	-
G20	6L6B	4L4B	6L8B	5L1S6B	6L1S8B	5L8B	5L6B	5L1S6B	5L1S6B	5L1S4B	4L4B	4L2B	5L2B	5L2B	6L2B	5L2B	2L2B	2L2B	1L
G21	4L1S2B	4L1S2B	4L1S2B	4L1S2B	3L1S2B	4L2S4B	4L2S4B	3L2S4B	3L1S4B	4L1S2B	5L1S4B	4L1S2B	5L1S2B	6L1S	5L1S	1L	-	-	-
G22	1L	1L	2L	2L	2L	2L	2L	2L	2L	2L	2L	2L	2L	2L	1L	-	-	-	-
G23	-	-	-	2B	2B	2B	4B	4B	4B	4B	4B	4B	4B	4B	4B	-	-	-	-
G24	2L	2L	2L	2L	2L	2L	2L	2L	2L	1L	1L	1L	1L	1L	1L	-	-	-	-



G25	IL	4L	4L	5L	5L	5L	5L	5L	5L	5L	4L	4L	4L	3L	3L	4L	2L	2L	1L	1L	1L
G26	IL	-	1L	1L	1L	1L	1L	1L	1L	1L	-	-	-	1L	1L	1L	-	-	-	-	-
G27	-	2B	4B	4B	4B	4B	4B	4B	4B	4B	4B	4B	4B	2B	2B	-	-	-	-	-	-
G28	2L	2B	2L2B	1L2B	2L2B	2L2B	2L2B	2L2B	2L2B	2L2B	1L	2L	2L	2L	2L	2L	1L	1L	-	-	-
G29	IL1S10B	IL1S14B	IL1S16B	IL1S16B	IL1S16B	IL1S16B	IL1S16B	IL1S16B	IL1S16B	IL1S16B	IL1S4B	IL2S4B	IL2S2B	IL1S2B	2S	2S	IS	IS	IS	IS	IS
G30	1L	1L2B	1L6B	1L8B	1L8B	1L8B	1L8B	1L8B	1L8B	1L8B	1L8B	1L8B	1L4B	1L4B	1L4B	1L4B	1L4B	1L2B	1L4B	1L4B	4B
G31	2B	2B	10B	14B	10B	10B	10B	12B	10B	10B	4B	4B	2B	4B	2B	4B	4B	-	-	-	-
G32	-	-	4B	2B	2B	2B	2B	2B	2B	2B	2B	2B	2B	2B	2B	2B	-	-	-	-	-
G33	-	-	4B	2B	2B	4B	4B	2B	4B	4B	2B	2B	2B	-	-	2B	2B	2B	2B	2B	2B
G34	4B	4B	6B	10B	8B	8B	8B	6B	6B	6B	6B	6B	6B	4B	4B	4B	4B	2B	2B	-	-
G35	-	1L1S	1L1S	1L1S	2L1S	1L	1L1S	1L1S	1L	1S	1S	1S	1S	1S	1S	-	-	-	-	-	-
G36	4L4S2B	2L2S	4L3S	4L4S	4L4S	4L4S	4L4S	3L2S2B	4L2S	2L4S4B	3L4S2B	3L4S2B	3L4S	2L4S2B	2L4S2B	3L2S2B	2L2S2B	2L2S	2L1S	2L1S	2L1S
G37	3L3S	2L1S2B	3L1S2B	1L3S2B	1L3S2B	2L3S2B	2L3S2B	2L2S2B	3L2S2B	3L1S	3L1S	1L1S	1L1S	2L	2L1S	2L1S	1L1S	2L1S	2L1S	2L1S	1L1S
G38	-	-	2B	2B	2B	2B	2B	2B	2B	2B	-	2B	2B	2B	2B	2B	2B	-	-	-	-
G39	-	-	-	1L	1L2B	-	1L4B	2B	1L4B	2B	1L4B	2B	1L4B	2B	1L4B	1L	1L	1L	1L2B	2B	2B
G40	4L1S	1L	2L1S	3L1S	2L	1S	2L	2L	2L1S	1S	1L1S	1L1S	1L1S	3L1S	2L	2L	3L	2L	2L1S	1L	1L
G41	2L2B	1L	1L	1L	2B	2B	-	4B	-	4B	4B	4B	4B	2B	2B	1L2B	2B	1L2B	1L	1L	1L
G42	-	1L2B	-	1L	1L	1L	1L	-	-	-	-	-	-	-	-	1L2B	1L4B	1L4B	-	-	-



472 *4.2 Driving factors of vegetation changes*

473 On a glacial-interglacial scale, observed land-cover changes in northern Asia are
474 generally consistent with the global climate signal (e.g. sea-surface temperature,
475 Pailler and Bard 2002; ice-core, Andersen et al., 2004; solar insolation, Laskar et al.
476 2004; cave deposits, Cheng et al. 2016). For example, the relatively high arboreal
477 cover at 40 ka (e.g. G20) corresponds with the warm MIS3 recorded in the Baikal
478 region (Swann et al., 2005). The open landscape at 25 ka and 21 ka (e.g. G25, G36)
479 reflects the cold and dry last glacial maximum (e.g. Swann et al., 2010). Furthermore,
480 the relatively high arboreal cover during the Holocene is consistent with the warm and
481 wet climate (occurring in most site-groups). The primary vegetation change in
482 north-eastern China (G29, G30) occurs in the early Holocene (11.5 and 10.5 ka),
483 caused by the rapid increase in abundance of temperate deciduous trees, which may
484 reflect the warmer climate and enhanced summer monsoon known from that region at
485 the beginning of the Holocene (Hong et al., 2009, Liu et al., 2014).

486 A sensitivity analysis of model-based biome estimation reveals that precipitation plays
487 an important or even dominant role in controlling vegetation changes in arid central
488 Asia (e.g. Tian et al., 2018). The climate of central Asia during the early Holocene is
489 inferred to be quite dry and the end of moisture increase occurs at ca. 8 ka by a series
490 of multi-proxy syntheses (Chen et al., 2008, 2016; Xie et al., 2018) and model-based
491 estimations (Jin et al., 2012). In the taiga-steppe transition zone (south-eastern Siberia
492 and north-central Asia; e.g. G6, G12, G14, G18), relatively open landscape is
493 reconstructed for the early Holocene and abundances of forest taxa increase after ca. 8
494 ka, which are consistent with the moisture evolution, and imply the importance of
495 moisture in controlling vegetation changes. Our results support the prediction of an
496 expansion of steppe in the present forest–steppe ecotone of southern Siberia in
497 response to a warmer and drier climate in the future (Tchebakova et al., 2009).

498 High abundances of *Larix* or boreal deciduous woody taxa (mostly shrubs) pollen
499 occur in northern Siberia (e.g. G28, G38, G39, G40) during the middle Holocene,
500 which is now covered by tundra. This is consistent with non-vegetation climate



501 records of a mid-Holocene temperature maximum (e.g. Biskaborn et al, 2012;
502 Nazarova et al., 2013). This result indicates that the boreal treeline in northern Siberia
503 reacts sensitively to warming on millennial time-scales, which contrasts with the
504 observed lack of response on a decadal time-scale (Wieczorek et al., 2017). This may
505 point to a highly non-linear vegetation–climate relationship in northern Siberia.

506 Our results indicate that climate change is the major factor driving land-cover change
507 in northern Asia on a long temporal scale. However, climate change cannot fully
508 explain the changes in arboreal taxa abundance for the West Siberian Plain (G8, G9)
509 and sandy places in central Yakutia (G23, G24, G25). In addition to climate, changes
510 in permafrost condition (Vandenbergh et al., 2014) and fire regime may have played
511 a central role in vegetation change. *Larix* is the dominant arboreal taxon during the
512 early Holocene (ca. between 12 and 8 ka), which is replaced by evergreen conifer
513 trees, mostly pine and spruce at 8 or 7 ka. *Larix* can survive on permafrost with an
514 active-layer depth of <40 cm (Osawa et al., 2010) and a high fire frequency, while
515 pine trees can only grow on soil with >1.5m active-layer (Tzedakis and Bennett, 1995)
516 and spruce is a fire-avoider. Probably the compositional change of boreal trees was
517 not in equilibrium with climate but rather driven by changes in the permafrost and fire
518 characteristics that were themselves affected by forest composition, resulting in
519 complex feedbacks. This explanation would be in agreement with the finding of
520 Herzsuh et al. (2016) that the boreal forest composition of nearby refugia during the
521 glacial influences the initial interglacial forest composition that is then only slowly
522 replaced by a forest composition that is in equilibrium with climate.

523 Population changes of herbivores could also be an important factor for vegetation
524 change at a regional scale during certain intervals (Zimov et al., 1995; Guthrie, 2006).
525 As with our pollen-based land-cover reconstruction, a circumpolar ancient DNA
526 metabarcoding study confirms the replacement of steppe-like tundra by moist tundra
527 with abundant woody plants at the Pleistocene–Holocene transition (Willerslev et al.,
528 2014). According to Zimov et al., (1995, 2012) such a change cannot be explained by
529 climate change alone, and thus a reduced density of herbivores is considered to be a



530 major driving factor of steppe composition reduction, since a reduced number of
531 herbivores is insufficient to maintain the open steppe landscapes and so causes a
532 decrease in steppe area (Zimov et al., 1995; Guthrie, 2006). Our land-cover
533 reconstruction fails to address the contribution of herbivores to vegetation changes,
534 but the extinction of herbivorous megafauna would add to the complexity of the
535 interactions among vegetation, climate and permafrost.

536 **5. Conclusions**

537 Regional vegetation based on pollen data has been estimated using the REVEALS
538 model for northern Asia during the last 40 ka. Relatively closed land cover was
539 replaced by open landscapes in northern Asia during the transition from MIS 3 to the
540 last glacial maximum. Abundances of woody components increase again from the
541 early Holocene or last deglaciation. Our numerical analyses indicate that the
542 vegetation was quite stable during the Holocene, i.e. only slight changes in the
543 abundances of taxa were recorded rather than mass expansion of new taxa. From
544 comparisons of our results with other data we infer that climate change is likely the
545 primary driving factor for vegetation changes on a glacial-interglacial scale. However,
546 the extension of evergreen conifer trees since ca. 8~7 ka throughout Siberia could
547 reflect a vegetation-climate disequilibrium caused by the interaction of climate,
548 vegetation, fire, and permafrost.

549 **Data availability.** The used fossil pollen dataset with the re-established age-depth
550 model for each pollen record, and its full description will be made publicly available
551 in journal Earth System Science Data (ESSD).

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975 Appendixes

976 Appendix 1 Metadata for all pollen records used in this study.

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Group	Site	Lat.	Long.	Alt. (m)	Basin type	Pollen count	Area (ha)	Radius (m)	Dating method	Num. of dating	Time span (cal BP)
G1	Aral Lake	44.42	59.98	53	Lake	Yes	330000	32410	¹⁴ C	4U	8.7-0
G2	Mokhovoye	53.77	64.25	178	Bog	Yes	20	252	¹⁴ C	4C+1E	6.0-0
G2	Novienky peat bog	52.24	54.75	197	Bog	Yes	-	-	¹⁴ C	1U	4.5-0
G2	Zaboinoe Lake	55.53	62.37	275	Lake	Yes	6	138	¹⁴ C	1U	12.3-0.1
G2	Lake Fernshee	52.83	60.50	290	Lake	Yes	0	38	¹⁴ C	10A	9.1-0.4
G2	Pobochnoye	53.03	51.84	81	Bog	No	79	500	¹⁴ C	10C+6E	14.4-0
G3	Chesnok Peat	60.00	66.50	42	Bog	Yes	-	-	¹⁴ C	7C	10.6-0.5
G3	Komaritsa Peat	57.50	69.00	42	Bog	Yes	-	-	¹⁴ C	10C	10.5-0.5
G3	UstMashevskoe	56.32	57.88	220	Bog	Yes	30	309	¹⁴ C	5C	7.8-0
G3	Karasieozerskoe	56.77	60.75	230	Bog	Yes	914	1706	¹⁴ C	3A	5.9-0.1
G4	Nulsaveito	67.53	70.17	57	Bog	Yes	-	-	¹⁴ C	4A+1C	8.4-6.4
G4	Lyadhej-To Lake	68.25	65.75	150	Lake	Yes	197	792	¹⁴ C	14A+6E	12.5-0.3
G5	Nizhnee Lake	41.30	72.95	1371	Lake	No	-	70	¹⁴ C	4E	1.5-0
G5	Verkhnee Lake	41.30	72.95	1440	Lake	No	1	60	¹⁴ C	5E	1.5-0
G5	Ak Terk Lake	41.28	72.83	1748	Bog	No	-	-	¹⁴ C	2A	7.5-0
G5	Kosh Sas	41.85	71.97	1786	Bog	No	-	-	¹⁴ C	1A	3.5-0
G5	Ortok Lake	41.23	73.25	1786	Lake	No	-	60	¹⁴ C	5A	1-0
G5	Bakaly Lake	41.87	71.97	1879	Lake	No	1	50	¹⁴ C	4A	7-0
G6	Big Yarvoe Lake	52.85	78.63	79	Lake	Yes	6362	4500	inclination with	-	4.3-0



		Lake Biwa														
G6	Ozerki	50.40	80.47	210	Bog	Yes	-	-	¹⁴ C	3A+13C	14.5-0	300	Tarasov et al., 1997			
G6	Karas' Lake	53.03	70.22	435	Lake	Yes	17	235	¹⁴ C	6U	5.5-0	170	Tarasov and Kremenetski. 1995			
G6	Kotyrkol	52.97	70.42	439	Bog	Yes	-	-	¹⁴ C	8U	4.5-0.5	180	Tarasov and Kremenetski. 1995			
G6	Pashennoe Lake	49.37	75.40	871	Lake	Yes	64	451	¹⁴ C	5D+5E	9.5-0	280	Tarasov and Kremenetski. 1995			
G7	Gladkoye Bog	55.00	83.33	80	Bog	Yes	-	-	¹⁴ C	13C	11-0.5	170	Firsov et al., 1982			
G7	Chagnskoe Mire	56.45	84.88	80	Bog	Yes	10	175	¹⁴ C	2C	8.8-0	320	Blyakharchuk, 2003.			
G7	Kirek Lake	56.10	84.22	90	Lake	Yes	52	407	¹⁴ C	3G	10.5-1.5	190	Blyakharchuk, 2003			
G7	Tom' River Peat	56.17	84.00	100	Bog	Yes	-	-	¹⁴ C	6C	10.1-0.2	390	Arkipov and Votakh, 1980			
G7	Zhukovskoye mire	56.33	84.83	106	Bog	Yes	-	-	¹⁴ C	9C+6H	11.2-0	130	Borisova et al., 2011			
G7	Tolmachevsko	55.00	84.00	110	Bog	Yes	-	-	¹⁴ C	1A+3C	13-1.5	400	Volkov and Arkipov, 1978			
G7	Suminskoye	55.00	80.25	135	Bog	Yes	-	-	¹⁴ C	8A	3-0	200	Klimanov, 1976			
G7	Kayakskoye	55.00	81.00	150	Bog	Yes	-	-	¹⁴ C	5C	6.5-0	210	Levina et al., 1987			
G7	Kalistratikha	53.33	83.25	190	Bog	Yes	-	-	¹⁴ C	4A	39.0-12.7	1870	Zudin and Votakh, 1977			
G8	Petropavlovka	58.33	82.50	100	Bog	Yes	-	-	¹⁴ C	4C+1E	10.5-0.1	160	Blyakharchuk, 1989			
G8	Bugristoe	58.25	85.17	130	Bog	Yes	-	-	LSC	4C+1E	11.5-5.0	100	Blyakharchuk, 1989			
G8	Maksimkin Yar	58.33	88.17	150	Bog	Yes	-	-	¹⁴ C	4C	8.3-0.2	170	Blyakharchuk, 1989			
G8	Teguldet	57.33	88.17	150	Bog	Yes	-	-	LSC	3C	7.3-2.4	90	Blyakharchuk, 1989			
G9	Nizhnevartovsk	62.00	76.67	54	Bog	Yes	-	-	¹⁴ C	3A+7C	11.1-0	300	Neustadt and Zelikson, 1985			
G9	Nizhnevartovskoye	61.25	77.00	55	Bog	Yes	-	-	¹⁴ C	1A+12C+1E	12.6-0	380	Neishtadt, 1976			
G9	Entamoye Peat	59.00	78.33	65	Bog	Yes	-	-	¹⁴ C	5C	14.9-0.9	460	Neishtadt, 1976			
G9	Lukaschin Yar	61.00	78.50	65	Bog	Yes	-	-	¹⁴ C	13C	10.9-0.3	430	Neishtadt, 1976			
G10	Igarka Peat	67.67	86.00	45	Bog	Yes	244	881	¹⁴ C	1A+2C	10.9-5.9	230	Kats, 1953			
G10	Pur-Taz Peatland	66.70	79.73	50	Bog	Yes	5	126	¹⁴ C	5A	10.3-4.7	80	Peteet et al., 1998			
G10	Karginskii Cape	70.00	85.00	60	Bog	Yes	-	-	¹⁴ C	13C	8.9-3.5	290	Firsov et al., 1972			



G10	Yenisei	68.17	87.15	68	Bog	No	-	¹⁴ C	7C	6.5-1.6	110	Andreev and Klimanov, 2000
G10	Lake Lama	69.53	90.20	77	Lake	Yes	64245	¹⁴ C	26A+4D+4E	19.5-0	170	Andreev et al., 2004
G11	11-CH-12A Lake	72.40	102.29	60	Lake	Yes	3	¹⁴ C+Pb/Cs	8A+7E	7.0-0.1	110	Klemm et al., 2015
G11	Levinson-Lessing Lake	74.47	98.64	26	Lake	Yes	2145	¹⁴ C	29A+1B+19E	35.3-0	390	Andreev et al., 2003
G11	SAOI	74.55	100.53	32	Lake	Yes	456000	¹⁴ C	6A+5C	57.9-0	1320	Andreev et al., 2003
G12	Aibi Lake	45.02	82.83	200	Lake	Yes	100885	¹⁴ C	8E	12.6-0	65	Wang et al., 2013
G12	Ebinur Lake	44.55	82.45	212	Lake	Yes	46421	¹⁴ C	7U	13-0	900	Wen and Qiao, 1990
G12	Ebinur Lake_SW	45.00	82.80	212	Lake	Yes	46421	¹⁴ C	6U	8.5-1.5	780	Lin, 1994
G12	Caotianhu Lake	44.42	86.02	380	Bog	Yes	2760	¹⁴ C	5C	8.5-0	150	Zhang Y. et al., 2008
G12	Dongdaohaizi Lake	44.70	89.56	430	Lake	Yes	20	¹⁴ C	8U	5.5-0	85	Yan et al., 2004
G12	Siachanghu Lake	44.31	89.14	589	Lake	Yes	2000	¹⁴ C	4U	1-0	50	Zhang Y. et al., 2004b
G12	Bosten Lake	41.97	86.55	1050	Lake	No	96608	¹⁴ C	5U	13-0	420	Xu, 1998
G12	Chaiwopu Lake	43.55	87.78	1100	Lake	No	3101	¹⁴ C	2U	10-0	845	Li and Yan, 1990
G12	Sayram Lake	44.57	81.15	2072	Lake	Yes	45800	¹⁴ C	12E	13.8-0.1	90	Jiang et al., 2013
G13	Mamas Lake	45.83	85.92	251	Lake	Yes	55000	¹⁴ C	7C	13.5-1	210	Sun et al., 1994
G13	Wutungu Lake	47.22	87.30	479	Lake	Yes	67019	¹⁴ C+Pb/Cs	1C	9-0	80	Liu X.Q. et al., 2008
G14	Teletsikoye Lake	51.72	87.65	1900	Lake	Yes	16610	¹⁴ C+Pb/Cs	6E	1-0	20	Andreev et al., 2007
G14	Uzunkol Lake	50.48	87.11	1985	Lake	No	123	¹⁴ C	2A	17.5-0	210	Blyakharchuk et al., 2004
G14	Kenedegulkol Lake	50.51	87.64	2050	Lake	No	5	¹⁴ C	7E	16-1	260	Blyakharchuk et al., 2004
G14	Hoton Nur Lake	48.62	88.35	2083	Lake	Yes	5021	¹⁴ C	4A	6-0	60	Rudaya et al., 2009
G14	Tashkol Lake	50.45	87.67	2150	Lake	No	-	¹⁴ C	3C	16-3	250	Blyakharchuk et al., 2004
G14	Akkol Lake	50.25	89.63	2204	Lake	No	388	¹⁴ C	12E	13.5-0	250	Blyakharchuk et al., 2007
G14	Grusha Lake	50.38	89.42	2413	Lake	No	130	¹⁴ C	3A+13E	14-1.5	250	Blyakharchuk et al., 2007
G15	Bayan Nuur	50.00	93.00	932	Lake	No	2968	¹⁴ C	7E	15.7-0.2	210	Krengel, 2000



G15	Achit Nur Lake	49.50	90.60	1435	Lake	No	29700	9723	¹³ C	4E	14-0.5	700	Gunin et al., 1999
G15	Achit Nur	49.42	90.52	1444	Lake	No	29700	9723	¹³ C	10E	20.2-0	250	Sun et al., 2013
G16	Lop Nur_1998	40.28	90.25	780	Lake	No	535000	41267	¹³ C	3U	22-2	2000	Yan et al., 1998
G16	Lop Nur_1983	40.33	90.25	800	Lake	Yes	535000	41267	¹³ C	3U	22-0.5	1600	Yan et al., 1983
G16	Barkol Lake	43.62	92.80	1575	Lake	Yes	11300	5997	¹³ C	1A+10E	10-0	115	Tao et al., 2009
G16	Balikun Lake	43.68	92.80	1575	Lake	Yes	7897	5014	¹³ C	1D+5E	30.5-9	250	An et al., 2013
G17	Juyan Lake	41.89	101.85	892	Lake	Yes	72000	15139	¹³ C	5E	10.5-1.5	140	Herzschuh et al., 2004
G18	Gun Nur Lake	50.25	106.60	600	Lake	No	33	325	¹³ C	7E	11-0	320	Gunin et al., 1999
G18	Yamant Nur Lake	49.90	102.60	1000	Lake	No	58	430	¹³ C	4E	15.5-0.5	360	Gunin et al., 1999
G18	Ugri Nur Lake	47.77	102.77	1330	Lake	No	2456	2796	¹³ C	2C	9-0	85	Wang et al., 2011
G18	Dood Nur Lake	51.33	99.38	1538	Lake	No	6400	4514	¹³ C	2E	14-0	740	Gunin et al., 1999
G18	Hovsgol Lake	51.10	100.50	1645	Lake	Yes	276000	29640	¹³ C	5E	12-2.5	190	Prokopenko et al., 2007
G18	Khuistin Lake	46.60	101.80	2270	Lake	Yes	4	118	¹³ C+Pb/Cs	6E	1.2-0	17	Tian et al., 2013
G18	Daba Nur Lake	48.20	98.79	2465	Lake	No	157	707	¹³ C	5E	13-0	520	Gunin et al., 1999
G19	Bolshoe Eravnoe Lake	52.58	111.67	947	Lake	Yes	9503	5500	¹³ C	3E	7.3-0.2	710	Vipper, 2010
G20	Baikal Lake	52.08	105.87	130	Lake	No	3150000	100134	¹³ C	12A	22-0	370	Demske et al., 2005
G20	Baikal Lake-CON01-603-5	53.95	108.91	446	Lake	Yes	3150000	100134	¹³ C	10D	15.8-0	270	Demske et al., 2005
G20	Lake Kotokel_2010	52.78	108.12	458	Lake	Yes	6900	4687	¹³ C	11E	47-0	220	Bezrukova et al., 2010
G20	Lake Kotokel_2009	52.78	108.12	458	Lake	Yes	6900	4687	¹³ C	3E	15-0	500	Tarasov et al., 2009
G20	Chernoe Lake	50.95	106.63	500	Lake	Yes	-	250	¹³ C	4E	7-0.7	620	Vipper, 2010
G20	Baikal Lake-CON01-605-3	51.59	104.85	675	Lake	Yes	3150000	100134	¹³ C	5D	17.7-0	200	Demske et al., 2005
G20	Okunayka	55.52	108.47	802	Bog	Yes	-	-	¹³ C	6C	8.3-2.0	120	Bezrukova et al., 2011
G20	Ukta Creek-mouth	55.80	109.70	906	Bog	Yes	-	-	¹³ C	3U	5.1-0	160	Bezrukova et al., 2006
G20	Cheremushka Bog	52.75	108.08	1500	Bog	Yes	-	-	¹³ C	6C	33.5-0	460	Shichi et al., 2009



G20	Baikal Lake-CON01-605-5	51.58	104.85	492	Lake	Yes	3150000	100134	¹³ C	12D	11.5-0	130	Denske et al., 2005
G20	Khandia-I	55.44	107.00	867	Bog	Yes	-	-	¹³ C	3C	3.1-0.3	50	Bezrukova et al., 2011
G20	Khandia	55.44	107.00	867	Bog	Yes	-	-	¹³ C	6C	5.8-0	140	Bezrukova et al., 2011
G21	Qigianhu Lake	42.90	119.30	600	Lake	Yes	190	778	¹³ C	5E	12.1-6.7	35	Hu et al., 2016
G21	Wangyanggou	42.07	119.92	751	Lake	No	13	200	¹³ C	1A+3E	5-0	85	Li et al., 2006
G21	Wanguantun	40.27	113.67	800	Bog	Yes	-	-	¹³ C	1A+4F	8-3	310	Kong and Du, 1996
G21	Anguli Nur Lake	41.33	114.37	1000	Lake	Yes	4264	3684	¹³ C	2U	14-10.5	520	Li et al., 1990
G21	Qasq	40.67	111.13	1000	Bog	Yes	-	-	¹³ C	2E	10-0	90	Wang et al., 1997
G21	Daihai Lake_2004	40.58	112.67	1220	Lake	Yes	16000	7136	¹³ C	8E	11.5-0	215	Xiao et al., 2004
G21	Gaoximage Lake	42.95	115.37	1253	Lake	No	100000	17841	¹³ C	4E	6-0	150	Li C.Y. et al., 2003
G21	Haoluku Lake	42.96	116.76	1295	Lake	No	1384	2099	¹³ C	4E	11.5-0	250	Wang et al., 2001
G21	Bayanchagan Lake	41.65	115.21	1355	Lake	Yes	636	1423	¹³ C	2B+7E	11.5-0	250	Jiang et al., 2006
G21	Liuzhouwan Lake	42.71	116.68	1365	Lake	No	288	957	¹³ C	3E	13-0.5	470	Wang et al., 2001
G21	Diaojiaohai Lake	41.30	112.35	1800	Lake	Yes	30	309	¹³ C	4U	11.5-2.5	95	Song et al., 1996
G22	Hulun Nur Lake_1995	49.28	117.40	544	Lake	No	233900	27286	¹³ C	7U	19-0.5	190	Yang et al., 1995
G22	Hulun Nur Lake_2006	49.13	117.51	545	Lake	Yes	233900	27286	¹³ C	13E	11-0	65	Wen et al., 2010
G23	Derput	57.03	124.12	700	Bog	Yes	1	56	¹³ C	1A+4C	11.7-0.8	210	Andreev and Klimanov, 1991
G23	Suolakh	57.05	123.85	811	Bog	Yes	-	-	¹³ C	8C	12.8-3.7	180	Andreev et al., 1991
G24	Nuochaga Lake	61.30	129.55	260	Lake	Yes	120	618	¹³ C	4E	6.5-0	140	Andreev and Klimanov, 1989
G24	Chabada Lake	61.98	129.37	290	Lake	Yes	210	818	¹³ C	15U	13-0	110	Andreev and Klimanov, 1989
G25	Boguda Lake	63.67	123.25	120	Lake	Yes	2500	2821	¹³ C	7E	10.9-0.4	180	Andreev et al., 1989
G25	Khomustakh Lake	63.82	121.62	120	Lake	Yes	440	1183	¹³ C	9E	12.3-0.1	170	Andreev et al., 1989
G25	Madjuga Lake	64.83	120.97	160	Lake	Yes	1440	2141	LSC	7E	8.2-0.2	120	Andreev and Klimanov, 1989
G25	Bilyakh Lake	65.30	126.78	340	Lake	Yes	1678	2311	¹³ C	7A	14.1-0	180	Müller et al., 2009



G25	Lake Billyakh	PG1755	65.27	126.75	340	Lake	Yes	1634	2281	¹³ C	1A+10E	50.6-0.2	470	Müller et al., 2010
G26	Lake Kyryvunda	PG2022	69.63	123.65	66	Lake	Yes	468	1220	¹³ C	10E	10.8-0.3	360	Biskaborn et al., 2015
G27	Khocho		71.05	136.23	6	Bog	Yes	10	178	¹³ C	1C	10.4-0.4	300	Velichko et al., 1994
G27	Samandon		70.77	136.25	10	Bog	Yes	100	564	¹³ C	3A+8C+4E	7.9-0.2	280	Velichko et al., 1994
G28	Barbarina Tumsa		73.57	123.35	10	Bog	Yes	-	-	¹³ C	4C	4.9-0.3	240	Andreev et al., 2004
G28	Lake Nikolay		73.67	124.25	35	Lake	Yes	1500	2185	¹³ C	6A	12.5-0	600	Andreev et al., 2004
G28	Dolgoe Ozero		71.87	127.07	12	Lake	Yes	84	517	¹³ C	1A+9B	15.3-0	210	Pisarcic et al., 2001
G29	Maiti		42.87	122.88	155	Bog	No	-	-	¹³ C	5A	3-0	115	Ren and Zhang, 1997
G29	Dashan		44.88	124.85	200	Bog	Yes	-	-	¹³ C	5U	7.5-1	160	Xia et al., 1993
G29	Xiaonan		43.88	125.22	209	Bog	Yes	-	-	¹³ C	5U	5.5-0	290	Wang and Xia, 1988
G29	Shuangyang		43.45	125.75	215	Bog	Yes	-	-	¹³ C	12E	2.5-0	30	Qiu et al., 1981
G29	Charisu		42.95	122.35	249	Bog	Yes	-	-	¹³ C	10A	5.5-0	170	Li Y.H. et al., 2003b
G29	Jingbo Lake		43.91	128.75	350	Lake	Yes	9500	5499	¹³ C+LSC	3E+4	8.8-0	40	Li et al., 2011
G29	Harbaling		43.63	129.20	600	Bog	Yes	-	-	¹³ C	3U	3-0	150	Xia, 1988b
G29	Jinchuan		42.35	126.38	620	Bog	Yes	-	-	¹³ C	7A	5.5-0	105	Li Y.H. et al., 2003a
G29	Erhailongwan Lake		42.30	126.37	724	Lake	Yes	30	309	¹³ C	2A+14E	22-0	760	Liu Y.Y. et al., 2008
G29	Sihailongwan Lake		42.28	126.60	797	Lake	Yes	41	360	¹³ C+varve	40A	16.9-0.2	47	Stebich et al., 2015
G29	Hani		42.21	126.52	899	Bog	Yes	1800	2394	¹³ C	1C	9.5-0	455	Qiao, 1993
G29	Chichi Lake		42.03	128.13	1800	Bog	Yes	0	40	¹³ C	1C	1-0	140	Xu et al., 1994
G30	Belaya Skala		43.25	134.57	4	Bog	Yes	-	-	¹³ C	2A+1C	6.5-3	250	Korotky et al., 1980
G30	Chernyiy Yar		43.18	134.43	4	Bog	Yes	-	-	¹³ C	4C	10-0.5	260	Korotky et al., 1980
G30	Tikhangou		42.83	132.78	4	Bog	Yes	-	-	¹³ C	5U	12-0	500	Korotky et al., 1980
G30	Amba River		43.32	131.82	5	Bog	Yes	-	-	¹³ C	1A+1C+1U	5-2.5	300	Korotky et al., 1980
G30	Ryazanovka		42.83	131.37	6	Bog	Yes	-	-	¹³ C	7A	6-0.5	540	Shilo, 1987



G30	Ovrazhnyii	43.25	134.57	8	Bog	Yes	-	-	¹⁴ C	3A	7-1	200	Shilo, 1987
G30	Peschanka	43.30	132.12	12	Bog	Yes	-	-	¹⁴ C	3U	22-11	965	Anderson et al., 2002
G30	Xingkai Lake	45.21	132.51	69	Lake	Yes	419000	36520	¹⁴ C+Pb/Cs	3E	28.5-0	150	Ji et al., 2015
G31	Tongjiang	47.65	132.50	49	Bog	Yes	-	-	¹⁴ C	5C	6-0	130	Zhang and Yang, 2002
G31	Chuangye	48.33	134.47	50	Bog	Yes	-	-	¹⁴ C	3U	12-1	400	Xia, 1988a
G31	Minzhuqiao	47.53	133.87	52	Bog	Yes	-	-	¹⁴ C	4U	6.5-0.5	420	Xia, 1988a
G31	Qindeli	47.88	133.67	52	Bog	Yes	-	-	¹⁴ C	1F+7U	13.5-0.5	380	Xia, 1988a
G31	Beidawan	48.13	134.70	60	Bog	Yes	8	157	¹⁴ C	3U	5.5-0.5	350	Xia, 1988a
G31	Wuchanghai	47.22	127.33	200	Bog	Yes	-	-	¹⁴ C	9E	7-0	250	Xia, 1988b
G31	Tangbei	48.35	129.67	486	Bog	Yes	-	-	¹⁴ C	2A	5.5-1	160	Xia, 1996
G32	Venyukovka-3	47.12	138.58	5	Bog	Yes	-	-	¹⁴ C	1A+2C	5.8-3.2	140	Korotky et al., 1980
G32	Venyukovka-2	47.03	138.58	6	Bog	Yes	-	-	¹⁴ C	1A+1C	3.6-0.4	140	Korotky et al., 1980
G32	Oumi	48.22	138.40	990	Bog	Yes	-	-	¹⁴ C	5C	2.6-0.4	80	Anderson et al., 2002
G32	Opasnaya River	48.23	138.48	1320	Bog	Yes	-	-	¹⁴ C	7C	13.3-6.7	360	Korotky et al., 1988
G33	Il'inka Terrace	47.97	142.17	3	Bog	Yes	-	-	¹⁴ C	2C+1F	2.6-1.1	360	Korotky et al., 1997
G33	Mereya River	46.62	142.92	4	Bog	Yes	-	-	¹⁴ C	2C+2F	42.0-0.8	1530	Anderson et al., 2002
G33	Sergeevskii	49.23	142.08	6	Bog	Yes	-	-	¹⁴ C	8A+1C	8.4-2.2	110	Korotky et al., 1997
G34	Gurskii Peat	50.07	137.08	15	Bog	Yes	-	-	¹⁴ C	7C	13.1-1.5	380	Korotky, 1982
G34	Gur Bog	50.00	137.05	35	Bog	No	-	-	¹⁴ C	13C	22.1-0	340	Mokhova et al., 2009
G34	Tuqiang	52.23	122.80	400	Bog	Yes	-	-	¹⁴ C	10A+14E+8F	3-1	125	Xia, 1996
G34	Selikan-2	53.22	135.03	1300	Bog	Yes	-	-	¹⁴ C	4C	6.4-1.9	260	Volkov and Arkhipov, 1978
G34	Selikan-1	53.22	135.05	1320	Bog	Yes	-	-	¹⁴ C	6C	7.9-0	140	Korotky et al., 1985
G35	Two-Yurts Lake_PG1856-3	56.82	160.04	275	Lake	Yes	1168	1928	¹⁴ C	5A	6.0-2.8	140	Hoff et al., 2015
G35	Two-Yurts Lake_PG1857-2	56.82	160.07	275	Lake	Yes	1168	1928	¹⁴ C	5A	2.5-0.1	130	Hoff et al., 2015



G35	Two-Yurts Lake_PG1857-5	56.82	160.07	275	Lake	Yes	1168	1928	¹³ C	5A	4.4-2.5	120	Hoff et al., 2015
G35	Lake Sokoch	53.25	157.75	495	Lake	Yes	41	363	¹³ C	8E	9.7-0.3	250	Dirksen et al., 2012.
G36	Glukhoye Lake	59.75	149.92	10	Bog	Yes	-	-	¹³ C	5C	9.4-3.4	1000	Lozhkin et al., 1990
G36	Chistoye Lake	59.55	151.83	91	Bog	Yes	-	-	¹³ C	5C	7.0-0	540	Anderson et al., 1997
G36	Lesnoye Lake	59.58	151.87	95	Lake	Yes	13	200	¹³ C	8A	15.5-0	400	Anderson et al., 1997
G36	Pepef'noye Lake	59.85	150.62	115	Lake	Yes	0	18	¹³ C	2A	4.3-0	180	Lozhkin et al., 2000
G36	Alut Lake	60.14	152.31	480	Lake	Yes	63	448	¹³ C	1.6A+9B	50.4-0	430	Anderson et al., 1998
G36	Podkova Lake	59.96	152.10	660	Lake	Yes	114	602	¹³ C	5A	6.0-0	220	Anderson et al., 1997
G36	Maltan River	60.88	151.62	735	Bog	Yes	-	-	¹³ C	4A+7C	12.0-9.4	120	Lozhkin and Glushkova, 1997
G36	Taloye Lake	61.02	152.33	750	Lake	Yes	16	227	¹³ C	7A	10.3-0	290	Lozhkin et al., 2000
G36	Elikchan 4 Lake	60.75	151.88	810	Lake	Yes	329	1023	¹³ C	1.6U	55.5-0	440	Lozhkin and Anderson, 1995
G36	Goluboye Lake	61.12	152.27	810	Lake	Yes	12	192	¹³ C	1.1A+2B	9.7-0	240	Lozhkin et al., 2000
G36	Julietta Lake	61.34	154.56	880	Lake	Yes	11	189	¹³ C	2A+4E+11	36.1-1.4	270	Anderson et al., 2010
G36	Elgennya Lake	62.08	149.00	1040	Lake	Yes	455	1204	¹³ C	6A	16.0-0	310	Lozhkin et al., 1996
G37	Smorodinoye Lake	64.77	141.12	800	Lake	Yes	27	293	¹³ C	6A+5F	27.1-0	360	Anderson et al., 1998
G37	Vechernii River	63.28	147.75	800	Bog	Yes	-	-	¹³ C	1F	14.4-0.1	380	Anderson et al., 2002
G37	Jack London Lake	62.17	149.50	820	Lake	Yes	1213	1965	¹³ C	7F	19.5-0.2	320	Lozhkin et al., 1993
G37	Sosednee Lake	62.17	149.50	822	Lake	Yes	82	510	¹³ C	4E+1F	26.3-0	640	Lozhkin et al., 1993
G37	Rock Island Lake	62.03	149.59	849	Lake	Yes	5	124	¹³ C	2E	6.6-0	470	Lozhkin et al., 1993
G37	Oldcamp Lake	62.04	149.59	853	Lake	Yes	7	150	¹³ C	2E	3.7-0	370	Anderson, unpublished
G37	Gek Lake	63.52	147.93	969	Lake	Yes	2392	2759	¹³ C	8A+1B	9.6-0	440	Stetsenko, 1998
G37	Figurnoye Lake	62.10	149.00	1053	Lake	Yes	439	1182	¹³ C	4A	1.3-0	30	Lozhkin et al., 1996
G38	Kuropatoch'ya_Kurop7	70.67	156.75	7	Bog	Yes	-	-	¹³ C	3C	5.7-0.4	760	Anderson et al., 2002
G38	Kuropatoch'ya_Kurpeat	69.97	156.38	47	Bog	Yes	-	-	¹³ C	1A+4C	11.7-7.5	430	Lozhkin and Vazhenina, 1987



G39	Elygygyyn Lake	67.50	172.10	496	Lake	No	9503	5500	polarity	-	20.2-1.5	650	Melles et al., 2012
G39	Emnyneem_mammoth	68.17	165.93	400	Bog	Yes	50	399	¹³ C	2C+2F	36.4-9.3	2470	Lozhkin et al., 1988
G39	Emnyvaam River	67.42	172.08	490	Bog	Yes	18	239	¹³ C	1A+4C	10.6-4.3	630	Lozhkin and Vazhenina, 1987
G39	Emnyneem River	68.25	166.00	500	Bog	Yes	-	-	¹³ C	4C	10.7-4.0	420	Anderson et al., 2002
G40	Malyi Kreehet Lake	64.80	175.53	32	Lake	Yes	125	630	¹³ C	12A	9.6-0	400	Lozhkin and Anderson, 2013
G40	Melkoye Lake	64.86	175.23	36	Lake	Yes	1870	2440	¹³ C	21E	39.1-0	1260	Lozhkin and Anderson, 2013
G40	Sunset Lake	64.84	175.30	36	Lake	Yes	240	874	¹³ C	7A	14.0-0	260	Lozhkin and Anderson, 2013
G40	Gygykai Lake	63.42	176.57	102	Lake	Yes	99	561	¹³ C	1A+8E	32.3-0	470	Lozhkin et al., 1998
G40	Patricia Lake	63.33	176.50	121	Lake	Yes	40	357	¹³ C	3A+7E	19.1-0	290	Anderson and Lozhkin, 2015
G41	Konerino	65.90	-178.90	10	Bog	Yes	-	-	¹³ C	1C	9.8-0	900	Ivanov et al., 1984
G41	Lorino	65.50	-171.70	12	Bog	Yes	-	-	¹³ C	3C	17.9-5.1	850	Ivanov, 1986
G41	Dlinnoye Lake	67.75	-178.83	280	Lake	Yes	71	476	¹³ C	3A	1.3-0	130	Anderson et al., 2002
G41	Dikikh Olyenyeyii Lake	67.75	-178.83	300	Lake	Yes	64	450	¹³ C	1A+4C	50.3-0	1050	Anderson et al., 2002
G42	Blossom Cape	70.68	178.95	6	Bog	Yes	-	-	¹³ C	1C	13.8-0.2	3400	Oganesyan et al., 1993
G42	Jack London Lake	70.83	-179.75	7	Lake	Yes	69	469	¹³ C	5A+1E	16.1-0.3	790	Lozhkin et al., 2001
G42	Wrangel Island	71.17	-179.75	200	Bog	Yes	-	-	¹³ C	17A+3C	13.7-10.2	110	Lozhkin et al., 2001

978 LSC: liquid-scintillation counting; A: terrestrial plant macrofossil; B: non-terrestrial plant macrofossil; C: peat; D: pollen; U: unknown; E: total organic
 979 matter from silt; F: animal remains or shell; G: charcoal; H: CaCO₃; I: tephra.

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985 **Appendix 2** RPP estimates (with their standard errors; SEs) of 27 pollen taxa from 20 study areas. The excluded PPE ($SE \geq PPE$) are in italics.

Country	Poland	Russia	Sweden	Switzerland	Sweden	Swiss	Switzerland	Sweden	Finland	Estonia
Region	Białowieża Forest	Khatanga region	Southern Sweden	Jura Mountains	west-central	Alps	Moss	west-central	Fennoscandia	Southeast
sample type	Moss	Moss	Moss	Moss	Lake	Trap	Moss	Moss	Moss	Lake
Reference	Baker et al., 2016	Niemeyer et al., 2015	Broström et al., 2004	Sugita et al., 1999	Soepboer et al., 2007	Sjögren et al., 2008	Mazier et al., 2008	von Stedingk et al., 2008	Räsänen et al., 2007	Poska et al., 2011
Model	ERV-3	ERV-2	ERV-3	ERV-3	ERV-3	-	ERV-1	ERV-3	ERV-3	ERV-1
Poaceae	1 (0.00)	1 (0.00)	1 (0.00)	1 (0.00)	1 (0.00)	1 (0.00)	1 (0.00)	1 (0.00)	1 (0.00)	1 (0.00)
<i>Abies</i>					9.92 (2.86)		3.83 (0.37)			
<i>Pinus</i>	23.12 (0.24)		5.66 (0.00)		1.35 (0.45)	9 (0.00)		21.58 (2.87)	8.4 (1.34)	5.07 (0.06)
<i>Picea</i>			1.76 (0.00)		0.57 (0.16)	0.5 (0.00)	7.1 (0.2)	2.78 (0.21)		4.73 (0.13)
<i>Larix</i>		<i>0.00009 (0.1)</i>				1.4 (0.00)				
<i>Alnus</i> tree	15.95 (0.66)		4.2 (0.14)							13.93 (0.15)
<i>Betula</i> tree	13.94 (0.23)		8.87 (0.13)		2.42 (0.39)	20 (0.00)		2.24 (0.2)	4.6 (0.7)	1.81 (0.02)
<i>Juglans</i>										
<i>Fraxinus</i>			0.67 (0.03)		1.39 (0.21)					
<i>Quercus</i>	18.47 (0.10)		7.53 (0.08)		2.56 (0.39)					7.39 (0.2)
<i>Tilia</i>	0.98 (0.03)		0.8 (0.03)							
<i>Ulmus</i>										
<i>Alnus</i> shrub		6.42 (0.42)								
<i>Betula</i> shrub		1.8 (0.26)								
<i>Carpinus</i>	4.48 (0.03)				4.56 (0.85)					
<i>Corylus</i>	1.35 (0.05)		1.4 (0.04)		2.58 (0.25)			0.09 (0.03)		2.31 (0.08)
<i>Salix</i>			1.27 (0.31)					0.07 (0.04)		
Ericaceae										
<i>Ephedra</i>										
Cyperaceae		0.53 (0.06)	1 (0.16)				0.68 (0.01)	0.89 (0.03)	0.002 (0.0022)	1.23 (0.09)



<i>Artemisia</i>																									3.48 (0.19)	
Chenopodiaceae																										
Asteraceae																										0.17 (0.03)
<i>Thalictrum</i>																										0.24 (0.06)
Ranunculaceae																										3.85 (0.72)
Caryophyllaceae																										
Brassicaceae																										
Country	Region	sample type	Reference	Model	Czech	Norway	Greenland	England	England	Germany	China	China	China	China	China	China	China	China	China	China	China	China	China	China	China	
Poaceae																										
<i>Abies</i>																										
<i>Pinus</i>																										
<i>Picea</i>																										
<i>Larix</i>																										
<i>Alnus_tree</i>																										
<i>Betula_tree</i>																										
<i>Juglans</i>																										
<i>Fraxinus</i>																										
<i>Quercus</i>																										
<i>Tilia</i>																										
<i>Ulmus</i>																										
<i>Alnus_shrub</i>																										
<i>Betula_shrub</i>																										



<i>Corpinus</i>									8.684 (0.09)
<i>Corylus</i>								1.216 (0.00)	
<i>Salix</i>								2.736 (0.00)	
Ericaceae									
<i>Epilobium</i>									0.96 (0.14)
Cyperaceae									0.94 (0.079)
<i>Artemisia</i>								0.65 (0.4)	0.21 (0.07)
Chenopodiaceae								3.2 (0.6)	24.7 (0.36)
Asteraceae								5.3 (1.1)	6.74 (0.79)
<i>Thalictrum</i>									0.39 (0.16)
Ranunculaceae									1.06 (0.21)
Caryophyllaceae									3.06 (0.42)
Brassicaceae									7.48 (0.33)
									0.89 (0.18)

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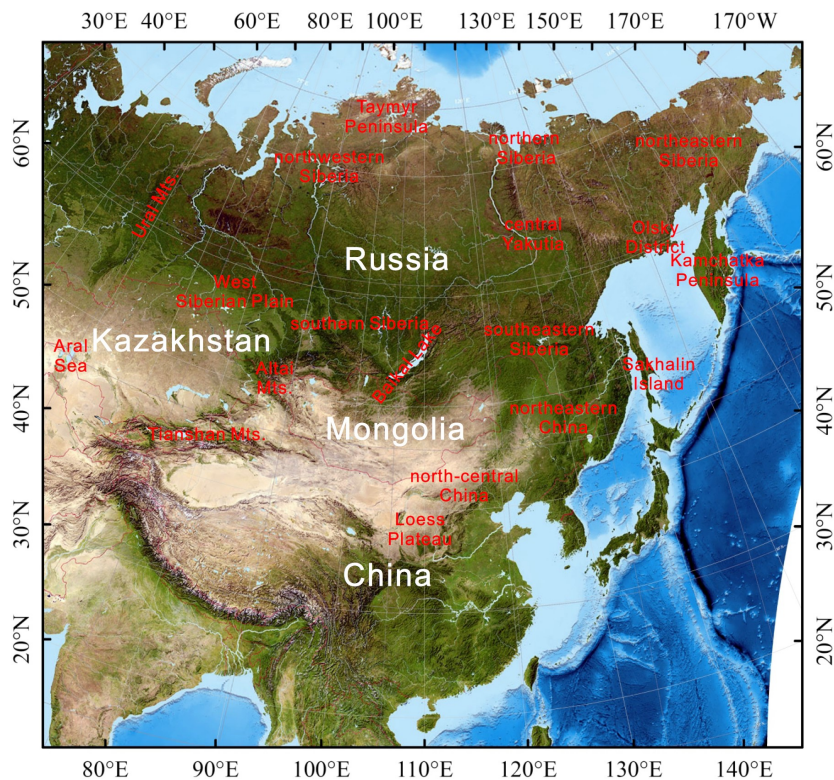
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999 Appendix 3 Map of the study area showing the geographic locations mentioned in the text.



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