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1 **Temperature and fire controls on vegetation dynamics in Northern Ural (Russia) boreal**
2 **forests during the Holocene based on brGDGT and pollen data**

3

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16

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18

19 **Abstract**

20 Boreal vegetation is influenced by multiple factors such as climate and fire, but interactions between long- and short-term effects of climate upon
21 fire activity are complex and remain poorly studied, especially in Eurasia. To understand the relationships between climate, fire and vegetation
22 in Eurasia, we reconstruct the climate changes during the Holocene for the western section of the Northern Urals region, in the southern part of
23 the Republic of Komi. We relate these temperature reconstructions to pollen and charcoal records from the same region (Yaksha site, Republic
24 of Komi, Russia). We use here a combined approach based on pollen and molecular biomarkers (branched Glycerol Dialkyl Glycerol Tetraethers
25 or brGDGTs) to provide independent estimates of past temperatures. Our objectives were: (1) to understand the relationships between climate,
26 fire, vegetation and human activity during the Holocene at the local scale of Yaksha and (2) to provide a robust regional-scale climatic
27 reconstruction of the southern part of the Republic of Komi. Our study shows that climate had a major influence on the regional vegetation
28 between 10,000 and 4000 cal. yr BP. Subsequently, fire activity had a joint and growing impact on vegetation dynamics between 4000 and 600
29 cal. yr BP. Finally, from 600 until the present (2016 AD), human presence and activities had a greater impact on the fire regime and vegetation
30 than earlier in time, and combined with climate to influence the dynamics of the boreal forest. At the regional scale of the Republic of Komi and
31 the local scale of Yaksha, the Holocene Thermal Maximum was detected between 6800 and 4000 cal. yr BP, using pollen-based temperature
32 estimates but in brGDGT calibration (at 4000 cal. yr BP) commonly shared in the literature, together with evidence from neighboring regions in
33 the Eurasian boreal biome which were studied for different proxies (pollen, chironomids), and also with reference to climate models (General
34 Circulation Models).

35

36 **Keywords:** brGDGT; Pollen; Quantitative climate reconstructions; Holocene; Republic of Komi, Northern Urals, boreal forests, fire histories

37

38 1. Introduction

39 Boreal regions are among the most sensitive regions to current and future climate change (IPCC-AR6, Pörtner *et al.*, 2022). Climate influences
40 boreal biomes through direct control of the biomass accumulation rates and shapes natural disturbance regimes such as wildfires. General
41 Circulation Models (GCMs) integrating these effects, suggest that the circumboreal zone will shrink by 2071-2100 (Feng *et al.*, 2014). The
42 simulated decline of the boreal biome is attributed to a precipitation increase (especially in winter), and a temperature increase (between +6° and
43 +8°C), driving an increase in fire activity (Goetz *et al.*, 2007; de Groot *et al.*, 2013; Feng *et al.*, 2014; Hoegh-Guldberg *et al.*, 2018).

44 Climate and fire are the main drivers of vegetation, but interactions between them are complex and poorly studied in Eurasian boreal forests
45 (Glückler *et al.*, 2020; Goldammer and Furyaev, 1996; Kharuk *et al.*, 2021). Climate impacts fire frequency, fire severity and burned area. An
46 increase in fire activity likely increases the share of serotinous tree species such as *Betula pendula* Roth., *B. pubescens* Ehrh. (hereafter *Betula*
47 spp.) and *Pinus sylvestris* L. (hereafter *Pinus sylvestris*) (de Groot *et al.*, 2013; Goetz *et al.*, 2007). In contrast, enhanced summer precipitation
48 counteracts this effect and favors *Picea abies* (L.) H.Karst. (hereafter *Picea abies*) and *Pinus sibirica* Du Tour (hereafter *Pinus sibirica*) (Feng
49 *et al.*, 2014; Hoegh-Guldberg *et al.*, 2018). In North American boreal forests, fire events were found to be influenced by climate and human
50 activity, but also by the type of vegetation (eg Ali *et al.*, 2012; Camill *et al.*, 2009; Girardin *et al.*, 2013; Hu *et al.*, 2006; Remy *et al.*, 2017). For
51 example, in Canada, during the Mid-Holocene (6000 cal. yr BP), forest dominated by boreal mixed woodland vegetation was associated with low
52 fire frequency, while the climate was warm and dry. But from 3000 cal. yr BP, despite colder and wetter conditions, fire frequency increased,
53 because of the vegetation shift toward a dense needleleaf landscape (Girardin *et al.*, 2013).

54 Recent regional climate synthesis studies have pointed out specific regional patterns of climate variability during the Holocene period (Kaufman
55 *et al.*, 2020; Marcott *et al.*, 2013; Marsicek *et al.*, 2018; Mauri *et al.*, 2015; Herzschuh *et al.*, 2022). In Europe, the climate synthesis by Kaufman
56 *et al.*, (2020) based on various proxies such as pollen, chironomids, and molecular biomarkers, indicated a warming trend in the Northern latitudes
57 during the Early Holocene followed by a cooling since 6000 yr BP. This study also showed that the climate patterns are proxy-specific. For
58 example, the temperature optimum was recorded at 10,000 years BP from reconstructions based on chironomids and at 6000 years BP from
59 reconstructions based on pollen (Kaufman *et al.*, 2020). The climate synthesis by Herzschuh *et al.* (2022) based on pollen data only, also indicate
60 a temperature optimum between 8000 to 6000 yrs cal BP, but the timing and the amplitude of this optimum is strongly dependent on latitude, and
61 appears more marked at high latitudes (70 to 80 °N) and less marked between 60 to 70°N. These global syntheses also highlight the poor “past
62 climate” coverage of Eurasia and particularly of Russia, despite their geographical extent and role in global biochemical cycles. The general lack

63 of data is particularly apparent in the Republic of Komi, West of the Northern Urals area (Golubeva, 2008), despite its climatic relevance, at the
64 confluence of several atmospheric meteorological mechanisms (Ural Blocking, Siberian High, Arctic Oscillations) (Wang et al., 2010; Dole et
65 al., 2011; Cheung et al., 2012; H. Cheung and Zhou, 2015). Our earlier investigations of pollen and charcoal records in the Republic of Komi, in
66 the Yaksha area, revealed a shift in the boreal forest tree species as well as increasing fire activity during the Holocene (Barhoumi et al., 2020,
67 2019). However, the role of climate in the interactions between fire and vegetation has not yet been well documented. The only study of Holocene
68 climate in this area reconstructs increasing temperatures between 6000 and 4800 cal. yr BP (Golubeva, 2008). In the neighboring sub-regions of
69 Northern Europe and Fennoscandia, several studies based on pollen and chironomids indicate an increase in temperatures between 8000 and 3500
70 cal. yr BP (e.g. Seppä *et al.*, 2009; Salonen *et al.*, 2011). On the eastern side of the Urals, some studies of the Holocene climate have been carried
71 out in the Taymyr peninsula (Andreev et al., 2002; Velichko et al., 2002). These studies suggest that in the Early Holocene (between 10,300 and
72 9000 cal. yr BP), temperatures were slightly cooler (-1 °C) than today, but wetter (+ 50 mm precipitation compared to present). At the Entarny
73 site (Velichko et al., 2002), the Early Holocene also showed colder temperatures (-2.5 °C), but also less precipitation (- 25 mm compared to
74 today). The main studies of Holocene climate-vegetation-fire relationships in the east of the Republic of Komi were carried out in Siberia, around
75 Lake Baikal (Barhoumi et al., 2021; Bezrukova et al., 2013, 2003; Demske et al., 2005; Feng et al., 2014; Tarasov et al., 2007, 2009). According
76 to these studies, from the Early Holocene to the Mid-Holocene (11,000-8000 cal. yr BP), conditions were colder and wetter. From 8000 to 5000
77 cal. yr BP, the Lake Baikal region experienced its climatic optimum with wet conditions. From 5000 to 3000 cal. yr BP temperatures and
78 precipitation decreased before increasing again from 3000 to the present day. Most of these studies are based on pollen records and transfer
79 functions (eg Chevalier *et al.*, 2020) and vegetation-independent studies are needed to provide more reliable climate reconstructions.

80 With this study, we reconstruct Holocene temperature and precipitation patterns in the Republic of Komi using a coupled approach including
81 pollen data and organic biomarkers Glycerol Dialkyl Glycerol Tetraethers (GDGTs) (Dugerdil et al., 2021; Martin et al., 2020; Ramos-Román et
82 al., 2022; Robles et al., 2022). GDGTs are membrane lipid molecules of bacterial origin (Damsté et al., 2000; Weijers et al., 2006b), ubiquitously
83 found in oceans, lakes and rivers, peats and soils. GDGT distributions in these environments broadly correlate to mean annual temperatures and
84 pH (e.g. Weijers et al., 2007a; Petersee et al., 2010). Different calibrations were performed on soils, lake sediments and peatlands to infer
85 temperatures for GDGTs and more specifically brGDGTs (branched-GDGTs, Damsté *et al.*, 2000; Weijers, Schouten, van den Donker, *et al.*,
86 2007; Weijers, Schouten, Sluijs, *et al.*, 2007; Peterse *et al.*, 2012; Foster *et al.*, 2016; Naafs *et al.*, 2017; Dearing Crampton-Flood *et al.*, 2020).
87 To our knowledge, there are very few Holocene temperature reconstructions based on pollen grains and brGDGTs, which are independent climate

88 proxies (Dugerdil et al., 2021; Martin et al., 2020; Ramos-Román et al., 2022; Robles et al., 2022), and the brGDGT calibrations have never been
89 used to reconstruct Holocene temperatures in Russia.

90 The objective of this study is first to understand the links between climate, fire regime, vegetation dynamics and human activity over the Holocene
91 at the local scale of the Yaksha area, and secondly, to provide a robust reconstruction of the climate changes during the Holocene in the southern
92 part of the Republic of Komi, in the Northern Urals area. Temperature reconstructions for Yaksha are based on two independent proxies, pollen
93 and brGDGT. They are discussed in relation to the dynamics of both fire regimes and forest vegetation reconstructed from charcoal and pollen
94 by Barhoumi *et al.*, (2019, 2020). We provide a regional perspective on the climate trends through the Holocene by applying the same pollen
95 transfer functions to the other pollen records available from the area. Finally, we compare our results with climate reconstructions developed for
96 Northern Europe and neighboring regions.

97

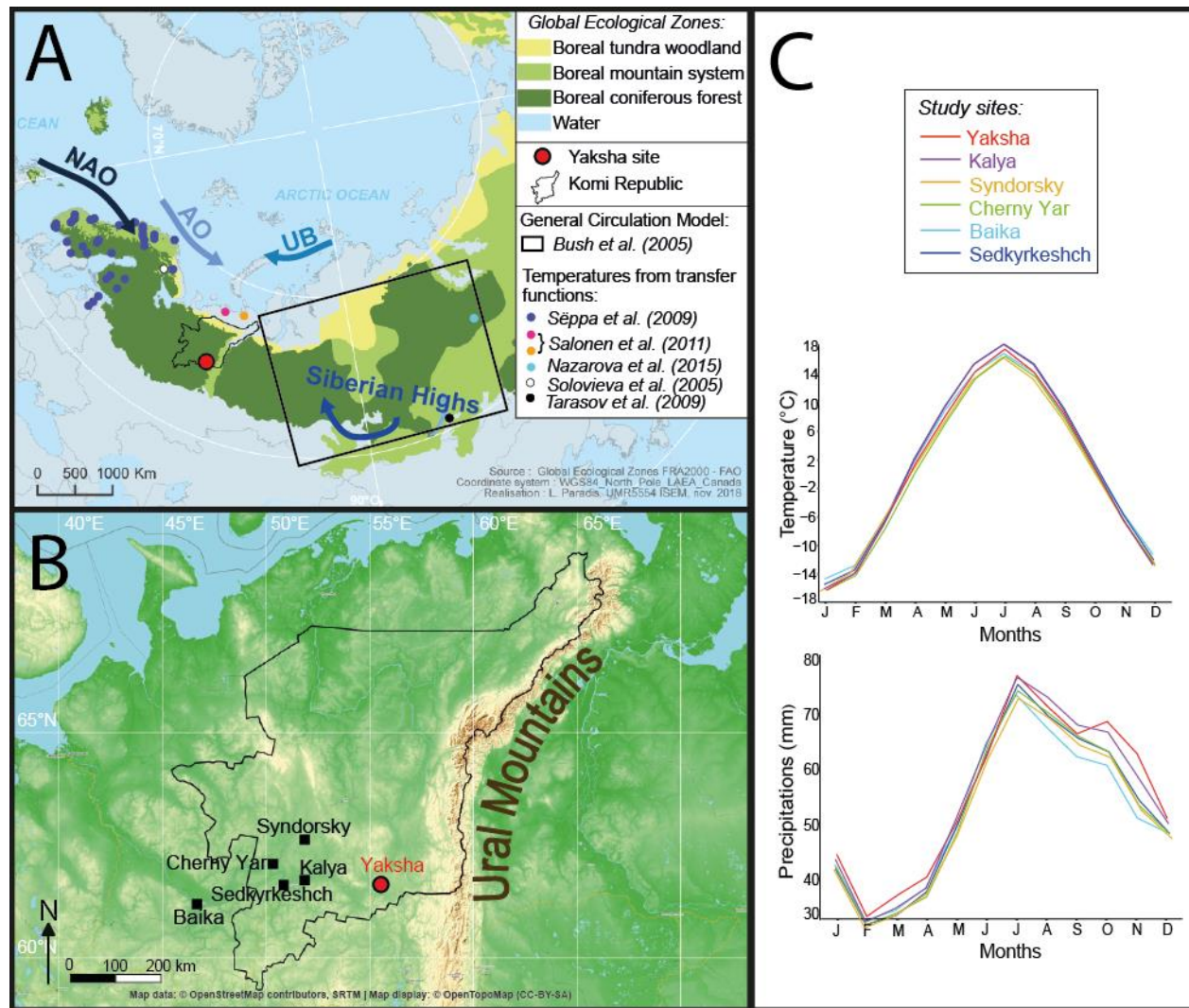
98 **2. Material and Methods**

99 *2.1 Environmental setting of the study area*

100 European boreal forests are constituted of patches of "light taiga" forests type dominated by *Pinus sylvestris*, *Larix sibirica* Ledeb. (hereafter
101 *Larix sibirica*) and *Betula* sp, associated with a surface fire regime in drier environments, and the "dark taiga" forests type, in wetter environments
102 dominated by *Picea abies*, *Pinus sibirica*, and *Abies sibirica*, where crown fires can occur (Goldammer, 2015; Lapenis et al., 2005; Schulze et
103 al., 2005; Shorohova et al., 2009). In the western part of the Northern Urals, the boreal vegetation is dominated by *Larix sibirica* and *Pinus* sp.

104 Yaksha. One of the study sites (Fig. 1, Table 1), is a forested peatbog of 4 hectares located in the south of the Republic of Komi (Barhoumi et al.,
105 2019, 2020). The Republic of Komi (Fig. 1) is a Russian administrative division of 415 900 km², occupying the western side of the Ural
106 Mountains. The soils of the region are mainly moraine and surface loams (Drobyshev et al., 2004a; Zaboeva, 1997), with podzolic soils and the
107 topography is flat except near the Ural Mountains (Naryshkin, 2003).

108 The local forest cover (assessed within a 10 km radius around the Yaksha site) consists today mainly of Scots pines (*Pinus sylvestris*, 84%),
109 spruce (*Picea abies*, 13%) and birch (*Betula pendula* and *B. pubescens*, 2%). In contrast, spruce forests dominate regionally.



110

111 *Figure 1 : A: The Republic of Komi in the Eurasian boreal biome (highlighted black contours). Location of the Yaksha coring site (red dot) as*
 112 *well as available temperature reconstructions cited in the text ((colored dots Solovieva, Tarasov and MacDonald, 2005; Seppä et al., 2009;*
 113 *Tarasov, Bezrukova and Krivonogov, 2009; Salonen et al., 2011; Nazarova et al., 2015a; Novenko and Olchev, 2015; Druzhinina et al., 2020).*
 114 *The black square corresponds to the zone for which climate outputs are available from the General Circulation Model GFDL (Bush, 2005), UB:*
 115 *Ural Blocking; AO: Arctic Oscillations; NAO: North Atlantic Oscillations. B: The Republic of Komi and the pollen records used for the Holocene*
 116 *climate regional synthesis (Yaksha – this study, Kalya, Syndorsky, Cherny Yar, Baika and Sedkyrkeshch (Borisova, 2002), Sedkyrkeshch*
 117 *(Golubeva, 2008), Kalya (Karmanov et al., 2011), Cherny Yar (Marchenko-Vagapova and Marieva, 2001) and Syndorsky (Golubeva, 2008)). C:*
 118 *Ombrothermic diagrams of each studied site (Grieser et al., 2006).*

119

120 In the Northern Urals region in Republic of Komi, a blocking, which is an anticyclonic or cyclonic vortex on a large scale and which remains
 121 quasi stationary, takes place (Ural Blocking, UB or also so-called Ural-Siberian Blocking, USB) (Cheung et al., 2013, 2012). UB (Fig. 1A) is
 122 generally more active and intense during boreal winter, acting as a barrier to Siberian Highs during this period, but amplifying its effect on the
 123 east-Asian sub-continent and causing harsher winters (Wang et al., 2010; Cheung et al., 2013; Cheung and Zhou, 2015). The intensity of UB

124 during winter is also linked to the phases of the Arctic Oscillation (AO) (Cheung et al., 2012). On the other hand, Rossby waves, another
125 atmospheric phenomena, occur and have an impact on the climate of Europe and Western Russia (Dole et al., 2011; Schubert et al., 2011, 2014).
126 For example, during summer 2010, strong heat waves occurred and had direct effects on wildfire activity in the Ural Mountains (Cheung et al.,
127 2013; Dole et al., 2011; Lau and Kim, 2012; Matsueda, 2011). In the study area, a UB occurring during the NAO positive phase may lead to a
128 regional warming in the atmospheric winter temperatures (Huang et al., 2017).

129 In the North of the Republic of Komi, the mean annual temperature is -6°C , while it is $+1^{\circ}\text{C}$ in the South (Figure 1C). Annual precipitation varies
130 between 450 and 700 mm (Drobyshev et al., 2004b; Grieser et al., 2006) (Figure 1C).

131

132 *2.2 Study sites and material*

133 We extracted two peat cores (Yak2-A and Yak3-A) using an 8-cm diameter Russian peat corer from the centers of the selected *Sphagnum*
134 peatlands. We built a composite sequence from the two cores Yak2-A and Yak3-A to obtain the longest chronology (Barhoumi et al., 2019, 2020).
135 The 0 to 300 cm interval of core Yak3-A provided the best temporal resolution of the Yaksha composite core. Although having a lower temporal
136 resolution than Yak3-A, the deeper part of core Yak2-A is constituted of organic-rich sediments reaching 11,000 cal. yr BP (Barhoumi et al.,
137 2019). The chronology was based on 12 radiocarbon dates, with the age model discussed in detail in Barhoumi et al. (2019) (see Appendix SI 1).
138 The Yaksha core provided both a charcoal record (Barhoumi et al., 2019) and a pollen record (Barhoumi et al., 2020). This study focuses on the
139 pollen-inferred climate reconstruction, the brGDGT analysis and the brGDGT-inferred temperature reconstruction.

140 We also benefited from five published pollen sequences (Fig. 1B, Table 1) located close to the Yaksha site to reconstruct the climate in the area
141 during the Holocene. From South to North, these pollen sequences were Baika (Borisova, 2002), Sedkyrkeshch (Golubeva, 2008), Kalya
142 (Karmanov et al., 2011), Cherny Yar (Marchenko-Vagapova and Marieva, 2001) and Syndorsky (Golubeva, 2008). Modern values for annual
143 temperatures and precipitation were established with the software New_Locclim (Grieser et al., 2006), a local climate estimator using the updated
144 FAOCLIM database (<https://www.faoswalim.org>). The 2010-2018 meteorological records for the coordinates of these sites, from the Worldclim
145 database, at a spatial resolution of 2.5 minutes, were used to verify the correlation between the mean annual temperatures, the mean summer
146 temperatures (June, July, August, corresponding to the fire season) and the mean temperatures of the months above 0°C (from April to October)
147 (Fick and Hijmans, 2017; Harris et al., 2014).

148

149 *Table 1: Pollen records selected for the climate reconstruction synthesis*

Name of the site	Coordinates	Elevation (a. s. l. in m)	Time covered (cal. yr BP)	References
Yaksha	61°43'N, 55°29'E 61°41'N, 55°34'E	135	10,047 to -50	This study; Barhoumi <i>et al.</i> , 2019, 2020.
Baika	61°16'N, 46°44'E	60	8775 - 50	Borisova, 2002
Cherny Yar	62°13'N, 50°17'E	90	8532 - 2876	Marchenko-Vagapova and Marieva, 2001
Kalya	61°48'N, 51°47'E	101	10,150 - 0	Karmanov <i>et al.</i> , 2011
Sedkyrkeshch	61°43'N, 50°51'E	95	4244 - 1197	Golubeva, 2008
Syndorsky	62°44'N, 51°51'E	138	9434 - 4727	Golubeva, 2008

150

151 These pollen sequences provide a vegetation synthesis in the Southern part of the Komi Republic as follows (Appendix SI 2):

152 At Yaksha, from 10,000 cal. yr BP to 5000 cal. yr BP, the vegetation was dominated by *Pinus sylvestris* and *Betula spp.* This vegetation fits with
 153 the present description of a light taiga system. From 6050 BP to 100 cal. yr BP the pollen assemblages show an increase of *Picea* and the
 154 occurrence of *Pinus sibirica*, suggesting the establishment of a predominantly dark taiga. From 3200 to 100 cal. yr BP, the dark taiga decreased
 155 slowly and the light taiga reappeared, with an increase of *Pinus sylvestris*. From 100 cal. yr BP to 0 cal. yr BP, there was a strong increase in
 156 *Betula spp.*

157 At Kalya, close to Yaksha, vegetation changes are consistent with the Yaksha ones: in the first half of the Holocene, from 9000 to 6000, light
 158 taiga taxa were predominant. In the Mid-Holocene, *Picea abies* disappeared. Then from 5000 to 3500 cal. yr BP *Picea abies* increased again but
 159 remained less numerous than *Pinus sylvestris* and *Betula spp.* From 3500 cal. yr BP, the light taiga was predominant with *Pinus sylvestris* and
 160 *Betula spp.*

161 In Sedkyrkeshch, Syndorsky and Cherny Yar, pollen diagrams only cover part of the Holocene. At Sedkyrkeshch, few changes were observed
 162 between 4000 and 1000 cal. yr BP. *Betula spp.* was the main taxa. *Pinus sylvestris* and *Picea abies* were equally present. In Syndorsky, *Betula*
 163 *spp.* dominated in the Early Holocene (from 9000 to 6500 cal. yr BP), followed by *Pinus sylvestris* from 6500 to 5000 cal. yr BP. *Picea abies*
 164 (dark taiga) culminated around 8000 cal. yr BP. In Cherny Yar, as in Yaksha and Kalya, the first half of the Holocene showed landscapes mostly
 165 consisting of forests dominated by *Betula spp.* up to 6000 cal. yr BP. From 6000 to 3000 cal. yr BP, *Betula*-dominated forests and dark taiga
 166 (*Picea abies*) were both present.

167 At Baika, before 10,000 cal. yr BP, the forests had not yet significantly developed; subsequently, *Picea abies*, *Pinus sylvestris* and *Betula spp.*
168 Forests developed. From 10,000 to 5000 cal. yr BP, dark taiga with *Picea abies* was predominant. From 5000 to 2500 cal. yr BP, *Picea abies*
169 decreased in favor of light taiga taxa, before developing again from 2500 cal. yr BP until the present day.

170

171 2.3 Pollen-inferred climate reconstructions: a multi-method approach

172 The pollen-based climate reconstructions were performed using two different methods, in order to increase the reliability of our reconstruction:
173 the Modern Analogue Technique (MAT; Guiot, 1990) and the Weighted Averaging Partial Least Squares Regression (WA-PLS; ter Braak and
174 Juggins, 1993). Transfer functions (such as WA-PLS) and assemblage approaches (such as MAT) require a robust modern pollen calibration
175 dataset. The MAT compares the composition of modern pollen assemblages compiled in the modern dataset with fossil pollen assemblages by
176 calculating a chord distance (a Euclidian distance on square-root-transformed abundances) (Guiot, 1990). When the chord distance reaches a
177 threshold value, modern pollen assemblages samples are rejected. On the other hand, the closest modern pollen samples are retained as the best
178 analogues, and the weighted average of their climate parameters is calculated to provide the past climate estimates (where the weights used are
179 the inverse of the chord distance) (Guiot, 1990). We chose between 6 to 8 analogues (depending on the site and the climatic parameters), using a
180 leave-one-out cross-validation test. WA-PLS is a transfer function, a regression method that assumes that the relationships between pollen
181 percentages and climate are unimodal, and that for each taxon there is an optimal climate variable value. With this method, the modern pollen
182 data set used can be considered as a large multidimensional matrix. Since there is collinearity between pollen taxa, and since some taxa are linked
183 to the climatic parameters of interest, it is possible to resize the dataset to a reduced number of components based on the linear predictors of the
184 parameter of interest and on the residual structure of the data when these predictors are removed (Peyron et al., 2013).

185 The modern dataset used here for the Yaksha and other sequences climate reconstructions was a sub-dataset from a Eurasian database (Peyron et
186 al., 2005), with more than 3000 sites (Peyron et al., 2008; Dugerdil et al., 2021). The sub-dataset selected here includes 2115 sites located mainly
187 in Russia but also in Northern and Central Europe. We chose to constrain the original dataset to increase the robustness of the climatic parameter
188 reconstruction. With that objective, we selected biomes comparable to the climate and ecosystems in the region of the Republic of Komi. The
189 sites corresponding to the biomes Cold Deciduous Forest, Cold Mixed Forest, Cold Coniferous Forest, Cold Steppe, Pioneer Environments, Taiga
190 forest and Tundra (Peyron et al., 1998; Prentice et al., 1996) were selected in the sub-dataset.

191 The R package ‘Rioja’ was used to reconstruct the past climate parameters with both methods (Juggins, 2009; Juggins and Juggins, 2020). Climate
192 parameters are: mean annual temperatures (TANN) and annual precipitation (PANN), mean summer temperatures (MTWA) and summer
193 precipitation (SUMMERPR). The performance of the two methods was tested on the database by randomly using 60% of it to calibrate and the
194 remaining 40% to test the transfer functions. The same test was carried out by selecting the 19 samples from the database between latitudes 40
195 and 50°N and longitudes 40 and 50°E, representing the closest samples from the database to the Yaksha site. The correlations between the
196 reconstructed values and the observed values of the database are presented in Appendix SI 3 and SI 4. A redundancy analysis (RDA) was
197 performed to compare the main pollen taxa (*Betula* spp., *Pinus sylvestris*, *Pinus sibirica*, *Picea abies*, *Abies sibirica* and Other taxa) with
198 reconstructed climate parameters inferred from pollen MAT (TANN, PANN, MTWA and SUMMERPR), fire activity (mFRI) and human
199 population density. The fire activity data come from Barhoumi et al. (2020, 2019) who calculated and computed temporally the mean Fire Return
200 Interval of Yaksha study site. The human population density numerical data come from the HYDE 3.1 database (Klein Goldewijk et al., 2011)
201 and were downloaded here: <https://landuse.sites.uu.nl/datasets/>.

202

203 *2.4 GDGT analysis*

204 Key samples representative of the sedimentary sequences and the lithologic transitions were processed for GDGT analyses at ENS de Lyon
205 (LGLTPE, France): 26 and 12 from Yak3-A and Yak2-A, respectively. Samples were freeze-dried and grounded. To aliquots of less than a gram,
206 a C₄₆ GDGT standard solution, at 10 ng.µL⁻¹ was added (Huguet et al., 2006). Then, lipids were microwaved (MARS, CEM) with dichloromethane
207 (DCM):MeOH (3:1). Total lipid extracts were separated into polar and apolar fractions on an Al₂O₃ column (1 g) with hexane:DCM (1:1) and
208 DCM/MeOH (1:1). The separated fractions were then analyzed using a High Performance Liquid Chromatography Mass Spectrometer (HPLC-
209 MS, Agilent 1200) (Hopmans et al., 2016; Davtian et al., 2018). The detected peak signals were integrated on the Agilent, LC/MS Chemstation
210 Software. Branched-GDGT compositions (brGDGTs, Damsté *et al.*, 2000; Weijers, Schouten, Sluijs *et al.*, 2007, 2007) were quantified.

211 The reproducibility and stability of the analytical process was assessed through regular chemistry and analysis of an internal standard peat sample.
212 Reproducibility of the measurements was calculated by replicate analyses of two contrasted samples of the sediment core.

213

214 *2.5 GDGT indices and temperature reconstructions*

215 BrGDGTs (see compound shape in Figure 1 from Naafs *et al.*, 2018) are distinguished by the proportions of tetra- (I), penta- (II) and hexa- (III)
 216 methylated forms and by the number of cyclopentane moieties, which can be 0 (a), 1 (b), or 2 (c). brGDGT fractional abundances were combined
 217 into several indices (Table 2) such as the Branched and Isoprenoid Tetraether Index (BIT - Hopmans *et al.*, 2004), the IIIa/IIa ratio (Xiao *et al.*,
 218 2016), in which we included the 5/6 and 7-Methylated form, the Cyclization ratio of Branched Tetraethers (CBT - Weijers *et al.*, 2007a) and the
 219 Methylation of Branched Tetraether (MBT' - Peterse *et al.*, 2012 and MBT'_{5Me} - De Jonge *et al.*, 2014b).

220 *Table 2: Indices and temperature calibrations based on brGDGT fractional abundances*

Indices/Temperature calibrations	Formula or model	References
CBT	$= -\log \left(\frac{Ib + IIb + IIb6Me}{Ia + IIa + IIa6Me} \right)$	(Weijers <i>et al.</i> , 2007b)
MBT'	$= \frac{Ia + Ib + Ic}{Ia + Ib + Ic + IIa' + IIa'' + IIa7Me + IIb' + IIb'' + IIc' + IIc'' + IIIa' + IIIa'' + IIIb' + IIIb'' + IIIc'}$	(Peterse <i>et al.</i> , 2012)
MBT' _{5Me}	$= \frac{Ia + Ib + Ic}{Ia + Ib + Ic + IIa + IIb + IIc + IIIa}$	(De Jonge <i>et al.</i> , 2014)
CI	$= \frac{Ia}{Ia + IIa + IIIa}$	(De Jonge <i>et al.</i> , 2019)
MAT _{Peterse}	$= 0.81 - 5.67 \times CBT + 31.0 \times MBT'$	(Peterse <i>et al.</i> , 2012)
MAT _{Naafs}	$= 52.18 \times MBT'_{5Me} - 23.05$	(Naafs <i>et al.</i> , 2017)
MAT _{Crampton-Flood}	<i>Bayesian regression model (BayMBT0, for mean annual temperatures above zero)</i>	(Dearing Crampton-Flood <i>et al.</i> , 2020)
MST _{Foster}	$= 18.7 + (80 \times Ib) - (23.05 \times II) - (19.4 \times III) + (369.9 \times IIIb)$	(Foster <i>et al.</i> , 2016)

221

222 Temperature reconstructions were based upon several indices, including the Methyl Index of Branched Tetraether (MBT - (Weijers *et al.*, 2007b).
 223 This has been modified by Peterse *et al.* (2012) to yield MBT', and by Naafs *et al.* (2017) to give MBT'_{5Me}, excluding brGDGT 6-methyl. We
 224 tested four calibration equations and models, assessed on global datasets of soils and peats. This allowed us to derive Mean Annual Air
 225 Temperature (hereafter called MAT_{Peterse} and MAT_{Naafs}), Mean Annual Temperature above 0°C (hereafter called MAT_{Crampton-Flood}) and Mean
 226 Summer Air Temperature (hereafter called MST_{Foster}). These calibrations are respectively based on Peterse *et al.* (2012), Naafs *et al.* (2017),
 227 Dearing Crampton-Flood *et al.*, (2020) and Foster *et al.*, (2016).

228

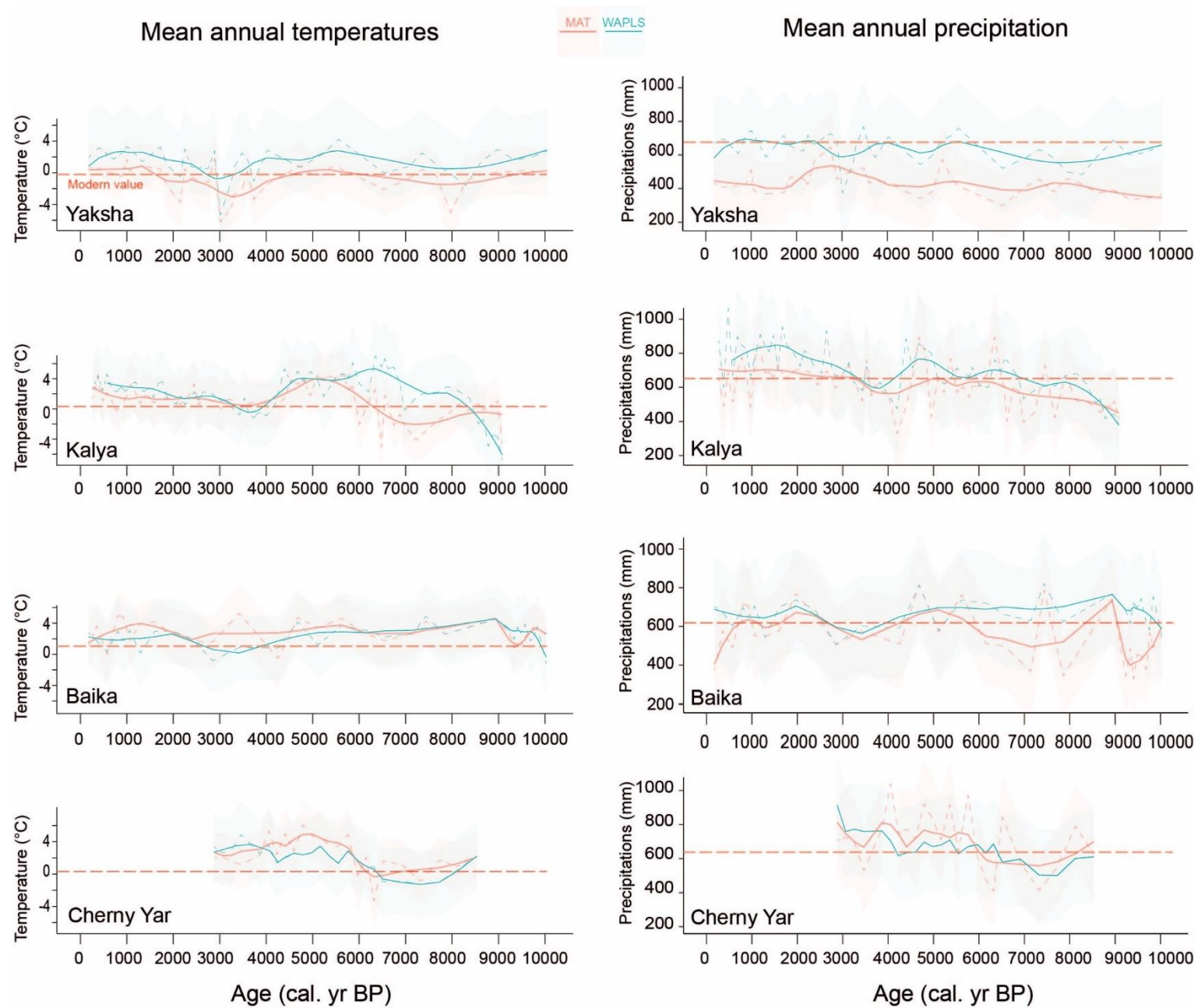
229 **3. Results**

230 *3.1 Pollen-inferred climate patterns*

231 The mean annual temperatures (TANN) and annual precipitation (PANN) of the Yaksha, Kalya, Baika and Cherny Yar sites are presented in Fig.
232 2. The two other sites (Sedkyrkeshch and Syndorsky), which cover only a small part of the Holocene, are presented in Appendix SI 5, as well as
233 mean summer temperatures (MTWA) and summer precipitation for each site.

234 During the Holocene, the mean annual temperatures reconstructed using the Modern Analogue Technique and the Weighted Averaging Partial
235 Least Squares Regression, from the different cores (Yaksha, Kalya, Baika, Cherny Yar) were broadly similar in terms of trends and amplitudes
236 (Fig. 2). In Yaksha, Kalya and Baika, the temperature values reconstructed from the most recent samples were very close to the measured modern
237 values (-0.37°C at Yaksha, $+0.39^{\circ}\text{C}$ at Kalya and $+1.46^{\circ}\text{C}$ at Baika). From 10,000 to 7000 cal. yr BP, higher than present day temperatures were
238 reconstructed for Yaksha and Baika ($+3^{\circ}\text{C}$). At Kalya, however, the temperature trends reconstructed with the two methods were similar only
239 from 5500 to 0 cal. yr BP (Fig. 2). Notably, the climate reconstruction began from 9000 cal. yr BP with lower values than today and the
240 temperature increased until 7000 cal. yr BP. Yaksha, Kalya and Baika records show a Holocene Thermal Maximum (HTM) extending between
241 6800 cal. yr BP and 4000 cal. yr BP, with temperature values from $+1^{\circ}\text{C}$ (MAT) to $+3^{\circ}\text{C}$ (WA-PLS) relative to the present. From 4000 to 3000
242 cal. yr BP, the results show a general decrease in temperatures, with values lower than today (Yaksha) or very close to modern values (Baika and
243 Kalya). Then, from 3000 to 0 cal. yr BP, the temperatures rose gradually and reach current values.

244 Mean annual precipitation (PANN) estimates at Yaksha show differences between the two methods but for Kalya, Baika and Cherny Yar, the
245 precipitation reconstructions were very similar for MAT and WA-PLS (Fig. 2). For all these sites (except Baika), there was a general increase in
246 precipitation during the Holocene. At the onset of the Holocene, between 10,000 and 8000 cal. yr BP, Yaksha and Kalya show precipitation values
247 slightly below the modern values (about 630 mm/year, especially with MAT results). Baika recorded a decrease of precipitation from 9000 to
248 8000 cal. yr BP. Then, from 8000 to 5000 cal. yr BP, the PANN at Baika shows an increasing trend, as do all the other sites. From 5000 cal. yr
249 BP, a precipitation decrease was observed (WA-PLS at Yaksha), up to about 3500 cal. yr BP. From 3500 cal. yr BP, PANN stabilized at modern
250 values for Yaksha (WA-PLS) and Baika. They increased up to 1500 cal. yr BP in Kalya, before gradually decreasing to the later values up to the
251 present day.



252

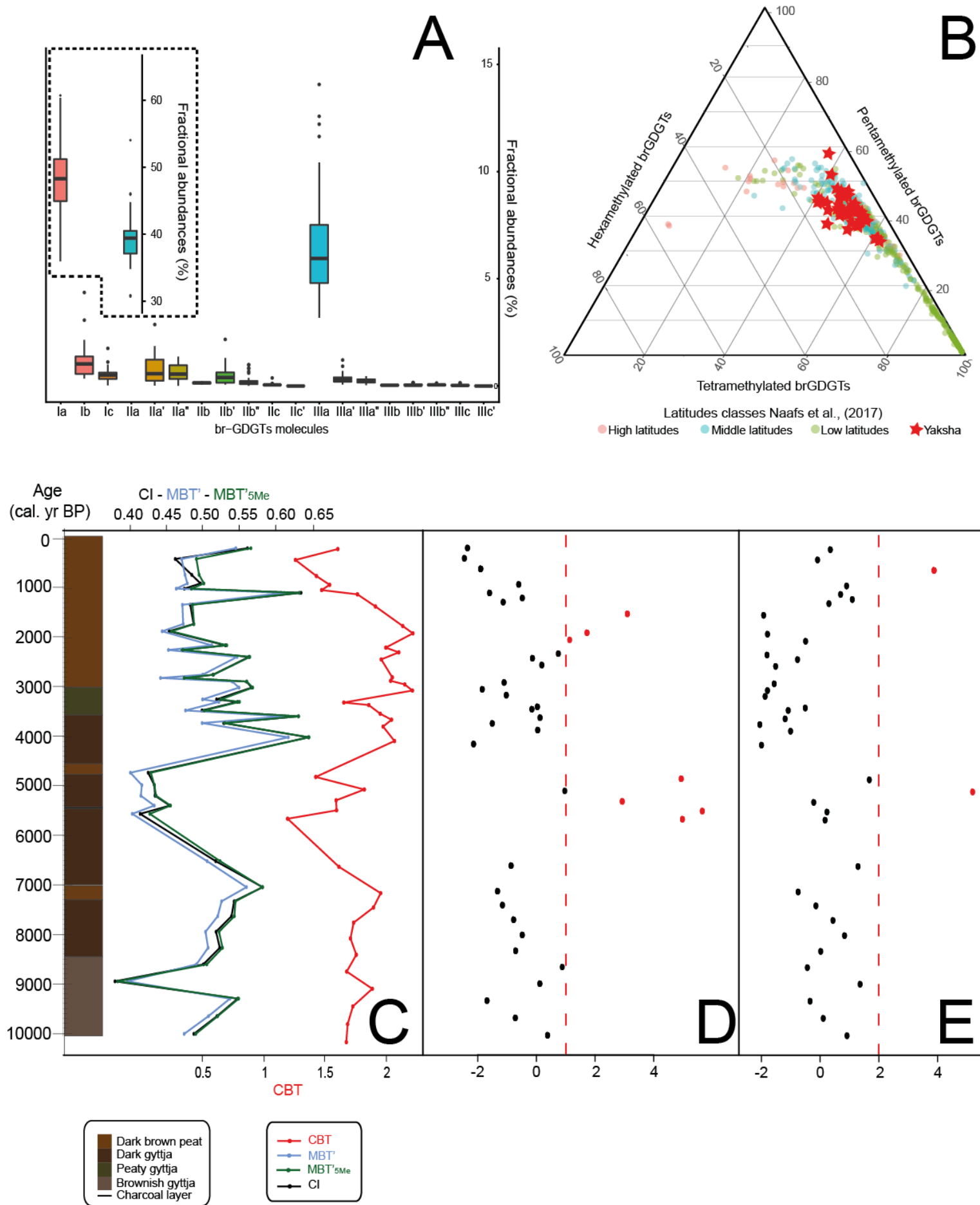
253 *Figure 2: Regional climatic synthesis for the Republic of Komi from pollen-based reconstructions. Mean annual temperature and mean annual*
 254 *precipitation (dashed lines) were calculated with the Modern Analogue technique (MAT) and the Weighted Averaging Partial Least Squares*
 255 *Regression (WA-PLS) and smoothed with Loess (span = 0.3, solid lines). Shaded areas are confidence interval. Red dashed lines are modern*
 256 *values for each site.*

257

258 *3.2 GDGT abundances and indices*

259 Within the Yaksha record, the majority of brGDGTs are tetramethylated Ia (48%) and pentamethylated forms IIa (39%) (Fig. 3A). The
260 hexamethylated form IIIa represents 6% of the total brGDGTs. The remaining brGDGTs are present at values below 2%. The GDGT signatures
261 from Yaksha were similar to those in the global database (Naafs *et al.*, 2017) and were characteristic of mid- and high-latitude sites (Fig. 3B).
262 The average BIT index is 0.998 ± 0.005 . The MBT'_{5Me} and MBT' signals (used to infer temperature) vary little along the core (Fig. 3C), but show
263 the lowest values (0.39 - 0.4) between 4740 and 5580 cal. yr BP and at 8980 cal. yr BP. The maximum value of 0.64 is at 4020 cal. yr BP. CI
264 (Community Index, Table 2, De Jonge *et al.*, 2019) shows the same variations as the MBT'_{5Me} and MBT' signals and values similar to those of
265 MBT'_{5Me}. These indices show high values at the very beginning of the Holocene, from 10,000 to about 9200 cal. yr BP. There are also high values
266 between 8600 and 6500 cal. yr BP, and again between 4500 cal. yr BP. until the end of the record. PCA of Yaksha brGDGTs was performed (see
267 SI 6). The eigenvalues of the first 2 axes of this PCA are presented in Fig. 3D (axis 1) and 3E (axis 2). Outlier brGDGT samples were highlighted
268 by cutoff values of 1 (for axis 1) and 2 (for axis 2).

269



271 *Figure 3: A: brGDGT fractional abundances in the Yaksha sequence measurement represented against two % scales. B: Ternary plot of the*
272 *relative abundances of tetra-, penta-, and hexamethylated brGDGTs compared to the general database from Naafs et al. (2017) sorted by latitude*
273 *classes. C: CBT, CI, MBT' and MBT'_{5Me} indices. D and E: Individual PCA eigenvalues according to axis 1 (D) and axis 2 (E). Red dots are*
274 *samples above the threshold separating main samples from outlier points*

275

276

277 **4. Discussion**

278 *4.1 Yaksha local temperature reconstructions: brGDGT and pollen comparison*

279 *4.1.1 brGDGT origins*

280 The brGDGT signal from the Yaksha study site is consistent with a terrigenous origin: the BIT index remains very close to 1 throughout the
281 sediment core (Hopmans et al., 2004).

282 BrGDGT forms without cyclopentane moieties, Ia and IIa, are the main compounds within the Yaksha sedimentary core (Fig. 3A). This agrees
283 with several studies on brGDGTs from soils and peatlands (Li et al., 2017; Loomis et al., 2014; Sun et al., 2011; Weijers et al., 2010, 2007b,
284 2006a, 2006b). This observation also confirms that the production of Yaksha brGDGTs is mainly of terrigenous origin since *in situ* production
285 contains more methyl groups and cycle forms (Loomis et al., 2014; Tierney et al., 2012, 2010). Form IIIa, which is the third most abundant
286 brGDGT compound here, is therefore likely to have come from the small amount which would have been produced *in situ*, when the peatland
287 was submerged (Buckles et al., 2014; Cao et al., 2017; Loomis et al., 2014, 2011; Tierney et al., 2010). The variations in CI appear to coincide
288 with the sample outliers indicated by the PCA eigenvalues of the brGDGTs samples. This could indicate a shift in brGDGT-producer communities,
289 since they may respond differently to varying atmospheric temperatures (De Jonge et al., 2019). These samples (at 400 cal. yr BP ; from 1330 to
290 1870 cal. yr BP and from 4740 to 5580 cal. yr BP) were therefore not considered in the discussion and interpretation of the results of the
291 temperature calibrations.

292 Moreover, peatland is an environment in which one part (catotelm) is anoxic and constantly saturated with water, while another part (acrotelm)
293 contains living *Sphagna* and exhibits large variability in oxygen content. Studies have shown that the concentration of brGDGTs is significantly
294 higher in catotelm than in acrotelm (Weijers et al., 2004). This differentiates the dynamics of brGDGT communities depending on the nature of
295 the sediment through the core and has an impact on reconstruction of the annual air temperatures. For this reason we tested four calibrations, one

296 for soil environments, $\text{MAT}_{\text{Peterse}}$ (Peterse et al., 2012), and two specific to peatland environments, $\text{MAT}_{\text{Naafs}}$ and $\text{MAT}_{\text{Crampton-Flood}}$, (Dearing
297 Crampton-Flood et al., 2020; Naafs et al., 2017). We tested another calibration, reconstructing summer temperatures or temperatures of the months
298 above 0°C, regionally adapted for Antarctic and sub-Antarctic lakes, $\text{MST}_{\text{Foster}}$ (Foster et al., 2016), which is close to the climate of the Republic
299 of Komi. (Fig. 4).

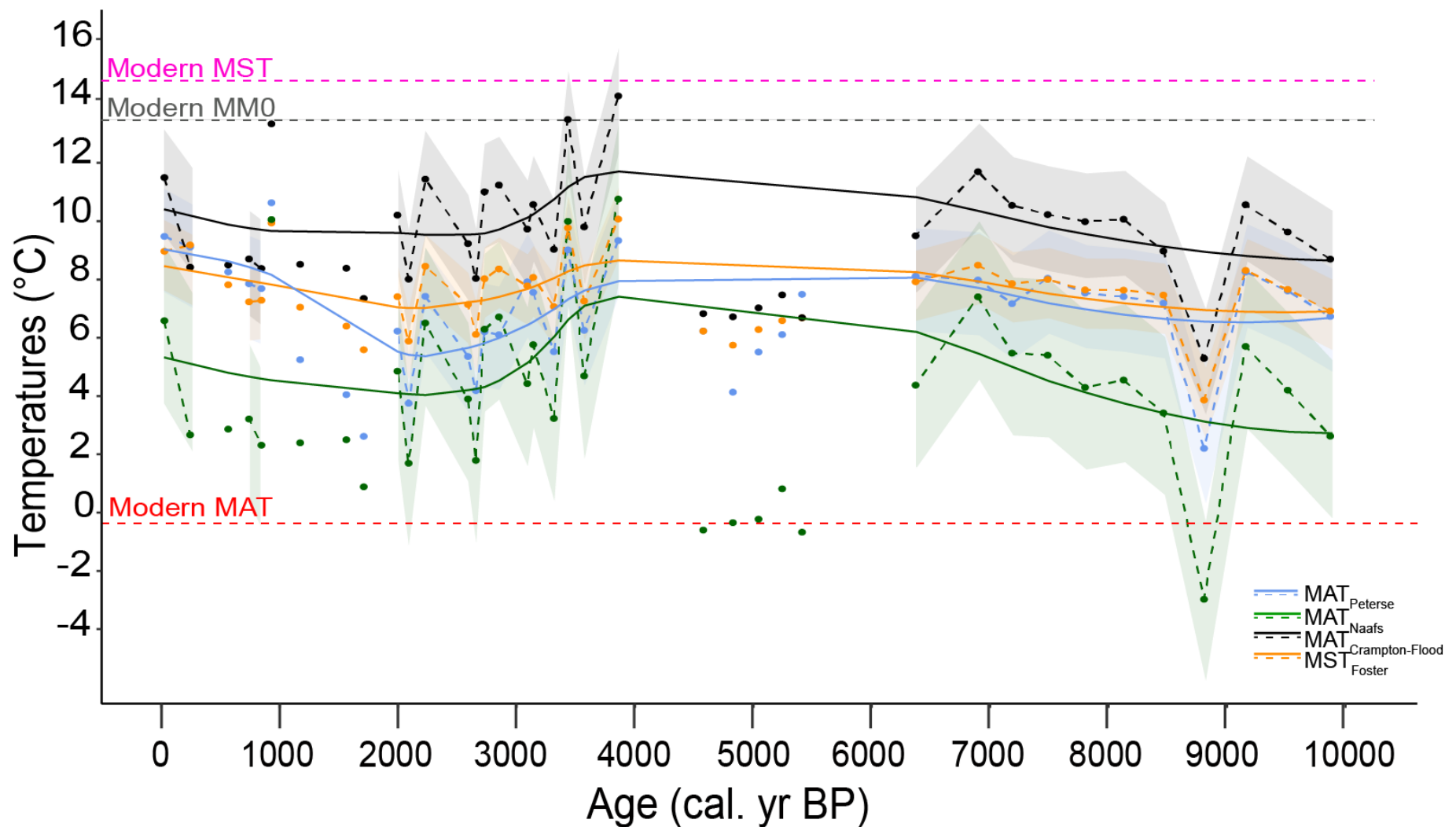
300

301 4.1.2 *brGDGT calibration for mean annual temperatures reconstruction*

302 The brGDGT reconstructed temperatures (Fig. 4) ranged between: $\text{MAT}_{\text{Peterse}}$: +2.5 to +10.5°C, $\text{MST}_{\text{Foster}}$: +5.5 to +9.9°C, $\text{MAT}_{\text{Naafs}}$: -3 to +10.6°C
303 and $\text{MAT}_{\text{Crampton-Flood}}$: +5.2 to +14.1°C. The four calibrations show similar patterns. The first half of the Holocene, from 10,000 to 6500 cal. yr
304 BP, shows a steady increase of the temperatures (+2°C). Then, from 4000 cal. yr BP to 2100 cal. yr BP, temperatures decrease before increasing
305 again in the Late Holocene. Both peat calibrations, $\text{MAT}_{\text{Naafs}}$ and $\text{MAT}_{\text{Crampton-Flood}}$, show more marked trends than the lake calibrations, $\text{MAT}_{\text{Peterse}}$
306 and $\text{MST}_{\text{Foster}}$. Highest temperature values are not reconstructed by the summer calibrations, but by the mean annual temperatures above zero
307 calibration from Crampton-Flood *et al.* (2020). The GDGT-based temperature values are higher than the current values, and differ from those of
308 pollen transfer-functions: we will therefore discuss trends rather than absolute values.

309 The warmest Holocene temperature appears to be at 4000 cal. yr BP, just before a temperature drop that spans the next 2000 years. This
310 corresponds to the end of the HTM time frame reconstructed by the pollen transfer functions. However, it should be noted that from 6500 to 4000
311 cal. yr BP and from 1870 to 1330 cal yr BP and at 400 cal. yr BP, there is no interpretation of the calibration results, these samples having been
312 excluded because of suspected correspondence to another community of brGDGTs. BrGDGTs analyzed in this study came from a peat sediment
313 core, which adds temperature reconstruction biases (Weijers et al., 2010). It is more notably more difficult to set up reconstructions of peatland
314 or soil temperatures, because the modern data are less well known and/or less available, and also generally less used in paleoecology (Weijers et
315 al., 2011, 2007b). The dual origin (terrestrial and lacustrine) of brGDGTs blurs the signal between the composition of brGDGTs and the
316 calculation of CBT and therefore contributes to the error that accompanies them (Sun et al., 2011). Other biases in the reconstruction of
317 temperatures from brGDGTs have been brought to light. The literature shows that brGDGT temperature calibrations are likely to both
318 underestimate past temperatures (Li et al., 2017; Pearson et al., 2011; Tyler et al., 2010; Zink et al., 2010) but and at other times to overestimate
319 them (Wang et al., 2012; Li et al., 2017), and this even with regional calibrations. The temperature seasonality, which is high in the region of the

320 study site, is a factor that enhances the overestimation of temperatures (Dearing Crampton-Flood et al., 2020) and this is what is clearly observed
321 with all the calibrations that have been tested, compared to the modern average annual temperatures at Yaksha. Although bacterial communities
322 are present and active in winter (Drotz et al., 2010; Nedwell, 1999), bacterial activity appears to be more intense in summer, with different
323 bacterial communities than in the winter season (Schostag et al., 2015; Sun et al., 2011). The calibrations provided for high latitudes such as that
324 of Foster *et al.* (2016), but also that of Dearing Crampton-Flood *et al.* (2020), more recently, with the use of their BayMBT0 model, would
325 therefore correspond more to growing season, rather than to the mean annual temperature. External factors can also influence brGDGT
326 distributions and temperature reconstructions, such as precipitation and humidity changes (Dearing Crampton-Flood et al., 2020). Finally,
327 vegetation can also be an element of variability in the brGDGT production (from soils and from the watershed) (Ayari et al., 2013; Huguet et al.,
328 2013; Naeher et al., 2014; Weijers et al., 2011). At Yaksha, the time periods that show the highest variability in the brGDGT signal are between
329 9100 and 8500 cal. yr BP, 5600 and 4700 cal. yr BP and 1500 cal. yr BP to the present day (Fig. 3C, CBT and IIIa/IIa indices, tetramethylated
330 brGDGTs, rings tetra- and pentamethylated 5 Me brGDGTs). The alternation of light taiga and dark taiga could therefore have played a role in
331 the diversity of the brGDGT present. This role is however not fully assessed so far (Buckles et al., 2014; Davtian et al., 2016; Weijers et al.,
332 2010).



333

334 *Figure 4: Yaksha GDGT temperature reconstructions. Blue: Mean Annual Temperature ($MAT_{Peterse}$) after Peterse et al. (2012), green: Mean*
 335 *Annual Air Temperature (MAT_{Naafs}), after Naafs et al. (2017), black: Mean Annual Temperature above 0 ($MAT_{Crampton-Flood}$), after Dearing*
 336 *Crampton-Flood et al. (2020), orange: Mean Sub-Arctic Air Temperature (MST_{Foster}) after Foster et al. (2016). The reconstructed temperatures*
 337 *are smoothed with the R function Loess (span = 0.3). Modern Mean Annual Temperature (Modern MAT) is represented in red dotted line, Modern*
 338 *Mean Summer Temperature (Modern MST) is represented in pink dotted line and Modern Mean Months above 0°C Temperature (Modern MM0)*
 339 *is represented in grey dotted line.*

340

341

4.1.3 Pollen-inferred climate reconstructions

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The reconstructed climatic parameters of the Holocene in the Republic of Komi show similar trends in the two-methods: MAT and WA-PLS (Fig. 2). A comparable agreement between the climate reconstructions obtained with the two methods can be observed at a more regional scale, namely the comparison between Europe and the Northern Hemisphere (Herzschuh et al., 2021). Here, the results from the MAT generally indicate more variability than the WA-PLS method, as has already been observed in other studies, because of the degree of sensitivity of the method (Birks

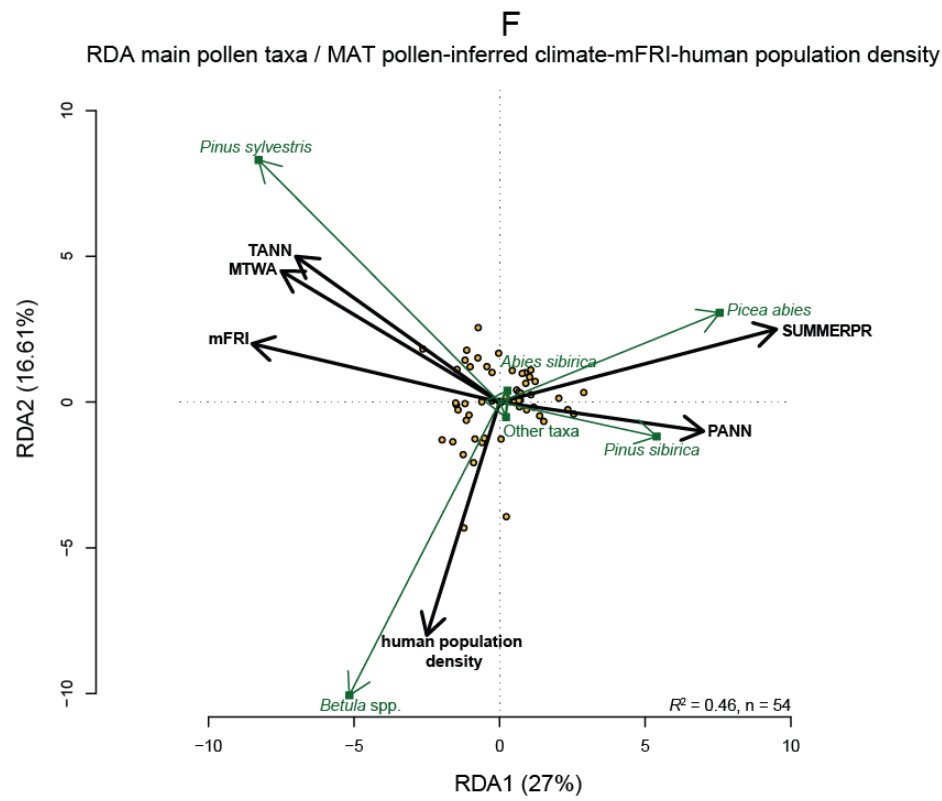
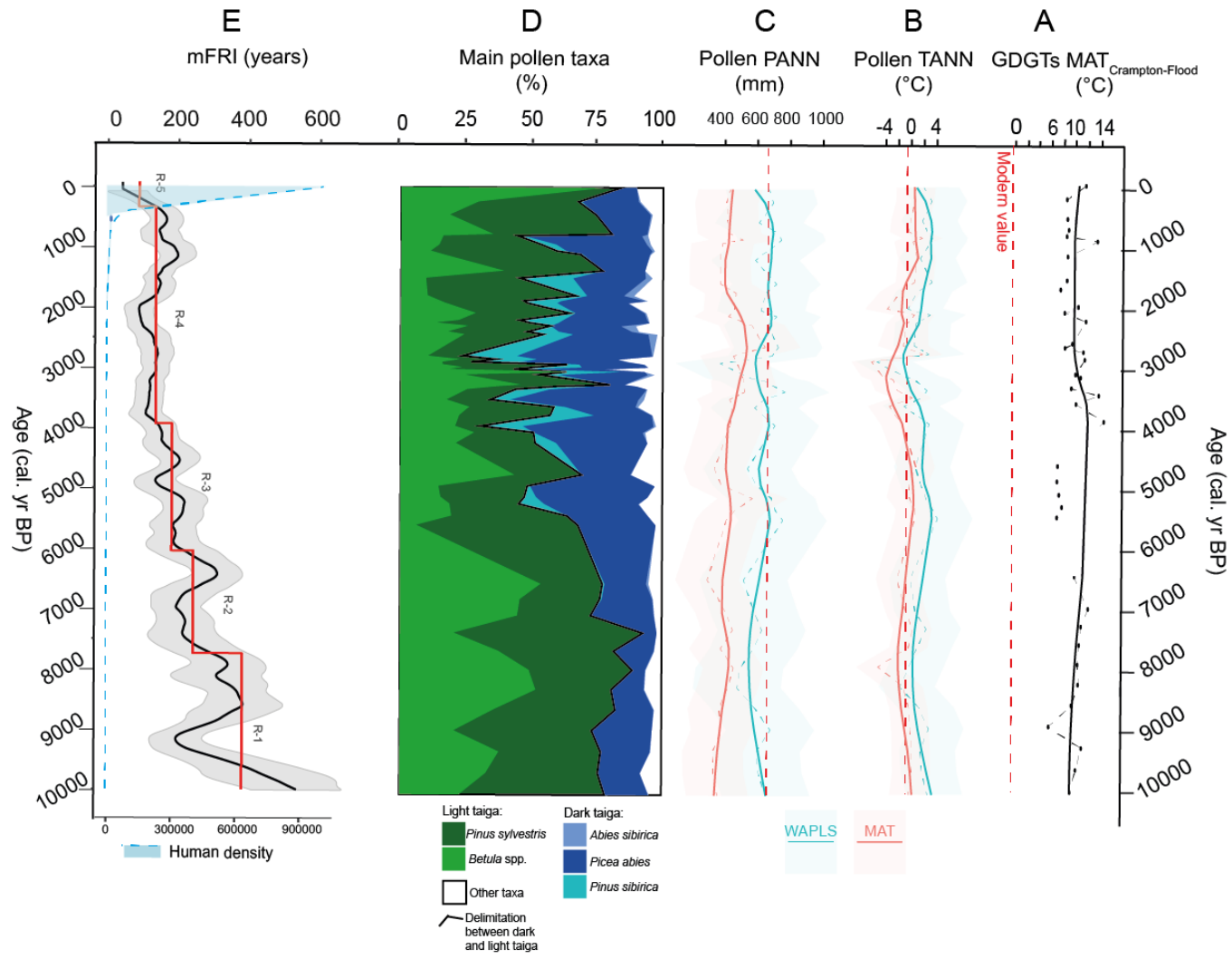
346 and Seppä, 2004; Brewer et al., 2008; Dugerdil et al., 2021; Robles et al., 2022). The MAT has been widely used to reconstruct the climate
347 changes in Europe over the Late Glacial and Holocene (Peyron et al., 2005, 2011, 2013; Mauri et al., 2015; Ponel et al., 2022) as the MAT is
348 usually more sensitive to minor variations in the pollen assemblage, compared to the WA-PLS (Brewer et al., 2008; Sinopoli et al., 2019, Hershuzh
349 et al., 2022). However, the MAT may be less reliable when the vegetation is only dominated by two or three taxa, as is the case in our study
350 (Salonen et al., 2012). This is the reason the WA-PLS has been more often used than the MAT to reconstruct Holocene temperatures in the boreal
351 regions of Scandinavia (Seppä et al., 2009; Salonen et al., 2011, 2012). The WA-PLS method is generally less efficient when the modern pollen
352 dataset is large (Chevalier et al., 2020; Dugerdil et al., 2021), but in this study the dataset was reduced to records comparable in terms of biomes,
353 which is also recommended as a method to increase the sensitivity of the MAT (Birks and Seppä, 2004). Moreover, the main disadvantage of
354 WA-PLS is that it tends to overestimate values (Birks, 1998), which is observed in the results of our study. Our results show that in the Republic
355 of Komi, the margins of error from the MAT (RSEP = 3.1 for TANN ; RSEP = 197.6 for PANN) are lower than those from the WA-PLS (RSEP
356 = 4.3 for TANN ; RSEP = 266.7 for PANN). However, both methods appear fairly reliable because they provide similar trends for the Holocene.

357

358 *4.1.4 Comparison of brGDGT- and pollen-inferred temperature reconstructions*

359 The reconstructions based on brGDGTs and pollen show different absolute values and amplitudes of variations (Fig. 5A, B). With the brGDGT
360 calibration of the temperatures, the amplitude of temperature variation is more than 7°C. In contrast with pollen records, the amplitude is around
361 4°C. However, the Holocene temperature variations comparing the two methods show more similarity. The Early Holocene begins with a slight
362 drop in pollen-inferred temperatures, till about 8000 cal. yr BP, from which time the temperature trends rise. This corresponds fairly well with
363 the brGDGT calibration MAT_{Crampton-Flood}, which shows an increase in temperatures during whole Early Holocene. The warmest period from
364 pollen-inferred temperatures is recorded between 6800 and 4000 cal. yr. BP. At 4000 cal. yr. BP., the MAT_{Crampton-Flood} calibration also shows its
365 highest temperature, thus presenting a shared identification of the HTM between the two temperature reconstruction methods (the mid-Holocene
366 part of the brGDGT temperature calibrations being put to one side and not compared with pollen-inferred temperatures). Thereafter, trends for
367 both signals are similar, since a synchronous decrease in temperatures is indicated after 4000 cal. yr BP, followed by a net increase from 3000
368 cal. yr BP for the pollen signal and from 2000 cal. yr BP for the brGDGT calibration.

369



371 *Figure 5: Yaksha local dynamics. A: brGDGT-inferred temperatures $MAT_{Crampton-Flood}$, after Dearing Crampton-Flood et al. (2020). B: Pollen-*
372 *inferred mean annual temperatures TANN. C: Pollen-inferred mean annual precipitation MAP. D: Main pollen taxa cumulative diagram. E:*
373 *Mean Fire Return Interval and human population density in the Republic of Komi (mFRI, Barhoumi et al., 2019, 2020). F: RDA for Yaksha main*
374 *pollen taxa, MAT reconstructed climate (TANN, PANN, MTWA, SUMMERPR); fire activity (mFRI) and human activity (human population*
375 *density).*

376

377 *4.2 Yaksha local dynamics: interactions between climate, vegetation, fire and human presence*

378 *4.2.1 From 10,000 to 4000 cal. yr BP: a first half of the Holocene mainly influenced by climate*

379 To evaluate the background for fire dynamics, a Pearson correlation test was carried out between modern annual temperatures (from 2010 to
380 2018), for the studied sites, and the mean temperatures of the warmest months, (June, July, August) , corresponding to the fire season, as well as
381 correlation with mean temperatures of the months above 0°C (Tabatabai et al., 2021). The Pearson's correlation indicates that modern mean annual
382 temperatures are positively correlated with mean modern summer temperatures (correlation of 0.45) and mean modern temperatures of months
383 above 0°C (correlation of 0.48). It is therefore assumed that past annual mean temperatures, reconstructed from pollen and brGDGTs were also
384 positively correlated with past mean summer temperatures and past mean temperatures of months above 0°C.

385 Temperatures close to the modern ones are reconstructed from 10,000 to 9000 cal. yr BP (Fig. 5B) with vegetation mainly representative of the
386 light taiga type, with the taxa *Pinus sylvestris* and *Betula* spp. being dominant (75 %, Fig. 5D). These results are consistent with those for the
387 modern period.

388 Even though the light taiga remained in the main forest system up to 5500 cal. yr BP, the warming occurring since 8000 and including the HTM,
389 which lasted until 4000 cal. yr BP, is associated with an increase of dark taiga taxa (increase in *Picea abies* and appearance of *Pinus sibirica*).
390 These two taxa seem to be influenced by the increase in the mean annual and summer precipitation, as shown by the RDA (Fig. 5F), which occurs
391 at the same time. The increase in dark taiga taxa is consistent with the recognised characteristics of this taiga system, which is favored by
392 precipitation (Goldammer and Furyaev, 1996; Golubeva, 2008; Schulze et al., 2005). The increase could also demonstrate the substantial influence
393 of climate on vegetation dynamics during this period. Moreover, between 10,000 and 6000 cal. yr BP, the mean Fire Return Interval (mFRI)
394 based on charcoal analysis (Barhoumi et al., 2019) is high (median mFRI greater than 200 years, Fig. 5E), which would be indicative of a boreal
395 forest with larger occurrence of the dark taiga type in the earlier part of the Holocene, because the dark taiga is usually associated with low fire
396 frequency (de Groot et al., 2013; Goldammer and Furyaev, 1996; Sannikov and Goldammer, 1996). Since the human presence and its impact on

397 the environment is negligible in the first half of the Holocene (between 10,000 and 5000 cal. yr BP; Drobyshev *et al.*, 2004; Karmanov *et al.*,
398 2011; Klein Goldewijk *et al.*, 2011), the climate appears to have been the main factor influencing the vegetation in Yaksha. This is consistent
399 with the conclusions of a previous study based on pollen analysis and vegetation cover modeled by REVEALS, over the period from 10,000 to
400 6000 cal. yr BP (Barhoumi *et al.* (2020).

401

402

4.2.2 From 4000 to 600: an increasing impact of fires

403 The period between 4000 and 2500 cal. yr BP corresponds to a significant decrease in temperature (Fig. 5A, B). The percentage ratio between
404 dark taiga and light taiga shows great variability and seems to demonstrate the establishment of a boreal forest consisting of dark and light taiga
405 mosaic patches, equally distributed, supported by high precipitation favouring dark taiga. However, this period coincides with the crossing of a
406 threshold in the fire regime of Yaksha: the mFRI goes from 180 years (Fig 5E, phase R-3) to 135 years (phase R-4) from 4000 cal. yr BP up to
407 600 cal. yr BP. An mFRI value of *circa* 200 years corresponds to a fire frequency still tolerable by the representative taxa of the dark taiga
408 (Goldammer and Furyaev, 1996; Sannikov and Goldammer, 1996). But from 4000 cal. yr BP, the mFRI value is well below this threshold and
409 should no longer allow dark taiga to develop (Goldammer and Furyaev, 1996; Schulze et al., 2005). A higher fire frequency would benefit the
410 maintenance of a light taiga system, while high precipitation would maintain the presence of dark taiga taxa such as *Picea abies*. The contrasting
411 influences of the climate and the fire regimes could explain the maintenance of a forest composed of a mosaic of patches of dark and light taiga
412 The gradual return to a light taiga dominance between 2500 and 600 cal. yr BP therefore seems favored by the increase of temperatures, but also
413 by the establishment of the lower mFRI, since this type of forest is made up of fire-tolerant species well adapted to high fire frequency (see RDA,
414 *Pinus sylvestris* correlated with mean temperatures and mFRI), (Goldammer and Furyaev, 1996; Schulze et al., 2005). Fire frequency could be
415 the cause of the decline of *Abies sibirica* and *Pinus sibirica*, which are not resistant to frequent fire events and whose seed production and life
416 cycle may need a longer time than the time interval available between two fire events during this phase (Goldammer and Furyaev, 1996; Sannikov
417 and Goldammer, 1996; Schulze et al., 2005). The dominant presence of light taiga over dark taiga from 2500 cal. yr BP, does not prevent *Picea*
418 *abies* remaining well established. Barhoumi *et al.*, (2020) suggested that this may be due to the local establishment of *Picea abies* tree stands,
419 growing along small streams and moist soils and with precipitation staying high between 3000 and 2000 cal. yr BP (Zaretskaya et al., 2014). As
420 these systems are also present in light taiga, it is surprising to note that *Picea abies* does not suffer drastically from the drop in mFRI to below
421 200 years. In theory, *Picea abies* cannot develop if surface fires reach its critical regeneration time range (about 200 years after a fire event)

422 (Goldammer and Furyaev, 1996; Schulze et al., 2005). We therefore suggest that these surface fires were not able to reach the peat wetlands on
423 which *Picea abies* grew. That interpretation was highlighted by the first study on the dynamics of fires of the Yaksha site by Barhoumi *et al.*
424 (2019). This study highlights that most of the recent fires revealed by the analysis of fire scars on trees at the Yaksha site, have affected the
425 vegetation in a very localized way, while others have affected the site Yaksha as a whole. This demonstrates that the surface fires at the Yaksha
426 site could have been mostly local, and so were not able to reach the populations of *Picea abies*, because of their location on highly moist soils.

427

428 *4.2.3 From 600 to modern times: the combined influence of human activity and climate?*

429 The period between 600 and 0 cal. yr BP shows slightly increasing temperature values to levels similar to those of the Early Holocene, and stable
430 precipitation (Fig. 5A). The light taiga is well established and *Betula spp.* is dominant (Fig. 5D). *Betula* is a pioneer species in a disturbed
431 environment and is also a sign of the opening of the boreal forest in this zone (Goldammer and Furyaev, 1996). The strong presence of *Betula*
432 *spp.* during this phase is strongly associated with human population density in the RDA (Fig. 5F) and could be a sign of a human influence on the
433 vegetation. In the Republic of Komi in particular, logging is now a highly developed activity and its production represents a major economic
434 resource for this region (Naryshkin, 2003). The mFRI is at its lowest value within the Holocene interval (less than 100 years, phase R-5, Fig. 5E).
435 This time frame corresponds to the highest density of the human population in the Republic of Komi and its increasing activity and impact on its
436 environment (Drobyshev et al., 2004b; Klein Goldewijk et al., 2011; Naryshkin, 2003). It therefore seems that fire events could have been induced
437 by human activity and that the generally high fire activity of this period could be related to both anthropogenic influences and a more favorable
438 climate (Drobyshev et al., 2004b; Naryshkin, 2003). However, a recent study has nuanced the impact of human presence during this period.
439 Different waves of human colonization during this period were indeed indicated, but were not synchronous with the changes in the fire cycles
440 reconstructed by dendrochronological analyses (Ryzhkova et al., 2022). These authors deduced that the climate was the main factor in the
441 dynamics of the forest and that the human impact on fire activity was more pronounced after the 1900s. This is also consistent with the increase
442 in temperature reconstructed by brGDGTs, which started from 1800 cal. yr BP but intensified from about 700 cal. yr BP (Fig. 5A).

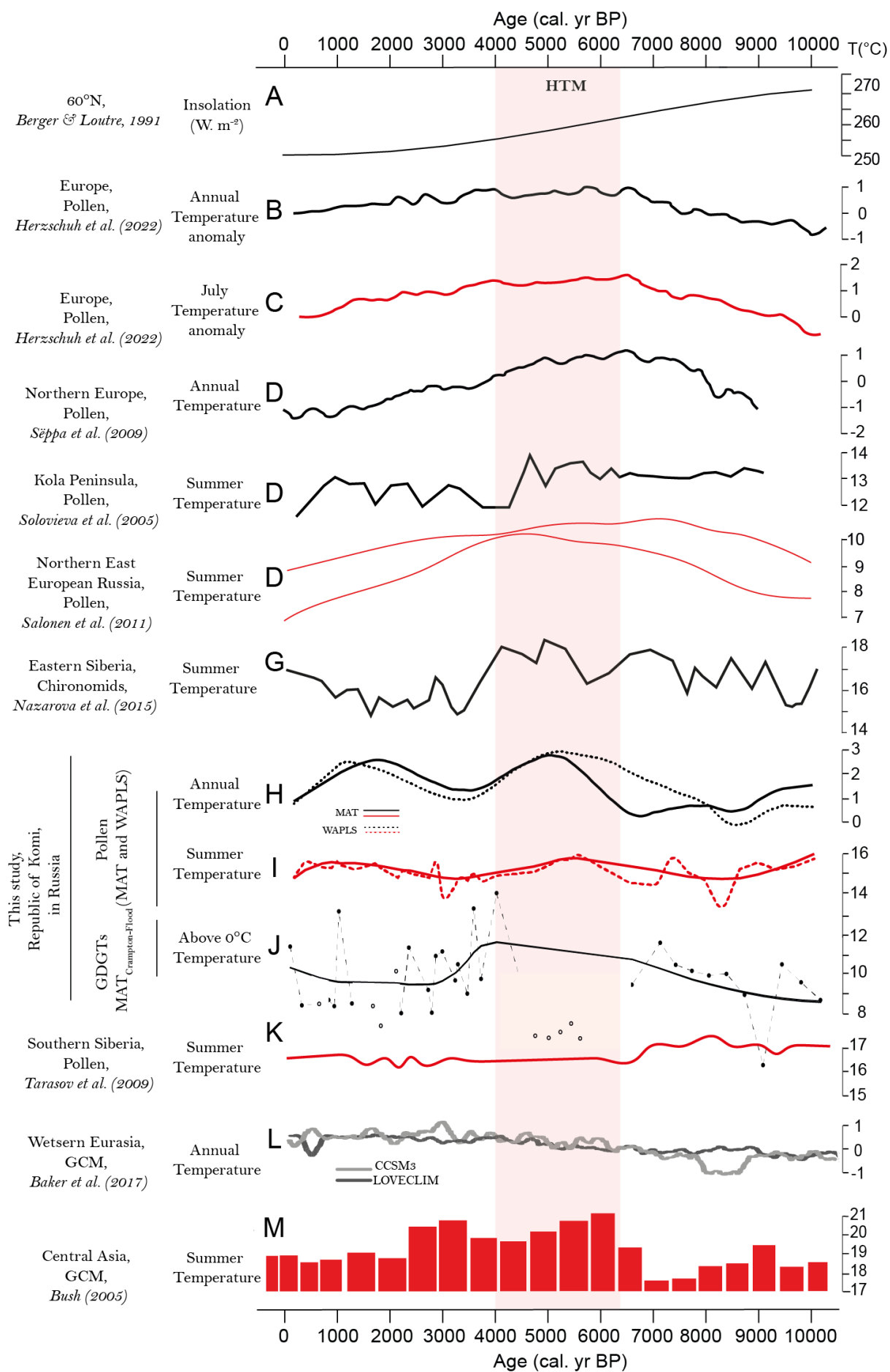
443

444 *4.3 Regional climate pattern in the South of the Republic of Komi*

445 *4.3.1 From 10,000 to 8000 cal. yr BP, a cold Early Holocene*

446 Although AO/NAO dynamics influence the climate of Republic of Komi region (*Raspopov et al., 2013*), climate records from the region can be
447 different from those recorded, for example, in Siberia because the Republic of Komi is located in a boundary zone, at the limit between the regions
448 positively or negatively influenced by atmospheric processes and solar irradiation (*Raspopov et al., 2013*). The regional climate signal in the
449 South of the Republic of Komi indicates a cooling and drying in the Early Holocene (Fig. 6H, 6I and 8A). This is in agreement with (1) the
450 brGDGT temperature calibration being the coldest of the records at the Yaksha site (Fig. 6J), (2) reconstructions of mean annual temperatures in
451 Eastern-central European Russia (from +1 to -1°C, Fig. 6E, Novenko and Olchev, 2015), summer temperatures in Eastern Siberia inferred from
452 chironomids (from +17 to +14°C, Fig. 6G, Nazarova *et al.*, 2015), (3) climate model simulations and mean temperature anomalies of Europe,
453 inferred from pollen (WA-PLS), showing the lowest temperatures of the Holocene during this time (between -1 to 0°C anomaly for annual
454 temperatures, Fig. 6B, C, Herzschuh *et al.*, 2022) The GCM outputs also simulate a drop in summer temperatures for Central Asia with a loss of
455 about 0.5°C, Fig. 6M, (Bush, 2005). However, in North Eastern European Russia, a rise in summer temperatures is reconstructed from pollen
456 data (+1°C approximately, Fig. 6D, Salonen *et al.*, 2011). The South of the Republic of Komi, therefore, seems to have undergone climatic
457 influences similar to those occurring in Western Russia and in Siberia.

458

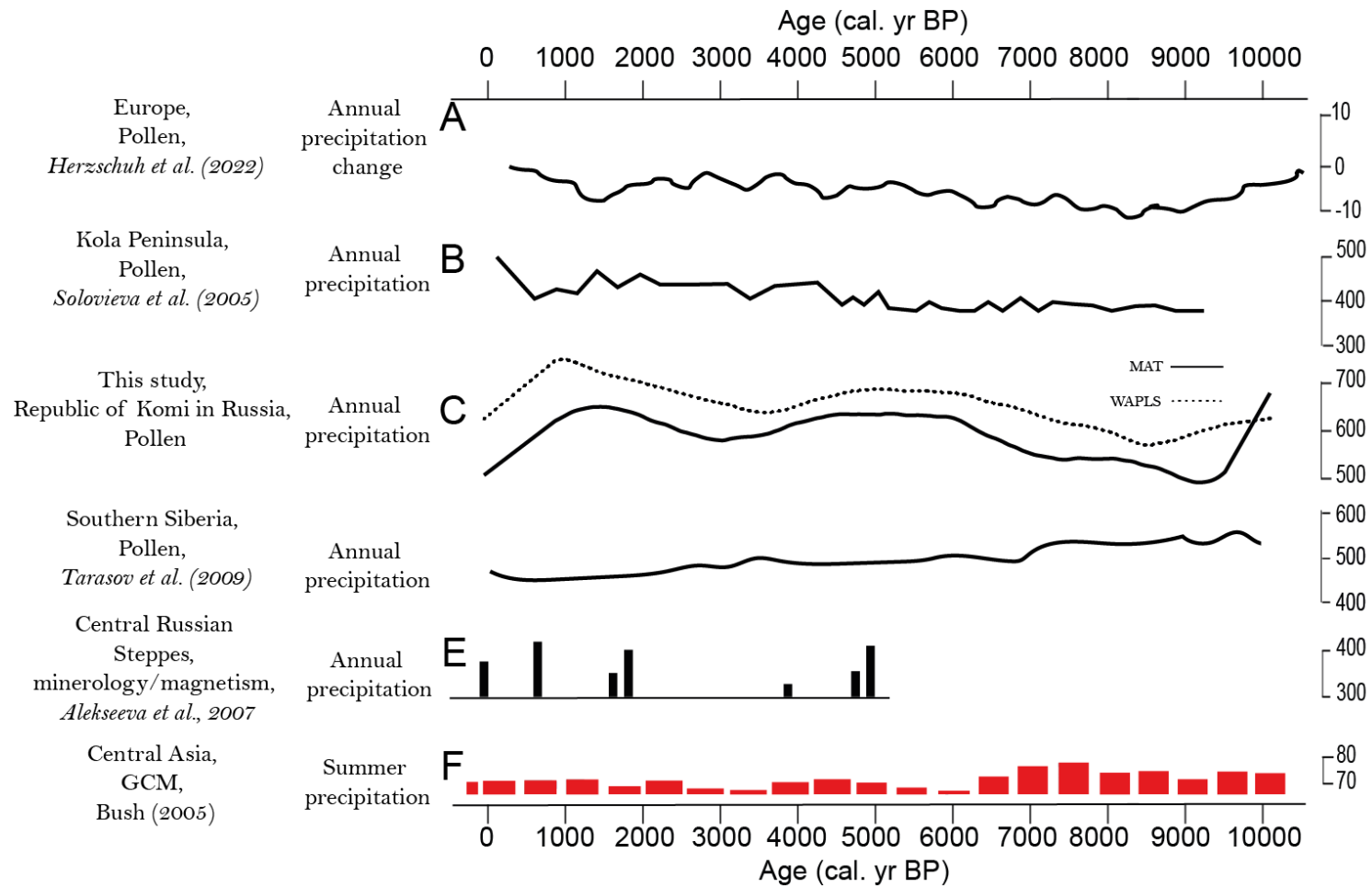


460 *Figure 6: Synthesis of Holocene temperature reconstructions in the Republic of Komi and neighboring regions, based on pollen, GDGTs,*
461 *chironomids and GCM outputs. Mean annual and summer temperatures are represented in black and in red, respectively. Location of the sites*
462 *are represented in Fig. 1. Insolation at 60°N after Berger and Loutre (1991). The red rectangle indicates the HTM period.*

463

464 4.3.2 Timing of the HTM

465 In the Republic of Komi, pollen results suggest the occurrence of the HTM between 6800 and 4000 cal. yr BP (this time frame includes the high
466 mean annual temperature values for both MAT and WA-PLS methods, Fig. 6H). This finding is consistent with the brGDGT MAT_{Crampton-Flood}
467 calibration, recording its warmest temperature value at 4000 cal. yr BP (Fig. 6J). The increase in annual temperatures in the Republic of Komi is
468 also associated with an increase in precipitation (Fig. 7B). This HTM time window is consistent with but broader than the one suggested by
469 Golubeva (2008), with the same pollen data set (except Yaksha site) but using other methods of temperature reconstruction (Klimanov, 1976).
470 This time-range for the HTM reconstructed with MAT/WA-PLS techniques is consistent with that reconstructed by Herzschuh *et al.* (2022),
471 showing a pollen-inferred (WA-PLS method) HTM at 5600 cal. yr BP for Europe annual temperatures. This time range is also consistent with
472 the Russian Arctic region and Kola Peninsula pollen-based temperature reconstructions (Fig. 6K; Tarasov *et al.*, 1999; Andreev and Klimanov,
473 2000; Solovieva, Tarasov and MacDonald, 2005), in the North of the Republic of Komi. The Russian Arctic HTM was explained because the
474 Arctic Ocean coast was about 100 to 300 km further North at this time than it is today, which contributed to a warmer and more continental
475 climate (Andreev and Klimanov, 2000; Baranskaya *et al.*, 2018). Studies from the west of the Republic of Komi, in Siberia and in Central Yakutia
476 also show an climatic optimum included in this interval (Biskaborn *et al.*, 2016; Blyakharchuk and Sulerzhitsky, 1999; Nazarova *et al.*, 2015b;
477 Subetto *et al.*, 2017; Ulrich *et al.*, 2017). Moreover, from 10,000 cal. yr BP until 4000 cal. yr BP, climate was the most moist of the Holocene
478 (Blyakharchuk and Sulerzhitsky, 1999; Tarasov *et al.*, 2009, 1999), which partially corresponds with the precipitation records from the Republic
479 of Komi (since it was low between 10,000 and 8500 cal. yr BP, and high between 6500 and 4000 cal. yr BP). The climate became moist again
480 between 3000 and 600 cal. yr BP. This time frame corresponds well with the annual precipitation reconstruction from Herzschuh *et al.* (2022),
481 suggesting that the Holocene increase in precipitation could be due to enhanced cyclonic activity. The HTM in the Republic of Komi is not as
482 long as in Northern Europe and Fennoscandia, where it began as early as 8000 cal. yr BP (Fig. 6B and 7D; Seppä *et al.*, 2009; Salonen *et al.*,
483 2011). Another extended HTM was observed by Kultti *et al.* (2003), still closer to Republic of Komi, between 9000 to 5200 cal. yr BP. Some of
484 the sites in the Kultti study were located at high altitudes in the Urals. The altitude may have had an impact on the different climatic influences
485 affecting the area from Arctic Russia to the Vychegda river basin in Republic of Komi. Many studies highlight the role of increased insolation in
486 global warming during the HTM (Bartlein *et al.*, 2011; Kultti *et al.*, 2003; Mayewski *et al.*, 2004; Wohlfarth *et al.*, 2007).



487

488 *Figure 7: Synthesis of Holocene precipitation reconstructions in the Republic of Komi and neighboring regions, based on pollen,*
 489 *minerology/magnetism and GCM outputs. Annual sum of precipitation is represented in black and the summer sum of temperatures, in red.*
 490 *Location of the sites are represented in Fig. 1*

491

492 Atmospheric processes could also explain this HTM period: a strong Westerly circulation, with a strong AO/NAO positive phase in winter (which
 493 would have generated warm and moist climates in Northern Europe) and a weaker AO/NAO positive phase in summer (warm and dry climate)
 494 (Mauri et al., 2015). Salonen *et al.* (2011) have also discussed the observed lags in HTM from Fennoscandia to the Ural region. Their assumptions
 495 are (1) there is a geographical timing gradient of the HTM; (2) some reconstructions may be wrong due to biases in the temperature inference
 496 methods used; (3) the different proxies for calculating temperatures may have non-synchronous responses to warming and (4) the complex history
 497 of tree lines in Russia may add uncertainties regarding pollen-based reconstructions.

498

500 A fluctuating and colder phase is marked in the Republic of Komi between 4000 and 2500 cal. yr BP. This cooling seems to have been also
501 registered in Siberia by chironomids (summer temperatures) (Nazarova et al., 2015b) and in Arctic Russia (Andreev and Klimanov, 2000). In
502 Northern Europe, a large period of continuous and gradual cooling has extended since the end of the HTM, around 4000 cal. yr BP, up to 1000
503 cal. yr BP, and has been largely explained by the influence of the decrease in summer insolation (Fig. 6D; Salonen *et al.*, 2011).

504 According to Seppä *et al.*, (2009), the Medieval Warm Period (MWP, 1550-650 cal. yr BP (Camill et al., 2009)) is not a distinct temperature peak
505 in Northern Europe, but “represents the final centuries of a longer warm period before the onset of cooling”. Pollen signals from the Republic of
506 Komi clearly indicate a period of warming between 2000 and 900 cal. yr BP. This signal is also registered by pollen assemblages from the Kola
507 Peninsula, which is located in the Northern part of European Russia (Solovieva et al., 2005) and a general slight increase in summer temperatures
508 has been simulated for Central Asia (Bush, 2005). This period coincides with the wettest recorded in the Republic of Komi, the Kola Peninsula
509 and the Central steppes of Russia, based on pollen grains and magnetism/minerological analysis (Fig. 7B, A and E; Solovieva, Tarasov and
510 MacDonald, 2005; Alekseeva *et al.*, 2007).

511 The subsequent short and rapid decrease in temperatures in the Republic of Komi from 500 cal. yr BP (WA-PLS), may correspond to the Little
512 Ice Age (LIA, 650-150 cal. yr BP (Camill et al., 2009)) . This cooling was also noted in records from Northern Europe by Seppä *et al.* (2009)
513 until ca. 400 cal. yr BP, in West-central Eurasia by the LOVECLIM model (Baker *et al.*, 2017), in Northern East European Russia by Salonen *et*
514 *al.* (2011), and in the Kola Peninsula (Solovieva et al., 2005). However, the resolution of our records is too low to corroborate (or to refute) these
515 results, but there are consistent with these observations.

516 At the end of the 19th century, a global warming trend was recorded by tree-rings in the Northern Urals (Moiseev et al., 2010) (Moiseev *et al.*,
517 2010) but in the Republic of Komi, the results do not show any general warming trend during this period, except for the sites Yaksha (MAT) and
518 Kalya. The brGDGT calibrations also showed also an increase in temperature over this interval.

519

520 5. Conclusions and remarks on the Republic of Komi boreal forest

521 This study presents (1) the first Holocene temperature reconstruction at a regional scale of the southern part of the Republic of Komi, based on
522 the study of pollen- transfer functions based on six different sites. (2) the first study of the local dynamics in Yaksha, between climate (based on
523 pollen-transfer functions and brGDGT temperature calibrations), fire, vegetation and human activities.

524 Regional climate reconstructions for the Republic of Komi show an increase in precipitation and a mid-Holocene HTM between 6800 and 4000
525 cal. yr BP which is in line with neighboring regions in Northern Europe, and also with Siberia, through the analysis of different proxies and
526 analytical methods (pollen, chironomids, model outputs).

527 At the local scale of Yaksha, the temperature reconstructions based on pollen assemblages and brGDGTs show common warmest temperature
528 phases around 4000 cal. yr BP. Further studies of cold environments are needed to improve the calibrations for brGDGTs, in particular for the
529 Holocene, where factors others than temperature influence the composition of brGDGT communities.

530 Finally, our study showed that climate had a major influence on the vegetation and dynamics of the boreal forest in Yaksha. Fires had an additional
531 and growing impact on vegetation dynamics between 4000 and 600 cal. yr BP. Finally, from 600 BP to the present day, both climate and increasing
532 human impacts have influenced the dynamics of the boreal forest in this region. In modern times, the fire regime induced by anthropogenic
533 activities corresponds to an overexploitation of the forest, whose coniferous species have rapidly declined in favor of a pioneer deciduous species
534 (the explosion of *Betula spp.* from 600 to the modern age is demonstrates this effect (Naryshkin, 2003; Sannikov and Goldammer, 1996). It is
535 likely that the wetter dark taiga growing on organic soils has been weakened by this fire regime. This can then lead to a reversal of the balance in
536 the carbon cycle, which could lead to massive releases into the atmosphere. This observation was made by Naryshkin, (2003) and Walker *et al.*
537 (2019): not only do these forests no longer play the role of carbon sinks as they have done in the past, but they are gradually becoming sources
538 of atmospheric carbon. With global warming, the temperature and dryness conditions of the environment may increase even more, and induce a
539 greater dryness of the soil, allowing the spread of fires even on previously more moist areas and therefore affect tree populations which were not
540 previously vulnerable. This was the case for example in the years 1972, 1974, 1977, 1982, 1987, 1998 in Siberia and in more recent years in
541 Siberia and in the Ural region (Goldammer et al., 2005; Goldammer and Furyaev, 1996). Managing the structure of forest stands by establishing
542 species more adapted to the new local climatic conditions may help to reverse the impact on the increase in fire activity that is evident today.

543

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557

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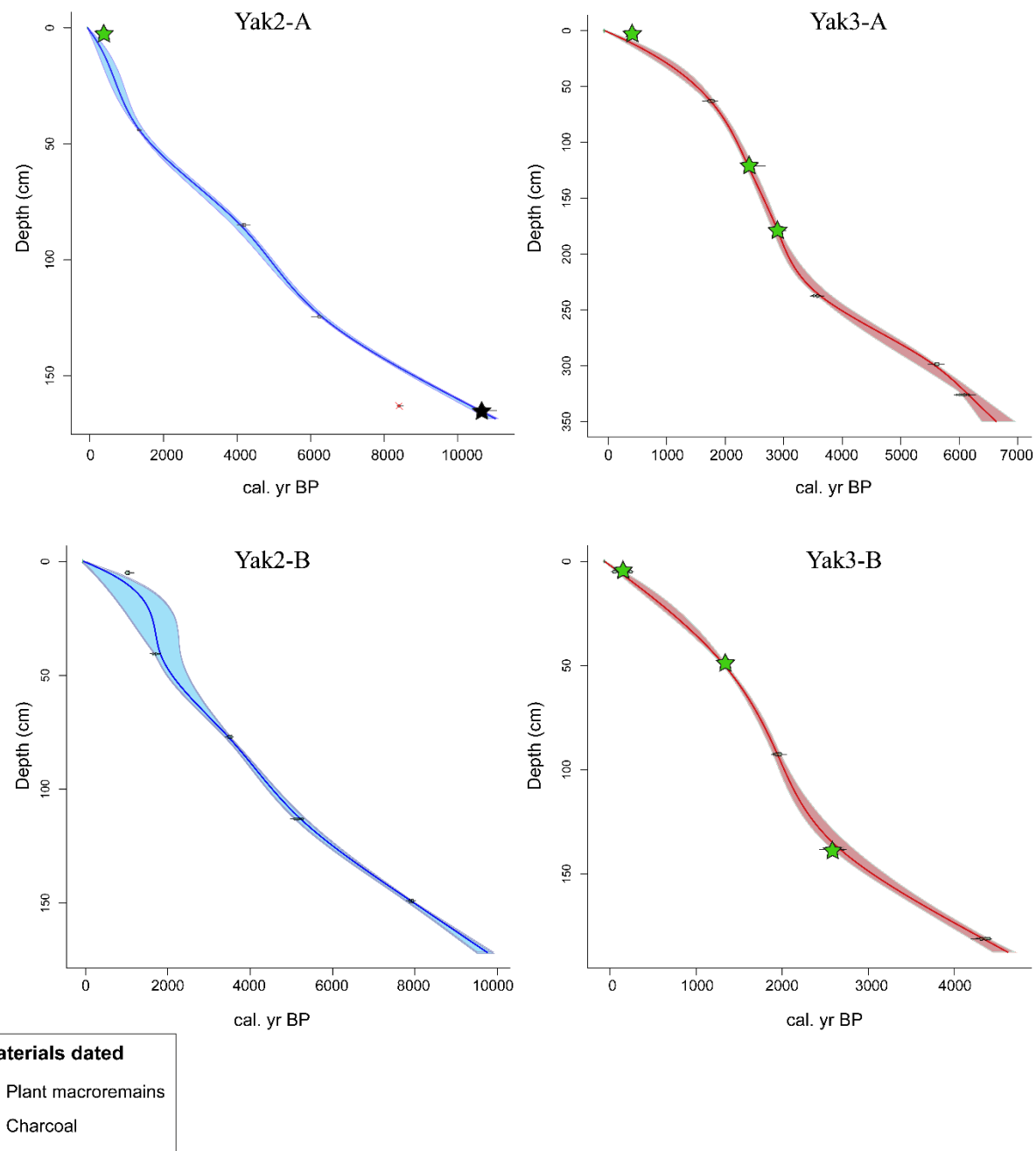
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913 **8. Supplementary Information**



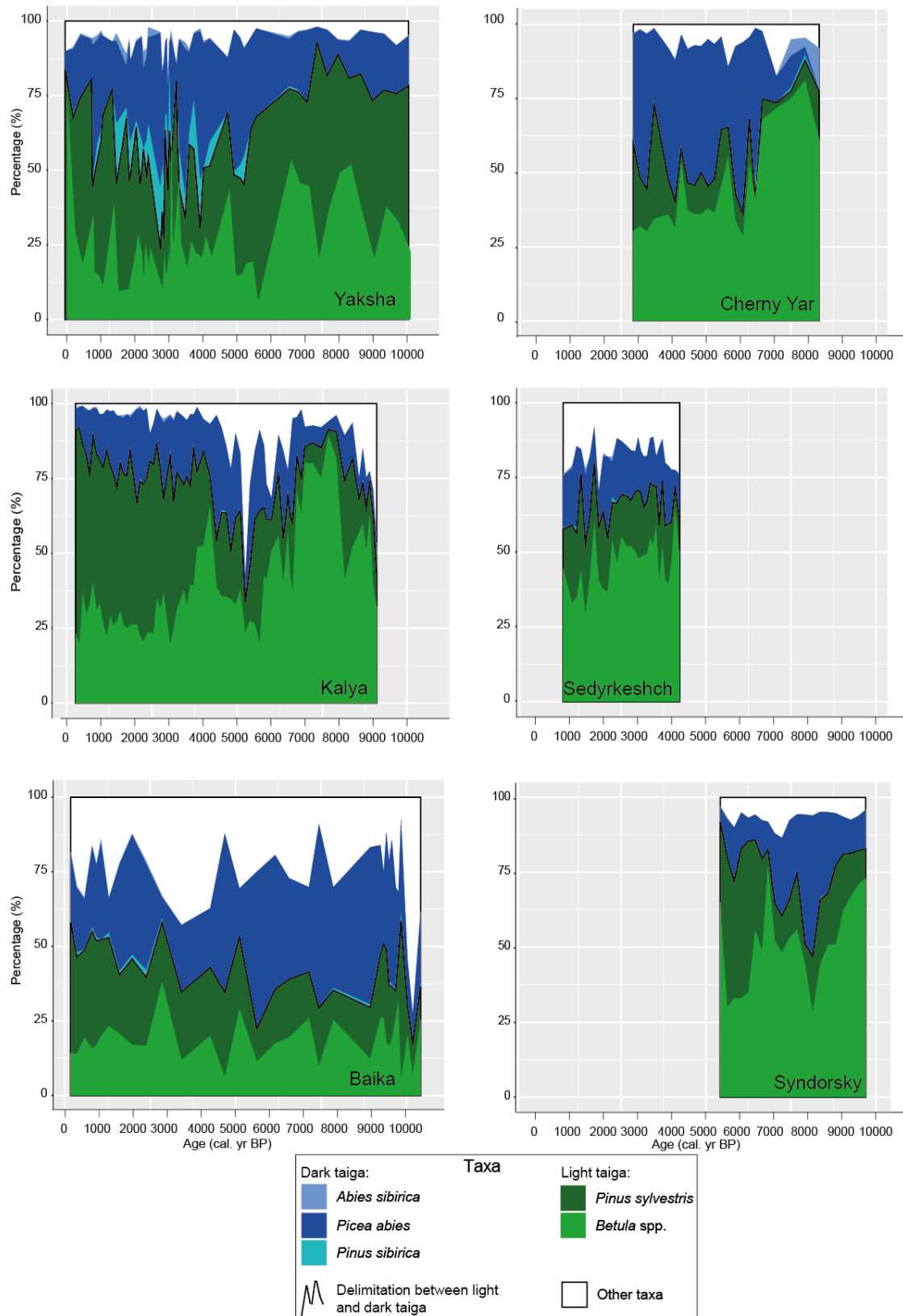
914

915 *SI 1: From Barhoumi et al. (2019): Age-depth model based on radiocarbon ages (see Table 2) from Yak2-A, Yak2-B, Yak3-A and Yak3-B cores.*
 916 *The materials dated by 14C are bulk (single black lines), plant macroremains (green stars), macrocharcoal (black star).*

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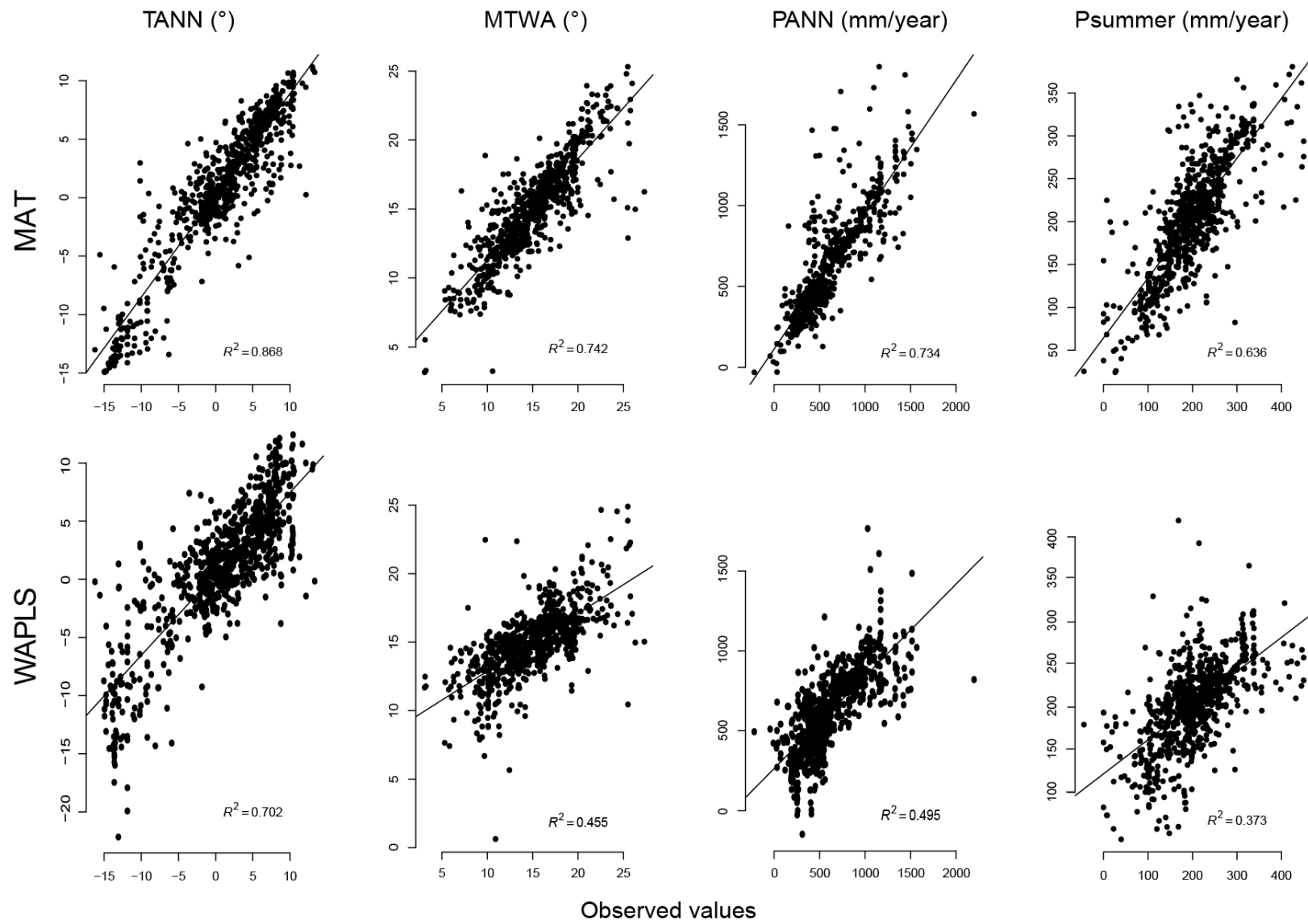


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921 *SI 2: Cumulative pollen percentage diagram of principal taxa for each site: Yaksha, Baika, Kalya, Cherny Yar, Sedyrkeshch and Syndorsky.*

922 *The main taxa shown are Betula spp. and Pinus sylvestris for the light taiga and Pinus sibirica, Picea abies and Abies sibirica for the dark taiga.*

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924

925 *SI 3: Correlations between the reconstructed values from the pollen transfer functions and the observed values of the randomly selected 40% of*
 926 *the database*

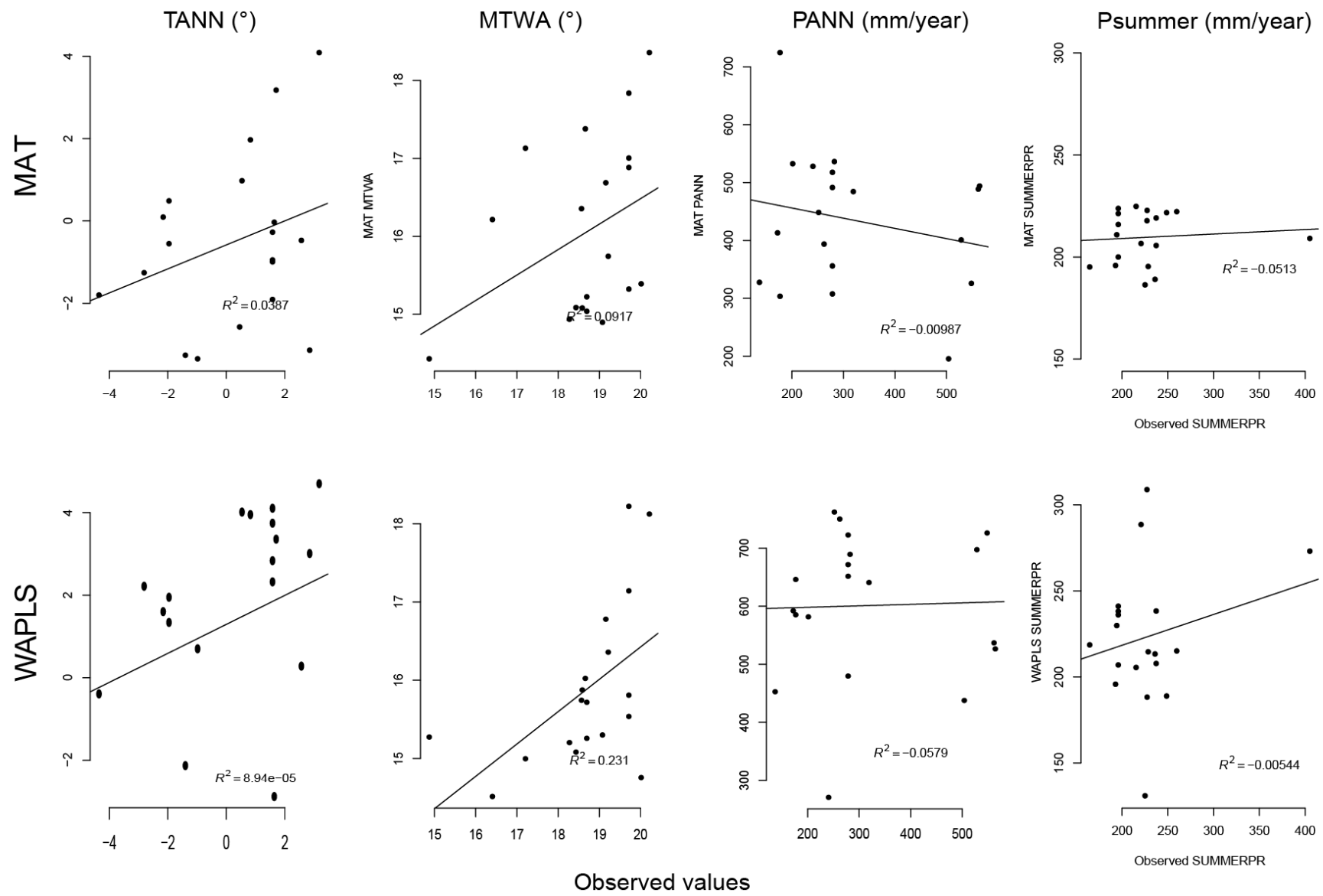
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933 *SI 4: Correlations between the reconstructed values from the pollen transfer functions and the observed values of the 19 samples situated between*
 934 *40-50°N, 40-50°E of the database*

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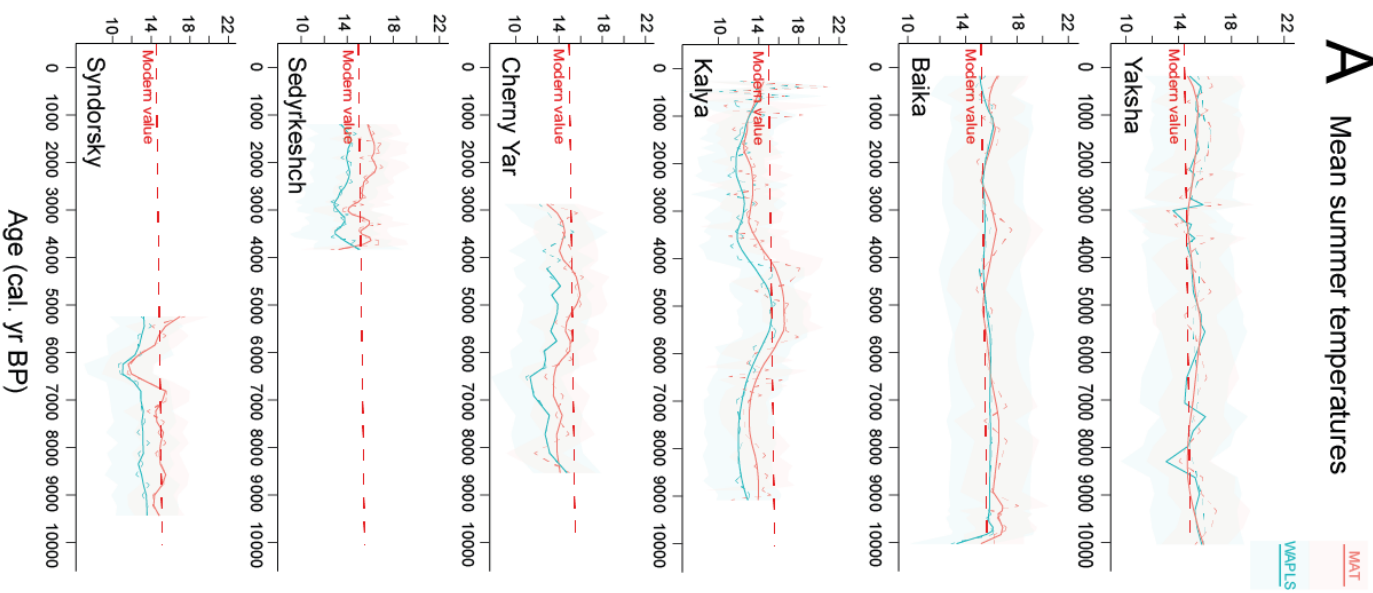
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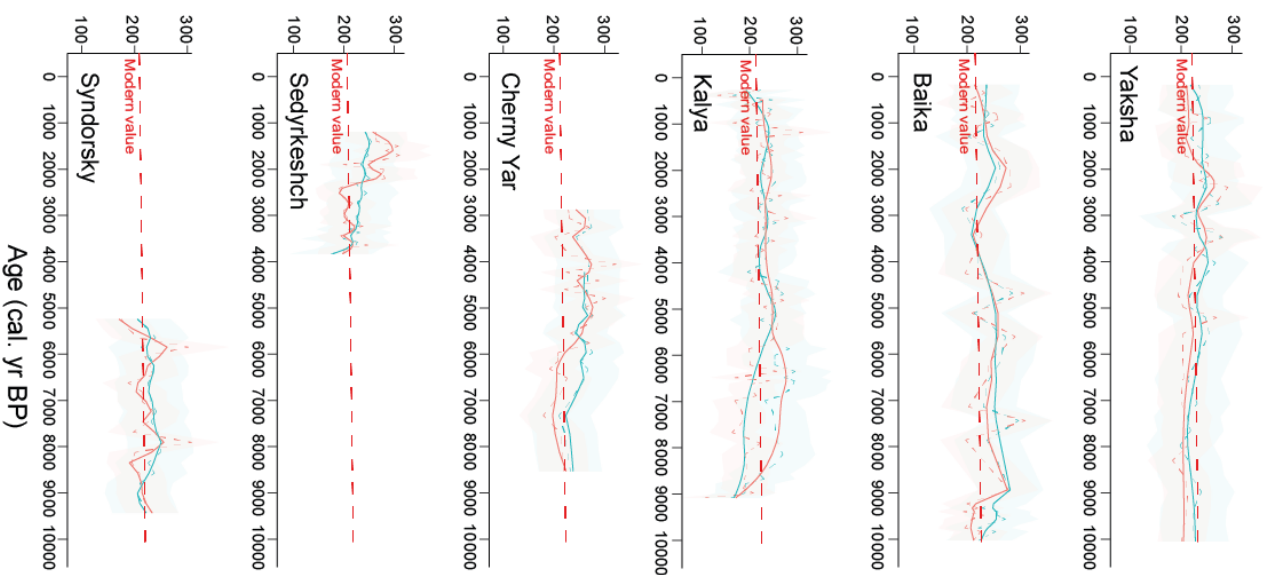
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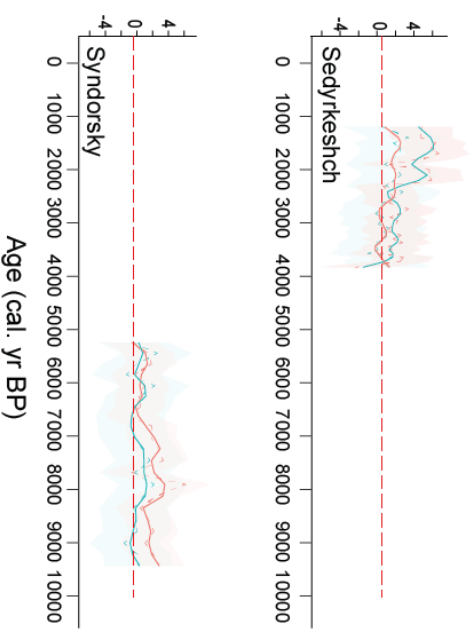
A Mean summer temperatures



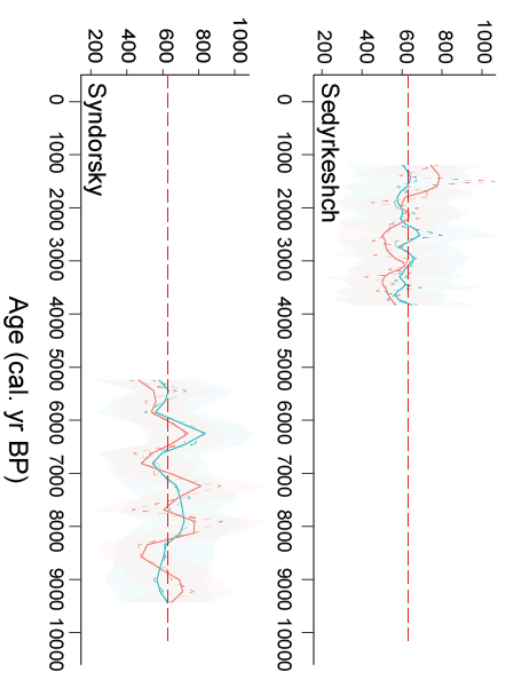
B Summer precipitation



C Mean annual temperatures



D Mean annual precipitation

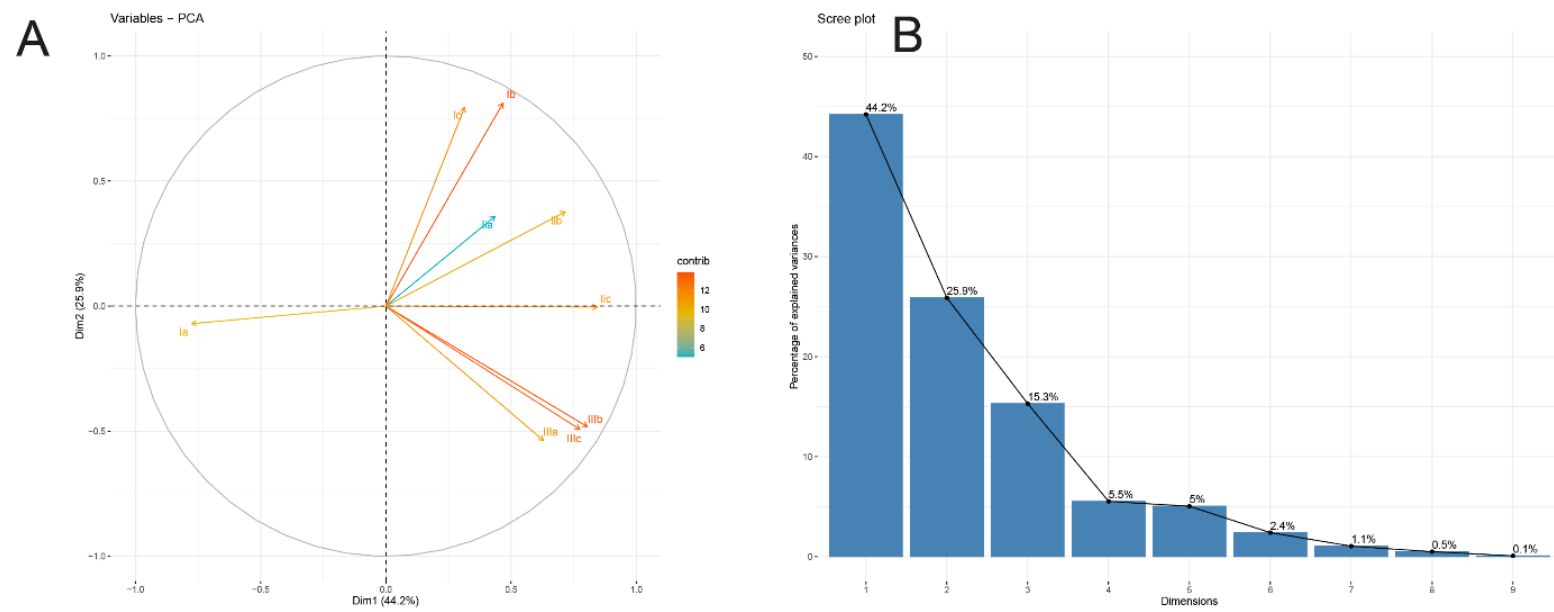


941 *SI 5: Regional climatic synthesis of the Republic of Komi of pollen-based climatic reconstructions. Mean summer temperature (A), summer*
 942 *precipitation (B) and mean annual temperatures and precipitations (C and D) were calculated using the modern analogue technique (MAT)*
 943 *and the weighted average partial Least squares regression (WA-PLS) and smoothed using Loess (span = 0.3, solid lines). Shaded areas are*
 944 *confidence intervals. Red dashed lines are modern values for each site.*

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948 *SI 6: A: Yaksha brGDGTs PCA (axis 1 and axis 2). B: Yaksha brGDGTs PCA percentage of explained variances for each axis.*

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