

1 **Holocene-scale fire dynamics of central European temperate spruce-beech forests**

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24 **Abstract**

25 This study investigated the long-term role and drivers of fire in the central European temperate
26 spruce-beech forests from Prášílské jezero, Czech Republic. The results illustrate the complex
27 relationship between broad-scale climate, vegetation composition, and local human activities on
28 fire throughout the Holocene. Biomass burning was the highest (average 3 fires/1000 years) and
29 most severe during the early Holocene when fire resistant taxa (*Pinus*, *Corylus* and *Betula*)
30 dominated. Using a Generalized Additive Model to assess the response of dominant canopy taxa
31 to changes in biomass burning and fire severity, response curves demonstrate a positive
32 relationship ($p < 0.01$) between fire resistant taxa and increases in biomass burning. Norway
33 spruce (*Picea abies*) established ~10,000 cal yr BP and expanded during peak biomass burning.
34 Response curves show a slight negative relationship with *Picea* and increasing biomass burning,
35 and a positive relationship with increasing fire severity. This suggests that central European
36 spruce forests may not be significantly impacted by fire. Regional biomass burning dramatically
37 decreased with the expansion of fire sensitive taxa (e.g. *Fagus sylvatica*) ~6500 cal yr BP, yet no
38 dramatic reduction in local fire frequency occurred. This suggests either human activities or rare
39 fire-promoting climatic events were important in shaping local fire regimes. Fire activity peaked
40 (6 fires/1000 years) ~2500 cal yr BP and paralleled increases in anthropogenic pollen indicators.
41 *Fagus* response curves illustrates a negative ($p < 0.01$) relationship with increasing biomass
42 burning and fire severity suggesting that natural *Fagus* forests may be increasingly vulnerable to
43 projected increases in wildfire occurrence.

44

45 **Keywords**

46 Climate; Fire; Holocene; Macrofossils; Paleoecology; Pollen; Sedimentary charcoal;

47

48 **Highlights**

- 49 • First high-resolution fire-history record to discuss fire frequency from natural spruce-
50 beech temperate forests in the Šumava Mountains, central Europe
- 51 • Fire has been an important disturbance agent in central Europe for the past 10,000 years
- 52 • Climate and vegetation were the primary drivers of fire in the early Holocene
- 53 • Humans activities were likely secondary drivers of fire throughout the Holocene
- 54 • Beech may be one of the most vulnerable species to projected increases in temperatures,
55 heat stress, and risk of wildfires in central Europe.

56

57 **1. Introduction**

58 Fire is an important disturbance agent driving changes in vegetation composition, ecosystem
59 structure and function, and nutrient cycling (Boerner, 1983; Bowman et al., 2009; Carcaillet et
60 al., 2002; Whitlock et al., 2003). Paleoecological studies have documented the vital role of
61 climate, vegetation, and human activities on global fire activity over millennia (Marlon et al.,
62 2013; Power et al., 2008). Yet, knowledge gaps pertaining to the long-term role of fire in
63 particular regions, specifically central Europe, still exist (Feurdean et al., 2012; Feurdean and
64 Vanni re, 2017). More important is the lack in understanding how forest canopy taxa will
65 respond to changing fire regimes as a result of anthropogenically-induced climate change.
66 Temperate forest fires in central Europe are often considered as a negligible ecosystem
67 disturbance (Ad mek et al., 2015) because of the assumed low flammability of deciduous forests
68 (Ellenberg, 1982). Yet, over the past decade emerging literature has demonstrated that fires have
69 occurred for millennia in central European forested ecosystems (e.g. Clark et al., 1989; Bobek et

70 al. 2017; Niklasson et al., 2010; Novák et al. 2012). However, crucial parameters of fire regimes
71 i.e. fire frequency and drivers of biomass burning, are neither fully understood nor discussed
72 (Niklasson et al., 2010), specifically from central European Norway spruce (*Picea abies*) and
73 European beech (*Fagus sylvatica*) forests.

74 Climate models predict more frequent and extreme climatic events such as heat-waves and
75 droughts throughout Europe (Rajczak et al., 2013; Seneviratne et al. 2012), which can elevate fire
76 risk and impact on vegetation (Camia et al., 2017; Lavelle et al., 2014; Linder et al., 2014). For
77 instance, as a result of increasing temperature and drought, the susceptibility of mountain plant
78 communities to mortality has increased (Allen et al., 2010). Because extreme climatic events also
79 contribute to an increase in fire risk, composition and structure of particular plant communities
80 may adapt to include more thermophilic species (Gottfried et al., 2012), thus favoring more fire-
81 prone ecosystems. As future projections suggest an increase in fire risk in central European
82 ecosystems by the end of the 21st century (Lung et al., 2013), it is important to understand long-
83 term fire dynamics in order to determine how increasing wildfire activity may impact future
84 temperate forests.

85 Fire activity is determined by both top-down (e.g. climate) and bottom-up (e.g.
86 vegetation and human activities) drivers which combine to create different fire regimes across
87 varying spatial and temporal scales. Climate variability is considered to be the dominant top-
88 down driver of fire through its influence on broad-scale energy budgets and variations in
89 moisture and temperature, which typically results in regional to continental-scale
90 synchronization of fire activity (Falk et al., 2011). Local factors such as topography (i.e. slope
91 and aspect) and fuel type (i.e. vegetation composition) typically create different mosaics of fire
92 severities (Falk et al., 2011). However, human land use also significantly influences local fire

93 regimes (Gill and Taylor, 2009), yet estimating the extent and magnitude of human-caused fires
94 and land-use activities on natural fire regimes has proven to be difficult (see Kaplan et al., 2016).
95 Because top-down and bottom-up factors vary spatially and temporally (Courtney-Mustaphi et
96 al., 2013; Gavin et al., 2003; Gedalof, 2011), long-term fire histories are necessary in order to
97 investigate the relationship between drivers of fire and their influence on local fire regimes
98 (Whitlock et al., 2010).

99 As the role of fire in central European temperate forests is often deemed unimportant,
100 there is a clear lack of understanding in: i) the relative importance and role of fire in these
101 forests, and ii) the relationship between the dominant forest canopy taxa and changing fire
102 regimes (i.e. changes in biomass burning and fire severities). To fill these gaps, we present a
103 ~11,500-year high-resolution paleoecological reconstruction of vegetation dynamics and fire
104 history from lacustrine sediments obtained from Prášílské jezero (Šumava Mountains, Czech
105 Republic). This record explores for the first time drivers of fire dynamics in these primary
106 temperate spruce-beech forests. The main objectives are to: 1) identify the key drivers of
107 Holocene fire regimes; and 2) assess the response of the dominant forest canopy to changes in
108 biomass burning and fire severities.

109

110 **2. Study area**

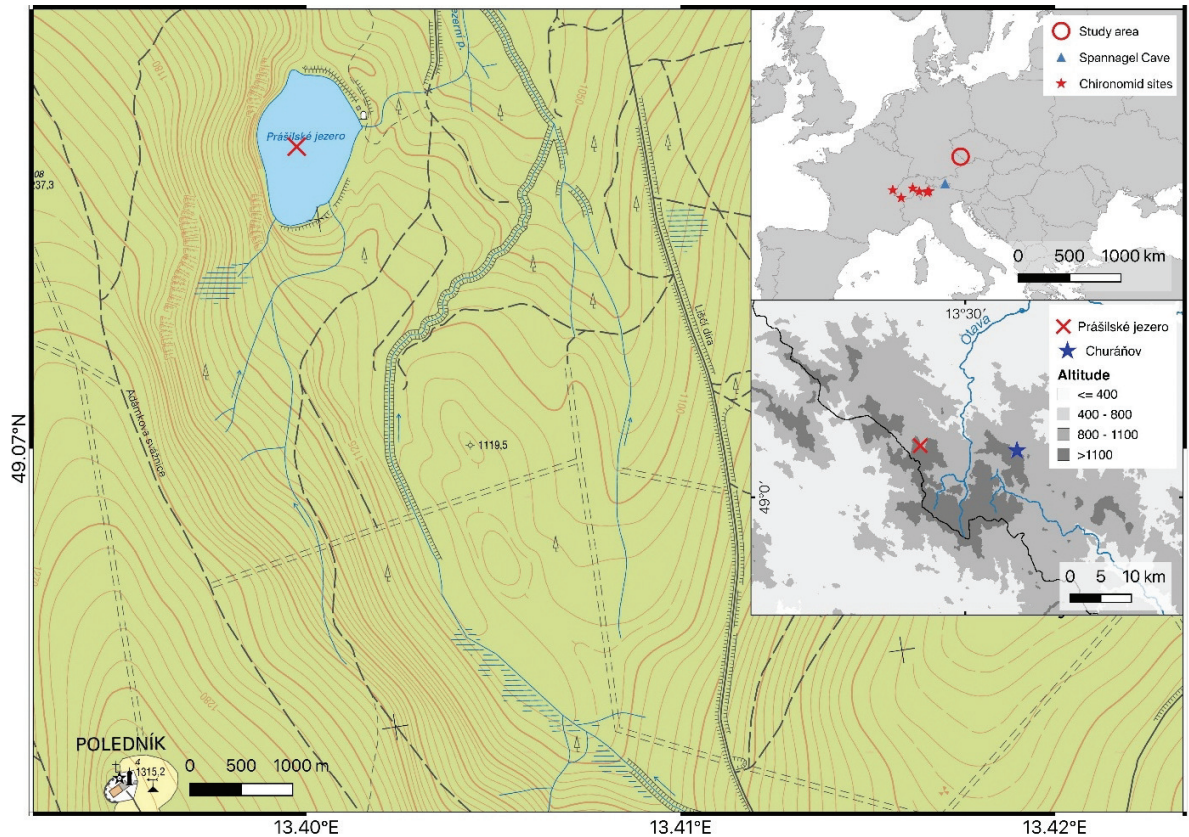
111 Prášílské jezero (49° 04' 30.684" N, 13° 23' 59.136" E, 1079 m a.s.l.) (Fig. 1) is located
112 within the unmanaged portion of Šumava National Park within a relatively steep glacial cirque,
113 which deglaciated ~14,000 years ago (Mentlík et al., 2010). Tree-covered flanks extend 200-300
114 m above the lake. It is a small oligotrophic lake (3.7 ha) with a relatively large (52 ha)
115 catchment, and a catchment area to lake volume ratio of 1.93 (Vrba et al., 1996, 2000). The

116 catchment bedrock is composed of metamorphic crystalline rocks with gneiss, migmatite, and
117 quartzite with local areas of granite (Mentlík et al., 2010; Pelc and Šebesta, 1994).

118 The surrounding vegetation is dominated by Norway spruce with minor components of
119 European beech, rowan (*Sorbus aucuparia* L.), silver birch (*Betula pendula* Roth), sycamore
120 maple (*Acer pseudoplatanus* L.), and silver fir (*Abies alba* Mill.). The understory is dominated
121 by common mountainous spruce forest vegetation such as grasses (*Avenella flexuosa* L.,
122 *Calamagrostis villosa* J.F. Gmel., *Luzula sylvatica* Huds.), herbs (*Prenanthes purpurea* L.,
123 *Senecio ovatus* Willd., *Soldanella montana* Willd., *Trientalis europaea* L.), and small shrubs
124 (*Rubus idaeus* L., *Vaccinium myrtillus* L., *V. vitis-idaea* L.). Sedges and shade-tolerant species
125 (*Carex canescens* L., *C. echinata* Murray, *Juncus effusus* L., *J. filiformis* L., *Oxalis acetosella*
126 L.) occur in shady and mesic areas along the inflowing stream, Jezerní potok. Ferns (*Athyrium*
127 *distentifolium* Tausch ex Opiz, *Blechnum spicant* L., *Dryopteris dilatata* Hoffm.) and ground
128 pine (*Lycopodium annotinum* L.) are also common in the understory vegetation.

129 Based on >50-year long meteorological data (Czech Hydrometeorological Institute) from
130 the closest weather station, Churáňov (Fig. 1), the modern Šumava region is characterized as a
131 semi-humid continental climate with wet and cold winters, and wet and mild summers with an
132 interpolated mean annual temperature and precipitation of 4.5°C and 941 mm year⁻¹.

133



134

135 Fig. 1. Site map of Prášilské jezero (red 'x') located in the Šumava Mountains of south-western
 136 Czech Republic (red circle). The red stars (Heiri et al., 2015) and blue triangle (Fohlmeister et
 137 al., 2013) show the localities used to reconstruct central European Holocene-climate.

138 Meteorological data from Churáňov weather station (blue star), located approximately 20 km
 139 from Prášilské jezero, were used in this study to create a local macrophysical climate model
 140 (Bryson, 2005).

141

142 3. Methods

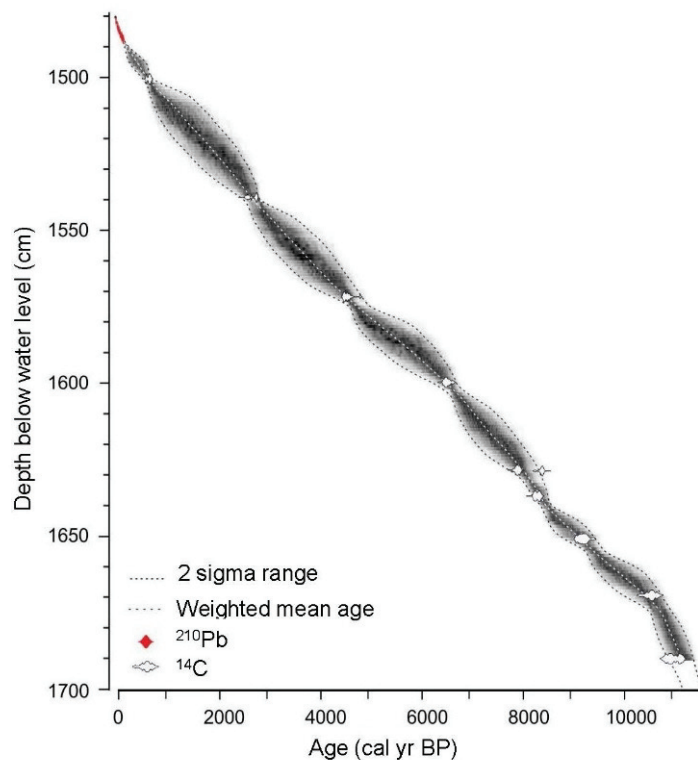
143 3.1 Core retrieval, sediment limnology and radiocarbon dating

144 In August 2015 a 2.18 m sediment profile comprising of one gravity core (PRA15-2GC)
 145 and two parallel and overlapping long-cores (PRA 15-2-1 and PRA 15-2-2) were collected

146 from the deepest (14.8 m) part of Prášilské jezero from a floating platform. The sediment-water
147 interface was collected using a gravity corer (Boyle, 1995), and the longer profiles with a
148 Russian corer (1.5 x 0.075 m). Sediments were taken back to the University of Liverpool where
149 they were subsampled at high-resolution (contiguous 0.5 cm intervals). Samples were then
150 shipped to Charles University where the paleoecological analyses were conducted.

151 Age-depth relationships were established using ten ^{14}C and a ^{210}Pb series (Appleby,
152 1978) (Table SI1). Age-depth relationships were modelled in a Bayesian framework using
153 'BACON' (Blaaw and Christen, 2011) using the ^{210}Pb and ^{14}C dates. All ^{14}C dates were
154 calibrated with the IntCal13 dataset (Reimer et al., 2013), and a Student- t distribution was used
155 to account for scatter in the ^{14}C measurements, and for statistical outliers (Blaauw and Christen,
156 2011). The weighted mean modelled ages against depth were smoothed using a 21-point moving
157 average (Fig. 2), and used to calculate sediment, pollen, and charcoal accumulation rates.

158



159

160 **Fig. 2.** Age-depth model for Prášilské jezero. Age-depth relationships were established using ten
 161 ^{14}C and a ^{210}Pb series (Appleby, 1978). The ages were modelled in ‘BACON’ (Blaauw and
 162 Christen, 2011) using the IntCal13 dataset for ^{14}C ages (Reimer et al., 2013). A Student- t
 163 distribution was used to account for both scatter in the measurements and statistical outliers.

164

165 **3.2 Plant macrofossils and pollen analysis**

166 To investigate the connection between the local fire history and local vegetation
 167 development, plant macrofossils were analyzed at 1 – 2.5 cm resolution. Sample volume was
 168 measured by measuring the displacement of water (on average 6 cm³), and then washed through
 169 a 100- μm sieve following Birks (2007). Plant macrofossils (needles, seeds, buds, bud scales,
 170 etc.) were counted under a stereomicroscope at 15 – 45 x magnification and identified with the
 171 aid of identification keys (Cappers et al., 2006; Bojňanský and Fargašová, 2007; Katz et al.,

172 1965; Tomlinson, 1985), and by comparing macrofossils with the reference material stored in the
173 Herbarium at Charles University. Identifiable charred macrofossil particles >1 mm were counted
174 in order to support the reconstruction of the local fire history (see section 3.3). Concentrations of
175 plant macrofossils were adjusted to a constant volume of 10 cm³. Seeds from terrestrial herbs and
176 small shrubs (*Asteraceae*, *Epilobium angustifolium*, *Epilobium* sp., *Poaceae*, *Rubus* agg.) were
177 summed together to estimate landscape openness.

178 Pollen analysis was conducted at 1 – 2 cm resolution to reconstruct the vegetation
179 history. For each sample, 0.5 cm³ was processed using standard procedures (Faegri et al., 1989).
180 Prior-to pollen processing, a *Lycopodium* tablet was added to each sample as an exotic tracer to
181 estimate pollen concentration and pollen accumulation rates (PAR; grains cm⁻² yr⁻¹) (Stockmarr,
182 1972). A minimum of 500 pollen grains were counted in each sample with the aid of reference
183 material and identification keys (Beug, 2004; Punt 1976 – 1996). Pollen counts were converted
184 into pollen percentages based on the abundance of each pollen type relative to the sum of all
185 identified terrestrial pollen. Total herb percentages were used to estimate landscape openness,
186 while the summed percentages of *Plantago lanceolata*, *Plantago*.sp., *Triticum*-type, *Secale*-type,
187 and *Cerealia*-type were used as traditional human indicator species. The pollen profile was
188 divided into statistically significant pollen assemblage zones based on optimal splitting the sum-
189 of-squares using the broken-stick model (Bennett, 1996). The plant macrofossil and pollen
190 records were visualized against the calibrated age-depth model using Tilia 2.0.41 software
191 (Grimm, 2004).

192

193 **3.3 Charcoal analysis**

194 *3.3.1. Sample treatment and microscope analysis*

195 Microscopic and macroscopic charcoal particles were used to reconstruct both regional
196 and local fire histories. Microscopic charcoal has been shown to be indicative of regional fire
197 activity within a radius of 20 – 100 km of a site (MacDonald et al., 1991; Tinner et al., 1998;
198 Whitlock and Larsen, 2001). Theoretical calibrations between fire and charcoal deposition
199 suggest that macroscopic charcoal peaks most accurately reflect local fires (<3 km from coring
200 site), while variations of total macroscopic charcoal abundance reflect regional biomass burning
201 trends (~50 km from coring site) (Higuera et al., 2007, 2010; Peters and Higuera, 2007; Adolf et
202 al., 2017).

203 Microscopic charcoal was counted on pollen slides and was identified as being black,
204 opaque, and angular in shape (Clark, 1988), while macroscopic charcoal was prepared (after
205 Mooney and Tinner, 2011) by disaggregating contiguous 0.4 – 1 cm³ samples in a 20 ml solution
206 of dilute sodium hexametaphosphate and 10 ml potassium hydroxide (5%). Macroscopic
207 charcoal samples were washed gently through a 250- μ m sieve and then bleached using 1 – 2 ml
208 of sodium hypochlorite (8%: NaOCl) for the minimum time (up to 12 hours) necessary to
209 achieve a consistent bleaching effect. The bleaching process was carefully monitored as bleach
210 digests charcoal particles that are not fully charred, thus potentially reducing their size,
211 particularly if the sample contains little organic material (Schlachter and Horn, 2010). The
212 samples were then washed gently through a 125- μ m sieve, and macroscopic charcoal particle
213 counts were recorded with the use of a low power binocular microscope. Charcoal area
214 measurements were made using digital greyscale images using a 137 – 255 greyscale threshold
215 in ImageJ software (<https://imagej.nih.gov/ij/>). Macroscopic charcoal counts and area
216 measurements were transformed to concentrations (particles cm⁻³) and accumulation rates

217 (particles $\text{cm}^{-2} \text{yr}^{-1}$; $\text{mm}^2 \text{cm}^{-3}$). Macroscopic charcoal accumulation rate will be denoted as
218 CHAR_C (the number of particles $\text{cm}^{-2} \text{yr}^{-1}$) and CHAR_A (the area of particles $\text{mm}^2 \text{cm}^{-2} \text{yr}^{-1}$).

219

220 3.3.2. Fire episode detection and change point analysis

221 To determine the regional fire history, the macroscopic charcoal records (CHAR_C and
222 CHAR_A) were first interpolated to a constant temporal resolution (median: 28 years sample^{-1}),
223 and then broken into a low-frequency component (charcoal background (BCHAR)) and a peak
224 component ($\text{CHAR}_{\text{peak}}$) using the CharAnalysis software (Higuera et al., 2009). The BCHAR
225 component was determined using a robust LOWESS regression with a moving-window width of
226 600 years which resulted in a robust signal-to-noise index (SNI) >3.0 (Kelly et al., 2011).

227 $\text{CHAR}_{\text{peak}}$ values were calculated as residuals from BCHAR, and $\text{CHAR}_{\text{peaks}}$ were evaluated
228 using the 99th percentile of a Gaussian mixture model that aimed at separating peak samples
229 representing actual fire events from surrounding noise in the $\text{CHAR}_{\text{peak}}$ series. The identified
230 $\text{CHAR}_{\text{peakC}}$ were further screened with the minimum count peak-screening test (Gavin et al.,
231 2006; Higuera et al., 2010). $\text{CHAR}_{\text{peakA}}$ were screened with the method proposed by Finsinger et
232 al. (2014) using the software, ARCO ('charcoal AREa-COunts.') v.1.0 (available at
233 github.com/wfinsinger/ARCO). Fire frequencies (fires kyr^{-1}) and fire-return intervals (FRI; the
234 total number of years between adjacent fire episodes) were smoothed using a 1000-year window.
235 Lastly, peak magnitude (the total charcoal abundance associated with each fire episode) was used
236 as a qualitative measure of fire severity (Colombaroli et al., 2010; Feurdean et al., 2017; Keeley,
237 2009; Minckley and Long, 2016; Robichaud, 2000).

238 Change point analysis was used to determine significant changes in biomass burning
239 based on variations in both the mean and variance of the total CHAR records (Killick et al.,

240 2012) using the ‘change point’ v2.2.2 package (Finsinger et al., 2016; Killick et al., 2014; R Core
241 Development Team, 2012). We also tested the potential effect of sedimentation-rate change on
242 change point detection following Finsinger et al. (2016).

243

244 **3.5 Regression analysis**

245 In order to describe the relationship between the dominant forest canopy taxa and
246 changes in fire regimes at Prášilské jezero, a Generalized Additive Model was used (GAM;
247 Hastie and Tibshirani, 1986) using the ‘mgcv’ v1.8-12 package (Wood, 2006). A GAM is a
248 semi-parametric extension of a generalized linear model that uses a link function to establish a
249 relationship between the mean response variable (i.e. the dependent variable; PAR of the six
250 dominant forest canopy taxa; *Abies*, *Betula*, *Corylus*, *Fagus*, *Picea*, and *Pinus*) and a smoothed
251 predictor variable(s) (i.e. the independent variable; CHAR_A and peak magnitude) (Birks, 2012).
252 The default setting for GAMs, a Gaussian error distribution and an identity link function, were
253 used in this study. Both the response variables and the predictor variables were logged to
254 stabilize the variance between the two datasets. *P*-values were implemented in the function
255 `summary.gam` of the ‘mgcv’ R package, v1.8-12.

256

257 **3.4 Climate model**

258 Locally derived paleoclimate proxies are scarce in central Europe making it difficult to
259 interpret macro-scale changes in climate and their influences on fuel and fire occurrence.
260 However, previous paleoecological studies have demonstrated the effectiveness of
261 macrophysical climate models (MCM) as independent climate data sources (Dreslerová, 2012;
262 Higgins and MacFadden, 2009; Jamrichová et al., 2014; Kuneš et al., 2015; Riehl et al., 2009).

263 The MCM is an alternative to iterative general circulation models (GCMs) and uses a top-down
264 approach rather than a bottom-up approach to model building. While MCMs are simpler than
265 GCMs, MCMs illustrate the main trends in site-specific climatic changes. Essentially the MCM
266 is a heat-budget model derived from the basic principles of synoptic climatology, and variations
267 in atmospheric transparency, as well as orbital forcing (Bryson, 2005). The model calculates
268 monthly values in 100-year intervals using modules that consist of internal boundary conditions
269 (i.e., subtropical highs, jet streams and Intertropical convergence), external orbital forcing, and
270 volcanic eruptions for the past 40,000 years. The modules are then assembled into a site-specific
271 model that is calibrated by using a locally derived time series of meteorological data (here, the
272 Churáňov weather station record).

273 In addition, we compared the MCM model with independent paleoclimate records
274 obtained from public repositories; a stacked reconstruction of July temperature from multiple
275 sites across central Europe (Heiri et al., 2015), and a reconstruction of winter temperature from
276 Spannagel Cave, Austria (Fohlmeister et al., 2013) (Fig. 1).

277

278 **4. Results**

279 ***4.1 Reconstructed fire history***

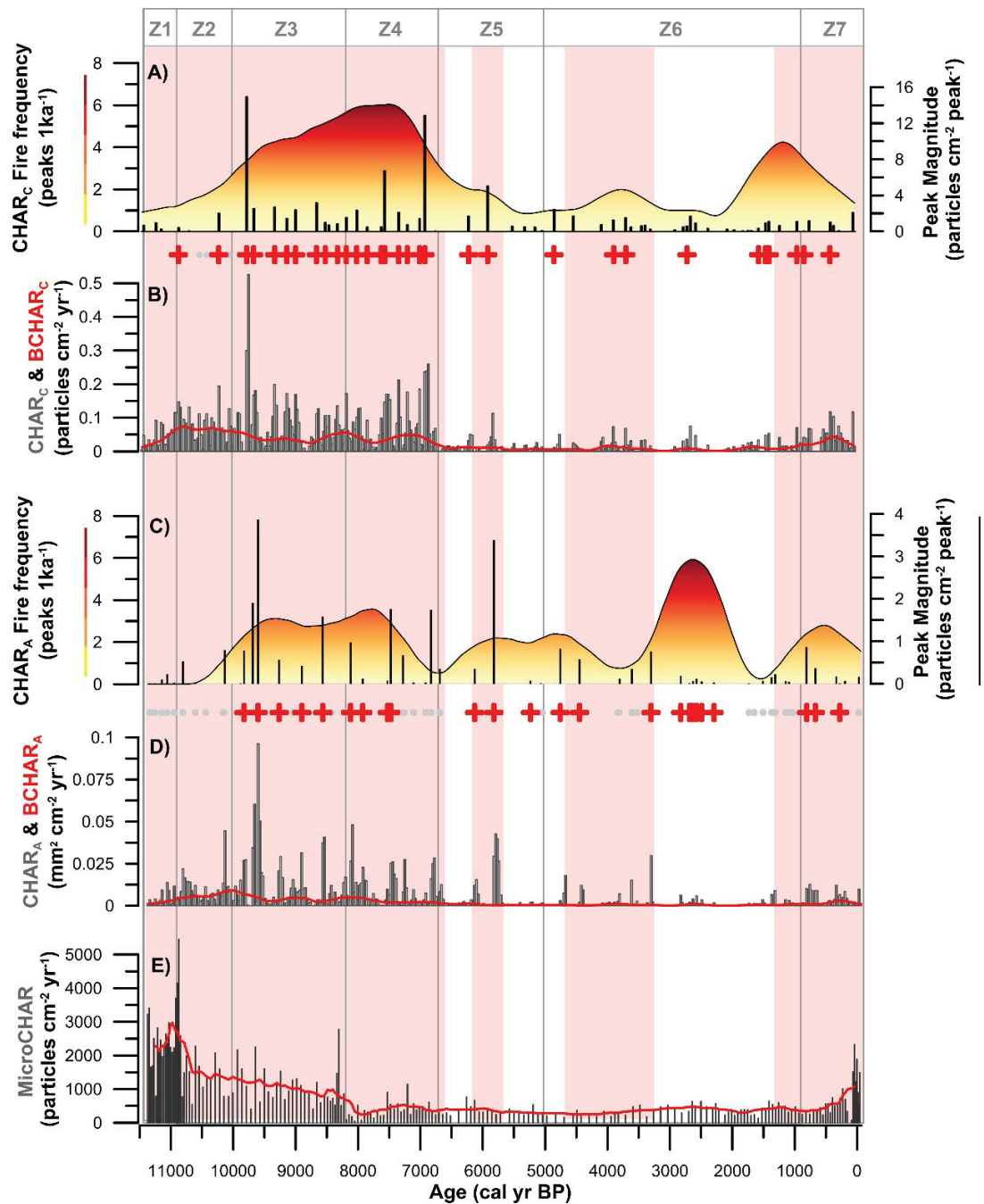
280 Macroscopic CHAR_C and CHAR_A are strongly correlated (Pearson's r coefficient = 0.74,
281 p-value < 0.001). CHAR_C and CHAR_A records show similar trends in biomass burning with the
282 highest BCHAR values occurring during the early Holocene between 11,000 and ~6500 cal yr
283 BP when CHAR abruptly decreased (Fig. 3). CHAR_A values increase again briefly ~6000 cal yr
284 BP, between 4600 and ~3300 cal yr BP, and over the past ~1800 years. These periods of
285 increased biomass burning correspond to the significant zones detected by change point analysis

286 (Fig. 4). Micro-CHAR similarly captures this general trend of increased values between 11,500
287 and ~8500 cal yr BP, minimum values between 8000 and 500 cal yr BP, and increasing values
288 over the past 500 years.

289 The SNI generally exceeded the critical threshold of 3.0 suggesting the records are both
290 suitable for peak-detection analysis during most periods of time (Kelly et al., 2011) (see
291 Appendix Fig. 1). Overall, CHAR_C identified 30 fire episodes, while CHAR_A identified 24 fire
292 episodes. Both CHAR_C and CHAR_A records show high fire frequencies centered in the early-to
293 mid-Holocene (10,000 – 7000 cal yr BP) and late Holocene (past c. 1,000 years) (Fig. 3a and c),
294 reflecting the regional biomass burning trends derived from the BCHAR record. However, the
295 fire frequency records based on CHAR_C and CHAR_A differ between 7000 – ~1000 cal yr BP;
296 whereas CHAR_C-inferred fire frequency is low, CHAR_A-inferred fire frequency is stable with the
297 highest values around 2500 cal yr BP. Reconstructed fire frequency based on CHAR_A suggests
298 an average of c. 3 fires/1000 years (FRI = ~333 years) between 10,000 – 7000 cal yr BP. CHAR_A
299 fire frequencies were slightly lower (average of 2 fires/1000 years (FRI = ~500 years)) between
300 6000 cal yr BP and present, except around ~2500 cal yr BP when CHAR_A fire frequency
301 increased to an average of 6 fires/1000 years (FRI = ~166 years).

302 While peak magnitudes varied in size (CHAR_C ranged between 0 and 15 particles cm⁻²
303 peak⁻¹; CHAR_A ranged between 0 and 3.9 particles cm⁻² peak⁻¹), the records show similar trends
304 of higher peak magnitudes in the early- to mid-Holocene, and lower peak magnitudes after
305 ~6500 cal yr BP.

306

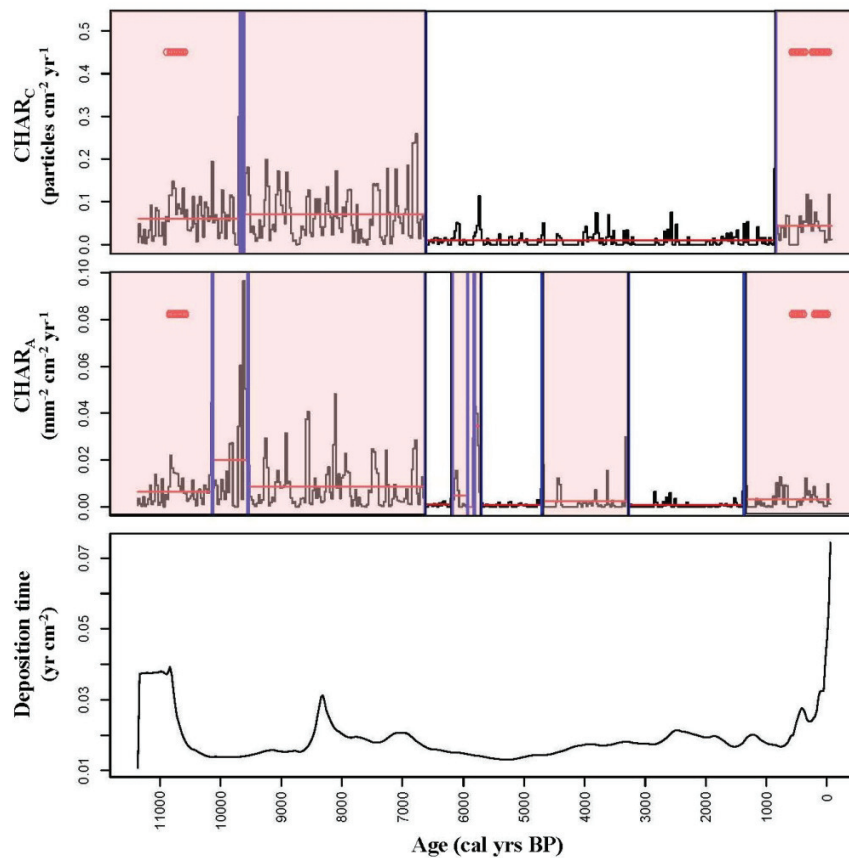


307

308 **Fig. 3.** Reconstructed fire history for Prášilské jezero based on macroscopic charcoal counts
 309 (CHAR_C : A-B), macroscopic charcoal areas (CHAR_A : C-D), and microscopic charcoal counts
 310 (MicroCHAR: E). A) and C): smoothed fire-frequency records (yellow-red shading), peak-
 311 magnitude records (black vertical bars), and significant fire episodes (red crosses) and non-

312 significant fire episodes (grey dots); B) and D): macroscopic charcoal accumulation rate (dark
 313 grey vertical bars), and the charcoal background records (BCHAR; red continuous line); E):
 314 MicroCHAR (dark grey vertical bars) values with a loess smoother using a window width of 11
 315 (red line). Pink vertical bands highlight periods of higher CHAR_A values as detected by change
 316 point analysis (see Fig. 4). Grey vertical lines are associated with the statistically significant
 317 pollen zones detected by broken stick analysis (labelled Z1 – Z7).

318



319

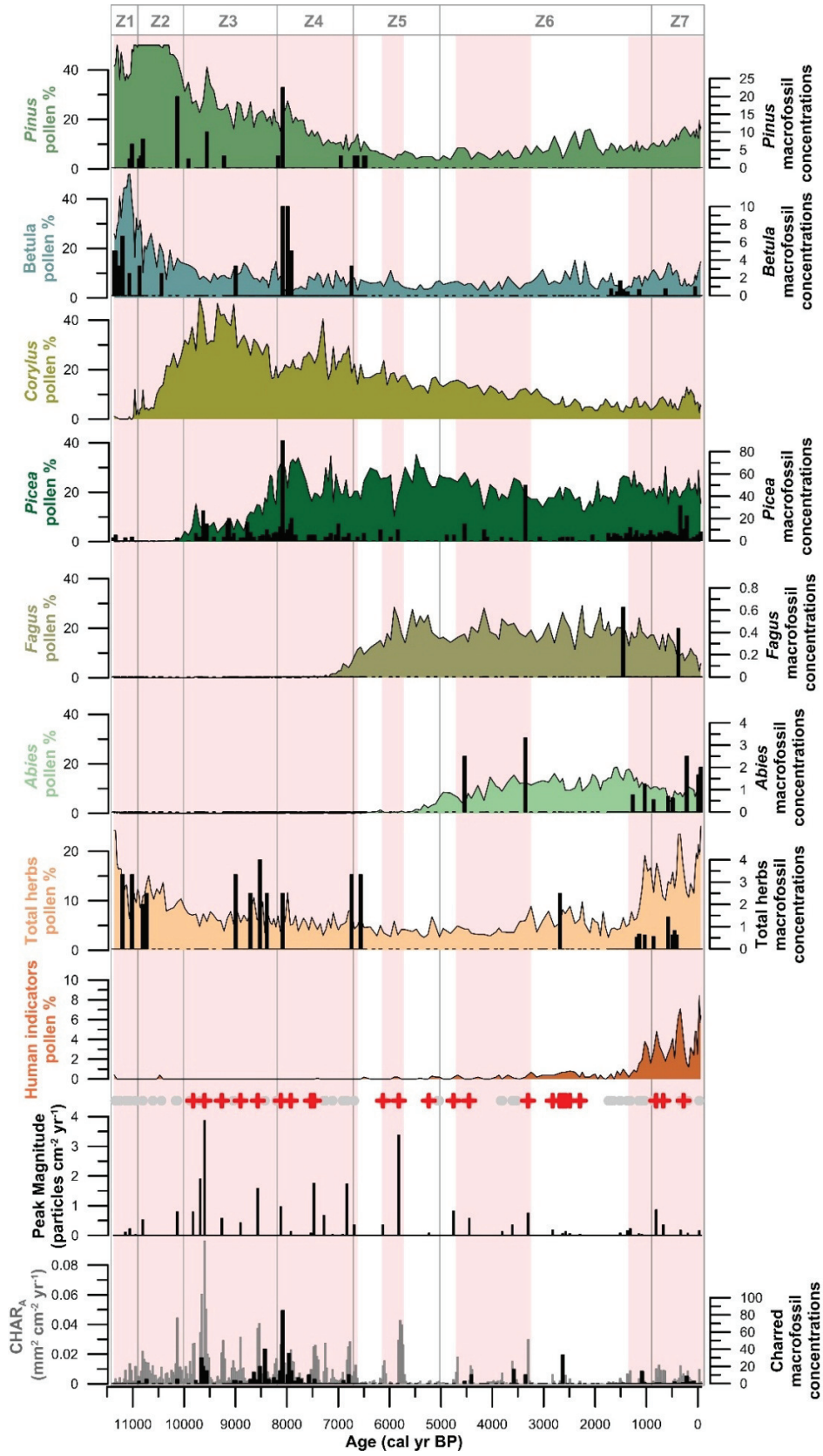
320 **Fig. 4.** Comparison between change point analysis based on macroscopic charcoal counts
 321 (CHAR_C ; top), macroscopic charcoal area (CHAR_A ; middle), and sample deposition time

322 (bottom) for Prášilské jezero. Vertical blue lines indicate change points in the CHAR records.

323 Primary zones of elevated biomass burning are depicted by the areas shaded in pink.

324 **4.2 Reconstructed vegetation history**

325 The pollen percentage profile was divided into seven statistically significant pollen-
326 assemblage zones. Zones 1 – 4 (11,500 – 6700 cal yr BP) are characterized by high percentages
327 of *Pinus*, *Corylus*, *Betula* and herbs (Fig. 5). High concentrations of *Pinus*, *Betula*, herbs, and
328 charred macrofossil remains (> 1 mm) were also found throughout Zones 1 – 4 (Fig. 5). High
329 concentrations of *Juncus* macrofossil remains were also present during Zones 1 – 4 (See
330 Appendix Fig. 2). During Zone 3 (10,000 – 8300 cal yr BP), *Picea* pollen percentages increased,
331 as did *Picea* macrofossil concentrations and the appearance of *Picea* stomata, suggesting the
332 local establishment and rise to dominance of *Picea*. Zone 4 (8300 – 6700 cal yr BP) illustrates
333 the dominance of *Picea* when *Corylus* was still abundant (Fig. 5), and when biomass burning
334 was at its highest (Fig. 3). *Fagus* pollen percentages increase towards the end of Zone 4 (~7000
335 cal yr BP) suggesting the local establishment of beech. The boundary between Zones 4 and 5 (c.
336 6700 cal yr BP) marks the transition of *Fagus* becoming a secondary component of the canopy
337 cover (comprising ~>20% of the canopy). Towards the end of Zone 5, *Abies* pollen percentages
338 increase, yet *Abies* macrofossil concentrations do not appear until Zone 6. The earliest findings
339 of human pollen indicator species occur in Zone 5. Around 2500 cal yr BP (middle of Zone 6;
340 5100 – 1000 cal yr BP), human pollen indicator species increase briefly, then decrease, and then
341 dramatically increase again starting ~1000 cal yr BP (onset of Zone 7). The latter half of Zone 6,
342 as well as Zone 7 are characterized by the decline in *Fagus* and *Abies* pollen percentages, and the
343 increase in herb pollen percentages and herb macrofossil concentrations (i.e. landscape
344 openness).



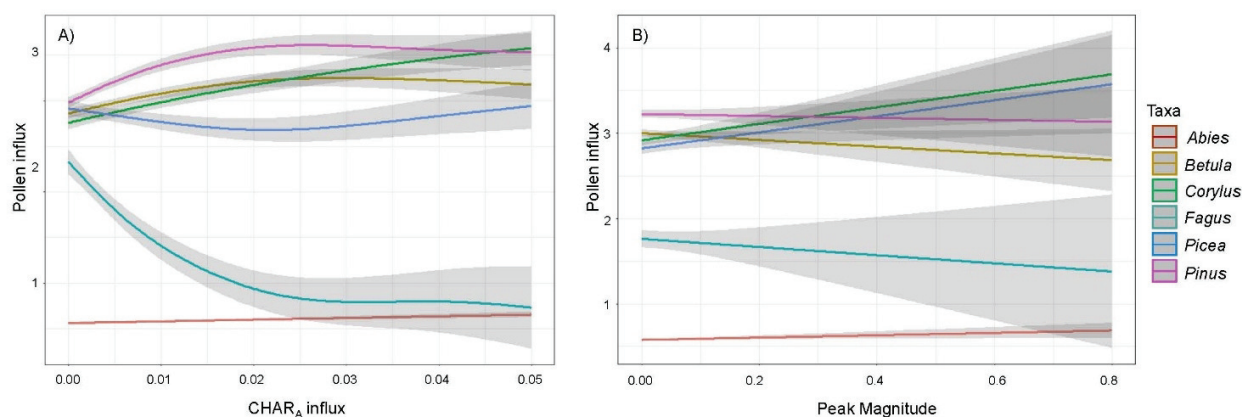
346 **Fig. 5.** Reconstructed vegetation history of the dominant forest canopy taxa at Prášilské jezero
347 using pollen percentages (filled coloured lines), and macrofossil data (black bars). Vegetation
348 data are compared to significant fire episodes (red crosses), non-significant fire episodes (grey
349 dots), peak magnitude (black vertical bars), CHAR_A (grey vertical bars), and the concentration of
350 charred macrofossil remains (black vertical bars). All y-axes were clipped at 50%. Pink vertical
351 bands highlight periods of higher CHAR_A values as detected by change point analysis (see Fig.
352 4). Grey lines are associated with the statistically significant pollen zones detected by broken
353 stick analysis (labelled Z1 – Z7).

354

355 **4.3 Regression analysis**

356 Response curves show that *Betula*, *Corylus* and *Pinus* have a statistically significant
357 positive relationship (e.g. at the 95% confidence interval) with increased biomass burning (i.e.
358 CHAR_A), whereas *Fagus* has a statistically significant negative relationship (Fig. 6a; Table 1).
359 While not statistically significant, *Corylus* illustrates a positive relationship with increasing fire
360 severities, while *Betula*, *Fagus*, and *Pinus* all have a negative relationship (Fig. 6b). *Picea* has a
361 slightly negative relationship with increased biomass burning, and a slight positive relationship
362 with increasing fire severities (Fig 6b), but these trends are not statistically significant. While
363 *Abies* shows a relatively positive relationship to both increased biomass burning and fire
364 severities, these relationship are too weak to make inferences about the species relationship with
365 fire in this study (Fig. 6a).

366



367
 368 Fig. 6. Taxa response curves illustrating the relationship between pollen accumulation rates of
 369 the six dominant forest canopy species and increases in biomass burning (i.e. CHAR_A)(A), and
 370 fire severity (i.e. peak magnitudes) (B). A) Response curves illustrate three different responses to
 371 changing fire regimes at Prášilské jezero, which correspond to fire resistance (*Betula*, *Corylus*,
 372 and *Pinus*), avoidance (*Picea*), and sensitive/intolerance (*Fagus*). B) Only *Corylus* and *Picea*
 373 illustrate a positive relationship with increasing fire severity.

374

Species names	CHAR _A r2 adj.	CHAR _A p-value	CHAR _A df	Peak Magnitude r2 adj.	Peak Magnitude p-value	Peak Magnitude df
<i>Abies</i>	0.03	0.009	2	0.0155	0.348	4.675
<i>Betula</i>	0.056	0.009	3.575	-0.003	0.623	2
<i>Corylus</i>	0.77	<0.001	2.742	0.0354	0.116	5.372
<i>Fagus</i>	0.162	<0.001	4.387	-0.002	0.508	2
<i>Picea</i>	0.008	0.419	3.342	0.003	0.191	2
<i>Pinus</i>	0.132	<0.001	4.38	-0.005	0.867	2

375

376

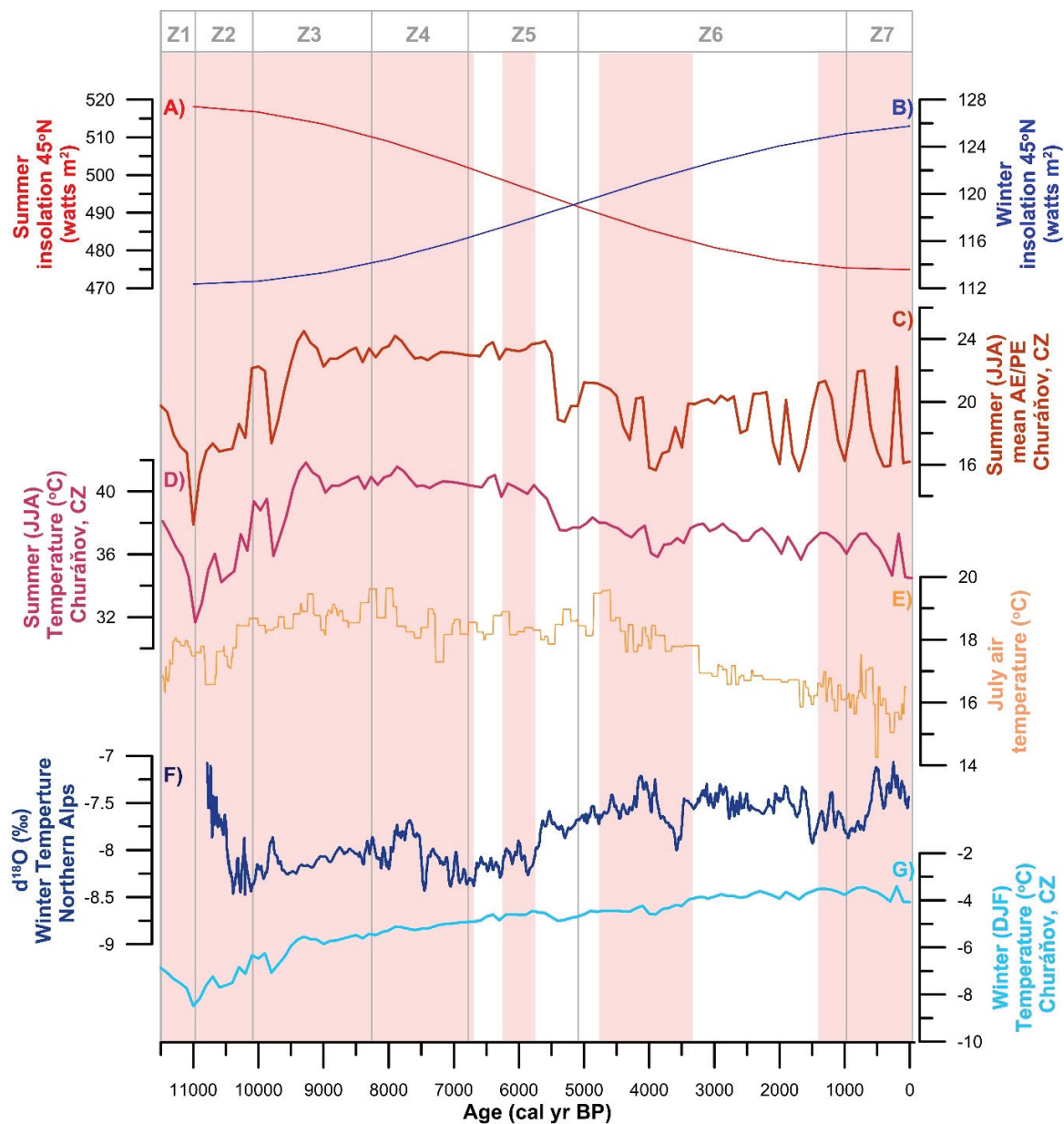
377 Table 1. Correlation between the dominant forest canopy taxa and macroscopic charcoal area
 378 (CHAR_A) and peak magnitudes at Prášilské jezero, as determined by a Generalized Additive
 379 Model.

380

381 ***4.4 Reconstructed climate***

382 The MCM model provided monthly means of temperature and evaporation in 100-year
383 intervals (Fig. 7C, D, G). Specifically, we selected averages of monthly means for winter (DJF)
384 and summer (JJA) temperature, and summer potential evaporation (AE/PE) in order to compare
385 with regional climate data. Two main climatic phases are present in the MCM model after the
386 postglacial warming from 11,500 to ~9500 cal yr BP. The first phase between 9500 and ~5500
387 cal yr BP was characterized by relatively low winter temperatures, higher-than-present summer
388 temperatures, and higher-than-present potential evaporation during the summer (i.e. warmer and
389 drier-than-present summer conditions). The second phase between ~5500 cal yr BP and present
390 was characterized by gradually increasing winter temperatures, decreasing summer temperatures,
391 and decreasing potential evaporation during the summer (i.e. gradually cooler and wetter-than-
392 previous summer conditions). Overall, the MCM outputs reflect the long-term millennial-scale
393 trends in winter and summer temperatures derived from regional proxy records (Fig. 7E, F).

394



395
 396 **Fig. 7.** Reconstructed climate from central Europe. A) summer and B) winter insolation curves
 397 for 45°N (Berger and Loutre, 1991); C) reconstructed summer AE/PE based on the MCM model,
 398 (this study); D) reconstructed summer temperature based on the MCM model (this study); E)
 399 reconstructed July temperature based on a stacked chironomid record from multiple sites across
 400 central Europe (Heiri et al., 2015); F) reconstructed winter temperature based on $\delta^{18}\text{O}$ isotopes
 401 from Spannagel Cave, Austria (Fohlmeister et al., 2013); G) reconstructed winter temperature

402 based on the MCM model (this study). Pink vertical bands highlight periods of higher CHAR_A
403 values as detected by change point analysis (see Fig. 4). Grey vertical lines are associated with
404 the statistically significant pollen zones detected by broken stick analysis (labelled Z1 – Z7).

405

406 **5. Discussion**

407 ***5.1. Using charcoal area to infer the local fire history***

408 Reconstructed CHAR_C and CHAR_A from Prášilské jezero illustrate similar long-term
409 patterns of higher biomass burning in the early-to mid-Holocene, and lower biomass burning
410 after 6500 cal yr BP (Fig. 3). The similarity supports previous studies reporting a strong
411 correlation between macroscopic charcoal count and area data (Finsinger et al. 2014; Tinner and
412 Hu, 2003).

413 Unlike the similarities in CHAR_C and CHAR_A, there appears to be differences in the
414 reconstructed fire episodes and fire frequency using both macroscopic charcoal counts versus
415 area. These differences could be associated with lab treatment and/or different user-defined
416 parameters within the software used (e.g. CharAnalysis and ARCO). For example, low count
417 sums in proxy data have been shown to reduce strongly the accuracy of palaeoecological
418 reconstructions (Finsinger and Tinner, 2005; Heiri and Lotter, 2001; Maher, 1972; Maher et al.,
419 2012). Charcoal counts were consistently low at Prášilské jezero and did not meet the preferred
420 rule of thumb that non-peak samples have >10 charcoal pieces and peak samples have at least 20
421 charcoal particles (Higuera et al., 2010). This likely made the identification of statistically
422 significant peaks difficult. Patterns of fire frequencies have been shown to vary little based on
423 charcoal counts and area data both without peak-screening tests (Ali et al., 2009), and with peak-
424 screening tests (Finsinger et al., 2014). By contrast, here we demonstrate that patterns of fire

425 frequencies and detected peak episodes differ substantially between charcoal counts and area
426 data. We suggest that low charcoal counts could have contributed to the different reconstructed
427 fire frequencies and detected fire episodes. Despite these limitations, here we infer relationships
428 between vegetation-dynamics and fire-frequency changes based on charcoal area rather than
429 charcoal counts. While it might be difficult to determine the spatial scales of fire frequency and
430 fire return interval (FRI) with CHAR records comprising particles >150 µm as in our study
431 (Adolf et al., 2017), support for this comes from the area-based screening-peak test (Finsinger et
432 al., 2014), which should reduce the influence of small charcoal particles derived from regional
433 background of CHAR (Tinner et al., 1998; Adolf et al., 2017).

434

435 ***5.2 Drivers of fire regimes in central European montane spruce-beech forests***

436 The history of fire in Europe is a complex product of top-down (i.e. climate) and bottom-
437 up (i.e. vegetation dynamics and human activities) drivers (Pyne, 2000). The Prášílské jezero fire
438 history reflects how these drivers facilitated in changing fire regimes over time. In the early
439 Holocene, broad-scale climatic forces such as the high contrast between colder-than-present
440 winters and warmer-than-present summers (Perić et al., 2017), and high summer insolation
441 induced warmer- and drier-than-present conditions (Fig. 7; Davis et al., 2003, Heiri et al., 2003,
442 Litt et al., 2009), resulted in fuel type more conducive for high and regionally synchronous
443 biomass burning. Fuel composition at Prášílské jezero was dominated by *Pinus* and *Corylus* in
444 addition to continuous fire-promoting fuels in the form of understory herbs in the early Holocene
445 (Fig. 5). While pollen and macrofossil analysis were unable to conclude whether *P. mugo* or *P.*
446 *sylvestris* dominated in the early Holocene, both *P. mugo* and *P. sylvestris* are favored by
447 frequent, low-intensity surface fires (Zackrisson, 1977; Delcourt and Delcourt, 1987; Engelmark

448 et al. 1994; Adámek et al., 2015). Thus either species would have benefited from the frequent
449 fire activity documented in the early Holocene. *Corylus avellana* is also known to colonize early
450 and spread quickly after fires (Delarze et al., 1992). However, because *Corylus maxima* also
451 occurred during previous Interglacials when conditions were drier-than-present (Wright, 1977),
452 the high abundance of *Corylus* in the early Holocene further supports that conditions were drier-
453 than-present. We thus interpret causality between relatively high fire frequency, high *Corylus*
454 abundance, and drier-than-present conditions at Prášílské jezero in the early Holocene,
455 supporting earlier formulated hypotheses (Huntley, 1993; Finsinger et al., 2006). High fire
456 activity and increased abundances of *Corylus* and *Pinus* have also been observed throughout
457 central Europe during this time (Feurdean et al., 2013; 2017; Finsinger et al. 2006; Tinner et al.,
458 1999).

459 *Picea abies* established and expanded during the early Holocene when regional biomass
460 burning and local fire severity were the highest of the entire record. Regionally, *Picea abies*
461 persisted throughout the Holocene in the Carpathians, enduring a low-to-moderate fire regime
462 and a variable FRI of 200 - 300 years (Feurdean et al., 2017), and 1000 - 4000 years (Finsinger
463 et al. 2016), which agrees with the estimated fire reoccurrence period in central European
464 mountain spruce forests (Tinner et al., 1999; Beer and Tinner, 2008). Previous paleoecological
465 studies documenting the expansion of *Picea abies* during periods of increasing fire activity
466 (Brown and Giesecke, 2014; Carcaillet et al., 2007) suggest that the combined effect of increased
467 fuel loads and periodic summer drought resulted in dry surface layers suitable for combustion
468 (Brown and Giesecke, 2014). Thus, the drier-than-present climatic conditions could have
469 supported the high biomass burning when *Picea abies* dominated in the early Holocene. Our
470 results support the findings of Feurdean et al. (2017) and Finsinger et al. (2016) in that *Picea* was

471 able to expand and persist in the early Holocene because climate conditions were dry enough
472 (high summer AE/PE ratio; Fig. 7C) to sustain high regional biomass burning with a relatively
473 high fire frequency and moderate-scale fire severity.

474 High biomass burning may have also been a result of Upper Paleolithic and Mesolithic
475 hunter and gatherers and their land-use activities, whom occupied the Šumava Mountains
476 between 13,950 - 7500 cal yr BP (Čuláková et al., 2012b; Vencl, 2006; Fröhlich, 2009; Šída et
477 al., 2011; Eigner et al., 2017). Mesolithic finds have been connected with the seasonal
478 exploitation of food resources, such as fishing and hunting, and the late summer source of berries
479 e.g. *Vaccinium* and *Oxycoccus* (Oliver, 2007), which mature later at higher elevations >500 m
480 a.s.l. Additionally, they would have exploited the high abundances of *Corylus* nuts (Divišová and
481 Šída, 2015), which was one of the dominant canopy species found regionally in the early
482 Holocene (Svobodová et al., 1996; 2000; 2002). While estimating the extent and magnitude of
483 fires caused by hunters and gatherers is difficult, Kaplan et al. (2016) suggest that hunter-
484 gatherers had mastered fire as a tool for landscape management, and for improving hunting and
485 foraging opportunities during the Last Glacial Maximum (LGM). However, increased burn area
486 during the LGM generally resulted in large reductions in forest cover (Kaplan et al., 2016).
487 However, in the early Holocene, there was no significant reduction in forest cover, nor any
488 significant increase in herbaceous pollen (i.e. landscape openness) (Carter et al., 2018), or
489 traditional anthropogenic pollen indicators at Prášílské jezero (Fig. 5). Additionally, *Corylus*
490 maxima also occurred during previous Interglacials (Wright, 1977) when human activities were
491 unlikely to have been a factor (Finsinger et al., 2006). Thus, despite the archeological evidence
492 suggesting humans occupied the region during the early Holocene, we conclude that because the
493 trend in biomass burning was similar to other records across Europe (Feurdean et al., 2012;

494 Finsinger et al., 2006; Olsson et al., 2010; Vanni re et al., 2016), as well as with global biomass
495 burning syntheses (Marlon et al. 2013; Power et al. 2008), climate and type of fuel were the
496 primary drivers of biomass burning at the regional-to-subcontinental-scale, but acknowledge that
497 local-scale human activities could have influenced the local fire regime (see Valese et al., 2014).

498 During the mid-Holocene, broad-scale changes in climate resulted in major shifts in
499 vegetation composition, and subsequently a decline in global biomass burning (Marlon et al.,
500 2013; Power et al., 2008). As summer insolation decreased, winter insolation increased resulting
501 in the long-term trend of increasing winter temperature (Fig. 7F, G). This led to the decline in the
502 strength of the westerlies inducing wetter and milder-than-previous winter conditions across
503 Europe (Benito et al., 2015). Pollen-based climate reconstructions highlight winter temperature
504 as the most important driver of mid-to late-Holocene warming in Europe (Mauri et al., 2015).
505 Because *Fagus sylvatica* is sensitive to cold winter temperatures and spring frost (Cheddadi et
506 al., 2017), it is likely that the spread of *Fagus* across Europe during the mid-Holocene, while not
507 spatially synchronous, may have been limited by colder-than-present winter temperatures (Fig.
508 7F, G). Feurdean et al. (2017) attributed the expansion of *Fagus* to either climate or a
509 combination of climate, fire, and human disturbances. Yet, Giesecke et al. (2007; 2017) suggest
510 that no single variable, such as climate, disturbances, or intrinsic biological factors can explain
511 the changes in *Fagus* distribution and abundance. Regardless of the causes leading to the
512 expansion of *Fagus* on regional to subcontinental-scales, the reconstructed CHAR_C and CHAR_A
513 corroborate the notion that once beech established as one of the main canopy species, regional
514 biomass burning declined illustrating bottom-up controls on biomass burning (Fig. 5).

515 Because regional biomass burning decreased with the expansion of beech forests, it can
516 be assumed that the local fire frequency would also decrease, yet the local fire frequency

517 remained relatively similar to that seen during the early Holocene (Fig. 3). Submontane beech
518 forests in central Europe are considered to have a low frequency fire regime with few fires
519 occurring under extreme climatic conditions (Xanthopoulos et al., 2012). For example, beech
520 forests in the Southern Alps experienced numerous, large fires under hot and dry weather during
521 the extremely dry summer of 2003 (Ascoli et al., 2013). Thus, the relatively stable local fire
522 frequency may be explained by complex interactions between climate and local human activities.
523 Chironomid- and pollen-based temperature reconstructions from Europe illustrate that summer
524 temperatures reached a maximum between ~6500 cal yr BP (Heiri et al., 2003) and 6000 cal yr
525 BP (Davis et al., 2003), which would have led to an increase in fire potential as a result of drier
526 fuel loads (Daniau et al., 2012). Coincidentally, between 6500 and 6000 cal yr BP, two local fire
527 events occurred simultaneous with a brief increase in regional biomass burning (Fig. 3). We
528 therefore suggest that the increase in biomass burning and two local fire events between 6500
529 and 6000 cal yr BP may be explained by fire conducive climatic conditions, despite the change
530 in more mesic fuel type during the mid-Holocene.

531 However, climate alone cannot explain the relatively stable local fire frequency, as the
532 continuous presence of human pollen indicators beginning ~6500 cal yr BP could also suggest
533 Neolithic human-induced influences on the fire regime in the region (Fig. 5). Despite the fact
534 that there is no direct evidence of human activities ca. 35 - 40 km from Prášílské jezero ~6500
535 cal yr BP (Dreslerová, 2016; Sommer, 2006), the timing of human indicators from Prášílské
536 jezero agrees with other records from the region suggesting Neolithic presence (Svobodová et
537 al., 2001; Svobodová 2002; 2004). Moreover, the appearance of hill-forts and hill-top settlements
538 in the region, as well as archaeological evidence from two sites ~5 km from Prášílské jezero
539 suggests the local settlement and occupation of humans during the Bronze and Iron Ages ~3000

540 and at ~2200 cal yr BP (Čuláková et al. 2012a; unpublished data; Dreslerová, D. unpublished
541 data), which correlates with the increases in human indicator pollen types (Fig. 5). Thus, the
542 increase in local fire frequency and fire occurrence ~2500 cal yr BP can be explained by the
543 presence of local Iron Age activities (Fig. 3). Cooler and wetter-than-previous summer
544 conditions likely inhibited regional fire occurrence (Fig. 7C, D, E), which is why this time period
545 was not identified as a statistically significant zone according to change-point analysis (Fig.4),
546 and why fires were of low severity as suggested by peak magnitudes (Fig. 3). However, fire
547 frequency was sufficiently high to trigger landscape openness and alter the forest canopy
548 composition with a slight decrease in spruce and brief increases in early-successional species
549 (i.e. *Pinus* and *Betula*) around 2500 cal yr BP (Fig. 5). As suggested by Kaplan et al. (2016), the
550 reductions in forest canopy in combination with increases in fire frequency ~2500 cal yr BP
551 further support human presence. Human activities over the last 500 years have significantly
552 altered the local forest composition, as shown by the general decline in *Fagus* and *Abies*, and
553 subsequent increase in landscape openness (Fig. 5). The decline in these two species over the
554 past 500 years is the result of intensive deforestation related to the glass industry and expansion
555 of pasture-land (Beneš, 1996).

556

557 ***5.3 Dominant forest canopy responses to varying fire regimes in central Europe***

558 Fire parameters such as fire frequency, severity, and drivers of biomass burning are not
559 fully understood in central European primary spruce-beech forests. Vegetation composition and
560 their species-level morphological traits significantly influenced the fire regime at Prášílské jezero
561 throughout the Holocene by creating mosaics of different fire regenerative strategies.
562 Specifically, we found three types of fire regenerative strategies; taxa that are classified as either

563 fire resistant, avoidant, or sensitive/intolerant (Fig. 6). Fire resistant taxa typically have thick
564 bark which protects the cambium and increases the species' chance of survival (Nikolov and
565 Helmisaari, 1992; Richardson and Rundel, 1998). Fires are typically more frequent when fire
566 resistant taxa dominate because of their low fire-induced mortality rates (Wooster and Zhang,
567 2004; Rogers et al., 2015). Not surprising, during the early Holocene when biomass burning was
568 the highest and fire severity was of moderate-scale, fire resistant taxa (*Pinus*, *Betula*, and
569 *Corylus*) dominated the landscape (Fig. 5). Modeled fire resistant taxa response curves clearly
570 demonstrate a positive response ($p < 0.01$) to increasing biomass burning (Table 1). *Pinus*
571 *sylvestris* is currently widespread throughout northern and central Europe (Fernandes, 2009), and
572 was the dominant tree species in Europe during the early Holocene (Giesecke et al., 2017). We
573 infer the species was likely present at Prášílské jezero in the early Holocene. *P. sylvestris*
574 responds favorably to fire as it possesses fire resistant morphological traits that enabled it to
575 survive the low-to-moderate fire intensities (Zackrisson, 1977) documented in the early
576 Holocene (Fig. 3). *Pinus* response curves demonstrate a negative relationship with increasing fire
577 severity (Fig. 6), further supporting that this species dominated in the early Holocene because of
578 the moderate-scale fire regime. *Betula* and *Corylus* are also considered fire resistant taxa because
579 of their morphological traits which allow the species to quickly colonize post-disturbance soils
580 and resprout vegetatively (Bradshaw et al. 2010; Delarze et al., 1992; Niklasson & Granström
581 2000; Feurdean et al., 2017). *Betula* is able to outcompete other species on freshly exposed
582 mineral soil (Clark et al., 1989), and *Corylus* is considered a fire-enhanced shrub (Tinner et al.,
583 2000). Interestingly, while not significant the *Corylus* response curve suggest a positive
584 relationship with increasing fire severity (Fig. 6). Together, the fire resistant morphological traits

585 described above support the recruitment and dominance of *Pinus* (likely *P. sylvestris*), *Betula*,
586 and *Corylus* during the early Holocene.

587 Fire avoidant taxa typically lack fire-adapted traits such as thick bark, and are usually
588 found in mesic environments where fires are infrequent (Rogers et al., 2015). *Picea abies* is
589 considered a fire avoider because it lacks morphological traits that allow it to survive or
590 recolonize quickly after a fire (Feurdean et al., 2017; Zackrisson, 1977; Pennanen, 2002).
591 Specifically, *Picea abies* has thin bark and shallow roots making it susceptible to both drought
592 and fire (Zackrisson, 1977). However, its low hanging branches create ladder fuels conducive for
593 crown fires during extreme climatic events (Grooth et al., 2013; Rogers et al., 2015; Feurdean et
594 al., 2017). Because of these morphological traits, we would expect a drastic change in biomass
595 burning with the arrival and expansion of *Picea*. Yet, the establishment and expansion of *Picea*
596 occurred when fire resistant taxa were still abundant (Fig. 5), and when biomass burning was at
597 its highest and most severe of the entire record (Fig. 3). Our results agree with other
598 paleoecological records that also document an increase in *Picea* during a period of high fire
599 activity (Carcaillet et al., 2007; Brown and Gisecke, 2014; Clear et al., 2015). However, there
600 appears to be some discrepancy regarding spruces' relationship with fire. For example, both
601 Clear et al. (2015) and Finsinger et al. (2016) documented the subsequent decline in fire activity
602 once *Picea* established as the dominant canopy, which differs from our findings. Feurdean et al.
603 (2017) also documented the decline in *Picea abies* abundance during times of increased fire
604 severity/area burned in the Carpathians Mountains. Lastly, Ohlson et al. (2011) synthesized 75
605 macroscopic charcoal records throughout Scandinavia and found that the expansion of *Picea* in
606 the late Holocene caused the decline in fire activity across the region by altering microclimate
607 conditions. While not statistically significant, the modeled response curve for *Picea abies* does

608 not show a dramatic decrease to increasing biomass burning (Fig. 6; Table 1). Rather, response
609 curves illustrate a positive relationship between *Picea* and increasing fire severity (Fig. 6).
610 Rogers et al. (2015) found that fire avoidant forests in Eurasian boreal forests exhibit
611 significantly higher severity metrics than fire resistant forests, highlighting the contradictions in
612 fire-related traits of *Picea abies*. The modeled response of *Picea* may suggest that central
613 European temperate spruce forests may not be as severely impacted by high levels of biomass
614 burning, and may benefit from infrequent high-severity fires. However, additional research is
615 needed to validate this relationship.

616 Lastly, similar to fire avoidant taxa, fire sensitive/intolerant taxa do not have fire-adaptive
617 traits. *Fagus sylvatica* is considered to be fire sensitive because of its morphological traits such
618 as relatively thin bark and shallow root systems, and the lack of persistent resprouting
619 capabilities (Peters, 1997; Packham et al., 2012). Not surprising, the greatest change in regional
620 biomass burning occurred when *Fagus* expanded ~6500 cal yr BP. The modeled *Fagus* response
621 clearly illustrates this statistically significant negative relationship with increases in biomass
622 burning, as well as with increasing fire severity (Table 1). These modeled results are similar to
623 those made by Tinner et al. (2000) who demonstrated a negative relationship with *Fagus* pollen
624 and increasing charcoal influxes. The authors classified *Fagus* as fire sensitive because fires
625 typically result in considerable decreases in the species, but surprisingly does not result in local
626 extinction (Tinner et al., 2000). Recent field observations demonstrate the potential of beech in
627 taking advantage of newly exposed soils after a single, mixed severity fire event (van Gils et al.
628 2010; Maringer et al., 2012; Ascoli et al., 2013), by favoring seed germination and seedling
629 emergence, and promoting diffuse light conditions via canopy openings (Ascoli et al., 2015).
630 Several paleoecological records from central Europe also demonstrate the benefit of mixed

631 severity fire regimes in beech forests (Tinner et al., 1999; Tinner and Lotter, 2006; Giesecke et
632 al., 2007). Beech can persist in a mixed severity fire regime as long as the fire return interval are
633 >50 years, which allows for trees to reach reproductive maturity (Ascoli et al., 2015). High
634 severity fires result in low seed production (Ascoli et al., 2015), which is supported by the
635 modeled response curve (Fig. 6b), and support existing literature that suggest that high-severity
636 fires are detrimental to the species. However, the modeled response curve does not support the
637 notion that mixed severity fires are beneficial for beech propagation. This could be explained by
638 the fact that our results are from a relatively high-elevation lake where spruce has been the
639 dominant forest canopy taxa for the past ~9000 years (Carter et al., 2018). Thus, these results
640 may not be representative of true beech-fire dynamics. Additional long-term research is needed
641 from pure beech and/or beech dominated forests to determine whether infrequent mixed severity
642 fires are beneficial in these forested systems.

643 Pollen and charcoal-based taxa response curves offer a deeper insight into the full suite of
644 ecological responses that may occur under future climate change. For instance, climate models
645 project a 3°C increase in temperatures in central Europe (Christensen et al., 2007), which may
646 increase the likelihood of more frequent and intense summer droughts across central and
647 southern Europe (Gao and Giorgi, 2008; Feyen and Dankers, 2009). As a result, the risk of fire
648 across central Europe is predicted to increase (Lung et al., 2013). Together, increased summer
649 droughts and fire risk may be detrimental for primary spruce and beech forests. Spruce is likely
650 to be the species most impacted by climate change (Bolte et al., 2009), with projections
651 predicting the loss of available habitat for spruce (Hanewinkel et al., 2012). Since 1920, reduced
652 rates of disturbance have contributed to the increase in disturbance susceptibility among primary
653 spruce forests across central and eastern Europe (Schurman et al., 2018) highlighting the species'

654 vulnerability to increasing exposure to extreme climatic events. Where beech naturally
655 predominates will also likely be threatened with increasing temperatures (Cheddadi et al., 2016).
656 Response curves demonstrate the fragility of primary beech forests to increased biomass burning,
657 while spruce forests may benefit from increased biomass burning. However, additional long-term
658 fire history research is strongly encouraged from central European primary spruce-beech forests
659 to determine how sensitive these forests may be as a result of changing fire regimes.

660

661 **6. Conclusions**

662 Currently, fire is considered a negligible disturbance agent in central European temperate
663 forests. Yet, the results of this study support emerging literature demonstrating that fires have
664 been an important disturbance agent throughout the Holocene in temperate forests (e.g. Clark et
665 al., 1989; Bobek et al. 2017; Niklasson et al., 2010; Novák et al. 2012). The results of this study
666 also illustrate the complex relationship between the primary drivers of fire (i.e. climate,
667 vegetation type, and human activities) in influencing the long-term fire regime. Climate and
668 vegetation type were likely the dominant drivers responsible for synchronizing regional biomass
669 burning in central Europe in the early Holocene. However, we acknowledge that human
670 occupation beginning as early as the Upper Palaeolithic/Mesolithic period may have contributed
671 to the local fire regime, but likely did not override climate as the dominant driver in the early
672 Holocene. When climatic conditions became more favorable for the more fire sensitive species
673 *Fagus* beginning ~6500 cal yr BP, regional biomass burning decreased. However, local fire
674 frequency only slightly decreased to an average of 2 fires/1000 years suggesting the relative
675 importance of either humans and/or rare fire-promoting climatic events post 6500 cal yr BP.
676 Human activities had a clear impact on the local fire regime ~2500 cal yr BP when the local fire

677 frequency increased to 6 fires/1000 years simultaneous to small increases in human pollen
678 indicators and small-scale changes in the forest canopy. Drastic changes in forest canopy
679 occurred over the past 1000 years as a result of human land-use activities, resulting in increases
680 in regional biomass burning and landscape openness.

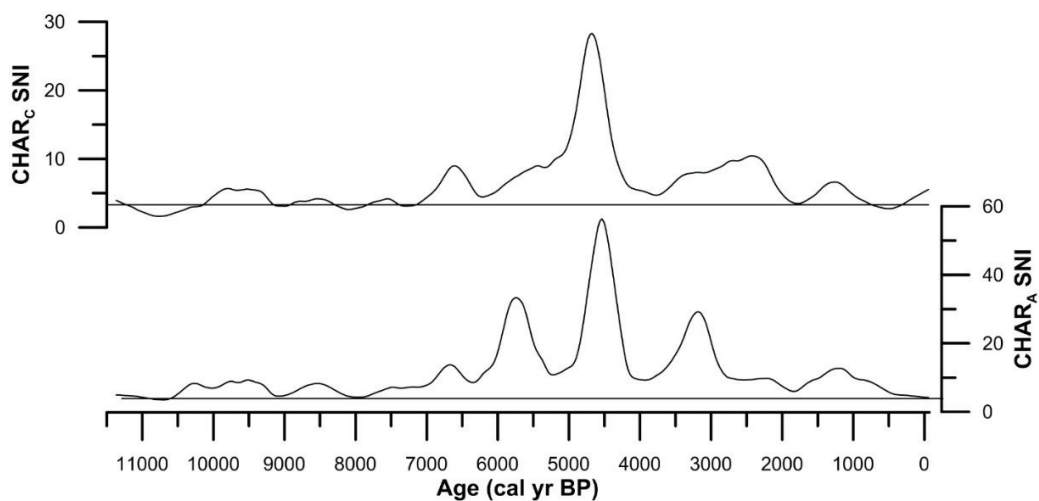
681 Vegetation composition significantly influenced the local fire regime at Prášilské jezero,
682 creating mosaics of different fire regenerative strategies; taxa that are classified as either fire
683 resistant, avoidant, or sensitive/intolerant. Response curves demonstrate that fire resistant taxa
684 *Pinus*, *Betula*, and *Corylus* thrived under high biomass burning, and a relatively frequent fire
685 regime comprised of moderate-scale fire severities during the early Holocene. *Picea*, established
686 ~10,000 cal yr BP and became the dominant canopy species by ~9000 cal yr BP. The rise of
687 *Picea* occurred when biomass burning and fire severities were the highest of the entire record.
688 While not statistically significant, response curves for this fire avoidant taxa suggest that *Picea*
689 may be less impacted by fire than conventionally thought. Finally, response curves for the fire
690 sensitive taxon, *Fagus* demonstrate the species intolerance to increased biomass burning and fire
691 severities. These modeled response curves disagree with emerging literature suggesting beech
692 forests may benefit from an infrequent (>50 years/fire) and mixed severity fire regime (Ascoli et
693 al., 2015). Rather, response curves demonstrate the fragility of primary beech forests to increased
694 biomass burning, while response curves suggest that primary spruce forests may benefit from
695 increased biomass burning. However, additional research is necessary from central European
696 spruce-beech forests to determine whether these modeled response curves are valid.

697 As climate projections forecast a 3°C increase in temperatures in central Europe
698 (Christensen et al., 2007), as well as the increased likelihood in extreme climate events such as
699 more frequent and intense heat-waves and drought (Gao and Giorgi, 2008; Feyen and Dankers,

700 2009; Rajczak et al., 2013; Seneviratne et al. 2012), these variables will likely lead to the
701 increased risk of wildfire in central Europe. With an increase in temperatures, heat stress, and
702 increased risk of wildfires (Lung et al., 2013), primary spruce and beech forests may be the one
703 of the most vulnerable forested ecosystems to climate change. Additional long-term fire histories
704 from central European temperate forests are crucial to determine how vulnerable spruce-beech
705 forests are to anthropogenically-induced climate change and increasing fire risk.

706

707 **Supplementary Information**

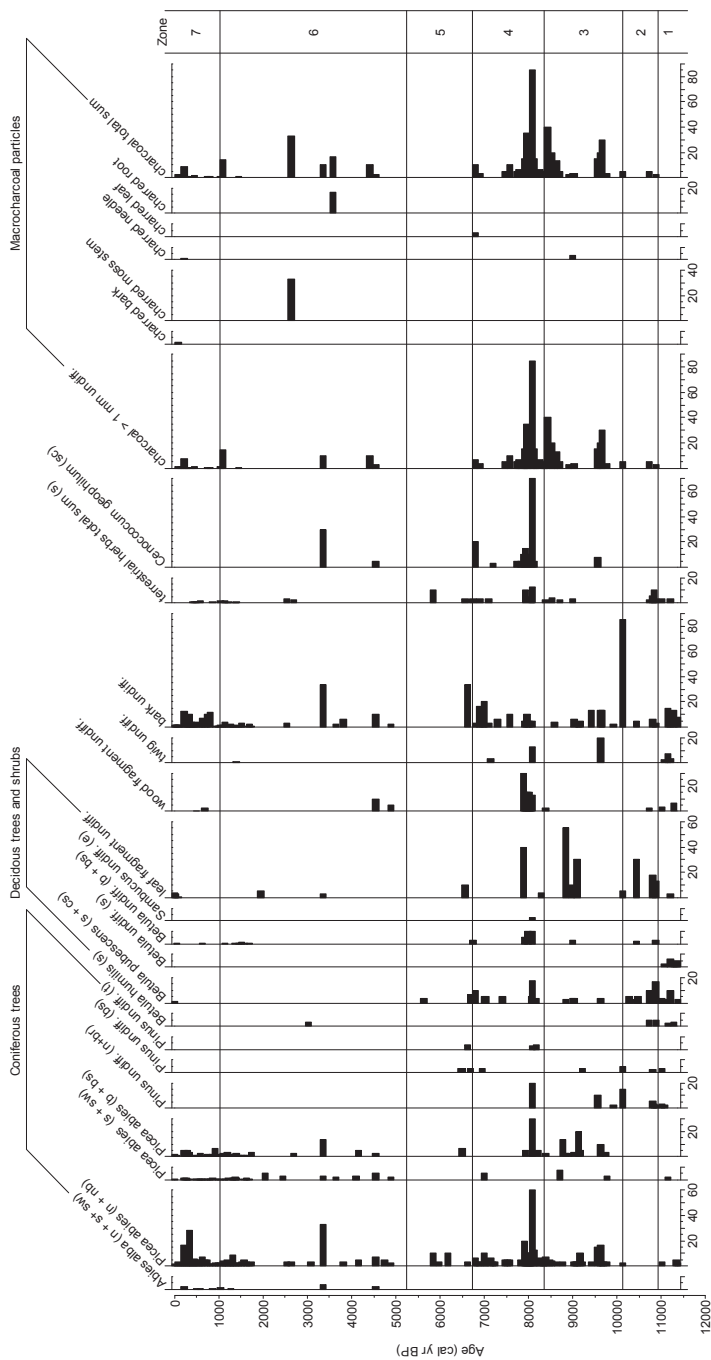


708

709

710 Appendix Fig. 1. Signal-to-noise (SNI) information for both CHAR_C and CHAR_A for Prášilské
711 jezero. Horizontal black line indicates robust signal-to-noise index threshold level of 3.0 (Kelly
712 et al., 2011).

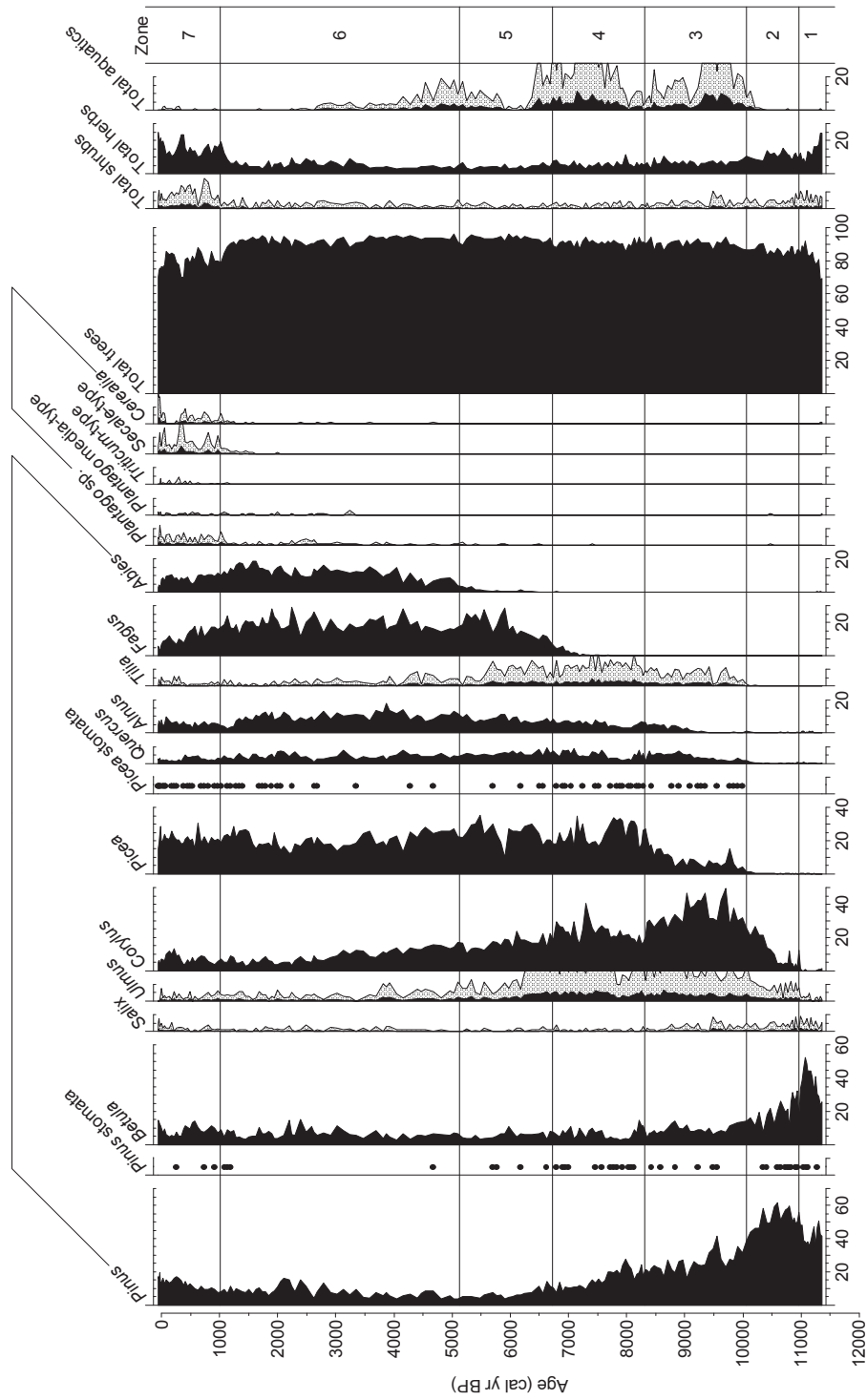
713



714

715 Appendix Fig. 2. Full macrofossil concentration diagram for Prášílské jezero. Abbreviations: b =
 716 bud, br = brachyblast, bs = bud scale, cs = catkin scale, e = endocarp, n = needle, nb = needle
 717 base, s = seed, sc = sclerotium, sw = seed wing, t = twig. Vegetation assemblage zones

718 correspond with the pollen assemblage zones, and were assessed using the broken stick model
 719 (Bennett, 1996).



720

721 Appendix Fig. 3. Condensed pollen percentage diagram for Prášilské jezero. Pollen vegetation
 722 assemblage zones were assessed using the broken stick model (Bennett, 1996).

Depth below water level (cm)	Core ID	¹⁴C Age ± 2σ_b	²¹⁰Pb age (Year AD)	Age (cal yr BP)	Material Dated	Lab ID number
1480	PRA 15- 2GC		2015 ± 1	-65		Surface
1480.5	PRA 15- 2GC		1995 ± 2	-55		Pb210-1
1481.5	PRA 15- 2GC		1986 ± 3	-36		Pb210-2
1482.5	PRA 15- 2GC		1976 ± 4	-26		Pb210-3
1483.5	PRA 15- 2GC		1963 ± 4	-13		Pb210-4
1484.5	PRA 15- 2GC		1943 ± 5	7		Pb210-5
1485.5	PRA 15- 2GC		1918 ± 7	32		Pb210-6
1486.6	PRA 15- 2GC		1889 ± 9	61		Pb210-7

1487.5	PRA 15- 2GC		1861 ± 12	89		Pb210-8
1500.5	PRA 15- 2-1	590 ± 30			Bulk sediment	Poz-84783
1539.2	PRA 15- 2-1	2545 ± 30			<i>Picea abies</i> needle	Poz-81580
1571.75	PRA 15- 2-2	4040 ± 35			<i>Picea abies</i> needles	Poz-81582
1599.75	PRA 15- 2-2	5700 ± 40			<i>Picea abies</i> needle	Poz-81583
1628.5	PRA 15- 2-1	7055 ± 40			<i>Picea abies</i> needle, and wood fragment	Poz-87722
1628.5	PRA 15- 2-2	7550 ± 40			<i>Picea abies</i> needles	Poz-80182
1637	PRA 15- 2-2	7460 ± 40			<i>Picea abies</i> needles	Poz-87724
1651	PRA 15- 2-2	8210 ± 50			<i>Picea abies</i> needle and <i>Picea abies</i> bud scale	Poz-84781

1669.5	PRA 15- 2-2	9330 ± 60			<i>Picea abies</i> needles, <i>Betula</i> bud scales, and leaf fragments	Poz-81780
1690.25	PRA 15- 2-2	9620 ± 50			<i>Picea abies</i> seed	Poz-80183

723

724 Supplementary Table 1. Summary of geochronological data (¹⁴C and ²¹⁰Pb measurements) for
725 Prášílské jezero.

726

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739

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742

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