

1 **Causes and mechanisms of synchronous succession trajectories in**
2 **primeval Central European mixed *Fagus sylvatica* forests**

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15 **Running headline**

16 Synchronous succession in *Fagus sylvatica* forests

17 **Abstract**

18 1. Natural succession trajectories of Central European forest ecosystems are poorly
19 understood due to the absence of long-term observations and the pervasive effects of past
20 human impacts on today's vegetation communities. This knowledge gap is significant given
21 that currently forest ecosystems are expanding in Europe as a consequence of global change.

22 2. Annually laminated sediments were extracted from two small lowland lakes (Moossee 521
23 m a.s.l.; Burgäschisee 465 m a.s.l.) on the Swiss Plateau. We combine high-resolution
24 palaeoecological and quantitative analyses to assess changes in vegetation during the
25 Neolithic. We test for regionally synchronous land-use phases and plant successional patterns
26 that may originate from complex interactions between human and climatic impacts.

27 3. Mixed *Fagus sylvatica* forests dominated the Swiss Plateau vegetation over millennia.
28 During the period 6,500–4,200 cal year BP, pronounced forest disruptions accompanied by
29 increased fire and agricultural activities occurred at c. 6,400–6,000 cal year BP, 5,750–5,550
30 cal year BP, around 5,400 cal year BP and at 5,100–4,600 cal year BP. Biodiversity increased
31 during these land-use phases, likely in response to the creation of new open habitats. After
32 decades to centuries of land-use, arboreal vegetation re-expanded. In a first succession stage,
33 heliophilous *Corylus avellana* shrubs were replaced by pioneer *Betula* trees. These open
34 arboreal communities were outcompeted within 150–200 years by late successional *F.*
35 *sylvatica* and *Abies alba* forests. Most strikingly, cross-correlations show that these
36 successions occurred synchronously (± 11 years) and repeatedly over large areas ($>1,000$ km²)
37 and millennia.

38 4. *Synthesis*. First notable human impact shaped the primeval mixed *F. sylvatica* forests in
39 Central Europe from c. 6,800–6,500 cal year BP on. Agrarian societies were susceptible to
40 climate changes and we hypothesize that climate-induced, simultaneous agricultural

41 expansion and contraction phases resulted in synchronous regional forest successions.
42 Currently forests are expanding in Central Europe as a result of land abandonment in marginal
43 areas. Our results imply that mixed *F. sylvatica* forests with *A. alba* and *Quercus* may re-expand
44 rapidly in these areas, if climate conditions will remain within the range of the mid-Holocene
45 climatic variability (with summers c. +1–2° C warmer than today).

46

47 **KEYWORDS**

48 Biodiversity, Charcoal, Climate change, Cross-correlations, Fire ecology, Forest resilience,
49 Non-pollen palynomorphs, Palaeoecology and land-use history, Pollen, Swiss Plateau

50

51 **1. INTRODUCTION**

52 European forest ecosystems have expanded over the last decades in response to global
53 change involving increasing land abandonment in marginal regions (FOREST EUROPE, 2015).
54 Most forests are still intensively managed and natural succession is restricted to a few
55 remnant areas (Ellenberg, 2009; Kaufmann, Hauck, & Leuschner, 2018). The direction of
56 ongoing forest change is difficult to assess since the projections are mostly based on short-
57 term observations alone (Willis & Birks, 2006). After disturbance, forest vegetation
58 spontaneously tends towards a late successional stage, which is often unknown because
59 modern forests have been strongly altered by humans over centuries to millennia (Ellenberg,
60 2009; Puhe & Ulrich, 2001). Studying long-term successional patterns in the past (>200 years)
61 provides unique information about vegetation dynamics under quasi-natural conditions, that
62 may help assess future vegetation dynamics (Foster, Schoonmaker, & Pickett, 1990).
63 Specifically, the assessment of vegetation shifts at the onset of the Neolithic, when humans
64 gradually became sedentary in Europe (Guilaine, 2015; Müller, 2015; Schier, 2015). This period

65 provides insights into successional patterns of moderately disturbed forests that were only
66 marginally shaped by human activities under environmental conditions comparable to today
67 (Kalis, Merkt, & Wunderlich, 2003). That information is crucial for nature conservation and
68 forest management in protected areas such as national parks (Feurdean & Willis, 2008;
69 Lindbladh, Niklasson, Karlsson, Björkman, & Churski, 2008; Valsecchi, Carraro, Conedera, &
70 Tinner, 2010).

71 Previous palaeoecological studies in Central Europe have nicely illustrated that early
72 successional (e.g. pioneer herbs, *Corylus avellana*, *Betula*) and late successional stages (*Fagus*
73 *sylvatica*, *Abies alba*) oscillated more frequently and pronouncedly after 6,500 cal year BP
74 (Ammann, 1989; Becker et al., 2006; Kleinmann, Merkt, & Müller, 2015; Rey et al., 2017).
75 Statistical analyses confirmed that prominent changes in vegetation were directly linked to
76 land-use (Gobet, Tinner, Hochuli, van Leeuwen, & Ammann, 2003; Rey et al., 2013; Schwörer,
77 Colombaroli, Kaltenrieder, Rey, & Tinner, 2015; Tinner, Hubschmid, Wehrli, Ammann, &
78 Conedera, 1999). Fires were commonly used to open landscapes to create space for
79 settlements, pastoral and arable land (Jacomet et al., 2016; Tinner, Conedera, Ammann, &
80 Lotter, 2005), primarily disadvantaging late-successional trees and favouring the expansion of
81 heliophilous herbs and shrubs (Conedera, Colombaroli, Tinner, Krebs, & Whitlock, 2017;
82 Tinner et al., 2000). Many studies numerically show that land-use substantially increased open
83 land biodiversity over the long-term (Colombaroli, Beckmann, van der Knaap, Curdy, & Tinner,
84 2013; Colombaroli & Tinner, 2013; Giesecke, Ammann, & Brande, 2014). However, one crucial
85 question still remains: were the marked vegetation changes spatially synchronous? This
86 question is important to assess the underlying causes of ecosystem change. Synchronism
87 would speak for a superimposed forcing such as climate (i.e. precipitation and/or temperature
88 changes) or, perhaps less likely, concerted cultural activities (Berglund, 2003; Tinner et al.,

89 2003), whereas diachronism would rather point to spatio-temporally randomized land-use
90 phases of local autarchic societies that were acting independently from each other (Rösch &
91 Lechterbeck, 2016). Until now, it was impossible to test these competing hypotheses because
92 available records lacked temporal precision and resolution (Berglund, 2003; Tinner et al.,
93 2003). In this study, we aim to resolve this long-standing question with high-resolution
94 palaeoecological and time-series analyses that rely on varved sediment chronologies reaching
95 exceptional temporal precision of c. ± 20 –50 cal years (Rey et al., 2018). The overarching goal
96 of the study is to explore the nature of re-occurring broad-scale successional patterns in mixed
97 beech forests after moderate human impact to refine existing projections of future forest
98 transformations (Bugmann et al., 2015; Ruosch et al., 2016) under global change conditions
99 that are currently triggering forest expansions in Central Europe and adjacent regions.

100

101 **2. MATERIAL AND METHODS**

102 **2.1. Study sites**

103 The study area is located on the western Swiss Plateau in southern Central Europe (Figure 1).
104 Moossee is a small lake close to the city of Bern at 521 m a.s.l. (47°1'17.0"N, 7°29'1.7"E). The
105 lake has a maximum water depth of 22 meters and a surface area of 0.31 km². Burgäschisee
106 is a small lake further to the northeast (c. 25 km from Moossee) at 465 m a.s.l. (47°10'8.5"N,
107 7°40'5.9"E). It has a maximum water depth of 31 meters and a surface area of 0.21 km². Both
108 lakes are eutrophic today with anoxic waters in the hypolimnion (Guthruf, Zeh, & Guthruf-
109 Seiler, 1999). The present climate is temperate with mean annual temperatures of 8.8°C and
110 an annual rainfall of 1,059 mm at Moossee (data from Bern/Zollikofen at c. 3 km distance,
111 MeteoSwiss, 2017). At Burgäschisee, it is slightly warmer and wetter with mean annual
112 temperatures of 9.1°C and an annual rainfall of 1,088 mm (data from Koppigen, at c. 6 km

113 distance, MeteoSwiss, 2017). The current vegetation at both lakes is dominated by mixed *F.*
114 *sylvatica* forests on the surrounding hills and scattered mixed *Alnus glutinosa-Fraxinus*
115 *excelsior* stands on the lake shores. Most of the flat areas around the lakes are intensively
116 used for agriculture. The region has been important for agricultural activities for millennia as
117 indicated by frequent local archaeological findings dating back to at least 6,800-6,500 cal year
118 BP (Hafner, Harb, Amstutz, Francuz, & Moll-Dau, 2012; Harb, 2017; Wey, 2012).

119

120 **2.2. Corings and chronologies**

121 In 2014, three parallel sediment cores at Moossee and two parallel sediment cores at
122 Burgäschisee were retrieved with a UWITEC piston corer (core diameter: 9 cm, core length:
123 200 cm) in deep parts of the lakes. A total of 7 m of lake sediments were sampled at each site
124 covering c. 9,000 years. For this study, we focus on the Neolithic to Early Bronze Age period
125 (6,500–3,800 cal year BP) during which the sediments are annually laminated (i.e. varved) at
126 both lakes (see Rey et al., 2018).

127 The Moossee chronology is based on 27 terrestrial plant macrofossils and varve counts
128 (Rey et al., 2018). The program OxCal 4.3 (V-sequence; Bronk Ramsey, 1994, 1995, 2001; Bronk
129 Ramsey, van der Plicht, & Weninger, 2001) and the IntCal13 calibration curve (Reimer et al.,
130 2013) were used to estimate the age-depth model (Figure 2a). The Burgäschisee chronology
131 is based on 22 terrestrial plant macrofossils and basic assumptions about the sedimentation
132 rates from a previous chronology (Rey et al., 2017, 2018). Here, the program OxCal 4.3 (U/P-
133 sequences; Bronk Ramsey, 1994, 1995, 2001, 2008; Bronk Ramsey & Lee, 2013) and the
134 IntCal13 calibration curve (Reimer et al., 2013) were used for the estimations of the age-depth
135 model (Figure 2b). Both records indicate fairly regular sedimentation rates for the investigated
136 time interval with an average of 26 years/cm at Moossee and 18.7 years/cm at Burgäschisee.

137

138 **2.3. Pollen, macrofossil, non-pollen palynomorphs and charcoal analyses**

139 All palaeoecological analyses were conducted on the same cores and for the same sample
140 depths (Moossee: 312 samples, Burgäschisee: 308 samples). We applied a contiguous,
141 approximately constant year sampling (10 ± 2 years/sample). For all microscopic analyses
142 (pollen, non-pollen palynomorphs (NPPs), microscopic charcoal), samples of 1 cm^3 were
143 treated with HCl, KOH, HF, acetolysis, sieved with a mesh size of $500 \mu\text{m}$ and mounted in
144 glycerine following standard palynological methods (Moore, Webb, & Collinson, 1991).
145 *Lycopodium* tablets (University of Lund batch no. 1031 with $20,848 \pm 3,457$ spores per tablet
146 for Moossee and University of Lund batch no. 177745 with $18,584 \pm 1,853$ spores per tablet
147 for Burgäschisee) were added prior to the chemical treatment to estimate microfossil
148 concentrations (Stockmarr, 1971). We used palynological keys (Beug, 2004; Moore, Webb, &
149 Collinson, 1991), photo atlases (Reille, 1992) and the reference collection at the Institute of
150 Plant Sciences (University of Bern) to identify pollen and spores under a light microscope at
151 $400\times$ magnification. Phase contrast under $1,000\times$ magnification was used to separate various
152 Cerealia-types (*Hordeum*-type, *Triticum*-type; Beug, 2004). The minimum number of
153 terrestrial pollen grains counted per sample was 500 with a total of 132 (Moossee) and 113
154 (Burgäschisee) identified terrestrial pollen types. The results are presented as percentages of
155 the terrestrial pollen sum (Figures 3 and 4), in which we excluded spores, pollen of aquatic
156 plants and other microfossils (e.g. stomata, algae cells). Pollen can be dispersed by wind over
157 large distances (up to 50 km) and generally represents extra-local to regional vegetation
158 dynamics (Conedera, Tinner, Cramer, Torriani, & Herold, 2006). However, since the sites are
159 rather small (Moossee: 0.31 km^2 , Burgäschisee 0.21 km^2), we assume that the pollen source

160 area only spans several hundred meters to at most a few kilometers (Conedera, Tinner,
161 Cramer, Torriani, & Herold, 2006; Sugita, 1994).

162 Samples for macrofossil analyses (including macroscopic charcoal) had mean volumes
163 of 17.5 cm³ (Moossee) and 11 cm³ (Burgäschisee) and were sieved with a mesh size of 200
164 µm. Terrestrial remains (e.g. *F. sylvatica* bud scales) were identified under a stereo
165 microscope. Macrofossil concentration (remains cm⁻³) were calculated and plotted in Figures
166 3 and 4. Plant macrofossils mainly indicate local vegetation as a result of short dispersal
167 distances (1–100 m; Birks, 2003).

168 Microscopic charcoal particles >10 µm and <500 µm were counted on pollen slides
169 following Tinner and Hu (2003) and Finsinger and Tinner (2005) and presented as microscopic
170 charcoal influx values (particles cm⁻² year⁻¹; Figures 3 and 4). These values were used as a proxy
171 for regional fire activity since microscopic charcoal particles are dispersed over distances of c.
172 20-50 km (Adolf et al. 2018; Tinner et al. 1998).

173 Macroscopic charcoal pieces >600 µm were identified under a stereo microscope
174 during macrofossil analysis. Their occurrence (pieces cm⁻³) may primarily reflect local fire
175 activity within few hundred meters distance (Adolf et al., 2018; Figures 3 and 4). This
176 procedure (large sampling volume, size threshold >600 µm) allows reducing the influence of
177 regional fires on macroscopic charcoal, without using de-trending and peak isolation
178 approaches (Adolf et al., 2018).

179 Green algae (*Botryococcus*, *Tetraedron*, *Coelastrum*) and akinetes of cyanobacteria
180 (*Anabaena*, *Aphanizomenon*) were counted on pollen slides to estimate changes in the trophic
181 levels. Although, single NPP taxa might occur under natural conditions, contemporaneous or
182 consecutive high numbers of green algae and cyanobacteria are considered as a proxy for
183 eutrophication during or after local anthropogenic impacts (van Geel, Mur, Ralska-

184 Jasiewiczowa, & Goslar, 1994; Hillbrand, van Geel, Hasenfratz, Hadorn, & Haas, 2014). All NPPs
185 are presented as percentages of the terrestrial pollen sum (Figures 3 and 4).

186 Local pollen assemblage zones (LPAZ; Figures 3 and 4) were delimited using optimal
187 sum-of-squares partitioning (Birks & Gordon, 1985) with the program ZONE 1.2 (Juggins,
188 1991). Statistically significant zones were assessed with the program BSTICK (Line & Birks,
189 unpublished software) following the broken-stick method (Bennett, 1996). The programs Tilia
190 2.0.41 and CorelDraw were used to plot the data for both high-resolution sequences (Figures
191 3 and 4).

192

193 **2.4. Biodiversity estimations**

194 Rarefaction analysis was used to calculate the palynological richness (PRI), which is commonly
195 used as a proxy for species richness at local to regional scale in many palaeoecological studies
196 (e.g. Birks & Line, 1992; Colombaroli & Tinner, 2013; Odgaard, 1999; Schwörer, Colombaroli,
197 Kaltenrieder, Rey, & Tinner, 2015). Rarefaction analysis allows estimating the number of taxa
198 per sample for a constant counting sum (Birks & Line, 1992), which was 500 at both sites. The
199 probability of interspecific encounter (PIE; Hurlbert, 1971) was used as a measure of
200 palynological evenness. In previous studies PIE was used to evaluate effects of few dominant
201 pollen producers (e.g. *C. avellana*; van der Knaap, 2009) on the palynological assemblages and
202 in particular on palynological richness. To assess such effects, PIE-derived evenness-detrended
203 palynological richness (DE-PRI) was calculated following Colombaroli, Beckmann, van der
204 Knaap, Curdy, and Tinner (2013). This approach aims at removing the evenness trend from
205 palynological richness by building an ordinary least square regression (OLS) between the
206 dependent (PRI) and the independent variable (palynological evenness). The resulting
207 residuals of pollen richness (= PRI - PIE) are then distributed around the original pollen richness

208 values (Colombaroli & Tinner, 2013). Only if PRI and DE-PRI show similar changes and trends,
209 we assume that the species richness estimates are unaffected by evenness effects. The DE-
210 PRI approach has proven to be valuable to estimate contemporary species richness patterns
211 at the European scale (Adolf, 2017). The program R statistics (R Development Core Team,
212 2016) was used for all calculations (see results in Figures 3 and 4).

213

214 **2.5. Time-series analyses (cross-correlations)**

215 Cross-correlations (Gobet, Tinner, Hochuli, van Leeuwen, & Ammann, 2003; Green, 1981; Rey
216 et al., 2013; Tinner, Hubschmid, Wehrli, Ammann, & Conedera, 1999) were calculated to
217 identify leads and lags between fire (microscopic charcoal influx values) and vegetation (pollen
218 percentages, PRI, PIE, DE-PRI) by using the program MYSTAT 12 (Systat, 2007). The time
219 window for all calculations was 6,500–4,150 cal year BP that included 209 samples at Moossee
220 (1 sample = 11.1 ± 0.2 cal years) and 266 samples at Burgäschisee (1 sample = 8.7 ± 0.6 cal
221 years). Cross-correlation coefficients for microscopic charcoal influx values vs. pollen
222 percentages, PRI, PIE and DE-PRI (see Figure 5) were calculated at ± 50 lags corresponding to
223 ± 555 cal years (Moossee) and ± 435 cal years (Burgäschisee), following Bahrenberg, Giese,
224 Mevenkamp, and Nipper (2008), with maximum lag numbers corresponding to one fourth of
225 the sample number N (lag number $\leq N/4$). The correlation coefficients at lag 0 between
226 microscopic charcoal and selected pollen types are represented as detailed correlograms
227 (Figure 6). For cross-correlation analyses between the two sites (e.g. *F. sylvatica* percentages
228 at Moossee vs. *F. sylvatica* percentages at Burgäschisee), the time series with higher time
229 resolution (Burgäschisee) was adjusted to the one with lower resolution (Moossee) by
230 combining neighbouring samples following Tinner et al. (2015). This led to a total of 209
231 samples (1 sample = 1 lag = 11.1 ± 0.2 cal years) and ± 50 lags (= ± 555 cal years) that were

232 included in the cross-correlation calculations (Figure 7). Variables were not de-trended prior
233 to the cross-correlation analyses because the vegetation type remains more or less uniform
234 for the whole time window without pronounced population trends (see Figures 3 and 4;
235 Tinner, Hubschmid, Wehrli, Ammann, & Conedera, 1999). The 95% (2σ) confidence intervals
236 of the correlations were estimated by computing ± 2 standard errors of the correlation
237 coefficients (Bahrenberg, Giese, Mevenkamp, & Nipper, 2008). This corresponds to a two-
238 sided significance level (α) of 5% (Tinner, Hubschmid, Wehrli, Ammann, & Conedera, 1999).

239

240 **3. RESULTS**

241 **3.1. Vegetational, agricultural and fire dynamics**

242 Both studied pollen records (Moossee: 7,000–3,900 cal year BP, Burgäschisee: 6,500–3,800
243 cal year BP) have a high temporal resolution of c. 10 cal years per sample and an extraordinary
244 chronological precision (Rey et al., 2018). Zonation analyses show a high number of significant
245 LPAZ (Moossee: 15, Burgäschisee: 14; see Figures 3 and 4), suggesting high variability of
246 vegetation composition over time. In general, *F. sylvatica* was dominant in the closed forests
247 (pollen percentages generally $\geq 20\%$). This pollen-based interpretation is supported by regular
248 finds of macrofossils (bud scales). Other important taxa in the forests included *Quercus* and *A.*
249 *alba*. The latter shows slightly higher pollen percentages at Burgäschisee (up to 10% instead
250 of 5%), probably as a result of increasing precipitation towards the east of the Swiss Plateau,
251 making the species more competitive under mesophilous conditions (Rey et al., 2017).
252 However, macrofossil and stomata finds of *A. alba* point to local occurrences of the species at
253 both sites. *Alnus glutinosa* was preferably growing on the wet soils at the lake shores as
254 indicated by high and fairly stable pollen percentages (around 25%) and abundant
255 macrofossils finds (e.g. *A. glutinosa* fruits). Pollen percentages of other subordinate taxa such

256 as *Tilia*, *Ulmus* and *Taxus baccata* steadily decrease until c. 5,000 cal year BP after which they
257 remain low (<2%, see *Ulmus*) or even disappear (see *Tilia* and *T. baccata*), most likely as a
258 result of overexploitation and fire disturbance (Rey et al., 2017; Tinner, Conedera, Ammann,
259 & Lotter, 2005). Distinct phases with low *F. sylvatica* pollen percentages (<10%), increased
260 cultural indicators (Cerealia-type, *Plantago lanceolata*, *Linum usitatissimum*-type), apophytes
261 (*Urtica*), other herbs (Poaceae, *Allium*-type) and heliophilous shrubs (*C. avellana*, *Juniperus*)
262 are apparent at both sites. A first phase is dated at 6,550–6,150 cal year BP at Moossee and
263 at 6,300–5,950 cal year BP at Burgäschisee. Subsequently, similar phases occurred at 5,750–
264 5,550 cal year BP, at around 5,400 cal year BP and at 5,100–4,600 cal year BP at both sites.
265 Finally, a last phase is dated around 3,900 cal year BP at Moossee. Periods of forest disruption
266 were generally accompanied by high regional fire activity as suggested by increasing
267 microscopic charcoal influx values (>5,000 particles cm⁻² yr⁻¹), sometimes overlapping with
268 local fire activity as inferred from macroscopic charcoal presence (≥600 μm). This finding is in
269 good agreement with local archaeological evidence (e.g. pile dwellings, light grey bars in
270 Figures 3 and 4). Some settlements around the lake had impacts on the water quality as shown
271 by high numbers of cyanobacteria (*Anabaena*, *Aphanizomenon*) and green algae (*Tetraedron*)
272 between 5,750 and 5,550 cal year BP at both lakes and around 4,600 cal year BP at Moossee.
273 Such blooms are best explained by strong lake water eutrophication. After the settlement
274 phases, *Betula* as a pioneer tree species quickly recolonized abandoned places (pollen
275 percentages up to 30% and abundant macrofossils). After intermediate phases often with *F.*
276 *excelsior*, *Ulmus* and *Tilia* expansions, these trees were unremittingly replaced within 150–200
277 years by late successional tree species (*F. sylvatica*, *A. alba*) if no further disturbances
278 occurred. These succession cycles were simultaneously repeated at both sites and are not only

279 visible in the pollen percentage data but are also confirmed by plant macrofossils, indicating
280 possible broad-scale succession trajectories.

281

282 **3.2. Biodiversity reconstruction**

283 Palynological richness (PRI) and evenness-detrended palynological richness (DE-PRI) show
284 good agreements (Figures 3 and 4), suggesting that overall trends in palynological richness are
285 not strongly affected by evenness. PRI and DE-PRI generally increase during phases with higher
286 human impact (>25 pollen types per sample), i.e. around 6,400 cal year BP, 4,600 cal year BP
287 and 3,900 cal year BP at Moossee, at 5,700–5,600 cal year BP at both sites, and around 4,900
288 cal year BP at Burgäschisee. These increases are directly related to vegetation openings and
289 the introduction of cultivated plants (*Hordeum*-type, *Triticum*-type, *L. usitastissimum*-type).
290 The establishment of open land for Neolithic farming created new habitats for short-lived
291 weeds (*P. lanceolata*), apophytes (*Urtica*) and light-demanding shrubs (*C. avellana*, *Sambucus*
292 *nigra*). Palynological evenness as inferred from PIE (Figures 3 and 4) is more or less stable (PIE
293 around 0.85). Slightly lower values of palynological evenness (PIE around 0.8) are recorded in
294 phases when either *Betula* or *F. sylvatica* pollen grains are dominant and the forests were
295 rather closed, suggesting that the expansion of monospecific stands may have affected species
296 evenness. On the other hand, phases with open forests (e.g. 5,700–5,600 cal year BP at both
297 sites) have usually high palynological evenness values (PIE ≥ 0.85), suggesting that vegetation
298 evenness is correlated to openness.

299

300 **3.3. Time-series analyses**

301 At both sites, pollen percentages of trees have significant negative correlations with
302 microscopic charcoal influx (maximum negative correlations at lag 0; Figure 5). *F. excelsior* is

303 a good example to illustrate immediate negative fire impacts. The negative correlations of *F.*
304 *sylvatica* pollen percentages is, however, markedly delayed at both sites (c. 320 years after a
305 fire at Moossee respectively c. 80 years after a fire at Burgäschisee), possibly indicating a
306 slightly higher fire tolerance compared to other tree species (Tinner et al., 2000). On the other
307 hand, pollen percentages of herbs (e.g. *Cerealia*-type) reach maximum positive correlations
308 with microscopic charcoal at lag 0, showing that agropastoral activities were strongly
309 connected to the use of fire. Similarly, correlations between microscopic charcoal influx and
310 PRI, DE-PRI and at Moossee also PIE suggest that biodiversity increased in the new habitats
311 (i.e. open areas) created by anthropogenic burning for agricultural purposes. Pollen
312 percentages of shrubs such as *C. avellana* and *Salix* also have significant positive correlations,
313 e.g. at Burgäschisee maximum positive correlations are reached at lag +4 for *C. avellana* (c. 35
314 years after a fire) and at lag 0 for *Salix* (Figure 5b). *Betula* shows maximum positive correlations
315 at lag +35 (c. 390 years after a fire; Figure 5a) at Burgäschisee and at lag +41 (c. 355 years after
316 a fire; Figure 5b) at Moossee. This result with *C. avellana* preceding *Betula* pollen percentages
317 is likely caused by the successional trajectories after fire disturbance. Later on, the recovery
318 of *F. excelsior* follows (lag +41 and lag +45, corresponding to c. 455 and c. 390 years) after the
319 fire-related decline (negative correlations) as well as *F. sylvatica* (lag +50 = c. 435 years; Figure
320 5b). Correlation coefficients at lag 0 between microscopic charcoal influx values and pollen
321 types or PRI, PIE and DE-PRI show similar linkages (Figure 6), with significant positive
322 correlations for cultural indicators (*Hordeum*-type, *Triticum*-type), other herbs (e.g. *Allium*-
323 type, *Mentha*-type, *Papaver rhoeas*-type, *Urtica*), PRI, DE-PRI and shrubs (e.g. *C. avellana*,
324 *Salix*, *S. nigra*). In contrast, most tree pollen types (e.g. *Quercus*, *F. excelsior*, *F. sylvatica*,
325 *Ulmus*, *T. baccata*) have significant negative correlations with microscopic charcoal,
326 suggesting that forest trees were most affected by anthropogenic burning. However, A.

327 *glutinosa*-type as an important tree pollen type is indifferent showing neither significant
328 positive nor negative correlations with charcoal-inferred fire incidence.

329 If cross-correlations are used to compare the two sites, a striking pattern appears
330 (Figure 7). Total shrubs and trees as well as some taxa (e.g. *C. avellana*, *Betula*, *F. sylvatica*,
331 *Tilia*) show pronounced positive correlations with maximum correlations at lag 0, suggesting
332 synchronous oscillations within the pooled sample resolution (11.1 ± 0.2 cal years). Cross-
333 correlations between pollen percentages of herbs (Moossee data vs. Burgäschisee data), *F.*
334 *excelsior* and *A. alba* only slightly differ and may reflect local vegetation variability, however,
335 significant positive correlations also center around lag 0 with maximum positive correlations
336 within c. ± 35 years. Of particular interest are the correlations for the cereals, that also show
337 this pattern, confirming that the cultural phases at the two sites were largely coeval with only
338 minor differences, possibly indicating positive synergy effects of cereal production in old and
339 new prehistoric centres. Similarly, also PRI and DE-PRI co-vary in time at the two sites. Taken
340 together, these results quantitatively show that the general succession patterns after
341 disturbance were not only similar as presented in Figures 3 and 4 but in fact synchronous at
342 the two sites.

343

344 **4. DISCUSSION**

345 **4.1. Impacts of land-use on temperate forests and synchronous patterns of forest** 346 **succession after disturbances**

347 The palaeobotanical data suggest the dominance of mixed beech forests over millennia at our
348 two study sites Burgäschisee and Moossee. Land-use phases contributed to openings and a
349 gradual conversion from mixed beech to almost pure beech forests. These general patterns
350 have been observed elsewhere in the lowlands of southern Central Europe after c. 7,000 cal

351 year BP (e.g. Ammann, 1989; Kleinmann, Merkt, & Müller, 2015; Rösch & Lechterbeck, 2015;
352 Tinner & Ammann, 2005; Tinner, Conedera, Ammann, & Lotter, 2005). However, local
353 differences in species composition resulted from dissimilar environmental conditions. For
354 instance in Switzerland, moisture availability increases towards higher elevations and to the
355 east. This moisture gradient may have led to the co-dominance of *A. alba* in the forests (Gobet
356 & Tinner, 2012; van der Knaap, van Leeuwen, & Ammann, 2004; Lotter, 1999; Wehrli, Tinner,
357 & Ammann, 2007), given that as the most shade tolerant and tallest tree species of Europe,
358 silver fir is particularly competitive under mesophilous conditions (Ellenberg, 2009; Ruosch et
359 al., 2016; Tinner et al., 2013). Conversely, drier conditions in the Lake District (Seeland) in the
360 rain shadow of the Jura Mountains may have promoted *Quercus* spp. including
361 submediterranean *Q. pubescens* (Ammann, 1989; Hadorn, 1992; Steiger, 2010).

362 Several diebacks of mixed *F. sylvatica* forests occurred between 6,400 and 6,000 cal
363 year BP, at 5,800–5,650 cal year BP, 5,400–5,300 cal year BP, at 5,100–4,700 cal year BP at
364 both sites and around 3,900 cal year BP at Moossee only. The combined charcoal and pollen
365 evidence as well as the cross-correlation analyses suggest that burning was used as a tool for
366 opening the mixed *F. sylvatica* forests, creating a mosaic of new habitats that advantaged
367 many herbaceous species, increasing the overall biodiversity (see biodiversity estimations in
368 Figures 3 and 4). A similar pattern has been reconstructed in previous studies and might be
369 typical for European landscapes (Colombaroli, Beckmann, van der Knaap, Curdy, & Tinner,
370 2013; Colombaroli & Tinner, 2013; Giesecke, Ammann, & Brande, 2014). Prehistoric slash-and-
371 burn activities were strong enough to release a wide-scale expansion of early-successional
372 shrublands, typically dominated by *C. avellana*, *Betula* and *Alnus* (Aaby, 1986; Tinner,
373 Conedera, Ammann, & Lotter, 2005; Tinner, Hubschmid, Wehrli, Ammann, & Conedera, 1999).
374 In contrast, most tree species were strongly reduced by fires and other human disturbances

375 such as logging, pollarding and browsing (e.g. Haas, Karg, & Rasmussen, 1998; Haas &
376 Schweingruber, 1993; Pott, 1985; Tinner, Hubschmid, Wehrli, Ammann, & Conedera, 1999).
377 Most interestingly, some tree species such as *F. sylvatica* and *A. alba* seem to have fully
378 recovered and even expanded after forest disruptions (within c. 150–200 years after a land-
379 use phase), suggesting long-term resilience to moderate human disturbance, while others
380 (*Ulmus*, *Tilia*, *Acer* and *T. baccata*) markedly diminished, suggesting high sensitivity of these
381 species. Ultimately, at c. 5,000 cal year BP (Figure 3 and 4) this process of repeated
382 disturbances led to a strong impoverishment in species diversity of forest ecosystems (Tinner
383 & Ammann, 2005), generating the advent of monospecific forests that are characteristic for
384 Central European landscapes today (e.g. almost pure spruce, beech, larch, oak stands,
385 depending on altitude and other environmental conditions; Ellenberg, 2009; Gobet, Vescovi,
386 & Tinner, 2010).

387 Here, we quantitatively demonstrate for the first time that forest succession cycles
388 over 3,000 years were regionally synchronous (Figure 7). The distance between the two sites
389 (c. 25 km) exceeds the expected pollen catchment expected for the two study sites (most
390 pollen from within a few hundred meters to at most a few kilometers; Conedera, Tinner,
391 Cramer, Torriani, & Herold, 2006), arguing for coeval population dynamics over the millennia
392 within the time resolution and precision available (c. 20–50 cal years; Rey et al., 2018).
393 Because this pattern was found in the cross-correlation analyses for several tree taxa as well
394 as for the tree percentage sum, we consider it to be very reliable. Synchronous forests
395 disruptions (tree pollen <80%) may have occurred at several distant sites in Central and
396 Southern Europe (Figure 8). The few available high-resolution (c. 10–20 years) and high-
397 precision (sufficient radiocarbon dates on terrestrial material) time series covering the entire
398 Neolithic and the onset of the Bronze Age reveal coeval tree population reductions at c. 6,400–

399 5,900 cal year BP, 5,750–5,600 cal year BP, 5,400 cal year BP, 5,100–4,700 cal year BP and
400 around 3,900 cal year BP (Ammann, 1989; Kleinmann, Merkt, & Müller, 2015; Lotter, 1999;
401 Rösch, Kleinmann, Lechterbeck, & Wick, 2014a, b; Tinner, Hubschmid, Wehrli, Ammann, &
402 Conedera, 1999; Wehrli, Tinner, & Ammann, 2007). One of these sites, Lago di Origlio, is
403 located in the lowlands south of the Alps (Sottoceneri), where environmental conditions are
404 typical for submediterranean Southern Europe (warmer summers, milder winters). We thus
405 hypothesize the existence of supra-regional synchronicity of forest disturbances during the
406 Neolithic, as it was formerly advocated for Central and Southern Europe (including Sicily) for
407 the Bronze Age, the Iron Age, the Roman Period and the subsequent early medieval times
408 (Finsinger & Tinner, 2006; Gobet, Tinner, Hochuli, van Leeuwen, & Ammann, 2003; Tinner et
409 al., 2003, 2009).

410

411 **4.2. Possible impacts of climate on land-use phases**

412 Simultaneous broad-scale deforestation phases over large areas caused by land-use may
413 mainly reflect superimposed causes such as climate change (e.g. Berglund, 2003; Tinner et al.,
414 2003, 2009). Our study sites showing coeval vegetation succession patterns are both located
415 in landscapes providing fertile arable lands (Guthruf, Zeh, & Guthruf-Seiler, 1999). They are
416 mostly lacking major in- and outflows, thus settlements around the lakes, especially at the
417 shores (e.g. pile dwellings) may have been affected by lake level changes (Guthruf, Zeh, &
418 Guthruf-Seiler, 1999). We here assume that people settled at lower elevations preferably near
419 lake shores/rivers during warm and dry phases and subsequently moved upwards to slightly
420 higher elevations during cool and wet phases. Thus, the more densely populated warm and
421 dry phases might be preferentially reflected in the archaeological and dendrochronological
422 records e.g. at Lake Biel (Fischer, Hafner, Stapfer, Marti, & Affolter, 2017; Hafner & Suter,

423 2000; Stöckli, 2016; Suter, 2017) and Lake Zurich (Bleicher et al., 2017), whereas the fewer
424 settlements on dry soils during cool and wet phases (e.g. hilltop sites) were more exposed to
425 erosion, hence artifacts are scarce.

426 Common land-use phases across Central and Southern Europe were possibly driven by
427 temperature oscillations, which were usually associated with moisture changes. After 8,200
428 cal year BP, warm periods in and around the Alps were generally associated with dry
429 conditions, while decadal to centennial scale cold excursions were wetter, comparable to the
430 conditions during the Little Ice Age (Haas, Richoz, Tinner, & Wick, 1998; Tinner & Lotter, 2006).
431 Indeed wet phases, as reconstructed from lake-level proxies occurred at around 6,300, 5,500
432 and 4,200 cal year BP (Magny, 2004, 2013), when crop production around the lakes was low.
433 The linkage to warm phases as reconstructed from tree-ring records (Bircher, 1982, 1986;
434 Renner, 1982) and the Greenland stable oxygen isotope records (Vinther et al., 2006) is less
435 pronounced (Figure 9). Although the Swiss tree-ring records of temperature change are well
436 in line with the Greenland stable oxygen isotope record, the chronological precision of these
437 records (c. ± 50 – 100 cal years) is lower than that of the dendrochronologically dated
438 archaeological evidence (c. ± 5 – 10 years). Previous studies have emphasized the good match
439 between the dendrochronologically dated archaeological phases and solar activity, as
440 reconstructed from the ^{14}C -residuals at multiannual to multidecadal scales (Gross-Klee &
441 Maise, 1997; Kleinmann, Merkt, & Müller, 2015; Magny, 2004, 2013). The link between solar
442 activity and archaeological evidence becomes again evident when comparing the land-use
443 phases at both study sites with the reconstructed average total solar irradiance (TSI;
444 Steinhilber, Beer, & Fröhlich, 2009; see Figure 9). Periods with high solar irradiance
445 corresponded with rather dry conditions (low lake levels) and increases of cultural indicators
446 (sum of cereals, *L. usitatissimum*, *P. lanceolata*), local–regional fires (macroscopic and

447 microscopic charcoal) and biodiversity (PRI). Conversely, periods with lower TSI and wetter
448 conditions (high lake levels) corresponded to land abandonment phases. We assume that
449 under adverse wet and cool conditions agricultural yields collapsed and human population
450 densities declined over large areas, as shown by the excellent agreement across distant sites
451 (Figure 8). Solar irradiance may have additionally advantaged crop production, given that the
452 cereals, which were the main source of calories, originate from the Near East and are adapted
453 to high insolation.

454

455 **4.3. Implications for global change ecology**

456 Our study shows that over the millennia temperate forests dominated by *F. sylvatica* and *A.*
457 *alba* were resilient to prehistoric human impacts in the Swiss Plateau. Forest succession after
458 disturbances generally started with light-loving pioneer species (*C. avellana*, *Betula*) and was
459 completed within 150–200 years by late successional mixed beech forests. Such
460 palaeoecological information might be crucial to develop sustainable strategies for nature
461 conservation and forest management (Feurdean & Willis, 2008; Lindbladh, Niklasson,
462 Karlsson, Björkman, & Churski, 2008; Valsecchi, Carraro, Conedera, & Tinner, 2010),
463 specifically under global-change conditions that are currently releasing forest ecosystem
464 expansions in abandoned rural areas (FOREST EUROPE, 2015). We assume that *F. sylvatica*
465 forests will remain key communities in Central Europe, if future (summer-) climate warming
466 does not exceed the Holocene variability range (c. +1–2°C compared to the 20th century; Heiri,
467 Tinner, & Lotter, 2004). Other trees such as *F. excelsior*, *Tilia* and *Ulmus* might also re-expand
468 under low disturbance levels (e.g. no browsing, no pollarding) provided that no further
469 devastating diebacks due to pathogenic diseases (e.g. *Ulmus*, *F. excelsior*) occur (see Brasier,
470 1991; McKinney, Nielsen, Hansen, & Kjær, 2011). Anticipated climate change (Appenzeller et

471 al., 2011; Kovats et al., 2014), however, with generally lower annual precipitation rates may
472 markedly disadvantage *F. sylvatica* and promote *A. alba* and *Quercus* spp. (including
473 submediterranean *Q. pubescens*) that are less-drought sensitive and thus more competitive
474 under drier conditions (Bugmann et al., 2015; Ellenberg, 2009; Ruosch et al., 2016; Tinner et
475 al., 2013). Predicted higher risk of forest fires (Kovats et al., 2014) may affect fire-sensitive *A.*
476 *alba* (Tinner et al., 2013), or conversely *A. alba* and the expansion of mediterranean evergreen
477 trees (e.g. *Quercus ilex*) may further reduce fire incidence because of positive feedbacks
478 mainly related to decreased biomass flammability (Henne et al., 2015, 2018).

479

480 **5. CONCLUSIONS**

481 We numerically demonstrate for the first time that vegetation dynamics at two distant sites
482 were synchronous over more than 2,000 years, with a pooled sampling resolution of 11 years.
483 Interactions between the first agrarian societies and their environment were complex, with
484 humans significantly shaping vegetation structure (creation of open land, shrublands) and
485 composition (shift in species). Conversely, the rise and fall of early farming societies was likely
486 dependent on climate. Favourable climatic conditions (i.e. warm and dry summers) probably
487 led to an increase in agricultural yields, the expansion of farming activities and resulting forest
488 openings, whereas unfavourable climatic conditions (i.e. cold and wet summers) likely caused
489 crop failures, abandonment of agricultural areas and forest succession. A better
490 understanding of the environmental and societal factors controlling coeval land-use
491 dynamics as shown in this study would require new climate proxy data (e.g. temperature
492 reconstruction from well dated and complete Holocene tree ring series). On the basis of our
493 results and considering the ongoing spread of temperate forests in lowland Central Europe,
494 we conclude that the existing beech forest ecosystems are resilient to anthropogenic

495 disturbances under a changing climate, if the amplitude does not exceed the range of
496 Holocene climate variability. Our results also indicate that abandoned agricultural land can
497 revert to quasi-natural mixed beech forests within 150–200 years. Climate warming exceeding
498 the Holocene variability range, however, has been identified as an important threshold that
499 might cause the rapid collapse of beech forests, giving way to novel communities that are
500 today restricted to Southern Europe.

501

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511

512 **AUTHORS' CONTRIBUTIONS**

513 F.R. performed all pollen, macrofossil and quantitative analyses, figure construction, and led
514 the writing; E.G. and W.T. initiated and designed the research project and wrote substantial
515 parts of the manuscript; C.S. helped to conduct the biodiversity estimations; A.H. and O.W.
516 provided archaeological data; W.T. and A.H. obtained funding. All authors contributed
517 critically to the drafts and gave final approval for publication.

518

519 **DATA ACCESSIBILITY**

520 The data will be available through the Alpine Palynological Database (ALPADABA) after
521 publication.

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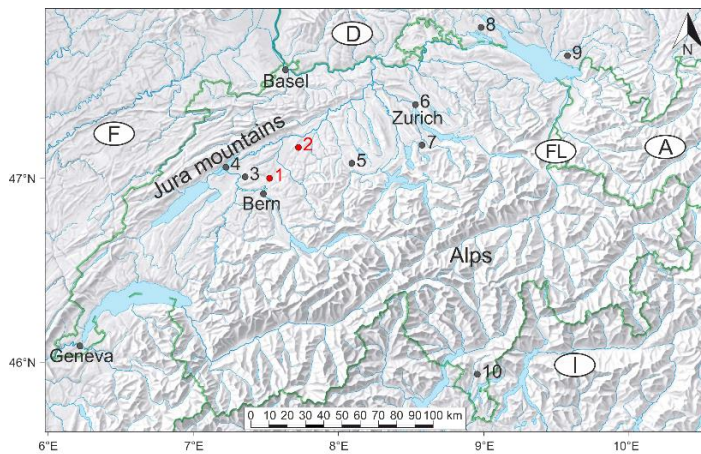
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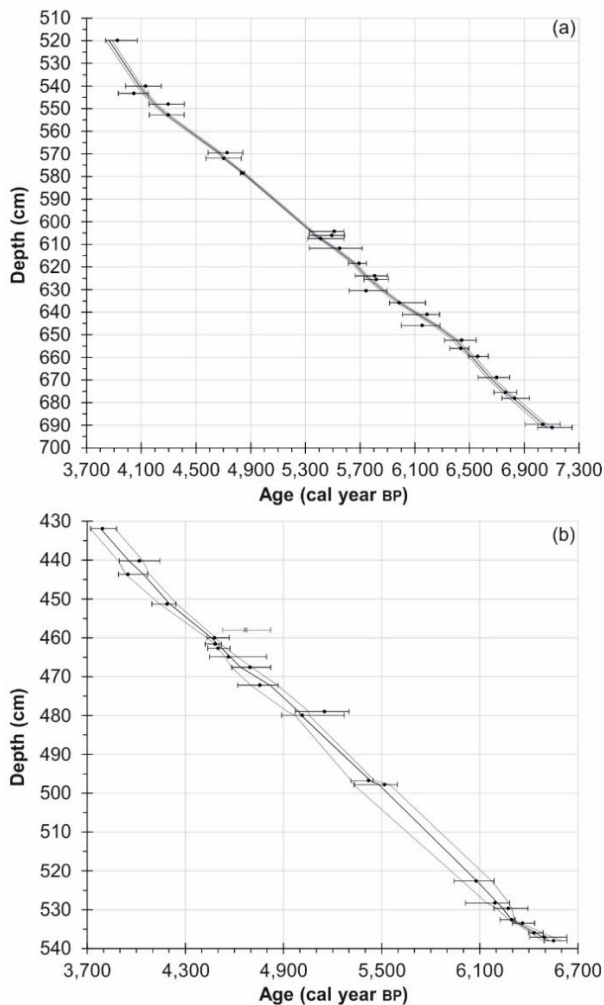
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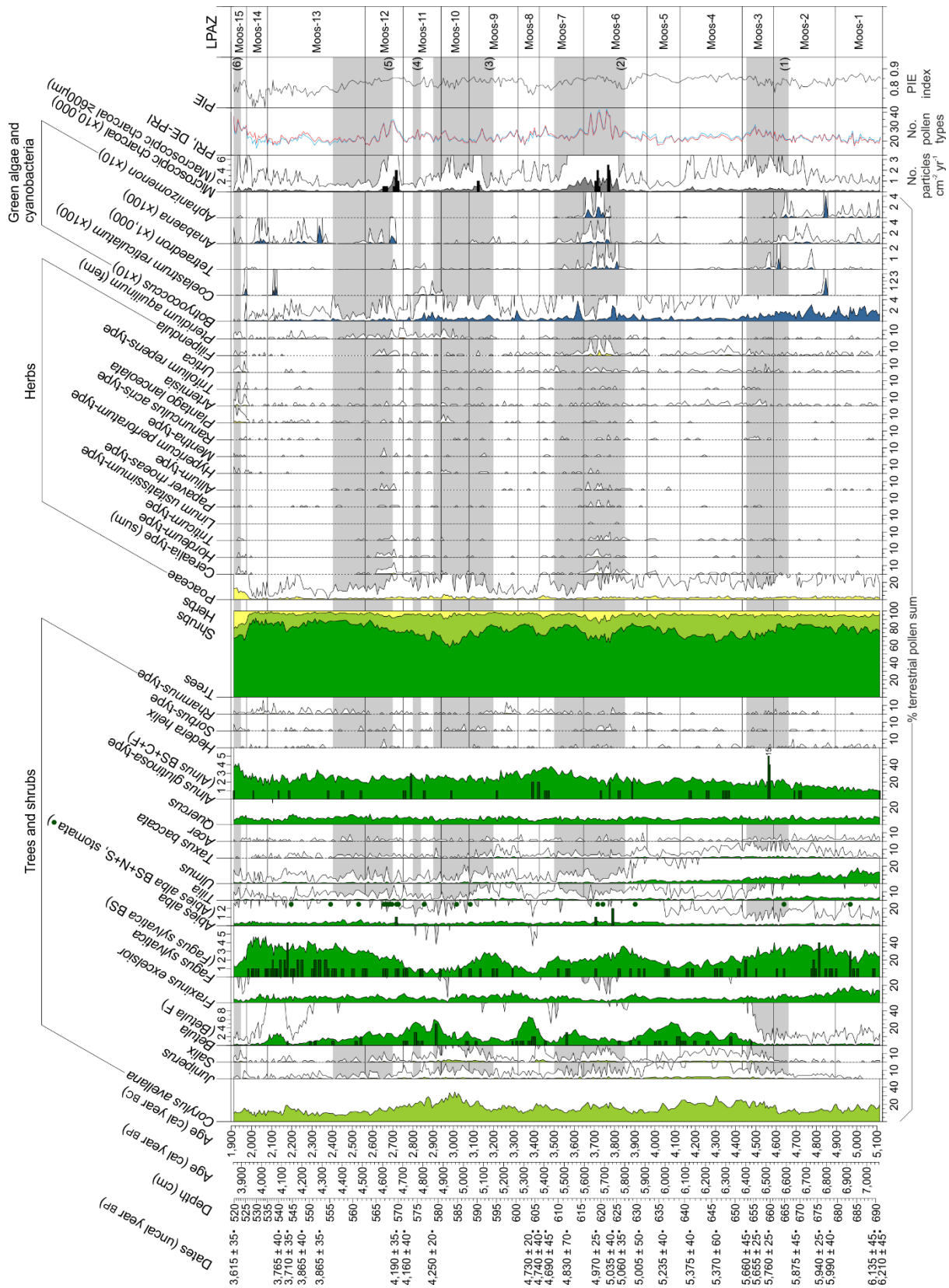
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FIGURE 1 Overview map of Switzerland and the neighbouring countries with the two sites of this study (in red) and other discussed sites. 1 Moossee; 2 Burgäschisee; 3 Lobsigensee (Ammann, 1989); 4 Lake Biel (Fischer, Hafner, Stapfer, Marti, & Affolter, 2017; Hafner & Suter, 2000; Stöckli, 2016; Suter 2017); 5 Soppensee (Lotter, 1999); 6 Zürich Opéra (Bleicher et al., 2017); 7 Egelsee (Wehrli, Tinner, & Ammann, 2007); 8 Mindelsee (Rösch, Kleinmann, Lechterbeck, & Wick, 2014a, b); 9 Degerssee (Kleinmann, Merkt, & Müller, 2015); 10 Lago di Origlio (Tinner, Hubschmid, Wehrli, Ammann, & Conedera, 1999). A = Austria, D = Germany, F = France, FL = Liechtenstein, I = Italy (topographic map: © swisstopo)



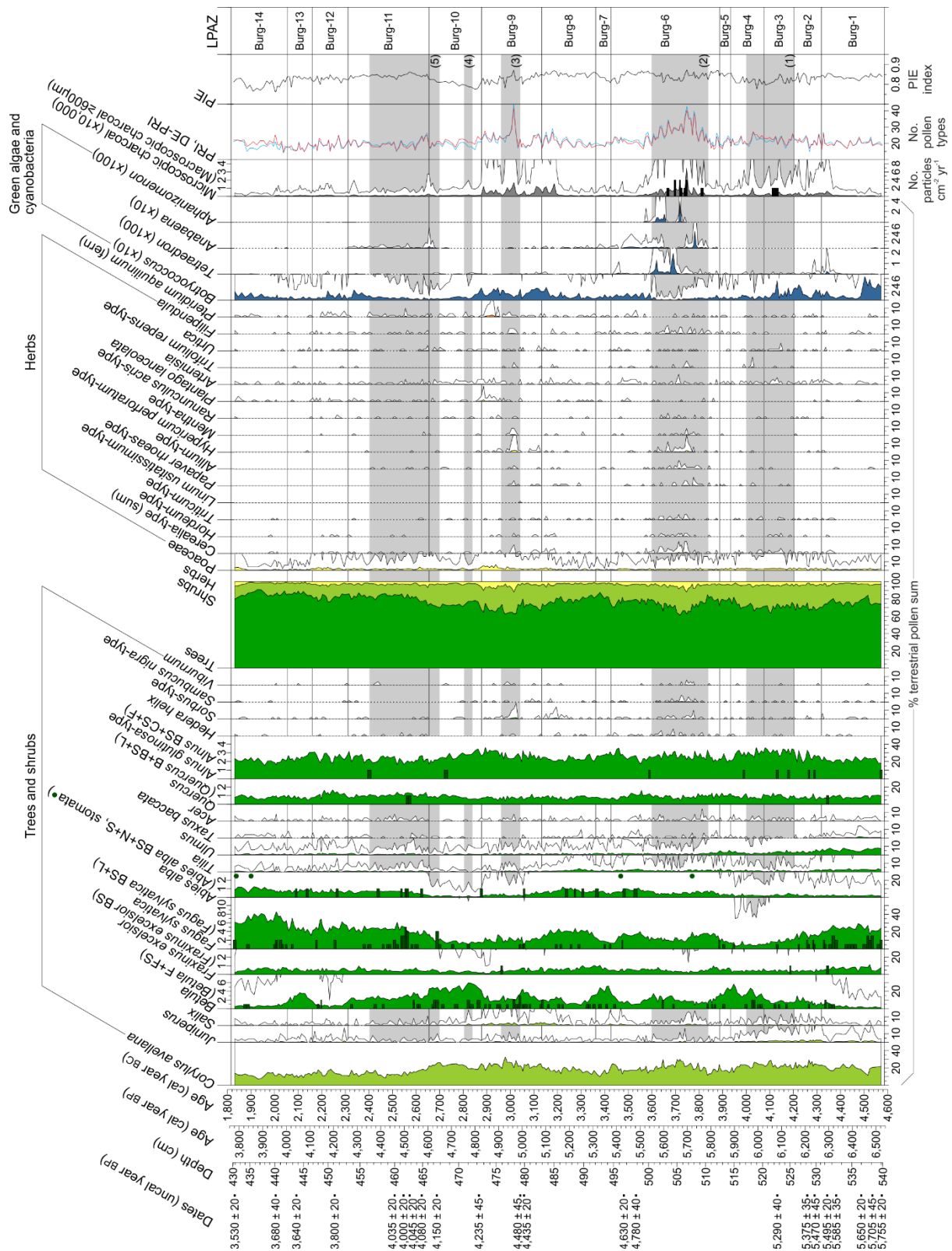
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FIGURE 2 Age-depth models of (a) Moossee and (b) Burgäschisee. Black dots show the calibrated ages with 95% (2σ) probabilities (IntCal13, Reimer et al., 2013). The black lines are the modelled chronologies (OxCal; Bronk Ramsey, 1994, 1995, 2001, 2008; Bronk Ramsey, van der Plicht, & Weninger, 2001; Bronk Ramsey & Lee, 2013). One age at Burgäschisee (dark grey x) was treated as an outlier. The grey lines indicate the 95% (2σ) probabilities of the models.



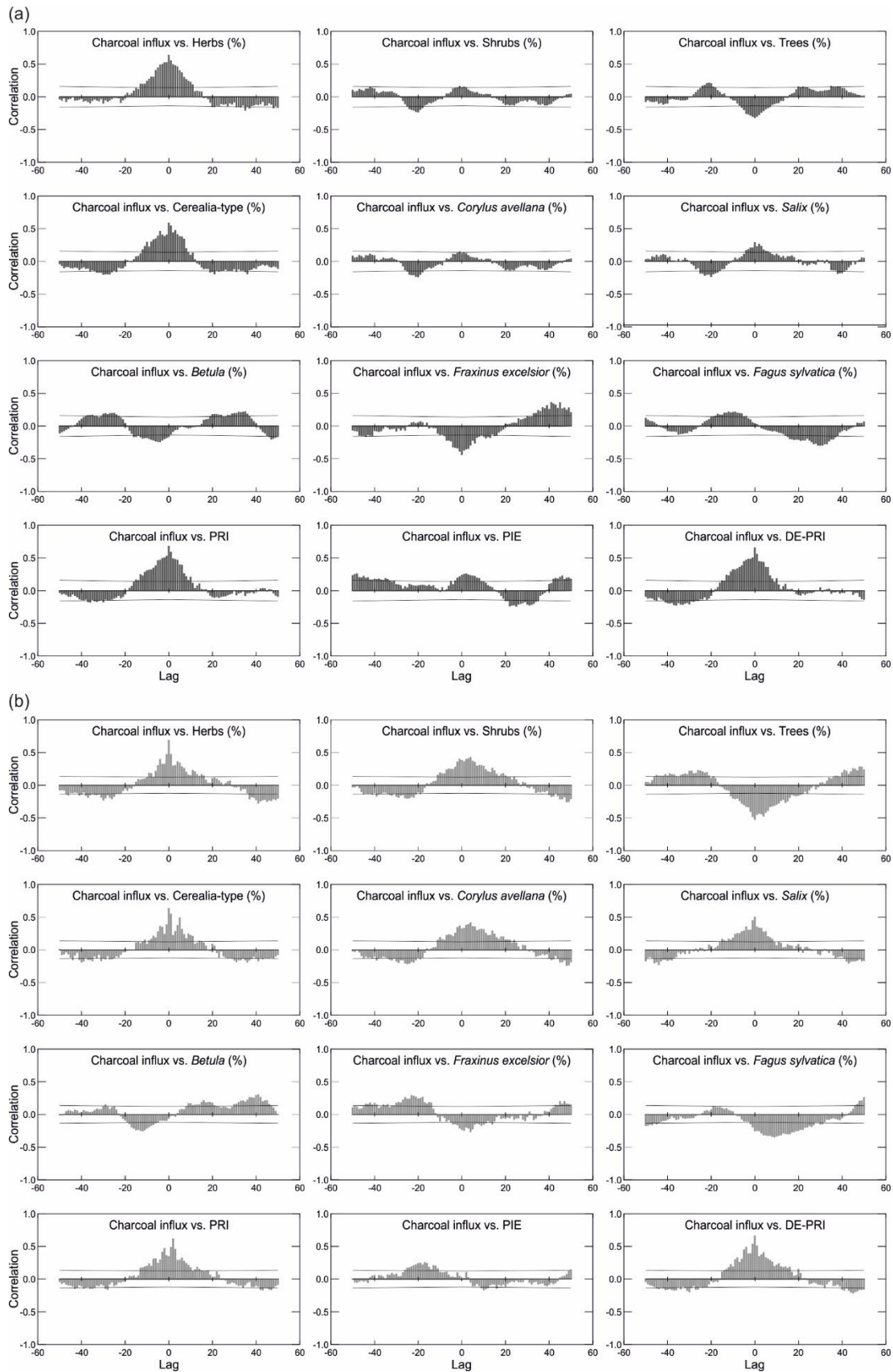
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FIGURE 3 Moossee high-resolution sequence. Presented are selected pollen, spore, algae and cyanobacteria percentages, microscopic charcoal influx values, macroscopic charcoal concentrations (concentration = number of particles $\geq 600 \mu\text{m}/17.5 \text{ cm}^3$, black bars, plotted on top axis), selected plant macrofossil concentrations (concentration = number of remains/ 17.5 cm^3 , dark green bars, plotted on top axis), presence of *Abies alba* stomata (dark green dots), palynological richness (PRI, light blue), evenness-detrended palynological richness (DE-PRI, red) as well as palynological evenness (PIE). Empty curves show 10 \times exaggerations. Light grey bars indicate the time windows of local archaeological findings reflecting settlement phases (1–6). BS = bud scales, C = cones, F = fruits, N = needles, S = seeds.



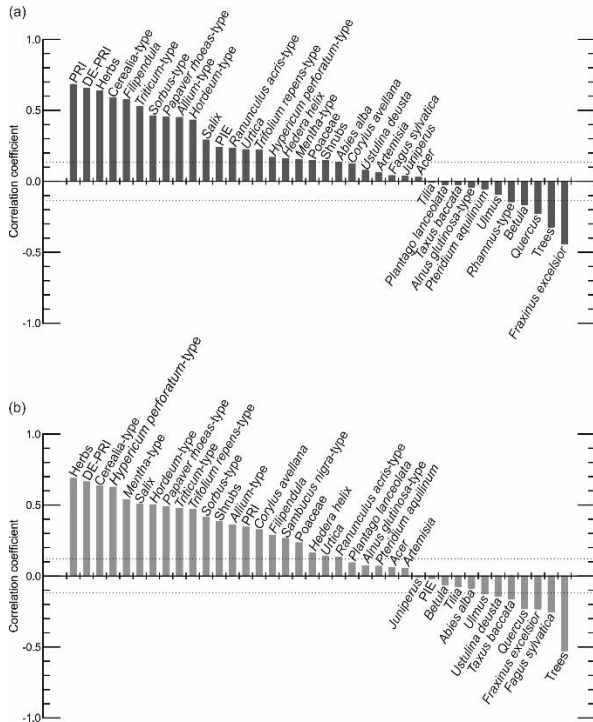
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FIGURE 4 Burgäschisee high-resolution sequence. Presented are selected pollen, spore, algae and cyanobacteria percentages, microscopic charcoal influx values, macroscopic charcoal concentrations (concentration = number of particles $\geq 600 \mu\text{m}^3$ (standard volume), black bars, plotted on top axis), selected plant macrofossil concentrations (concentration = number of remains/11 cm^3 (standard volume), dark green bars, plotted on top axis), presence of *Abies alba* stomata (dark green dots), palynological richness (PRI, light blue), evenness-detrended palynological richness (DE-PRI, red) as well as palynological evenness (PIE). Empty curves show 10 \times exaggerations. Light grey bars indicate the time windows of local archaeological findings reflecting settlement phases (1–4). B = bud, BS = bud scales, CS = cone scales, F = fruits, FS = fruit scales, L = leaves, N = needles, S = seeds.



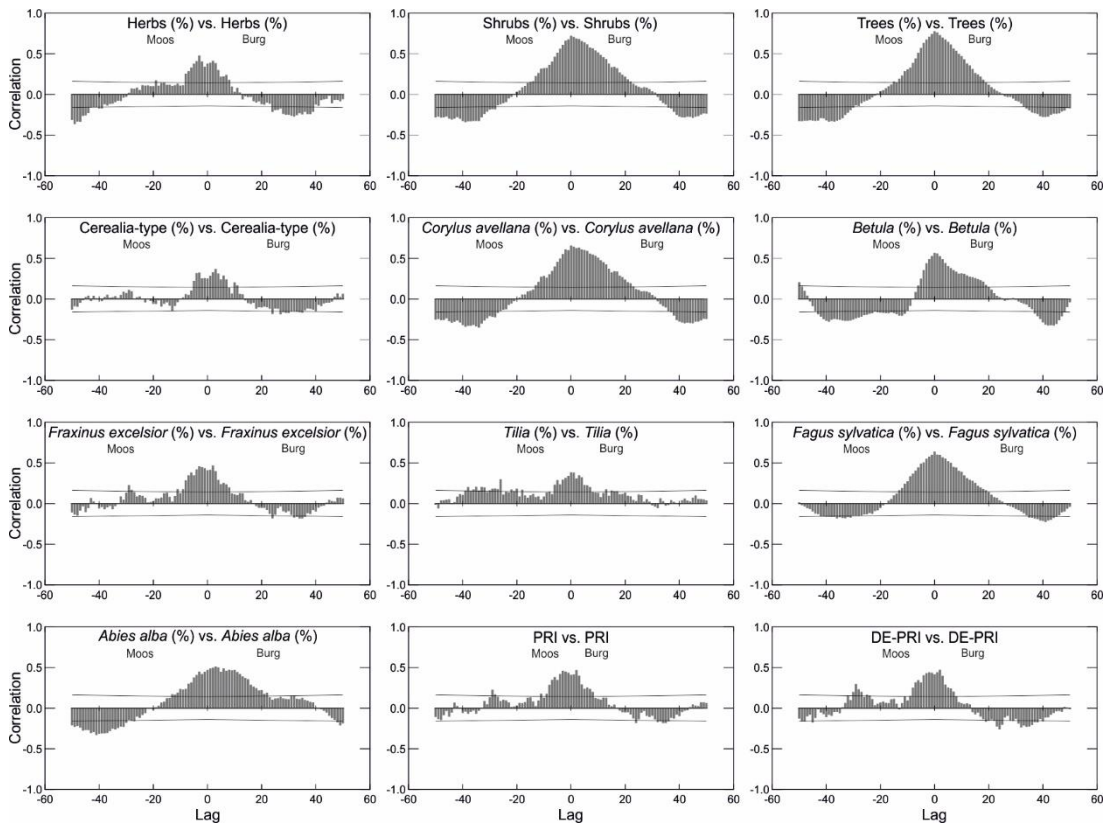
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FIGURE 5 Cross-correlation analysis of microscopic charcoal influx vs. percentages of selected pollen types, palynological richness (PRI), palynological evenness (PIE) and evenness-detrended palynological richness (DE-PRI) from (a) Moossee and (b) Burgäschisee (6,500–4,150 cal year BP). 1 lag = 11.1 ± 0.2 cal years (Moossee), 8.7 ± 0.6 cal years (Burgäschisee). The solid black lines mark the significance level ($P < 0.05$).



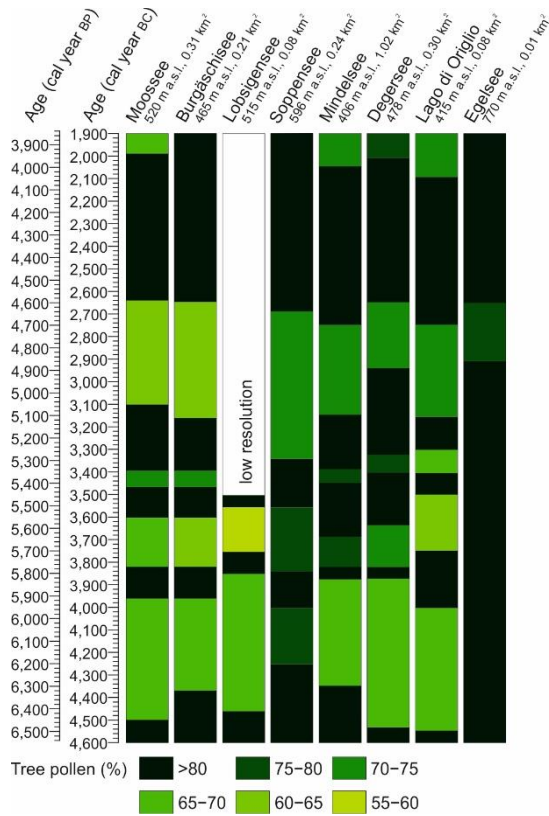
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FIGURE 6 Correlograms showing the correlation coefficients at lag 0 between microscopic charcoal influx and selected pollen types, spore types, palynological richness (PRI), palynological evenness (PIE) and evenness-detrended palynological richness (DE-PRI) for (a) Moossee and (b) Burgäschisee (6,500–4,150 cal year BP). The dotted lines mark the significance level ($P < 0.05$).



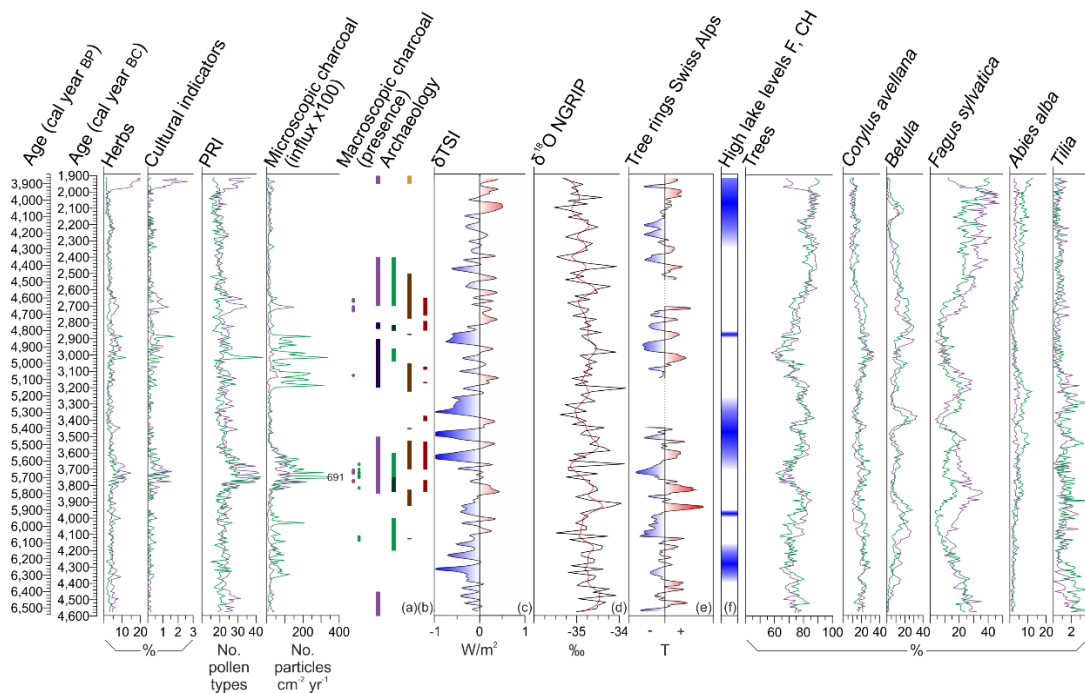
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FIGURE 7 Cross-correlation analysis of percentages of selected pollen types, palynological richness (PRI) and evenness-detrended palynological richness (DE-PRI) from Moossee (Moos) vs. percentages of selected pollen types, PRI and DE-PRI from Burgäschisee (Burg) (6,500–4,150 cal year BP). 1 lag = 11.1 ± 0.2 cal. years. The solid black lines mark the significance level ($P < 0.05$).



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FIGURE 8 Tree pollen percentages from selected sites (see Figure 1). Dark green bars indicate periods with fairly closed forests (tree pollen % >80). Light green bars indicate phases with forest openings (tree pollen % <80).



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FIGURE 9 Percentages of selected pollen types, palynological richness (PRI), microscopic charcoal influx, macroscopic charcoal presence ($\geq 600 \mu\text{m}$) and local archaeological findings at Moossee and Burgäschisee compared to palaeoclimatic proxies. Purple graphs = Moossee, green graphs = Burgäschisee. Cultural indicators = \sum Cerealia-type + *Plantago lanceolata* + *Linum usitatissimum*-type. Bottom labelling, center: (a) Local archaeological settlement phases within the city of Zurich (Bleicher et al., 2017). (b) Dendrochronologically dated settlement phases at Lake Biel (Fischer, Hafner, Stapfer, Marti, & Affolter, 2017; Hafner & Suter, 2000; Stöckli, 2016; Suter 2017). Dark coloured bars (archaeology) indicate dendrochronologically dated settlement phases (Moossee, Burgäschisee and Zurich). (c) δTSI (total solar irradiance) (Steinhilber, Beer, & Fröhlich, 2009). (d) $\delta^{18}\text{O}$ NGRIP (Vinther et al., 2006) with smoothing (loess = 0.05, red line). (e) Calibrated tree ring data from the Swiss Alps (Bircher, 1982, 1986; Renner, 1982). Dotted black lines mark data gaps (f) Periods of high lake levels in Eastern France (F) and Western Switzerland (CH) (Magny, 2004, 2013).