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7 **The role of fire disturbances, human activities and climate change for long-term forest**
8 **dynamics in upper-montane forests of the central Dinaric Alps**

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19
20 **Abstract**

21 We present the first high-resolution Holocene pollen, plant-macrofossil, and charcoal records from the
22 upper-montane zone in the central Dinaric Alps. Drawing on these new records from well-dated
23 lacustrine sediments of Zminje Jezero (ca. 1500 m a.s.l.; Montenegro) and on independent chironomid-
24 inferred summer temperatures, we explore long-term ecosystem responses to variations in climate, fire
25 disturbances and land use, as well as legacy effects of past environmental changes.

26 A mixed spruce-fir forest established in the upper-montane zone around 9500 cal BP, and *Fagus*
27 *sylvatica* became co-dominant with the two conifers after 5000 cal BP. Prehistoric land-use pressure
28 was overall remarkably low, but increased since 2000 cal BP and was highest after the Middle Ages.

29 We found a significant positive relationship between biomass burning and summer temperature,
30 indicating that fires were mostly climate driven. *Picea abies* was insensitive to summer temperature,
31 biomass burning and human impact, which supports the view that spruce forests may not be significantly
32 impacted by fire. In contrast, *Abies alba* and other disturbance-sensitive trees (*Tilia*, *Ulmus*, *Fraxinus*
33 *excelsior*-type) show significant negative responses to land-use pressure and positive responses to
34 summer temperature. This supports the notion that these species may be well-adapted to warmer-than
35 present summer temperatures and that their populations declined in recent millennia due to land-use
36 activities. Conversely, *F. sylvatica* was sensitive to summer temperatures but was promoted by low
37 biomass burning, indicating that its expansion in the spruce-fir dominated forest was enhanced by the
38 onset of cooler and possibly also moister climatic conditions as well as by fire disturbances.

39
40 **Keywords**

41 Holocene, vegetation dynamics, mountain forests, fire history, vegetation-fire interactions, Montenegro

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48 **Introduction**

49 Assessing the responses of European mountain forests to changing environmental conditions is crucial
50 to develop adaptation and management strategies to possible ecosystem shifts that may cause the loss
51 of important ecosystem services, such as risk prevention (from avalanches, landslides or rockfall),
52 recreation, and the maintenance and promotion of biodiversity (Klopčič et al., 2017). Such assessments
53 are particularly important given that there is strong support for the hypothesis that climate change could
54 markedly modify disturbance regimes, with a likely increase of some disturbances (e.g. fire) in a
55 warming world (Seidl et al., 2017).

56 However, understanding natural ecological processes is challenging as processes often play out over
57 long time scales (centuries, millennia), particularly when long-lived species such as trees are involved.
58 The long time horizon of palaeoecological records permits to study ecosystem responses under
59 substantially different environmental conditions than the present ones, including temperatures analogous
60 to those predicted by future climate changes (approximately 1-2°C higher than present; Carter et al.,
61 2018; Morales-Molino et al., 2021; Samartin et al., 2017). Moreover, current ecosystems and ecological
62 processes often carry legacy effects of past environmental changes and anthropogenic impacts (Cagliero
63 et al., 2022; Feurdean et al., 2009; Grindean et al., 2019; Morales-Molino et al., 2022), which have often
64 altered species-environment relationships (Tinner et al., 2013). Thus, taking into account long-term
65 records may be important to gain more accurate environmental-change response assessments, especially
66 in Europe, where anthropogenic manipulation of nature started several millennia ago (Birks and Tinner,
67 2016).

68 The long-term history of mountain ecosystems varies across regions and is arguably contingent on
69 patterns of human settlement, land use, and socioeconomic development. In this context, the central
70 Dinaric Alps are an interesting area as its land-use history may differ from those of other European
71 mountain regions. There is little doubt that the Balkan Peninsula acted as a land bridge from the Near
72 East, across Asia Minor and towards Central and Western Europe (Forenbaher et al., 2013). While it
73 seems that the Neolithic spread mainly across the fertile plains along the Danube valley in the east
74 (Starčevo culture) and along the Adriatic coastal strip in the west (Impresso culture) around the 6th
75 millennium BCE (8000-7000 cal BP; Borić et al., 2019), there is evidence to suggest that the

76 mountainous hinterland of the central Dinaric Alps remained an agricultural frontier zone, eventually
77 even until the Late Neolithic (Forenbaier and Miracle, 2005). The frontier-zone hypothesis is consistent
78 with modelled anthropogenic deforestation (Kaplan et al., 2009), which suggests that during the past
79 3000 years relatively low forest clearance occurred when compared to other regions of Europe, and that
80 a large fraction of usable land in the region was not heavily exploited until the Middle Ages (600-1460
81 CE; 1350-490 cal BP). By contrast, charcoal production, mining activities, and grazing likely occurred
82 in the interior area of the Dinaric Alps since the Bronze Age (3500-600 BCE; 5450-2550 cal BP), and
83 intensified during the Iron Age (600-200 BCE; 2550-2150 cal BP) and the Ottoman Empire (1460-1800
84 CE; 490-150 cal BP) (Kranjc, 2009; Longman et al., 2018). However, it is not clear if these activities
85 were widespread across the mountain region, or whether human activities rather concentrated in some
86 areas. In the latter case, large forested regions in the interior range may have remained relatively intact
87 until the present (Nagel et al., 2017) or managed with low intensity silvicultural systems during recent
88 centuries (Boncina, 2011). Low historical forest clearance in the montane belt may have preserved fir
89 (*Abies alba* Mill.), beech (*Fagus sylvatica* L.), and spruce (*Picea abies* (L.) Karst.) old-growth forests
90 (Cagliero et al., 2022; Motta et al., 2011; Sabatini et al., 2018). As these tree species are widespread and
91 often form mixed forests in European mountains (Hilmers et al., 2019), exploring their long-term
92 responses under low land-use pressure may be useful to improve knowledge on the role of disturbances
93 by fire and climate. However, the impact of Neolithic and of more recent cultures on the interior
94 mountain region is still weakly constrained. In contrast to other European mountain regions, the area is
95 both archeologically and palaeoecologically under-documented (Borić et al., 2019; Finsinger et al.,
96 2017; Vander Linden et al., 2014).

97 Thus, to provide new insights into the Holocene vegetation dynamics and into vegetation responses to
98 disturbances by fire and to changes in climate and land use we studied sediments from Zminje Jezero
99 (Fig. 1), a lake at 1535 m a.s.l., thus in the montane belt of the central Dinaric Alps. Our main aims are
100 to (1) assess the long-term Holocene vegetation dynamics of mixed montane forests, (2) characterize
101 the Holocene land-use and fire histories, (3) investigate the influence of the main drivers of fire
102 dynamics (climate and human impact), and (4) track responses of the dominant montane trees (*A. alba*,

103 *F. sylvatica*, *P. abies*, as well as of other disturbance-sensitive trees such as *Ulmus*, *Tilia*, and *Fraxinus*
104 *excelsior*) to variations in climate, fire and human impact.

105

106

107 **Material and methods**

108

109 *Study area and study site*

110 In the Dinaric Alps, vegetation is influenced by the interaction of mountainous reliefs, pedological
111 conditions, and proximity to the Adriatic Sea (Horvat et al., 1974; Nagel et al., 2017). Mediterranean
112 evergreen sclerophyllous vegetation dominated by *Pinus halepensis* Mill., *Quercus ilex* L. and *Olea*
113 *europaea* L. occurs near the coast. Mixed submediterranean deciduous woodlands with *Carpinus betulus*
114 L., *Fraxinus ornus* L., deciduous *Quercus* L., *Ostrya carpinifolia* Scop., *Carpinus orientalis* Mill., and
115 *Castanea sativa* Mill. occur up to c. 700 m asl. The valley floodplains are commonly occupied by *Alnus*
116 *glutinosa* (L.) Gaertn., *Quercus robur* L., *Fraxinus* sp. and *Ulmus minor* Mill.. In the montane belt (from
117 700 to 2000 m asl), forests are dominated by *Pinus nigra* J.F. Arnold, *F. sylvatica*, and mixed beech-fir-
118 spruce forests. Other species occurring in the montane belt include *Pinus sylvestris* L., *O. carpinifolia*,
119 *Acer* L., *Ulmus* L., *Tilia* L., and *Fraxinus excelsior* L.. The subalpine vegetation belt is generally above
120 c. 2000 m asl and is dominated by *Pinus mugo* Turra, *Juniperus communis* L., and *Alnus viridis* (Chaix)
121 DC.

122 Zminje Jezero (Snake lake; 43°09'21" N 19°04'14" E; 1535 m asl) is a small 1.2-ha large and 9.5-m
123 deep glacial-origin lake (Fig. 1) whose water is drained into the Crno Jezero (1460 m asl) by a small
124 stream. The lake is located on the northwest part of a high karst plateau in the Durmitor massif (Annys
125 et al., 2014) in a valley adjacent to the one currently hosting the last surviving glacier in Montenegro,
126 Debeli namet (Hughes et al., 2011). Given its elevation, Zminje Jezero is within the limits of terminal
127 moraines that were deposited before the Lateglacial Interstadial (Hughes et al., 2011).

128 The vegetation in the surroundings of the lake is dominated by a dense spruce-fir forest (Fig. 1) with
129 lesser amounts of beech, *Acer* sp., *Sorbus aucuparia* L., *Rhamnus fallax* Boiss., and *Vaccinium myrtillus*
130 L.. However, *P. sylvestris*, *Pinus nigra* subsp. *nigra*, *Betula pendula* Roth, and *Pinus heldreichii* H.

131 Christ are also well represented in the Durmitor massif. To the east, there is a town (Žabljak; 1450 m
132 asl) with pastures and agriculture lands. The lake shores host a rich community of wetland plants,
133 including *Molinia caerulea* (L.) Moench, *Comarum palustre* L., *Carex* sp., *Sphagnum* sp., *Parnassia*
134 *palustris* L., *Filipendula ulmaria* (L.) Maxim., and *Eriophorum vaginatum* L.. The current tree line is at
135 c. 1950 m asl and is mainly formed by spruce with beech (Bui, 1975). Above the tree line are *P. mugo*
136 and *J. communis* shrublands, alpine meadows, and rocks.

137 Climate is continental with a mean annual air temperature of 5.1°C and a mean annual precipitation of
138 c. 1450 mm at Žabljak (Annys et al., 2014). In the northern and central parts of the mountain range,
139 bedrock consists of Mesozoic sedimentary rocks and thick Middle and Upper Triassic and Upper
140 Jurassic limestones, while in the southern part Upper Cretaceous flysch are predominant (Mirković,
141 1985).

142 Zminje Jezero is located in a zone of special protection of the Durmitor National Park, where only
143 cutting of naturally collapsed trees (so-called “sanitary cuttings”), clearing of forest roads, and tourism
144 are allowed (Srdanović and Pavić, 2013; UNESCO and IUCN, 2018). Before the establishment of the
145 National Park in 1952 CE, the area was informally protected since 1907 CE.

146

147 *Field work and sediment-core correlation*

148 We studied the lake floor with an echo sounder connected to a Garmin GPS device (Fig. 1d) and
149 collected two overlapping sediment cores (sections 1-m long and 6 cm in diameter) from the deepest
150 part of the lake at a water depth of 9.3 m using a modified Livingstone piston corer and an UWITEC
151 gravity corer. All core sections were split longitudinally and photographed at ISEM (University of
152 Montpellier) to visually describe the sediments and align the sections with the aid of Corelyzer v2.1.1
153 (CSDCO/LacCore-University of Minnesota). To assess sediment composition, we used an X-ray
154 fluorescence (XRF) AVAATECH core scanner at 5 mm resolution (with the two following settings: 10
155 kV/0.09 mA for 15 s and 30 kV/0.09 mA for 30 s), and then normalised the values using the centre-log-
156 ratio method (CLR, Weltje et al., 2015). We correlated the sections based on marker layers and on
157 selected XRF records. Thereafter, one core half was cut into 1-cm slices and samples were stored in zip-
158 lock bags at 4°C.

159

160 *Chronology*

161 We modelled the depth-age relationship (Fig. 2) with RBacon v2.4.1 (Blaauw and Christen, 2011) using
162 41 control points (Table 1 and Table S1), including 19 AMS ^{14}C dates from terrestrial plant macrofossils
163 calibrated using the IntCal20 dataset (Reimer et al., 2020), one pollen-inferred age (onset of the
164 Holocene; Giesecke et al., 2014), and 21 control points derived from a chronology of short-lived
165 radionuclides (^{210}Pb and ^{137}Cs ; Fig. S1) that was built with the constant flux constant sedimentation
166 (CFCS) using the serac package (Brueel and Sabatier, 2020). We excised visually identified event-deposit
167 layers matching peaks of K, Ti, Rb, Zr, and Sr (Fig. 2), as they most probably represent sediment
168 deposition that occurred over very short time spans (Finsinger et al., 2021; Heiri et al., 2003).

169

170 *Pollen, spores and plant-macrofossils analyses*

171 We processed 78 1-cm³ samples for pollen analysis following standard physical and chemical
172 treatments, including treatments with HCl, KOH, sieving with a 500- μm mesh and decanting, HF,
173 acetolysis, and mounted the fuchsin-stained residues on slides with glycerol. To calculate influxes (#
174 cm⁻² yr⁻¹), we added *Lycopodium* tablets (Stockmarr, 1971). We identified and counted pollen, stomata
175 and the dung-fungi *Sporormiella* spore using determination keys and photographic atlases (Beug, 2004;
176 Cagliero et al., 2022; Davis, 1987; Finsinger and Tinner, 2005; Moore et al., 1998; Reille, 1992) as well
177 as the pollen and stomata reference collections at ISEM (University of Montpellier). We counted at least
178 300 terrestrial pollen grains at 400x magnification and calculated percentages relative to the terrestrial
179 pollen sum, which includes pollen of trees, shrubs, upland herbs, ferns, and vascular cryptogams and
180 excludes pollen of obligate aquatic plants.

181 The pollen diagram was divided into pollen assemblage zones using optimal partitioning by sums-of-
182 squares with square-root-transformed proportions of pollen types included in the terrestrial pollen sum,
183 and exclusion of rare taxa (abundance <5%; Birks and Gordon 1985). The number of statistically
184 significant zones was determined by comparison with the broken-stick model (Bennett, 1996) with
185 Psimpoll v4.26 (Bennett, 2008).

186 For plant-macrofossils analyses, we processed 203 samples. We measured sample volumes (5.6 ± 1.0
187 cm^3) by water displacement and then sieved them with a 100- μm mesh sieve. We identified and counted
188 macrofossils with a stereomicroscope at 7.5-60x magnification using atlases (Birks, 2017; Katz et al.,
189 1965; Schoch et al., 1988) and the reference collection at ISEM (University of Montpellier) and stored
190 them at -18°C in Milli-Q water. Plant-macrofossil abundances are expressed as concentrations ($\# \text{cm}^{-3}$).
191 To assess land-use pressure, we used the abundances of *Secale cereale* pollen (a primary anthropogenic
192 indicator), secondary indicators (as the sum of adventives and apophytes), and cultural indicators (as the
193 sum of Cerealia-type and *Plantago lanceolata*-type pollen) (Behre, 1981; Tinner et al., 2003). These
194 indexes include pollen of cultivated plants, ruderals, and plants of meadows (Deza-Araujo et al., 2020).
195 *Veratrum album* was added to the apophyte category, as it is avoided by cattle due to its toxicity
196 (Spiegelberger et al., 2006). We also assessed land-use pressure in the wider region using the OJC index
197 (Mercuri et al., 2013), which is based on the abundance of woody crops (*Olea europaea* L., *Juglans*
198 *regia* L., and *Castanea sativa* Mill.) that grow at lower elevations and along the coast of the Adriatic
199 Sea. Despite their presence in uncultivated areas, an increase in their abundances is often due to broad-
200 scale cultivation (Deza-Araujo et al., 2020).

201

202 *Charcoal analyses*

203 We counted microscopic charcoal particles in 42 pollen slides spread along the sediment core (Finsinger
204 and Tinner, 2005; Tinner and Hu, 2003) to obtain a low-resolution record of regional fire activity. For
205 macroscopic charcoal analyses, we took contiguous 1- cm^3 samples and treated them without the use of
206 an orbital shaker with a 5% NaPO_3 solution overnight and then with a 15% H_2O_2 solution for 24h
207 (Schlachter and Horn, 2010). Subsequently, samples were sieved through a 150- μm mesh (Higuera et
208 al., 2005) and charcoal particles were identified and counted under a stereomicroscope at 7.5-60x
209 magnification. The area of charcoal particles was not estimated since it is generally highly correlated to
210 charcoal counts (Finsinger et al., 2014; Tinner et al., 1998). To account for variations in sedimentation
211 rate (Whitlock and Larsen, 2001), both microscopic and macroscopic charcoal counts were converted
212 to charcoal-accumulation rates (influx; $\# \text{cm}^{-2} \text{yr}^{-1}$), hereafter denoted mCHAR and MCHAR,
213 respectively.

214

215 *Fire episodes and fire-regime changes*

216 To reconstruct regional fire activity and landscape-scale biomass burning we used the long-term trends
217 of two complementary proxies, mCHAR and MCHAR. While their potential source areas are similar (c.
218 40-km distance from study sites; Adolf et al., 2018), the records may differ, with MCHAR potentially
219 reflecting fires within a smaller distance (Finsinger et al., 2017). To determine significant changes in
220 landscape-scale biomass burning, we identified change points based on the mean and the variance in
221 MCHAR and tested their independence from variations in the modelled sediment-accumulation rates
222 (Finsinger et al., 2018).

223 To detect fire episodes within a few km distance around the study site (Higuera et al., 2010), we analysed
224 the MCHAR record with tapas v0.1.2 (Finsinger and Bonnici, 2022). This analysis involved resampling
225 the record to a constant resolution of 33 years (i.e. the 3rd quartile of the sampling-interval distribution).
226 Thereafter, we decomposed the record into a low-frequency background and a high-frequency peak
227 component using a loess robust to outliers with a smoothing-window width of 2000 years. The suitability
228 of the record for peak detection was evaluated through the signal-to-noise index (Kelly et al., 2011).
229 Peaks were evaluated using the 95th percentile of the modelled noise distribution obtained with locally
230 defined Gaussian mixture models for each 2000-year portion of the record (Higuera et al., 2009). The
231 peaks were further screened (Higuera et al., 2010) before calculating the fire return intervals (FRI: years
232 between adjacent fire episodes).

233

234 *Ecosystem responses*

235 We used generalized additive models (GAMs) to investigate ecosystem responses to variations in
236 climate, fire and land use. GAMs are suited for this purpose as they can unfold nonlinear relationships
237 between a response variable and a smoothed function of the predictor variable (Hastie and Tibshirani,
238 1986). Specifically, we explored the responses of fires to variations in climate and land-use pressure,
239 and the responses of dominant forest canopy taxa (*P. abies*, *A. alba*, *F. sylvatica*, *F. excelsior*-type, *Tilia*,
240 and *Ulmus*) to variations in climate, fires and land-use pressure (Carter et al., 2020; Colombaroli et al.,
241 2010; Morales-Molino et al., 2021).

242 As climate data, we used chironomid-inferred summer (July) surface-air temperature anomalies from
243 Lago Verdarolo (1390 m asl) (Samartin et al., 2017) that is in a biogeographically comparable ecosystem
244 in the Tuscan-Emilian Apennines where current vegetation is dominated by fir and beech. Comparisons
245 between instrumental data and climate model runs (Samartin et al., 2017) show that at interannual to
246 multidecadal timescales summer temperature variations in the Tuscan-Emilian Apennines are well
247 correlated with grid cells in Montenegro (Pearson's correlation coefficients are 0.8-1 for multidecadal
248 variability and 0.6-0.7 for interannual variability).

249 We assumed a quasi-Poisson distribution, log-transformed both the response and the predictor variables
250 to stabilize their variances, and fitted GAMs using restricted maximum likelihood (REML) smoothness
251 selection (Carter et al., 2020) with mgcv v1.8-38 (Wood, 2017). We chose a base period from 8000 cal
252 BP to the present because secondary anthropogenic indicators were very abundant during the early
253 Holocene, when human impact was negligible (Carter et al., 2020).

254

255

256 **Results and interpretation**

257

258 *Chronology and sediment composition*

259 The sediments cover part of the Younger Dryas and the entire Holocene, from c. 12,340 cal BP to present
260 (Fig. 2). The reliability of the chronology in its most recent part is broadly confirmed (Fig. S2) by the
261 match between the expected and modelled ages of Pb peaks during the Roman period and the Middle
262 Ages (McConnell et al., 2018; Renberg et al., 2001). Sediment deposition times vary between 6-65 years
263 cm^{-1} (median = 21.6 years cm^{-1}).

264 At the base, from 615 cm to 575 cm (12,340-11,640 cal BP), the sediments consist of light-brown sandy
265 and silty clay (Fig. 2). From 575 cm to 479 cm (11,640-10,300 cal BP), there are 1-2-cm thick light grey
266 silty-clay layers that alternate with darker and organic-richer layers (gradual boundaries), and a c. 28-
267 cm thick sequence of five graded deposits (529-500 cm), each one characterized by a distinct fining-
268 upward trend. Above 479 cm, sediments are mainly composed of dark-brown organic gyttja, which is
269 interrupted by three minerogenic layers of fine grey detrital clay with sharp stratigraphic boundaries at

270 445-441 cm, 413-410 cm, and 283-281 cm depth. In keeping with the visual assessment of the sediments,
271 minerogenic elements (K, Ti, Rb, Zr, and Sr) are most abundant below 479 cm (10,300 cal BP) as well
272 as in conjunction with the minerogenic layers.

273

274 *Long-term vegetation dynamics*

275 The pollen record (Figs. 3-4) was divided into four statistically significant assemblage zones at 566.5,
276 455.5, and 359.5 cm (corresponding to 11,500, 9410, and 6400 cal BP) and three non-significant
277 subzones with boundaries at 200.5 cm and 58.5 cm (2090 and 430 cal BP).

278 Pollen assemblages from 12,340 to 11,500 cal BP (ZMN-1; 615-566.5 cm) are dominated by *Pinus* and
279 herb pollen (mainly *Artemisia*, Poaceae and Chenopodiaceae). Both stomata and plant macrofossils
280 attest the local presence of *Betula* and *Pinus*, the latter presumably as low-density stands of dwarf
281 mountain pine (*P. mugo*) or pine trees (*P. sylvestris*, *P. heldreichii*, or *P. nigra*). Cerealia-type pollen
282 are likely associated with wild Poaceae, as Cerealia-type pollen were also found elsewhere long before
283 the development of agriculture (Dörfler, 2013). Such assemblages are typical of the Central European
284 Younger Dryas (12,850-11,650 cal BP; Rasmussen et al., 2014) and are indicative of an open and arid
285 steppe-tundra with cold-tolerant pine woodlands. Rising arboreal pollen (from c. 45 to 65%) indicate a
286 gradual closure of the woodland during the Younger Dryas cold stage, including mixed oak woodlands
287 at lower altitude.

288 *Picea abies* stomata unequivocally indicate a rapid altitudinal shift of this tree species at the Younger
289 Dryas-Holocene transition, when a rapid climatic change including a warming of c. 2-4°C occurred
290 (Heiri et al., 2014; Tóth et al., 2015). The woodlands closed further from 11,500 to 9410 cal BP (ZMN-
291 2; 566.5-455.5 cm), as attested by an increase of arboreal pollen (from c. 65% to 80%). *F. excelsior*-
292 type, *Ulmus*, and *Tilia* pollen first appeared at 11,500 cal BP marking the expansion of meso-
293 thermophilous trees at lower altitude, a characteristic feature of pollen records from the Balkan
294 Peninsula and the adjacent European Alps (Caf et al., 2022; Vescovi et al., 2007; Willis, 1994). *Betula*
295 populations were denser than during the Younger Dryas, as shown by both pollen and plant macrofossils.
296 However, the abundance of light-demanding pioneer trees and shrubs (*Ephedra*, *Juniperus* and *Betula*)
297 decreased in conjunction with the local expansion of spruce and fir populations starting between 10,400

298 and 9600 cal BP. Finds of *Sporormiella* dung-fungi spores indicate the presence of wild herbivores
299 around the lake between 11,500 and 10,400 cal BP, as also observed on the Swiss Plateau (Rey et al.,
300 2017) and in the Maritime Alps (Finsinger et al., 2021).

301 The shift to a *Picea-Abies* dominated forest was mostly concluded shortly after 9410 cal BP (onset of
302 ZMN-3; 455.5-359.5 cm), as also observed at Prokoško Jezero (1670 m asl, Bosnia Herzegovina;
303 Dörfler, 2013). Plant-macrofossils show that both *Pinus* and *Betula* were still intermixed in the spruce-
304 fir dominated forest until around 8000 cal BP, when a low-density population of beech likely
305 established, as suggested by the continuous pollen curve. At lower altitudes, vegetation was
306 characterized by mixed oak forests with a higher share of *Corylus* between 9410 and 6000 cal BP.
307 Around 7250 cal BP, *Ostrya*-type pollen increased indicating the expansion of *O. carpinifolia*, *C.*
308 *orientalis*, or of both species.

309 This expansion was followed by an increase of *Fagus* and *C. betulus* pollen starting around 6400 cal BP
310 (onset of ZMN-4a; 359.5-200.5 cm). Although the *Fagus* expansion at Zminje Jezero occurred
311 approximately 2500-1000 years later than in pollen records from the Central Dinaric mountain area
312 (Prokoško Jezero, Crveni Potok), it broadly coincided with the expansion of *Ostrya* and *Carpinus*
313 *betulus*, as often seen in pollen records from the region (Prokoško Jezero, Lake Ohrid, Lake Prespa, and
314 Crveni Potok; Dörfler, 2013; Finsinger et al., 2017; Panagiotopoulos et al., 2013; Wagner et al., 2009).
315 The admixture of *Fagus* in the *Picea-Abies* dominated forest involved a c. 2000-years long build-up
316 phase (6400-4600 cal BP), as attested by rising pollen abundance, after which *Fagus* plant macrofossils
317 and stomata regularly occur. As both *C. betulus* and *Fagus* are shade-tolerant and favoured by moist
318 habitats on upland soils (Houston Durrant et al., 2016; Sikkema et al., 2016), an increase in humidity
319 during the growing season may have occurred (Finsinger et al., 2017). In keeping with this, plant
320 macrofossils of more light-demanding and better drought-resistant *Pinus* are absent in this zone, though
321 stomata occasionally indicate their scattered presence. *Secale cereale* pollen first appear in this zone and
322 occur mostly between 5800 and 3800 cal BP, suggesting its presence as a weed among other cereals
323 during the Bronze Age (Behre, 1992). Some secondary anthropogenic-indicator pollen types (e.g. *P.*
324 *lanceolata*-type, *Melampyrum*) increased as well. However, tree pollen abundance was highest in this
325 time interval, suggesting that land-use pressure was minor. Similarly, a slightly lower tree-pollen

326 abundance between 3800 and 2100 cal BP suggests moderate presence of forest openings that are,
327 however, not matched by rising abundance of anthropogenic-indicator pollen types.

328 By contrast, anthropogenic-indicator pollen document higher land-use pressures from Roman times
329 onwards (*c.* after 2100 cal BP; ZMN-4b and ZMN-4c). *Secale cereale* pollen is mostly present around
330 the Roman period and regularly occurs since the Ottoman Empire (ZMN-4c; 58.5-0 cm; 430 cal BP to
331 present). Similarly, both cultural and secondary indicators are slightly higher during the Roman period
332 and substantially rise since 430 cal BP in conjunction with a substantial tree-pollen decrease. Thus,
333 pollen overall document two land-use phases characterized respectively by moderate land-use pressure
334 (Roman period) and increasing and reaching highest land-use pressure since the Ottoman Empire. These
335 two land-use phases were interrupted by a phase with minor land-use pressure during the Middle Ages
336 (ZMN-4b; 200.5-58.5 cm; 2090-430 cal BP).

337 The frequent occurrence of *C. sativa* and *O. europaea* pollen since 1800 cal BP is consistent with a
338 human-mediated spread of chestnut populations since Roman times (Conedera et al., 2004) and the
339 cultivation of olive trees in Roman territories (Mercuri et al., 2013), including Montenegro, which was
340 conquered by the Romans during the 2nd century BCE. Further, as in other records in the region (Dörfler,
341 2013; Finsinger et al., 2017), pollen of *Juglans* first appear at *c.* 1500 cal BP and occur more regularly
342 after 500 cal BP.

343 Although *Abies* pollen abundance was substantially lower after 2100 cal BP, a mixed *Abies-Picea-Fagus*
344 was still present locally until 430 cal BP, as confirmed by stomata and plant macrofossils. However,
345 lower pollen percentages and the absence of plant macrofossils of *Fagus* in conjunction with rare finds
346 of *Abies* macrofossils since 430 cal BP suggest a major shift towards a *Picea*-dominated forest. Forest
347 cover increased during the last century, perhaps due to the protection of the area since 1907 CE.

348

349 *Charcoal-inferred fire history*

350 Regional fire activity, inferred based on microscopic charcoal (mCHAR), was highest over the past 2000
351 years and was moderately high between 12,000 and 10,000 cal BP (Figs. 3-4). By contrast, landscape-
352 scale biomass burning (MCHAR trend) was highest between 11,400 and 6000 cal BP, and overall
353 decreasing from 6000 cal BP to the present (Figs. 3-4 and S4). The signal-to-noise index (Fig. S5) shows

354 that the macroscopic charcoal-accumulation rate (MCHAR) record is suitable for peak-detection
355 analysis (Kelly et al., 2011). A total of 35 fire episodes were identified over the past 12,500 years, with
356 a median fire-return interval (mFRI) of 260 years (FRI range: 79-790 years). Longest FRI values (>530
357 years) occur before 8000 and after 2000 cal BP. Charred *A. alba* and *P. abies* needles document the
358 occurrence of local fires in the conifer-dominated mountain ecosystem, mostly between 5600 and 500
359 cal BP (Figs. 3-4).

360

361 *Response of fire to variations in climate and land-use pressure*

362 Landscape-scale biomass burning (MCHAR trend) and regional fire activity (mCHAR) show different
363 responses to climate and land-use pressure. Whereas biomass burning significantly increases in response
364 to summer temperatures, fire activity significantly decreases (Fig. 5a; Table 2). Similarly, whereas
365 biomass burning significantly decreases in response to land-use pressure, regional fire activity shows a
366 hump-shaped response including an increase for the lower range of anthropogenic indicator pollen
367 values (Fig. 5b).

368

369 *Response of forest canopy species to variations in climate, fire and land use*

370 *Picea*'s responses to variations in climate, land use and biomass burning are not statistically significant
371 (Fig. 5c-e). *Fagus* shows a significant negative response, and *Abies*, *F. excelsior*-type, *Ulmus*, and *Tilia*
372 show significant positive responses to both summer temperature and biomass burning (Fig. 5c and e;
373 Table 2). *Abies*, *F. excelsior*-type and *Ulmus* show significant negative responses to land-use pressure
374 (Fig. 5d).

375

376

377 **Discussion**

378

379 *Regional vs local land-use*

380 The investigation of long-term vegetation dynamics in relation to land-use pressure and disturbances
381 requires a detailed understanding of land-use history. This is particularly important for southern Europe,

382 where forest clearances and agriculture often involved the use of fire. Moreover, land-use phases were
383 often interspersed by periods of abandonment and secondary forest establishment as the result of the
384 development and expansion of more permanent land-use practices, such as animal husbandry,
385 ploughing, crop cultivation, and woodland management (Birks and Tinner, 2016). However, identifying
386 the start and inferring the intensity of land-use pressure using palaeoecological records is challenging,
387 particularly in regions where independent documentation by archaeological evidence is poor (Deza-
388 Araujo et al., 2020), as is the case for the Durmitor.

389 Stomata and plant macrofossils indicate the local presence of taxa, mostly within some decametres
390 around a site (Ammann et al., 2014; Birks, 2017). Thus, the continuous presence of plant macrofossils
391 and stomata of trees (*Picea*, *Abies*, and *Fagus*) indicates that tree cover persisted in the surroundings of
392 Zminje Jezero at least throughout the past 9000 years (Fig. 3). In keeping with this, high arboreal pollen
393 (generally >80%) and AP/NAP ratio values (generally >4; Fig. 4) qualitatively indicate the presence of
394 closed forest (Deza-Araujo et al., 2020). A persistently high forest cover was also found in the internal
395 Dinaric Alps at Crveni potok (Finsinger et al., 2017), but contrasts with results from Prokoško Jezero
396 (Dörfler, 2013) where arboreal pollen values decreased to 50% during the past 2000 years. This
397 contrasting evidence would support the hypothesis that some of the forested regions in the interior range
398 of the Dinaric Alps have been left relatively intact until the present (Nagel et al., 2017).

399 Conversely, if land-use pressure was regionally heterogeneous, reconstructions based on pollen may not
400 necessarily covary with those based on plant macrofossils and stomata. Pollen from the wider region
401 may reach small lakes such as Zminje Jezero even if their relevant pollen source area is relatively small
402 (some kilometres at most; Sugita, 1994). Indeed, despite persistence of closed forest in the surroundings
403 of Zminje Jezero, anthropogenic indicators unambiguously document increasing land-use pressure in
404 the region since the Roman period. Cultural indicators, secondary indicators, as well as OJC-index
405 values rise around 2000 cal BP, when the region currently belonging to Montenegro was conquered by
406 the Romans (2nd century BCE). At that time, land-use pressure probably reached the Durmitor, as
407 attested by the construction of roads, including the one connecting Nikšić and Komini. The further rise
408 of anthropogenic indicators around 500 cal BP (15th century CE) is coherent with the first local
409 settlements in the Durmitor. For instance, the so-called stećci sites (medieval tombstones and graveyards

410 from the 13th-17th century; Erdeljan, 2018) attest to the local presence of settlements on the Durmitor
411 during the Middle Ages and the Ottoman Empire, and churches and monasteries from the 15th-19th
412 century CE document the presence of local settlements during the Ottoman Empire. Thus, these results
413 add a finer-scale scale documentation of past land-use pressure in comparison to modelled
414 anthropogenic deforestation patterns (Kaplan et al., 2009), which suggest that relatively low forest
415 clearance occurred during the past 3000 years and that the region was not heavily exploited until the
416 Middle Ages.

417 Similarly, regional heterogeneity of land-use pressure may also have occurred in pre-Roman times.
418 Anthropogenic indicators do not show distinct signs of Bronze and Iron Age land use, despite the
419 probable connection between coastal and inland settlements (Bulatović et al., 2020) and Illyrian and
420 Celtic Iron Age settlements (Cozzolino et al., 2020). However, *Secale cereale* pollen finds at Zminje
421 Jezero suggest its presence as a weed among other cereals (Behre, 1992) since about 6000 cal BP, as
422 also observed in archaeobotanical samples from Neolithic sites in the mountain hinterland (e.g. at
423 Okolište, Bosnia-Herzegovina; de Vareilles et al., 2022). While this is about 1000 years later than the
424 age of Neolithic settlements on the shores of the lowland Lake Ohrid (Hafner et al., 2021) and 2000
425 years later than the earliest Starčevo and Butmir culture Neolithic settlements in the inland of Bosnia-
426 Herzegovina (Vander Linden et al., 2014), the *Secale* pollen finds support the view that Neolithic
427 novelties, albeit with a certain time lag, spread in the hinterland of Montenegro (Borić et al., 2019).
428 Although Neolithic sites have not yet been found in the Durmitor area, there is evidence of Neolithic
429 occupation sites at 20-35 km distance (Odmut rock shelter; Borić et al., 2019), suggesting that inland
430 mountain areas may be archeologically under surveyed (Vander Linden et al., 2014). Thus, the
431 palaeoecological records agree with the hypothesis that the mountain hinterland remained an agricultural
432 frontier zone for much of the Neolithic (Forenbaher and Miracle, 2005) and possibly even until the
433 Roman Age.

434

435 *Regional vs local fires*

436 We found contrasting responses of fire to climate and land-use pressure over the past 8500 years (Fig.
437 5a-b), pointing to different drivers of fire dynamics at landscape and regional scales. Landscape-scale

438 biomass burning, as inferred based on MCHAR, responded positively and significantly to summer
439 temperature, as expected based on the strong influence (summer) temperature has on fire activity (Jain
440 et al., 2022; Westerling et al., 2006) and as often observed with sedimentary charcoal records (Daniau
441 et al., 2012; Power et al., 2008). As fuel was not a limiting factor in the moist and productive mountain
442 forests, higher mean July temperatures perhaps coupled with prolonged dry seasons (Holocene Thermal
443 Maximum; Samartin et al., 2017) likely improved fuel flammability (Pausas and Paula, 2012). By
444 contrast, surprisingly regional fire activity, as inferred based on mCHAR, responded negatively to
445 summer temperature. A disconnect between fire-history reconstructions can arise both when comparing
446 paleofire records from sites located near each other (Finsinger et al., 2018; Gavin et al., 2006), as well
447 as different paleofire proxies from the same site (Finsinger et al., 2017) if fire occurrence was not
448 spatially homogeneous. While charcoal records from additional sites may be necessary to better
449 constrain the spatial heterogeneity of fire occurrence in the region, it is likely that mCHAR captures fire
450 activity at greater distance from the site than MCHAR (Finsinger et al., 2017). This interpretation is
451 supported by the positive response of fire activity (mCHAR) to land-use pressure (Fig. 5b), which likely
452 occurred in a wider region, including lower-elevation areas where submediterranean deciduous
453 woodlands occur. The slightly earlier rise of regional fire activity, which started around the Iron Age
454 (Fig. 4), may be connected to land use in the region that remained undetected by the anthropogenic
455 indicators from Zminje Jezero. Biomass burning, instead, responded negatively to land-use pressure
456 (Fig. 5c). It is unlikely that this relationship is the result of feedbacks arising from human-induced
457 deforestation (e.g. lower fuel availability, fragmentation; Bowman et al., 2011) because biomass burning
458 decreased predominantly at the Neolithic/Bronze Age transition, when land-use pressure was low. The
459 overall decreasing biomass burning suggests that humans did not extensively use fire in the Durmitor.
460 While this overall contrasts with paleofire evidence from other southern European mountains (e.g. the
461 Apennines; Morales-Molino et al., 2021), the lower biomass burning rates in recent millennia fit with
462 the notion that fires are currently rare in the Dinaric Alps (Nagel et al., 2017). However, charred *Picea*
463 and *Abies* needles unambiguously document the occurrence of fires in the mixed spruce-fir-beech
464 mountain forests of the Durmitor.

465

466 *Species-response curves and legacies of past environmental changes*

467 Species-response curves are useful to assess factors that have driven long-term vegetation dynamics,
468 thereby unfolding legacies of past environmental changes (Carter et al., 2020; Colombaroli et al., 2010;
469 Morales-Molino et al., 2021). We found similar species responses to summer temperature and biomass
470 burning (Fig. 5c and 5e). Given the strong and positive relationship among these two predictors (Fig.
471 5a), it is difficult to disentangle their roles separately. However, as (summer) temperature currently has
472 a strong influence on fire activity (Jain et al., 2022; Westerling et al., 2006), the response curves may
473 yield valuable insights into the long-term fire ecology of the analysed species (*P. abies*, *F. sylvatica*, *A.*
474 *alba*, *Ulmus*, *Fraxinus excelsior*, and *Tilia*), which are widespread and often dominant in European
475 mountain forests. The right-skewed responses of *Fagus* to biomass burning and temperature (Fig. 5c
476 and 5e) suggest that it was favoured under low biomass-burning and cooler conditions. Overall, these
477 response curves support the notion that *Fagus* became more competitive in mixed fir-spruce forests with
478 the onset of cooler and moister summers and fire disturbance, as observed in the ecologically similar
479 Northern Apennines (Morales-Molino et al., 2021). Indeed, *Fagus* requires moist summers for its
480 germination (Giesecke et al., 2017) and is more sensitive than *Abies* to drought due to its shallow root
481 system (Cheddadi et al., 2016; Tinner et al., 2013). *Fagus* is a shade-tolerant species and its regeneration
482 can establish and grow with low light levels under the forest canopy for years before rapidly expanding
483 and achieving dominance when light conditions improve after disturbances (Gardner and Willis, 1999).
484 Thus, fire occurrence after 5000 cal BP may have promoted the recruitment of *Fagus* and its admixture
485 into the mixed *Picea-Abies* forest. This matches with evidence suggesting that during the initial phase
486 of stand establishment, *Fagus* is favoured by mixed-severity fire and intermediate human disturbances
487 (Bradshaw and Lindbladh, 2005; Giesecke et al., 2007; Tinner and Lotter, 2006) thanks to its capacity
488 to occupy newly exposed soils and canopy openings (Carter et al., 2018) more rapidly than its two main
489 competitors (*Abies* and *Picea*). Despite lacking ecological adaptations to fire and being identified as a
490 fire-sensitive species that is affected by higher biomass burning and temperatures (Carter et al., 2018;
491 Morales-Molino et al., 2021; Tinner et al., 2000), *Fagus* can be advantaged by fire incidence as long as
492 it is not excessive (Maringer et al., 2020). In keeping with this, the change-point analysis shows a
493 decrease in biomass burning during the establishment of *Fagus* (Fig. 4), corroborating the view that

494 beech establishment occurs in conjunction with a shift to a lower fire activity (Bobek et al., 2019;
495 Feurdean et al., 2017).

496 Further, similar to observations from the ecologically similar Northern Apennines (Morales-Molino et
497 al., 2021), we found that *Abies* and disturbance-sensitive deciduous taxa such as *Ulmus*, *F. excelsior*,
498 and *Tilia* were promoted by warmer-than-present summer temperatures (up to ca. 2.5°C; Fig. 5c).
499 However, our findings also suggest that these taxa responded positively to increasing biomass burning
500 (Fig. 5e). This contrasts with several records showing that both high-severity infrequent fires and low-
501 severity frequent fires led to their rapid decline and to local extinctions in recent millennia (Morales-
502 Molino et al., 2021; Tinner et al., 2000, 2013). On the one hand, the striking positive response of these
503 disturbance-sensitive taxa to biomass burning could simply arise from the positive relationship between
504 landscape-scale biomass burning and summer temperatures (Fig. 5a). On the other hand, the significant
505 negative response of *Abies*, *Ulmus*, and *F. excelsior* to land-use pressure (Fig. 5d) as well as to regional
506 fire activity (Fig. S6 and Table S2) indicates that their populations declined even in the wider region
507 due to land use, probably with the use of fires. Indeed, the decline of *Abies* coincides with the rise in
508 land-use pressure (pasturing and small-scale cultivation) and of regional fire activity since 2000 cal BP.
509 Conversely, the local persistence of *Abies* in the surroundings of Zminje Jezero until present-day
510 suggests that land-use pressure was not widespread across the montane forest belt, leaving relatively
511 undisturbed patches of forests in a landscape mosaic (Fig. 1). Indeed, *Abies* can be resistant to fire
512 disturbances when fires are rare (Henne et al., 2013) and its populations strongly reduce under excessive
513 human-induced fire activity (Feurdean and Willis, 2008; Finsinger et al., 2021; Tinner et al., 2013),
514 which was not the case around Zminje Jezero but may have been the case to the East of Žabljak and
515 elsewhere in the upper-montane zone of the central Dinaric Alps.

516 *Picea*'s response curves suggest that neither temperature nor biomass burning and land use significantly
517 influenced its populations (Fig. 5c-e). Indeed, *Picea* remained relatively stable even under higher-than-
518 present summer temperatures (Fig. 4), as also observed with palaeoecological records from the
519 Carpathians (Carter et al., 2018). Its insensitivity to summer temperatures may simply imply that past
520 climatic conditions did not exceed the species' tolerance range. Moreover, the lack of a significant
521 response to biomass burning agrees with evidence showing that *Picea* can persist thanks to vigorous

522 post-fire regeneration from wind-dispersed seeds (Bobek et al., 2018) even with median FRI as low as
523 260 years as at Zminje Jezero (Brown and Giesecke, 2014; Feurdean et al., 2017; Finsinger et al., 2018).
524 Although fires may have been fuelled by *Picea*'s traits that promote fire spread (high resin content,
525 flammable litter, and a ladder-canopy structure), its well-established populations persisted at Zminje
526 Jezero despite fire occurrence in the mixed spruce-fir-beech forests.

527 The species-response curves may also be useful to explain the relatively recent shift from a *Picea-Abies-*
528 *Fagus* mixed forest to one dominated by *Picea* that occurred in the surroundings of Zminje Jezero
529 around 430 cal BP (15th century CE; Fig. 4). Fir populations, which are more sensitive to land-use
530 pressure than *Picea* and *Fagus* (Fig. 5d), could have been reduced due to the establishment of the local
531 pastoral katun society (c. 1477 CE; Turkish Land Registry). Around 1400 CE, the Balkan Peninsula was
532 under the influence of the Republic of Venice and from 1496 CE Montenegro fell under the domain of
533 the Ottoman Empire (Rastoder, 2003). In the mid-16th century, local land-owners started seizing
534 monastery estates and hunting grounds in the lower parts of Montenegro. This resulted in the retreat of
535 considerable parts of the population in mountain areas (Rastoder, 2003), including the Durmitor, whose
536 forests probably started to be more intensively exploited. An alternative, or additional explanation could
537 involve the lower sensitivity of spruce to declining winter temperatures (Cheddadi et al., 2016). In this
538 scenario, the development of a *Picea*-dominated forest could be linked to the onset of cooler conditions
539 during the Little Ice Age (1450-1850 CE). Indeed, due to its shallow root system *Picea* is more
540 vulnerable to drought than *Abies* (Henne et al., 2011), and spruce-dominated stands in the Dinaric Alps
541 mostly occur in habitats with significantly colder and moister microclimates (Nagel et al., 2017).

542

543

544 **Conclusions**

545 Vegetation of forest ecosystems is often the result of complex interactions between vegetation dynamics
546 and variations in climate, disturbances (e.g. fire), and human activities. However, understanding the
547 ecological processes underlying these interactions is challenging as processes often play out over long
548 time scales (centuries, millennia), particularly for forests where long-lived species such as trees are

549 involved. The long-term perspective of palaeoecological records permits to study ecosystem responses
550 under substantially different environmental conditions than the present ones.

551 In this study, we sought to investigate the Holocene vegetation and fire history in the upper-montane
552 zone of the central Dinaric Alps, where fires are currently rare and forests mainly include beech-
553 dominated stands and mixed forests dominated by varying amounts of beech, fir, and occasionally
554 spruce (Nagel et al., 2017). While records from different elevations may be necessary to better support
555 our interpretation, our results support the view that at least some parts of the central Dinaric Alps
556 remained an agricultural frontier zone during the Neolithic (Forenbaher and Miracle, 2005) and that
557 land-use pressure was low until the Middle Ages (Kaplan et al., 2009).

558 Response curves indicate that fires in the upper-montane zone were mostly driven by variations in
559 climatic conditions, as expected based on the strong influence (summer) temperature has on fire activity
560 today (Jain et al., 2022; Westerling et al., 2006). *Picea* was insensitive to variations in summer
561 temperature, biomass burning and human impact, which supports the view that spruce forests may not
562 be significantly impacted by fire (Carter et al., 2018). In contrast, *Abies* and other disturbance-sensitive
563 deciduous trees (*F. excelsior*-type, *Tilia*, and *Ulmus*) show a significant positive relationship with
564 summer temperatures and a significant negative relationship with land-use pressure. This supports the
565 notion that these tree species may be well-adapted to warmer-than-present summer temperatures and
566 that their populations declined in recent millennia due to land-use activities (Morales-Molino et al.,
567 2020; Tinner et al., 2000, 2013). Conversely, *Fagus* emerges as a species sensitive to summer
568 temperatures whose expansion in the *Picea-Abies* dominated forest was enhanced by the onset of cooler
569 and possibly moister climatic conditions as well as by fire disturbances.

570

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579

580

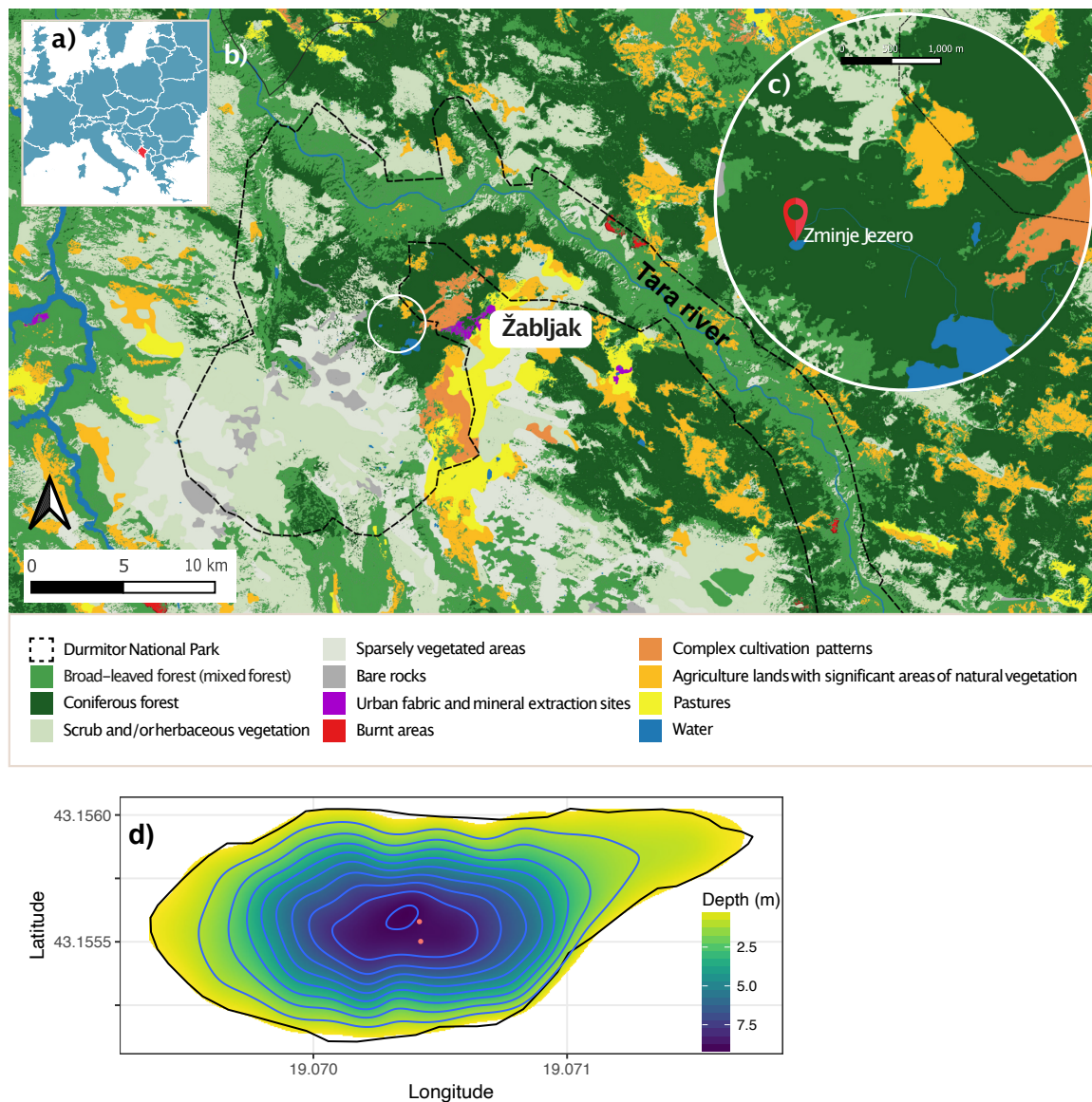
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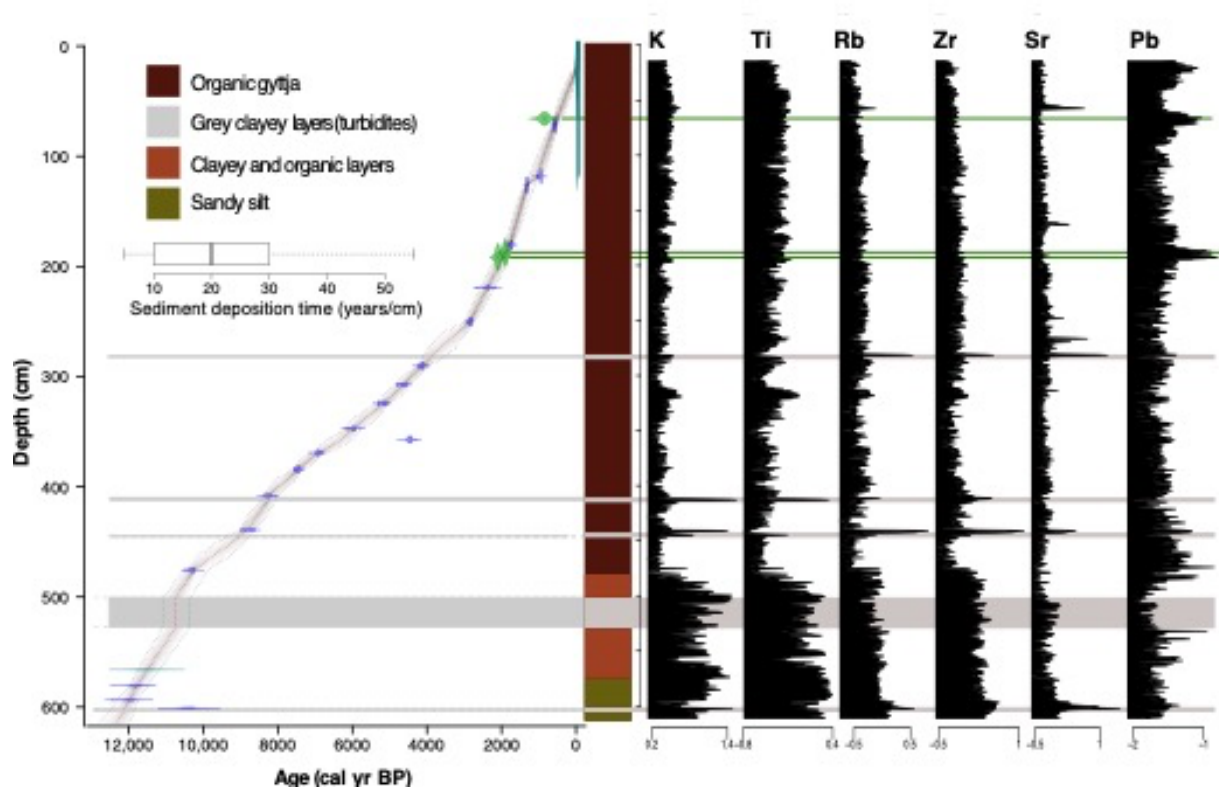
584

585 **Data**

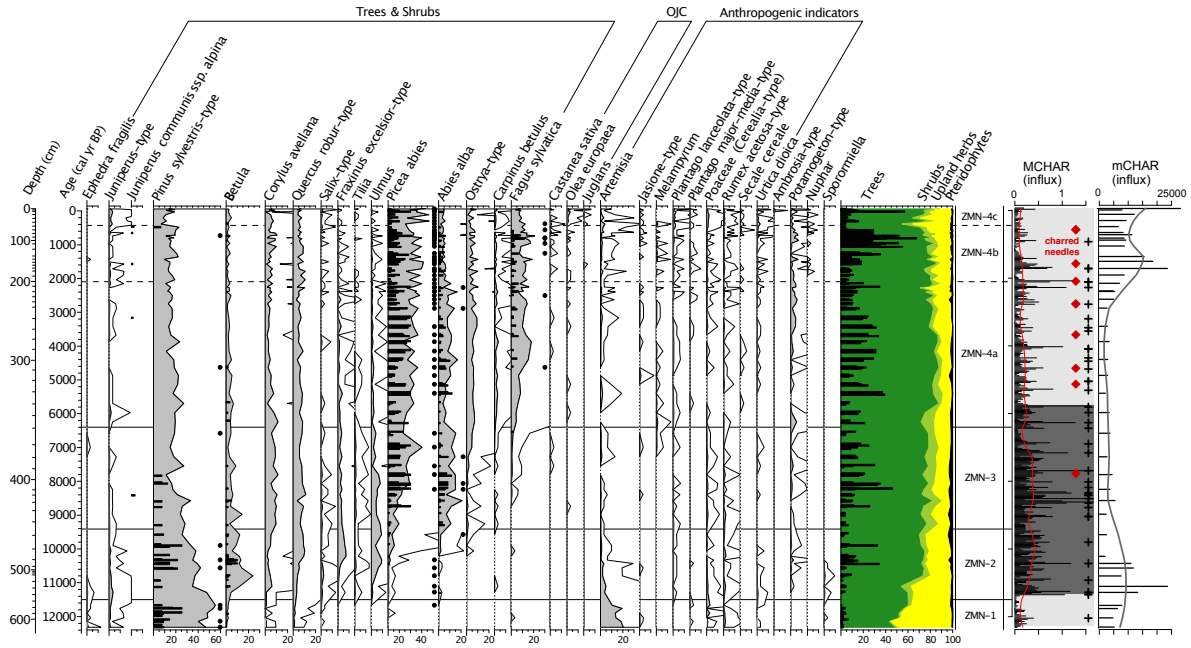
586 The palaeoecological data (pollen, spores, stomata, plant macrofossils, charcoal, and XRF records) will
587 be uploaded to the Neotoma database (DOI: 10.21233/XYZZ-XYZZ) through the European Pollen
588 Database.



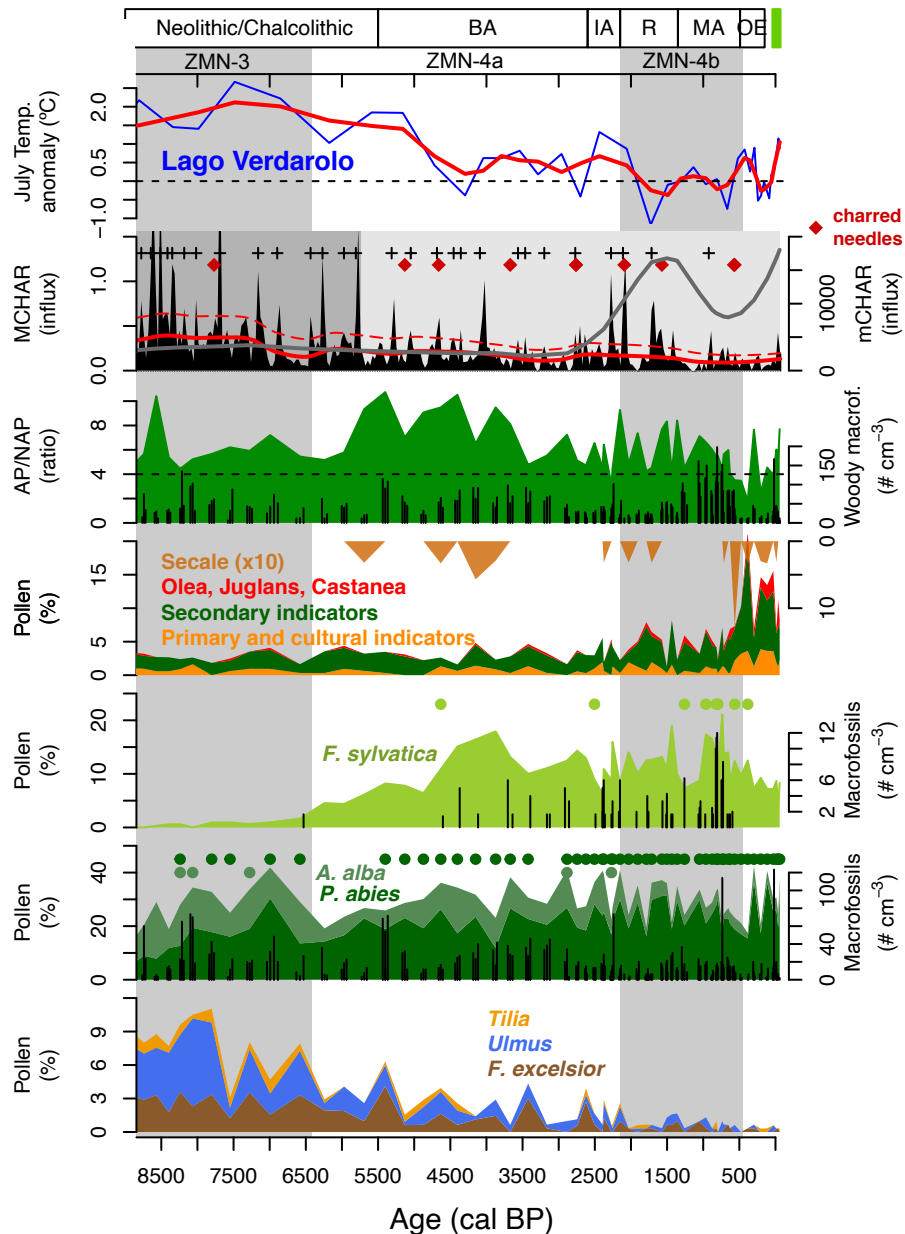
590
 591 **Fig. 1** a-c) Location of the study site at decreasing spatial scales. b-c) Map showing the distribution of
 592 land cover types (CORINE Land Cover 2018) in the Durmitor National Park and surroundings. d)
 593 bathymetric map of Zminje Jezero with contour lines at 1-m intervals and coring locations (red circles).
 594



595
 596 **Fig. 2** Depth-age model for the Zminje Jezero sediment core. The active control points used to constrain
 597 the model (Table 1) are based on ^{14}C , ^{210}Pb , and ^{137}Cs dates as well as on a pollen-inferred age estimate
 598 (onset of the Holocene). Passive control points based on local maxima in the XRF-Pb record (McConnell
 599 et al., 2018; Renberg et al., 2001) are shown in green (see also Fig. S2). Grey horizontal bands indicate
 600 turbidite layers that were excluded from the model. Lithological and XRF geochemical profiles of the
 601 sediment core are shown on the right. The inset shows the distribution of sediment deposition time
 602 within the sequence (median = 21 years cm^{-1})
 603

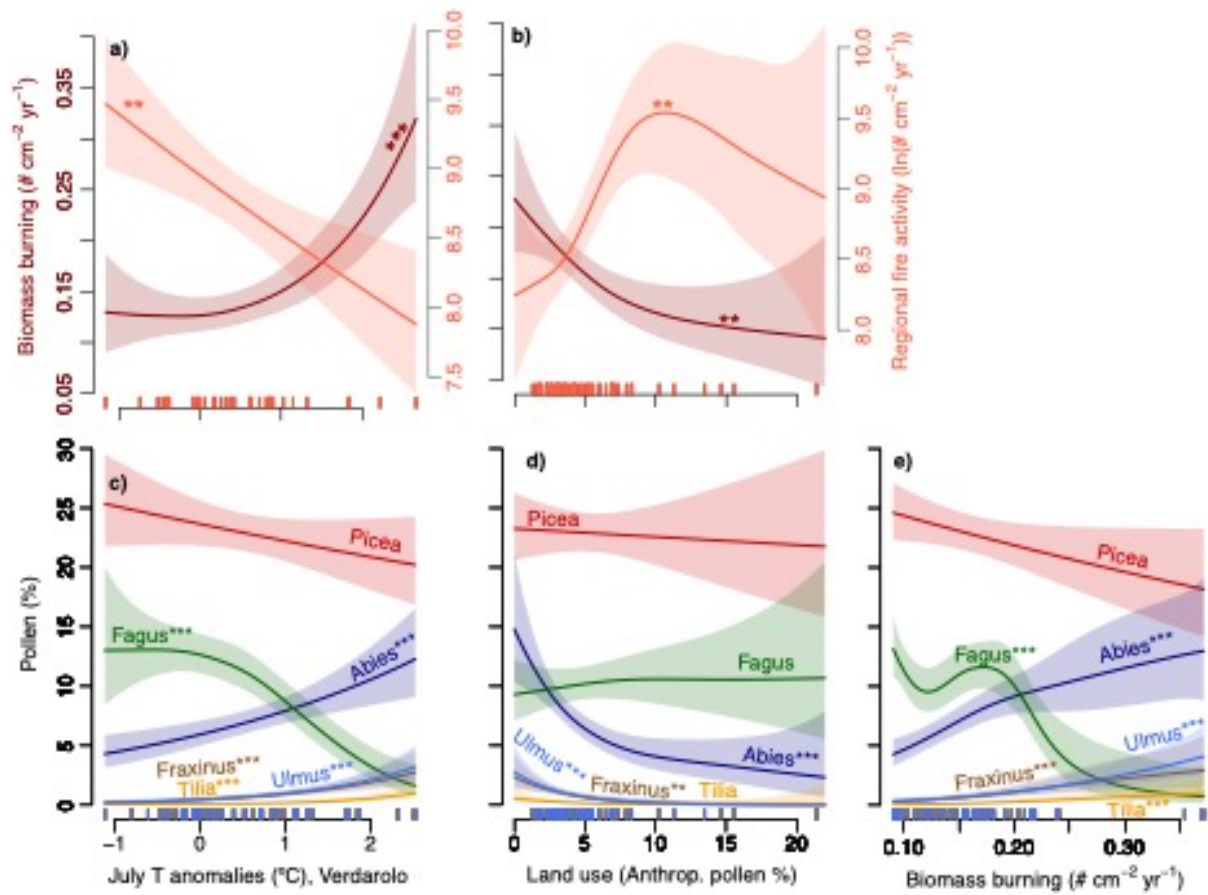


605
 606 **Fig. 3** Vegetation and fire history from Zminje Jezero sediments. Left: synthetic pollen diagram with
 607 selected pollen and spore percentages of the terrestrial pollen sum (grey curves; empty curves show 10x
 608 exaggerations of the percentage values), presence/absence of stomata (black circles), and plant-
 609 macrofossil concentrations (black vertical bars, dimensionless) for selected genera and for all woody
 610 taxa of the Zminje Jezero. The continuous horizontal and dashed lines indicate statistically significant
 611 and non-significant pollen-assemblage zones, respectively. See Fig. S3 for a more detailed plant-
 612 macrofossil diagram. To the right: macroscopic-charcoal accumulation rate (MCHAR) and microscopic-
 613 charcoal accumulation rate (mCHAR) as black bars, their long-term trends (red and black lines), fire
 614 episodes (black crosses), and presence of charred conifer needles (red diamonds).
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Fig. 4 Comparison of the main proxies for vegetation dynamics, fire and land-use history from Zminje Jezero, and chironomid-inferred July-air temperature (T_{July}) anomalies from Lago Verdarolo (Samartin et al., 2017). Microscopic charcoal (mCHAR, thick dark-grey line) documenting regional fire activity and macroscopic charcoal (MCHAR, black filled area) documenting landscape-scale biomass burning (red continuous line), local fire episodes (black crosses), periods of biomass burning as determined by the change-point analysis (grey-shaded areas), and charred *Picea* and *Abies* needles (red diamonds). Temporal changes of dominant forest canopy taxa and of anthropogenic indicator pollen types (filled polygons: pollen percentages; black vertical bars: plant macrofossils concentrations; grey circles: stomata). Grey vertical shaded areas represent pollen zone boundaries (see Fig. 3).



627
 628 **Fig. 5** Generalized Additive Models showing (a-b) the responses of landscape-scale biomass burning
 629 and regional fire activity to climate and land-use pressure, and (c-e) the responses of dominant forest
 630 canopy taxa to climate, land-use pressure, and biomass burning.

Table 1 Control points used to establish the depth-age model for the ZMN-19 sediment core from Zminje jezero (Durmitor Massif, Montenegro). For a detailed description of the terrestrial plant macrofossils used for radiocarbon dating see Table S1.

Depth (cm)	Lab-code	Material	Dry weight (mg)	Sample Thickness (cm)	Age (^{14}C yr BP) (cal yr BP)*
0	^{210}Pb	Bulk sediment	/	0	$-69 \pm 5^*$
0.5	^{210}Pb	Bulk sediment	/	0	$-65 \pm 1^*$
1.5	^{210}Pb	Bulk sediment	/	0	$-62 \pm 1^*$
2.5	^{210}Pb	Bulk sediment	/	0	$-58 \pm 1^*$
3.5	^{210}Pb	Bulk sediment	/	0	$-54 \pm 1^*$
4.5	^{210}Pb	Bulk sediment	/	0	$-51 \pm 1^*$
5.5	^{210}Pb	Bulk sediment	/	0	$-47 \pm 2^*$
6.5	^{210}Pb	Bulk sediment	/	0	$-44 \pm 2^*$
7.5	^{210}Pb	Bulk sediment	/	0	$-40 \pm 2^*$
8.5	^{210}Pb	Bulk sediment	/	0	$-36 \pm 3^*$
9.5	^{137}Cs peak	Bulk sediment	/	0	$-36 \pm 1^*$
9.5	^{210}Pb	Bulk sediment	/	0	$-33 \pm 3^*$
10.5	^{210}Pb	Bulk sediment	/	0	$-29 \pm 3^*$
12.5	^{210}Pb	Bulk sediment	/	0	$-22 \pm 4^*$
13.5	^{210}Pb	Bulk sediment	/	0	$-19 \pm 4^*$
14.5	NWT ^{137}Cs	Bulk sediment	/	0	$-15 \pm 5^*$
14.5	^{210}Pb	Bulk sediment	/	0	$-13 \pm 1^*$
15.5	^{210}Pb	Bulk sediment	/	0	$-11 \pm 5^*$
16.5	^{137}Cs	Bulk sediment	/	0	$-8 \pm 5^*$
16.5	^{210}Pb	Bulk sediment	/	0	$-5 \pm 5^*$
17.5	^{210}Pb	Bulk sediment	/	0	$-4 \pm 6^*$
71.5	DeA-33892	Terrestrial plant macrofossils	2.25	1	565 ± 19
118.5	DeA-23961	Terrestrial plant macrofossils	20	1	1054 ± 24
126.5	DeA-32618	Terrestrial plant macrofossils	16.8	1	1427 ± 20
180.5	DeA-31441	Terrestrial plant macrofossils	9.8	1	1844 ± 23
219.5	DeA-33893	Terrestrial plant macrofossils	3.5	1	2335 ± 55
250.5	DeA-31442	Terrestrial plant macrofossils	8	1	2755 ± 22
290.5	DeA-31091	Terrestrial plant macrofossils	8.5	1	3762 ± 22
307.5	DeA-23962	Terrestrial plant macrofossils	194	1	4108 ± 30
324.5	DeA-31093	Terrestrial plant macrofossils	17.8	1	4532 ± 25
347.5	DeA-33890	Terrestrial plant macrofossils	1.18	1	5212 ± 51
357.5	DeA-23963	Terrestrial plant macrofossils	266.5	1	3980 ± 30
369.5	DeA-31440	Terrestrial plant macrofossils	17.6	1	6060 ± 28
384.5	DeA-23964	Terrestrial plant macrofossils	170.2	1	6552 ± 37
408.5	DeA-33891	Terrestrial plant macrofossils	1.6	1	7449 ± 60
439.5	DeA-23967	Terrestrial plant macrofossils	148.5	1	7908 ± 39
476	DeA-23965	Terrestrial plant macrofossils	532.3	0.5	9139 ± 44
566.5	/	Pollen inferred (onset Holocene)	/	1	$11500 \pm 250^*$
581	Poz-10170	Terrestrial plant macrofossils	0.4	2	10170 ± 60
594	Poz-143126	Terrestrial plant macrofossils	3	2	10260 ± 60
601.5	Poz-143573	Terrestrial plant macrofossils	0.08	3	9190 ± 120

Table 2 Ecosystem responses to variations in climate, fire and land use at Zminje jezero (Durmitor Massif, Montenegro), as determined by Generalized Additive Models (GAMs) based on the pollen percentages and charcoal-accumulation rate records (this study) as well as chironomid-inferred July temperatures from Lago Verdarolo (Samartin et al., 2017). Effective degrees of freedom indicate the complexity of the smooth (a value = 1 indicates a straight line); significance of smooth terms: * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$.

Independent variable	Response variable	Effective degrees of freedom	Reference degrees of freedom	F-value	Deviance explained (%)
Climate (chironomid-inferred July temperature anomalies)	Biomass burning***	2.54	3.08	11.2	52.2
	Regional fire**	1	1	12.18	28.3
	<i>P. abies</i>	1	1	2.2	4.07
	<i>A. alba</i> ***	1	1	14.31	22.4
	<i>F. sylvatica</i> ***	3.07	3.88	11.47	57
	<i>F. excelsior-type</i> ***	1	1	21.72	28.9
	<i>Tilia</i> ***	1.88	2.35	10.02	31.1
	<i>Ulmus</i> ***	1	1	33.14	37.2
Biomass burning (long-term trend of MCHAR)	<i>P. abies</i>	1.0	1.0	3.88	7.1
	<i>A. alba</i> ***	2.32	2.78	10.65	39.1
	<i>F. sylvatica</i> ***	4.33	5.2	5.61	53
	<i>F. excelsior-type</i> ***	1.83	2.21	0.2	32.4
	<i>Tilia</i> ***	1.79	2.16	12.26	37
	<i>Ulmus</i> ***	1.65	1.99	23	46.5
Land-use pressure (anthropogenic indicator pollen)	Biomass burning**	1.89	2.37	6.55	26.3
	Regional fire***	3.32	4.07	7.13	38.4
	<i>P. abies</i>	1	1	0.11	0.21
	<i>A. alba</i> ***	2.26	2.83	11.14	41.7
	<i>F. sylvatica</i>	1.34	1.61	0.12	1.6
	<i>F. excelsior-type</i> **	1.08	1.16	10.37	25.2
	<i>Tilia</i>	1.48	1.82	2.59	13.7
	<i>Ulmus</i> ***	1.03	1.05	12.8	30.7

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<p>Table 2 Ecos Montenegro), charcoal-accu Verdarolo (Sa 1 indicates a s</p>
