



HAL
open science

Legacies of past human activities on one of the largest old-growth forests in the south-east European mountains

Eleonora Cagliero, Donato Morresi, Laure Paradis, Milic Curovic, Velibor Spalevic, Niccolò Marchi, Fabio Meloni, Ilham Bentaleb, Renzo Motta, Matteo Garbarino, et al.

► To cite this version:

Eleonora Cagliero, Donato Morresi, Laure Paradis, Milic Curovic, Velibor Spalevic, et al.. Legacies of past human activities on one of the largest old-growth forests in the south-east European mountains. *Vegetation History and Archaeobotany*, 2022, 31, pp.415-430. 10.1007/s00334-021-00862-x . hal-03446641

HAL Id: hal-03446641

<https://hal.science/hal-03446641>

Submitted on 18 Jan 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Legacies of past human activities on one of the largest old-growth forests in south-east European mountains

Eleonora Cagliero^{1,2}, Donato Morresi³, Laure Paradis², Milić Čurović⁴, Velibor Spalevic⁵, Niccolò Marchi¹, Fabio Meloni³, Ilham Bentaleb², Renzo Motta³, Matteo Garbarino³, Emanuele Lingua¹, Walter Finsinger²

¹ Department of Land, Environment, Agriculture and Forestry (TESAF), University of Padova, 35020 Legnaro (PD), Italy

² University of Montpellier, ISEM, CNRS, IRD, EPHE, Montpellier, France

³ Department of Agricultural, Forest and Food Sciences (DISAFA), University of Torino, 10095 Grugliasco (TO), Italy

⁴ University of Montenegro, Biotechnical Faculty, Podgorica, Montenegro

⁵ University of Montenegro, Faculty of Philosophy – Geography Department, Nikšić, Montenegro

The authors do not recommend the distribution of this version of this article.

The published version of this article is freely available upon request.

To receive a free complimentary copy, please send a request to Walter Finsinger: walter.finsinger@umontpellier.fr

Walter Finsinger

*Institut des Sciences de l'Evolution-Montpellier (ISEM)
CNRS – EPHE - IRD
Montpellier
France*

Correspondence and requests should be addressed to:
walter.finsinger@umontpellier.fr, +33 (0)6 69 61 07 42

35 **Abstract**

36 The Dinaric Mountains are a region considered as a hotspot for remaining late-successional montane mixed *Abies*
37 *alba-Fagus sylvatica-Picea abies* old-growth forests presumably because historical deforestation levels were
38 substantially lower than in other European regions. We present new well-dated stand-scale palaeoecological
39 records (pollen, spores, stomata, macrofossils, macroscopic charcoal, and magnetic susceptibility), an extensive
40 dataset of current forest structures and a detailed land-cover types map from the Biogradska Gora forest to provide
41 new insights into the long-term vegetation dynamics of old-growth forests in the montane zone of the Dinaric
42 Mountains. Land use (cereal crop cultivation, cattle herding, and fire) during the Middle Ages caused a reduction
43 of the *A. alba* and *P. abies*-dominated forest. After a major land-abandonment event around the Black Death
44 pandemic (mid-14th century) and more moderate land-use phases associated with fire episodes, which favoured
45 the short-term expansion of light-demanding pioneer species (*Corylus* and *Betula*), *F. sylvatica*-dominated stands
46 developed in the more accessible outer part of the forest. The legacy of past land uses is still visible as the structure
47 of the almost pure *F. sylvatica* stands shows less old-growth characteristics. Most strikingly and markedly in
48 contrast to decreasing tree cover due to generally intensifying land use elsewhere in Europe, tree cover increased
49 several centuries before the formal protection of the forest (1878 CE), supporting the view that historical land-use
50 pressures played an important role for the small extent and the continuity of disturbance-sensitive *A. alba* and *P.*
51 *abies*-dominated old-growth stands.

52

53 **Keywords**

54 disturbance history; forest structure; land-use legacy; mountain ecosystem; old-growth forest; palaeoecology

55 **Introduction**

56 Forest ecosystems that have developed for a long period of time without important anthropogenic disturbance are
57 rare (<3% of the total forest extent), small and fragmented in Europe (Sabatini et al. 2018; Barredo et al. 2021).
58 Major human imprints on many, if not all, forest ecosystems, including high conversion rates to agriculture (often
59 with the use of fire) for millennia and intense forest exploitation (Kaplan et al. 2009; Birks and Tinner 2016) are
60 generally viewed as causes for their current small extent (Nagel et al. 2017; Sabatini et al. 2020). Despite their
61 small extent, these primary and old-growth forests provide valuable opportunities to study forest dynamics and
62 biotic responses to non-anthropogenic disturbances (Foster et al. 1996), thereby contributing to the development
63 of close-to-nature forest management methods (Bauhus et al. 2009; Schütz et al. 2016) and guiding restoration and
64 adaptation to environmental changes (Mazziotta et al. 2016). Even if generally protected and particularly the
65 smaller ones (<1000 ha), these forests are vulnerable to both biotic and abiotic disturbances (Nagel et al. 2017;
66 Sabatini et al. 2020), climate change (Elsen et al. 2020) as well as by land-use and altered disturbance regimes
67 (e.g. fires) in surrounding areas (Hansen and DeFries 2007) that may hinder the development of features associated
68 with old-growth stage.

69 Old-growth forests are typically characterised by functional, structural and compositional features which
70 distinguishes them from forests of younger age classes: high amounts and size of deadwood, presence of old trees
71 approaching their natural longevity and a mosaic of heterogeneous stands arising through gap dynamics (Wirth et
72 al. 2009). These features indirectly reflect the length of time an area has been continuously wooded without human
73 influence and major stand-replacing disturbances, as well as the history of land-use and forest management
74 (Buchwald 2005). However, features reflecting the old-growthness of current forest structures cannot provide
75 information on their longer-term history and dynamics. Paleoecology, instead, is sometimes the best and only tool
76 for evaluating the history and ecosystem responses to past environmental changes such as climate, fire and land
77 use (Whitlock et al. 2018). Moreover, palaeoecology can document the legacies of land-use history, climate change
78 and disturbances such as fire on present-day forest composition (Lindbladh 1999; McLachlan et al. 2000; Birks
79 2019), which is a critical information for clarifying conservation objectives and evaluating outcomes (Whitlock et
80 al. 2018; McMullin and Wiersma 2019).

81 The distribution of primary and old-growth forests is uneven in Europe, likely because the intensity and extent of
82 human pressure differed among regions (Sabatini et al. 2020). Old-growth forests in east-central Europe have
83 captured the attention of foresters long ago (Leibundgut 1959; Horvat et al. 1974) as their dominant tree species
84 (*Abies alba* Mill., *Fagus sylvatica* L., and *Picea abies* (L.) Karst) prevail in the montane belt of central Europe.

85 For instance, the Dinaric Mountains is considered a hotspot for late-successional montane old-growth forests
86 (Sabatini et al. 2018) presumably due to early protection of forests during the 19th century and lower historical
87 human pressure compared to other mountain ranges in Europe due to the extent of rugged mountain areas and land
88 with low agricultural productivity (Diaci 1999; Kaplan et al. 2009; Nagel et al. 2017). However, records
89 documenting long-term vegetation dynamics in conjunction with environmental changes are lacking for the
90 montane zone in this region (Finsinger et al. 2017). Thus, the factors leading to their fragmentation and the extent
91 to which the current landscape retains legacies of past land-uses and natural components (Vale 2002; Whitlock et
92 al. 2018) are largely unknown. For instance, in the montane zone of the Apennines, monospecific beech forests
93 established in relatively recent times following the decline of *Abies alba* and other mesophilous deciduous trees
94 due to enhanced fire activity and multi-millennial land-use intensification superimposed on late-Holocene cooling
95 and moistening (Morales-Molino et al. 2020).

96 Here, we present novel multi-proxy palaeoecological data (pollen, spores, macrofossils, macroscopic charcoal,
97 and magnetic susceptibility) and current forest structure data from Biogradska Gora (central Dinaric Mountains,
98 Montenegro) to provide new insights into the long-term vegetation dynamics of old-growth forests in the montane
99 zone of the Dinaric Mountains. The forest has been continually under protection for the past 140 years and includes
100 one of the largest central-southern European old-growth stands dominated by mixed fir and beech with sparse
101 spruce that is surrounded by almost pure beech stands (Motta et al. 2015a). Our specific aims are: (1) to assess
102 differences in current forest structure within the old-growth stands and the surrounding forest, (2) to track stand-
103 scale long-term vegetation dynamics and occurrence of past disturbances by fire, and (3) assess potential legacy
104 effects on present-day forests.

105

106 **Materials and Methods**

107 *Study area*

108 The Biogradska Gora valley (Fig. 1) is located on the Bjelasica massif, which bears relatively small amounts of
109 carbonate bedrocks compared to the rest of the Dinaric mountain system, where limestone substrata are prevalent.
110 Dystric cambisols (brown soils) on eruptive rock are the dominant type of soil (Čurović et al. 2011). The climate
111 is influenced by continental and maritime airstreams, with annual average precipitation of *c.* 1960 mm, lowest
112 rainfall in July-August and monthly temperatures ranging between -2 and 16 °C (Motta et al. 2015a; Fick and
113 Hijmans 2017).

114 Tree cover in the valley is dominated by beech, fir and spruce, with minor amounts of *Acer pseudoplatanus* L., *A.*
115 *platanooides* L. and *A. heldreichii* Orph. ex Boiss, *Fraxinus excelsior* L., *Ulmus montana* With., *Ulmus glabra*
116 Huds., and *Sorbus aucuparia* L. (Stijovic 2017). *Betula* L. and *Pinus mugo* Turra occur at the upper treeline in
117 adjacent valleys, and *Pinus peuce* Griseb, *P. leucodermis* Ant., and *P. sylvestris* L. are absent in the valley but
118 sparsely occur on the Bjelasica (Černjavski 1937).

119 The forest is protected since 1878 CE, when the area was set aside as a royal hunting reserve (Motta et al. 2015a).
120 The area is included in the Biogradska Gora National Park since 1952 to protect the forest from exploitation by
121 logging companies (Luburić 2016) and has been proclaimed Biosphere Reserve in 1977 (UNESCO 2010). This
122 includes a 2830-ha strictly protected core area (IUCN category II) where land-use activities (logging, farming,
123 grazing) are prohibited. The core area is surrounded by a buffer zone characterised by meadows (Fig. 1) and groups
124 of shepherds' huts (locally called "katun") whose presence possibly dates back to the Middle Ages when pasturing
125 was widespread in Montenegro (Pluskowski and Seetah 2006). The number of occupied huts has declined
126 considerably during the past decades due to rural areas depopulation and many of them have been converted for
127 tourism purposes.

128

129 ***Current forest composition and structure***

130 We surveyed 51 plots predominantly in the outer part of the forest (Fig. 1). Their location was guided by a
131 preliminary segmentation of a SPOT5 satellite image that identified polygons of homogeneous forest canopy
132 composition and structure (Motta et al. 2015a).

133 In each circular plot (radius = 14 m), we recorded the species and measured the diameter at breast height (DBH)
134 of all living stems with a $DBH \geq 7.5$ cm and the heights (H) of at least three individuals for each species and in
135 different diameter classes when available. We measured the minimum and maximum diameter and length (D_{min} ,
136 D_{max} , L) of all coarse woody debris (CWD) with $L \geq 100$ cm and $D_{min} \geq 10$ cm, classifying the deadwood as snags
137 (standing dead trees), logs (lying deadwood), or stumps ($H < 130$ cm). In a smaller area (radius = 6 m) centred on
138 each plot centroid we identified and counted the regeneration ($DBH < 7.5$ cm).

139 We pooled our 51-plots dataset with the 30-plots dataset recorded by Motta et al. (2015), which were concentrated
140 in a small (50 ha) portion of the inner part of the forest, and for each plot calculated variables to assess the current
141 old-growthness and forest structure. Then we estimated the overall tree density (De; #/ha), basal area (BA; m^2/ha),
142 and amount of regeneration (Re; #/ha). To estimate the volume of living wood biomass (V; m^3/ha) we used a local
143 volume table, deriving tree heights from species-specific hypsometric curves. We computed CWD volumes

144 (m^3/ha) for CWD classes, and the dead to live wood ratio (Öder et al. 2021). To estimate tree species diversity, we
145 computed the Brillouin index (Brillouin 1956). To measure the structural diversity, we calculated the DBH
146 standard deviation, Tree Diameter Diversity index (TDD) to 5 cm DBH classes of living stems (Rouvinen and
147 Kuuluvainen 2005), and the Gini coefficient (Gini 1912; Weiner and Solbrig 1984), which quantifies the structural
148 heterogeneity in tree diameters (G_{DBH}) and basal areas (G_{BA}) (Table S1).

149 Subsequently, we identified forest structural types (FST) using a Hierarchical Cluster Analysis (HCA) based on
150 selected structural and compositional variables and tested the statistical differences among FSTs using a non-
151 parametric Kruskal-Wallis test, followed, in the case of significance, by a Dunn's post hoc test (see ESI1 for further
152 details).

153 To explore the influence of accessibility, we calculated Spearman's correlations between variables describing
154 forest structure and a proxy for potential human pressure namely the cost of access, that is the minimum
155 accumulative distance (m) to each plot from the main roads (see ESI1 for further details), following Garbarino et
156 al. (2013).

157 To assess the distribution of land-cover types and to upscale FSTs at a landscape scale we used an object-based
158 image analysis. We pre-processed two high-resolution satellite images (Table S2) by pan-sharpening multispectral
159 bands through the nearest neighbour diffusion (NNDiffuse) algorithm (Sun et al. 2014) and by co-registering them
160 to the Bing satellite image with ENVI software (v5.3.1; Exelis Visual Information Solutions, Boulder, Colorado).

161 We then created image objects through the Large-Scale Mean-Shift (LSMS) segmentation algorithm (Michel et
162 al. 2015) implemented in Orfeo ToolBox v7.0 (Grizonnet et al. 2017), using a raster stack formed by the near
163 infrared band, the Normalized Difference Vegetation Index (NDVI) and textural data derived from granulometric
164 analysis based on the opening procedure (see ESI1 for further details). We performed a supervised classification
165 of image objects using the Random Forest (RF) algorithm implemented in the 'ranger' R package (Wright and
166 Ziegler 2017), employing the spectral and textural information of the image objects as predictor variables for the
167 RF model (Table S3). We trained the RF model using 1457 objects that were classified through on-screen visual
168 interpretation. Most of the training objects ($n=1305$) intersected the 81 ground-survey plots and belonged to one
169 of the following land-cover types: broadleaved trees, conifers and forest canopy gaps. We identified training
170 objects of land-cover types that we did not survey (grasslands, bare ground and water) through on-screen
171 interpretation. We assessed the performance of the RF model by computing the average overall accuracy and
172 Cohen's Kappa statistic obtained from a 5-fold cross-validation procedure. We performed the analyses separately
173 for two satellite images and then merged the land-cover maps.

174

175 ***Long-term vegetation and fire disturbance histories***

176 We collected a 245-cm long sediment sequence from a small pond (0.047 ha; 42°54'5.898"N; 19°35'53.538"E;
177 1155 m a.s.l.; Fig. 1) located in the beech-dominated outer part of the forest to reconstruct stand-scale vegetation
178 dynamics. We combined two parallel and overlapping cores (drives 1-m long and 8 cm in diameter) collected near
179 to the centre of the basin with a Russian-type corer at 5 cm water depth.

180 To constrain the depth-age model, we used eight AMS ¹⁴C dates from terrestrial plant macrofossils (Table S4)
181 calibrated using the IntCal13 dataset (Reimer et al. 2013). We built the model using the R Bacon v2.4.1 package
182 (Blaauw and Christen 2011) and verified the accuracy in its most recent part by comparing the expected and actual
183 ages of the first occurrence of *Ambrosia artemisiifolia* L. pollen. Documentary evidence (Makra et al. 2005;
184 Csontos et al. 2010) indicates that ragweed (*Ambrosia*) became invasive in Central and Eastern Europe around
185 1910-1920 CE.

186 We measured the magnetic susceptibility at 1-cm intervals with a Bartington MS2E surface-scanning sensor
187 following Nowaczyk (2001). Magnetic susceptibility is influenced by the amount of minerogenic input that results
188 from erosion. Negative magnetic-susceptibility values are found in sediments with minerals that do not contain Fe
189 (e.g. quartz and calcite) and in organic-rich sediments.

190 We used macroscopic charcoal analyses to reconstruct long-term fire activity (Whitlock and Larsen 2001;
191 Conedera et al. 2009). We counted charcoal particles in contiguous 1-cm³ samples, and additionally measured
192 areas of charcoal particles for 42 samples (6-cm resolution) using an image-analysis software (see ESI1). We
193 transformed charcoal concentrations to charcoal accumulation rates (CHAR) based on the chronology.

194 To uncover local-scale vegetation dynamics, we analysed 41 plant macrofossil samples in conjunction with pollen
195 and stomata (see Fig. S1 and ESI for details of laboratory and identification methods used) (Birks and Birks 2000;
196 Ammann et al. 2014; Finsinger and Tinner 2020). We calculated pollen percentages relative to the terrestrial pollen
197 sum, which included pollen from trees, shrubs, herbs and *Pteridium* spores. A sum of at least 250 pollen and spores
198 was counted for each sample. However, the lowermost sample has a substantially lower pollen sum (n=36) due to
199 an extremely low pollen concentration.

200 To evaluate human impact, we considered the abundances of primary anthropogenic indicators, secondary
201 adventives and apophytes (Behre 1981; Deza-Araujo et al. 2020), which include pollen of cultivated plants,
202 ruderals, and plants of meadows. In addition, we used *Sporormiella*-type dung-fungi spores, which are linked to
203 the presence and abundance of large herbivores (Davis 1987; Baker et al. 2013), and *Tilletia caries*-type spores

204 (see ES11), a pathogen associated mostly with grasses, including cereals (Mazurkiewicz-Zapałowicz and
205 Okuniewska-Nowaczyk 2015). Abundances of non-pollen palynomorphs are presented as influx (number cm⁻²
206 year⁻¹).

207 We determined pollen assemblage zones based on terrestrial pollen taxa (excluding taxa with maximum abundance
208 <5%) using optimal partitioning by sums-of-squares (Birks and Gordon 1985) in Psimpoll v4.26 (Bennett 2008).
209 The number of statistically significant zone boundaries was determined by comparison with the broken-stick
210 model (Bennett 1996).

211 We analysed the CHAR data using CharAnalysis v1.1 (Higuera et al. 2009) to determine centennial-scale trends
212 in CHAR that were interpreted as relative changes in biomass burned over time (Marlon et al. 2008; Higuera et al.
213 2010a), and to identify peaks in charcoal, which were interpreted as fire episodes. The analysis involved
214 interpolating CHAR values to a constant sampling resolution, decomposing that record into a background and a
215 peak component using a robust LOWESS, and evaluating peak samples using both the 99th percentile of the
216 modelled noise distribution obtained with a Gaussian mixture model and a peak-screening test. The suitability of
217 the record for peak detection was assessed with the signal-to-noise index (SNI; Kelly et al. 2011). We calculated
218 fire return intervals (FRI) using the screened peak record.

219 We used change-point analysis to determine significant changes in biomass burning and test the potential effect
220 of sedimentation rates on change-point detection (Finsinger et al. 2018).

221 To test the simultaneity between fire and erosion events, thereby allowing identification of high-severity local
222 catchment fires (Chileen et al. 2020), we used Event Coincidence Analysis (ECA; Siegmund et al. 2017). We
223 determined erosion events as (i) peaks of magnetic susceptibility, which respond to increases in minerogenic input
224 that often follow fire events as a result of erosion, and to in-washing of secondary ferromagnetic minerals that are
225 formed when soils with a high concentration of convertible Fe are heated (Thompson and Oldfield 1986;
226 Millspaugh and Whitlock 1995), and (ii) peaks of *Cenococcum geophilum* Fr. sclerotia influx, whose abundances
227 are linked to soil erosion (Van Geel 1978). The two datasets were analysed with a custom-made computer code
228 (R Core Team 2020) in a similar way to the CHAR record to statistically identify distinct peaks. We performed
229 the ECA using two binary event time series (CHAR peaks and erosion peaks), a lag of 8 years, and a tolerance
230 window 8-48 years that detects erosion events within 10-50 years of fire episodes, and tested the significance
231 based on the assumption of independent and sparse Poisson processes ($\alpha=0.05$).

232 To identify leads and lags between fire activity (macroscopic charcoal influx values) and vegetation and land-use
233 change (pollen percentages and dung-fungi spores' influx), we used cross-correlation analyses (Green 1981;

234 Tinner et al. 1999; Valsecchi et al. 2008). We performed the analyses for two time intervals that show different
235 intensity of human pressure: 970-1350 CE (higher pressure); 1600 CE to the present (lower pressure). Within the
236 selected time intervals, the sampling resolution was relatively stable (32 ± 3 and 21 ± 3 years between samples,
237 respectively). The cross-correlations' span was restricted to one-fourth of the sample number N (lag number \leq
238 $N/4$).

239

240 **Results**

241 *Present vegetation composition and forest structure*

242 The forest includes plots characterized by large trees (up to 148 cm of DBH; Fig. 2) and by a high CWD volume
243 (up to $791.6 \text{ m}^3 \text{ ha}^{-1}$; Fig. 3). Plots having a complex horizontal and vertical structure are present as shown by high
244 volume of living trees (V ; up to $1781.9 \text{ m}^3 \text{ ha}^{-1}$) and high values of structural diversity indices (G_{BA} up to 0.8)
245 (Table 1). CWD consists mostly of logs (65%) and snags (33%) and rarely stumps (2%). Although beech is the
246 species with the highest overall stems density, beech trees are generally smaller than fir and spruce trees.

247 The HCA (Fig. S2) identified three forest structural types (FST) that differ significantly from each other (Table 1;
248 Fig. 3). Their overlap on the land-cover type map that we obtained through remote-sensing analysis (Fig. 1; see
249 ESII Table S5 for assessment of accuracies) shows that FST1 plots predominantly occur in the beech-dominated
250 outer part of the forest. These plots are dominated by small and mostly multi-stemmed beech trees (DBH generally
251 <40 cm from single stools), and have negligible amounts of CWD, and low BA and density of conifers and other
252 deciduous species. We found an inactive charcoal kiln in one of these plots, and cut stumps in two plots. FST2 and
253 FST3 plots are in a 957-ha conifer-dominated area (34% of the core area) and are dominated by fir (FST3) and
254 predominantly co-dominated by fir and spruce (FST2). FST2 also includes a plot dominated by sycamore maple.
255 CWD and dead to live wood ratio values are significantly higher, and BA and density of beech are significantly
256 lower than in FST1 plots.

257 The indices of structural diversity (DBH_{SD} , H_{SD} , G_{DBH} , G_{BA}) indicate that plots in the inner part of the forest are
258 structurally more heterogeneous than those in the outer part. FST2 plots have the highest species and structural
259 diversity (Table 1) as they consist of large fir and spruce trees (up to 148 cm in DBH), and small to intermediate
260 beech trees (mostly 10-65 cm in DBH). In FST3 plots, spruce trees are extremely rare, and the prevalent species
261 are fir (intermediate to large diametric classes, up to 115 cm) and beech (small to intermediate diametric classes).
262 Moreover, the DBH_{mean} and volume are significantly lower and the amount of CWD and dead to live wood ratio

263 values are significantly higher. Regeneration of spruce is very scarce in all plots, while regeneration of fir and
264 beech is significantly higher in FST1 and FST3, respectively.

265 Median cost of access is lower for FST1 plots in the outer part of the forest (Fig. 3). Cost of access is significantly
266 and positively correlated to BA of fir (Spearman's $\rho=0.43$, $P<0.001$) and negatively to BA of beech (Spearman's
267 $\rho=-0.36$, $P<0.01$). Positive significant correlations of cost of access are also found with CWD amount (Spearman's
268 $\rho=0.44$, $P<0.001$), dead to live wood ratio (Spearman's $\rho=0.38$, $P<0.001$) and heterogeneity as described by the
269 DBH standard deviation (Spearman's $\rho=0.29$, $P<0.05$) and Gini indices (Spearman's $\rho=0.35$ for G_{DBH} and 0.30
270 for G_{BA} , $P<0.01$).

271 The difference among forest structures is also supported by the textural analysis of the forest canopy (Figs S3a-c),
272 which are finer and more homogeneous in the outer part, whereas more complex and heterogeneous canopies,
273 probably arising from gap dynamics, are common in the inner part. Most (99%) of the detected gaps occur in the
274 conifer-dominated area. Gap sizes are highly variable (mean: 210 m²; range: 3.33-5636 m²) and their distribution
275 is right-skewed (76% of gaps <200 m², only 2% >1000 m²).

276

277 ***Long-term environmental changes***

278 The sediment core spans the past *c.* 1000 years (Fig. S4a). The reliability of the chronology in its most recent part
279 is confirmed by the first occurrence of *Ambrosia* pollen around 1920 CE (Fig. 4). Sediment deposition time (Fig.
280 S4b) varies little (3-8 years cm⁻¹; median=4.4 years cm⁻¹). Sediments deposited before 1300 CE are lighter in
281 colour than the darker-brown detritus gyttja deposited thereafter (see ESI1 for further details on sediment
282 composition and the chronology).

283 The pollen record (Fig. 4, see ESI1 Fig. S5-S6 for more detailed pollen and macrofossil diagram) was divided into
284 three statistically significant assemblage zones at 123.5 and 52 cm depth (*c.* 1600 and 1850 CE, respectively).
285 However, to better illustrate the long-term vegetation changes we additionally selected a non-significant pollen
286 zone boundary at 171.5 cm (*c.* 1350 CE).

287 The lowermost pollen assemblages (950-1150 CE) of zone 1a are characterized by decreasing abundance of tree
288 pollen (from 80% to 40%), particularly pollen of conifers (*Abies*, *Pinus sylvestris*-type and *Picea*) and of fern
289 spores (e.g. *Athyrium filix-femina*), which grow in fresh and shaded understorey environments (Ellenberg 2009).

290 The continuous finds of pollen and plant macrofossils of the half-shade demanding *Sambucus* from 950 to 1150
291 CE indicate the presence of clearings. The transition to a land-use phase (1150-1350 CE), which is demonstrated

292 by high abundance of primary anthropogenic indicators and adventives as well as by *Sporormiella* and *Tilletia*
293 spores, is marked by a short-term expansion of *Rhamnus* (1050-1150 CE).

294 Anthropogenic indicators and herb pollen abundances distinctly decrease around 1350 CE (onset of zone 1b)
295 indicating a sudden abandonment of pasture and cultivation. Higher abundance of arboreal pollen percentages in
296 conjunction with angiosperm leaves and fern spores indicates the establishment of broadleaf trees with a fern
297 understorey. *Picea* was present in the surroundings, as shown by stomata and plant-macrofossil finds. The pollen
298 record shows the expansion of trees and shrubs that typically colonise abandoned pastures (*Sambucus*, *Betula*,
299 *Alnus*, *Ulmus* and *Acer*). A century later (around 1450 CE) pollen, stomata and plant-macrofossils of shade-tolerant
300 *Abies* and *Fagus* trees increased. The development of a mixed woodland was interrupted by a short-term and
301 milder land-use phase (1500-1600 CE), as suggested by the slight rise of primary and secondary anthropogenic
302 indicators, fire-adapted *Pteridium* and upland herbs.

303 Local conifer populations collapsed during this second land-use phase (onset of zone 2: 1590 CE) and a *Fagus*-
304 dominated forest gradually established around the site. Pollen and plant macrofossils indicate that light-demanding
305 woody species (*Corylus*, *Betula*) expanded faster than the shade-tolerant *Fagus*, which peaked around 100 years
306 later (1700 CE). *Fagus* and *Fraxinus* pollen as well as their plant macrofossils markedly decreased between 1760
307 and 1850 CE in conjunction with a slight rise in *Sporormiella* and *Veratrum* spores, which indicates a third land-
308 use phase characterised by grazing.

309 During the past 170 years (zone 3; 1850 CE to present), a *Fagus*-dominated forest type developed with increasing
310 abundance of *Ulmus*, *Alnus*, *Fraxinus* and *Acer*, low abundance of anthropogenic indicators, and decreasing
311 abundance of pioneer trees and shrubs (*Corylus* and *Betula*). Tree cover has been highest since 1950 CE.

312 Macroscopic charcoal concentration values ranged between 0 and 271 (median = 34 pieces cm⁻³). Charcoal counts
313 and charcoal areas are significantly correlated ($R^2=0.91$, $P<0.001$). Peak analyses based on different parameters
314 are highly comparable among one another with mean SNI values generally higher than the critical threshold (Table
315 S6; Figs S8-S9). The periods of shorter fire-return intervals (1000-1150 CE, FRI=25 years; 1460-1520 CE, FRI=60
316 years; and 1730-1810 CE, FRI=75 years) occur predominantly during phases of high biomass burning (1000-1030,
317 1340-1730, and 1730-1850 CE, Figs 5 and S10). A large majority (75%, $P=0.05$) of the erosion events occurred
318 10-50 years after fire episodes (Fig. S11). This is the case for erosion events occurring at the onset of the Middle
319 Ages (1050 CE), towards the end of the Middle Ages (1500-1550 CE), and during the 20th-century. The
320 coincidence between fire episodes and erosion events suggests that these were triggered by higher-severity

321 catchment fires, whereas fire episodes occurring during the medieval land-use phase (1050-1150 CE) and around
322 1800 CE were of lower intensity or occurred outside the catchment.

323 We used cross-correlation analyses (Fig. 6) to explore leads and lags between fire activity and vegetation and land-
324 use change separately for (i) the Middle Ages when human pressure was higher (970-1350 CE; zone 1b), and (ii)
325 the more recent centuries (1600 CE to the present; zones 2-3) when human pressure was lower and the forest was
326 protected. Significant negative correlation coefficients ($P < 0.05$) between charcoal-accumulation rates (CHAR)
327 and arboreal pollen, *Abies*, *Picea* and *Fagus* in the Middle Ages indicate that fires contributed considerably to the
328 decline of late seral species. We found the highest correlation coefficients when CHAR lagged primary indicators
329 and dung spores by 30 years, consistently with mechanisms of charcoal taphonomy leading to delayed deposition
330 at a coring location (Duffin et al., 2008; Higuera et al., 2010). Thus, the significant positive correlations between
331 CHAR and primary anthropogenic indicators and dung spores at negative lags support the hypothesis of human-
332 driven fires used to create open areas for agriculture and grazing.

333 For the time interval when human pressure was lower (1600 CE to the present) arboreal pollen is negatively
334 correlated with fire, and primary anthropogenic indicators are positively correlated with fire at lag 0, thus
335 corroborating the link between cultivation and fire. Dung fungi also show positive significant correlations with
336 fire, though the highest coefficients are found at positive lags, suggesting a delayed increase of grazing ca. 60
337 years after fire activity rises. By contrast, in this time interval the correlation coefficients between CHAR and
338 *Abies*, *Picea* and *Fagus* are not significant. However, *Corylus* and *Betula* show positive significant correlations
339 ahead of the charcoal peaks (at lags -4 and -5), suggesting that these light-demanding pioneer species acted as fire
340 precursors, and *Fraxinus* shows a negative significant correlation at lag 0. It thus seems likely that land-use and
341 fires mainly occurred in gaps within the overall *Fagus*-dominated forest.

342

343 **Discussion**

344 ***Current forest structure within the old-growth stands and the surrounding forest***

345 Our extensive ground surveys and the detailed remote-sensing analyses show that the Biogradska Gora forest is
346 characterised by a large compositional and structural variability. We detected a fine-scale variability due to gap
347 dynamics within the conifer-dominated matrix in the inner part, which allow the recruitment of more light-
348 demanding species, like sycamore maple, in larger gaps (Nagel et al. 2014). In addition to this fine-scale variability,
349 we identified three forest structural types (FSTs) showing different degrees of old-growthness (Fig. 3) that are
350 unevenly distributed within the forest (Fig. 1). The structural and compositional variability supports the notion

351 that plots placed in a limited area that is considered representative of old-growth characteristics may lead to an
352 overestimation of average old-growthness (Peck et al. 2015; Carrer et al. 2018).

353 The structure in the inner part of the forest (FST2 and FST3) is comparable to that of other mixed old-growth
354 forests such as Perućica, Lom, and Jani in Bosnia-Herzegovina (Motta et al. 2011, 2015b, a; Keren et al. 2014,
355 2020; Zenner et al. 2015; Chivulescu et al. 2020), both in terms of variables assessed previously (BA, V, and
356 CWD) by Motta et al. (2015a) as well as in terms of dead to live wood ratio and structural diversity (Table 1, Figs
357 2 and 3). Moreover, the heterogeneous texture of the forest canopy with small-scale gaps also shows that the
358 conifer-dominated stands in the inner part of the forest likely had the time to develop typical old-growth attributes
359 (Spies and Franklin 1988; Wirth et al. 2009).

360 The HCA confirms prior studies showing that the old-growth forest includes two structural types, their main
361 differences being the rarity of spruce (Motta et al. 2015a) and significantly higher dead biomass (CWD and dead
362 to live wood ratio values) in the fir-dominated FST3 plots (Fig. 3). Because spruce is rare in these plots, their
363 significantly higher amount of dead biomass could be linked to higher spruce mortality. This would fit with the
364 persisting decline of the spruce population, as indicated by its extremely low seedling regeneration and the absence
365 of spruce saplings in all plots (Table 1). The decline of spruce may agree with evidence showing that at the southern
366 boundary of its distributional range populations of the cold-adapted spruce are more vulnerable to drought than fir
367 and beech (Hanewinkel et al. 2013; Zang et al. 2014). In agreement with this, in the Dinaric Alps spruce dominated
368 stands are common in karst depressions and sinkholes where temperature inversions cause significantly colder
369 microclimates (Nagel et al. 2017). Conversely, the low spruce regeneration could be explained by the scarcity of
370 expanded gaps, as spruce is less shade tolerant than beech and fir (Stancioiu and O'Hara 2006a) and beech is the
371 main gap filler species in a small-scale disturbance regime (Petritan et al. 2014) typical of old-growth forests.

372 In the beech-dominated outer part of the forest (FST1) CWD consists mostly of logs with a lesser number of snags,
373 as often observed in old-growth stands (Nilsson et al. 2003) and as observed in the inner part of the forest.
374 However, the FST1 plots have substantially lower CWD values than FST2 and FST3 plots. While this is relatively
375 unsurprising given that broadleaved trees produce a lower deadwood accumulation (Harmon et al. 2004) due to
376 their lower height and volume, and their deadwood decays faster than deadwood of conifer species (e.g. 20-40
377 years for *Fagus*, and within 58-191 years for conifer snags on moist sites; Vacek et al. 2015; Hararuk et al. 2020),
378 these plots also have substantially lower CWD values than other European beech-dominated old-growth forests
379 (Burrascano et al. 2013; Meyer et al. 2021). Interestingly, CWD and dead to live wood ratio values are closer to
380 those found in currently managed forests or in those recently withdrawn from regular management (Motta et al.

381 2015b). Moreover, the lower structural diversity of these plots and the finer texture of the forest canopy rather
382 reflect a homogeneous structure and even-aged cohorts.

383

384 *Stand-scale long-term vegetation dynamics, land-use changes and disturbances by fire*

385 Despite the importance of pollen loading from regional sources, the proportion of pollen loading coming to the
386 0.05-ha-pond in the beech-dominated area from the relevant pollen source area (200-300 m for such sites) is
387 adequate to reflect local vegetation composition (Sugita 1994; Hofstetter et al. 2006). This is also supported by
388 the coherence between the pollen and the plant-macrofossil and stomata records (Fig. 7) that are generally
389 dispersed over substantially shorter distances than pollen (Birks and Bjune 2010; Ammann et al. 2014). Similarly,
390 while the source area of macroscopic charcoal particles can be relatively large (up to 30-50 km; Oris et al. 2014;
391 Adolf et al. 2018), both empirical and simulated data support the assumption that charcoal peaks most accurately
392 reflect fire episodes within 1–3 km of coring sites (Higuera et al. 2010b). Moreover, the coincidence of peaks in
393 charcoal and erosion-indicators helped us to pinpoint the occurrence of local higher-severity catchment fire
394 episodes (Fig. 7). Thus, our palaeoecological record predominantly documents local-scale vegetation dynamics,
395 land-use and fire occurrence for the currently beech-dominated outer part of the forest.

396 During the Middle Ages, tree cover was substantially lower and cereal crop cultivation and cattle herding were
397 more widespread than today (Fig. 7). Finds of spores of common bunt (*Tilletia sp.*) suggest that pathogens affected
398 cultivated crops, as these pathogens can cause devastating yield reductions by up to 50% (Kiesselbach and Lyness
399 1939). Bunt was one of the most severe diseases of winter wheat (*Triticum aestivum* L.) in the Middle Ages
400 (Gaudet and Menzies 2012) and harvest failures were important factors for social vulnerability, particularly for
401 people living in rural areas in pre-industrial economies (Pfister and Brázdil 2006). These constraints on crop
402 cultivation favoured abandonment of the fields surrounding the pond, thereby causing the tree cover increase
403 around 1350 CE when the Black Death pandemic rapidly spread and substantially reduced population density
404 (Green 2014; Luterbacher et al. 2020).

405 Despite setbacks due to the occurrence of more moderate and transient local land-use phases with the use of fire,
406 tree cover increased after 1350 CE. This trajectory markedly contrasts with decreasing tree cover due to
407 intensifying land-use since the 15th-16th century (Fig. 7) documented for nearby Bosnia-Herzegovina (Prokoško
408 Jezero; Dörfler 2013), the coastal region of Albania-Montenegro (Shkodra Jezero; Sadori et al. 2015), as well as
409 for elsewhere in Europe (Fyfe et al. 2015; Conedera et al. 2017), and as suggested by models (Kaplan et al. 2009).
410 The absence of evidence for intensifying land-use after the 15th century at Biogradska Gora could be due to the

411 transition to cooler temperatures and the beginning of the Little Ice Age (LIA), which may have discouraged
412 cultivation and pasturing in the valley. Indeed, years with unusually cold spring seasons during the LIA had serious
413 consequences on grain harvests and on cattle in the meridional Balkans and in Serbia (Xoplaki et al. 2001; Mrgic
414 2018). An alternative, or additional, explanation could be the small pollen source area, which predominantly
415 captured pollen from the surrounding expanding beech stand despite ongoing land use on the hilltops where
416 meadows still exist today. Regardless, the tree-cover increase and decreasing land-use pressure that started around
417 1500-1600 CE suggests that the 19th century's formal protection of the forest eventually took advantage of the pre-
418 existing situation, supporting the view that historical land-use pressure is a significant predictor for the occurrence
419 of primary and old-growth forests (Sabatini et al. 2018).

420 The longer continuity of the conifer-dominated old-growth stands is currently not supported by firm evidence due
421 to the lack of palaeoecological sites in that area. On one hand, these stands may have developed after the 15th-16th
422 century, when land-use declined. This would fit with age estimates of deadwood showing that trees up to 400-500
423 years old occurred in the conifer-dominated stands (Motta et al. 2015a). On the other hand, the presence of stomata
424 and plant macrofossils before the 15th-16th century in the currently beech-dominated outer part of the forest (Fig.
425 7) rather supports the hypothesis that the area of fir and spruce-dominated old-growth forest was reduced during
426 the Middle Ages. In Central and in southern European mountains fir declined several millennia earlier (Büntgen
427 et al. 2014; Morales-Molino et al. 2020) than at Biogradska Gora, and it is plausible to hypothesise that fir declined
428 earlier in more accessible mountain areas. The higher cost of access may have prevented human activities in the
429 old-growth forest, and land-use activities were probably limited to the outer part of the forest, as observed at
430 Biogradska Gora (Černjavski 1937) and as is often the case for protected ecosystems (Hansen and DeFries 2007).
431 Fires either did not propagate into the inner part of the forest, or their severity was not high enough to affect the
432 fire-sensitive fir population. Overall, this supports the notions that human pressure played an important role for
433 the small extent of old-growth forests (Nagel et al. 2017; Sabatini et al. 2018) and that buffer zones are key for
434 protecting old-growth forests (Barredo et al. 2021).

435

436 *Legacies of past human activities*

437 Forest composition in the surroundings of the small pond shifted from a mixed fir-spruce-broadleaf stand to one
438 dominated by beech at the transition to cooler LIA temperatures and in conjunction to a land-use pressure decline
439 around 1500-1600 CE (Fig. 7). Analogous expansions of beech at the expense of fir are well documented in mid-
440 late Holocene pollen records from central-southern Europe, and evidence suggests that despite the two species

441 currently sharing large parts of the ecological niche (Houston Durrant et al. 2016; Mauri et al. 2016), beech became
442 more competitive after the decline of *Abies alba* and with the onset of cooler and moister summers and human fire
443 disturbance (Vescovi et al. 2010; Morales-Molino et al. 2020). While it is difficult to disentangle the effects of
444 climate and land-use, it seems likely that land-use and fire occurrence probably played an important role in driving
445 the vegetation shift. The conifer population was strongly reduced due to increased local fire activity (Fig. 6) in
446 conjunction with land-use during the Middle Ages, and the local conifer population finally collapsed in 1500 CE
447 when two higher-severity local fires occurred at the onset of a moderate land-use phase (Fig. 7). This is in line
448 with a wealth of evidence showing that conspicuous canopy gaps (from fires and land-use) can cause a reshuffling
449 of the dominant tree species in mixed fir, beech and spruce forests. Spruce, for instance, does not survive or re-
450 sprout after high severity fires (Niklasson et al. 2010; Feurdean et al. 2019) despite bearing traits promoting fires
451 (high resin content, ladder canopy structure) and being able to persist with a low to moderate fire severity
452 (Feurdean et al. 2017). Similarly, both large-infrequent and small-frequent fires lead to a rapid local extinction of
453 the fire-intolerant *Abies* (Tinner et al. 2013). By contrast, human activities and disturbance by fire can favour the
454 spread of beech at the stand level (Bradshaw and Lindbladh 2005; Tinner and Lotter 2006). Beech quickly re-
455 sprouts and regenerates successfully after small or intermediate human and natural disturbances (windthrow,
456 cutting, fire; Motta et al. 2011; Nagel et al. 2014; Maringer et al. 2016). Importantly, beech regenerates faster than
457 fir and spruce in canopy gaps and overstorey releases (Stancioiu and O'Hara 2006b; Bolte et al. 2014).
458 Additionally, beech encircles competitors and fills gaps after disturbances (Pretzsch and Schütze 2005; Bolte et
459 al. 2014) as it rapidly takes advantage of more favourable light conditions due to higher morphological plasticity
460 of foliage and crown structures (Dieler and Pretzsch 2013). Thus, frequent small or intermediate-scale disturbances
461 (Delarze et al. 1992), such as those created by land-use associated with the use of fire, can promote beech (Bolte
462 et al. 2014). An additional explanation could involve clear-cutting and extraction of conifer timber in stands that
463 are accessible for harvest (Büntgen et al. 2014). Other forms of land-use, such as coppicing, also could have
464 favoured beech to obtain firewood or wood charcoal, as observed elsewhere in marginal areas of coniferous
465 woodland in Central Europe (Winkler 1963). Coppicing and clear-cutting practices developed greatly due to
466 increasing wood demand and demographic growth in the 16th-17th centuries and after 1850 CE (McEvedy and
467 Jones 1978). At Biogradska Gora, these practices are attested to by multi-stemmed beech trees and traces of
468 charcoal kilns in some plots in the more accessible outer part of the forest.

469 The protected old-growth forest of Biogradska Gora should be sufficiently large (>1000 ha) to buffer the effects
470 of small-scale natural disturbances (Sabatini et al. 2018). Moreover, population density in mountain areas is

471 predicted to decrease over the 21st century in eastern Europe due to abandonment of pastoral and agricultural
472 activities (Wu et al. 2015). This may also be beneficial to the majority of primary and old-growth forests that are
473 substantially smaller (<100 ha) (Sabatini et al. 2018). However, old-growth forests may be at risk due to predicted
474 environmental changes. For instance, despite the rare natural fire occurrence and the much greater importance of
475 other disturbance agents (bark beetle outbreaks, windthrows; Nagel et al. 2017), forest fires are predicted to
476 increase in the region, which could potentially become a new fire-prone area (Krawchuk et al. 2009; Wu et al.
477 2015). Warmer and drier conditions that may lead to increased fires will also likely affect vegetation structure
478 modifying fuel type, fuel load and therefore fire intensity and spread, increasing mortality rates. For instance, as
479 fir is known to be more drought tolerant than beech (Morales-Molino et al. 2020) its population may recover if
480 other disturbances (e.g. fires) do not prevent the expansion of this fire-sensitive tree species.

481

482 **Conclusions**

483 The multi-proxy palaeoecological records (pollen, spores, stomata, macrofossils, macroscopic charcoal, and
484 magnetic susceptibility) coupled with the extensive survey of current forest structures and with the map of land-
485 cover types from the Biogradska Gora forest provide new insights into the long-term vegetation dynamics of old-
486 growth forests in the montane zone of the Dinaric Mountains. The stand-scale palaeoecological records show that
487 human activities (agriculture, and pastures) as well as fires, which are rare today in these forest types (Nagel et al.
488 2017) reduced the area of fir and spruce-dominated forest during the Middle Ages. Despite the local land-use
489 decline 500-400 years ago and the early protection of the forest 140 years ago, the legacies of past land-use
490 activities are still visible, as the conifer-dominated mixed forest in the inner part of the valley has more old-growth
491 characteristics than the almost pure beech forest in the outer part. However, the continuity and increase of tree
492 cover in the outer part of the forest since the 16th century markedly contrasts with the widespread high conversion
493 rates to agriculture and forest exploitation elsewhere in Europe during the past millennium (Kaplan et al. 2009;
494 Fyfe et al. 2015; Birks and Tinner 2016), thereby supporting the view that historical land-use pressure played an
495 important role for the small extent and the continuity of disturbance-sensitive *A. alba* and *P. abies*-dominated old-
496 growth stands.

497 Our study shows that combining stand-scale long-term ecological records with assessments of contemporary forest
498 structure can generate valuable insights (Foster et al. 1996), as the structures and spatial patterns of ecosystems
499 are often a result of legacy effects arising from complex interactions between natural and human disturbances

500 (McLachlan et al. 2000; Vale 2002; Willis and Birks 2006; Whitlock et al. 2018), which is critical information for
501 guiding forest management and conservation measures (Conedera et al. 2017).

502

503

504 **Figures and Figure captions**

505 **Fig. 1** Map showing the distribution of land-cover types in the Biogradska Gora National Park obtained through
506 the remote-sensing analysis of Pléiades satellite images. Circles indicate the locations of field-survey plots (colour-
507 coded by forest structural type, FST). The star shows the location of the palaeoecological site. The inset shows the
508 study area location in a larger spatial context

509 **Fig. 2** Cumulative diametric (DBH) class distributions in the field-survey plots grouped by forest structural type

510 **Fig. 3** Boxplots illustrating differences among forest structural types in the Biogradska Gora forest. Whiskers
511 represent the first and third quartiles of the distributions, and the horizontal black lines are referred to the median
512 values. Y-axis indicates values of coarse woody debris (CWD), dead to live wood ratio, Tree diameter diversity
513 index (TDD), Gini index referred to the basal area (G_{BA}), diameter standard deviation (DBH_{SD}), basal area (BA)
514 and path distance

515 **Figure 4** Pollen percentage (continuous curves) and plant macrofossil (black bar plots) concentrations diagram
516 of selected taxa from the small pond in the Biogradska Gora valley. Horizontal continuous and dotted lines
517 represent significant and non-significant pollen zone boundaries, respectively. See ESI1 for more detailed pollen
518 and plant-macrofossil diagrams

519 **Fig. 5** Comparison between erosion and charcoal-derived fire history. a) Magnetic susceptibility (MS); b)
520 Macroscopic charcoal accumulation rate (CHAR) interpolated to 8 years (black), charcoal background modelled
521 using a 500-year smoothing window (grey line), while red line indicates final positive and negative threshold
522 values for peaks identification. Identified CHAR peaks are marked with “+” symbols. Grey shaded areas refer to
523 periods of relatively stable biomass burning as determined by the change-point analysis (the darker the shade the
524 higher the mean CHAR values are). See ESI1 for results obtained with other user-determined parameters
525 (interpolation and smoothing-window widths). c) Fire return interval (FRI) values. Vertical continuous and
526 dotted lines represent significant and non-significant pollen zone boundaries, respectively

527 **Fig. 6** Cross-correlograms of charcoal accumulation rates (CHAR), selected pollen percentages and dung-fungi
528 spores’ influxes for two phases of different intensity of human pressure. (i) The Middle Ages when human pressure
529 was higher (970-1350 CE; <1350 CE) and (ii) the more recent centuries when human pressure was lower (1600

530 CE to the present; > 1600 CE). Horizontal axis shows the lag. One lag is equal to *c.* 30 years for phase (i) and to
531 *c.* 20 years for phase (ii). Vertical axis: correlation coefficients; dashed horizontal lines: 95% confidence limits
532 **Fig. 7** Comparison between vegetation dynamics (pollen and non-pollen palynomorphs: filled areas; plant
533 macrofossils: black barplots; stomata: full circles), macroscopic charcoal (CHAR) inferred fire history (red
534 crosses: higher-severity fire events), and magnetic-susceptibility (MS) inferred erosion history (black and blue
535 crosses: erosion events) at Biogradska Gora, and warm-season (May-August, MAMJJA) temperature (see ES11
536 for further details). The bottom panels show the tree cover at Prokoško Jezero, Bosnia-Herzegovina (Dörfler, 2013)
537 and the abundance of total closed forest in Europe (Fyfe et al., 2015)

538

539 **Acknowledgements**

540 We are grateful to D. D'Aprile for help during fieldwork, to I. Figueral, L. Bouby and F. Wagner-Cremer for help
541 with identification of plant-macrofossil, wood and charcoal pieces and *Fagus* stomata, and to R. Marzano, D.
542 Ascoli, C. Urbinati, D. McKey, E. Ilardi, and D. Barbaro for discussions. We thank the Biogradska Gora National
543 Park for granting permission to collect sediments and perform the field surveys.

544

545 **Declarations**

546

547 **Funding:** EC was financially supported by the Land Environment Resources and Health (L.E.R.H.) doctoral
548 course of the University of Padova (DOR1957359/19; “Disturbi naturali in foresta: Studio su una old-growth
549 forest dei Balcani”) and by the Fondazione Ing. Aldo Gini. This work was supported by public funds received in
550 the framework of GEOSUD, a project (ANR-10-EQPX-20) of the program "Investissements d'Avenir" managed
551 by the French National Research Agency.

552 **Availability of data and material:** All data will be made publicly available upon acceptance. The
553 palaeoecological data (pollen, spores, stomata, plant macrofossils, macroscopic charcoal, and magnetic
554 susceptibility) will be uploaded to the Neotoma database (DOI: 10.21233/XYZZ-XYZZ) through the European
555 Pollen Database. The forest structure and composition data will be uploaded to Figshare (figshare.com).

556 **Code availability** (software application or custom code): The custom-made computer code in R will be
557 available on GitHub (<https://github.com/wfinsinger>) and archived in Zenodo (<https://zenodo.org/>) upon
558 acceptance.

559 **Authors' contributions**

560 WF, RM, EL, MG, and EC conceived the ideas and designed methodology; EC, WF, EL, MG, NM, FM, LP
561 collected the data; EC, WF and DM analysed the data; EC, WF, and EL led the writing of the manuscript; MG,
562 RM, LP, NM, FM, MC, VS, IB reviewed the manuscript. All authors contributed critically to the drafts and gave
563 final approval for publication.

564

565 **References**

- 566 Adolf C, Wunderle S, Colombaroli D, et al (2018) The sedimentary and remote-sensing reflection of biomass
567 burning in Europe. *Glob Ecol Biogeogr* 27:199–212. <https://doi.org/10.1111/geb.12682>
- 568 Ammann B, Knaap WO van der, Lang G, et al (2014) The potential of stomata analysis in conifers to estimate
569 presence of conifer trees: examples from the Alps. *Veg Hist Archaeobotany* 23:249–264.
570 <https://doi.org/10.1007/s00334-014-0431-9>
- 571 Baker AG, Bhagwat SA, Willis KJ (2013) Do dung fungal spores make a good proxy for past distribution of
572 large herbivores? *Quat Sci Rev* 62:21–31. <https://doi.org/10.1016/j.quascirev.2012.11.018>
- 573 Barredo JI, Brailescu C, Teller A, et al (2021) Mapping and assessment of primary and old-growth forests in
574 Europe. Luxembourg
- 575 Bauhus J, Puettmann K, Messier C (2009) Silviculture for old-growth attributes. *For Ecol Manag* 258:525–537.
576 <https://doi.org/10.1016/j.foreco.2009.01.053>
- 577 Behre K-E (1981) The interpretation of anthropogenic indicators in pollen diagrams. *Pollen Spores* 23:225–245
- 578 Bennett KD (2008) *Psimpoll v. 4.26*
- 579 Bennett KD (1996) Determination of the number of zones in a biostratigraphical sequence. *New Phytol*
580 132:155–170
- 581 Birks HH, Birks HJB (2000) Future uses of pollen analysis must include plant macrofossils. *J Biogeogr* 27:31–
582 35
- 583 Birks HH, Bjune AE (2010) Can we detect a west Norwegian tree line from modern samples of plant remains
584 and pollen? Results from the DOORMAT project. *Veg Hist Archaeobotany* 19:325–340.
585 <https://doi.org/10.1007/s00334-010-0256-0>
- 586 Birks HJB (2019) Contributions of Quaternary botany to modern ecology and biogeography. *Plant Ecol Divers*
587 12:189–385. <https://doi.org/10.1080/17550874.2019.1646831>
- 588 Birks HJB, Gordon AD (1985) *Numerical Methods in Quaternary Pollen Analysis*. Academic Press, London
- 589 Birks HJB, Tinner W (2016) Past forests of Europe. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, et al. (eds)
590 *European Atlas of Forest Tree Species*. Publications Office of the European Union, Luxembourg, pp
591 36–39
- 592 Blaauw M, Christen JA (2011) Flexible Paleoclimate Age-Depth Models Using an Autoregressive Gamma
593 Process. *Bayesian Anal* 6:457–474. <https://doi.org/10.1214/11-BA618>
- 594 Bolte A, Hilbrig L, Grundmann BM, Roloff A (2014) Understorey dynamics after disturbance accelerate
595 succession from spruce to beech-dominated forest—the Siggaboda case study. *Ann For Sci* 71:139–
596 147. <https://doi.org/10.1007/s13595-013-0283-y>
- 597 Bradshaw RHW, Lindbladh M (2005) Regional spread and stand-scale establishment of *Fagus sylvatica* and
598 *Picea abies* in Scandinavia. *Ecology* 86:1679–1686

- 599 Brillouin L (1956) Science and Information Theory. Academic Press, New York (USA)
- 600 Buchwald E (2005) A hierarchical terminology for more or less natural forests in relation to sustainable
601 management and biodiversity conservation. FAO, Rome, 17–19 January 2005, p 17
- 602 Büntgen U, Tegel W, Kaplan JO, et al (2014) Placing unprecedented recent fir growth in a European-wide and
603 Holocene-long context. *Front Ecol Environ* 12:100–106. <https://doi.org/10.1890/130089>
- 604 Burrascano S, Keeton WS, Sabatini FM, Blasi C (2013) Commonality and variability in the structural attributes
605 of moist temperate old-growth forests: A global review. *For Ecol Manag* 291:458–479.
606 <https://doi.org/10.1016/j.foreco.2012.11.020>
- 607 Carrer M, Castagneri D, Popa I, et al (2018) Tree spatial patterns and stand attributes in temperate forests: The
608 importance of plot size, sampling design, and null model. *For Ecol Manag* 407:125–134.
609 <https://doi.org/10.1016/j.foreco.2017.10.041>
- 610 Černjavski P (1937) Zur Kenntnis der Glaziation und des Buchenwaldes bei Biogradsko Jezero in Montenegro.
611 *Bull Inst Jard Bot Univ Beogr* 4:24–41
- 612 Chileen BV, McLaughlan KK, Higuera PE, et al (2020) Vegetation response to wildfire and climate forcing in a
613 Rocky Mountain lodgepole pine forest over the past 2500 years. *The Holocene* 30:1493–1503.
614 <https://doi.org/10.1177/0959683620941068>
- 615 Chivulescu S, Ciceu A, Leca S, et al (2020) Development phases and structural characteristics of the Penteleu-
616 Viforâta virgin forest in the Curvature Carpathians. *IForest - Biogeosciences For* 13:389.
617 <https://doi.org/10.3832/ifor3094-013>
- 618 Conedera M, Colombaroli D, Tinner W, et al (2017) Insights about past forest dynamics as a tool for present and
619 future forest management in Switzerland. *For Ecol Manag* 388:100–112.
620 <https://doi.org/10.1016/j.foreco.2016.10.027>
- 621 Conedera M, Tinner W, Neff C, et al (2009) Reconstructing past fire regimes: methods, applications, and
622 relevance to fire management and conservation. *Quat Sci Rev* 28:555–576.
623 <https://doi.org/10.1016/j.quascirev.2008.11.005>
- 624 Csontos P, Vitalos M, Barina Z, Kiss L (2010) Early distribution and spread of *Ambrosia artemisiifolia* in
625 Central and Eastern Europe. *Bot Helvetica* 120:75–78. <https://doi.org/10.1007/s00035-010-0072-2>
- 626 Čurović M, Stešević D, Medarević M, et al (2011) Ecological and structural characteristics of monodominant
627 montane beech forests in the National park Biogradska Gora, Montenegro. *Arch Biol Sci* 63:429–440
- 628 Davis OK (1987) Spores of the dung fungus *Sporormiella*: increased abundance in historic sediments and before
629 Pleistocene megafaunal extinction. *Quat Res* 28:290–294
- 630 Delarze R, Calderari D, Hainard P (1992) Effects of fire on forest dynamics in southern Switzerland. *J Veg Sci*
631 3:55–60
- 632 Deza-Araujo M, Morales-Molino C, Tinner W, et al (2020) A critical assessment of human-impact indices based
633 on anthropogenic pollen indicators. *Quat Sci Rev* 236:106291.
634 <https://doi.org/10.1016/j.quascirev.2020.106291>
- 635 Diaci J (ed) (1999) Virgin forests and forest reserves in Central and East European countries: history, present
636 status and future development: proceedings of the invited lecturers' reports presented at the COST E4
637 management committee and working groups meeting in Ljubljana, Slovenia, Ljubljana, 25–28 April,
638 1998. Dept. of Forestry and Renewable Forest Resources, Ljubljana
- 639 Dieler J, Pretzsch H (2013) Morphological plasticity of European beech (*Fagus sylvatica* L.) in pure and mixed-
640 species stands. *For Ecol Manag* 295:97–108. <https://doi.org/10.1016/j.foreco.2012.12.049>

- 641 Dörfler W (2013) Prokoško Jezero: An environmental record from a subalpine lake in Bosnia-Herzegovina. In:
642 Müller J, Rassmann K, Hofmann R (eds) Okolište 1 – Untersuchungen einer spätneolithischen
643 Siedlungskammer in Zentralbosnien. Habelt Verlag, Bonn, pp 311–340
- 644 Ellenberg H (2009) Vegetation ecology of Central Europe, 4th Edition. Cambridge University Press
- 645 Elsen PR, Monahan WB, Dougherty ER, Merenlender AM (2020) Keeping pace with climate change in global
646 terrestrial protected areas. *Sci Adv* 6:eaay0814. <https://doi.org/10.1126/sciadv.aay0814>
- 647 Feurdean A, Florescu G, Vanni ere B, et al (2017) Fire has been an important driver of forest dynamics in the
648 Carpathian Mountains during the Holocene. *For Ecol Manag* 389:15–26.
649 <https://doi.org/10.1016/j.foreco.2016.11.046>
- 650 Feurdean A, Tonkov S, Pfeiffer M, et al (2019) Fire frequency and intensity associated with functional traits of
651 dominant forest type in the Balkans during the Holocene. *Eur J For Res* 138:1049–1066.
652 <https://doi.org/10.1007/s10342-019-01223-0>
- 653 Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int*
654 *J Climatol* 37:4302–4315. <https://doi.org/10.1002/joc.5086>
- 655 Finsinger W, Fevre J, Orb an I, et al (2018) Holocene fire-regime changes near the treeline in the Retezat Mts.
656 (Southern Carpathians, Romania). *Quat Int* 477:94–105. <https://doi.org/10.1016/j.quaint.2016.04.029>
- 657 Finsinger W, Morales-Molino C, Ga ka M, et al (2017) Holocene vegetation and fire dynamics at Crveni Potok,
658 a small mire in the Dinaric Alps (Tara National Park, Serbia). *Quat Sci Rev* 167:63–77.
659 <https://doi.org/10.1016/j.quascirev.2017.04.032>
- 660 Finsinger W, Tinner W (2020) New insights on stomata analysis of European conifers 65 years after the
661 pioneering study of Werner Trautmann (1953). *Veg Hist Archaeobotany* 29:393–406.
662 <https://doi.org/10.1007/s00334-019-00754-1>
- 663 Foster DR, Orwig DA, McLachlan JS (1996) Ecological and conservation insights from reconstructive studies of
664 temperate old-growth forests. *Trends Ecol Evol* 11:419–424. [https://doi.org/10.1016/0169-5347\(96\)10047-1](https://doi.org/10.1016/0169-5347(96)10047-1)
- 666 Fyfe RM, Woodbridge J, Roberts N (2015) From forest to farmland: pollen-inferred land cover change across
667 Europe using the pseudobiomization approach. *Glob Change Biol* 21:1197–1212.
668 <https://doi.org/10.1111/gcb.12776>
- 669 Garbarino M, Lingua E, Weisberg PJ, et al (2013) Land-use history and topographic gradients as driving factors
670 of subalpine *Larix decidua* forests. *Landsc Ecol* 28:805–817. <https://doi.org/10.1007/s10980-012-9792-6>
- 671 6
- 672 Gaudet D, Menzies J (2012) Common bunt of wheat: an old foe remains a current threat. In: Sharma I (ed)
673 *Disease Resistance in Wheat*. CABI, pp 220–235
- 674 Gini C (1912) Variabilit a e Mutabilit a (Variability and Mutability). C. Cuppini, Bologna, Italy
- 675 Green DG (1981) Time Series and Postglacial Forest Ecology. *Quat Res* 15:265–277
- 676 Green MH (2014) Taking ‘‘Pandemic’’ Seriously: Making the Black Death Global. *Mediev Globe* 1:27–62
- 677 Grizonnet M, Michel J, Poughon V, et al (2017) Orfeo ToolBox: open source processing of remote sensing
678 images. *Open Geospatial Data Softw Stand* 2:15. <https://doi.org/10.1186/s40965-017-0031-6>
- 679 Hanewinkel M, Cullmann DA, Schelhaas M-J, et al (2013) Climate change may cause severe loss in the
680 economic value of European forest land. *Nat Clim Change* 3:203–207.
681 <https://doi.org/10.1038/nclimate1687>

- 682 Hansen AJ, DeFries R (2007) Ecological mechanisms linking protected areas to surrounding lands. *Ecol Appl*
683 17:974–988. <https://doi.org/10.1890/05-1098>
- 684 Hararuk O, Kurz WA, Didion M (2020) Dynamics of dead wood decay in Swiss forests. *For Ecosyst* 7:36.
685 <https://doi.org/10.1186/s40663-020-00248-x>
- 686 Harmon ME, Franklin JF, Swanson FJ, et al (2004) Ecology of coarse woody debris in temperate ecosystems. In:
687 *Advances in Ecological Research*. Academic Press, pp 59–234
- 688 Higuera PE, Brubaker LB, Anderson PM, et al (2009) Vegetation mediated the impacts of postglacial climate
689 change on fire regimes in the south-central Brooks Range, Alaska. *Ecol Monogr* 79:201–219
- 690 Higuera PE, Gavin DG, Bartlein PJ, Hallett DJ (2010a) Peak detection in sediment–charcoal records: impacts of
691 alternative data analysis methods on fire-history interpretations. *Int J Wildland Fire* 19:996.
692 <https://doi.org/10.1071/WF09134>
- 693 Higuera PE, Whitlock C, Gage JA (2010b) Linking tree-ring and sediment-charcoal records to reconstruct fire
694 occurrence and area burned in subalpine forests of Yellowstone National Park, USA. *The Holocene*
695 21:327–341. <https://doi.org/10.1177/0959683610374882>
- 696 Hofstetter S, Tinner W, Valsecchi V, et al (2006) Lateglacial and Holocene vegetation history in the Insubrian
697 Southern Alps—New indications from a small-scale site. *Veg Hist Archaeobotany* 15:87–98.
698 <https://doi.org/10.1007/s00334-005-0005-y>
- 699 Horvat I, Glavač V, Ellenberg H (1974) *Vegetation of Southeast Europe*. Gustav Fischer Verlag, Stuttgart
- 700 Houston Durrant T, de Rigo D, Caudullo G (2016) *Fagus sylvatica* in Europe: distribution, habitat, usage and
701 threats. In: San Miguel-Ayanz J, de Rigo D, Caudullo G, et al. (eds) *European Atlas of Forest Tree*
702 *Species*. Publ. Off. EU, Luxembourg, p e012b90+.
- 703 Kaplan JO, Krumhardt KM, Zimmermann N (2009) The prehistoric and preindustrial deforestation of Europe.
704 *Quat Sci Rev* 28:3016–3034. <https://doi.org/10.1016/j.quascirev.2009.09.028>
- 705 Kelly R, Higuera PE, Barrett CM, Hu FS (2011) A signal-to-noise index to quantify the potential for peak
706 detection in sediment–charcoal records. *Quat Res* 75:11–17.
707 <https://doi.org/10.1016/j.yqres.2010.07.011>
- 708 Keren S, Motta R, Govedar Z, et al (2014) Comparative structural dynamics of the Janj mixed old-growth
709 mountain forest in Bosnia and Herzegovina: Are conifers in a long-term decline? *Forests* 5:1243–1266.
710 <https://doi.org/10.3390/f5061243>
- 711 Keren S, Svoboda M, Janda P, Nagel TA (2020) Relationships between structural indices and conventional stand
712 attributes in an old-growth forest in southeast Europe. *Forests* 11:4. <https://doi.org/10.3390/f11010004>
- 713 Kiesselbach TA, Lyness WE (1939) The effects of stinking smut (Bunt) and seed treatment upon the yield of
714 winter wheat. *Hist Res Bull Neb Agric Exp Stn 1913-1993* 110:1–25
- 715 Krawchuk MA, Moritz MA, Parisien M-A, et al (2009) Global pyrogeography: the current and future
716 distribution of wildfire. *PLOS ONE* 4:e5102. <https://doi.org/10.1371/journal.pone.0005102>
- 717 Leibundgut H (1959) Über Zweck und Methodik der Struktur und Zuwachsanalyse von Urwäldern. *Schweiz Z*
718 *Für Forstwes* 110:111–124
- 719 Lindbladh M (1999) The influence of former land-use on vegetation and biodiversity in the boreo-nemoral zone
720 of Sweden. *Ecography* 22:485–498. <https://doi.org/10.1111/j.1600-0587.1999.tb01277.x>
- 721 Luburić V (2016) The introduction of new management measures in protected areas with the aim of improving
722 models of nature protection of Montenegro. PhD, University of Novi Sad

- 723 Luterbacher J, Newfield TP, Xoplaki E, et al (2020) Past pandemics and climate variability across the
724 Mediterranean. *Euro-Mediterr J Environ Integr* 5:46, s41207-020-00197–5.
725 <https://doi.org/10.1007/s41207-020-00197-5>
- 726 Makra L, Juhász M, Béczi R, Borsos E (2005) The history and impacts of airborne *Ambrosia* (Asteraceae) pollen
727 in Hungary. *Grana* 44:57–64. <https://doi.org/10.1080/00173130510010558>
- 728 Maringer J, Conedera M, Ascoli D, et al (2016) Resilience of European beech forests (*Fagus sylvatica* L.) after
729 fire in a global change context. *Int J Wildland Fire* 25:699. <https://doi.org/10.1071/WF15127>
- 730 Marlon JR, Bartlein PJ, Carcaillet C, et al (2008) Climate and human influences on global biomass burning over
731 the past two millennia. *Nat Geosci* 1:697–702. <https://doi.org/10.1038/ngeo313>
- 732 Mauri A, de Rigo D, Caudullo G (2016) *Abies alba* in Europe: distribution, habitat, usage and threats. In: San-
733 Miguel-Ayanz J, de Rigo D, Caudullo G, et al. (eds) *European Atlas of Forest Tree Species*. Publ. Off.
734 EU, Luxembourg, p e01493b+
- 735 Mazurkiewicz-Zapałowicz K, Okuniewska-Nowaczyk I (2015) Mycological and palynological studies of early
736 medieval cultural layers from strongholds in Pszczew and Santok (western Poland). 10
- 737 Mazziotta A, Heilmann-Clausen J, Bruun HH, et al (2016) Restoring hydrology and old-growth structures in a
738 former production forest: Modelling the long-term effects on biodiversity. *For Ecol Manag* 381:125–
739 133. <https://doi.org/10.1016/j.foreco.2016.09.028>
- 740 McEvedy C, Jones R (1978) *Atlas of World Population History*. Penguin Books, London
- 741 McLachlan JS, Foster DR, Menalled F (2000) Anthropogenic ties to late-successional structure and composition
742 in four New England Hemlock stands. *Ecology* 81:717–733. [https://doi.org/10.1890/0012-9658\(2000\)081\[0717:ATTLSS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[0717:ATTLSS]2.0.CO;2)
- 744 McMullin RT, Wiersma YF (2019) Out with OLD growth, in with ecological continNEWity: new perspectives
745 on forest conservation. *Front Ecol Environ*. <https://doi.org/10.1002/fee.2016>
- 746 Meyer P, Aljes M, Culmsee H, et al (2021) Quantifying old-growthness of lowland European beech forests by a
747 multivariate indicator for forest structure. *Ecol Indic* 125:107575.
748 <https://doi.org/10.1016/j.ecolind.2021.107575>
- 749 Michel J, Youssefi D, Grizonnet M (2015) Stable mean-shift algorithm and Its application to the segmentation of
750 arbitrarily large remote sensing images. *IEEE Trans Geosci Remote Sens* 53:952–964.
751 <https://doi.org/10.1109/TGRS.2014.2330857>
- 752 Millspaugh SH, Whitlock C (1995) A 750-year fire history based on lake sediment records in central
753 Yellowstone National Park, USA. *The Holocene* 5:283–292.
754 <https://doi.org/10.1177/095968369500500303>
- 755 Morales-Molino C, Steffen M, Samartin S, et al (2020) Long-term responses of mediterranean mountain forests
756 to climate change, fire and human activities in the northern Apennines (Italy). *Ecosystems*.
757 <https://doi.org/10.1007/s10021-020-00587-4>
- 758 Motta R, Berretti R, Castagneri D, et al (2011) Toward a definition of the range of variability of central
759 European mixed *Fagus – Abies – Picea* forests: the nearly steady-state forest of Lom (Bosnia and
760 Herzegovina). *Can J For Res* 41:1871–1884. <https://doi.org/10.1139/x11-098>
- 761 Motta R, Garbarino M, Berretti R, et al (2015a) Structure, spatio-temporal dynamics and disturbance regime of
762 the mixed beech–silver fir–Norway spruce old-growth forest of Biogradska Gora (Montenegro). *Plant*
763 *Biosyst - Int J Deal Asp Plant Biol* 149:966–975. <https://doi.org/10.1080/11263504.2014.945978>
- 764 Motta R, Garbarino M, Berretti R, et al (2015b) Development of old-growth characteristics in uneven-aged
765 forests of the Italian Alps. *Eur J For Res* 134:19–31. <https://doi.org/10.1007/s10342-014-0830-6>

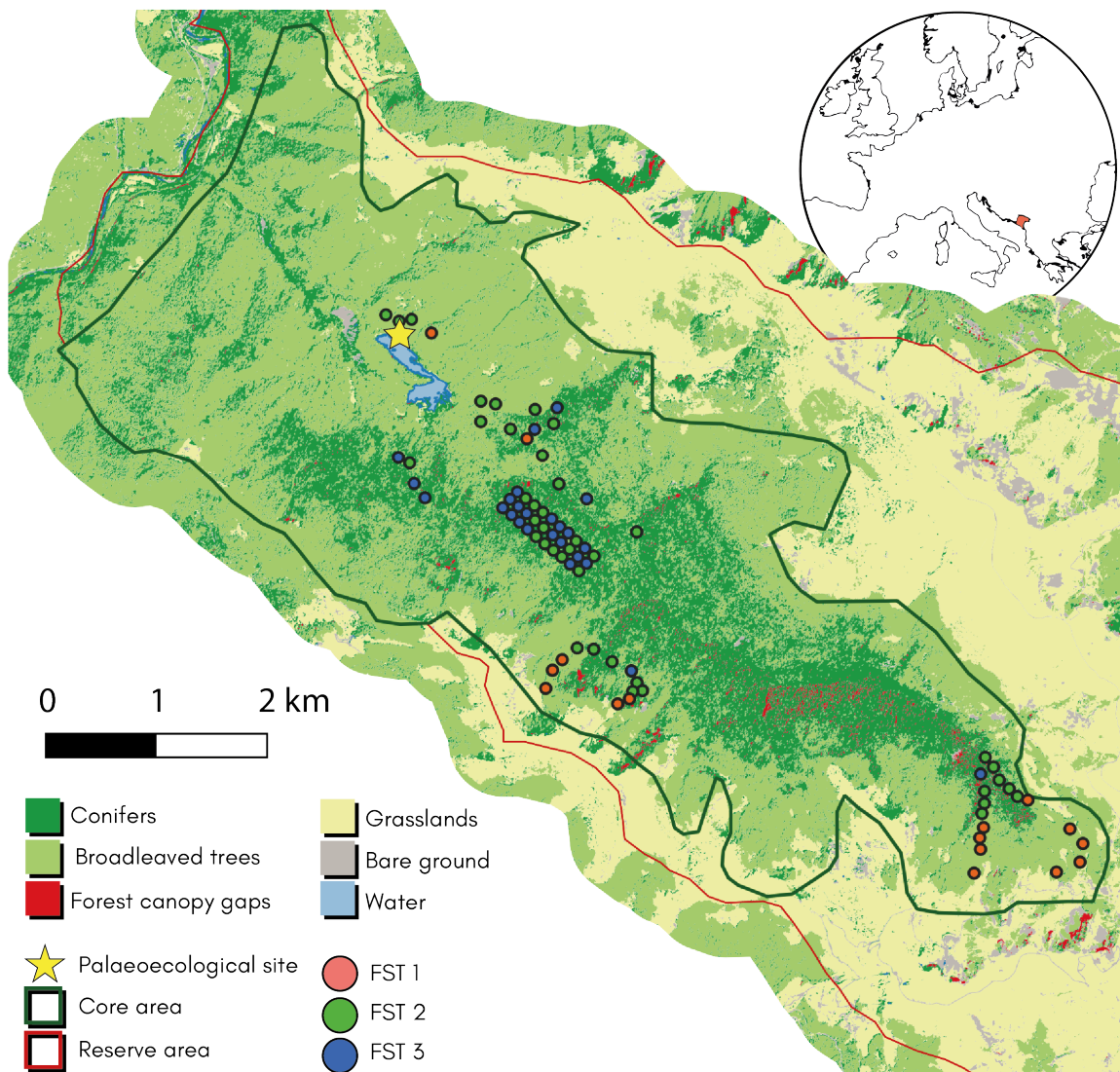
- 766 Mrgic J (2018) Intemperate weather in violent times – narratives from the Western Balkans during the Little Ice
767 Age (17-18th centuries). *Cuad Investig Geográfica* 44:137. <https://doi.org/10.18172/cig.3380>
- 768 Nagel TA, Mikac S, Dolinar M, et al (2017) The natural disturbance regime in forests of the Dinaric Mountains:
769 A synthesis of evidence. *For Ecol Manag* 388:29–42. <https://doi.org/10.1016/j.foreco.2016.07.047>
- 770 Nagel TA, Svoboda M, Kobal M (2014) Disturbance, life history traits, and dynamics in an old-growth forest
771 landscape of southeastern Europe. *Ecol Appl* 24:663–679
- 772 Niklasson M, Zin E, Zielonka T, et al (2010) A 350-year tree-ring fire record from Białowieża Primeval Forest,
773 Poland: implications for Central European lowland fire history. *J Ecol* 98:1319–1329.
774 <https://doi.org/10.1111/j.1365-2745.2010.01710.x>
- 775 Nilsson SG, Niklasson M, Hedin J, et al (2003) Erratum to “Densities of large living and dead trees in old-
776 growth temperate and boreal forests.” *For Ecol Manag* 178:355–370. [https://doi.org/10.1016/S0378-1127\(03\)00084-7](https://doi.org/10.1016/S0378-1127(03)00084-7)
- 778 Nowaczyk NR (2001) Logging of magnetic susceptibility. In: *Tracking Environmental Change Using Lake*
779 *Sediments. Volume 1: Basin Analysis, Coring, and Chronological Techniques.* Kluwer Academic
780 Publishers, Dordrecht, The Netherlands, pp 155–170
- 781 Öder V, Petritan AM, Schellenberg J, et al (2021) Patterns and drivers of deadwood quantity and variation in
782 mid-latitude deciduous forests. *For Ecol Manag* 487:118977.
783 <https://doi.org/10.1016/j.foreco.2021.118977>
- 784 Oris F, Ali AA, Asselin H, et al (2014) Charcoal dispersion and deposition in boreal lakes from 3 years of
785 monitoring: Differences between local and regional fires. *Geophys Res Lett* 41:6743–6752.
786 <https://doi.org/10.1002/2014GL060984>
- 787 Peck JE, Commarmot B, Hobi ML, Zenner EK (2015) Should reference conditions be drawn from a single 10 ha
788 plot? Assessing representativeness in a 10,000 ha old-growth European beech forest. *Restor Ecol*
789 23:927–935. <https://doi.org/10.1111/rec.12258>
- 790 Petritan IC, Marzano R, Petritan AM, Lingua E (2014) Overstory succession in a mixed *Quercus petraea*–*Fagus*
791 *sylvatica* old growth forest revealed through the spatial pattern of competition and mortality. *For Ecol*
792 *Manag* 326:9–17. <https://doi.org/10.1016/j.foreco.2014.04.017>
- 793 Pfister C, Brázdil R (2006) Social vulnerability to climate in the “Little Ice Age”: an example from Central
794 Europe in the early 1770s. *Clim Past* 2:115–129. <https://doi.org/10.5194/cp-2-115-2006>
- 795 Pluskowski A, Seetah K (2006) The animal bones from the 2004 excavation at Stari Bar, Montenegro. In:
796 Gelichi S (ed) *The Archaeology of an abandoned town. The 2005 Project in Stari Bar.* All’Insegna del
797 Giglio, Florence, pp 97–111
- 798 Pretzsch H, Schütze G (2005) Crown allometry and growing space efficiency of Norway spruce (*Picea abies*
799 [L.] Karst.) and European beech (*Fagus sylvatica* L.) in pure and mixed stands. *Plant Biol Stuttg Ger*
800 7:628–639. <https://doi.org/10.1055/s-2005-865965>
- 801 R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical
802 Computing, Vienna, Austria
- 803 Reimer PJ, Bard E, Bayliss A, et al (2013) IntCal13 and Marine13 radiocarbon age calibration curves 0-50,000
804 years cal BP
- 805 Rouvinen S, Kuuluvainen T (2005) Tree diameter distributions in natural and managed old *Pinus sylvestris*-
806 dominated forests. *For Ecol Manag* 208:45–61. <https://doi.org/10.1016/j.foreco.2004.11.021>
- 807 Sabatini FM, Burrascano S, Keeton WS, et al (2018) Where are Europe’s last primary forests? *Divers Distrib*
808 24:1426–1439. <https://doi.org/10.1111/ddi.12778>

- 809 Sabatini FM, Keeton WS, Lindner M, et al (2020) Protection gaps and restoration opportunities for primary
810 forests in Europe. *Divers Distrib* 26:1646–1662. <https://doi.org/10.1111/ddi.13158>
- 811 Sadori L, Giardini M, Gliozzi E, et al (2015) Vegetation, climate and environmental history of the last 4500
812 years at lake Shkodra (Albania/Montenegro). *The Holocene* 25:435–444.
813 <https://doi.org/10.1177/0959683614561891>
- 814 Schütz J-P, Saniga M, Diaci J, Vrška T (2016) Comparing close-to-nature silviculture with processes in pristine
815 forests: lessons from Central Europe. *Ann For Sci* 73:911–921. <https://doi.org/10.1007/s13595-016-0579-9>
816
- 817 Siegmund JF, Siegmund N, Donner RV (2017) CoinCalc —A new R package for quantifying simultaneities of
818 event series. *Comput Geosci* 98:64–72. <https://doi.org/10.1016/j.cageo.2016.10.004>
- 819 Spies TA, Franklin JF (1988) Old growth and forest dynamics in the Douglas-fir region of Western Oregon and
820 Washington. *Nat Areas J* 8:190–201
- 821 Stancioiu PT, O’Hara KL (2006a) Morphological plasticity of regeneration subject to different levels of canopy
822 cover in mixed-species, multiaged forests of the Romanian Carpathians. *Trees* 20:196–209.
823 <https://doi.org/10.1007/s00468-005-0026-2>
- 824 Stancioiu PT, O’Hara KL (2006b) Regeneration growth in different light environments of mixed species,
825 multiaged, mountainous forests of Romania. *Eur J For Res* 125:151–162.
826 <https://doi.org/10.1007/s10342-005-0069-3>
- 827 Stijovic A (2017) Bazna studija o sumama u Nacionalnom parku Biogradska Gora (Podloga za upravljanje
828 sumama). *JP Nacionalni parkovi Crne Gore*
- 829 Sugita S (1994) Pollen representation of vegetation in Quaternary sediments - theory and method in patchy
830 vegetation. *J Ecol* 82:881–897
- 831 Sun W, Chen B, Messinger D (2014) Nearest-neighbor diffusion-based pan-sharpening algorithm for spectral
832 images. *Opt Eng* 53:013107. <https://doi.org/10.1117/1.OE.53.1.013107>
- 833 Thompson R, Oldfield F (1986) *Environmental magnetism*. Allen & Unwin Ltd, London
- 834 Tinner W, Colombaroli D, Heiri O, et al (2013) The past ecology of *Abies alba* provides new perspectives on
835 future responses of silver fir forests to global warming. *Ecol Monogr* 83:419–439.
836 <https://doi.org/10.1890/12-2231.1>
- 837 Tinner W, Hubschmid P, Wehrli M, et al (1999) Long-term forest fire ecology and dynamics in southern
838 Switzerland. *J Ecol* 87:273–289
- 839 Tinner W, Lotter AF (2006) Holocene expansions of *Fagus sylvatica* and *Abies alba* in Central Europe: where
840 are we after eight decades of debate? *Quat Sci Rev* 25:526–549
- 841 UNESCO (2010) UNESCO Global Strategy: the Man and the Biosphere Programme. In: UNESCO World Herit.
842 Cent. <https://whc.unesco.org/en/tentativelists/5569/>. Accessed 17 May 2021
- 843 Vacek S, Vacek Z, Bílek L, et al (2015) The dynamics and structure of dead wood in natural spruce-beech forest
844 stand – a 40 year case study in the Krkonoše National Park. *Dendrobiology* 73:21–32.
845 <https://doi.org/10.12657/denbio.073.003>
- 846 Vale TR (2002) The Pre-European landscape of the United States. In: Vale TR (ed) *Fire, native peoples, and the*
847 *natural landscape*. Island Press, Washington, D.C.
- 848 Valsecchi V, Finsinger W, Tinner W, Ammann B (2008) Testing the influence of climate, human impact, and
849 fire on the Holocene population expansions of *Fagus sylvatica* in the southern Prealps (Italy). *The*
850 *Holocene* 18:603–614. doi: 10.1177/0959683608089213

- 851 Van Geel B (1978) A palaeoecological study of Holocene peat bog sections in Germany and The Netherlands,
852 based on the analysis of pollen, spores and macro- and microscopic remains of fungi, algae,
853 cormophytes and animals. *Rev Palaeobot Palynol* 25:1–120. [https://doi.org/10.1016/0034-](https://doi.org/10.1016/0034-6667(78)90040-4)
854 [6667\(78\)90040-4](https://doi.org/10.1016/0034-6667(78)90040-4)
- 855 Vescovi E, Ammann B, Ravazzi C, Tinner W (2010) A new Late-glacial and Holocene record of vegetation and
856 fire history from Lago del Greppo, northern Apennines, Italy. *Veg Hist Archaeobotany* 19:219–233.
857 <https://doi.org/10.1007/s00334-010-0243-5>
- 858 Weiner J, Solbrig OT (1984) The meaning and measurement of size hierarchies in plant populations. *Oecologia*
859 61:334–336. <https://doi.org/10.1007/BF00379630>
- 860 Whitlock C, Colombaroli D, Conedera M, Tinner W (2018) Land-use history as a guide for forest conservation
861 and management. *Conserv Biol* 32:84–97. <https://doi.org/10.1111/cobi.12960>
- 862 Whitlock C, Larsen C (2001) Charcoal as a fire proxy. In: Smol JP, Birks HJB, Last WM, Last WM (eds)
863 Terrestrial, Algal, and Siliceous Indicators. Kluwer Academic Publishers, Dordrecht, The Netherlands,
864 pp 75–97
- 865 Willis KJ, Birks HJB (2006) What is natural? The need for a long-term perspective in biodiversity conservation.
866 *Science* 314:1261–1265
- 867 Winkler E (1963) Beiträge zur Klimatologie hochalpiner Lagen der Zentralalpen. *Berichte*
868 *Naturwissenschaftlich-Med Ver Innsbr* 53:209–223
- 869 Wirth C, Messier C, Bergeron Y, et al (2009) Old-growth forest definitions: a pragmatic view. In: Wirth C,
870 Gleixner G, Heimann M (eds) *Old-Growth Forests*. Springer Berlin Heidelberg, Berlin, Heidelberg, pp
871 11–33
- 872 Wright MN, Ziegler A (2017) ranger: A fast implementation of random forests for high dimensional data in C++
873 and R. *J Stat Softw* 77:1–17. <https://doi.org/10.18637/jss.v077.i01>
- 874 Wu M, Knorr W, Thonicke K, et al (2015) Sensitivity of burned area in Europe to climate change, atmospheric
875 CO₂ levels, and demography: A comparison of two fire-vegetation models: Projected future burned area
876 in Europe. *J Geophys Res Biogeosciences* 120:2256–2272. <https://doi.org/10.1002/2015JG003036>
- 877 Xoplaki E, Maheras P, Luterbacher J (2001) Variability of climate in meridional Balkans during the periods
878 1675-1717 and 1780-1830 and its impact on human life. *Clim Change* 48:581–615.
879 <https://doi.org/10.1023/A:1005616424463>
- 880 Zang C, Hartl-Meier C, Dittmar C, et al (2014) Patterns of drought tolerance in major European temperate forest
881 trees: climatic drivers and levels of variability. *Glob Change Biol* 20:3767–3779.
882 <https://doi.org/10.1111/gcb.12637>
- 883 Zenner EK, Sagheb-Talebi K, Akhavan R, Peck JE (2015) Integration of small-scale canopy dynamics smoothes
884 live-tree structural complexity across development stages in old-growth Oriental beech (*Fagus*
885 *orientalis* Lipsky) forests at the multi-gap scale. *For Ecol Manag* 335:26–36.
886 <https://doi.org/10.1016/j.foreco.2014.09.023>

887

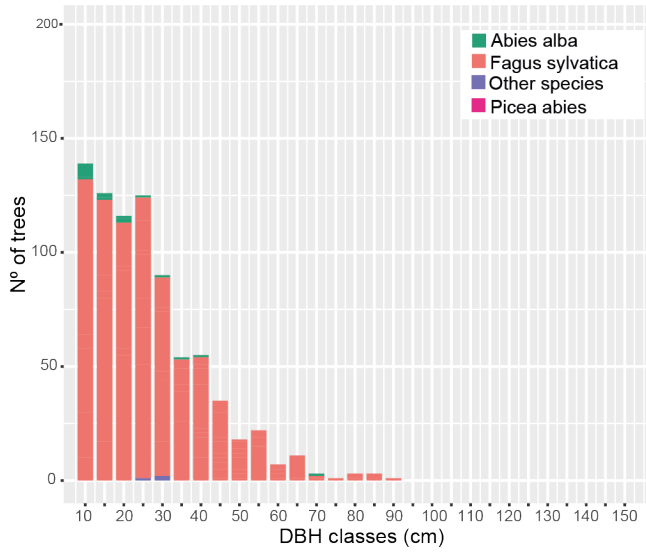
888



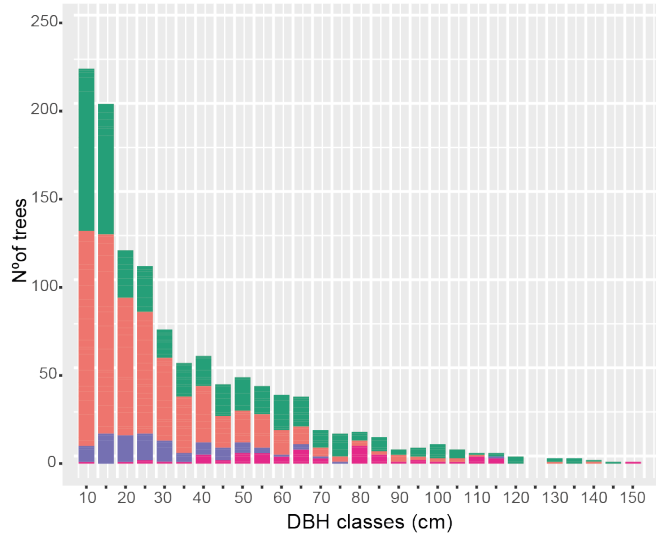
889

890

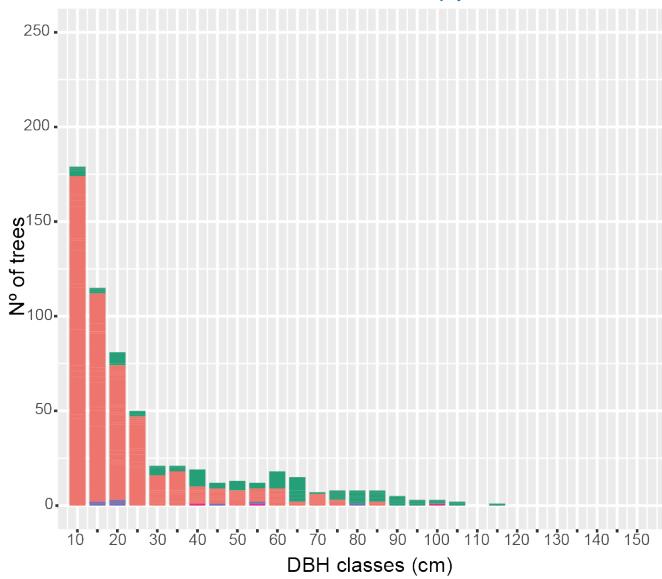
Forest structural type 1

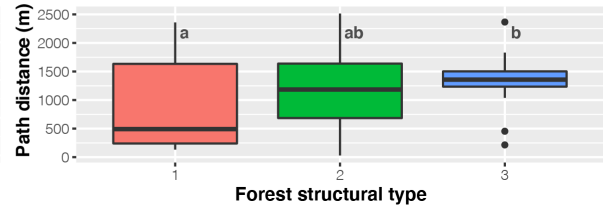
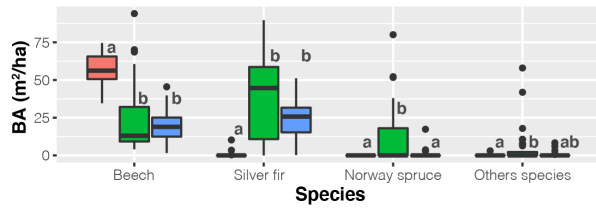
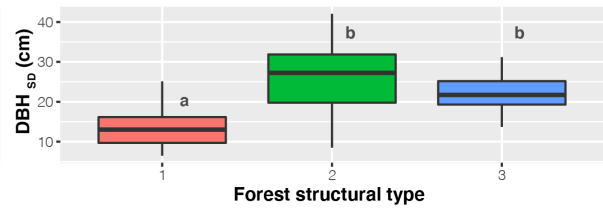
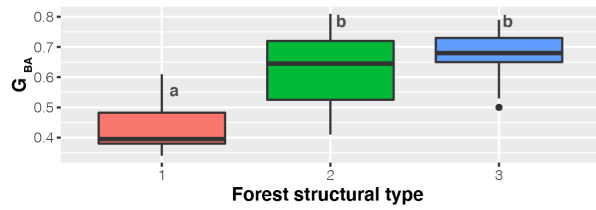
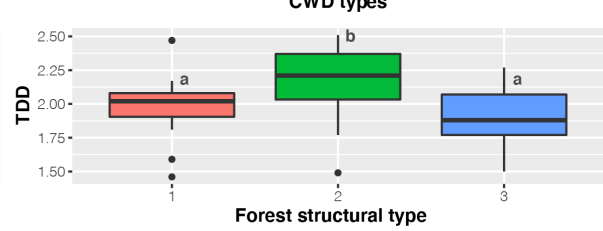
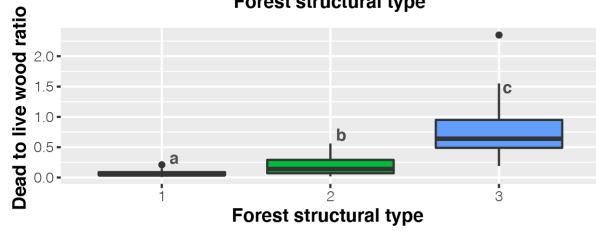
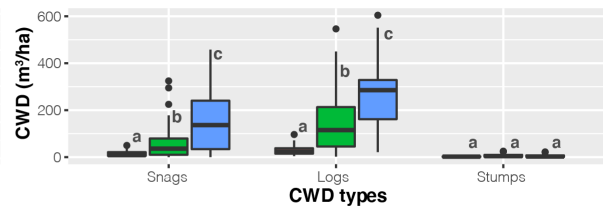
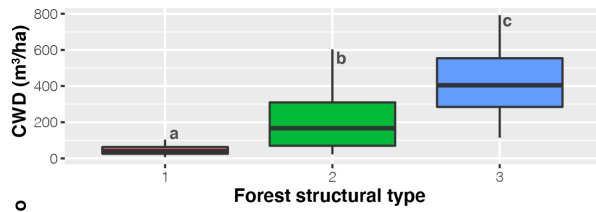


Forest structural type 2



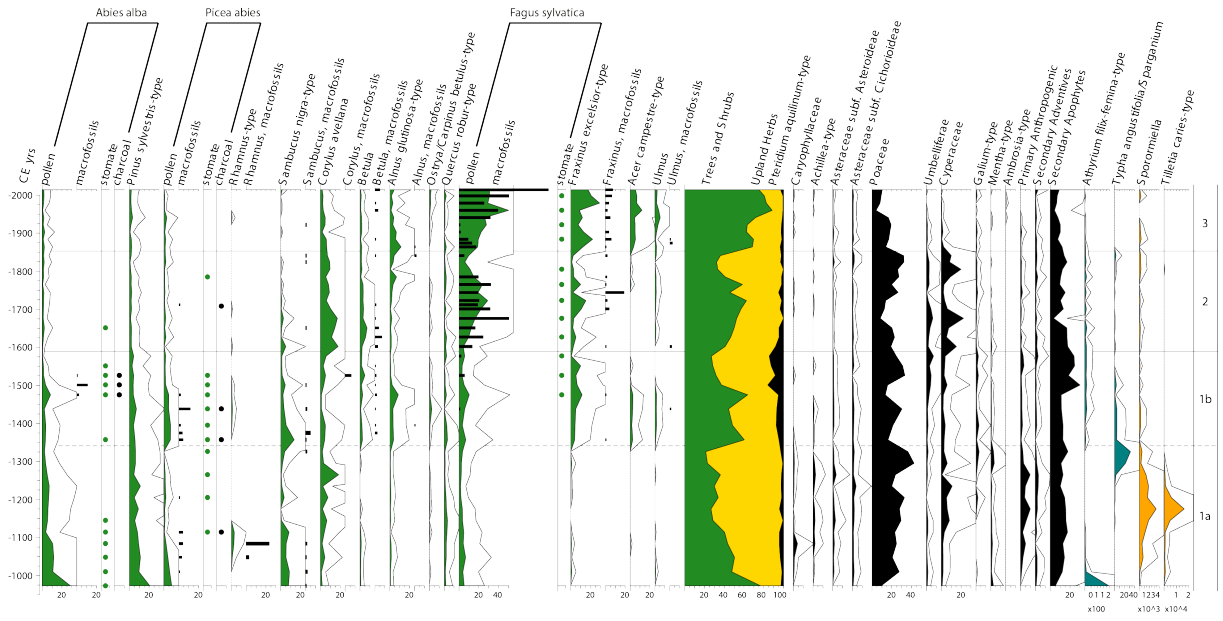
Forest structural type 3





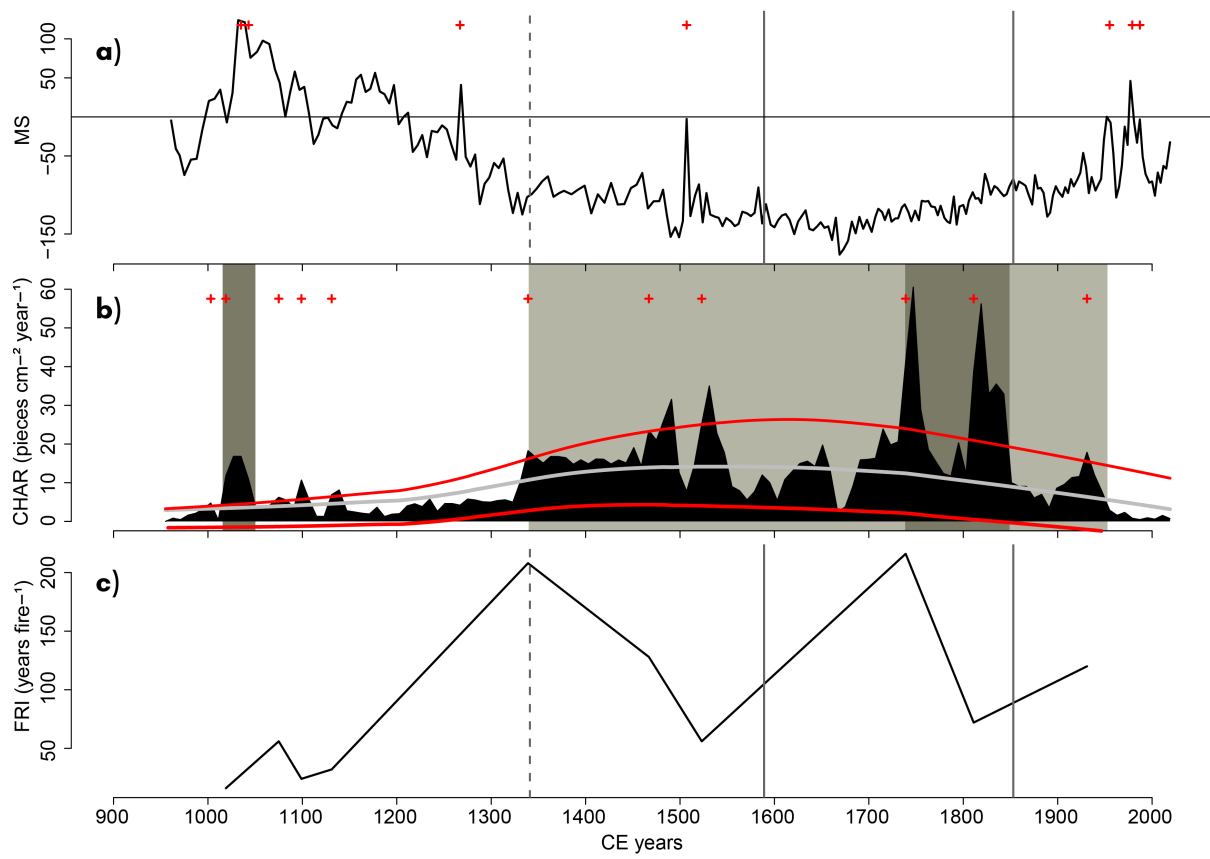
893

894



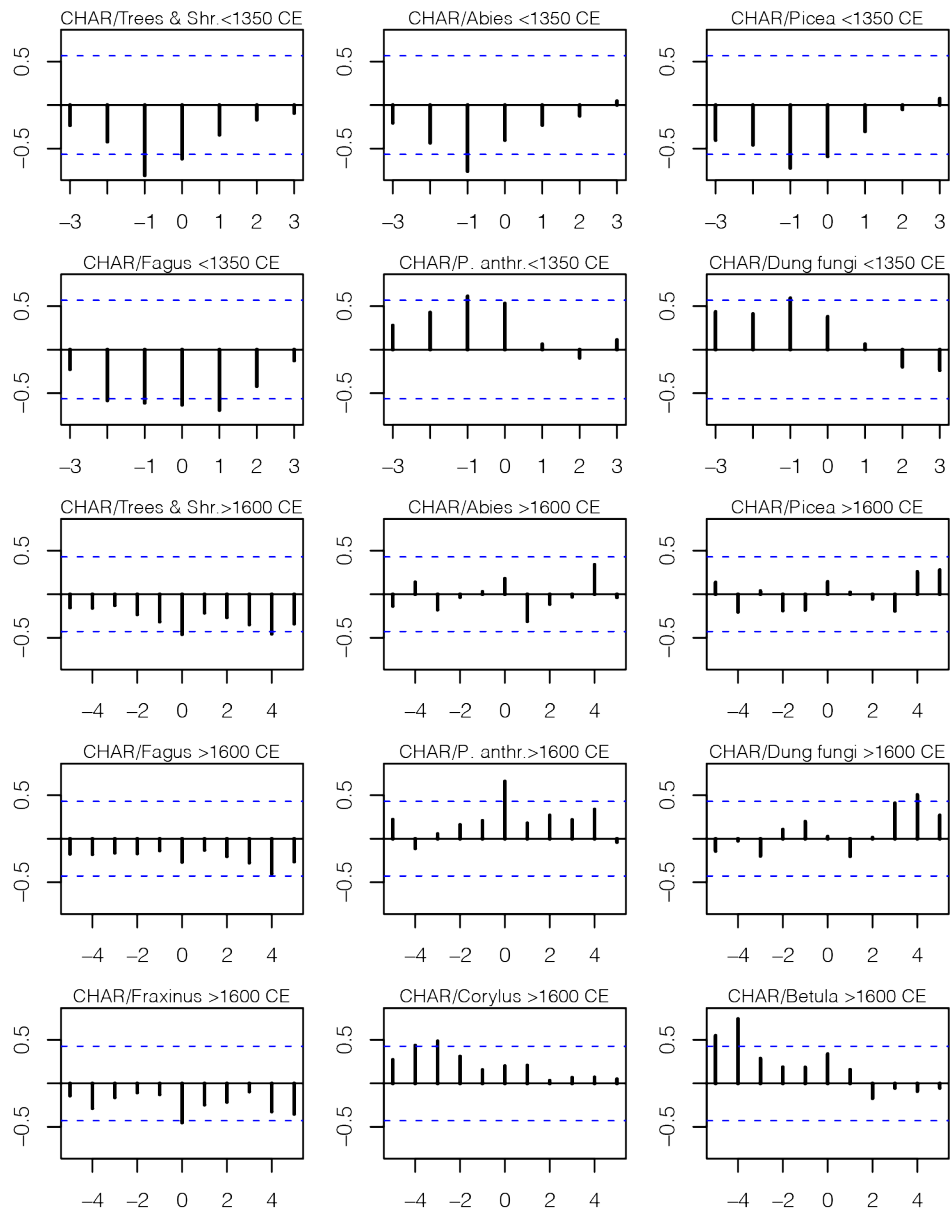
895

896



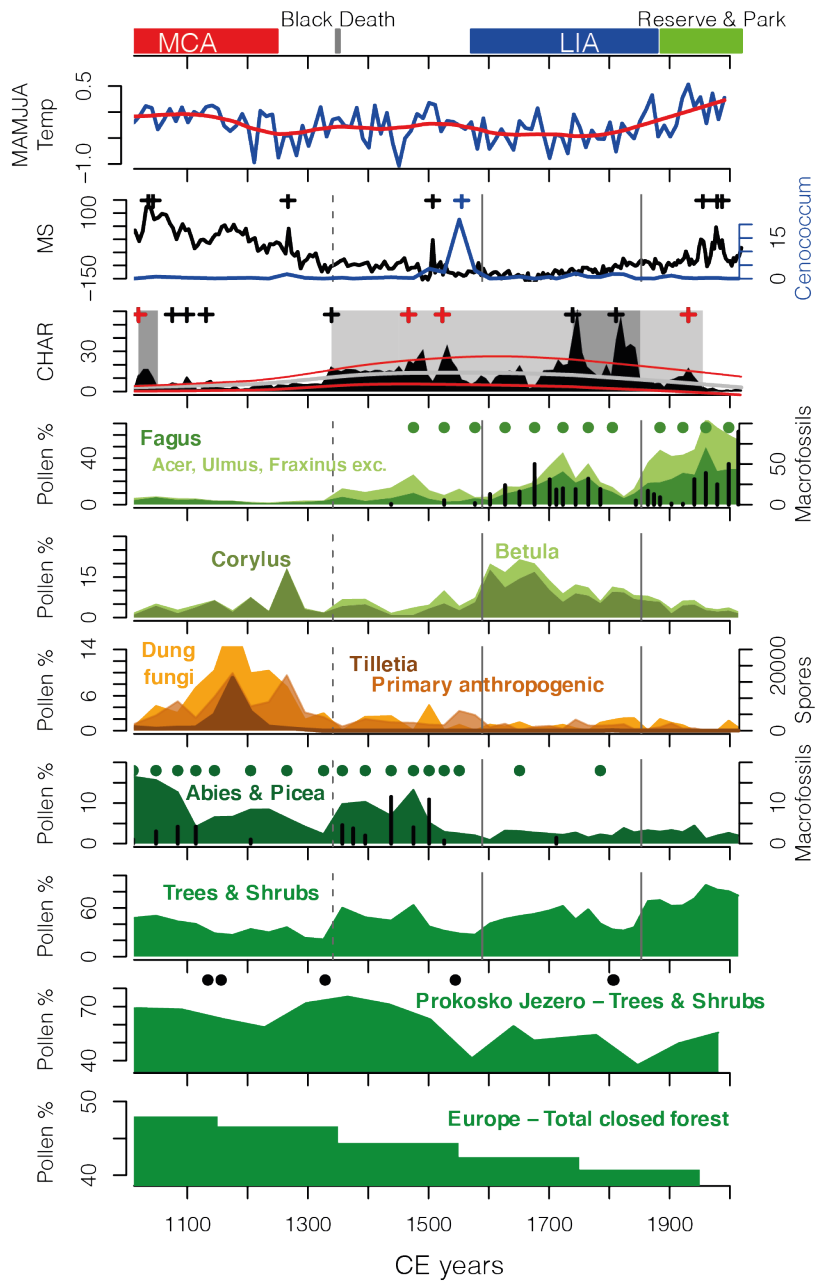
897

898



899

900



901