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

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Abstract

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

A mixed spruce-fir ~~(*Picea abies – Abies alba*)~~ forest established in the upper-montane zone around 9500 cal BP, and beech (*Fagus sylvatica*) became co-dominant with the two conifers after 5000 cal BP. Prehistoric land-use pressure was overall remarkably low, but increased since 2000 cal BP and was highest after the Middle Ages.

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

Keywords

Holocene, vegetation dynamics, mountain forests, fire history, vegetation-fire interactions, ~~Dinaric Alps~~Montenegro

Introduction

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

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

The long-term history of mountain ecosystems varies across regions and is arguably contingent on patterns of human settlement, land use, and socioeconomic development. In this context, the central Dinaric Alps are an interesting area as its land-use history may differ from those of other European mountain regions. There is little doubt that the Balkan Peninsula acted as a land bridge from the Near East, across Asia Minor and towards Central and Western Europe (Forenbaher et al., 2013). While it seems that the Neolithic spread mainly across the fertile plains along the Danube valley in the east (Starčevo culture) and along the Adriatic coastal strip in the west (Impresso culture) around the 6th millennium BCE (8000-7000 cal BP; Borić et al., 2019), there is evidence to suggest that the mountainous hinterland of the central Dinaric Alps remained an agricultural frontier zone, eventually even until the Late Neolithic (Forenbaher and Miracle, 2005). The frontier-zone hypothesis is consistent with modelled anthropogenic deforestation (Kaplan et al., 2009), which suggests that during the past 3000 years relatively low forest clearance occurred when compared to other regions of Europe, and that a large fraction of usable land in the region was not heavily exploited until the Middle Ages (600-1460 CE; 1350-490 cal BP). By contrast, charcoal production, mining activities, and grazing likely occurred in the interior area of the Dinaric Alps since the Bronze Age (3500-600 BCE; 545~~50~~0-~~2600~~ 2550 cal BP), and intensified during the Iron Age (600-200 BCE; 255~~60~~0-2150 cal BP) and the Ottoman Empire (1460-1800 CE; 490-150 cal BP) (Kranjc, 2009; Longman et al., 2018). However, it is not clear if these activities were widespread across the mountain region, or whether human activities rather concentrated in some areas. In the latter case, large forested regions in the interior range may have remained relatively intact until the present (Nagel et al., 2017) or managed with low intensity silvicultural systems during recent centuries (Boncina, 2011). Low historical forest clearance in the montane belt may have preserved fir (*Abies alba* Mill.), beech (*Fagus sylvatica* L.), and spruce (*Picea abies* (L.) Karst.) old-growth forests (Cagliero et al., 2022; Motta et al., 2011; Sabatini et al., 2018). As these tree species are widespread and often form mixed forests in European mountains (Hilmers et al., 2019), ~~knowledge of~~exploring their long-term responses under low land-use pressure may be useful to improve knowledge on the role of disturbances by fire and climate. However, the impact of Neolithic and of more recent cultures on the interior mountain region is still weakly constrained. In contrast to other European mountain regions, the area is both archeologically and palaeoecologically under-documented (Borić et al., 2019; Finsinger et al., 2017; Vander Linden et al., 2014).

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

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

Material and methods

Study area and study site

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

~~Zminje jezero~~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 deep glacial-origin lake (Fig. 1) whose water is drained into the Crno Jezero (1460 m asl) by a small stream. The lake is located on the northwest part of a high karst plateau in the Durmitor massif (Annys et al., 2014) in a valley adjacent to the one currently hosting the last surviving glacier in Montenegro, Debeli namet (Hughes et al., 2011). Given its elevation, ~~Zminje jezero~~Zminje Jezero ~~may be~~is within the limits of terminal moraines that were deposited ~~either~~ before ~~or during~~ the Lateglacial Interstadial (Hughes et al., 2011).

The vegetation in the surroundings of the lake is dominated by a dense spruce-fir forest (Fig. 1) with lesser amounts of beech, *Acer* sp., *Sorbus aucuparia* L., *Rhamnus fallax* Boiss., and *Vaccinium myrtillus*

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

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

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

Field work and sediment-core correlation

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

Chronology

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

Pollen, spores and plant-macrofossils analyses

We processed 78 1~~one~~-cm^{-3} samples for pollen analysis following standard physical and chemical treatments, including treatments with HCl, KOH, sieving with a 500-µm mesh and decanting, HF, a~~A~~cetolysis, and mounted the ~~Fuchsin~~fuchsin-stained residues on slides with glycerol. To calculate influxes (# cm^{-2} yr^{-1}), we added *Lycopodium* tablets (Stockmarr, 1971). We identified and counted pollen, stomata and the dung-fungi *Sporormiella* spore using determination keys and photographic atlases (Beug, 2004; Cagliero et al., 2022; Davis, 1987; Finsinger and Tinner, 2005; Moore et al., 1998; Reille, 1992) as well as the pollen and stomata reference collections at ISEM (University of Montpellier). We counted at least 300 terrestrial pollen grains at ~~x~~400x magnification and calculated percentages relative to the terrestrial pollen sum, which excludes pollen of obligate aquatic plants, spores of ferns and fungi.

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

For plant-macrofossils analyses, we processed 203 samples. We measured sample volumes (~~c.~~ 5.6±1.0 cm^3) by water displacement and then sieved them with a 100-µm mesh sieve. We identified and counted macrofossils with a stereomicroscope at ~~x~~7.5-60x magnification using atlases (Birks, 2017; Katz et al., 1965; Schoch et al., 1988) and the reference collection at ISEM (University of Montpellier) and stored them at -18°C in Milli-Q water. Plant-macrofossil abundances are expressed as concentrations (# cm^{-3}).

To assess land-use pressure, we used the abundances of *Secale cereale* pollen (a primary anthropogenic indicator), secondary indicators (as the sum of adventives and apophytes), and cultural indicators (as the sum of Cerealia-type and *Plantago lanceolata*-type pollen) (Behre, 1981; Tinner et al., 2003). These indexes include pollen of cultivated plants, ruderals, and plants of meadows (Deza-Araujo et al., 2020). *Veratrum album* was added to the apophyte category, as it is avoided by cattle due to its toxicity (Spiegelberger et al., 2006). We also assessed land-use pressure in the wider region using the OJC index (Mercuri et al., 2013), which is based on the abundance of woody crops (*Olea europaea* L., *Juglans regia* L., and *Castanea sativa* Mill.) that grow at lower elevations and along the coast of the Adriatic Sea. Despite their presence in uncultivated areas, an increase in their abundances is often due to broad-scale cultivation (Deza-Araujo et al., 2020).

Charcoal analyses

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

Fire episodes and fire-regime changes

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

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

Ecosystem responses

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

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

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

Results and interpretation

Chronology and sediment composition

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

At the base, from 615 cm to 575 cm (12,340-11,640 cal BP), the sediments consist of light-brown sandy 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 silty-clay layers that alternate with darker and organic-richer layers (gradual boundaries), and a c. 28-cm thick sequence of five graded deposits (529-500 cm), each one characterized by a distinct finingupward trend. Above 479 cm, sediments are mainly composed of dark-brown organic gyttja, which is interrupted by three minerogenic layers of fine grey detrital clay with sharp stratigraphic boundaries at 445-441 cm, 413-410 cm, and 283-281 cm depth. In keeping with the visual assessment of the sediments, minerogenic elements (K, Ti, Rb, Zr, and Sr) are most abundant below 479 cm (10,300 cal BP) as well as in conjunction with the minerogenic layers.

Long-term vegetation dynamics

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

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

Picea abies stomata unequivocally indicate a rapid altitudinal shift of this tree species at the Younger Dryas-Holocene transition, when a rapid climatic change including a warming of c. 2-4°C occurred (Heiri et al., 2014; Tóth et al., 2015). The woodlands closed further from 11,500 to 9410 cal BP (ZMN-2; 566.5-455.5 cm), as attested by an increase of arboreal pollen (from c. 65% to 80%). *F. excelsior*-type, *Ulmus*, and *Tilia* pollen first appeared at 11,500 cal BP marking the expansion of meso-thermophilous~~thermophilus~~ trees at lower altitude, a characteristic feature of pollen records from the Balkan Peninsula and the adjacent European Alps (Caf et al., 2022; Vescovi et al., 2007; Willis, 1994). *Betula* populations were denser than during the Younger Dryas, as shown by both pollen and plant macrofossils. However, the abundance of light-demanding pioneer trees and shrubs (*Ephedra*, *Juniperus* and *Betula*) decreased in conjunction with the local expansion of spruce and fir populations starting between 10,400 and 9600 cal BP. Finds of *Sporormiella* dung-fungi spores indicate the presence of ~~large~~ wild herbivores around the lake between 11,500 and 10,400 cal BP, as also observed on the Swiss Plateau (Rey et al., 2017) and in the Maritime Alps (Finsinger et al., 2021).

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

This expansion was followed by an increase of *Fagus* and *C. betulus* pollen starting around 6400 cal BP (onset of ZMN-4a; 359.5-200.5 cm). Although the *Fagus* expansion at ~~Zminje jezero~~Zminje Jezero occurred approximately 2500-1000 years later than in pollen records from the Central Dinaric mountain area (Prokoško Jezero, Crveni Potok), it broadly coincided with the expansion of *Ostrya* and *Carpinus betulus*, as often seen in pollen records from the region (Prokoško Jezero, Lake Ohrid, Lake Prespa, and Crveni Potok; Dörfler, 2013; Finsinger et al., 2017; Panagiotopoulos et al., 2013; Wagner et al., 2009). The admixture of *Fagus* in the ~~local~~ *Picea-Abies* dominated forest involved a c. 2000-years long build-up phase (6400-4600 cal BP), as attested by rising pollen abundance, after which *Fagus* plant macrofossils and stomata regularly occur. As both *C. betulus* and *Fagus* are shade-tolerant and favoured by moist habitats on upland soils (Houston Durrant et al., 2016; Sikkema et al., 2016), an increase in humidity during the growing season may have occurred (Finsinger et al., 2017). In keeping with this, plant macrofossils of more light-demanding and better drought-resistant *Pinus* are absent in this zone, though ~~occasional~~ stomata occasionally~~finds~~ indicate their scattered presence. *Secale cereale* pollen first appear in this zone and occur mostly between 5800 and 3800 cal BP, ~~unambiguously documenting cultivation~~suggesting its presence as a weed among other cereals during the ~~Copper~~ Bronze Age (Behre, 1992). Some secondary anthropogenic-indicator pollen types (e.g. *P. lanceolata*-type, *Melampyrum*) increased as well. However, tree pollen abundance was highest in this time interval, suggesting that land-use pressure was minor. Similarly, a slightly lower tree-pollen abundance between 3800 and 2100 cal BP suggests moderate presence of forest openings that are, however, not matched by rising abundance of anthropogenic-indicator pollen types.

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

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

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

Charcoal-inferred fire history

Regional fire activity, inferred based on microscopic charcoal (mCHAR), was highest over the past 2000 years and was moderately high between 12,000 and 10,000 cal BP (Figs. 3-4). By contrast, landscape-scale biomass burning ~~macroscopic charcoal~~ (MCHAR trend) ~~documents~~ was ~~highest burned biomass~~ between 11,400 and 6000 cal BP, and overall decreasing ~~biomass burning~~ from 6000 cal BP to the present (Figs. 3-4 and S4). The signal-to-noise index (Fig. S5) shows that the macroscopic charcoal-accumulation rate (MCHAR) record is suitable for peak-detection analysis (Kelly et al., 2011). A total of 35 fire episodes were identified over the past 12,500 years, with a median fire-return interval (mFRI) of 260 years (FRI range: 79-790 years). Longest FRI values (>530 years) occur before 8000 and after 2000 cal BP. Charred *A. alba* and *P. abies* needles document the occurrence of local fires in the conifer-dominated mountain ecosystem, mostly between 5600 and 500 cal BP (Figs. 3-4).

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

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

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

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

Discussion

Regional vs local land-use

The investigation of long-term vegetation dynamics in relation to land-use pressure and disturbances requires a detailed understanding of land-use history. This is particularly important for southern Europe, where forest clearances and agriculture often involved the use of fire. Moreover, land-use phases were often interspersed by periods of abandonment and secondary forest establishment as the result of the development and expansion of more permanent land-use practices, such as animal husbandry, ploughing, crop cultivation, and woodland management (Birks and Tinner, 2016). However, identifying the start and inferring the intensity of land-use pressure using palaeoecological records is challenging, particularly in regions where independent documentation by archaeological evidence is poor (Deza-Araujo et al., 2020), as is the case for the Durmitor.

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

Conversely, if land-use pressure was regionally heterogeneous, ~~pollen~~ reconstructions based on pollen may not necessarily covary with those based on plant macrofossils and stomata. Pollen from the wider region ~~including from lower elevations~~ may reach small lakes such as ~~Zminje jezero~~Zminje Jezero even if their relevant pollen source area is relatively small (some kilometres at most; Sugita, 1994). ~~Thus, reconstructions based on plant macrofossils and stomata may not necessarily covary with those based on pollen if land-use pressure was not homogeneous across the region.~~ Indeed, despite persistence of closed forest in the surroundings of Zminje Jezero, anthropogenic indicators unambiguously document increasing land-use pressure in the region since the Roman period. Cultural indicators, secondary indicators, as well as OJC-index values rise around 2000 cal BP, when the region currently belonging to Montenegro was conquered by the Romans (2nd century BCE). At that time, land-use pressure probably reached the Durmitor, as attested by the construction of roads, including the one connecting Nikšić and Komini. The further rise of anthropogenic indicators around 500 cal BP (15th century CE) is coherent with the first local settlements in the Durmitor. For instance, the so-called stećci sites (medieval tombstones and graveyards from the 13th-17th century; Erdeljan, 2018) attest to the local presence of settlements on the Durmitor during the Middle Ages and the Ottoman Empire, and churches and monasteries from the 15th-19th century CE document the presence of local settlements during the Ottoman Empire~~the presence of *Secale cereale* pollen unambiguously documents that~~. Thus, these results add a finer-scale scale documentation of past land-use pressure in comparison to modelled anthropogenic deforestation patterns (Kaplan et al., 2009), which suggest that relatively low forest clearance occurred during the past 3000 years and that the region was not heavily exploited until the Middle Ages.

Similarly, regional heterogeneity of land-use pressure may also have occurred in pre-Roman times. Anthropogenic indicators do not show distinct signs of Bronze and Iron Age land use, despite the probable connection between coastal and inland settlements (Bulatović et al., 2020) and Illyrian and Celtic Iron Age settlements (Cozzolino et al., 2020). However, *Secale cereale* pollen finds at Zminje Jezero suggest its presence as a weed among other cereals (Behre, 1992) since about 6000 cal BP, as also observed in archaeobotanical samples from Neolithic sites in the mountain hinterland (e.g. at Okolište, Bosnia-Herzegovina; de Vareilles et al., 2022). ~~cultivation started in the region at least around 6000 cal BP, during the Copper Age.~~ While this is about 1000 years later than the age of Neolithic settlements on the shores of the lowland Lake Ohrid (Hafner et al., 2021) and 2000 years later than the earliest Starčevo and Butmir ~~-~~culture Neolithic settlements in the inland of Bosnia-Herzegovina (Vander Linden et al., 2014), the *Secale* pollen finds support the view that Neolithic novelties, albeit with a certain time lag, spread in the hinterland of Montenegro (Borić et al., 2019). Although Neolithic sites have not been found yet in the Durmitor area~~On the other hand~~, there is ~~some~~ evidence ~~for~~of Neolithic occupation sites inland, such as the Odmut cave at 20-35 km from the Durmitordistance (Odmut rock shelter; Borić et al., 2019), suggesting that inland mountain areas may be archeologically under surveyed (Vander Linden et al., 2014). Nevertheless

On the one hand, the sparse occurrence of *Secale* pollenpalaeoecological records may agree with the hypothesis that the mountain hinterland remained an agricultural frontier zone for much of the Neolithic (Forenbaher and Miracle, 2005) and possibly even until the Copper Roman Age. On the other hand, there is some evidence for Neolithic occupation sites inland, such as the Odmut cave 20-35 km from the Durmitor (Borić et al., 2019), suggesting that inland mountain areas may be archeologically under surveyed (Vander Linden et al., 2014). Similarly, anthropogenic indicators do not show distinct signs of Bronze and Iron Age land use, despite the probable existence of connections between coastal and inland settlements (Bulatović et al., 2020) and Illyrian and Celtic Iron Age settlements (Cozzolino et al., 2020). By contrast, anthropogenic indicators unambiguously document increasing land-use pressure since the Roman period. Cultural indicators, secondary indicators, as well as OJC-index values rise around 2000 cal BP, when the region currently belonging to Montenegro was conquered by the Romans (2nd century BCE). At that time, land-use pressure probably reached the Durmitor, as attested by the construction of roads, including the one connecting Nikšić and Komini. The further rise of anthropogenic indicators around 500 cal BP (15th century CE) is coherent with the first local settlements in the Durmitor. For instance, the so-called stećci sites (medieval tombstones and graveyards from the 13th-17th century; Erdeljan, 2018) attest to the local presence of settlements on the Durmitor during the Middle Ages and the Ottoman Empire, and churches and monasteries from the 15th-19th century CE document the presence of local settlements during the Ottoman Empire.

Regional vs local fires

We found contrasting responses of fire to climate and land-use pressure over the past 8500 years (Fig. 5a-b), pointing to different drivers of fire dynamics at landscape and regional scales. Landscape-scale Biomass biomass burning, as inferred based on MCHAR, responded positively and significantly to summer temperature, as expected based on the strong influence (summer) temperature has on fire activity (Jain et al., 2022; Westerling et al., 2006) and as often observed with sedimentary charcoal records (Daniau et al., 2012; Power et al., 2008). As fuel was not a limiting factor in the moist and productive mountain forests, higher mean July temperatures perhaps coupled with prolonged dry seasons (Holocene Thermal Maximum; Samartin et al., 2017) likely improved fuel flammability (Pausas and Paula, 2012). By contrast, surprisingly regional fire activity, as inferred based on mCHAR, responded negatively to summer temperature. A disconnect between fire-history reconstructions can arise both when comparing paleofire records from sites located near each other (Finsinger et al., 2018; Gavin et al., 2006), as well as different paleofire proxies from the same site (Finsinger et al., 2017) if fire occurrence was not spatially homogeneous. While charcoal records from additional sites may be necessary to better constrain the spatial heterogeneity of fire occurrence in the region, it is likely that mCHAR captures fire activity at greater distance from the site than MCHAR (Finsinger et al., 2017). This interpretation is supported by the positive response of fire activity (mCHAR) to land-use pressure (Fig. 5b), which likely occurred in a wider region, including lower-elevation areas where ~~sub-Mediterranean~~submediterranean deciduous woodlands occur. The slightly earlier rise of regional fire activity, which started around the Iron Age (Fig. 4), may be connected to land use in the region that remained undetected by the anthropogenic indicators from ~~Zminje jezero~~Zminje Jezero. Biomass burning, instead, responded negatively to land-use pressure (Fig. 5c). It is unlikely that this relationship is the result of feedbacks arising from human-induced deforestation (e.g. lower fuel availability, fragmentation; Bowman et al., 2011) because biomass burning decreased predominantly at the Neolithic/Bronze Age transition, when land-use pressure was low. The overall decreasing biomass burning suggests that humans did not extensively use fire in the Durmitor. While this overall contrasts with paleofire evidence from other southern European mountains (e.g. the Apennines; Morales-Molino et al., 2021), the lower biomass burning rates in recent millennia fit with the notion that fires are currently rare in the Dinaric Alps (Nagel et al., 2017). However, charred *Picea* and *Abies* needles unambiguously document the occurrence of fires in the mixed spruce-fir-beech mountain forests of the Durmitor.

Species-response curves and legacies of past environmental changes

Species-response curves are useful to assess factors that have driven long-term vegetation dynamics, thereby unfolding legacies of past environmental changes (Carter et al., 2020; Colombaroli et al., 2010;

Morales-Molino et al., 2021). We found similar species responses to summer temperature and biomass burning (Fig. 5c and 5e). Given the strong and positive relationship among these two predictors (Fig. 5a), it is difficult to disentangle their roles separately. However, as (summer) temperature currently has a strong influence on fire activity (Jain et al., 2022; Westerling et al., 2006), the response curves may yield valuable insights into the long-term fire ecology of the analysed species (*P. abies, F. sylvatica, A. alba, Ulmus*, *Fraxinus excelsior*, and *Tilia*), which are widespread and often dominant in European mountain forests. The right-skewed responses of *Fagus* to biomass burning and temperature (Fig. 5c and 5e) suggest that it was favoured under low biomass-burning and cooler conditions. Overall, these response curves support the notion that *Fagus* became more competitive in mixed fir-spruce forests with the onset of cooler and moister summers and fire disturbance, as observed in the ecologically similar Northern Apennines (Morales-Molino et al., 2021). Indeed, *Fagus* requires moist summers for its germination (Giesecke et al., 2017) and is more sensitive than *Abies* to drought due to its shallow root system (Cheddadi et al., 2016; Tinner et al., 2013). *Fagus* is a shade-tolerant species and its regeneration can establish and grow with low light levels under the forest canopy for years before rapidly expanding and achieving dominance when light conditions improve after disturbances (Gardner and Willis, 1999). Thus, fire occurrence after 5000 cal BP may have promoted the recruitment of *Fagus* and its admixture into the mixed *Picea*-*Abies* forest. This matches with evidence suggesting that during the initial phase of stand establishment, *Fagus* is favoured by mixed-severity fire and intermediate human disturbances (Bradshaw and Lindbladh, 2005; Giesecke et al., 2007; Tinner and Lotter, 2006) thanks to its capacity to occupy newly exposed soils and canopy openings (Carter et al., 2018) more rapidly than its two main competitors (*Abies* and *Picea*). ~~However~~Despite~~,~~ lacking ecological adaptations to fire~~,~~ and being identified as ~~*Fagus* is~~ a fire-sensitive species that is affected by higher biomass burning and temperatures (Carter et al., 2018; Morales-Molino et al., 2021; Tinner et al., 2000), *Fagus* can be advantaged by fire incidence as long as it is not excessive (Maringer et al., 2020). In keeping with this, the change-point analysis shows a decrease in biomass burning during the establishment of *Fagus* (Fig. 4), corroborating the view that beech establishment occurs in conjunction with a shift to a lower fire activity (Bobek et al., 2019; Feurdean et al., 2017).

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

Picea's response curves suggest that neither temperature nor biomass burning and land use significantly influenced its populations (Fig. 5c-e). Indeed, *Picea* remained relatively stable even under higher-than-present summer temperatures (Fig. 4), as also observed with palaeoecological records from the Carpathians (Carter et al., 2018). Its insensitivity to summer temperatures may simply imply that past climatic conditions did not exceed the species' tolerance range. Moreover, the lack of a significant response to biomass burning agrees with evidence showing that *Picea* can persist thanks to vigorous post-fire regeneration from wind-dispersed seeds (Bobek et al., 2018) even with median FRI as low as 260 years as at ~~Zminje jezero~~Zminje Jezero (Brown and Giesecke, 2014; Feurdean et al., 2017; Finsinger et al., 2018). Although fires may have been fuelled by *Picea's* traits that promote fire spread (high resin content, flammable litter, and a ladder-canopy structure), its well-established populations persisted at ~~Zminje jezero~~Zminje Jezero despite fire occurrence in the mixed spruce-fir-beech forests.

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

Conclusions

Vegetation of forest ecosystems is often the result of complex interactions between vegetation dynamics and variations in climate, disturbances (e.g. fire), and human activities. However, understanding the ecological processes underlying these interactions is challenging as processes often play out over long time scales (centuries, millennia), particularly for forests where long-lived species such as trees are involved. The long-term perspective of palaeoecological records permits to study ecosystem responses under substantially different environmental conditions than the present ones.

In this study, we sought to investigate the Holocene vegetation and fire history in the upper-montane zone of the central Dinaric Alps, where fires are currently rare and forests mainly include beech-dominated stands and mixed forests dominated by varying amounts of beech, fir, and occasionally spruce (Nagel et al., 2017). ~~We performed the first detailed palaeoecological study from this region (including pollen, plant macrofossils, microscopic and macroscopic charcoal analysis) on well-dated sediments from Zminje jezero (Durmitor massif, Montenegro) and assessed the response of the dominant canopy taxa (*P. abies*, *A. alba*, *F. sylvatica*, *F. excelsior-type*, *Tilia*, and *Ulmus*) to variations in climate, fire and land-use pressure.~~

~~Vegetation in the upper-montane zone was dominated by *Pinus* and *Betula* during the Younger Dryas and until 9500 cal BP, when a *Picea-Abies* forest established. This mixed forest remained relatively stable until 5000 cal BP, when *Fagus* expanded in the mixed forest. Biomass burning gradually decreased during the past 8500 years in the upper-montane zone, though fire episodes did occur there throughout that period of time. Land-use pressure was overall remarkably low in the montane zone until the Roman period (2000 cal BP) but increased substantially after the Middle Ages. By contrast, regional fire activity rose since *c*. 2500 cal BP (Iron Age) as a result of higher land-use pressure in the wider region, probably including areas at lower elevation.~~ While records from different elevations may be necessary to better support ~~these~~ our ~~results~~interpretation, our results support the view that at least some parts of the central Dinaric Alps remained an agricultural frontier zone during the Neolithic (Forenbaher and Miracle, 2005) and that land-use pressure was low until the Middle Ages (Kaplan et al., 2009).

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

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Data

All data will be made publicly available upon acceptance. The palaeoecological data (pollen, spores, stomata, plant macrofossils, charcoal, and XRF records) will be uploaded to the Neotoma database (DOI: 10.21233/XYZZ-XYZZ) through the European Pollen Database.

Figures (with captions) and Tables

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

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

Fig. 3 Vegetation and fire history from ~~Zminje jezero~~Zminje Jezero sediments. Left: synthetic pollen diagram with selected pollen and spore percentages of the terrestrial pollen sum (grey curves; empty curves show 10x exaggerations of the percentage values), presence/absence of stomata (black circles), and plant-macrofossil concentrations (black vertical bars, dimensionless) for selected genera and for all woody taxa of the ~~Zminje jezero~~Zminje Jezero. The continuous horizontal and dashed lines indicate statistically significant and non-significant pollen-assemblage zones, respectively. See Fig. S3 for a more detailed plant-macrofossil diagram. To the right: macroscopic-charcoal accumulation rate (MCHAR) and microscopic-charcoal accumulation rate (mCHAR) as black bars, their long-term trends (red and black lines), fire episodes (black crosses), and presence of charred conifer needles (red diamonds).

Fig. 4 Comparison of the main proxies for vegetation dynamics, fire and land-use history from ~~Zminje jezero~~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).

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

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