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# Climate and biomass control on fire activity during the late-glacial/ early-Holocene transition in temperate ecosystems of the upper Rhone valley (France)

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# ABSTRACT

The main objective of this study is to document paleofire activity during the late-glacial/early-Holocene transition in temperate ecosystems. For this purpose, we cored lakes Paladru and Moras (Rhone valley, France) and quantified sedimentary charcoal accumulation rate and fire frequency. To assess the role of climate and vegetation in paleofire activity, charcoal data were compared to vegetation dynamics based on pollen analyses and to climate reconstructions. The first increase in paleofire activity occurred at the beginning of the Bølling/Allerød Interstadial period (14,500 cal yr BP), synchronous with temperature and fire-prone vegetation increases. During the Younger Dryas, paleofire activity first decreased (12,600–12,200 cal yr BP) and then abruptly increased (12,200–11,600 cal yr BP). This change corresponds to a known climate partitioning that occurred during the Younger Dryas and implies that a sufficient quantity of biomass was available during the second period. At the beginning of the Holocene, fire activity remained high. This is in agreement with the increases in temperature and vegetation density. The change in forest composition since ca. 11,200 cal yr BP partly explains the decrease in paleofire activity, whereas warm climate conditions seem suitable for fire ignition and propagation.

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# Introduction

Fire is an important driver of environmental processes that affect global ecosystem patterns through changes in vegetation cover, climate and the carbon cycle (Cofer et al., 1997; Bowman et al., 2009). Climate variations control fire regime through vegetation and soil moistures, biomass composition and structure, and fire-conductive weather patterns (Pausas, 2004). At the same time, fire induces feedback control on climate changes through greenhouse and aerosol emissions, albedo surface changes and the restriction of forest cover expansion (Daniau et al., 2012). Thus, it is crucial to anticipate the future effects of climate change on fire regimes in the current period of climate warming (Schneider et al., 2007).

Fire activity depends on interactions between climate, vegetation and human activities (Whitlock et al., 2010). The use of fire for land clearing in Western Europe has occurred as a consequence of the agricultural expansion during the Neolithic period (e.g., Colombaroli et al., 2008; Doyen et al., 2013a) while the significant human influence on biomass burning seemed to start ca. 4000 cal yr BP (Vannière et al., 2008; Rius et al., 2011; Doyen et al., 2013b). Therefore, since the development of farming activities (i.e., 7000 years ago), it has been difficult to

\* Corresponding author. *E-mail address*: el.doyen@laposte.net (É. Doyen). disentangle the respective influence of climate and vegetation changes on fire activity independent of human impacts (Vannière et al., 2011).

The period between the late-glacial ice recession and the early Holocene was marked by rapid and strong climate changes, while the influence of hunter-gatherers on the environment was negligible and/or restricted to small areas (Brown, 1997; Kalis et al., 2003). Thus, this time period can be used to assess the interactions between climate. vegetation and fire activity without the possible confounding influence of human activities. Undisturbed sediments that accumulated in lacustrine systems since the glacial retreat are appropriate archives to study the late-glacial/early-Holocene transition (e.g., Magny et al., 2006a). Most of the published studies specifically dedicated to paleofire reconstructions during the late-glacial/early-Holocene transition have been carried out in North America (e.g., Higuera et al., 2009; Marlon et al., 2009). In Europe, available studies have focused on the Mediterranean basin (Tinner et al., 2005; Magny et al., 2006a; Kaltenrieder et al., 2010; Vescovi et al., 2010; Connor et al., 2012; Leys et al., 2013), and some records document the history of fires in temperate areas during these periods (Clark et al., 1989; Feurdean et al., 2012; Rius et al., in press).

The objectives of the present study are: (*i*) to reconstruct the fire history of Lake Paladru and Lake Moras, two sites located in the upper Rhône valley (eastern France) and (*ii*) to assess the biomass burning response to high-amplitude climate and vegetation changes during the late-glacial/early-Holocene transition. The relationship between fire







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activity and vegetation dynamic was studied using pollen analyses (in percentages and concentrations) from these two lacustrine records. The relationship between fire regime and climatic changes was studied by comparing results from charcoal analysis with regional climate dynamics provided by a vegetation-independent proxy (i.e., chironomidinferred summer air temperatures reconstructed from the neighboring Jura mountains; Heiri and Millet, 2005).

### Material and methods

### Environmental settings

Lake Paladru (45°27′18″N, 5°32′06″E, 492 m a.s.l.) and Lake Moras (45°40′55″N, 05°16′06″E, 304 m a.s.l.) are located 32 km apart in the French Alpine foreland, in the upper Rhône valley (Fig. 1a). The area is characterized by a sub-continental climate: the mean annual precipitation rate is 1060 mm/yr; mean July and January temperatures are 19.9°C and 2.2°C, respectively.

The study sites are two moraine-dammed lakes formed during the last glacial maximum. Lake Paladru has an area of 392 ha, a catchment area of 5200 ha and a maximum depth of 36 m (Fig. 1b). The watershed (maximum elevation: 780 m a.s.l.) is composed of molasse and is covered in several places by moraine deposits. Two small streams feed the lake. Lake Moras is smaller, with an area of 20 ha, a catchment of 400 ha and a maximum depth of 12.5 m (Fig. 1c). Water drains into the lake from a small watershed (maximum elevation: 420 m a.s.l.) that is composed of Jurassic calcareous substratum (184 ha) and is covered in several places by moraine deposits (167 ha). The water is supplied to the lake by underground springs; discharge is into a small stream at the southern extremity of the lake.

### Coring and geophysical logging

In each lake, overlapping cores were taken at the deepest part of the basin (Fig. 1b–c) using a stationary piston corer (UWITEC system) operated from a surface platform. Magnetic susceptibility and gamma density were measured at 5-mm intervals with a Multi Sensor Core Logger (Geotek). Sediment color variations were checked using high-resolution pictures. These three parameters were used to correlate the sedimentary levels of the core sections to create a master core without gaps for each lake. All further analyses were performed on these master cores (550–370 cm section for Lake Paladru) and (555–470 cm section for Lake Moras).

### Pollen analyses

Samples (2 cm<sup>3</sup>) from Lake Paladru were taken at 8-cm intervals between 550 and 425 cm core section and at 16-cm intervals between 425 and 370 cm of the sediment core section, while Lake Moras was sampled at 5-cm intervals along the 555 to 470 cm section. Samples were prepared for pollen analysis using the standard procedure described by Faegri and Iversen (1989). Lycopodium clavatum tablets were added to each subsample to calculate pollen concentration in Lake Moras (Stockmaar, 1971), while the volumetric method was used to calculate pollen concentration in Lake Paladru. Pollen was identified and counted at 500  $\times$  magnification. A mean of 1060 (±550) pollen grains from terrestrial plants (Total Land Pollen, hereafter referred to as TLP) were counted in each subsample using transmitted light. Pollen identification was based on identification keys (Beug, 2004), photography books (Reille, 1992, 1998) and a reference collection of modern pollen types. Pollen counts were expressed as percentages of TLP, excluding pteridophytes, aquatics and indeterminable grains from the total pollen sum and as concentrations (number pollen grains/cm<sup>3</sup>). In the discussion part, TLP concentration and AP/TLP ratio were used as proxy for biomass/fuel load and woody cover, respectively.

### Sediment analyses

Geochemical core logging was undertaken using an ITRAX XRF core scanner (CEREGE laboratory, Aix-en-Provence, France) to track the occurrence of allochtonous mineral inputs. The relative abundances of calcium (Ca), titanium (Ti) and potassium (K) were measured using a Chromium tube with a count-time of 15 s and a sampling step of 5 mm set at 30 kV.

### Charcoal analyses

Fire history was reconstructed from macro- and microscopic charcoal particles accumulated in lake sediments.

The size of a charcoal particle partly determines its ability to be transported (Clark, 1988). Micro-charcoal analysis (particles between 10 and 200  $\mu$ m) is generally considered to reflect regional fire activity (within a radius of ca. 20–50 km around the lake; Tinner et al., 1998); whereas macro-charcoal analysis (particles larger than 200  $\mu$ m) mainly traduce local fire history (within a radius approximately between 1 and 2 km around the lake; Higuera et al., 2007).



Figure 1. a) Location of Lake Moras and Lake Paladru, b) bathymetric map of Lake Paladru and location of the core samples, c) bathymetric map of Lake Moras and location of the core samples.

Two centimeter thick contiguous subsamples (2  $\text{cm}^3$  in volume) were taken along the Lake Paladru master core (a total of 107) and 1-cm<sup>3</sup> subsamples were taken at 5-cm intervals along the Lake Moras sequence (a total of 13) for micro-charcoal analysis. Micro-charcoal particles were extracted using the procedure described by Turner et al. (2008), which involves the removal of carbonates using HCl, bleaching of non-charred organic material with H2O<sub>2</sub>, sieving to 200 µm and density separation using LST (Lithium heteropolytungstate with a specific density of 2.5). L. clavatum tablets were added to each subsample to estimate the concentration of charcoal in the sediment (Stockmaar, 1971). Micro-charcoal was identified under transmitted light as black and opaque particles with angular contours (Clark, 1988). Identifications were checked using reflective light (using an oil immersion technique) to distinguish micro-charcoal from black opaque non-reflective organic matter. Charcoal measurements (area, length and width) were performed using image analysis software (Qwin Standard). Charcoal concentrations (mm<sup>2</sup>/cm<sup>3</sup>) were converted to charcoal accumulation rates (micro-CHAR in  $mm^2 cm^{-2} yr^{-1}$ ) based on the sedimentation rate estimated by the age-depth models.

For macro-charcoal analysis, 1-cm-thick contiguous subsamples (2 cm<sup>3</sup> in volume) were taken from Lake Moras (a total of 72) and Lake Paladru (a total of 213). Charcoal particles were extracted by soaking samples in HCl (10%), in H<sub>2</sub>O<sub>2</sub> (10%) and by sieving the samples at 200  $\mu$ m (Rhodes, 1998; Whitlock and Larsen, 2001). Charcoal particles were counted and measured under a binocular microscope at 50× magnification with a reticule grid of 62.5 × 10<sup>-3</sup> mm<sup>2</sup> (10 × 10 squares). Charcoal identification was based on criteria defined in the literature (Umbanhowar and McGrath, 1998). Charcoal concentrations (mm<sup>2</sup>/cm<sup>3</sup>) were converted to charcoal accumulation rates (macro-CHAR in mm<sup>2</sup> cm<sup>-2</sup> yr<sup>-1</sup>) based on the sedimentation rate estimated by the age–depth models.

Fire frequency was calculated based on the decomposition of charcoal data in the background component ( $C_{back}$ ) and the peaks component ( $C_{peak}$ ). This method (Long et al., 1998) was thoroughly described by Higuera et al. (2008, 2009) and consists of a decomposition of the charcoal accumulation rate (CHAR) according to the following steps:

- The CHAR was re-sampled to constant 25-yr time steps corresponding approximately to the mean temporal resolution of the record.
- (2) To estimate the low varying component (C<sub>back</sub>), the re-sampled CHAR (C<sub>int</sub>) was smoothed with a locally weighted regression model (moving mode) using a 250-yr moving window that best fit the low varying components.
- (3) The peak component was calculated by subtracting  $C_{back}$  from the re-sampled CHAR ( $C_{peak} = C_{int} - C_{back}$ ).  $C_{peak}$  is usually represented by two subpopulations of values: the lowest values are interpreted as analytical noise, while the positive highest values recorded above the threshold value (Tv) are assumed to represent fire episodes that occurred around the lake. The 99th percentile of the distribution was selected as the threshold value for fire episode detection.
- (4) Inferred Fire Frequency (IFF) was estimated by smoothing fire episodes over a 500-yr moving window.

All of these numerical treatments were performed only for Lake Paladru macro-CHAR using the program CharAnalysis (Higuera et al., 2009; http://CharAnalysis.googlepages.com). For Lake Moras, the temporal resolution of the sediment was too low and prevented the calculation of fire frequency (mean sediment accumulation rate 93 years/cm between 15,000 and 8000 cal yr BP).

# Chronology

Sixteen samples from Lake Paladru and seven samples from Lake Moras were taken for radiocarbon analysis. Macro-remains of terrestrial origin (leaf, seed or wood) were hand-picked under a stereomicroscope after sieving the sediment at 200  $\mu$ m. Radiocarbon analyses were performed at the Poznan Radiocarbon Laboratory and at the Laboratory LMC14 in Gif-sur-Yvette. Ages were calibrated at  $2\sigma$  ranges with CALIB 6.0.1 using the IntCal09 calibration curve (Reimer et al., 2009; Table 1).

Age–depth models for both lakes were constructed using the Clam code (smooth spline model; Blaauw, 2010).

### Table 1

AMS-radiocarbon dates from Lake Paladru and Lake Moras calibrated with the CALIB 6.0.1 program using the Intcal09 calibration curve and ages estimated for the main late-glacial/ early-Holocene transitions which were indicated by the pollen stratigraphy and by geochemistry data (in italic).

Site name	Laboratory code	Sample depth (cm)	AMS 14C (radiocarbon BP)	Age cal yr BP (2σ range)
PALADRU	Poz-37099	58.3-61.3	$750 \pm 60$	561-790
	Poz-37096	97.7-99.7	$1250 \pm 30$	1082-1273
	SacA-20695	99.7-101.7	$1245 \pm 25$	1120-1270
	SacA-20696	124.7-126.7	$1525 \pm 25$	1350-1520
	Poz-37098	161.2-162.2	$2220\pm60$	2064-2347
	SacA-20699	190-192	$2670\pm30$	2750-2840
	SacA-20697	230-232	$3410\pm30$	3580-3720
	Poz-37094	260-262	$4210\pm40$	4616-4853
	SacA-20701	265.6-267.1	$4270\pm35$	4810-4880
	SacA-20700	300-302	$5055\pm30$	5730-5900
	Poz-37093	330-332	$6650\pm80$	7427-7656
	Poz-37095	394-396	$8670\pm50$	9534-9770
	Poz-37100	428-430	$9880\pm90$	11,155-11,650
	SacA-20694	428-430	$10,590 \pm 45$	12,420–12,640 <sup>a</sup>
	Poz-37092	480-482	$12,470 \pm 80$	14,151–15,052 <sup>a</sup>
	SacA-20698	510-511	$12,020 \pm 50$	13,750-14,010
	Χ	440	Χ	11,500-11,700
	Χ	470	Χ	12,600-12,800
	Χ	515	Χ	14,500-14,700
MORAS	Poz-27997	144-145	$720\pm30$	568-722
	Poz-27993	206-209	$1190\pm35$	988-1236
	Poz-27998	273.5-274.5	$2090\pm30$	1992-2143
	Poz-27999	341.5-342.5	$2980\pm40$	3005-3323
	SacA-12346	404.5-405.5	$4170\pm30$	4584-4831
	Poz-27994	459.8-462	$6480\pm50$	7279-7477
	SacA-12347	516.5-518.5	$11340 \pm 45$	13,117–13,321
	Χ	502	Χ	11,500-11,700
	Χ	513	Χ	12,600-12,800
	X	531	X	14,500-14,700

<sup>a</sup> Dates rejected.

### Results

### Pollen-inferred vegetation dynamics

Pollen analyses from both lakes provided very similar results, so they will be described together using common Pollen Assemblage Zones (PAZ) (Figs. 2 and 3).

### PAZ 1 (537 to 517 cm for Lake Paladru; 557 to 529 cm for Lake Moras)

The vegetation dynamic of this zone was mainly documented using pollen data from Lake Moras because pollen grains from Lake Paladru were poorly preserved. The vegetation was dominated by steppic and heliophilous herb species, such as Poaceae, *Artemisia*, Chenopodiaceae, *Helianthemum*, *Thalictrum* and *Rumex*-type and with numerous taxa associated with meadows (e.g., Anthemideae, Brassicaceae, Rubiaceae, Caryophyllaceae and Cyperaceae). Several heliophilous shrubs (*Salix*, *Betula*, Hippophae, *Juniperus*, *Ephedra distachya* and *Ephedra fragilis*) were also present. *Pinus* percentages (ca. 10 to 20%) most likely corresponded to long distant transportation of pollen. Throughout this period, the concentration of TLP remained low, without significant fluctuations (Figs. 2b and 3b). This phase of treeless, herbaceous-dominated vegetation with scattered shrubs is characteristic of the Oldest Dryas period for the area (Clerc, 1988; Ruffaldi, 1991).



Figure 2. a) Synthetic pollen diagram of Lake Paladru (in %) with exaggerated curves (5×). b) concentration diagram in pollen grains/cm<sup>3</sup> (histograms) and their percentages in gray.

PAZ 2 (517 to 502 cm for Lake Paladru; 529 to 520 cm for Lake Moras)

The percentages and concentrations of *Juniperus* were high at the beginning of PAZ 2. Other shrubs, such as *Salix* and *Hippophae* increased during this zone. *Betula* percentages and concentrations progressively increased and become dominant at the end of PAZ 2. Therefore, percentages of arboreal pollen were higher than non-arboreal pollen percentages at the end of this zone (AP/TLP was approximately 60% for both lakes). The percentage and concentration of heliophilous and meadows taxa decreased, except for Poaceae and *Artemisia*, which remained high until the end of the zone. These vegetation changes can be considered similar to the ones described during the Bølling zone in the area (Eicher et al., 1981; Richard and Bégeot, 2000).

# PAZ 3 (502 to 469 cm for Lake Paladru; 520 to 513 cm for Lake Moras)

The decrease in *Betula, Juniperus, Salix* and *Hippophae* percentages and concentrations were synchronous with the strong expansion of *Pinus* (percentages over 50% for both lakes), indicating the development of a pine forest around the lakes. The occurrence of some taxa such as Poaceae, *Artemisia* and *Rumex*-type suggested the presence of treeless or wet areas colonized by *Filipendula* and Cyperaceae. This type of vegetation is largely described in the region (Clerc, 1988; Argant et al., 2008) and is considered to be typical of the Allerød period.

# PAZ 4 (469 to 445 cm for Lake Paladru; 513 to 503 cm for Lake Moras)

Betula percentages and concentrations largely decreased, while heliophilous shrubs (Juniperus), herbs (Poaceae, Artemisia,

Chenopodiaceae, *Helianthemum*, *Thalictrum* and *Rumex*-type) and meadows (Anthemideae, Brassicaceae, Rubiaceae, Caryophyllaceae and Cyperaceae) increased. *Pinus* percentages and concentrations remained high (above 50% for both lakes). This return of steppic vegetation may correspond to the Younger Dryas period and was largely described at the regional scale (Ruffaldi, 1991; Argant et al., 2008) and in western Europe (Lotter et al., 1992; Ammann et al., 1993).

# PAZ 5 (445 to 417 cm for Lake Paladru; 503 to 493 cm for Lake Moras)

The beginning of PAZ 5 was marked by a new expansion of *Betula* and the maintenance of *Pinus* percentages in high values. Then, percentages and concentrations of *Betula*, *Pinus*, heliophilous herbs and meadows taxa decreased, while the AP/TLP reached its highest values. This increase most likely resulted from the growth of the meso-thermophilous forest (mainly composed of *Corylus*, *Quercus* and *Ulmus*) at the expense of the pine–birch forest. This vegetation dynamic corresponds to the Preboreal period (Eicher et al., 1981; de Beaulieu et al., 1994).

# PAZ 6 (417 to 377 cm for Lake Paladru; 493 to 469 cm for Lake Moras)

*Betula* and *Pinus* reached low percentage values, while *Corylus* sharply increased and become dominant. The increase of *Quercus* and *Ulmus* was recorded later and was followed by the appearance and expansion of *Tilia*, *Acer* and *Fraxinus*. Percentages of herb taxa were low and the AP/TLP ratio reached 95% for the two lakes. This *Corylus*-dominated vegetation phase has been described to be characteristic of the Boreal period (Clerc, 1988; Ruffaldi, 1991). This classical pollen



Figure 3. a) Synthetic pollen diagram of Lake Moras (in %) with exaggerated curves (5×). b) Concentration diagram in pollen grains/cm<sup>3</sup> (histograms) and their percentages in gray.

assemblage for the Boreal period, with a domination of Corylus taxa, was easily noticeable in Lake Moras but not in Lake Paladru.

### Geochemistry

The variations in Ti and K values were quite similar in both lakes and could be divided into four zones (Fig. 4). Maximum levels were recorded in S1 (Oldest Dryas; bottom of the sequences), medium values were recorded in S3 (Younger Dryas; between 470 and 441 cm in Lake Paladru and between 513 and 501 cm in Lake Moras) and two phases of low values were recorded in S2 (Bølling/Allerød Interstadial; between 515 and 470 cm in Lake Paladru and between 531 and 513 cm in Lake Moras) and in S4 (early Holocene; top of the sequences).

In Lake Paladru, Ca values increased at the S1/S2 transition and remained stable until the top of the sequence. In Lake Moras, Ca values were high in S1, rapidly decreased to low values in S2, increased again during S3 (with a short decrease during the middle of this zone), abruptly decreased at the beginning of S4 and then strongly increased and remained high until the top of the sequence (Fig. 4).

# Age/depth model

To obtain a robust chronology for the two lakes, composite agedepth models were built using a smooth spline model from (i) the accepted radiocarbon dates (fourteen for Lake Paladru and seven for Lake Moras) and (ii) ages estimated for the main late-glacial/early-Holocene transitions (three ages), which were indicated by the pollen stratigraphy and by geochemistry data (Fig. 5a–b and Table 1).

For Lake Paladru, two radiocarbon dates were rejected because they were outliers compared to dates from similar depths (Fig. 5a), and because they were not in accordance with the regional palynostratigraphy. In particular, the age obtained at 480–482 cm (14,151–15,052 cal yr BP) was too old to match the vegetation composition dominated by Pinus, which was characteristic of the Allerød period, between 13,500 and 12,700 cal yr BP (Lotter, 1999; David, 2001). Two samples at 428-430 cm depth have been dated by two laboratories (Poz-37100 and SacA-20694) and yield two different ages (Table 1). At this depth, pollen spectrum shows a pine-birch forest and some mesothermophilous taxa typical of the Preboreal period, which occurred from 11,700-11,500 cal yr BP (Birks and Ammann, 2000; Magny et al., 2006b). Therefore, the age obtained for the first date (SacA-20694; approximately 12,420-12,640 cal yr BP) appears to be too old and was rejected, while the second age (Poz-37100; approximately 11,155-11,650 cal yr BP) was judged to be correct.

Due to the paucity of terrestrial plant remains in sediments corresponding to the late-glacial period, other data were used to improve the chronology of both sequences. Thanks to the large number of available <sup>14</sup>C-dated pollen diagrams for the region (Lotter, 1999; Birks and Ammann, 2000; David, 2001; Magny et al., 2006b), the radiocarbon age of the zone boundaries was relatively well constrained and was



Figure 4. Results of ITRAX analysis of calcium (Ca), titanium (Ti) and potassium (K) values in the two lakes.

used to provide ages for the late-glacial/early-Holocene transitions of our sequences. This method of improving the age-depth model has already been used in several studies for the same time period (e.g., Heiri et al., 2007; Lotter et al., 2012; Millet et al., 2012). The transition depths in each sequence were determined by changes in vegetation composition observed in the pollen data (Figs. 2 and 3) and by breaks in sedimentation composition determined using geochemistry diagrams (Fig. 4). Because the analytical resolution of geochemistry analyses is higher than for pollen analyses, more precise transition depths could be obtained using this method. Changes in vegetation composition



Figure 5. Lithology, age depth-model with expected ages (in black) along the sequence (bold line), 95% confidence intervals (gray line), 2 $\sigma$  range probability distribution and ages fixed by pollen and sedimentation transition (in white) of Lake Paladru (a) and Lake Moras (b).



Figure 6. CHAR of macroscopic and microscopic analysis of Lake Paladru and Lake Moras and Inferred Fire Frequency (IFF) of Lake Paladru from 15,000 to 8000 cal yr BP.

largely described in the literature for the region (Birks and Ammann, 2000; Richard and Bégeot, 2000; Magny et al., 2006b) suggested that the date of the Oldest Dryas/Bølling transition is ca. 14,600 cal yr BP (PAZ1/PAZ2; S1/S2: 515 cm for Lake Paladru and 531 cm for Lake Moras), the date of the Allerød/Younger Dryas is ca. 12,700 cal yr BP (PAZ3/PAZ4; S2/S3: 470 cm for Lake Paladru and 513 cm for Lake Moras) and the date of the Younger Dryas/Holocene is ca. 11,600 cal yr BP (PAZ4/PAZ5; S3/S4: 440 cm for Lake Paladru and 502 cm for Lake Moras; Table 1). These dates were integrated to construct the age–depth model of the two sequences (Fig. 5a–b). An error interval of two hundred years ( $\pm$ 100 years) was added to these three dates, corresponding to the interval generally described by regional pollen data.

### Charcoal record and fire frequency

From 15,000 cal yr BP to 14,300 cal yr BP, macro-CHAR values from Lake Paladru remained low (Fig. 6a). The strongest increase was recorded at ca. 14,300 cal yr BP. Then, macro-CHAR values were high but progressively decreased until 12,600 cal yr BP. Between 12,600 and 12,200 cal yr BP they reached their lowest values  $(0.02 \text{ mm}^2 \text{ cm}^{-2} \text{ yr}^{-1})$ . From 12,200 cal yr BP, macro-CHAR values sharply increased and remained high (approximately 0.06 mm<sup>2</sup> cm<sup>-2</sup> yr<sup>-1</sup>) until 11,200 cal yr BP. Then, they progressively decreased, reaching again low values ca. 10,000 cal yr BP.

Micro-CHAR values from Lake Paladru (Fig. 6b) were low until 14,100 cal yr BP, when started to increase to approximately 0.01 mm<sup>2</sup> cm<sup>-2</sup> yr<sup>-1</sup>. Then they remained constant until 12,600 cal yr BP. Between 12,600 and 12,200 cal yr BP, these values decreased and reached their minimum value of 0.005 mm<sup>2</sup> cm<sup>-2</sup> yr<sup>-1</sup>. Between 12,200 and 11,500 cal yr BP, micro-CHAR increased and reached their

highest values (around 0.015  $\text{mm}^2 \text{cm}^{-2} \text{yr}^{-1}$ ). From 11,000 cal yr BP, the values sharply declined and stayed low until 8000 cal yr BP.

The variation in fire frequencies may be reconstructed applying the decomposition approach to the macro-CHAR data (Fig. 6c). Between 14,200 and 13,200 cal yr BP, IFF values oscillated approximately around 6 fire episodes/500 yr. From 13,200 to 12,200 cal yr BP, IFF values decreased (ca. 4 fire episodes/500 yr). From 12,200 to 11,200 cal yr BP, IFF values reached the highest values recorded (7 fire episodes/ 500 yr). Finally, from 11,200 to 8000 cal yr BP, IFF values progressively decreased to 5 fire episodes/500 yr.

The macro-CHAR record from Lake Moras increased to  $0.04 \text{ mm}^2 \text{ cm}^{-2} \text{ yr}^{-1}$  from 14,500 cal yr BP and reached high values at around 14,100 cal yr BP (Fig. 6d). The values remained high and then decreased at 13,100 cal yr BP and reached very low values (0.005 mm<sup>2</sup> cm<sup>-2</sup> yr<sup>-1</sup>) at 12,600 cal yr BP. Between 12,600 to 9500 cal yr BP several oscillations of CHAR values were observed, although they were small compared to the ones recorded during the previous period.

Micro-CHAR values from Lake Moras were counted at a low analytical resolution and could only be used as indicative information. The micro-CHAR values were high between 14,500 and 12,500 cal yr BP, and then decreased between 12,500 and 11,500 cal yr BP (Fig. 6e). From 11,500 cal yr BP until 10,800 cal yr BP, micro-CHAR values increased. From 10,800 to 8000 cal yr BP, low values were recorded, except around ca. 9200 cal yr BP.

### Discussion

The linkages between fire regime, climate and vegetation were discussed following the four main phases of climate changes that occurred between 15,000 and 8000 cal yr BP (Fig. 7). To facilitate the



Figure 7. Synthesis with fire (macro-CHAR), vegetation and erosion dynamics for Lake Paladru and regional and global temperature reconstructions from 15,000 to 8000 cal yr BP.

comparison and discussion, the data set was also presented in Table 2, in a chronological framework.

# Oldest Dryas (<14,600 cal yr BP)

Fire activity was very low during this period. The absence of woody cover and the low fuel load were indicated by the presence of scattered vegetation, which was mainly composed of steppic heliophilous grasses and shrubs (*Juniperus* and *Betula*). The high values of terrigenous elements (K and Ti) attested a strong erosion of the watershed due to the lack of a dense vegetation cover (de Klerk, 2008). The development of vegetation seemed to be limited by drought condition and low summer temperature (Heiri and Millet, 2005). The presence of a scattered vegetation imply also a low connectivity landscape that may have prevented the spread of fires during the Oldest Dryas period (Whitlock et al., 2010; Briles et al., 2012). These results were in accordance with the low fire activity recorded between 21,000 and 15,000–14,500 cal yr BP in Europe (Rius et al., in press) and around the world (e.g., Power et al., 2008).

# Bølling/Allerød interstadial period (14,600 to 12,600 cal yr BP)

Concomitant increases of fire occurrence and frequency (with a maximum of 6 fire episodes/500 yr at Lake Paladru) were recorded in the two sites between ca. 14,500 and 13,200 cal yr BP. These increases

in fire activity were correlated with an increase in the amount of fuel available and with the progression of woody cover at the expense of steppic heliophilous herbaceous taxa. Indeed the increase in Betula pollen over 25% evidenced the local development of a birch forest (Huntley and Birks, 1983). A direct relationship between increases in woody cover and fire activity has been documented in several studies (e.g., Marlon et al., 2006). This vegetation development was most likely the main driver for the synchronous decreases recorded in the local erosion of soils. From ca. 14,700 cal yr BP, the climate became warmer (Rasmussen et al., 2006). At the regional scale, a significant increase of summer temperature of ca. 3-3.5°C occurred between 14,600 to 14,200 cal yr BP and a more gradual increase was recorded until 13,700 cal yr BP (Fig. 7, Heiri and Millet, 2005). The combination of summer warming with increase in woody biomass may have induced the increase in fire activity recorded at Lake Moras and Lake Paladru. This assumption was supported by comparable results obtained in Europe from ca. 14,500 cal yr BP (Power et al., 2008; Feurdean et al., 2012).

During the Allerød, two centennial-scale summer temperature decreases of 1.5–2.0°C (centered on ca. 13,200 cal yr BP and on ca. 12,900 cal yr BP) were recorded in the neighboring Jura Mountains (Heiri and Millet, 2005). From ca. 13,200 cal yr BP, the frequency of fires and the trend of macro-CHAR values decreased around Lake Paladru and Lake Moras (Fig. 6). No vegetation changes in composition and amount of fuel were recorded concomitantly to these decreasing fire frequency and these minor climate oscillations. Indeed the shift

scription of mai	r vegetation, charcoal and geochen	nistry results in chronological f	framework.					
Age (cal yr BP)	Pollen data of both lakes	Charcoal data (age in cal yr l	BP)			Geochemical data (age in c	al yr BP)	Glacial periods
		Paladru micro-	Paladru macro-	Moras micro-	Moras macro-	Paladru	Moras	
15,000 to 14,600	AP/TLP ~ from 30 to 45% (Paladru) and from 15 to 30% (Moras) domination of steppic and heliophilous herbs	No charcoal or very Iow values				Ti and K values are higher Ca values remain stable	Ti and K values are higher Ca values > progressively	Oldest Dryas
(4,600 to 13,500	AP/TLP ~ to 60% (Paladru) and to 70% (Moras) domination of steppic and heliophilous herbs and shrubs	Low values and ~ from 14100	Low values and / from 14300	Low values and ~ from 14,500	Low values and / from 14,100	Ti and K values ≻ from 14,300 Ca values ∕ from 14,300 and stay high	Ti and K values > from 14,100 Ca > to reach lower values	Bølling
l3,500 to 12,700	AP/TLP $\checkmark$ to $\approx$ 80% domination of <i>Pinus</i>	Stabilization of values	Gradual × of values until 12,600	Stabilization in high values	Stabilization in high values and \ from 13,100 to 12,600	Ti and K values are low and ~ slightly from 13,000 Ca values remain high	Ti and K values are low and ~ slightly around 13,000 Ca values remain low	Allerød
12,700 to 11,600	AP/TLP < to 70% domination of <i>Pinus</i>	> between 12,600 and 12,200 < from 12,200	<ul> <li>&gt; between 12,600 and</li> <li>12,200 ≤ from 12,200</li> </ul>	between 12,500     and 11,500	abrupt > from 12,600	Ti and K values ~ from 12,600 to 11,700 Ca values remain high	Ti and K values < from 12,600 to 11,700 Ca values <, shortly < at 11,900 and < after	Younger Dryas
11,600 to 8000	AP/TLP $\lambda \approx 95\%$ domination of <i>Pirus</i> until 10,600 and then domination of mesothermophilous taxa	Stabilization in high values and \ from 11,000	Values remain high and from 11,200 to reach low values at 10,000	✓ from 11,500 and > from 10,800	Stabilization in low values	Ti and K values < from 11,700 and reach lower values until 8000 Ca values remain high	Ti and K values $\sim$ Ca values $\sim$ , remain low except around 11,800 and $\sim$ from 10,200 to reach high values until 8000	Early Holocene

able

from birch forest to coniferous forests mainly composed by *Pinus* was previously recorded by pollen data, from 13,500 cal yr BP. Nevertheless, some decreases in macro-CHAR values in Lake Paladru seem to be correlated with these short-lived cold events. However, the resolution of charcoal and pollen analyses should be improved to be able to link potential fire and vegetation changes with climatic events of short duration and low magnitude.

At the end of the Allerød, significant higher values of macro-CHAR and micro-CHAR were recorded in Lake Paladru. This increase of fire activity was well correlated with the highest temperature of summer recorded at the end of this period at the regional scale (Heiri and Millet, 2005).

# Younger Dryas (12,600 to 11,600 cal yr BP)

From ca. 12,600 to 12,200 cal yr BP, fire activity synchronously decreased around the two lakes and fire frequencies at Lake Paladru remained low. Fuel availability remained at the same levels as during the Bølling–Allerød whereas vegetation composition changed with a decrease in *Betula* and a new, but limited, expansion of shrubs (*Juniperus*) and steppic herbaceous taxa. This shift involved a change in vegetation structure with less dense forests, involving the development of areas with less combustible material available.

At the same time, increases in terrigenous elements in the sediment indicated that there was another phase of soil erosion, but less intense than during the Oldest Dryas. Soil erosion was induced by the partial substitution of forest cover by steppic vegetation (Zolitschka, 1998). These environmental changes, typical from the onset of the Younger Dryas period (Isarin and Bohncke, 1999; Birks and Ammann, 2000; Magny et al., 2006b), were induced by colder summer temperatures (Heiri and Millet, 2005; Rasmussen et al., 2006) and led to a decrease of fire frequency.

Fire frequency increased from 12,200 cal yr BP, especially around Lake Paladru, with the highest CHAR values and a high fire frequency (ca. 7 fires episodes/500 yr) occurring during the late-glacial period. In Lake Moras, the increase in macro-CHAR values was barely noticeable and suggested that there were few fires. At a regional scale, after the gradual decrease of summer temperatures during the first part of the Younger Dryas, a gradual increase was recorded from 12,200 cal yr BP from chironomid assemblages (Heiri and Millet, 2005). Several regional studies, which attempted to reconstruct the temperatures during the late-glacial/early-Holocene transition using other proxies, highlighted climate fluctuations during the Younger Dryas period. Pollen-inferred temperature (Lotter et al., 1992; Peyron et al., 2005), pollen-inferred vegetation history (Ruffaldi, 1991) or palaeo-hydrological dynamics (Magny and Ruffaldi, 1995; Magny, 2001) revealed two phases during the Younger Dryas period: a cold phase followed by a warmer/drier phase (Magny et al., 2006b). Thus, the variability in fire activity observed in Lake Paladru seemed to correspond to a climatic partitioning during the Younger Dryas period, which has been evidenced at the regional scale. In North America (Marlon et al., 2009), variation in fire activity has also been recorded and reflected the variable climate that occurred during the Younger Dryas period at a larger scale. Thus, during the second part of the Younger Dryas period, a sufficient quantity of biomass mainly dominated by Pinus (55-75%) a fire-prone taxa and an increase in summer temperatures seemed to have been favorable for fire ignition and propagation.

### Early Holocene (11,600 to 8000 cal yr BP)

At Lake Paladru, fire activity over the Younger Dryas/early Holocene transition (ca. 11,600 cal yr BP) remained high. During the early Holocene, the vegetation dynamic was characterized by increases of woody cover and biomass availability. This most likely corresponded to an expansion of birch species and a decrease in steppic herbaceous and heliophilous shrubs (*Juniperus*). Concomitant decreases in terrigenous

inputs of the two lakes marked the stabilization of soils. Global and regional studies described a clear increase in temperatures during the same period (Heiri and Millet, 2005; Rasmussen et al., 2006). The increase in available biomass (mainly pine–birch forest) associated with warmer temperature and drier conditions were favorable for high fire activity (Vannière et al., 2008; Leys et al., 2013). High fire activity has also been illustrated during the early Holocene from ca. 11,600 cal yr BP in Europe (Tinner et al., 1999; Power et al., 2008; Olsson et al., 2010; Rius et al., 2011).

On the contrary, around Lake Moras, the frequency of fires was still low. The differences in fire reconstructions between the two lakes may be largely explained by the difference in their watershed sizes. A site with a large watershed relative to the lake size will magnify the allochthonous inputs (Higuera et al., 2007) and the probability of fire ignition and propagation in a large watershed (i.e., Lake Paladru) is higher than in a small watershed (i.e., Lake Moras) (Whitlock and Millspaugh, 1996). Moreover, the expansion of dense hardwoodforests since 11,600 cal yr BP constituted a filter (Blackford, 2000), which may have limited charcoal inputs more strongly in a small catchment than in a large one.

Since 11,200 cal yr BP, fire activity decreased and the vegetation changed from pine–birch forests to deciduous forests. The biomass availability, mainly composed by woody cover, was always present (75–80%) but its composition changed. This enabled better fixation of soils (Ranger and Nys, 1994; Zolitschka, 1998; Leroux et al., 2008) due to the more developed root system of hardwood trees. Moreover, this vegetation stabilization implied increasing soils thickness through pedogenic processes: soils under deciduous forests were less subject to droughts, and thus to fire ignition and propagation, than soils under coniferous forests.

#### Conclusion

This study illustrated the sensitivity of fire activity, recorded in temperate areas, to the main climatic changes during the late glacial/ Holocene transition. The fire dynamics evolved according to the different periods of climate warming or cooling, and in relation with changes in vegetation composition and distribution. The fluctuations of fire activity were the result of complex interactions between climate and vegetation in which the respective roles of these two forcing factors are difficult to clearly disentangle.

This study highlights expected relations of cause-and-effect between fire, climate and vegetation. During cooling periods such as the Oldest Dryas (15,000 to 14,600 cal yr BP) and the first part of the Younger Dryas (12,600 to 12,200 cal yr BP), low fire activity was due to limited biomass availability and low summer temperature. Conversely, during warming periods such as the Bølling/Allerød (14,600 to 12,600 cal yr BP) and the beginning of the early Holocene (11,600 to 11,000 cal yr BP), the increase of summer temperatures and drought condition combined with the increase in biomass availability involved an increase of fire activity.

However, during the second part of the Younger Dryas and during the early Holocene, these fire–vegetation–climate relationships did not follow the patterns previously described. During the cooling phase of the Younger Dryas, an increase in fire activity was recorded (12,200 to 11,600 cal yr BP) in parallel to an increase of summer temperatures, while the vegetation composition remained characteristic of cold climatic conditions. During the early Holocene, summer temperatures were warmer and biomass was available but the fire activity decreased (from ca. 11,000 cal yr BP). In this case, the shift from coniferous to deciduous forests (less-flammable) seemed to be the cause of decreasing fire activity.

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