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Historical range of fire frequency is not the Achilles' heel of the Corsican black pine ecosystem

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Summary

1. This study investigated the fire-vegetation relationship by reconstructing the long-term fire and vegetation dynamics around a small lake in the Mediterranean montane belt on Corsica Island. The vegetation is characterised by forests dominated by *Pinus nigra* ssp. *laricio*, an endemic subspecies that is currently threatened. Populations of this taxon are geographically restricted, and their ranges are decreasing, possibly because of disturbance, that is, fire and logging.

2. Here, we examine the role of fire in vegetation dynamics and its effect on diversity since the lateglacial at a montane site using sedimentary plant macrofossils and charcoal to reconstruct local vegetation and fire frequency, respectively.

3. Macrofossils of *P. laricio* provide evidence for its growth around the Lac de Creno since 13 200 cal. years BP, which is consistent with its natural origin in Corsica. The onset of the Holocene (~11 700 cal. years BP) was marked by a rapid shift in the treeline, the establishment of *P. laricio*-dominated woodlands with low species turnover, and a long-term increase in taxa richness as a result of successive expansions of broadleaved deciduous trees. In spite of fire-return intervals (FRIs) fluctuating between 30 and 490 years during the Holocene, *P. laricio*-dominated woodlands persisted for several millennia, and fires likely played an ecological role in the functioning of these woodlands. The 12 000 year record of mean FRI (80 years between fires; i.e. frequency of 12.5 fires 1000 year^{-1}) can be used to define a baseline for the management and conservation of *P. laricio* montane forests. Our findings demonstrate that *P. laricio* has a long history, a natural origin in Corsica, and that Corsican pine forests have survived to a wide range of burning conditions over the last 13 200 years.

4. *Synthesis*: We present multimillennial fire and vegetation histories of a Mediterranean montane site. *Pinus nigra* ssp. *laricio* has been present near the study site since approximately 13 200 cal. years BP, demonstrating that this pine was present on the island prior to the arrival of pre-historic humans. The long-term records also show that *P. laricio* woodlands were mixed with deciduous broadleaf trees (*Betula* sp. and *Fagus sylvatica*), and other needleleaf trees (*Abies alba*), at least, and were not influenced by changes in fire frequency. We conclude that (i) fire is a natural component of the ecosystem and (ii) fires likely played an important ecological role in the functioning of the Corsican black pine woodland ecosystem.

Key-words: diversity, fire ecology, forest, Mediterranean, palaeoecology and land-use history, *Pinus nigra laricio*

Introduction

Due to the seasonal warm and dry climate that leads to a summer drought, the Mediterranean basin is well known for being a fire-prone region with an annual season of fire risk (Keeley *et al.* 2011b). As a result of changes in both climate and land use, relationships between vegetation, climate and disturbances in the Mediterranean basin are likely to change in the near future (Pausas 2004; Parry *et al.* 2007). On one hand, climate models forecast that the late 21st century is likely to be warmer and drier than was the 20th century, with longer summers and winter dry spells (Pal, Giorgi & Bi 2004; Giorgi & Lionello 2008). On the other hand, the ongoing abandonment of agro-pastoral land uses in mountainous and hilly areas may lead to higher forest connectivity (Debussche, Lepart & Dervieux 1999; Sheffer 2012), higher amounts of biomass and greater fuel loads (Fournier *et al.* 2012; Chauchard, Guibal & Carcaillet 2013), which in turn could facilitate more frequent ignition and the spread of fire, increasing both the burned area and the fire risk (Cary *et al.* 2006; Dury *et al.* 2011).

Current knowledge about post-fire-vegetation dynamics is mostly based on short-term studies, that is, < 100 years

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(Retana *et al.* 2002; Capitanio & Carcaillet 2008; Millington *et al.* 2009) that use models of vegetation dynamics (Mouillot, Rambal & Joffre 2002; Pausas & Fernández-Muñoz 2011). Therefore, we are unable to predict ecosystem responses to environmental conditions that are different to those that have occurred in recent decades. In addition, because Mediterranean land cover has been modified by previous human activities (Millennium Ecosystem Assessment 2005), 100-year observations of fire-vegetation relationships are potentially biased due to multisecular human-driven processes, for example landscape fragmentation, logging, agriculture and fire ignition. As a result, the natural vegetation dynamics with regard to fire disturbance are poorly understood. Spatially and temporally precise fire and vegetation records are needed to identify the mechanisms linking vegetation composition and fire regimes at time scales greater than 100 years. Current ecosystem management rarely takes into account baseline data about the ecosystem processes and disturbances, as fire frequency or grazing must be maintained to preserve biodiversity. This is even more important in the case of island ecosystems, where the risk of species loss may be exaggerated due to relatively small population sizes, large proportions of endemic taxa and a lack of potentially suitable habitats under future climate conditions (Whittaker & Fernández-Palacios 2007).

Corsica harbours several endemic taxa, including the Corsican black pine (*Pinus nigra laricio* (Poir.) Maire, hereafter *P. laricio*), which forms ~16 000 ha of pure woodlands in the montane belt (Barbet-Massin & Jiguet 2011). These woodlands are currently considered a priority habitat by the Council Directive 92/43/EEC and include protected and managed areas in the Natura 2000 network targeting the Corsican nuthatch (*Sitta whiteheadi*). Forestry in the area has focused on increasing *P. laricio* timber productivity. Model-based studies (Barbet-Massin & Jiguet 2011) suggest that the natural area of *P. laricio* is altered by natural disturbance (wildfires) and by human activities (logging and fires). Moreover, its future distribution is possibly threatened by logging and increased climate- and human-induced fire risk. However, several challenging questions remain unanswered in spite of research efforts focusing on *P. laricio* (Reille *et al.* 1997; Barbet-.Massin & Jiguet 2011; Pimont, Prodon & Rigolot 2011) such as when and how did *P. laricio*-dominated woodlands emerge on the island? How did fire regimes and climatic changes affect the composition of the woodlands? What was the natural range of variability in fire-return intervals? Palaeoecological studies allow the assessment of long-term relationships between plant assemblages and fire regimes (Willis & Bhagwat 2010) and are therefore useful to address these questions.

By collecting sediment cores from Lac de Creno (Corsica), which is surrounded by a montane forest of *P. laricio*, and extracting charcoals and plant macrofossils (e.g. needles, seeds or buds), we established a time-series that we compared to the published pollen records (Reille *et al.* 1997, 1999) and thus investigated the relationship between endemic vegetation dynamics and fire frequency during the past 18 000 years. This lake is a key paleobotanical study site on Corsica and in the western Mediterranean basin due to (i) the length of the chronology (18 000 years), (ii) its nearly constant rate of sedimentation over the past 18 000 years (Reille *et al.* (1997, 1999)) and due to (iii) its small lake surface, which is well suited to the reconstruction of local fire episodes and vegetation composition because of the small charcoal source area (Peters & Higuera 2007), the short transport distance for macrofossils and the relatively small pollen source area (Sugita 1994).

The long history of sedimentation allows for the reconstruction of vegetation and fire-regime changes from ca. 18 000 cal. years BP up to the present, which are associated with a number of different climatic conditions. Since the Last Glacial to present day, several climatic oscillations are known: colder conditions in the lateglacial (18 000–14 700 cal. years BP) and the Younger Dryas (12 700–11 700 cal. years BP) contrast with warmer conditions during the Bølling/Allerød (14 700–12 700 cal. years BP) and the Holocene (the last 11 700 years) (Lotter *et al.* 2012; Shuman 2012). We hypothesised a higher fire frequency related to warmer climatic conditions, possibly correlated with changes of vegetation dynamics (i.e. composition and/or abundance) as it was demonstrated in Northern America (Marlon, Bartlein & Whitlock 2006), Southern Europe (Piñol, Terradas & Lloret 1998) or at the global scale (Marlon *et al.* 2008; Daniau *et al.* 2012). Moreover, land-use activities in more recent times could have modified the vegetation composition and the fire frequency by pastoral activities, human-induced fires and/or forest management (Piñol, Terradas & Lloret 1998; Carcaillet *et al.* 2009).

Earlier palynological investigations from Lac de Creno (Reille *et al.* 1997, 1999) indicated that *Pinus* pollen increased in abundance at the onset of the Holocene and that *Pinus, Fagus*, *Betula* and deciduous *Quercus* dominated regional vegetation during most of the Holocene. The authors assumed that the fluctuations of pollen percentage of all taxa were due to changes in climate and possibly fire. But, particularly in mountain regions, pollen records are not unambiguous to infer the local occurrence of plant taxa contrary to plant macroremains (Lang 1994; Birks & Birks 2000). Moreover, a charcoal record was urgently needed to address vegetation-fire relationships at Lac de Creno. Our new high-resolution plant macroremains and charcoal records allow us to test the role of fire frequency on the vegetation and to determine when *P. laricio* arrived and expanded in the lake catchment area.

Materials and methods

STUDY AREA AND CORE LOCATIONS

Lac de Creno (1310 m a.s.l.; 42°12′17″N, 08°56′45″E) is located in the south-eastern part of the Rotondo massif (western Corsica, west Mediterranean basin). The lake is part of a Regional Natural Park established in 1972. The 6.5-m deep, 1.5-ha area lake is situated on a narrow crest. It has no permanent inflow and receives water from a small catchment (~25 ha) with a bedrock of monzonitic granite. Ecologically, the lake is situated in the lower montane belt, which is characterised by mixed conifer forests of *P. laricio*, *Fagus sylvatica*

L. (beech), and *Abies alba* Mill. (white fir) with an understorey of *Genista corsica* DC and tall heather species from Ericaceae (mainly *Erica arborea* L.) (Gamisans & Jeanmonod 1993; Gamisans, Badia & Rafols 2000). Today, the vegetation surrounding the lake and within the lakes' watershed is dominated by *P. laricio* with scattered *F. sylvatica* trees and patches dwarf shrubs (*G. Corsica*).

The supra-Mediterranean belt, which lies below the montane belt, is characterized by mixedwoods with Corsican pine (*Pinus nigra laricio* (Poir.) Maire), maritime pine (*P. pinaster* Aiton), deciduous oaks (*Q. petraea* (Matt.) Liebl., *Q. pubescens,* Wild.) and chestnut (*Castanea sativa* Mill.). At lower elevation, the meso-Mediterranean belt is dominated by evergreen broadleaved oak (*Quercus ilex* L.) woodlands or tall shrublands (*Arbutus unedo* L.) with maritime pine. In all of these three belts, pyrogenic tall shrubs, such as *Erica arborea*, *E. scoparia* L., *Cistus mospeliensis* L. or *C. salvifolius* L., dominate the understorey.

AGE-DEPTH MODEL

Parallel overlapping cores were extracted in 2009 from the lake centre at a water depth of ~6 m using a Russian corer (diameter = 7.5 cm, length = 100 cm) and a Kajak–Brinkhurst corer (diameter = 8.0 cm), which allowed us to sample the uppermost water-saturated sediments. The longest sedimentary sequence, measuring 700 cm in length, was used for the analyses of charcoal and terrestrial plant macrofossils.

^{210}Pb and ^{137}Cs measurements were used to build an accurate age-depth model for the upper sediments. The depositional model was extended down the core using 11 ^{14}C dates measured by accelerator mass spectrometry (AMS) on plant macrofossils or on the total organic matter of bulk sediments when macrofossils were not sufficiently abundant (Table 1). Radiocarbon ages were calibrated in calendar years before present (hereafter cal. year BP) using CALIB v6.1 (Stuiver & Reimer 1993) with the Intcal09 data set (Reimer *et al.* 2009). The age-depth model was established using a smoothing spline (span = 0.1) with the MCAgeDepth program (Higuera 2008), which applies a Monte Carlo resampling technique to assess median ages and generate confidence intervals (CI) for the model based on the probability distribution of each date.

To test the robustness of the age-depth model for periods of widespread large climate variations, such as the Younger Dryas–Holocene transition (11 700 cal. years BP), we estimated sediment composition changes using loss-on-ignition (LOI). LOI was determined at 550 °C for 1 h (Heiri, Lotter & Lemcke 2001) at 1-cm intervals along the core to estimate the relative abundance of organic matter and ignition residue, principally minerogenic sediment components. LOI was not measured in the top 20 cm of the core sequence because the sediment volume was too small.

CHARCOAL ANALYSIS AND LOCAL FIRE-EPISODES RECONSTRUCTION

Local fire episodes were inferred from the macrocharcoal record using the decomposition approach (Lynch, Clark & Stocks 2004), which separates the charcoal peaks ($CHAR_{peak}$), indicative for local fire episodes, and the charcoal background ($CHAR_{background}$) component, that is indicative for regional area burned (Whitlock & Anderson 2003). The optimal sampling interval for detecting local fire episodes using macroscopic charcoal records is < 0.1–0.2 times the mFRI (Higuera *et al.* 2007), which is approximately 15 years based on the current estimated fire frequency on Corsica (Mouillot, Rambal & Joffre 2002). To determine the sampling resolution of our new sediment core before obtaining ^{14}C measurements, we estimated the deposition time using ^{14}C dates from core labelled Creno 8 (Reille *et al.* 1999) that were fitted with a smoothing spline (span = 0.1) with MCAgeDepth. Based on this age-depth model, the sediments were sampled at 0.5-cm intervals (1290 samples) to obtain a sampling resolution < 20-year sample^{-1}.

Sediment samples (1 cm^3) were first treated with NaClO and then sieved (160-μm mesh size) under a gentle water spray (Carcaillet *et al.* 2001). Subsequently, charcoal particles > 250 μm^2 were identified and tallied, and their size was measured using digital image-analysis software (WinSeedle 2007, © Regent Instruments Inc., QC, Canada). Charcoal measurements were reported as charcoal concentrations per area (mm^2 cm^{-3}) and as charcoal accumulation rates ($CHAR_{area}$: mm^2 cm^{-2} year^{-1}) according to the robustness measurements and methods, for processing and quantifying charcoal samples, especially in a Mediterranean context (Leys *et al.* 2013).

To decompose the $CHAR_{area}$ series, we first interpolated the $CHAR_{area}$ record to equal sampling resolution using the median of the sediment-accumulation rate (i.e. 14 years) and then separated the $CHAR_{background}$ and $CHAR_{peak}$ components using a locally weighted polynomial regression (LOWESS) with a locally defined threshold type. A moving time window of 600 year was used to maximise the signal-to-noise index SNI (Kelly *et al.* 2011) and the goodness-of-fit between the empirical data and the $CHAR_{background}$ data. Although we cannot rule out the possibility of charcoal pieces larger than 160 μm to extraordinarily be transported on long distances (Pisaric

Table 1. Accelerator mass spectrometry (AMS) radiocarbon dating. Terrestrial plant macrofossils are needles of *Pinus laricio* or seeds of *Betula* sp. Measurements on bulk sediments were carried out on the total organic matter

Depth (cm)	Lab code	^{14}C years BP	Calibrated age range, cal. years BP (2 σ)*	Dated material
90–95	Poz-36753	1415 ± 30	1287–1365	Plant macrofossils
175–180	Poz-36754	3360 ± 35	3483–3689	Plant macrofossils
240–245	Poz-36755	4705 ± 35	5321–5580	Plant macrofossils
355–360	Poz-38609	7740 ± 60	8410–8627	Plant macrofossils
370–375	Poz-36803	8150 ± 50	9004–9257	Bulk sediment
385–390	Poz-38612	8350 ± 60	9140–9491	Plant macrofossils
435–440	Poz-36758	9630 ± 50	10 774–11 180	Plant macrofossils
495–500	Poz-36759	11 250 ± 60	12 954–13 297	Plant macrofossils
526–531	Poz-36802	12 850 ± 80	14 928–16 053	Bulk sediment
580–585	Poz-36760	13 130 ± 70	15 242–16 506	Bulk sediment
670–675	Poz-38611	14 430 ± 90	17 180–17 891	Bulk sediment

*Calibration via Calib 6.0 (INTCAL09; last accessed 17 August 2013).

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2002; Tinner *et al.* 2006), empirical and modelling studies indicate that peaks of CHAR are indicative of fire occurrence within a distance of 1.0–3.0 km from the lake shore (Higuera *et al.* 2007; Higuera, Whitlock & Gage 2011) and that more than 90% of charcoal particles are transported over just a few metres (Clark *et al.* 1998; Ohlson & Tryterud 2000; Lynch, Clark & Stocks 2004) in the absence of run-off transportation within the catchment area (Carcaillet *et al.* 2007).

The ages of the reconstructed local fire episodes were used to calculate the fire-return interval (FRI: years between two consecutive fires, year fire^{-1}) and the fire frequency (FF: number of fires per unit of time, smoothed over a 1000-year smoothing window, fires kyear^{-1}). Mean FRI (mFRI) values were estimated by fitting a two-parameter Weibull model, which passed a Kolmogorov–Smirnov goodness-of-fit test ($P > 0.10$), to the FRI distribution. Reconstructions of FRI and FF were performed using the CharAnalysis, v.1.1 program (Higuera *et al.* 2009).

The statistical analyses of the charcoal record resulted in the estimation of two among the three complementary components of the fire regime i.e., temporal component, spatial component and fire behaviour (Whelan 1995; Hély & Alleaume 2006). The FRI and FF describe the temporal component of the fire regime, whereas the fire severity characterises the fire behaviour by the degree of burned biomass, for example tree mortality, depth of burned litter and fire size. Although we do not have a direct estimate of fire severity, we used $CHAR_{background}$ as a proxy for the regional burned area, which is correlated with fire size in a rolling landscape (Higuera *et al.* 2010), with gentler slopes compared with those surrounding the Lac de Creno.

PLANT MACROFOSSIL ANALYSES AND VEGETATION HISTORY RECONSTRUCTION

To estimate plant macrofossil concentrations, the 700-cm-long core was sliced into 695 contiguous 1-cm-thick slices, and the volume (~12 cm^3) of each slice was measured by water displacement. The macrofossils were extracted by water-sieving (250-μm mesh size) and identified under a stereomicroscope (x6.3-50) with the aid of a reference collection and macrofossil atlases (Martin & Barkley 1973; Cappers, Bekker & Jans 2006). Abundances of macrofossils were expressed as accumulation rates based on deposition time as computed by the age~depth model (number of fragments cm^{-2} year^{-1}). The macrofossil record was compared with published pollen percentages for most abundant pollen taxa from the same site (Reille *et al.* 1997, 1999) to illustrate relationships between local macrofossil-inferred vegetation changes, that is, the local vegetation changes in the watershed, and pollen-derived regional vegetation changes. The pollen diagrams were digitised using ImageJ software, v 1.45 s (Abràmoff, Magalhães & Ram 2004).

QUANTITATIVE ANALYSES

To reduce noise in the data set, the macrofossils record was smoothed using a moving average (window width of 100 year) prior to the subsequent quantitative analyses. Taxonomic richness of macrofossils was estimated as the number of taxa per sample (*S*) to compare the richness of the macrofossils over time. Macrofossil assemblages do not fully reflect plant communities because of the differential production of macrofossils, differences in their preservation (macrofossils of evergreen woody taxa are often overrepresented relative to macrofossils of deciduous and herbaceous plants) and because the chance of finding macrofossils strongly depends on the population size (Jackson & Booth 2007; Blarquez *et al.* 2012). Therefore, this richness estimated differs from alpha diversity (i.e. the floristic richness in a single locality) and may be indicative, within the limits of resolution of macrofossil records, of taxa richness of macrofossils' assemblages (Blarquez, Finsinger & Carcaillet 2013). Based on the richness values, we performed a constrained hierarchical clustering (CONISS) analysis using a distance matrix, with the clusters constrained by sample order (Gordon & Birks 1972; Grimm 1987). We compared the distribution of the hierarchical classification obtained from a broken stick model (Bennett 1996) to determine the number of significant zone boundaries. Zonation was performed using the Rioja package in R (Juggins 2012).

The compositional turnover of plant macrofossil assemblages based on β-diversity, a turnover index (Hill & Gauch 1980), was estimated by a detrended canonical correspondence analysis DCCA (Ter Braak 1986) constrained by age. As for the richness index, the compositional turnover reflects changes to the macrofossils assemblage composition. The DCCA was performed with square-root-transformed percentages, detrended by segments, nonlinear rescaled, and without down weighting of rare taxa. DCCA directly scales the first ordination axis in standard deviation units (SD-units) to estimate compositional turnover over time (Birks 2007). A turnover ≥ 4 SD-units would mean that the assemblages experienced a complete turnover, that is, a given assemblage shares no species with the previous assemblage (Hill & Gauch 1980).

Principal component analyses (PCA), standardised by taxa with log-transformed concentration data (Ammann *et al.* 2000), were used to visualise the relationships among taxa inferred from macrofossils accumulation rates. We carried out two PCA analyses: one included all samples, and the second used only the samples that contained at least two taxa. Samples younger than 500 cal. years BP were excluded from all of the PCAs due to potential bias from high sediment-accumulation rates in that section of the core. To visualise the relationships between the local fire-episodes regime and the local vegetation inferred from macrofossil assemblages, $CHAR_{background}$ (proxy of the burning area) and FRI (proxy of local fire episodes) were added passively in the PCA ordination plots. All ordinations were carried out in Canoco v4.5 (Ter Braak & Smilauer 2002).

Results

AGE-DEPTH MODEL, SAMPLING RESOLUTION AND SEDIMENT COMPOSITION

Sediment-accumulation rates showed little variation between 500 cm and 50 cm depth, corresponding to the Holocene. The top 50 cm, corresponding to the last 500 years, displays the poorly compacted sediments and, at the opposite end, sediments below 500 cm, corresponding to the lateglacial, were characterised by the lowest sediment-accumulation rates (Fig. 1a). The estimated last glacial sedimentation rates (18 000–14 700 cal. years BP) showed a large degree of uncertainty, with confidence intervals (CI) ranging from 0.2 to 0.8 mm year^{-1} (Fig. 1c). The median deposition time for the entire age-depth model was ~27 year cm^{-1}. Therefore, the median sample resolution for the charcoal record was ~13-year sample^{-1}, which met our sampling goal for the local fire-episode reconstruction (Fig. 1d).

Organic matter percentage (Fig. 1b) was low with a mean of 8.5% of sediment dry weight (dw%) from 18 000 to

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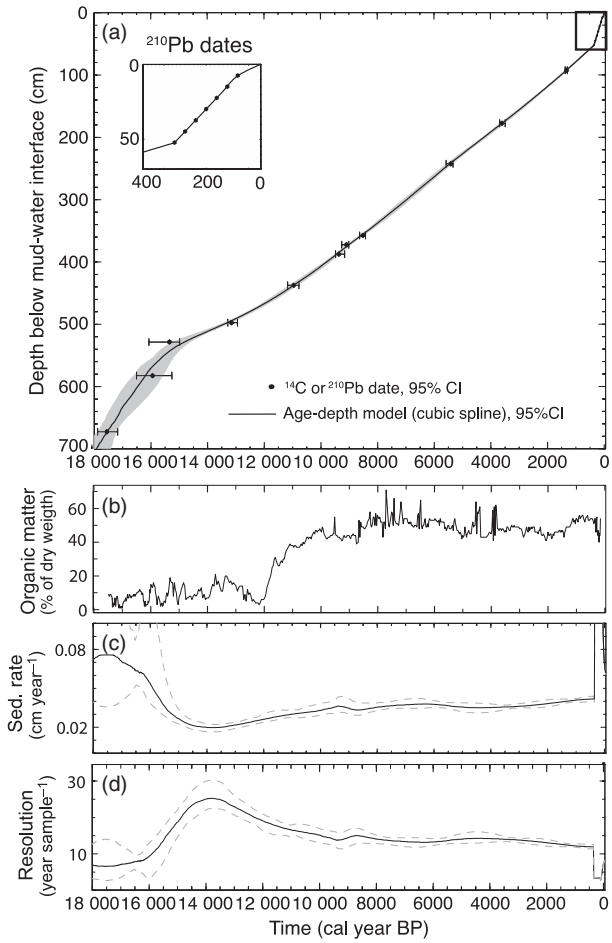

Fig. 1. (a) Age-depth model for the Lac de Creno record (horizontal whiskers: confidence intervals (CI = 2σ) for the calibrated ^{14}C ages; grey shaded area: 95% uncertainties of the model); insert: ^{210}Pb dates plotted against depth. (b) Abundance of organic matter (as a percentage of dry weight). (c) Sediment-accumulation rate (cm year^{-1}) and (d) sample resolution (year sample^{-1} for a 0.5-cm sample) (dashed lines = 95% CI).

11 950 cal. years BP. The estimated ages of a decrease in organic matter at ~12 500 cal. years BP (12 617–12 308 cal. years BP) and an increase in organic matter at ~11 900 cal. years BP (12 108–11 793 cal. years BP) are consistent with the age estimates for the beginning and end of the Younger Dryas based on $\delta^{18}O$ records from Greenland (Rasmussen *et al.* 2006; Steffensen *et al.* 2008). Organic matter content increased from 8 to 45 dw% starting from ~11 900 cal. years BP, corresponding to the onset of the Holocene, and levelled off after 9900 cal. years BP at approximately 50 dw%.

FIRE HISTORY

The fire reconstruction analysis identified 95 local fire episodes over the past 18 000 years (Fig. 2a,b). These 95 fire episodes, inferred from the $CHAR_{peak}$ component of $CHAR_{area}$, (Fig. 2a) could be clearly distinguished from the $CHAR_{background}$. The signal-to-noise index was 6.6 on average, indicating that the peaks were well differentiated from the background noise (Kelly *et al.* 2011).

The fire-return interval (FRI) during the Holocene ranged from 30 to 490 year fire^{-1} with a median of 98 year fire^{-1} (Fig. 2b). From the end of the last glacial maximum to the onset of the Holocene (18 000–11 700 cal. years BP), local fire episodes were rare (mFRI 1540 year fire^{-1}, corresponding to a fire frequency (FF) of 0.65 fires kyear^{-1}, Fig. 2c) and regional area burnt was low ($CHAR_{background}$ was lowest). The regional vegetation largely dominated by herbs (Reille *et al.* 1997, 1999) could explain the low abundance of charcoal fragments (low fuel load) and the small amount of sediment organic matter (~15%). Local fire episodes became more frequent starting in 11 800 cal. years BP (mFRI = 135 year fire^{-1}; FF = 7.5 fires kyear^{-1}, Fig. 2b,c). During the Holocene, fire frequency peaked 3 times, with the maxima centred at approximately 11 000 cal. years BP (12.0 fires kyear^{-1}), 4300 cal. years BP (12.3 fires kyear^{-1}) and 1500 cal. years BP (11.0 fires kyear^{-1}, Fig. 2c). Between the two last maxima at 4300 and 1500 cal. years BP, the fire frequency was lower with 4.9 fires kyear^{-1} at 3000 cal. years BP. The last 500 years were characterised by a low FRI value, similar to the values reconstructed for the period 9000–8000 cal. years BP, that is, 3.4 fires kyear^{-1}. The last reconstructed fire episode was dated to 150 cal. years BP, that is, approximately 210 years before our sampling year.

VEGETATION DYNAMICS AND RICHNESS INFERRED FROM MACROFOSSILS

Overall, 21 taxa were identified in the macrofossils from the 695 analysed samples. The assemblages were largely dominated by woody taxa (97% of total macrofossils, Fig. 3) with the most abundant taxa being *P. laricio*, *Fagus sylvatica*, *Betula* sp. and Ericaceae (mainly *Erica arborea* seeds, with a few occurrences of *Vaccinium* sp., Appendix S1 in Supporting Information). As also shown by the pollen record (Reille *et al.* 1997, 1999), the lateglacial flora was dominated by herbaceous taxa. Macrofossils found in this section include mainly seeds of *Poa sp.* and Cyperaceae, with fewer occurrences of Polygonaceae (Appendix S1 in Supporting Information). The first occurrences of *P. laricio* macrofossils were found at ~13 200 cal. years BP. At ~11 900 cal. years BP (about the onset of the Holocene), the abundance of macrofossils of woody taxa rapidly increased, indicating a likely shift in the treeline resulting in the establishment of mixed woodlands with *Abies*, *P. laricio, Betula* and *Fagus* among the trees and *Juniperus* and Ericaceae among the shrubs. With the exception of a phase between 9500 and 8500 cal. years BP, for which only Ericaceae macrofossils were found, tree taxa consistently dominated the assemblages throughout the Holocene. The pollen and plant macrofossil records display similar changes (Fig. 4), with increases in macrofossil accumulation rates when relative pollen abundances increased (e.g. *Betula* at ~8000 cal. years BP, *Pinus* at ~11 900 cal. years BP, *Abies* at ~3000 cal. years BP). However, for several taxa such as *Betula, Fagus, Abies* and Ericaceae macrofossils occurred earlier in the record than pollen or when relative pollen abundances were minimal. This clearly attests to the

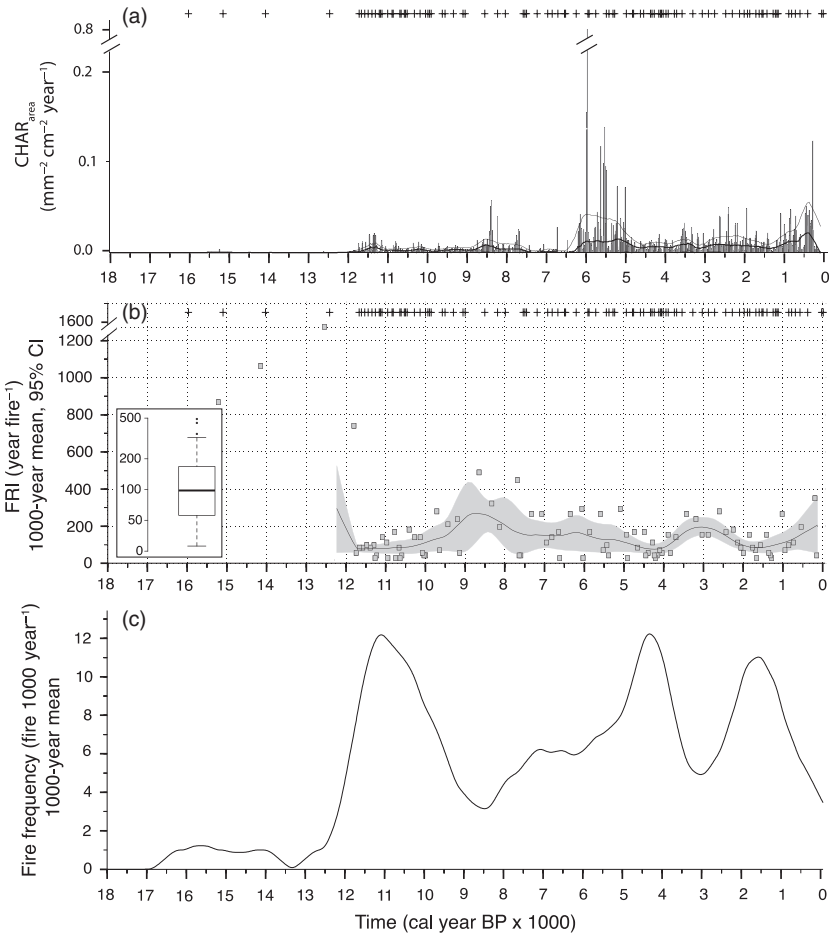

Fig. 2. Fire-history reconstruction at Lac de Creno. (a) $CHAR_{area}$ (histograms), Charcoal background fitted with a LOWESS curve (black line) and 95 percentile of noise distribution (grey line), and Charcoal peak components (portion of histograms above black line); local fire episodes are depicted as black crosses (+). (b) LOWESS-smoothed fire-return intervals [FRI, 1000-year smoothing window, 95% CI (grey)] and a log-scaled boxplot illustrating the distribution of FRIs over the past 12 000 years (median: horizontal black line; first and the third quartiles: box; 95th and 5th percentiles: whiskers). (**c**) LOWESS-smoothed fire frequency (1000-year smoothing window).

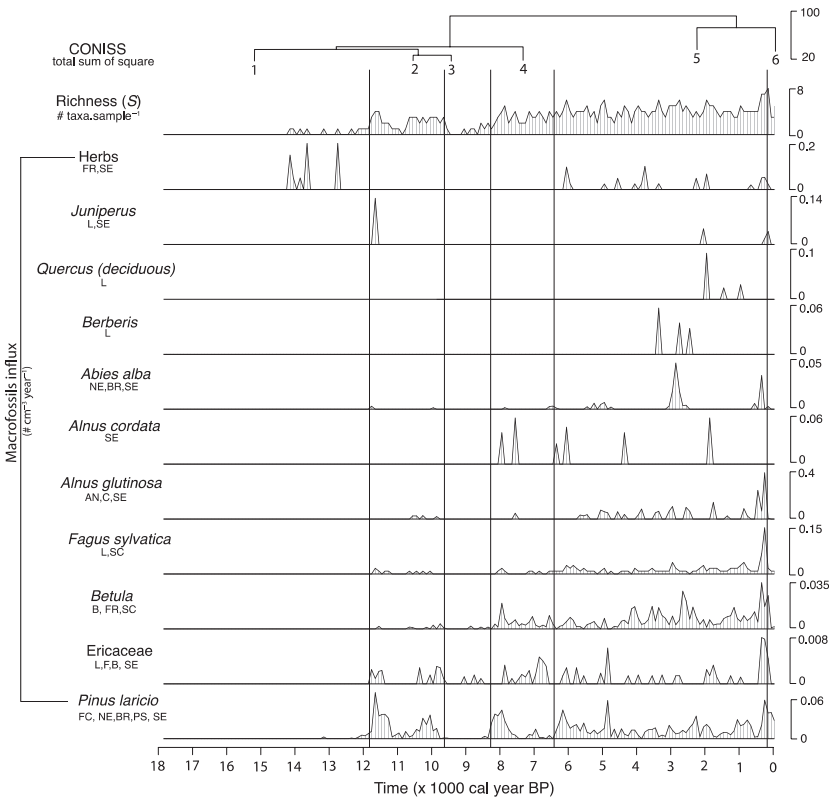

Fig. 3. Diagrams of macrofossil richness (fragments sample^{-1}) and plant macrofossil accumulation rate (# fragments cm^{-2} year^{-1}) records at Lac de Creno. Vertical lines indicate the five statistically significant zone boundaries in the richness record (CONISS cluster analysis). FC, female cone; NE, needle; BR, brachyblast, PS, pollen sac; B, bud; SE, seed; SC, bud scale; L, leaf; AN, anther; C, cone; F, flower; FR, fruit. All macrofossil accumulation rate records were smoothed with a 100-year moving average.

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local presence of low-population densities prior to their rapid population expansion, as also noted in other pollen and macrofossil records (Lang 1994).

The occurrence of *P. laricio*, Ericaceae, *Fagus* and *Betula* macrofossils throughout this period confirms the long-term persistence of those species near the lake. The discontinuous presence of *Abies* macrofossils, and its changes in pollen percentage (Fig. 4), may indicate short-term population expansions of white fir, even if a rare local presence of this species throughout the last 6000 years with a lack of macrofossil records is not excluded. The first occurrences of other tree taxa, appeared at ~8000 cal. years BP (*Alnus glutinosa*, *Alnus cordata*) and ~6000 cal. years BP (deciduous *Quercus*); and shrubs taxa (*Berberis* sp.) around 4000 cal. years BP, indicated the relatively late population expansions of these species in the lower montane belt (Fig. 3). These taxa display sporadic records, except for *Alnus glutinosa*, which could indicate a rare presence of these taxa possibly explained by the transition zone between the montane and supra-Mediterranean belts, corresponding to the limit of their distributions. From ~6000 cal. years BP onwards, herbs macrofossils reoccurred in the record. The macrofossil accumulation rates of several taxa increased abruptly at the top of the sequence possibly due to an artefact in the age-depth model (Fig. 1c).

The richness record (*S*; Fig. 3) was divided into six statistically significant zones. Richness was null from 18 000 to 14 100 cal. years BP and low from 14 100 to 11 900 cal. years BP (zone 1; mean $S = 0.2$), then increased rapidly beginning in 11 900 cal. years BP (zone 2, 11 900 to 9700 cal. years BP; $1 \leq S \leq 4$; mean $S = 2.3$). From 9700 to 8300 cal. years BP (zone 3), richness decreased (mean $S = 0.7$) due to the absence of most taxa except for Ericaceae. In zones 4 and 5 (8300–6400 and 6400–150 cal. years BP, respectively), richness increased (mean *S* of 3.1 and 4.2, respectively), followed by a decrease in *S* ($S = 3$) during the past 200 years (zone 6).

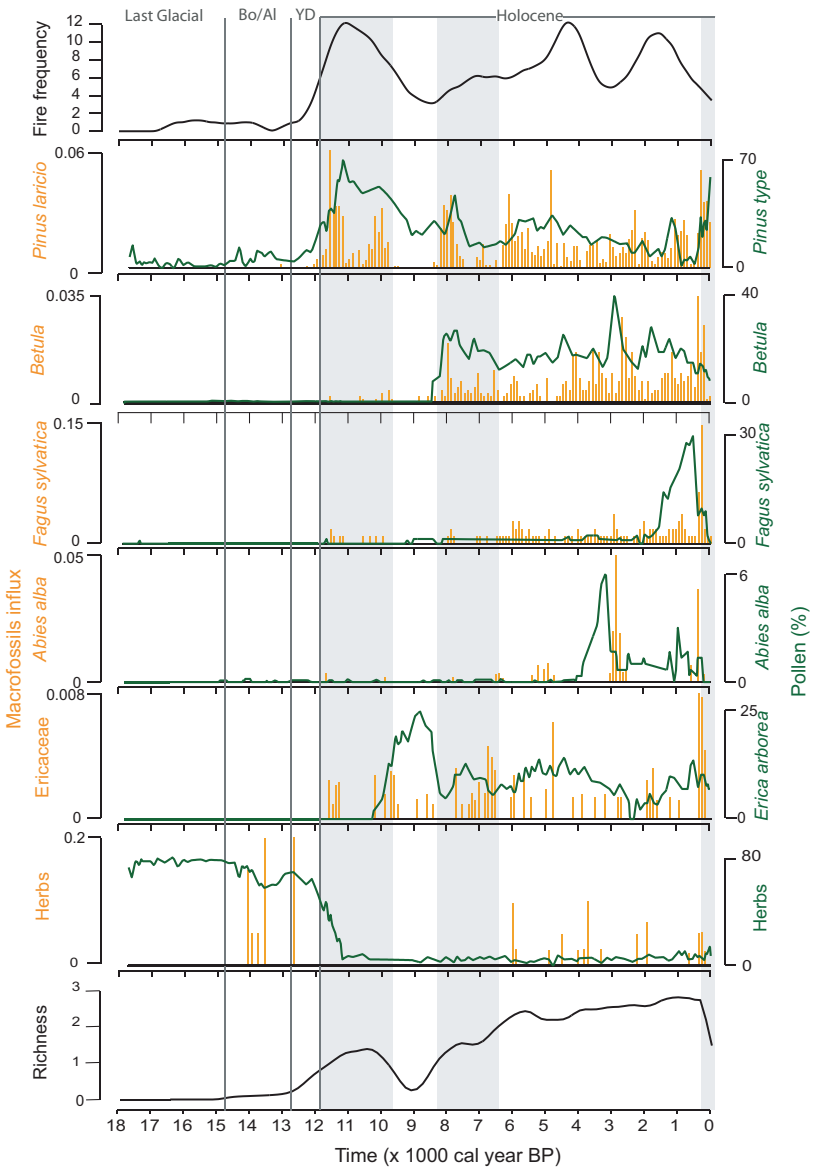

Fig. 4. Comparison between long-term local fire and vegetation dynamics (selected taxa only) at Lac de Creno. From top to bottom: fire frequency (fire kyear^{-1}); macrofossils accumulation rate (# fragments cm^{-2} year^{-1}) (orange histograms); pollen abundance (%) (green lines), digitalised from Reille *et al.* (1997, 1999); and macrofossil taxa richness (number of taxa sample^{-1}). Vertical grey and white zones: statistically significant zones, as in Fig. 3. Vertical grey lines: main biozones with ages from the Greenland NGRIP stable oxygen isotope record (Rasmussen *et al.* 2006): Last Glacial (18 000–14 700 cal. years BP), Bølling/Allerød (Bo/Al, 14 700–12 700 cal. years BP), Younger Dryas (YD, 12 700–11 700 cal. years BP), and Holocene (11 700 cal. years BP to present).

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LINKS BETWEEN FIRE AND VEGETATION DYNAMICS AT THE LOCAL SCALE

Two different patterns of population dynamics in response to local fire frequency were observed in the macrofossils analysis. First, a number of macrofossil taxa were present throughout the Holocene, and their abundances varied independently from changes in the fire regime (Figs 2 and 3). Specifically, *P. laricio, Betula*, *Fagus* and Ericaceae appeared to be resistant to fires for FRIs ranging between 30 and 750 years. Similarly, the isolated occurrence of other taxa (*A. glutinosa, A. cordata, Berberis, Quercus, Juniperus* and herbs) showed no visual relationship with changes in fire frequency. In contrast, the abundance of *Abies* macrofossils peaked distinctly at ~3000 and ~500 cal. years BP, when FRIs were long (approximately ~200 years; Figs 2 and 3), suggesting that low fire frequency was more favourable to maintain *Abies* populations.

The PCAs were used to highlight the relationships among macrofossil taxa (Fig. 5) and visually assess differences in the historical behaviour of woody taxa populations. In both PCAs, the taxon with the highest loading on axis 1 ($\lambda = 0.65$) was *P. laricio,* whereas axis 2 ($\lambda = 0.15$) was associated primarily with *Abies* and *Betula.* Other taxa associated with the PCA axis 1 were *Juniperus*, *Quercus and* Ericaceae*,* while taxa with relatively small loadings on the axis 2 included *Berberis, A. glutinosa and Fagus.* The variables describing changes in the fire regime (FRI and $CHAR_{background}$, respectively) did not show distinct relationships with either of the first two PCA axes, suggesting that the changes in vegetation as reflected by macrofossils assemblages were independent of the local changes in fire regime (i.e. FRI and burned area reflecting by $CHAR_{background}$).

RICHNESS AND TURNOVER

Macrofossil richness (Fig. 6b) was lowest from 18 000 to 14 700 cal. years BP, when herbs dominated the landscape (Figs 3 and 4), and slightly higher (mean $S = 0.2$) from 14 700 to 11 700 cal. years BP and from 9500 to 8500 cal. years BP (zone 3), when woody taxa occurred (Figs 3 and 4). Richness rapidly increased ca. 11 500 cal. years BP during the Younger Dryas-Holocene transition (mean $S = 2.3$, zone 2) and remained stable until 150 cal. years BP (zone 5, mean $S = 4.1$, Fig. 6a). Turnover (beta diversity) ranged over the entire record from 0.0 to 3.0 SD (mean: 1.1 SD; Fig. 6c) and showed high intersample variability. The smoothed record indicates that turnover was higher at 12 500 cal. years BP (~1.5 SD) than during the Holocene (< 1 SD). A slight increase in compositional turnover was found in zone 3 (9700 to 8300 cal. years BP; ~2 SD) where the total abundance of macrofossils and the number of taxa were low. Turnover gradually decreased until ~200 cal. years BP, suggesting greater stability in community composition over the last 7500 years.

Both richness and turnover changed when fire frequency changed (Fig. 6d), that is, at the lateglacial – Holocene transition and at approximately 9500–8500 cal. years BP (zone 3). In contrast, the macrofossil assemblages showed lower temporal variability in richness and turnover during the past ~6000 years. The low variability of macrofossil richness shows assemblages composed by the same number of woody taxa since 6000 cal. years BP, and the low turnover suggests that the macrofossil assemblages had similar composition, in spite of large changes in the fire regime (Fig. 6 c). This is consistent with the PCA result, which showed an absence of relationship between macrofossils assemblage and fire regime for the whole Holocene (Fig. 5).

Discussion

Since the establishment of Corsican pine woodlands around Lac de Creno, fire has been a permanent component of this Mediterranean ecosystem. The following discussion analyses, the historical establishment of these woodlands and the vegetation dynamics and plant diversity in relation to the long-term fire-regime, climatic changes and land-use changes. In addition, we determined the historical range in fire frequency to develop guidelines for the conservation of Corsican pine woodlands.

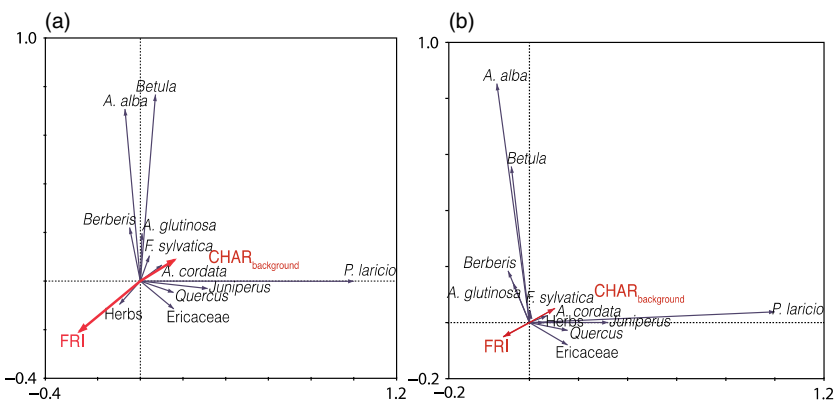

Fig. 5. Taxa plots of the principal component analysis (PCA) on the macrofossils data with environmental variables, FRI and $CHAR_{background}$, added passively (thick red arrows). (a) PCA for the entire record from 13 200 to 500 cal. years BP. (b) PCA for only the Holocene period, excluding the samples from zone 3 (9500–8000 cal. years BP) and the last 500 years. Samples younger than 500 cal. years BP were excluded from all of the PCAs due to potential bias from high sediment-accumulation rates in that section of the core.

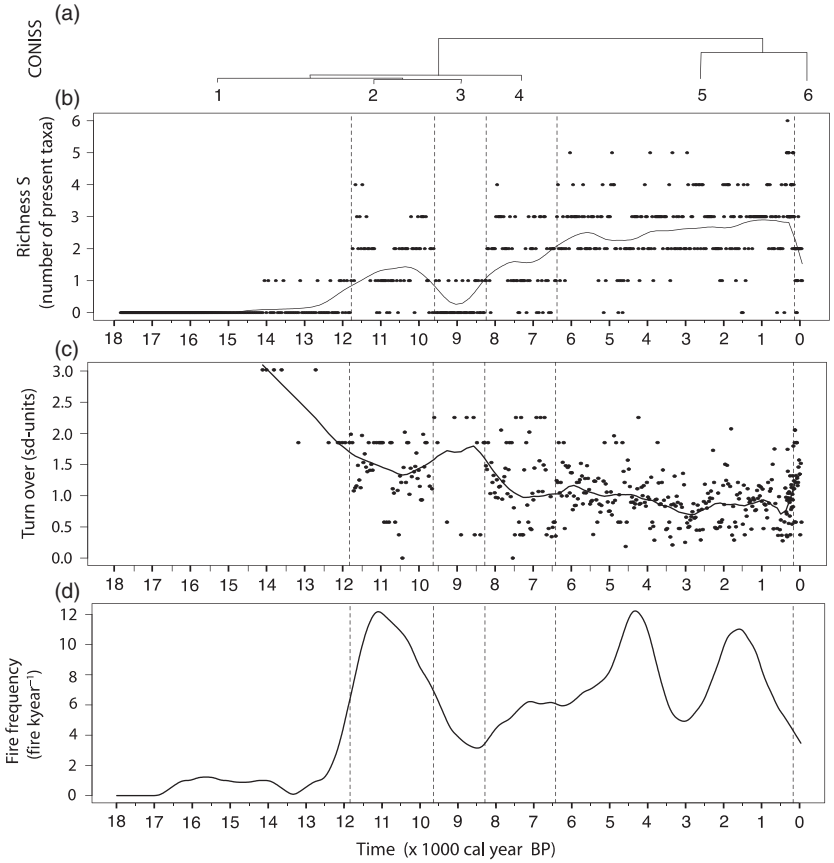

Fig. 6. Macrofossils taxa richness–fire frequency relationships. (a) Dendrogram of the CONISS cluster analysis (see Fig. 3), (b) Macrofossils taxa richness (taxa number sample^{-1}), (c) compositional turnover of macrofossils assemblages (β-diversity, in standard deviation (SD) units), (d) fire frequency (fires kyear^{-1}). Vertical dashed lines: statistically significant zone boundaries (see Fig. 3). The main trends of (b), (c), and (d) are highlighted with a smoothing spline (1000-year smoothing window).

ESTABLISHMENT OF *PINUS NIGRA LARICIO*-DOMINATED WOODLANDS

The question on the naturalness status of *Pinus* species in the Mediterranean basin is commonly debated. For instance, in the Iberian Peninsula, *Pinus sylvestris* and *Pinus nigra* are recorded since the last glacial maximum in the North and in the South (Carrión & Van Geel 1999; Múgica *et al.* 2001; Figueiral & Carcaillet 2005; Rubiales, Garcìa-Amorena & lvarez, S.G. & Manzaneque, F.G. 2008; López-Merino *et al.* 2012), whereas their presence was recorded only since the last 7000 years in the central part of the Peninsula (Rubiales *et al.* 2007). They disappeared in the central and in the southern part of Iberian Peninsula likely because of human activities (Carrión *et al.* 2003; Figueiral & Carcaillet 2005; Rubiales, Garcìa-Amorena & lvarez, S.G. & Manzaneque, F.G. 2008). Consequently, the interpretations of paleodata are not consensual on site-specific causes leading to population expansions or decreases for these species.

Today, *P. laricio* is an endemic subspecies in Corsica that covers ~16 000 ha of pure forest (Barbet-Massin & Jiguet 2011). Based on the pollen record, Reille *et al.* (1997) hypothesised that pre-historic peoples introduced *P. laricio* during the early Holocene. They thus concluded that this subspecies was not native on the island but also acknowledged 'that only an earlier occurrence of macrofossils could cast doubt upon the palynological evidence' (Reille *et al.* 1997), which suggested that *P. laricio* appeared in Corsica at about 11 500 cal. years BP. In fact, the low frequencies of *Pinus* pollen during the last glacial and the lateglacial were interpreted by Reille *et al.* (1997) as being indicative of an extra-regional pollen source rather than of the presence of a few island-like stands or a low-density population of *P. laricio* on Corsica. With the exception of the present study, there are no other palaeoecological records based on macrofossils that could cast doubt on this interpretation.

Although their interpretation requires caution, plant macrofossils can be extremely informative in the reconstruction of local vegetation histories (Birks & Birks 2000). As explained in the Material and methods section, the biases of macrofossil records due to transport and preservation of macrofossils suggest that the absence of a taxon in a macrofossil assemblage cannot be used as evidence for the absence of that species at a site. Thus, the absence of woody macrofossils prior to 13 200 cal. years BP at Lac de Creno, which is consistent with the high abundance of herb pollen (Fig. 4) and the low content of organic matter, suggests that either the treeline was located at a lower elevation or that woody species were scattered within an open grass-dominated vegetation prior to the onset of the Holocene. In spite of these potential biases, our results clearly show that *P. laricio* was present on the island at least three millennia earlier than suggested by Reille *et al.* (1997) because the first *Pinus* needles were recorded at 13 200 cal. years BP. However, as *Pinus* pollen abundances (Fig. 4) remained relatively low (~10%) at that time, it is likely that populations of pines, including *P. laricio,* were already present before 13 200 cal. years BP but sparsely distributed on the island.

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Interestingly, *Betula* macrofossils and pollen were not abundant during the lateglacial, even though *Betula* fruits and catkin scales are released in large quantities and easily transported over long distances (Freund, Birks & Birks 2001). In the Alps, *Betula* generally dominates macrofossil and pollen assemblages during the Bølling (Tinner *et al.* 2005; Hofstetter *et al.* 2006; Genries *et al.* 2009). The absence of *Betula* macrofossils and pollen, since the onset of the lateglacial to the end of the Younger Dryas, suggests an unfavourable environment at Lac de Creno for birches. These species requiring lower levels of moisture (e.g. *Betula*, *P. Laricio*) present low abundance of pollen and macroremains since the lateglacial to the onset of the Holocene, whereas species requiring higher levels of moisture (e.g. *Abies alba*, *Fagus sylvatica*, *Alnus cordata*, and *A. glutinosa*) appear later in the record.

Despite the lack of synchrony between changes in macrofossils-inferred vegetation and changes in fire regime over the last 13 200 years (Fig. 5), the timing of the increase in *Pinus* macrofossil and pollen abundance coincides with the widespread colder Younger Dryas climate episode (~12 750–11 750 cal. years BP) (Alley *et al.* 1993; Rasmussen *et al.* 2006) that is observed in several southern European records (Pèrez-Obiol & Julià 1994; Cacho *et al.* 2001; Cacho, Grimalt & Canals 2002). This climatic episode corresponds to a treeline shift in the European Alps (Vescovi *et al.* 2007) and drier climate conditions in the west Mediterranean basin (Guiter *et al.* 2005; Finsinger *et al.* 2008). *P. laricio* macrofossils and *Pinus* pollen both increased during the onset of the Holocene, indicating a rapid expansion of woodlands near the study site and an upward shift in the treeline to elevations >1300 m that likely occurred in response to the rapid change to more humid and warm climate conditions.

The largest compositional turnover (β diversity) occurred between 13 200 and 11 500 cal. years BP when *P. laricio*-dominated woodlands became established at Lac de Creno, suggesting that transformations in the local woody composition were of major importance at that time. Nevertheless, macrofossil richness gradually increased throughout the Holocene with the subsequent expansions of *Fagus*, *Alnus*, Ericaceae, *Abies*, *Quercus* and *Betula*. As suggested by the turnover estimates (SD$\ll$ 4; Fig. 6b), the vegetation as recorded by macrofossils did not experience a complete turnover in composition (Hill & Gauch 1980). In contrast, our results suggest the co-occurrence of mixed woodlands of evergreen needleleaf trees and deciduous broadleaf trees and shrubs during most of the past 11 500 years. It would be tempting to investigate whether similar patterns emerge also with pollen records, which are richer in taxa and are less biased by preservation than plant macrofossils (Blarquez, Finsinger & Carcaillet 2013).

DEVELOPMENT OF MIXED WOODLANDS IN RELATION TO FIRE REGIME

Long mean fire-return intervals (mFRI: >1000 year fire^{-1}) between 18 000 and 11 900 cal. years BP were likely a result of a fuel-limited community dominated by herbs (Fig. 4) compared with the onset of the Holocene, when the establishment of an ecosystem in which woody biomass and fire covaried and interacted. The steppe–tundra ecosystem characterized by *Artemisia* (Reille *et al.* 1997) was characterised by long FRIs, which were most likely connected to cold and dry climatic conditions along the northern border of the Mediterranean basin that did not favour biomass productivity (Peyron *et al.* 1998). With the establishment of woody vegetation at approximately 11 900 cal. years BP, the fire regime at Lac de Creno markedly changed (mFRI = 140 year fire^{-1}), suggesting that the establishment of vegetation was concomitant with the higher fire frequency. It is likely that fuel availability and plant cover were important drivers leading to more frequent fires at the onset of the Holocene rather than the direct effects of climate change (Pausas & Keeley 2009).

Similarly, the longer mean fire-return intervals (mFRI = 260 year fire^{-1}) between 9700 and 8200 cal. BP were possibly connected to lower fuel availability because the vegetation near the site was dominated by Ericaceae scrublands as shown by both the macrofossil and pollen records (Fig. 4). This period coincides with a period of drier climate conditions on the central Italian coast (Magny *et al.* 2007; Finsinger *et al.* 2010) and in the southern Iberian Peninsula (Carrión *et al.* 2010). We could suppose that the effects of climate on fire are complex and were modulated by fuel abundance (Pausas 2004). A sustained drier climate would first favour fires and then would finally result in less woody species due to more vegetation mortality and less primary productivity, conducing to a decrease in local fire frequency.

For the period after 6000 cal. years BP, climatic reconstructions from the western Mediterranean basin indicate contradictory patterns. Whereas in the south of the Iberian Peninsula climate conditions became wetter (Reed, Stevenson & Juggins 2001), at Lago dell'Accesa, Central Italy, climate changed to drier and warmer conditions (Colombaroli, Marchetto & Tinner 2007; Finsinger *et al.* 2010). However, a synthesis of climatic conditions of western Mediterranean basin sites (Magny, Miramont & Sivan 2002) highlights a change towards drier conditions around 6000 cal. years BP, before shifting again towards more humid conditions at ~4500 cal. years BP. Although climate reconstructions are not available for Corsica, we assume that the broad Northern Mediterranean border land climate trends depicted by Magny, Combourieu Nebout & Beaulieu, J.d., Bout-Roumazeilles, V., Colombaroli, D., Desprat, S., Francke, A., Joannin, S., Peyron, O. & Revel, M. (2013), which confirm the trends recorded in Lago dell'Accesa located 1° further north than Corsica (Colombaroli, Marchetto & Tinner 2007; Finsinger *et al.* 2010), are the most relevant for a comparison with vegetation dynamics at Lac de Creno for the last 6000 years.

This period was marked by two increases in fire frequency at Lac de Creno, centred on 4300 cal. years BP (12.3 fires kyear^{-1}) and 1500 cal. years BP (11.0 fires kyear^{-1}, Fig. 4). *Fagus sylvatica* is known as a fire resilient species at the opposite of *Abies alba*, which is a fire-intolerant species (Tinner *et al.* 1999; Colombaroli, Marchetto & Tinner 2007). It is therefore not surprising to observe the persistence of

Betula over the Holocene, and the expansion of *Abies alba* populations when fire-return intervals became longer (Fig. 4). The late expansion of *Abies alba* and deciduous *Quercus* at Lac de Creno is consistent with records from Lago di Origlio (Southern Switzerland; Tinner *et al.* 1999) and Lago di Annone (Northern Italy; Wick & Môhl 2006) where they expanded with the onset of colder or moister climate conditions.

In spite of these changes in fire frequency, local woodland composition remained largely unchanged and macrofossils-inferred vegetation is not related to fire regime (Fig. 5). Whereas *Pinus* pollen frequencies decreased between 6000 and 500 cal. years BP possibly due to a regional decline of this taxon, *P. laricio* macrofossils abundances remained stable indicating that a population was maintained around the lake throughout the last 6000 years (Fig. 4). This suggests that the fuel availability was sufficiently high to maintain this fire frequency and that temperature and moisture varied sufficiently to alter the fire frequency without exceeding the tolerance limits of Corsican pine.

Alternatively, agricultural land use (e.g. forest clearance for seasonal grazing by domestic herbivores) would have altered the fire regime during the period from the Neolithic (4300 cal. years BP) to the Middle Ages (1500 cal. years BP). However, there is no pollen evidence to support the influence of human activities on vegetation around Lac de Creno until the Middle Ages (*ca.* 1500–500 cal. years BP), when the percentage of non-arboreal pollen slightly increased (Reille *et al.* 1999). Furthermore, the archaeological record from Corsica shows only a few seasonal late Neolithic settlements in inland areas around 900 m in altitude (Tozzi & Weiss 2001), while most of the permanent pre-historic settlements remained near the coast (Vigne 1995). In Corsica, social activities and human settlements remained centred on the coastal areas until the Middle Ages, when Barbarian and Saracen invasions changed land occupation and uses in favour of inner villages and widespread pasturing of livestock in the mountains (Neboit 1981). Consequently, during most of the Holocene, vegetation dynamics and composition in the Corsican montane belt likely interacted with climate changes and natural disturbances (including fire) rather than with land use.

RANGE OF FIRE-RETURN INTERVALS AND FOREST MANAGEMENT

Pine woodlands in the Mediterranean basin are considered to be fire-sensitive, particularly to crown fires (Pausas *et al.* 2009). In keeping with this, some studies (Barbet-Massin & Jiguet 2011; Pimont, Prodon & Rigolot 2011) suggest that *P. laricio* populations are decreasing due to natural disturbance as wildfires or human-induced fire and logging. In addition, climate change might further threaten this taxon, either directly, through a shift in suitable climatic conditions upwards in elevation, or indirectly, by increasing the frequency or intensity of wildfires. The resilience threshold of *P. laricio*-dominated forests to fires and logging is poorly constrained (Barbet-Massin & Jiguet 2011). This ecosystem would be sensitive to high-severity fires because of their lack of seed production before they attain 15–20 years after fire regeneration and the absence of cone serotiny preventing the aerial seed-bank that would release their seeds after fires (Pimont, Prodon & Rigolot 2011). However, other studies show that *P. nigra* populations can support low-intensity surface fires with small burned areas (Tapias *et al.* 2001; Christopoulou *et al.* 2013). Today, there are no accounts of fire history in ecosystems dominated by *P. laricio*; this study provides thus the first quantitative reconstruction of the long-term fire-vegetation history on such an ecosystem.

During the last 250 years, and especially since 1970s, fires were actively suppressed at Lac de Creno, as well as in all *P. laricio* forests. Historically, forestry was dedicated to *P. laricio* timber exploited notably for boat construction during the 18th and 19th centuries, with livestock grazing in the understorey (Riffard 2006; Barbet-Massin & Jiguet 2011), including at Lac de Creno, where cattle and pigs are abundant. This type of forest management generally contributed to the development of a low-diversity understorey in the *P. laricio*-dominated forests. The dominance of *P. laricio* macrofossils and the decrease in taxa richness at Lac de Creno since *ca.* AD 1800 (Appendix S2 in Supporting Information) most likely mirrors the changes in land use, that is, the Corsican pine exploitation and pastoralism (understorey practically completely browsed at present). While currently the canopy at Lac de Creno is virtually monospecific with a low-density understorey of Ericaceae, elsewhere in the lower montane belt (~1300 m), the forests are characterised by higher tree richness. At these elevations, in the absence of grazing and fire (Brown 1960), these forests could be dominated by shade-tolerant trees (*Abies* and *Fagus*). At present, this site is composed of young shallow soils on bedrock, which do not facilitate the establishment of *Abies*. In the past, the combination of drought stress, which was certainly more pronounced during the early Holocene (Colombaroli, Marchetto & Tinner 2007; Finsinger *et al.* 2010) and long periods of high fire frequency, might have prevented the local establishment of *Abies alba*, which is more moisture demanding than *P. laricio*. The rare local occurrence of *Abies* macrofossils during periods with long FRI is consistent with its known sensitivity to both small frequent and large infrequent fires (Henne *et al.* 2012; Tinner *et al.* 2013).

The vegetation around Lac de Creno was a *P. laricio*-dominated woodland, which was characterised by an admixture of shade-tolerant species and the occurrence of local fire episodes for most of the Holocene. It is possible that this ecosystem has also tolerated grazing by large herbivores (i.e. pigs, cattle and cows) during past centuries, as it is observed at present. Although pine-dominated woodlands are often considered to be the result of secondary succession following past anthropogenic activities, long-term ecological records from Mexico show that burning in combination with the occurrence of seasonal drought can maintain such ecosystems for millennia (Willis & Bhagwat 2010). Therefore, the *P. laricio*-dominated forest and their association with fire represent a natural legacy and should be managed accordingly. However, the spatial distribution of past vegetation reconstructed is

unknown, that is, the structure and the density of taxa recorded. Nevertheless, the macrofossil and charcoal records pinpoint the mixed composition of vegetation and their relation to fire frequency. The structure and the distribution of vegetation are almost as important as the composition for management policy, and further studies on past vegetation distributions are needed (e.g. spatial models of vegetation distribution).

The Holocene FRIs at Lac de Creno (30–490 year) are consistent with recent observations in Greek black pine forests (Christopoulou *et al.* 2013), but show a much wider range of variability than the modern-simulated FRI (~70 ± 30 years) in Corsica (Mouillot, Rambal & Joffre 2002). Therefore, the modern FRI does not appear to exceed the long-term range of variability remaining within the historical range of variability as observed the past 11 500 years (30 < FRI< 490; Fig. 2). We expected a distinct change in the fire regime during the late Middle Ages, as a result of forest grazing by livestock (Neboit 1981; Rius, Vannière & Galop 2009). Although a potential bias on the kinetic of this change is not excluded within the last 500 years due to the modelled age-depth relation, we conclude that modern human activity has not altered the fire regime outside of its historical range at this site.

The persistence of *P. laricio*-dominated woodlands with FRIs as short as 30 years through the Holocene could be explained by the occurrence of low-intensity fires or small burned areas that did not affect mature trees, which are more resistant to burning (Pimont, Prodon & Rigolot 2011). Similar small and frequent fires have been observed in some ecosystems in the Mediterranean basin (Fulé *et al.* 2008; Christopoulou *et al.* 2013). In Corsica, for the maritime pine woodlands (*Pinus pinaster*), simulated fire-return intervals under current climate conditions are estimated at ~70 ± 30 years (Mouillot, Rambal & Joffre 2002). Historical fire regimes (mostly human-induced) in lower-elevation *Quercus ilex* and *P. pinaster* forests are characterised by frequent fires with small burned areas, *that is,* 2–12% of surveyed areas (Mouillot *et al.* 2003). This type of fire pattern is assumed to exist in fragmented landscapes resulting from land-use intensification and forest clearance during historical times (Henne *et al.* 2012).

These low-severity fires contrast with modern fire regimes in the Mediterranean basin. Indeed, wildfires are becoming increasingly characterised by larger burned areas and higher intensity burns, likely due to higher biomass availability in more connected landscapes as a result of the land abandonment (Pausas & Fernández-Muñoz 2011). As it is generally the case for ecosystems in the Mediterranean biome (Keeley *et al.* 2011a), fires appear to be an integral component of the Corsican pine ecosystem.

Conclusion

We recorded an 18 000 year-long vegetation and fire history in the montane belt of Corsica, characterised by extensive woodlands dominated by the endemic *Pinus laricio*. Although the native status of *P. laricio* is debated, our findings clearly show that this subspecies was present on the island since 13 200 year, at least, during a time when humans had not yet occupied Corsica. Moreover, *P. laricio*-dominated woodlands have locally persisted at the site since at least 11 900 cal. years BP and species richness has gradually raised due to a progressive increase in the abundance of moisture-requiring deciduous broadleaved taxa, in consistence with the climatic change at the Younger Dryas–Holocene transition. Because of the site location on a remote mountain in the inland areas of Corsica, human activity most likely did not influence vegetation dynamics and rates of biomass burning until the late Middle Ages. Instead, climate variability probably controlled fire frequency directly by favourable seasons of fire ignition and indirectly by influencing fuel availability through biomass growth. During the driest climate conditions (e.g. before 11 700 cal. years BP and between 9400 and 8000 cal. years BP), local woody biomass was markedly reduced and FRI was significantly longer compared with most of the Holocene.

We may speculate that during the Holocene, and particularly the last 6000 years, frequent low-severity fires with small burned areas, most likely played an important ecological function in preventing the expansion of more fire-sensitive trees for millennia (e.g. *Abies alba*), thereby maintaining the *Pinus laricio*-dominated woodlands. The modern remnants of these woodlands therefore represent an important natural legacy and should be managed accordingly. Although recent studies suggest that Corsican black pine forests are threatened by logging and increased fire risk, our long-term reconstruction of fire frequency suggests that these woodlands can persist with FRI ranging between 30 and 490 years. Conservation practises should be aimed at preserving the historical variability of fire disturbance to maintain the ecological functions and services of these forests.

Acknowledgements

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References

Abràmoff, M.D., Magalhães, P.J. & Ram, S.J. (2004) Image processing with ImageJ. *Biophotonics International*, **11**, 36–42.

Alley, R.B., Meese, D., Shuman, C., Gow, A., Taylor, K., Grootes, P., White, J., Ram, M., Waddington, E. & Mayewski, P. (1993) Abrupt increase in Greenland snow accumulation at the end of the Younger Dryas event. *Nature*, **362**, 527–527.

Ammann, B., Birks, H.J.B., Brooks, S.J., Eicher, U., von Grafenstein, U., Hofmann, W., Lemdahl, G., Schwander, J., Tobolski, K. & Wick, L. (2000) Quantification of biotic responses to rapid climatic changes around the Younger Dryas – a synthesis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **159**, 313–347.

Barbet-Massin, M. & Jiguet, F. (2011) Back from a predicted climatic extinction of an Island endemic: a future for the Corsican Nuthatch. *PLoS ONE*, **6**, e18228.

Bennett, K.D. (1996) Determination of the number of zones in a biostratigraphical sequence. *New Phytologist*, **132**, 155–170.

Birks, H.J.B. (2007) Estimating the amount of compositional change in late-Quaternary pollen-stratigraphical data. *Vegetation History and Archaeobotany*, **16**, 197–202.

Birks, H.H. & Birks, H. (2000) Future uses of pollen analysis must include plant macrofossils. *Journal of Biogeography*, **27**, 31–35.

Blarquez, O., Finsinger, W. & Carcaillet, C. (2013) Assessing paleo-biodi versity using low proxy influx. *PLoS ONE*, **8**, e65852.

Blarquez, O., Carcaillet, C., Elzein, T.M. & Roiron, P. (2012) Needle accumulation rate model-based reconstruction of palaeo-tree biomass in the western subalpine Alps. *The Holocene*, **22**, 579–587.

Brown, J. (1960) The Corsican Pine in its native land. Part I. *Empire Forestry Journal*, **39**, 294–318.

Cacho, I., Grimalt, J. & Canals, M. (2002) Response of the Western Mediterranean Sea to rapid climatic variability during the last 50,000 years: a molecular biomarker approach. *Journal of Marine Systems*, **33**, 253–272.

Cacho, I., Grimalt, J.O., Canals, M., Sbaffi, L., Shackleton, N.J., Schönfeld, J. & Zahn, R. (2001) Variability of the western Mediterranean Sea surface temperature during the last 25,000 years and its connection with the Northern Hemisphere climatic changes. *Paleoceanography*, **16**, 40–52.

Capitanio, R. & Carcaillet, C. (2008) Post-fire Mediterranean vegetation dynamics and diversity: a discussion of succession models. *Forest Ecology and Management*, **255**, 431–439.

Cappers, R.T.J., Bekker, R.M. & Jans, J.E.A. (2006) *Digitale Zadenatlas van Nederland*. Digital Seed Atlas of the Netherlands (Groningen Archaeological Studies 4). 502 pp.

Carcaillet, C., Bouvier, M., Fréchette, B., Larouche, A.C. & Richard, P.J. (2001) Comparison of pollen-slide and sieving methods in lacustrine charcoal analyses for local and regional fire history. *The Holocene*, **11**, 467–476.

Carcaillet, C., Perroux, A.-S., Genries, A. & Perrette, Y. (2007) Sedimentary charcoal pattern in a karstic underground lake, Vercors massif, French Alps: implications for palaeo-fire history. *The Holocene*, **17**, 845–850.

Carcaillet, C., Ali, A.A., Blarquez, O., Genries, A., Mourier, B. & Bremond, L. (2009) Spatial variability of fire history in subalpine forests: from natural to cultural regimes. *Ecoscience*, **16**, 1–12.

Carrión, J.S. & Van Geel, B. (1999) Fine-resolution Upper Weichselian and Holocene palynological record from Navarrès (Valencia, Spain) and a discussion about factors of Mediterranean forest succession. *Review of Palaeobotany and Palynology*, **106**, 209–236.

Carrión, J.S., Sánchez-Gómez, P., Mota, J.F., Yll, R. & Chaín, C. (2003) Holocene vegetation dynamics, fire and grazing in the Sierra de Gádor, southern Spain. *The Holocene*, **13**, 839–849.

Carrión, J.S., Fernández, S., González-Sampériz, P., Gil-Romera, G., Badal, E., Carrión-Marco, Y., López-Merino, L., López-Sáez, J.A., Fierro, E. & Burjachs, F. (2010) Expected trends and surprises in the Lateglacial and Holocene vegetation history of the Iberian Peninsula and Balearic Islands. *Review of Palaeobotany and Palynology*, **162**, 458–475.

Cary, G.J., Keane, R.E., Gardner, R.H., Lavorel, S., Flannigan, M.D., Davies, I.D., Li, C., Lenihan, J.M., Rupp, T.S. & Mouillot, F. (2006) Comparison of the sensitivity of landscape-fire-succession models to variation in terrain, fuel pattern, climate and weather. *Landscape Ecology*, **21**, 121–137.

Chauchard, S., Guibal, F. & Carcaillet, C. (2013) Land-use legacies: multi-centuries years-old management control of between-stands variability at the landscape scale in Mediterranean mountain forests, France. *Journal of Forest Science*, **59**, 1–7.

Christopoulou, A., Fulé, P.Z., Andriopoulos, P., Sarris, D. & Arianoutsou, M. (2013) Dendrochronology-based fire history of *Pinus nigra* forests in Mount Taygetos, Southern Greece. *Forest Ecology and Management*, **293**, 132–139.

Clark, J.S., Lynch, J., Stocks, B.J. & Goldammer, J.G. (1998) Relationships between charcoal particles in air and sediments in west-central Siberia. *The Holocene*, **8**, 19–29.

Colombaroli, D., Marchetto, A. & Tinner, W. (2007) Long term interactions between Mediterranean climate, vegetation and fire regime at Lago di Massaciuccoli (Tuscany, Italy). *Journal of Ecology*, **95**, 755–770.

Daniau, A.L., Bartlein, P.J., Harrison, S.P., Prentice, I.C., Brewer, S., Friedlingstein, P. *et al.* (2012) Predictability of biomass burning in response to climate changes. *Global Biogeochemical Cycles*, **26**, GB4007.

Debussche, M., Lepart, J. & Dervieux, A. (1999) Mediterranean landscape changes: evidence from old postcards. *Global Ecology and Biogeography*, **8**, 3–15.

Dury, M., Hambuckers, A., Warnant, P., Henrot, A., Favre, E., Ouberdous, M. & François, L. (2011) Responses of European forest ecosystems to 21st century climate: assessing changes in interannual variability and fire intensity. *iForest: Biogeosciences and Forestry*, **4**, 82–99.

Figueiral, I. & Carcaillet, C. (2005) A review of Late Pleistocene and Holocene biogeography of highland Mediterranean pines (*Pinus* type *sylvestris*) in Portugal, based on wood charcoal. *Quaternary Science Reviews*, **24**, 2466–2476.

Finsinger, W., Belis, C., Blockley, S.P., Eicher, U., Leuenberger, M., Lotter, A.F. & Ammann, B. (2008) Temporal patterns in lacustrine stable isotopes as evidence for climate change during the late glacial in the Southern European Alps. *Journal of Paleolimnology*, **40**, 885–895.

Finsinger, W., Colombaroli, D., De Beaulieu, J.L., Valsecchi, V., Vannière, B., Vescovi, E., Chapron, E., Lotter, A.F., Magny, M. & Tinner, W. (2010) Early to mid-Holocene climate change at Lago dell'Accesa (central Italy): climate signal or anthropogenic bias? *Journal of Quaternary Science*, **25**, 1239–1247.

Fournier, T.P., Brossier, B., Gauthier, O. & Carcaillet, C. (2012) Post-fire dynamics and spatial heterogeneity of woody debris associated with *Pinus halepensis* in an oak-pine Mediterranean ecosystem. *Ecoscience*, **19**, 356–363.

Freund, H., Birks, H.H. & Birks, H.J.B. (2001) The identification of wingless Betula fruits in Weichselian sediments in the Gross Todtshorn borehole (Lower Saxony, Germany)-the occurrence of *Betula humilis* Schrank. *Vegetation History and Archaeobotany*, **10**, 107–115.

Fulé, P.Z., Ribas, M., Gutierrez, E., Vallejo, R. & Kaye, M.W. (2008) Forest structure and fire history in an old *Pinus nigra* forest, eastern Spain. *Forest Ecology and Management*, **255**, 1234–1242.

Gamisans, J., Badia, J.N. & Rafols, E.S. (2000) *La Végétation de la Corse*. Edisud, 391 pp.

Gamisans, J. & Jeanmonod, D. (1993) *Catalogue des Plantes Vasculaires de la Corse*. Complements au Prodrome de la flore corse, 258pp. Conservatoire et Jardin botaniques de la Ville de Geneve.

Genries, A., Muller, S.D., Mercier, L., Bircker, L. & Carcaillet, C. (2009) Fires control spatial variability of subalpine vegetation dynamics during the Holocene in the Maurienne valley (French Alps). *Ecoscience*, **16**, 13–22.

Giorgi, F. & Lionello, P. (2008) Climate change projections for the Mediterranean region. *Global and Planetary Change*, **63**, 90–104.

Gordon, A. & Birks, H. (1972) Numerical methods in Quaternary palaeoecology. I. Zonation of pollen diagrams. *New Phytologist*, 961–979.

Grimm, E. (1987) CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers & Geosciences*, **13**, 13–35.

Guiter, F., Andrieu-Ponel, V., Digerfeldt, G., Reille, M., de Beaulieu, J.L. & Ponel, P. (2005) Vegetation history and lake-level changes from the Younger Dryas to the present in Eastern Pyrenees (France): pollen, plant macrofossils and lithostratigraphy from Lake Racou (2000 m a.s.l.). *Vegetation History and Archaeobotany*, **14**, 99–118.

Heiri, O., Lotter, A.F. & Lemcke, G. (2001) Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of Paleolimnology*, **25**, 101–110.

Hély, C. & Alleaume, S. (2006) Fire regimes in dryland landscapes. Dryland ecohydrology, pp. 283–301. Springer.

Henne, P.D., Elkin, C., Colombaroli, D., Samartin, S., Bugmann, H., Heiri, O. & Tinner, W. (2012) Impacts of changing climate and land use on vegetation dynamics in a Mediterranean ecosystem: insights from paleoecology and dynamic modeling. *Landscape Ecology*, **28**, 819–833.

Higuera, P. (2008) MCAgeDepth 0.1: Probabilistic age-depth models for continuous sediment records. Montana State University. Available at: http://www. montana.edu/phiguera.

Higuera, P.E., Whitlock, C. & Gage, J.A. (2011) Linking tree-ring and sediment-charcoal records to reconstruct fire occurrence and area burned in subalpine forests of Yellowstone National Park, USA. *The Holocene*, **21**, 327–341.

Higuera, P.E., Peters, M.E., Brubaker, L.B. & Gavin, D.G. (2007) Understanding the origin and analysis of sediment-charcoal records with a simulation model. *Quaternary Science Reviews*, **26**, 1790–1809.

Higuera, P.E., Brubaker, L.B., Anderson, P.M., Hu, F.S. & Brown, T.A. (2009) Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. *Ecological Monographs*, **79**, 201–219.

Higuera, P.E., Gavin, D., Henne, P. & Kelly, R. (2010) Recent advances in the analysis and interpretation of sediment-charcoal records. *Open Ecology Journal*, **3**, 6–23.

Hill, M.O. & Gauch, H. (1980) Detrended correspondence analysis: an improved ordination technique. *Plant Ecology*, **42**, 47–58.

Hofstetter, S., Tinner, W., Valsecchi, V., Carraro, G. & Conedera, M. (2006) Lateglacial and Holocene vegetation history in the Insubrian Southern Alps, New indications from a small-scale site. *Vegetation History and Archaeobotany*, **15**, 87–98.

Jackson, S.T. & Booth, R.K. (2007) Plant macrofossil methods and studies | Validation of pollen studies. *Encyclopedia of Quaternary Science* (ed. A.E. Editor-in-Chief: Scott), pp. 2413–2422. Elsevier, Oxford.

Juggins, S. (2012) Rioja: analysis of Quaternary science data. R package version 0.8-5. Available at http://cran.r-project. org/package= rioja.

Keeley, J.E., Bond, W.J., Bradstock, R.A., Pausas, J.G. & Rundel, P.W. (2011a) Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, **16**, 406–411.

Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J. & Bradstock, R.A. (2011b) Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, **16**, 406–411.

Kelly, R.F., Higuera, P.E., Barrett, C.M. & Hu, F.S. (2011) A signal-to-noise index to quantify the potential for peak detection in sediment-charcoal records. *Quaternary Research*, **75**, 11–17.

Lang, G. (1994) *Quartäre Vegetationsgeschichte Europas: Methoden und Ergebnisse*. Spektrum Akademischer Verlag, Heidelberg.

Leys, B., Carcaillet, C., Dezileau, L., Ali, A.A. & Bradshaw, R.H. (2013) A comparison of charcoal measurements for reconstruction of Mediterranean paleofire frequency in the mountains of Corsica. *Quaternary Research*, **79**, 337–349.

López-Merino, L., Silva Sánchez, N., Kaal, J., López-Sáez, J.A. & Martínez Cortizas, A. (2012) Post-disturbance vegetation dynamics during the Late Pleistocene and the Holocene: an example from NW Iberia. *Global and Planetary Change*, **92**, 58–70.

Lotter, A.F., Heiri, O., Brooks, S., van Leeuwen, J.F.N., Eicher, U. & Ammann, B. (2012) Rapid summer temperature changes during Termination 1a: high-resolution multi-proxy climate reconstructions from Gerzensee (Switzerland). *Quaternary Science Reviews*, **36**, 103–113.

Lynch, J.A., Clark, J.S. & Stocks, B.J. (2004) Charcoal production, dispersal, and deposition from the Fort Providence experimental fire: interpreting fire regimes from charcoal records in boreal forests. *Canadian Journal of Forest Research*, **34**, 1642–1656.

Magny, M., Combourieu Nebout, N., Beaulieu, J.D., Bout-Roumazeilles, V., Colombaroli, D., Desprat, S., Francke, A., Joannin, S., Peyron, O. & Revel, M. (2013) North–south palaeohydrological contrasts in the central Mediterranean during the Holocene: tentative synthesis and working hypotheses. *Climate of the Past Discussions*, **9**, 1901–1967.

Magny, M., Miramont, C. & Sivan, O. (2002) Assessment of the impact of climate and anthropogenic factors on Holocene Mediterranean vegetation in Europe on the basis of palaeohydrological records. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **186**, 47–59.

Magny, M., De Beaulieu, J.L., Drescher-Schneider, R., Vannière, B., Walter-Simonnet, A.V., Miras, Y., Millet, L., Bossuet, G., Peyron, O. & Brugiapaglia, E. (2007) Holocene climate changes in the central Mediterranean as recorded by lake-level fluctuations at Lake Accesa (Tuscany, Italy). *Quaternary Science Reviews*, **26**, 1736–1758.

Marlon, J., Bartlein, P.J. & Whitlock, C. (2006) Fire-fuel-climate linkages in the northwestern USA during the Holocene. *The Holocene*, **16**, 1059–1071.

Marlon, J.R., Bartlein, P.J., Carcaillet, C., Gavin, D.G., Harrison, S.P., Higuera, P.E., Joos, F., Power, M.J. & Prentice, I.C. (2008) Climate and human influences on global biomass burning over the past two millennia. *Nature Geoscience*, **1**, 697–702.

Martin, A.C. & Barkley, W.D. (1973) *Seed Identification Manual*. University of California Press, Berkeley and Los Angeles.

Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-Being: Wetlands and Water: Synthesis*. World Resources Institute, Washington, DC.

Millington, J.D.A., Wainwright, J., Perry, G.L.W., Romero-Calcerrada, R. & Malamud, B.D. (2009) Modelling Mediterranean landscape succession-disturbance dynamics: a landscape fire-succession model. *Environmental Modelling & Software*, **24**, 1196–1208.

Mouillot, F., Rambal, S. & Joffre, R. (2002) Simulating climate change impacts on fire frequency and vegetation dynamics in a Mediterranean-type ecosystem. *Global Change Biology*, **8**, 423–437.

Mouillot, F., Ratte, J.P., Joffre, R., Moreno, J.M. & Rambal, S. (2003) Some determinants of the spatio-temporal fire cycle in a mediterranean landscape (Corsica, France). *Landscape Ecology*, **18**, 665–674.

Múgica, F.F., Antón, M.G., Ruiz, J.M., Juaristi, C.M. & Ollerol, H.S. (2001) The Holocene history of *Pinus* forests in the Spanish Northern Meseta. *The Holocene*, **11**, 343–358.

Neboit, R. (1981) *La Forêt Méditerranéenne Française Depuis 10 000 ans, Daprés des Travaux Récents*. Annales de Géographie, Vol. 90, pp. 445–450. Société de géographie, France.

Ohlson, M. & Tryterud, E. (2000) Interpretation of the charcoal record in forest soils: forest fires and their production and deposition of macroscopic charcoal. *The Holocene*, **10**, 519–525.

Pal, J.S., Giorgi, F. & Bi, X. (2004) Consistency of recent European summer precipitation trends and extremes with future regional climate projections. *Geophysical Research Letters*, **31**, L13202.

Parry, M., Canziani, O., Palutikof, J., Van der Linden, P. & Hanson, C. (2007) *IPCC, 2007: Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.

Pausas, J. (2004) Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean basin). *Climatic Change*, **63**, 337–350.

Pausas, J.G. & Fernández-Muñoz, S. (2011) Fire regime changes in the Western Mediterranean Basin: from fuel-limited to drought-driven fire regime. *Climatic Change*, **110**, 215–226.

Pausas, J.G. & Keeley, J.E. (2009) A burning story: the role of fire in the history of life. *BioScience*, **59**, 593–601.

Pausas, J.G., Llovet, J., Rodrigo, A. & Vallejo, R. (2009) Are wildfires a disaster in the Mediterranean basin? – A review. *International Journal of Wildland Fire*, **17**, 713–723.

Pèrez-Obiol, R. & Julià, R. (1994) Climatic change on the Iberian Peninsula recorded in a 30,000-yr pollen record from Lake Banyoles. *Quaternary Research*, **41**, 91–98.

Peters, M.E. & Higuera, P.E. (2007) Quantifying the source area of macroscopic charcoal with a particle dispersal model. *Quaternary Research*, **67**, 304–310.

Peyron, O., Guiot, J., Cheddadi, R., Tarasov, P., Reille, M., de Beaulieu, J.L., Bottema, S. & Andrieu, V. (1998) Climatic reconstruction in Europe for 18,000 yr BP from pollen data. *Quaternary Research*, **49**, 183–196.

Pimont, F., Prodon, R. & Rigolot, E. (2011) Comparison of postfire mortality in endemic Corsican black pine (*Pinus nigra* ssp. *laricio*) and its direct competitor (*Pinus pinaster*). *Annals of Forest Science*, **68**, 425–432.

Piñol, J., Terradas, J. & Lloret, F. (1998) Climate warming, wildfire hazard, and wildfire occurrence in coastal eastern Spain. *Climatic Change*, **38**, 345–357.

Pisaric, M.F. (2002) Long-distance transport of terrestrial plant material by convection resulting from forest fires. *Journal of Paleolimnology*, **28**, 349–354.

Rasmussen, S., Andersen, K., Svensson, A., Steffensen, J., Vinther, B., Clausen, H., Siggaard-Andersen, M., Johnsen, S., Larsen, L. & Dahl-Jensen, D. (2006) A new Greenland ice core chronology for the last glacial termination. *Journal of Geophysical Research*, **111**, D06102.

Reed, J.M., Stevenson, A.C. & Juggins, S. (2001) A multi-proxy record of Holocene climatic change in southwestern Spain: the Laguna de Medina, Cádiz. *The Holocene*, **11**, 707–719.

Reille, M., Gamisans, J., deBeaulieu, J.L. & Andrieu, V. (1997) The late-glacial at Lac de Creno (Corsica, France): a key site in the western Mediterranean Basin. *New Phytologist*, **135**, 547–559.

Reille, M., Gamisans, J., Andrieu-Ponel, V. & de Beaulieu, J.L. (1999) The Holocene at Lac de Creno, Corsica, France: a key site for the whole island. *New Phytologist*, **141**, 291–307.

Reimer, P.J., Baillie, M.G.L., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Ramsey, C.B., Buck, C.E., Burr, G.S. & Edwards, R.L. (2009) IntCal09 and Marine09 radiocarbon age calibration curves, 0-50,000 years cal BP. *Radiocarbon*, **51**, 1111–1150.

Retana, J., Espelta, J.M., Habrouk, A., Ordonez, J.L. & de Sola-Morales, F. (2002) Regeneration patterns of three Mediterranean pines and forest changes after a large wildfire in northeastern Spain. *Ecoscience*, **9**, 89–97.

Riffard, O. (2006) La politique forestière en Corse et le role de l'Office du développement agricole et rural de Corse. *Forêt Méditerranéenne*, **27**, 214–216.

Rius, D., Vannière, B. & Galop, D. (2009) Fire frequency and landscape management in the northwestern Pyrenean piedmont, France, since the early Neolithic (8000 cal. BP). *The Holocene*, **19**, 847–859.

Rubiales, J.M., Garcìa-Amorena, I., lvarez, S.G. & Manzaneque, F.G. (2008) The Late Holocene extinction of *Pinus sylvestris* in the western Cantabrian Range (Spain). *Journal of Biogeography*, **35**, 1840–1850.

Rubiales, J., García-Amorena, I., Génova, M., Gómez Manzaneque, F. & Morla, C. (2007) The Holocene history of highland pine forests in a submediterranean mountain: the case of Gredos mountain range (Iberian Central range, Spain). *Quaternary Science Reviews*, **26**, 1759–1770.

Sheffer, E. (2012) A review of the development of Mediterranean pine-oak ecosystems after land abandonment and afforestation: are they novel ecosystems? *Annals of Forest Science*, **69**, 429–443.

Shuman, B. (2012) Patterns, processes, and impacts of abrupt climate change in a warm world: the past 11,700 years. *Wiley Interdisciplinary Reviews: Climate Change*, **3**, 19–43.

Steffensen, J.P., Andersen, K.K., Bigler, M., Clausen, H.B., Dahl-Jensen, D., Fischer, H., Goto-Azuma, K., Hansson, M., Johnsen, S.J. & Jouzel, J. (2008) High-resolution Greenland ice core data show abrupt climate change happens in few years. *Science*, **321**, 680–684.

Stuiver, M. & Reimer, P.J. (1993) Extended 14C data base and revised CALIB 3.0 14C age calibration program. *Radiocarbon*, **35**, 215–230.

Sugita, S. (1994) Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. *Journal of Ecology*, **82**, 881–897.

Tapias, R., Gil, L., Fuentes-Utrilla, P. & Pardos, J.A. (2001) Canopy seed banks in Mediterranean pines of south-eastern Spain: a comparison between *Pinus halepensis* Mill., *P. pinaster* Ait., *P. nigra* Arn. and *P. pinea* L. *Journal of Ecology*, **89**, 629–638.

Ter Braak, C.J.F. (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, **67**, 1167–1179.

Ter Braak, C.J.F. & Smilauer, P. (2002) *Canoco 4.5: Reference Manual and Canodraw for Windows. User's Guide: Software Form Canonical Community Ordination (Version 4.5)*. Microcomputer Power, Ithaca.

Tinner, W., Hubschmid, P., Wehrli, M., Ammann, B. & Conedera, M. (1999) Long-term forest fire ecology and dynamics in southern Switzerland. *Journal of Ecology*, **87**, 273–289.

Tinner, W., Conedera, M., Ammann, B. & Lotter, A.F. (2005) Fire ecology north and south of the Alps since the last ice age. *The Holocene*, **15**, 1214–1226.

Tinner, W., Hofstetter, S., Zeugin, F., Conedera, M., Wohlgemuth, T., Zimmermann, L. & Zweifel, R. (2006) Long-distance transport of macroscopic charcoal by an intensive crown fire in the Swiss Alps-implications for fire history reconstruction. *The Holocene*, **16**, 287–292.

Tinner, W., Colombaroli, D., Heiri, O., Henne, P., Steinacher, M., Untenecker, J., Vescovi, E., Allen, J., Carraro, G. & Conedera, M. (2013) The past ecology of *Abies alba* provides new perspectives on future responses of silver fir forests to global warming. *Ecological Monographs*, **83**, 419–439.

Tozzi, C. & Weiss, M.C. (2001) Nouvelles données sur le Néolithique ancien de l'aire corso-toscane. *Bulletin de la Société Préhistorique Française*, **98**, 445–458.

Vescovi, E., Ravazzi, C., Arpenti, E., Finsinger, W., Pini, R., Valsecchi, V., Wick, L., Ammann, B. & Tinner, W. (2007) Interactions between climate and vegetation during the Lateglacial period as recorded by lake and mire sediment archives in Northern Italy and Southern Switzerland. *Quaternary Science Reviews*, **26**, 1650–1669.

Vigne, J.D. (1995) Préhistoire du Cap Corse: les abris de Torre d'Aquila, Pietracorbara (Haute-Corse)-La faune. *Bulletin de la Société Préhistorique Française*, **92**, 381–389.

Whelan, R.J. (1995) *The Ecology of Fire*. Cambridge University Press, Cambridge.

Whitlock, C. & Anderson, R.S. (2003) Fire history reconstructions based on sediment records from lakes and wetlands. *Fire and Climatic Change in Temperate Ecosystems of the Western Americas*, pp. 3–31. Springer, New York.

Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island Biogeography: Ecology, Evolution, and Conservation*. Oxford University Press, USA.

Wick, L. & Möhl, A. (2006) The mid-Holocene extinction of silver fir (*Abies alba*) in the Southern Alps: a consequence of forest fires? Palaeobotanical records and forest simulations. *Vegetation History and Archaeobotany*, **15**, 435–444.

Willis, K. & Bhagwat, S. (2010) Questions of importance to the conservation of biological diversity: answers from the past. *Climate of the Past*, **6**, 759–769.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Complete diagram of macrofossils recorded in the sediments of the Lac de Creno.

Appendix S2. Extension of the last millennium of fire and vegetation history.

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