Original Article

The anthropogenic influence on wildfire regimes: charcoal records from the Holocene and Last Interglacial at Ioannina, Greece

I. T. Lawson[1*], P. C. Tzedakis[2], K. H. Roucoux[1] and N. Galanidou[3]

[1]School of Geography, University of Leeds, Leeds LS2 9JT, UK, [2]Environmental Change Research Centre, Department of Geography, University College London, London WC1E 6BT, UK, [3]Department of History and Archaeology, University of Crete, Rethymno 74100, Greece

*Correspondence: I.T. Lawson, School of Geography, University of Leeds, Leeds LS2 9JT, UK.

E-mail i.t.lawson@leeds.ac.uk.

Running headline: Fire during the Holocene and Last Interglacial

ABSTRACT

Aim To characterize the changing fire regime of a Mediterranean landscape during the Holocene and the Last Interglacial and, by comparing the two periods, to improve our understanding of the extent and timing of human alteration of natural fire regimes.

Location Lake Ioannina, north-western Greece (39° 45′ N, 20° 51′ E).

Methods Using a long sequence of lake sediments, we measured the charcoal content of the sediment over the course of the Holocene and the Last Interglacial. We compared the charcoal data with pollen data for the same periods.

Results Charcoal was present in all samples analysed. Charcoal influx was greater during interglacials, which at Ioannina were forested, than during glacials, when tree populations were small. Charcoal influx was greater and more variable during the Holocene than during the Last Interglacial.

Main conclusions Fire was a persistent feature throughout the periods studied, under both glacial and interglacial conditions. Overall, more biomass was burned during interglacials than during glacials, and peak burning occurred at intermediate values of moisture availability. There is little evidence that the composition of forests significantly affected burning regimes. Enhanced burning during the Holocene relative to the Last Interglacial may reflect human impact, as well as climatic or vegetational differences between the two periods.

Keywords

Biomass burning, climate, fire, human impact, lake sediments, Mediterranean, microcharcoal, palaeoecology, pollen analysis.

INTRODUCTION

Wildfire is an important process in ecosystems around the world. Fire shapes many plant and animal communities, influencing succession, evolution and global biogeography (Bond *et al.*, 2005). It is important to the carbon cycle and climate system, mediating the release of CO_2, CH_4 and black carbon aerosols (Butler *et al.*, 2005; Bowman *et al.*, 2009) and converting biomass to biochar, which may effectively sequester carbon in soils for millennia (Druffel, 2004; Preston & Schmidt, 2006). Fire is also destructive of human life and property. Some current coupled general circulation and Earth system models incorporate fire processes, and most predict that wildfire activity will increase in many regions over the coming decades as a result of climatic change, which may lead to more instances of the hot, dry spells that encourage wildfires (e.g. Schumacher & Bugmann, 2006; Flannigan *et al.*, 2009). These models are, however, poorly constrained by data on the processes that determine wildfire behaviour. Thus there is a need from both basic and applied research perspectives for a better understanding of the pattern and process of vegetation burning.

Fire scientists have often made a distinction between 'natural' and 'anthropogenic' fire regimes (Bowman *et al.*, 2011). The idea of a 'natural' fire regime is a useful concept because, for example, there is evidence that natural fires and anthropogenic fires have different characteristics in terms of spatial extent and duration (Archibald *et al.*, 2009); managers often advocate reinstating a 'natural' fire regime, rather than trying to suppress all fires (Jensen & McPherson, 2007). However, it is difficult to determine what the natural fire regime is in a given environment, because even in sparsely populated parts of the world, people probably start the majority of fires today. For example, 86% of recorded fires in protected forests in boreal Russia between 1986 and 1995 were anthropogenic (Shvidenko *et al.*, 1998), while in the Mediterranean today *c*. 95% of fires are anthropogenic, accounting for > 90% of the total area burned (Ganteaume *et al.*, 2012; Keeley *et al*., 2012).

A key research aim is therefore to understand the behaviour of natural wildfires. Historical data sets based on satellite observations (in the last few years only) or on records kept by organizations such as governmental forestry departments inevitably conflate anthropogenic and natural ignitions. Such data sets cannot give us insights into, for example, whether regular burning is an inherent property of certain vegetation types. An alternative source of evidence for fire regimes is the palaeoecological record. Charred particles produced during fires are often preserved in lake, mire and marine sediments. Compilations of such records (e.g. Power *et al.*, 2008; Marlon *et al.*, 2009a,b, 2013; Vannière *et al.*, 2011) have produced useful global and regional syntheses of Lateglacial to Holocene fire regimes. In many lightly populated parts of the world, for example the boreal forests of Canada and Siberia, these fire records may reflect wholly natural processes for most of the Holocene. In more heavily populated regions, such as Europe, disentangling natural and anthropogenic causes of changing fire regimes has proven more problematic. The deliberate use of fire for cooking by hominins may have begun as early as 2 Ma (million years ago; Wrangham *et al.*, 1999) and firm evidence for the use of fire as early as 790 ka has emerged from Israel (Goren-Inbar *et al.*, 2004), while archaeological evidence from European sites suggests that habitual and controlled use of fire by hominins began between *c*. 400 and 200 ka (Karkanas *et al*., 2007; Roebroeks & Villa, 2011). A wealth of literature has argued for the widespread use of fire by non-industrial societies, both hunter-gatherer and agro-pastoralist, as a tool for hunting, vegetation clearance, and deflection of succession (e.g. Stewart, 1956; James, 1989; Lupo & Schmitt, 2002). Prehistoric people may also have started fires accidentally, and their indirect effects on ecosystems may have changed burning regimes: for example, a reduction in large herbivore populations through hunting could have increased the available fuel load (Caldararo, 2002; Gill *et al.*, 2009).

This paper has three aims.

1. To present new palaeoecological proxy records for biomass burning for selected periods from north-western Greece, a region from which such records are lacking.
2. To investigate the relationship between vegetation, climate and fire under conditions of minimal hominin disturbance, during the Last Interglacial.
3. To assess when and how past human activity may have affected biomass burning.

We addressed these aims by measuring the influx of sub-fossil charcoal, a proxy for the quantity of biomass burning, in a long, continuous sequence of lake sediments from the Ioannina basin, Epirus, north-western Greece (Fig. 1). Ioannina lies in a mountainous landscape in a transition zone between Mediterranean sclerophyllous vegetation and mixed deciduous and coniferous woodland. The charcoal record presented here includes the Holocene and the end of the last glacial (24–0 cal. kyr BP), and the Last Interglacial and part of the preceding (or penultimate) glacial and subsequent stadial (c. 133–110 ka, including parts of Marine Isotope Stages 6, 5e and 5d; Frogley *et al.*, 1999; Tzedakis *et al.*, 2002a,b, 2003; chronological terms are summarized in Table 1).

Sometimes a natural 'before-and-after' experiment can be used to determine the extent of human impact. For example, McWethy *et al.* (2010) showed that the arrival of the first humans in New Zealand was accompanied by a substantial step change in ecosystem behaviour, including fire regimes. Such an experiment is not possible in long-occupied regions such as Europe. Although we could, in principle, compare the Holocene with conditions before the earliest known presence of hominins at *c*. 1.2 Ma (Carbonell *et al.*, 2008), the vegetation and climate of such old interglacials are very different from those of the Holocene, and poorly understood. Here we instead compare the Holocene with the Last Interglacial. Two advantages of working on the Last Interglacial are that: (1) we can use data from the same sediment sequence from one site for both periods, thus holding site and depositional parameters as constant as possible; and (2) the climate and vegetation of the Last Interglacial are relatively well understood compared with older interglacials. Specifically, the Last Interglacial was characterized by higher peak summer temperatures than the Holocene, and was one of the strongest interglacials of the past 800 kyr (Lang & Wolff, 2011). This was related to large positive summer insolation anomalies across the Northern Hemisphere between 130 and 127 ka and an earlier deglaciation compared to the Holocene. Reconstructions based on coral terraces suggest that maximum sea level reached *c*. 5.5–9 m higher than present (Dutton & Lambeck, 2012). In Greece, the interval of maximum summer insolation during the Last Interglacial was characterized by enhanced seasonality of precipitation, with highly evaporative summer conditions, but also increased winter precipitation (Tzedakis, 2007; Milner *et al.*, 2012).

We proceed with the understanding that hominins may have been active in our study area during the Last Interglacial, but with the assumption that their lower population densities, at least by comparison with *Homo sapiens* of the Neolithic and later, mean that we can still gain insights into what a ‘more natural’ wildfire regime might be like in the Mediterranean. That assumption is supported by archaeological data as follows.

Taking into account the preservation biases in the archaeological record, the evidence for hominin occupation of north-western Greece during the Last Interglacial is nevertheless limited. A hominin cranium from Petralona in Greek Macedonia and Lower Palaeolithic stone tools from Kokkinopilos in Epirus indicate that hominins were present in Greece, at least intermittently, after 300 ka at the latest (Galanidou, 2004; Harvati *et al.*, 2009). There are abundant finds of Middle Palaeolithic lithic industries, which are associated with *Homo neanderthalensis*; some of them might be as old as the Last Interglacial, including finds from Ormos Odysseos in coastal Epirus (Runnels & van Andel, 2003) and sites in the southern Peloponnese (e.g. Reisch, 1985; Harvati *et al*., 2011), but very few can be dated with precision. The only Middle Palaeolithic site in the region to return a date which could place it within the Last Interglacial, Anavatis on the coast of Epirus, is constrained by an infrared stimulated luminescence date to < 128 ± 23 ka (Zhou *et al*., 2000). By contrast, there is abundant evidence for sustained occupation of sites in and around the Ioannina basin by *Homo sapiens* during the latter part of the Last Glacial and during the Holocene. There are numerous sites dating to the Upper Palaeolithic (including some well-known caves and rockshelters in the Ioannina basin and nearby; Bailey, 1997; Galanidou *et al*., 2000; Galanidou & Tzedakis, 2001), Mesolithic (sites in the wider region; Harrold *et al*., 1999; Gjipali, 2006; Galanidou, 2011), and Neolithic (sites within the Ioannina basin at Asfaka and on Kastritsa hill, and in the wider region at Gouves and Doliana; Dousougli, 1996; Dousougli & Zachos, 2002; Youni, 2010). There may have been a hiatus in activity during the Early and the Middle Bronze Age (*c*. 5.0–3.6 ka), followed by intensified settlement and exploitation during the Late Bronze Age (3.6–3.1 ka, with over 40 sites known from the Ioannina basin), continuing into the Early Iron Age (12 sites reported from the same area; Zachos, 1997; Vasileiou, 2010). Since then the basin has probably remained continuously occupied until the present day.

MATERIALS AND METHODS

Core I-284 (39° 45′ N, 20° 51′ E, 472 m a.s.l.; Fig. 1) was retrieved from the Ioannina basin by the Greek Institute of Geological and Mineral Exploration using a truck-mounted coring rig. The core is 319 m long and, beneath *c*. 4 m of sand and gravel, consists of olive-grey lake silts with varying carbonate content (Frogley, 1997). The age model (Table 2) and pollen data used here have been published previously (Frogley *et al.*, 1999; Tzedakis *et al.*, 2002a,b, 2003; Lawson *et al.*, 2004).

We assume that the influx of charcoal to the sediment is an index of the quantity of biomass burning (by which we mean the amount of biomass burnt during a given period within a certain area around the core site, which would have units of kg yr^{-1} ha^{-1}). The area of (assumed planar) charcoal in the pollen slides was quantified using the point-count technique (Clark, 1982) with a square grid graticule. Using sedimentation rates derived from the age model, this yields influxes in mm^2 (of charcoal) cm^{-2} (of lake bed) yr^{-1}. At least 200 objects (> 30 charcoal ‘points’ and > 30 exotic marker grains of *Lycopodium clavatum*; Stockmarr, 1971) were counted in each sample.

Figure 2 shows the climatic context of the two intervals studied here. Contiguous sampling is impractical over such a long sequence, and the sampling interval is variable due to previous sub-sampling. The estimated mean time interval between samples is 220 years. Each sample represents a 1-cm thickness of sediment which represents between 4 and 30 years of deposition. The Ioannina sediments are not laminated, which indicates that the sediments have been mixed after deposition by bioturbation and/or wave action. Furthermore, the Ioannina basin is large (the lake had a maximum extent of 35 km × 11 km), and charcoal was probably recruited from at least within the entire hydrological catchment (absolute limits of the airborne charcoal source area are undefinable; cf. Prentice, 1985), an area large enough (420 km^2) that even the largest fires might not have affected the whole area. Fire return intervals, a potentially very useful index of past fire regimes, can only reasonably be estimated using unmixed, annually laminated sedimentary records with contiguous sampling, in lakes with catchments small enough to only be affected by one fire at a time; this is not the case at Ioannina. Instead, when we discuss 'burning regimes' in this paper, we interpret each sample in the charcoal record as containing information about the amount of biomass burnt over a period of several years, averaged over the catchment as a whole. Changes in the rate of biomass burning over time should be discernible in our record, even though not every fire event will be captured by the discontinuous sampling.

We compared the two interglacials with reference to peaks in the 40° N 21 June insolation curve (Fig. 3; Laskar *et al*., 2004). Comparing interglacials in this way is justified because (1) orbital parameters are well established to be the pacemaker of glacial-interglacial climatic variability (Hays *et al.*, 1976); (2) summer insolation is a good predictor of local summer temperatures today (Huybers, 2006) and can therefore be expected to exert a strong control on peak fire season temperatures in locations far from oceans and ice sheets; and (3) the pattern of vegetational succession in both periods is most similar when they are aligned on the insolation peak (Magri & Tzedakis, 2000). Informal subdivisions are made as follows (Table 2): the 'full glacial', > 3.5 kyr before the insolation peak, when arboreal pollen (AP) is at typically low glacial values; the 'late glacial', 0.5–3.5 kyr before the insolation peak, during which AP gradually rises to interglacial values; the 'early interglacial', from 0.5 kyr before to 2.3 kyr after the insolation peak, during which maquis taxa are abundant, indicating summer aridity (Tzedakis, 2007); the 'mid interglacial', 2.3–5.2 kyr after the insolation peak; the 'late interglacial', 5.2–11.2 kyr after the insolation peak, which during the Holocene is characterized by loss of forest cover, soil erosion, and other changes attributed to human impact on the landscape; and, in the Last Interglacial part of the record only, the 'interglacial/stadial transition' (including part of the end of the forested interglacial and the beginning of the ensuing unforested interval), beginning 11.2 kyr after the insolation peak.

The climate at Ioannina today has the typical mediterranean climatic features of mean winter temperatures above freezing and a strong summer drought, although the elevation of the basin means that temperatures are lower and rainfall is higher than in the coastal lowlands. Mean January and July temperatures at the Ioannina meteorological station at 483 m a.s.l. are 4.7 °C and 24.8 °C, respectively, and monthly precipitation varies from a maximum of 175 mm in December to a minimum of 31 mm in August with an annual total of 1082 mm (mean values for the period 1956–1997; HNMS, 2012).

RESULTS

The charcoal data are presented in Fig. 3, together with pollen data from the same samples. The charcoal data are summarized in box-and-whisker plots in Fig. 4, which emphasize the median values rather than the extremes and reduce the effect of small uncertainties in the age model. Microcharcoal, typically ranging in size from 5 to 150 μm, was present in all samples analysed.

During the Last Interglacial and the part of the penultimate glacial studied here, charcoal influx values show subdued variations. They are small during the earliest recorded part of the glacial (typically 6 $mm^2\ cm^{-2}\ yr^{-1}$), increase slightly to *c*. 15 $mm^2\ cm^{-2}\ yr^{-1}$ at 127 ka during the transition to the interglacial, decline to *c*. 10 $mm^2\ cm^{-2}\ yr^{-1}$ after *c*. 124 ka during the middle part of the interglacial, increase to c. 15 $mm^2\ cm^{-2}\ yr^{-1}$ after 120 ka in the late part of the interglacial, then decline again to c. 6 $mm^2\ cm^{-2}\ yr^{-1}$ after 112 ka.

In the Holocene and last glacial part of the record, charcoal influx is low from 24–11.5 ka, similar to the end of the penultimate glacial but not showing a rise during the transition to the interglacial. Charcoal influxes increase substantially at the start of the Holocene; from 11.6–10 ka, influxes are very variable, reaching larger values than any seen in the Last Interglacial and penultimate glacial part of the record; however, these are matched by fluctuations in the pollen influxes in the same samples. Influxes remain large, *c*. 20–30 $mm^2\ cm^{-2}\ yr^{-1}$, until *c*. 6 ka when they first decrease to less than 10 $mm^2\ cm^{-2}\ yr^{-1}$, then recover to *c*. 30 $mm^2\ cm^{-2}\ yr^{-1}$. During this period AP declines substantially from *c*. 75% to *c*. 20%, rebounds to *c*. 70%, then declines to *c*. 15%.

Table 3 presents coefficients for Spearman's rank correlation between the charcoal data and selected pollen taxa shown in Fig. 3. The strongest correlations occur in the Last Interglacial (excluding the preceding glacial), where charcoal influx is strongly negatively correlated with the proportions of AP and most tree taxa, and positively correlated with the proportions of grass and steppe taxa.

Table 4 presents significance tests to accompany the box-and-whisker plots in Fig. 4. They suggest that charcoal influx differs significantly between the mid interglacial and, more marginally, late interglacial parts of the records.

DISCUSSION

The presence of charcoal in every sample analysed indicates that fire was a persistent element in both glacial and interglacial environments throughout the periods studied.

The Last Interglacial and penultimate glacial

The charcoal record from the Last Interglacial and penultimate glacial offers insights into the functioning of fire regimes under, at least, less anthropogenic influence than today.

There is a positive correlation between charcoal influx and deciduous tree pollen percentages (Table 3), suggesting that interglacial forests supplied more charcoal per unit time to the lake sediments than the more open steppic grasslands of the glacials (the same is true for the last glacial/Holocene). Other authors have considered that in semi-arid environments, total biomass (fuel load) may be the dominant long-term control on charcoal abundance in sediments, not the occurrence of climates favouring spells of fire weather. Turner *et al*. (2008), for example, found that charcoal abundance in their Holocene record from Anatolia (Turkey) increased during wetter periods, probably in response to increased biomass. Linstädter & Zielhofer (2010) found a similar pattern in north-eastern Morocco.

If we consider just the forested part of the Last Interglacial, palynological indicators of the degree of woodland openness (AP, steppe taxa, Gramineae) are correlated with the charcoal data (Table 3) so as to suggest that, within an interglacial, open woodland produces more charcoal than dense woodland. This suggests that peak charcoal production occurs at intermediate levels of aridity, because under very arid conditions biomass is low and there is not much material to burn, while under very wet conditions fires are infrequent (Krawchuk & Moritz, 2011).

There is little evidence of enhanced burning around the Last Interglacial insolation peak relative to other parts of the Last Interglacial, when summer drought was probably most severe and abundances of mediterranean sclerophylls peaked. In fact, the correlation between summer drought-tolerant taxa and charcoal abundance is negative. (Positive correlations between charcoal influx and maquis taxa during the Holocene as a whole are largely due to the expansion of these taxa during the second half of the Holocene, probably associated with human activity.) This supports the conclusion of Colombaroli *et al.* (2009), based on Holocene data alone, that fire is not important in assisting the establishment of broadleaved evergreen maquis vegetation.

In general, low correlation coefficients between the abundance of individual taxa (or groups of related taxa) and charcoal suggest that, within the wooded ecosystems represented in our record, the composition of the woodland was less important than the overall biomass in determining the total amount of burning in the long term. In particular, there is no relationship between charcoal influx and the abundance of *Pinus* (pine) pollen. Some species of pine, particularly lowland species such as *Pinus halepensis*, burn readily and may benefit competitively from fires (Grove & Rackham, 2001, p. 219). The Ioannina record, with its mountainous catchment, may be dominated by less fire-adapted upland species such as *Pinus nigra* (Roucoux *et al*., 2011).

Holocene and last glacial fire regimes, and human activity

During the part of the last glacial studied here, charcoal influxes were low and similar to those of the penultimate glacial (Fig. 4).

During the early and middle parts of the Holocene, before 6 ka, charcoal influx values are usually rather higher, and much more variable, than in the orbitally equivalent parts of the Last Interglacial (Fig. 4). This would suggest more intensive burning during the early and middle part of the Holocene. One possible explanation is that humans may have altered fire dynamics during that period. However, pollen influxes are also much higher in the early Holocene than in the equivalent part of the Last Interglacial and there are considerable differences in the pollen assemblages, both of which suggest that a third factor is involved. Possibly, some additional transport pathway was bringing both pollen and charcoal to the lake in the early Holocene, perhaps linked to changes in basin morphology or erosional changes (but there is no sedimentological support for this: Lawson *et al*., 2004). More plausibly, the lower AP percentages in the early Holocene suggest a more open landscape (perhaps due to human activity or climatic differences) which could have led both to more burning and to greater charcoal and pollen transport (because wind speeds are higher in more open forests).

Our observation that charcoal influx increased during the last glacial–interglacial transition, with more burning during the Holocene than during the Last Glacial Maximum (LGM, *c*. 20 ka), agrees with the synthesis of Power *et al.* (2008), which showed that this pattern is typical across Europe. However, the increase in charcoal influx is much weaker during the transition from the penultimate glacial to the Last Interglacial. While climatic differences between the two transitions could explain the difference in fire behaviour, it is equally possible that the increased activity of humans is the critical factor, either through their direct use of fire, or as an indirect consequence, for example by opening up dense woodland or reducing herbivore populations (e.g. Caldararo, 2002; Gill *et al.*, 2009).

This raises the question of the extent to which early Holocene charcoal records in similar Mediterranean situations necessarily provide insights into purely natural processes of burning. While climate and/or vegetation change are probably the dominant drivers of fire regime change in most situations (Vannière *et al*., 2011; Marlon *et al*., 2013), some other records spanning more than one interglacial indicate that fire activity has generally increased over the last *c*. 50 kyr, across different ecosystem types, and previous authors have concluded that this increase is probably due to human activity. For example, van der Kaars *et al.* (2000) found increased evidence of burning after 37 ka in a > 170 kyr marine sequence from the Banda Sea, Indonesia; Thevenon *et al.* (2004), working on a 360 kyr marine sequence from north of Papua New Guinea, found evidence for unprecedented levels of burning after 55 ka; Wang *et al*. (2005) found higher burning in the Holocene than in the two previous interglacials in records from the Chinese Loess Plateau. However, other long records of biomass burning show no evidence for increased burning during the Holocene compared with earlier periods that could be linked to human activity (e.g. Bird & Cali, 1998, 2002; Daniau *et al*., 2007, 2010; Mooney *et al.*, 2011). This lack of agreement could be due to problems with the interpretation of individual records, perhaps arising from taphonomic complications with marine records (Verardo & Ruddiman, 1996), as well as the inevitable complications of taphonomy and changing depositional environment in lake sequences. Equally, this disagreement may reflect genuine spatial variation in the importance of humans (and/or climate and vegetation) in determining Holocene biomass burning regimes. Further records would help to distinguish between these explanations. Although no past interglacial can be a perfect ‘undisturbed’ analogue for the Holocene, a larger sample of Holocene/past interglacial comparisons would clarify the extent to which the fire history of the Holocene is unusual.

The Ioannina pollen record indicates a pronounced decline in deciduous woodland extent beginning *c*. 6 ka and proceeding in two stages (separated by a period of partial reafforestation). By the end of this process, the deciduous oak-dominated woodlands of the mid-Holocene had been replaced by more open vegetation; grasses dominate the pollen record, but maquis species such as evergreen oaks are also important, along with possible crops [olive (*Olea europaea*) and cereals]. The sedimentological record at Ioannina indicates significant soil erosion accompanying the deforestation phases (Lawson *et al.*, 2004), though this does not seem to have transported additional charcoal to the lake. Elsewhere in Greece a similar transformation of the landscape occurred at different times and rates in different places, often around 9 ka and generally intensifying around 4 ka (during the Bronze Age; e.g. van Andel *et al*., 1990; Bintliff, 2002; Fuchs, 2007). Charcoal influx values in this part of the Ioannina record largely mirror the changes in AP, which suggests that again, biomass was the main control on charcoal production. However, after *c*. 3 ka, high charcoal influx values persist despite low AP and low pollen influx, which suggests more intense burning. Increased charcoal abundance in later Holocene deposits is common in Mediterranean sequences and the consensus view is that it represents the effect of human-induced intensification of burning regimes (e.g. Colombaroli *et al.*, 2009; Kaltenrieder *et al.*, 2010; Vannière *et al.*, 2011).

CONCLUSIONS

Our record shows that fire has been important at Ioannina since at least 133 kyr BP and appears to have played a role in shaping local ecosystems over a long period. The important role of fire should therefore be considered when managing similar ecosystems today.

Although the steppe-grasslands of glacial periods were subject to burning, woodlands produced more charcoal per unit time; peak burning occurred under conditions of intermediate moisture availability. In the wooded ecosystems of the Last Interglacial, woodland composition was less important than total biomass in determining total charcoal production.

Fire regimes throughout the Holocene were different from those of the Last Interglacial. More burning took place during the early Holocene, between 11.5 and 6 ka, than during the orbitally-equivalent part of the Last Interglacial. The greater presence of humans during the Holocene could explain this difference, but climatic differences between the two interglacials may also be responsible. Charcoal influx declined between 6 and 3 ka, possibly responding to reduced biomass due to deforestation, but increased again after 3 ka, perhaps reflecting more intensive use of fire by humans. Thus, although climatic change remains an important process in determining fire regimes, our results underline the need for caution in interpreting early–middle Holocene fire records as representing purely natural events.

ACKNOWLEDGEMENTS

We thank J. Corr for technical support and M.R. Frogley, R.C. Preece and the Greek Institute of Geology and Mineral Exploration for their role in making this study possible. We also thank three anonymous referees and the editor for constructive comments.

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BIOSKETCHES

The authors are three palaeoecologists and an archaeologist specializing in the reconstruction of environmental change and past human/environment interactions using a range of analytical techniques. The team has published extensively on lake and cave sediment records from the Ioannina basin, as well as from other locations in Greece and elsewhere in the Mediterranean.

Author contributions: I.T.L. generated the charcoal data, undertook the statistical analyses, and led the writing. P.C.T. and I.T.L. generated the pollen records. All co-authors made substantial contributions to writing the manuscript.

Editor: Jack Williams

Tables

Table 1 Chronological terms used in this paper, especially Fig. 4 and Table 4. The 21 June insolation peak took place at 126.8 ka during the Last Interglacial and at 11.2 ka in the Holocene (Laskar *et al.*, 2004)

Period	**Holocene time range**	**Last Interglacial time range**	**Explanation**
'Full glacial'	24.3–14.7 ka	133.0–130.3 ka	From the start of the data set to 3.5 kyr before each insolation peak, when arboreal pollen is at typically low glacial values
'Late glacial'	14.7–11.7 ka	130.3–127.3 ka	0.5–3.5 kyr before the insolation peak in each interglacial, during which AP gradually rises to interglacial values
'Early interglacial'	11.7–8.9 ka	127.3–124.5 ka	0.5 kyr before to 2.3 kyr after the insolation peak, during which maquis taxa are abundant, indicating summer aridity (Tzedakis, 2007)
'Mid interglacial'	8.9–6.0 ka	124.5–121.6 ka	2.3 to 5.2 kyr after the insolation peak
'Late interglacial'	6.0–0 ka	121.6–115.6 ka	5.2 to 11.2 kyr after the insolation peak. During the Holocene this interval is characterized by loss of forest cover, soil erosion, and other changes attributed to human impact on the landscape. In the Last Interglacial this period was characterized by the development

			of late successional forest.
‘Interglacial/stadial transition’	Not present	115.6–109.9 ka	Beginning 11.2 kyr after the insolation peak, this period has no analogue in the Holocene (it has not yet happened). Includes part of the end of the forested interglacial and the beginning of the subsequent unforested stadial.

Table 2 Age control points in core I-284. The radiocarbon dates presented here are discussed in Lawson *et al*. (2004), and are based on microcharcoal concentrates (the most amenable material for dating in this hard-water lake). Additional age control points (Tzedakis *et al.*, 2002b) are derived through (1) astronomical tuning of particular palynological events (peaks in pollen from sclerophyllous taxa) to specific configurations of the Earth's orbit (perihelion occurring in northern summer), as initially proposed by Magri & Tzedakis (2000); (2) phase-locking the midpoint of post-Heinrich cold-to-warm transitions during the last glacial to the North Atlantic–Greenland time-scale, using marine-pollen sequences in the western Mediterranean as a stepping-stone. The Greenland chronology used here is that of the GISP2 ice core, based on annual layer counting (Meese *et al.*, 1997). The age model used in this paper to calculate microcharcoal and pollen influx values (objects cm^{-2} yr^{-1}) is derived by linear interpolation between the age control points. The charcoal/pollen concentration ratios are independent of the age model, as concentration calculations (objects cm^{-3}) do not include time as a factor.

Control point depth (m)	**Age (ka)**	**Explanation**
0.00	-0.03	Assumed top of sequence in AD 1984
7.20	2.54	^{14}C (Lawson *et al.*, 2004)
9.17	5.88	^{14}C (Lawson *et al.*, 2004)
11.55	7.81	^{14}C (Lawson *et al.*, 2004)
15.10	11.63	^{14}C (Lawson *et al.*, 2004)
17.17	18.33	^{14}C (Lawson *et al.*, 2004)
23.01	23.30	Alignment to GISP2 (Tzedakis *et al.*, 2002b)
26.90	29.33	Alignment to GISP2 (Tzedakis *et al.*, 2002b)
29.40	38.30	Alignment to GISP2 (Tzedakis *et al.*, 2002b)
30.80	45.36	Alignment to GISP2 (Tzedakis *et al.*, 2002b)
34.50	52.23	Alignment to GISP2 (Tzedakis *et al.*, 2002b)

36.00	59.00	Astronomical calibration (Tzedakis *et al.*, 2002a)
42.80	66.00	Astronomical calibration (Tzedakis *et al.*, 2002a)
46.40	68.70	Alignment to GISP2 (Tzedakis *et al.*, 2002b)
49.80	73.00	Alignment to GISP2 (Tzedakis *et al.*, 2002a)
60.98	83.00	Astronomical calibration (Tzedakis *et al.*, 2002b)
66.20	88.50	Astronomical calibration (Tzedakis *et al.*, 2002b)
82.80	111.00	Astronomical calibration (Tzedakis *et al.*, 2002b)
96.25	126.60	Astronomical calibration (Tzedakis *et al.*, 2002b)
102.00	133.00	Astronomical calibration (Tzedakis *et al.*, 2002b)

Table 3 Spearman's rank correlation coefficients between charcoal influx values and selected pollen oercentages in the I-284 sequence.

	Holocene (and last glacial)	**Last Interglacial (and penultimate glacial)**	**Holocene only**	**Last Interglacial only**
Arboreal pollen	0.446	0.281	0.029	-0.460
Pinus	-0.158	-0.112	0.138	0.107
All conifers	-0.164	-0.009	0.033	0.022
Deciduous *Quercus*	0.443	0.485	0.111	0.243
All deciduous trees	0.477	0.335	0.009	-0.254
Evergreen *Quercus*	0.402	0.107	-0.028	-0.347
All maquis trees	0.586	0.112	-0.079	-0.271
Gramineae	-0.338	-0.232	-0.020	0.486
All steppe taxa	-0.711	-0.308	-0.069	0.361

Table 4 *P*-values from Wilcoxon rank sum tests between charcoal influx values for equivalent periods (illustrated in Fig. 4). The alternative hypothesis, accepted when $P < 0.05$ (entries in bold), is that the samples from the two periods are not drawn from the same population.

	Late interglacial	Mid interglacial	Early interglacial	Late glacial	Full glacial
P-value	**0.048**	**< 0.001**	0.074	0.082	0.580

Figure Captions

Figure 1 (a) Map showing the location of Ioannina in north-western Greece; (b) the Ioannina basin and surrounding area, showing the location of core I-284.

Figure 2 Total tree pollen percentage data for the Ioannina basin core I-284 from the last climatic cycle, *c*. 133 kyr BP to present (Tzedakis *et al.*, 2002b), atmospheric CO_2 concentrations from the Dome C and Vostok ice cores (Loulergue *et al*., 2008), and mean daily insolation for 21 June at 40° N (Laskar *et al*., 2004). The sections of the sequence investigated in this paper are shaded.

Figure 3 Charcoal, pollen and insolation data plotted against time. The left hand panel shows the data from the Holocene and last glacial [with the period of marked anthropogenic influence in the pollen data [Lawson *et al.*, 2004] shaded grey], and the right hand panel the data from the Last Interglacial and penultimate glacial. The position of peak 21 June insolation is marked by the vertical dashed line in each panel. From top: charcoal influx, expressed as the area of charcoal per area of sediment surface per year; charcoal to pollen ratio (with 5× exaggeration, dashed curve); total terrestrial pollen influx; total steppe pollen percentage (includes *Artemisia*, Chenopodiaceae, *Ephedra*); total maquis pollen percentages (includes *Olea*, *Phillyrea*, *Pistacia*, evergreen *Quercus*); total deciduous tree pollen percentages (all tree taxa excluding maquis and conifers); *Pinus* pollen percentages; atmospheric CO_2 concentrations from the Dome C and Vostok ice cores (Loulergue *et al*., 2008); and mean daily insolation for 21 June at 40° N (Laskar *et al*., 2004). The pollen data are from Frogley *et al.* (1999), Tzedakis *et al.* (2002a,b), and Lawson *et al.* (2004).

Figure 4 Box-and-whisker plots showing the distribution of charcoal data in comparable intervals (note that there is no Holocene equivalent of the interglacial–stadial transition). Asterisks indicate the two intervals for which the charcoal influxes are significantly different. Numbers below the *x*-axis indicate sample sizes.

624 Fig. 1

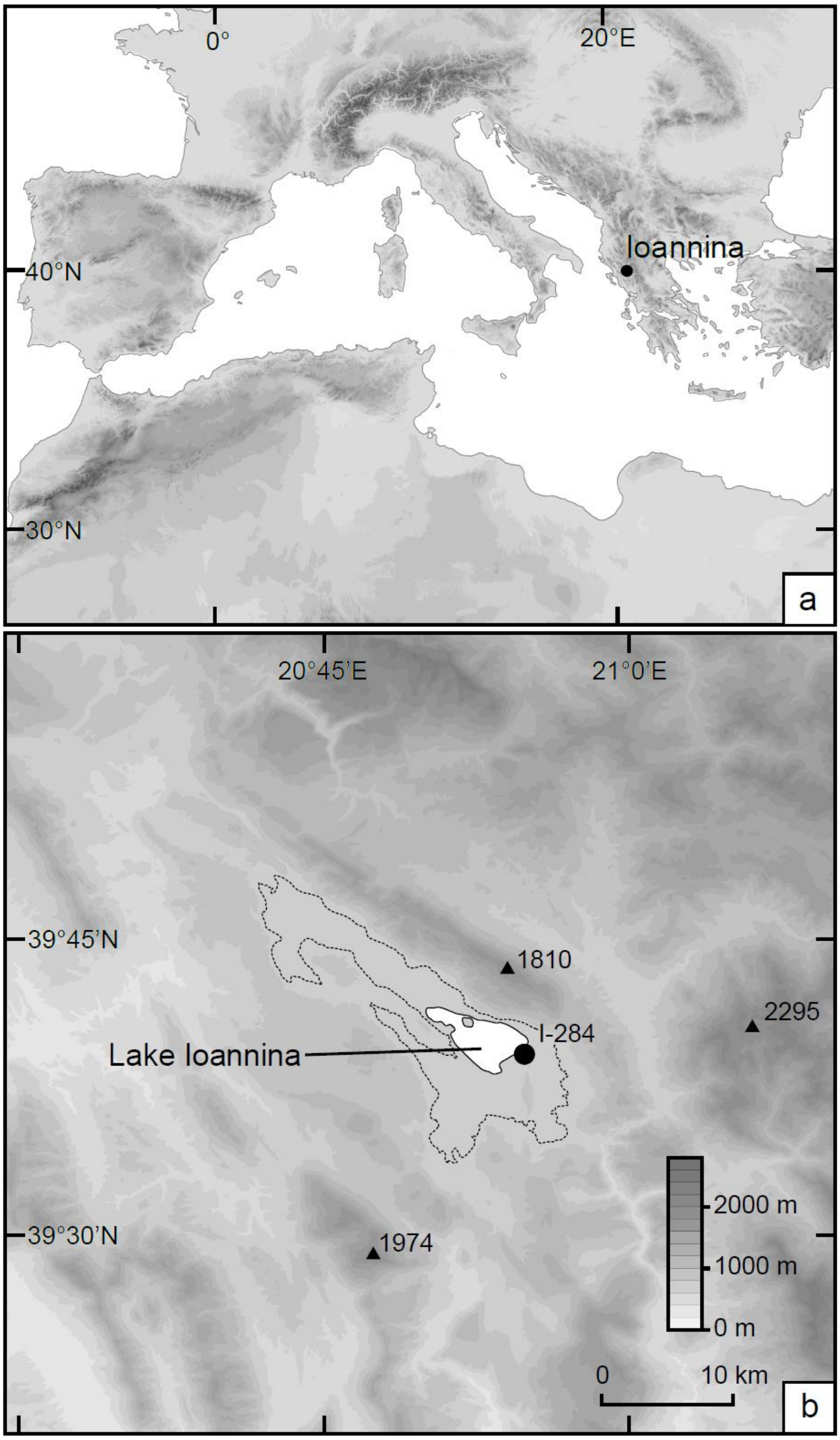

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Fig. 2

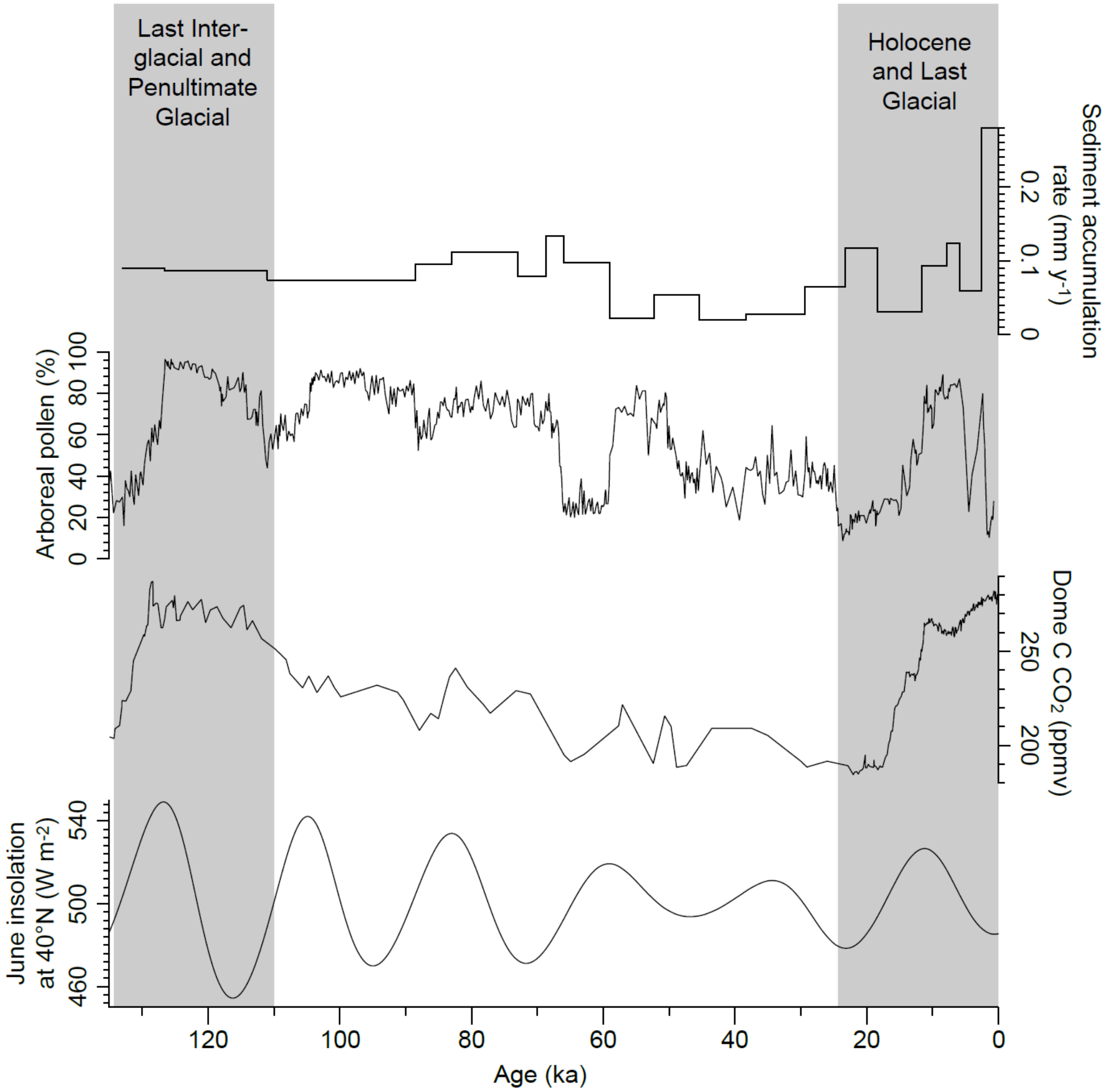
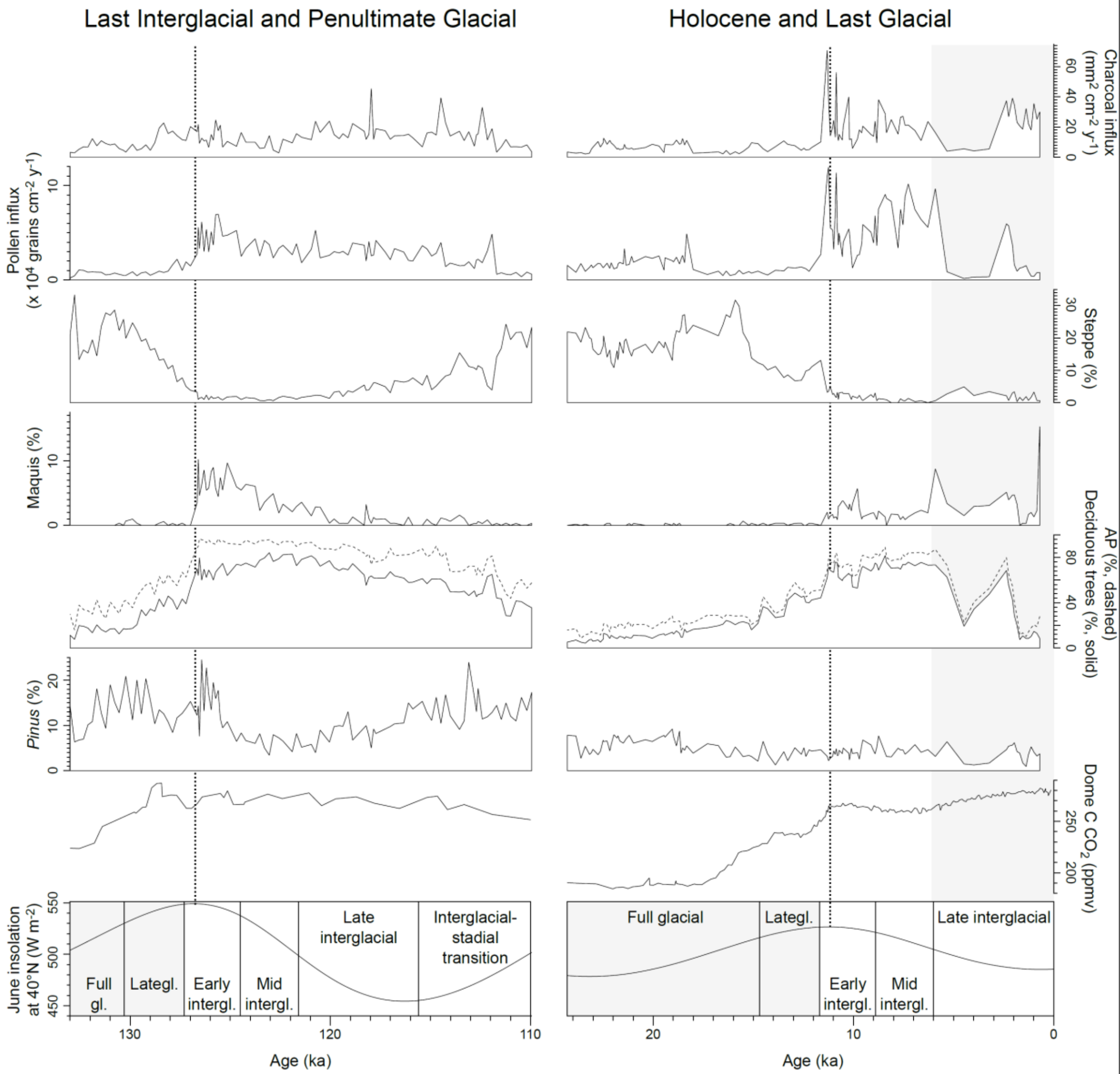
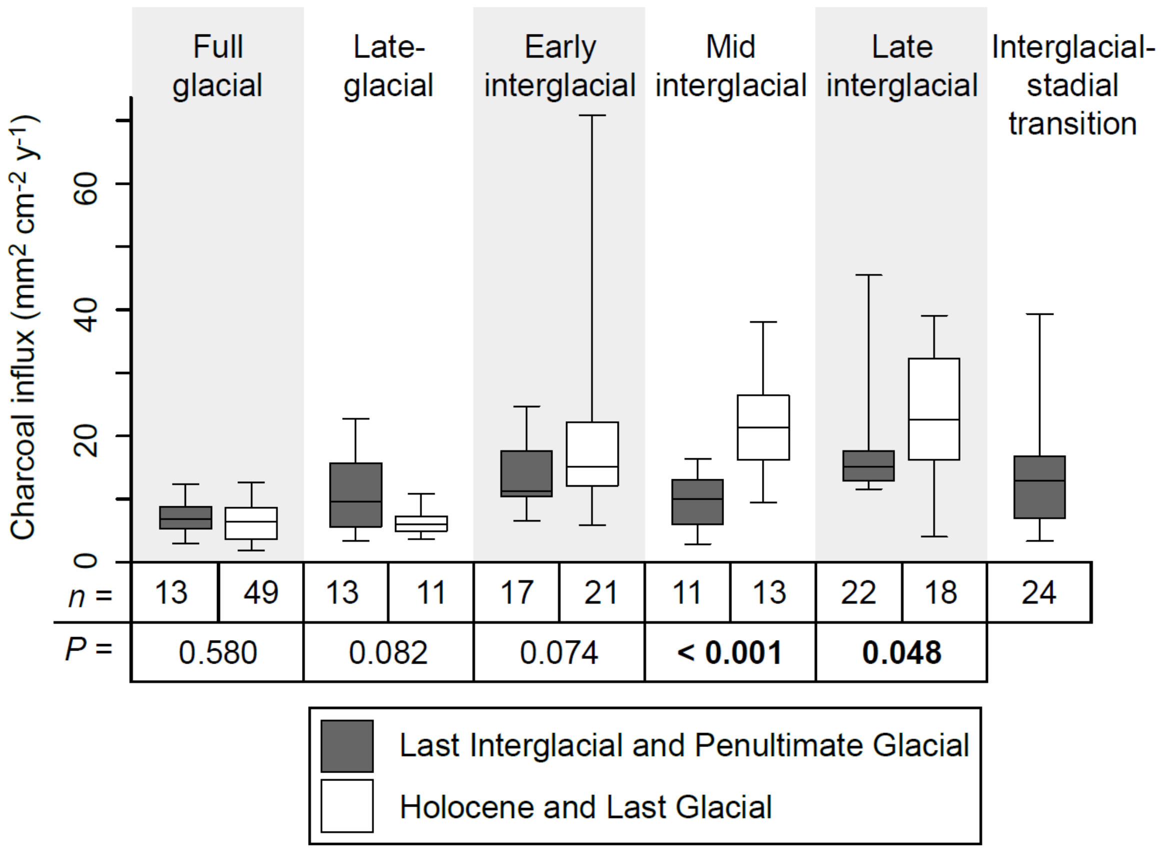

Last Inter-
glacial and
Penultimate
Glacial
Holocene
and Last
Glacial
Sediment accumulation
rate (mm y-1)
0
0.1
0.2
Arboreal pollen (%)
0
20
40
60
80
100
Dome C CO2 (ppmv)
200
250
June insolation
at 40°N (W m-2)
460
500
540
120
100
80
60
40
20
0
Age (ka)

Fig. 3



Last Interglacial and Penultimate Glacial
Holocene and Last Glacial
Charcoal influx (mm^2 cm^{-2} y^{-1})
Pollen influx (x 10^4 grains cm^{-2} y^{-1})
Steppe (%)
Maquis (%)
AP (%, dashed)
Deciduous trees (%, solid)
Pinus (%)
Dome C CO_2 (ppmv)
June insolation at 40°N (W m^{-2})
Full gl.
Lategl.
Early intergl.
Mid intergl.
Late interglacial
Interglacial-stadial transition
Full glacial
Lategl.
Early intergl.
Mid intergl.
Late interglacial
Age (ka)
Age (ka)

Fig. 4


Full glacial
Late-glacial
Early interglacial
Mid interglacial
Late interglacial
Interglacial-stadial transition
Charcoal influx (mm2 cm-2 y-1)
0
20
40
60
n =
13
49
13
11
17
21
11
13
22
18
24
P =
0.580
0.082
0.074
< 0.001
0.048
Last Interglacial and Penultimate Glacial
Holocene and Last Glacial