Quaternary Science Reviews 29 (2010) 1082–1092

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

Holocene fire activity and vegetation response in South-Eastern Iberia

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A R T I C L E I N F O

Article history:
Received 17 November 2008
Received in revised form
30 December 2009
Accepted 12 January 2010

A B S T R A C T

Since fire has been recognized as an essential disturbance in Mediterranean landscapes, the study of long-term fire ecology has developed rapidly. We have reconstructed a sequence of vegetation dynamics and fire changes across south-eastern Iberia by coupling records of climate, fire, vegetation and human activities. We calculated fire activity anomalies (FAAs) in relation to 3 ka cal BP for 10–8 ka cal BP, 6 ka cal BP, 4 ka cal BP and the present. For most of the Early to the Mid-Holocene uneven, but low fire events were the main vegetation driver at high altitudes where broadleaved and coniferous trees presented a highly dynamic post-fire response. At mid-altitudes in the mainland Segura Mountains, fire activity remained relatively stable, at similar levels to recent times. We hypothesize that coastal areas, both mountains and lowlands, were more fire-prone landscapes as biomass was more likely to have accumulated than in the inland regions, triggering regular fire events. The wet and warm phase towards the Mid-Holocene (between ca 8 and 6 ka cal BP) affected the whole region and promoted the spread of mesophytic forest co-existing with *Pinus*, as FAAs appear strongly negative at 6 ka cal BP, with a less important role of fire. Mid and Late Holocene landscapes were shaped by an increasing aridity trend and the rise of human occupation, especially in the coastal mountains where forest disappeared from ca 2 ka cal BP. Mediterranean-type vegetation (evergreen oaks and *Pinus pinaster-halepensis* types) showed the fastest post-fire vegetation dynamics over time.

1. Introduction

There is increasing evidence of the role of fire in explaining the history of the natural landscapes of the Mediterranean (Pausas and Keeley, 2009). Fire is a well known disturbance in Mediterranean ecosystems, and significant progress in fire ecology of these ecosystems has been achieved during recent decades (e.g. Keeley, 1991; Bond and Midgley, 2001; Bradstock et al., 2002; Pausas et al., 2004). Fire is now considered an inherent element of many ecosystems, including those of the Mediterranean (e.g. Ojeda et al., 2005; Pausas et al., 2008); however changes in fire activity may greatly impact the sustainability of some ecosystems (Lavorel et al., 1998; Elmqvist et al., 2003; Moritz and Stephens, 2008). Hence the understanding of long-term relationships between vegetation, climate change and fluctuations in fire and human activity in the Mediterranean basin may help to assess the ecosystem's resilience to changing fire activities and human impact. Since conventional ecology is often limited when addressing issues within time frames beyond instrumental records, palaeoecological methods may serve as an adequate alternative, as proven by the abundant literature that has been produced across the European Mediterranean region (Colombaroli et al., 2007, 2008; Sadori and Giardini, 2007; Vannière et al., 2008; Tinner et al., 2009). This is especially relevant under the current scenario of increasing temperatures in Southern Europe (Pausas, 2004), where fire management may be critical in the near future for biodiversity and landscape management.

The southern European peninsulas are characterized by a long history of human occupation which has also determined the vegetation structure and its response to rapid environmental fluctuations. In this sense the Iberian Peninsula is no different, and its southern sector has been shaped by cultural transitions, from metallurgic to agro-pastoral societies that have occupied the area at various times and places.

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doi:10.1016/j.quascirev.2010.01.006

This study is focused on understanding Holocene vegetation history and the local fire activity of south-eastern Spain (Fig. 1). Specifically, we aim 1) to explore the change in fire activity and vegetation throughout the Holocene in SE Iberia; and 2) to infer the role of climate and human activity as drivers for vegetation change. To answer these questions we combined the results from six pollen and charcoal records from an altitudinal gradient in order to analyze the long-term post-fire vegetation response to different degrees of human occupation and topographical complexity.

2. Study area

The six sites studied are situated along an environmental gradient from 225 to 1900 masl (Fig. 1, Table 1) in south-eastern Iberia. This region includes several of the most arid territories of Europe (Puigdefábregas and Mendizábal, 1998) although the topographical complexity makes rainfall and temperature vary considerably from the highest Baetic Mountains to the Tabernas Desert. The region is a hotspot of plant diversity (Médail and Quézel, 1999) lying on the Baetic–Rifan complex, and subject to increasing human pressure due to growing population density and all the direct and indirect impacts associated with it (Blondel and Aronson, 1999).

2.1. Vegetation patterns

The current vegetation of the study area is dominated by Mediterranean shrublands with some patches of forest. High-elevation areas above 1400 m are dominated by scrublands of *Berberis hispanica* and *Juniperus oxycedrus*, with *Crataegus monogyna*, *Quercus rotundifolia*, *Lonicera arborea*, *Prunus ramburii* and a ground cover of hard-leaved grasses; *Pinus nigra* and *P. sylvestris* are the conifers representative of the uppermost forest belts. Prostrate thorns, such as *Vella spinosa*, *Hormatophylla spinosa*, *Erinacea anthyllis*, or *Echinospartum boissieri*, become the dominant vegetation in the wind-exposed areas above 1800–1900 m. The area between 800 and 1400 m is dominated by evergreen holm oaks while the deciduous oak forests are restricted to the most humid sites on deep soils. These prevail in the west and northwest slopes in Siles, dominated by *Quercus faginea*, occasionally

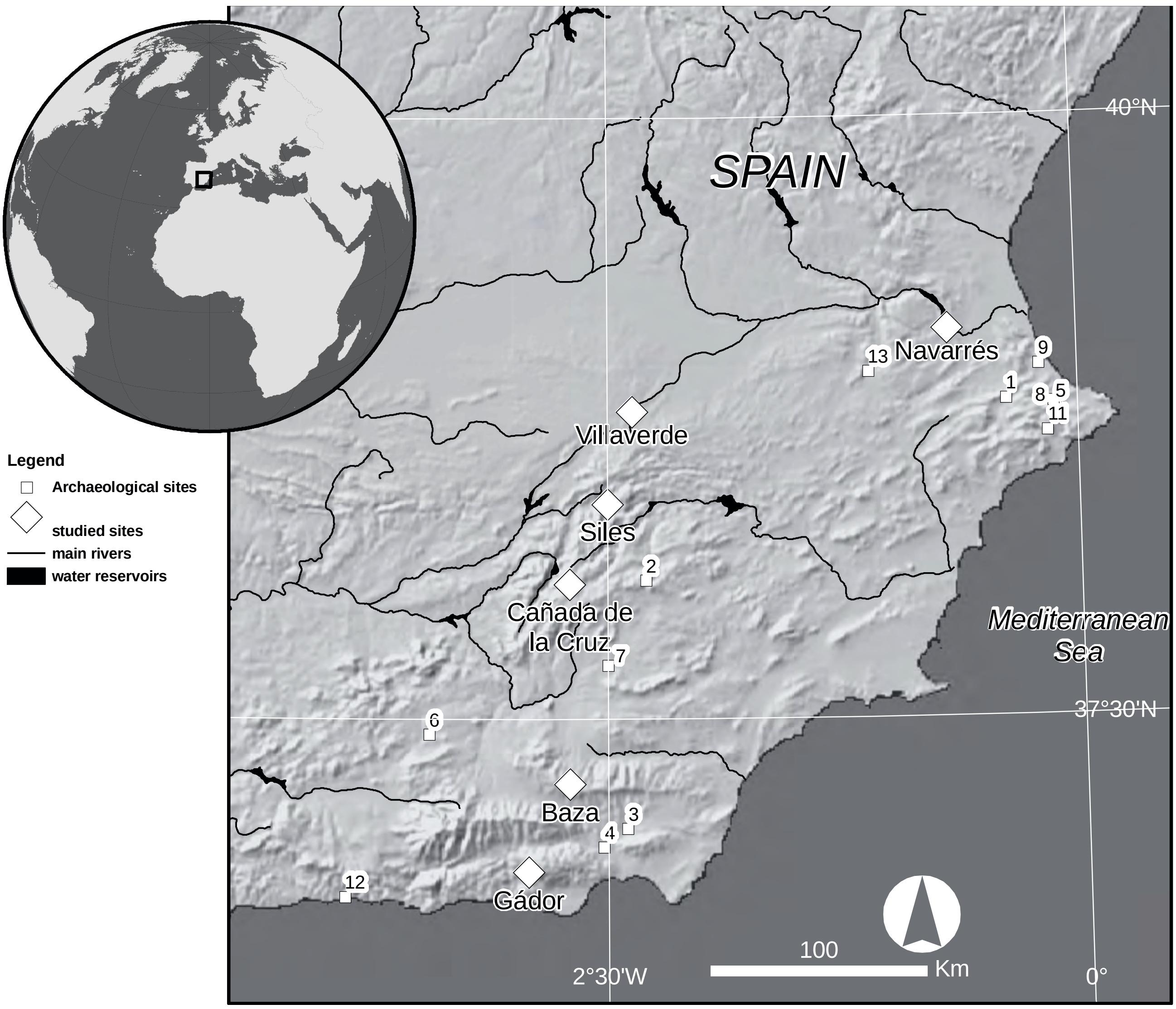

Fig. 1. Location map for the studied locations (white diamonds) and the archaeological sites (white squares): 1, Cova de l'Or; 2, Cueva del Nacimiento; 3, Terrera Ventura; 4, Los Millares; 5, Les Jovades; 6, Carihuela; 7, Cerro de la Virgen; 8, Cova Ampla; 9, Cova de la Recambra; 10, Cueva del Toro; 11, Les Cendres; 12, Nerja; 13, San Benito. Further details for the study and archaeological sites are shown in Tables 1 and 2 respectively.

Table 1
Physical settings of the six sites analyzed including the time span recorded in every chronology. MAT: Mean annual temperature (°C), MAP: Mean annual precipitation (mm), Ref: original references where more information about vegetation history can be found: 1. Carrión et al. (2007), 2. Carrión et al. (2001a) 3. Carrión et al. (2003a), 4. Carrión (2002), 5 Carrión et al. (2001b), 6. Carrión and Van Geel (1999).

Locality	Type	Lat.	Long.	Alt. (masl)	Modern vegetation	Climate	MAT	MAP	Time span (cal yrs BP)	Ref
Baza	Peat deposit	37°14′	2°42′	1900	Mosaic of pine, oak and mixed pine-oak woodlands	Oromediterranean, cold continental	4–8	500–600	160–8390	1
Cañada de la Cruz	Shallow lacustrine deposit	38°04′	2°42′	1595	Dwarf junipers (*Juniperus sabina* and *J. communis*), some *Pinus nigra* stands and a thorny prostrate scrub	Oro/Supramediterranean, cold continental	5–8	700–800	1955AD–9350	2
Gádor	Shallow lacustrine deposit	36°52′	2°55′	1530	Sparse presence of trees: *Pinus*, *Quercus* with a continental understorey	Supramediterranean, cold continental	11–12	450–500	1160–6850	3
Siles	Lake	38°24′	2°30′	1320	Patches of *Pinus nigra*, *P. pinaster* and evergreen *Quercus* . *Juniperus* is relatively frequent	Mesomediterranean, cold subhumid	10–11	800–1000	504–9840	4
Villaverde	Tufaceous peat	38°47′	2°22′	870	Patches of evergreen *Quercus*, scattered *Juniperus* and *Pinus* (*P.Pinaster* and *P. nigra*) woodlands in the adjacent mountains	Mesomediterranean, dry continental	13–14	400–450	1160–9730	5
Navarrés	Peat overlying a lacustrine deposit	39°7′	0°41′	225	Garrigue and cultures with patches of evergreen *Quercus*	Thermomediterranean	15–16	500–550	3378–10186	6

accompanied by *Acer granatense* and rarely *Taxus baccata*, with relict *Corylus avellana* forests developed in shady valleys. The zone between 200 and 800 m is characterized by rich communities of *Pistacia lentiscus*, *Quercus coccifera*, *Chamaerops humilis*, *Ephedra fragilis*, *Olea europaea*, and a diversity of thorny Fabaceae. Xerosclerophyllous brushwood characterized by Ibero-North African species as *Maytenus europaeus*, *Ziziphus lotus*, *Periploca angustifolia*, *Withania frutescens* and perennial chenopods, are abundant along the southern and eastern slopes below 400 m.

2.2. Archaeological settings

Archaeological sites in the region are very diverse, both continuity and age wise. However, human occupation has been apparent since early Neolithic times and particularly intense at some of the sites (Table 2). The settlement pattern has been featured by phases of intense occupation alternating with episodes of abandonment, and it is likely that the early human communities were unevenly distributed across SE Iberia (Carrión et al., 2007).

Human occupation was earlier in the mountain areas of Baza and Gádor than at lower elevations at Siles and Villaverde (Sánchez-Quirante, 1998). At Siles, pastoralism and deforestation are recorded since 7.5 ka cal BP (Castro et al., 1999; Barandiaran et al., 2002) while Villaverde, by contrast, was not occupied probably because these inland sites have a rough topography with arduous access conditions, include fairly unproductive soils and harsh, continental climates. In the other extreme is Navarrés, where its temperate setting, fertile land and sheltered situation at the bottom of a valley have supported human settlements since the Upper Palaeolithic and early Neolithic (Martí et al., 1980; Martí, 1988; Díaz-Andreu and Keay, 1997), with yet stronger human pressure since 4 ka BP (Butzer, 2005; McClure et al., 2008). Well documented archaeological settlements also appear at Baza and Gádor (Sánchez-Quirante, 1998). The occupation of these areas expanded in the Bronze Age (Chalcolithic and Argaric periods in the regional terminology) and Roman period (Díaz-Andreu and Keay, 1997; Rodríguez-Ariza and Moya, 2005).

In the inland mountains (Cañada, Siles and Villaverde) archaeological evidence is not as clear, and anthropogenic activity is difficult to trace prior to the Roman occupation (ca 2000 yr BP) (Díaz-Andreu and Keay, 1997; Rodríguez-Ariza and Moya, 2005). Livestock grazing may have been present for longer, since these are montane areas suitable for summer pastures and livestock was already present in the peripheral lowlands (Martí, 1988).

The increasing human impact before and from the Roman period has been extensively documented (Rodríguez-Ariza and Ruiz-Sánchez, 1993; Cámalich and Martín, 1999; Rodríguez-Ariza

Table 2
Number, names and age of the archaeological sites in Figs. 1 and 4. Meso refers to Mesolithic.

Number	Archaeological site	Age
1	Cova de l'Or	Neolithic
2	Cueva del Nacimiento	Neo-Chalcolithic
3	Terrera Ventura	Chalcolithic
4	Los Millares	Chalcolithic
5	Les Jovades	Chalcolithic
6	Carihuela	Neolithic
7	Cerro de la Virgen	Chalcolithic
8	Cova Ampla	Neolithic
9	Cova de la Recambra	Chalcolithic
10	Cueva del Toro	Neolithic
11	Les Cendres	Meso-Neolithic
12	Nerja	Neolithic
13	San Benito	Neolithic

Mesolithic, 12–7.4 cal ka BP; Neolíthic, 7.4–5.7 cal ka BP; Chalcolithic, 5.7–4.5 cal ka BP.

and Moya, 2005). Social and economic development increased with demographic pressure. This population pressure would have caused a considerable environmental transformation in order to satisfy the agricultural, and trade demands of the Roman Republic (Blázquez Martínez, 1974). Similarly, the Roman occupation brought the expansion of species with economic value such as *Olea* (Rodríguez-Ariza and Moya, 2005).

2.3. *Current fire activity*

Fire frequency in peninsular Spain for the period 1974–2000 has been analyzed by Vázquez et al. (2006) in 10 × 10 km grid units. While the national average is ca 56 fire events per grid, Vázquez et al. (2006) report between 5 and 25 fires over the 26 years in most of the six study site grids, except for Navarrés where the number of fires is between 25 and 100. The relatively high fire activity in Navarrés is probably related to human activities since this site shows a higher population density; this fact, together with important landscape changes, increases the probability of starting and spreading fires (Pausas, 2004).

3. Materials and methods

3.1. *Pollen, charcoal and dating*

The Holocene vegetation and fire records are derived from lacustrine and peaty sediments (Carrión and Van Geel, 1999; Carrión et al., 2001a,b, 2003a, 2007; Carrión, 2002) (Table 1) where fossil pollen, micro- and macrocharcoal have been analyzed. When possible, two types of *Pinus* pollen were distinguished; *pinaster-halepensis* type and *sylvestris-nigra* type. For the purposes of this paper, the palynomorphs found have been grouped under different functional types based on life form, leaf type and post-fire regeneration strategy (Table 3). Microscopic charcoal particles in pollen slides were counted following the method proposed by Tinner and Hu (2003) and Finsinger and Tinner (2005). Charcoal concentration particles (cm^{-3}) were estimated with the same method as for pollen; charcoal area ($mm^2\ cm^{-3}$) was calculated following Tinner and Hu (2003). Charcoal accumulation rate (CHAR, $mm^2\ cm^{-2}\ yr^{-1}$) was used in order to have a time-fitted value of charcoal. Contiguous core sampling would provide the temporal resolution necessary to detect individual fire events and therefore would help reconstructing local fire regimes. Since our charcoal record is based on pollen-slide charcoal counting, in widely spaced core samples, we cannot accurately reconstruct fire frequencies. However changes in charcoal abundance provide valuable information for comparisons of fire activity between periods (Whitlock et al., 2006).

Chronologies are based on radiocarbon-dated bulk sediment from every core following conventional and AMS methods. Dates were calibrated using the curve INTCAL98 included in CALIB 4.3 (Stuiver et al., 1998) (Table 1). Age–depth models were based on linear interpolation between adjacent pairs of dates. Pollen diagrams were produced using the software Tilia and TiliaGraph (Grimm, 1991) and edited with Corel Draw X3©.

3.2. *Fire activity anomalies (FAAs)*

In order to understand the fire dynamics at critical phases of climate change of human occupation we calculated the fire activity anomalies (FAAs) of target periods versus 3 ka cal BP, when more intensive human activities are reported across the area (Martí, 1988). Therefore the anomalies correspond to the difference in CHAR at particular times in comparison with the 3 ka cal BP values. A similar approach was used by Whitlock et al. (2007) to determine the climatic controls of Holocene fire patterns in South America in reference to the European arrival.

Prior to anomalies estimation, CHAR series were normalized following Carcaillet et al. (2002). As explained by these authors, CHAR normalization allows series to be assessed using a comparable scale for all the sequences (Fig. 2a and c), reducing the variability due to sedimentation rate, vegetation type or catchment physiography. Normalized charcoal series (NCHAR) were averaged per millennium, so each data point to calculate FAA is centred on a millennium, e.g. 6 ka corresponds to time elapsed between 6500 and 5500 calibrated years before present. When data were available, NCHAR was averaged for the present which corresponds to the last 500 years (Carcaillet et al., 2002).

We have characterized FAAs for four different periods as positive, negative, strongly negative or without change in comparison to the fire activity during 3–2 ka BP. The NCHAR values used for the FAA estimation correspond to the Early Holocene, defined as 10–8 ka BP – because some of the chronologies record less than 10 ka (Baza and Gádor); Mid-Holocene, corresponding to 6 ka cal BP; Late Holocene, which corresponds to 4 ka cal BP and the Present which is referred to the last 500 years.

4. Results

4.1. *Holocene fire activity in south-eastern Iberia*

Fire activity, deduced from NCHAR sequences (Figs. 2, 3a and b), shows a general stability during the early Holocene, with decreasing values towards the early- mid-holocene transition and a widespread increase since ca 3 ka cal BP. In spite of this general regional trend in fire activity, abrupt fire fluctuations and inter-site variability should not be overlooked. The coastal mountains sites, and the lowland site of Navarrés show unstable NCHAR values since the early Holocene. In particular Baza and Gádor were subject to rapidly fluctuating fire activity for most of the first half of the Holocene, finally increasing since 3–2 ka cal BP. The more continental locations at middle altitudes show minor changes in fire activity for much of the Holocene, especially in the case of Cañada and Villaverde, while fire activity at Siles oscillates faster. The FAAs compared to 3 ka cal BP suggest a general concurrence of negative

Table 3
Plant type, life form and regeneration strategy after crown-fire of the taxa discussed in this paper.

Acronym	Plant type	Taxa included	Life form (or functional type)	Post-fire response strategy
MES	Mesophytes	*Fraxinus, Salix, Acer, Castanea, Corylus, Betula, Alnus*	Broadleaf deciduous trees	Obligate resprouters
Querdec	Deciduous *Quercus*	*Quercus faginea*	Broadleaf deciduous trees	Obligate resprouters
MED	Mediterranean	*Pistacia, Phyllirea, Olea, Rhamnus*	Broadleaf evergreen trees and shrubs	Obligate resprouters
Querever	Evergreen *Quercus*		Broadleaf evergreen trees/shrubs	Obligate resprouters
Quersub	*Quercus suber*		Broadleaf evergreen trees/shrubs	Obligate resprouters
Pinpin	*Pinus pinaster, P.halepensis*		Needleleaf evergreen trees	Obligate seeder
Pinnig	*Pinus nigra, P. sylvestris*		Needleleaf evergreen trees	Without any strategy
ANTHR	Anthropic elements	*Juglans, Plantago, Cerealia, Centaurea, Papaver*	Variable	Variable
XER	Xerophytes	*Artemisia*, Asteraceae, Chenopodiaceae, *Ephedra*, Lamiaceae	Variable (mainly shrubs and scrubs)	Variable

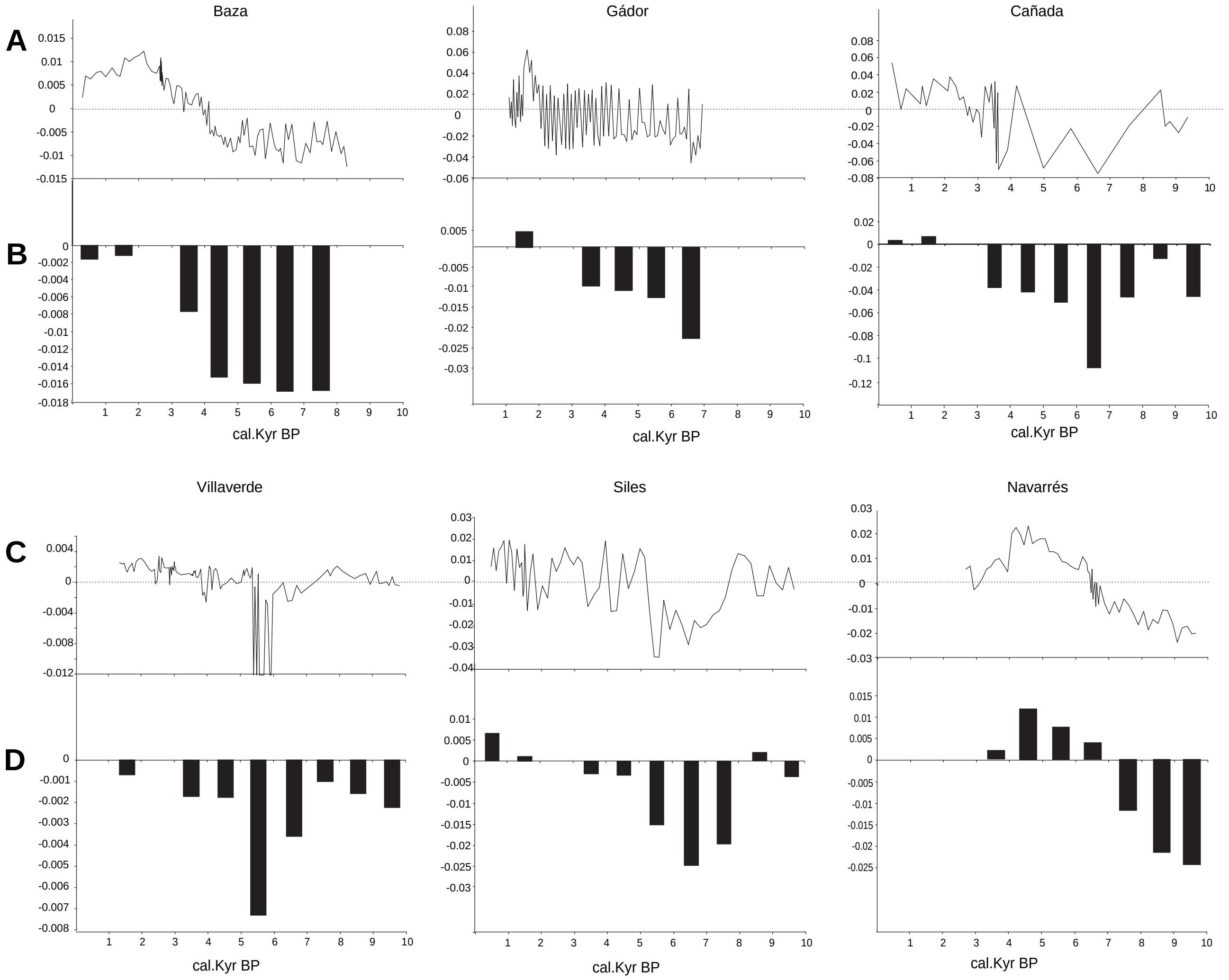

Fig. 2. NCHAR (A and C) and millennial averaged FAA (B and D) for the sites studied in this paper. NCHAR and FAA have no units (see details in text).

anomalies at 10–8 ka cal BP that becomes strongly negative during 6 ka BP to reach a stable negative value at 4 ka BP (Fig. 4). Interestingly, positive FAAs are almost absent for most of the Holocene but in the case of Navarrés and for other inland sites during the last two millennium, confirming the overall regional increase of fire activity for the last three thousand years.

4.2. *Regional vegetation change inferred from fossil pollen*

Despite different chronologies and time resolution over the sequences, it is possible to describe a general pattern of vegetation change comprising four main phases (Fig. 3a and b):

1. Early Holocene (10–7.5 ka cal BP). During this period of *Pinus* forests dominate at most of the sites. All the localities show plant assemblages where the mesic component is scarce while *Pinus* is abundant; especially *Pinus nigra-sylvestris*. The woodlands represent a legacy of the lateglacial developments where *Pinus* has a key role in the woodlands while preserving a poor understory (Carrión et al., 2001a).
2. Middle Holocene (7.5–6 to 4.5 ka cal BP). A regional increase in mesophytes and deciduous *Quercus* is remarkable. Pines progressively decline although not synchronously at all of the sites. Microfossils indicative of relatively high lake levels (e.g. *Botryococcus*) prevail during this period (Carrión, 2002). Different trends in lake level occurred, with these indicators decreasing in Gádor and increasing in Navarrés through time.
3. Mid-late Holocene transition (4.5–2 ka cal BP). The landscape in eastern Iberia shows an important reduction in tree cover and a greater role of the herbaceous layer dominated by xerophytes and Poaceae. The remaining woody elements include Mediterranean scrub and evergreen *Quercus* and a fluctuating occurrence of *Pinus* and deciduous oaks.
4. Late Holocene (2 ka BP to the present). There is a general opening of the landscape where the grasses, thorny scrub, and xerophyte component become dominant. A prominent increase in the anthropogenic pollen indicators is identified in Siles, concurrent with *Pinus* re-expansion in most of the records except at Baza.

5. Discussion

The existence of long-term fire activity patterns in the Mediterranean Basin has been proved in different local and regional approaches (Wick et al., 2003; Colombaroli et al., 2007; Sadori and Giardini, 2007; Sadori et al., 2008; Turner et al., 2008; Vannière et al., 2008; Tinner et al., 2009). These approaches show in some cases synchronous trends but also many unexpected ecosystem responses

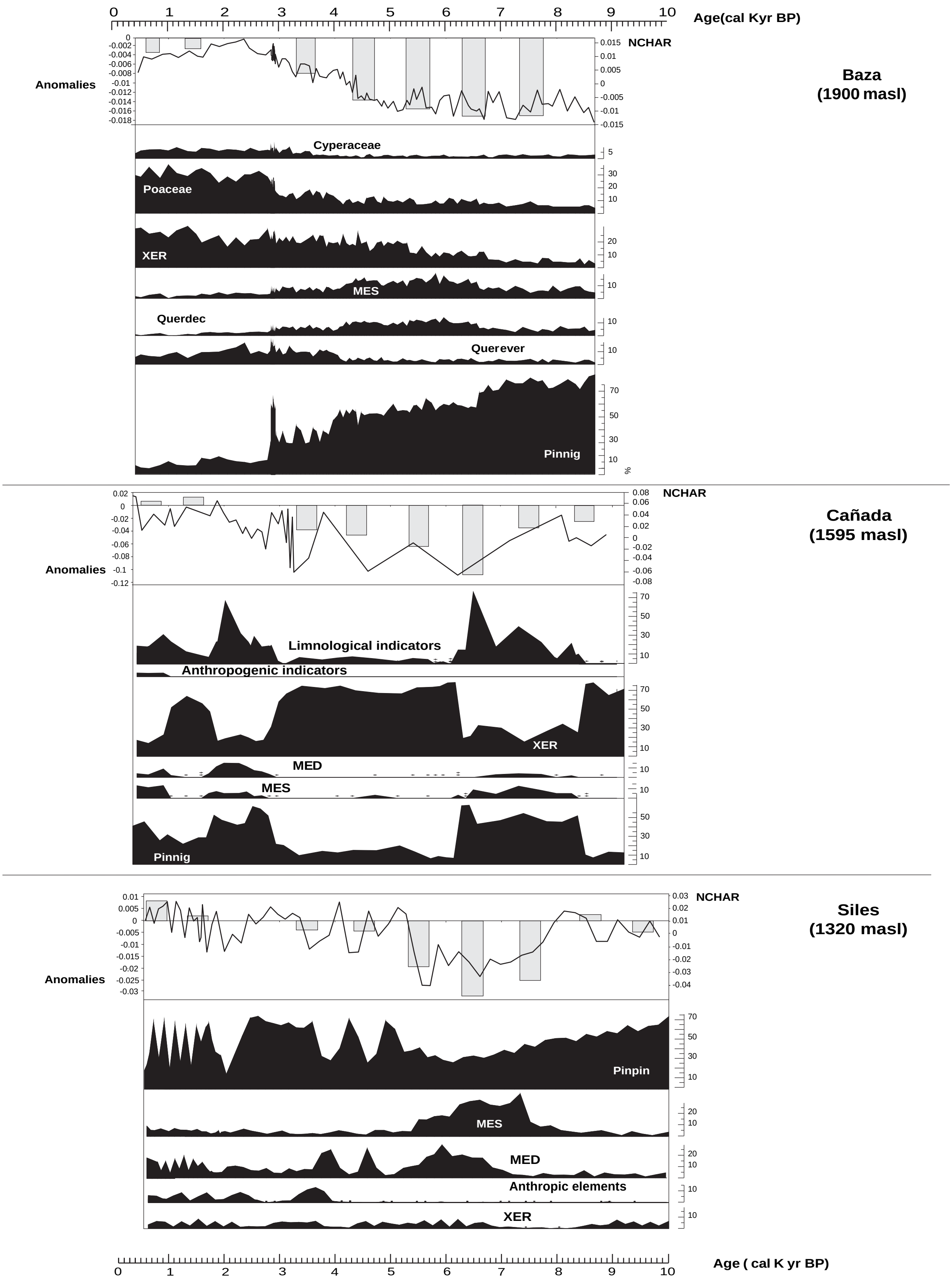

Fig. 3. (a) Synthetic pollen percentage diagrams for Baza, Cañada and Siles, with the NCHAR and millennial averaged FAA sequences shown on top. The taxa are grouped according to plant functional types in Table 3. (b) Synthetic pollen diagrams for Gádor, Villaverde and Navarrés, with the NCHAR and millennial averaged FAA sequences shown on top. The taxa are grouped according to plant functional types in Table 3.

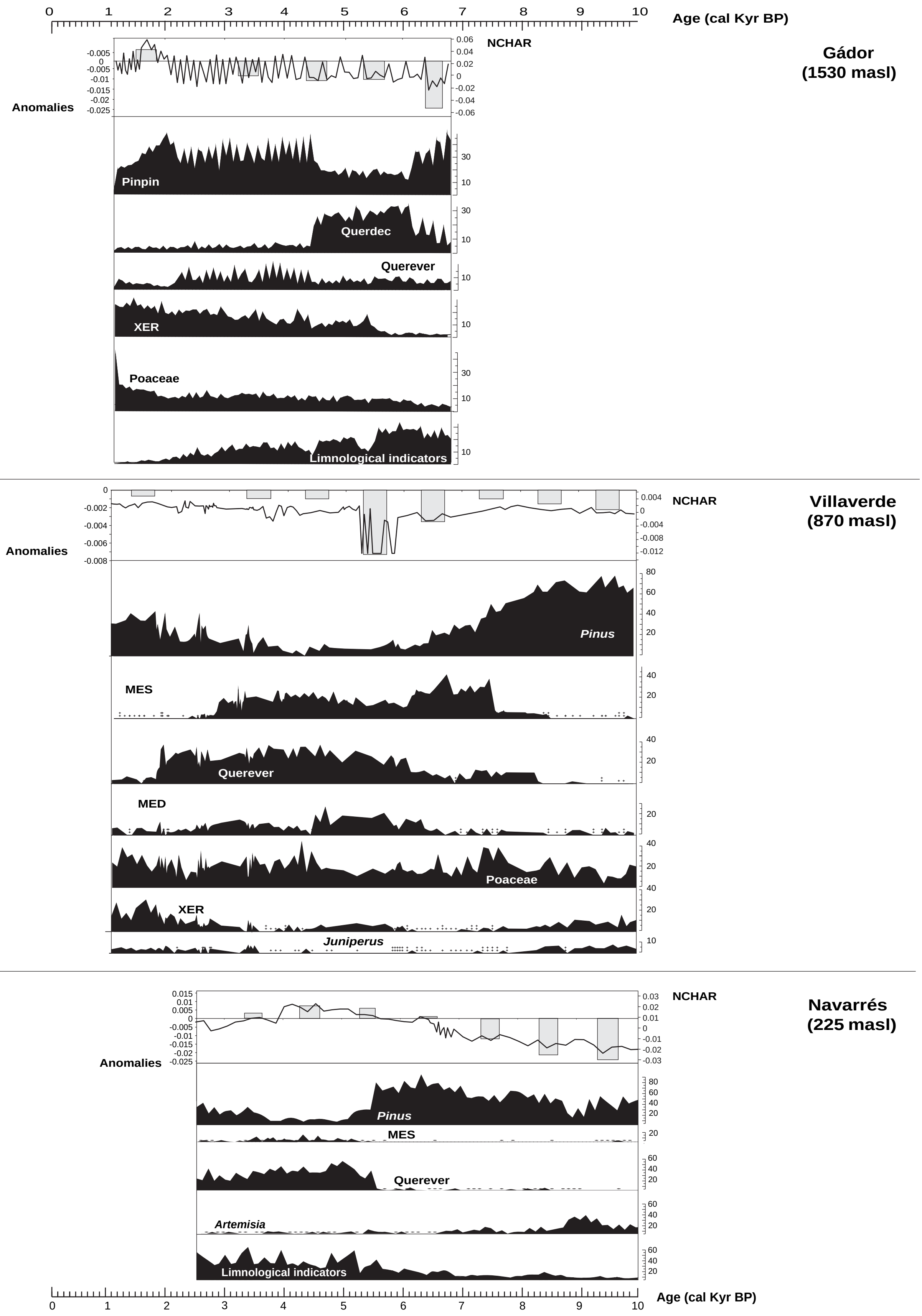

Fig. 3. (*continued*).

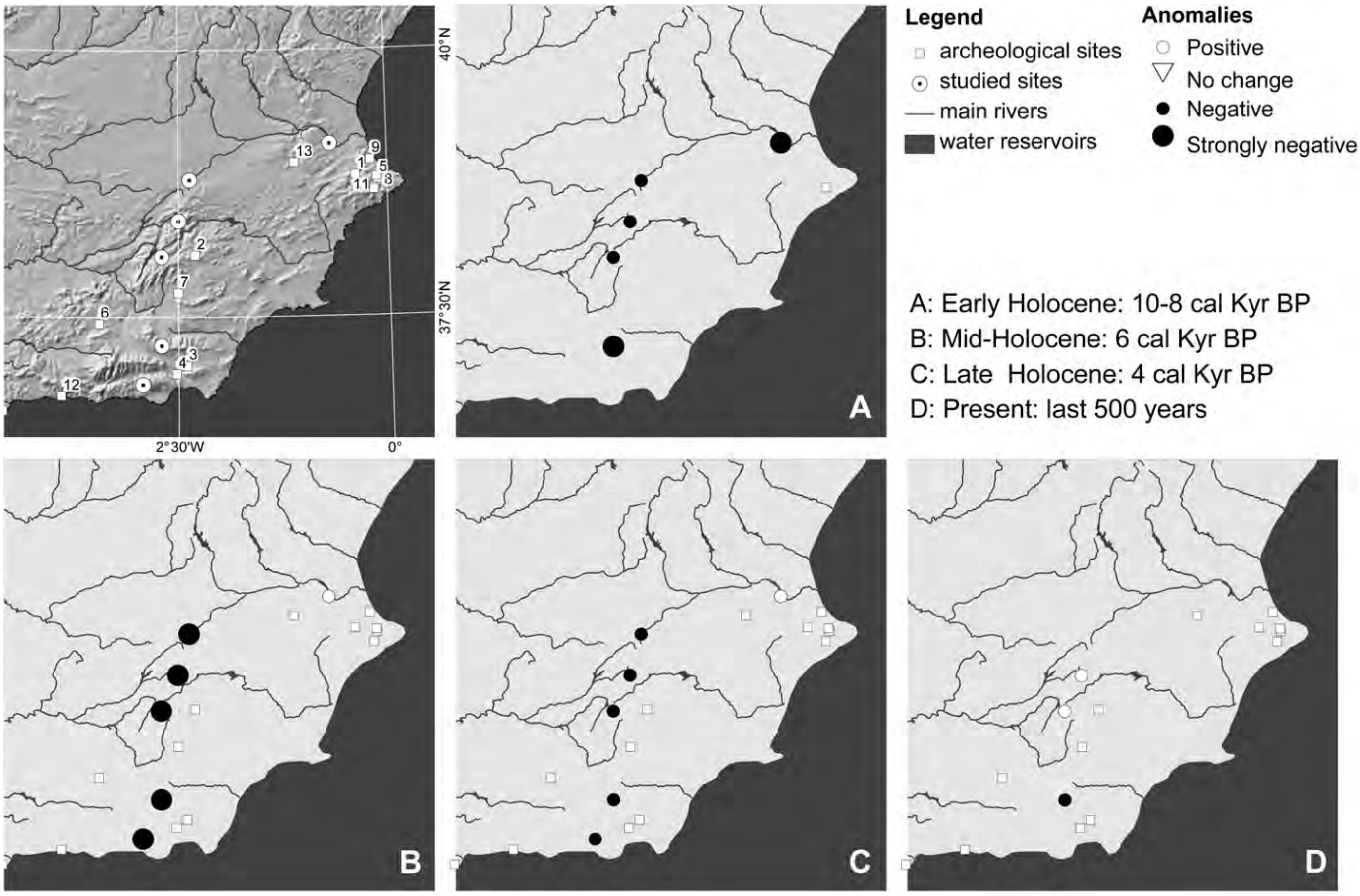

Fig. 4. Fire anomalies based on NCHAR differences between the target periods and 3 ka cal BP. This difference is qualitatively represented in every map period as strongly negative (large dark dots), negative (small dark dots), no change (inverted triangles) or positive (empty dots). Archaeological sites are represented as empty squares in every map (see details in text and Table 2).

due to particular physical settings, microclimatic aspects and different models of human agency. South-eastern Iberian forest dynamics agree with this sub-continental framework and, as illustrated in this paper, fire activity has fluctuated temporally but also spatially throughout the Holocene (Figs. 3a, b and 4). This finding is in agreement with current fire activity in Mediterranean ecosystems, which has been demonstrated to be very erratic in time and space depending on land use, population density, biomass fragmentation and fuel availability (Pausas, 2004; Vannière et al., 2008).

5.1. Fire activity anomalies and vegetation response: the role of fire in south-eastern Iberia

Relatively colder conditions than those of today would have prevailed in the region during the onset of the Holocene. The decreasing difference between January and July insolation at 37°N would have produced a lessening of temperature seasonality during the Early Holocene, with warmer winters and cooler summers. Under this early holocene climate, cooler than today's, but not necessarily drier, pine woodlands developed under post-glacial conditions were still successful. Some of these wooded areas in the mountains were probably Scots or European black pine forest supported by the low fire activity – negative FAA across the region. These pines lack any particular post-fire strategy (Table 3) (Tapias et al., 2001; Pausas et al., 2008) and therefore they are less successful than the Aleppo and Maritime pines (with serotinous cones) under intense canopy fire regimes. Thus during this period fires would have been limited to the understory level.

The Holocene temperature rise in the Mediterranean Basin has been widely discussed across different regions (Cheddadi et al., 1996; Prentice and Webb, 1998; Sadori et al., 2008; Tinner et al., 2009) as well as in the Iberian Peninsula (García Antón et al., 1995, 1997; Franco Múgica et al., 1998, 2001; Carrión et al., 2001a,b; Benito Garzon et al., 2007; Gil García et al., 2007; Morellón et al., 2008). These studies report a more benign climate with a shorter drought season between ca 8.5 and 5.5 ka cal BP. Broadly speaking a tendency towards warmer and wetter climate is found in all the records considered in the present analysis where broadleaved trees – both evergreen and deciduous – replaced conifers in most sites. Some of these areas would have acted as glacial refugia, enclosing some marginal oak forests that would have remained over the glacial and postglacial period (Brewer et al., 2002; Petit et al., 2002; Carrión et al., 2003b). Broadleaved elements were continuously present at the coastal mountain areas since the beginning of the Holocene, while in the intramontane regions and the lowlands the spreading of deciduous forest began abruptly at ca 8 ka cal BP as a consequence of the favourable climatic conditions. Thus deciduous *Quercus* and mesophytes reached their maximum expansion between 7.5 and 6 ka cal BP, when the lowest fire activity (low levels of both CHAR and FAA) is registered, except at Navarrés where the mid-Holocene presented positive FAAs (Figs. 2, 3a, b and 4). If fire activity is reduced, mesophytes become superior competitors to Aleppo and Maritime pines, which are shade intolerant and obligate seeders (i.e., they germinate readily after fire and increase their population size in the open spaces generated by the fire). On the whole, a likely mid-holocene scenario in the SE

Iberian Peninsula would imply the initial expansion of mesophytes and evergreen *Quercus* owing to warmer and wetter conditions as fire activity decreased due to shorter dry seasons produced by a less marked seasonal insolation. These results are coherent with the mid-holocene vegetation response found at similar latitudes in Southern Europe (Sadori and Giardini, 2007; Tinner et al., 2009), where decreasing fire activity aided by growing moisture availability permitted the expansion of broadleaved forests (Vannière et al., 2008).

Interestingly all sites, but Navarrés, show similarly negative FAA at 4 ka cal BP, indicating an increment in fire activity compare to the previous Mid-Holocene phase, but still not as high as the fire activity after 3 ka cal BP (Fig. 4). Arid events over the second half of the Holocene in the Mediterranean Basin have been extensively recognized, although happening at different intervals in different regions (Tinner et al., 2009). After the benign climate during the mid-Holocene, arid conditions were probably strengthened in south-eastern Iberia through recurrent drought spells (Carrión et al., 2007). Fire activity steadily intensified since ca 6 ka cal BP, being particularly strong from ca 4 ka BP onwards (Vannière et al., 2008), promoting the regional spread of Mediterranean and xerophytic taxa.

Increasing aridity and fire activity would have triggered fast threshold responses in the *Quercus* and *Pinus* forests (Carrión 2002), with fast but resilient changes between 5 and 2 ka cal BP, as happened in the mountains of Gádor. Simultaneously, the changing fire pattern between 6 and 4 ka cal BP probably facilitated the succession from the southern Iberian mesophytic woodlands into a more Mediterranean scrub composition. This reaction would not be exclusively dependent on the post-fire strategy as deciduous and evergreen *Quercus*, as well as many other Mediterranean taxa, are resprouters (Table 3), responding effectively to fire. However, only the schlerophylls would have been able to spread faster than mesophytes within the increasingly arid conditions. A likely regional landscape during the mid-late holocene transition would be one where, under higher fire activity than the Mid-Holocene and increasing aridity, the evergreen component thrived better.

During the Late Holocene, from ca 3 ka cal BP onwards, forests became relatively unstable and very responsive to the strong fire dynamics. Fire activity, although not necessarily stronger in terms of intensity and frequency – since these are parameters difficult to assess from pollen-slide charcoal counts – turned into abrupt episodes, as those at Siles or Gádor. Thus oak forest and mountain pines contracted and xerophytes expanded as fire activity became more dynamic in all sites recorded. The last millennium shows positive FAA in Siles and Cañada and still negative in Baza, where the maximum fire activity occurred at 3–2 ka cal BP.

5.2. *Fire pattern in the context of climate and human driven changes*

Differences in the fire signal recorded in the six sites suggest that fires are sensitive to the environmental gradient separating more continental mid-altitude sites from high altitude coastal ranges. This is noticeable in the mountain areas of Baza and Gádor where FAAs are relatively negative in all the time slices selected. At the inland sites, Villaverde, Siles and Cañada, CHAR values fluctuated synchronously, from levels similar to those reached at the Roman Period – ca 2 cal ka BP – to strongly negative, with a later rise. This pattern could be due to differences in the vegetation composition and to variable climatic constraints, but also to a heterogeneous pattern of human occupation. Thus while the inner part of the Segura mountains, Siles and Villaverde, have been much less inhabited (Jordán, 1992; Burjachs, 1997; Carrión, 2002) with a late human impact on vegetation, the southern mountains of Baza and Gádor have a long history of human occupation (Buxó, 1997; Sánchez-Quirante, 1998; Carrión et al., 2003a,b, 2007) as in the coastal area of Navarrés (Fig. 1 and Table 2).

Coastal mountains remained more humid than the continental sites under the early holocene climatic conditions. These areas experienced a faster forest expansion due to the Mediterranean influence while fire activity kept highly fluctuating levels. These fires were most likely climatically induced, although early grazing pressure cannot be rejected as the practice of burning to form new pastures has been recognized in these mountains during the Neolithic. Increasing human pressure over the Holocene would have changed fire controls from climatic to more human related. Thus mining activities have been very prevalent in the southern mountains being one of the oldest areas of Europe presenting metallurgy as a common practice. Chalcolithic settlements in this region occur between ca 5–4.9 and 4.4–4.2 ka cal BP (Castro et al., 1999; Nocete, 2001) (Fig. 4) and these would have implied an increasing need of wood resources. As late holocene aridity and human pressure continued towards Roman times, vegetation composition changed at high altitudes, leading to a *Pinus-Quercus* forest. These forests would have been resilient to fire between 6 and 2 ka BP to eventually recede in favour of more xerophytic elements and giving way to open landscapes. These would have represented a positive feedback to the increasing fire activity, so both human and climatic induced changes accelerated the fire dynamics from the mid-Holocene.

A different scenario appears in the more continental mid-altitude sites of the Segura range. Vegetation seems less responsive to fire activity, as this remained at relatively stable levels over time (Fig. 3a and b). Only in Siles was fire activity rather dynamic conditioning the *Pinus* forest response, with a strong positive feedback to fire activity as these are obligate seeding Mediterranean-type pines. Human pressure in these areas, although present, has always been less important than in the coastal sector; fewer settlements have been found and most of all them are from Roman-Medieval times. There is some evidence of grazing and hunter-gathering populations during the Neolithic but it is not clear the extent of agriculture in this area at that time (Buxó, 1997).

Navarrés constitutes a counterintuitive case of this regional model. This is the only site presenting a positive FAA during the Mid-Holocene while the spread of *Quercus* was delayed compared to other sites. It is worth considering that the same warm and wet mid-holocene phase provoked a different fire response in Navarrés. Increasing winter rainfall during the Mid-Holocene would have provoked the spread of a fire-prone biomass in the coastal lowlands and therefore more likely fire events as the precipitation–evapotranspiration ratio remained the same (Turner et al., 2008). Additionally, human activity could explain the increasing fire activity from 5 to 4 ka cal BP as these easily accessible valleys of Navarrés have been heavily populated since the Neolithic (Badal, 1988). Different phases of agriculture intensification have been recognized in these settlements from as early as 7 ka cal BP (Martí, 1988), as well as slash and burn in pine woodlands, although these are not easily recognizable in our record. These mid-Holocene fires would have promoted the forest change from Scots and European Black pine to oak and Aleppo pine, while a positive selection of oaks by humans could be possible owing to the fodder value of acorns for livestock. These hypothesis are not mutually exclusive and probably human agency, the mid-holocene biomass growth as well as the aridity trend imposed from the Mid to Late Holocene, would explain the positive FAA in Navarrés from ca 6 ka cal BP.

A plausible hypothesis explaining the differences in fire activity across the whole south-eastern region is that reduced moisture availability in the Segura range always conditioned slow forest development and biomass accumulation so open landscapes were more common than at higher altitudes, preventing fast and abrupt fire events. As human occupation increased at high altitudes, anthropogenic pressure became a superimposed factor influencing vegetation and accelerating fire dynamics with the subsequent vegetation response until the final forest collapse two thousand years ago. Since human impact was relatively scarce in the Segura area until relatively recent times, vegetation and fire dynamics would have always been primarily controlled by climate fluctuations and scarce fuel accumulation. The coastal lowlands were subject of increasing rainfall patterns during the Mid-Holocene promoting the biomass expansion and therefore a higher fire activity.

6. Conclusions

Through the combined analyses of fire activity and Holocene vegetation history from six localities in south-eastern Iberia we have improved our understanding of the long-term post-fire vegetation response and the fire–climate–vegetation relationship.

We have shown how Mediterranean forests in south-eastern Iberia experienced increasing fire activity phases for much of the Holocene up to the last 3 ka cal BP, from relatively negative fire activity anomalies during the early Holocene becoming strongly negative during the mid-Holocene to reach its maximum ca 3 ka cal BP. The different post-fire responses of the vegetation types partially explain the long-term vegetation dynamics. Accordingly mountain pines were probably worse competitors than oaks and Mediterranean scrub taxa under increasing fire activities, while Mediterranean pines (*Pinus pinaster-halepensis*) were more resilient to fire changes.

Despite regional discrepancies due to different environmental features, the coastal highlands have always been more populated than the inland ones presenting earlier and more abrupt fire activities. The coastal lowland vegetation responded positively to the mid-holocene increasing rainfall, spreading a mesophilous biomass and therefore the fire activity. The presence of human activity since the Neolithic would have enhanced the effects of the mid-late holocene arid pulses, increasing fire activity. In the Segura mountains climate conditions have controlled fire and vegetation dynamics for much of the Holocene, where only at ca 2 ka cal BP has anthropogenic action become evident. Overall, this study shows that long-term fire records are essential to address questions linked to forest resilience and threshold responses in Mediterranean landscapes, and are relevant to conservation and landscape management strategy.

Acknowledgements

This paper has been funded by the projects CGL2006-2956-BOS, GRACCIE CONSOLIDER INGENIO 2010 Ministerio de Ciencia e Innovación of Spain, and PaleoDiversitas Fundación Séneca, Murcia. We are thanked to Drs. Mitchell Powell and Philip Higuera, who made relevant suggestions for the quantitative analyses and to Dr. Thomas Gillespie for reviewing an early draft of this manuscript.

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