Patterns and processes of Late Quaternary environmental change in a montane region of southwestern Europe

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Abstract

This paper examines the Late Quaternary (c. 20,300–< 505 cal yr BP) environmental history of Siles, a lake situated at 1320 m in the Segura mountains of southern Spain, with the goal of establishing the mechanisms exerting control on vegetation change. Palaeoecological indicators include pollen, microcharcoal, spores of terrestrial plants, fungi, and non-siliceous algae, and other microfossils. The Siles sequence is shown to be sensitive to climatic change, although the control exerted by climate on vegetation is ultimately shaped by disturbances and species interactions, determining the occurrence of century-scale lags and threshold responses. Biotically induced changes of vegetation are also shown at the intrazonal level of variation. The new sequence is placed in the context of two previous records to postulate a picture of Holocene environmental change for the Segura region. The existence of mid-elevation glacial refugia for a number of temperate and Mediterranean trees is shown. A mid-Holocene phase (c. 7500–5200 cal yr BP) emerges regionally as the time of maximum forest development and highest lake levels. The early Holocene occurs as a generally dry, pyrophytic period of pine forests, with grassland scrub in high altitudes, and the late Holocene as a period of protracted vegetation sensitivity, with return to development of pine forests, spread of xerophytic communities, and increased fire activity, under the context of dry spells, localized anthropogenic disturbance, and shallowing and desiccation of lakes. Several events described here correlate with established times of abrupt transitions in the climates of northern Europe, the Mediterranean basin, north Africa, and the Sahel. © 2002 Elsevier Science Ltd. All rights reserved.

1. Introduction

Vegetation change can be conceived as result of a tension between historical accident and the determinism of the climatic system, that is between random and non-random processes. In the search for contingent explanations of current distributional patterns and models of ecosystem vulnerability, detailed studies of vegetational sequences at particularly sensitive areas such as southern Mediterranean Spain may be pertinent. It is challenging that concepts developed from research in north Europe may not be applicable in southern latitudes, where floras would have remained relatively stationary, and where biotic interactions among existing populations may be of further importance (Bennett and Willis, 1995). Indeed, available records from the southernmost areas of Europe do not show persistent trends through time or correlation with major climatic events of global scale (Valero and González, 1999; Carrión et al., 2000a). Unexpected trajectories in vegetation dynamics are therefore more a rule than an exception.

Two sequences from the Segura mountains, Betic Cordillera of southern Spain highlight the influence of ecosystem properties in the long-term dynamics of Mediterranean vegetation. The pollen record of Villaverde features the existence of lags, resilience, and thresholds in the response of forests to climatic change (Carrión et al., 2001a). In contrast, the pollen record of Cañada de la Cruz, illustrates the rapidity in the response of timberline vegetation to climatic change (Carrión et al., 2001b). This paper examines the Late Quaternary environmental history of Siles, a mountain lake lying in altitudinal sequence with Villaverde and Cañada de la Cruz within the same cordillera (Fig. 1). The objective is to establish the main pieces in the puzzling system of mechanisms exerting control on vegetation change at the sequence level. A second goal will be to correlate the new sequence of events with those in Villaverde and Cañada de la Cruz in order to

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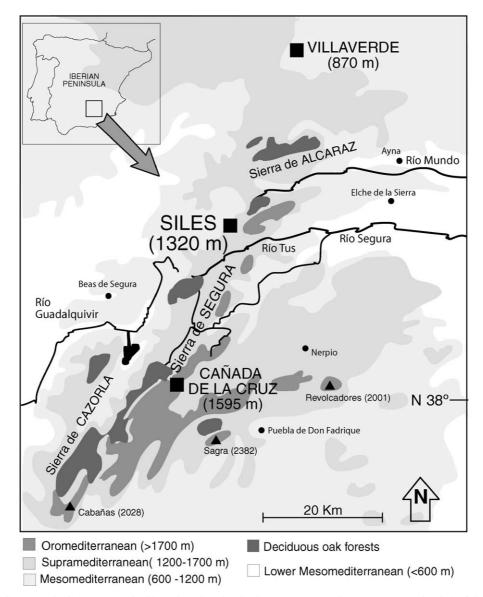*E-mail address:* carrion@um.es (J.S. Carrión).

Fig. 1. Location of Siles, Cañada de la Cruz, and Villaverde pollen sites in the Segura mountain system. Vegetation belts follow Valle et al. (1989). Siles lake lies within the supra–mesomediterranean ecotone, in close proximity to the oro- and dry, lower-mesomediterranean belt, and to wet territories characterized by deciduous forests. Cañada de la Cruz is located within the high-elevation treeline of southern Sierra de Segura. Villaverde is a tufaceous peat deposit in a submontane plateau, facing north is the humid Sierra de Alcaraz, and northwest is the arid Murciano–Almeriense phytoprovince.

postulate a picture of environmental change for the Segura region. The value of this study relies on the following facts:

(i) Absence of a comparable pollen sequence from supramediterranean Spain that spans the period from the end of the Last Glacial to nearly present. As the northern Betics were ice free during the Late Pleistocene (Gutiérrez, 2001), their vegetation history could be crucial in understanding postglacial dynamics in the southern Iberian peninsula.

(ii) The ecotonal character of the territory, which lies near transitions between oro-, supra-, and mesomediterranean zones, in the vicinity of areas of steep topographic gradients. This confers potentiality to locate glacial refugia of arboreal vegetation, and to record altitudinal shifts of vegetation belts.

(iii) The possibility of obtaining, from the same core, biological indicators of vegetation change, fire incidence, hydrological conditions, and human activities.

(iv) The concurrence of three sedimentary sequences with good palynomorph preservation, continuity,

potential for radiocarbon dating and correlation, and acceptable taxonomic and stratigraphic resolution. It must be emphasized that palaeoecological success with Quaternary sequences in southern Spain is still, to a great extent, a matter of luck.

2. Setting

2.1. Study site

Siles lake (2°30′W, 38°24′N, 1320 m a.s.l.) is located 6 km west of the village of Siles, Jaén province, 2 km south of the Albacete limit, in the northern Segura mountains, calcareous Betic Cordillera of southern Spain (Fig. 1). The lake consists of two basins separated by a low ridge. The study basin is the largest and extends up to 45×60 m^2 (maximum depth of 3.5–4.0 m) during high-rainfall years, and normally dries up for no more than one month a year, if ever completely. The lake has no connections with streams and is fed by direct precipitation and surface runoff from the catchment, which covers $\sim 3.1 \times 1.6$ km^2. Losses are mainly due to summer evaporation, although some infiltration cannot be excluded. The region is karstic and the lake itself is part of a relatively flat-floored, polje, 350×700 m^2, formed in Cretaceous limestones that subhorizontally overlie impermeable Triassic marls (López Vélez, 1996). Dissolution of the lake margins is not marked, like in other regional lakes where slumping of the sedimentary sequences along steep margins has been recognized. The sediment consists of massive brown clay with sparse basal, angular clasts (c. 1 cm^3) grading upwards into a more organic-rich clay.

2.2. Climate

Climate in the Segura mountains above 1000 m is cold continental Mediterranean. Siles lake is located in the supramediterranean bioclimatic belt, close to the mesomediterranean, and oromediterranean (Fig. 1). Local mean annual temperature and precipitation average 10–11°C and 800–1000 mm, respectively. Regional precipitation is, however, highly variable from year to year and distributed unevenly across the mountains due to elevational gradients and localized rainshadow effects. Precipitation increases with altitude, often exceeding 1300 mm, but dropping below 400 mm along the southeastern slopes. Snowdrifts accumulate during the winter in the high-elevation areas and often persist into the spring. Although occasional intense rainstorms account for much of the summer precipitation, generally summer drought is severe. Frost can occur in any month of the year, but is rare from June to August.

2.3. Vegetation

Local hydrophytes include *Potamogeton*, *Myriophyllum*, *Callitriche*, and *Ranunculus* species. Littoral vegetation is characterized by *Scirpus tabernaemontani*, several *Carex* species, *Typha dominguesis*, *Mentha pulegium*, *Juncus tenageia*, *Phragmites australis*, and *Bellis annua*. The surroundings of the lake are characterized by forest patches of *Pinus nigra*, *P. pinaster*, and *Quercus rotundifolia*, with several *Juniperus* species (*J. communis*, *J. oxycedrus*, *J. phoenicea*, and *J. thurifera*), thorny shrubs (*Berberis hispanica*, *Rhamnus saxatilis*, *Erinacea anthyllis*, and *Echinospartium boissieri*), and a basal layer of grasses. A treeline of *P. nigra* occurs throughout the 1600–2100 m zone in the Segura mountains, and correlates with an abrupt change in thermal lapse rate and wind speed (Valle et al., 1989). Dwarf junipers with hard-leaved grasses and thorny shrubs dominate these non-forested areas of high altitude. Oak forests occur below c. 1600 m in the supra- and mesomediterranean belts. Deciduous oak forests prevail in the west and northwest slopes. These are dominated by *Quercus faginea*, occasionally accompanied by *Acer granatense* and rarely *Taxus baccata*, with relict *Corylus avellana* forests developed in shady valleys. *Quercus pyrenaica* occurs on the less frequent siliceous outcrops. Evergreen *Q. rotundifolia* forests are frequent below c. 1400 m. Mixed oak–pine forests including *P. pinaster* are even commoner at mid-altitudes. Thermophilous *Quercus coccifera*, *Pistacia lentiscus*, and *Phillyrea angustifolia* understorey communities are characteristic of the lower, more xerophytic mesomediterranean belt.

3. Methods

A sediment core was raised from the central point in a dry area of the lake during late summer using a 6-cm diameter piston sampler. Coring was stopped at 172 cm due to the hardness of the bottom. The sediment was extruded in the field, wrapped in cling film, and placed in labelled sections of PVC guttering cut lengthways. Subsamples of sediment were taken at 2-cm intervals throughout the core. No macrofossil remains were found throughout the sediment core. Extraction of palynomorphs follows the standard procedure described in Moore et al. (1991). Mineral separation with heavy liquid density 2.0 was used for all the samples. Exotic *Lycopodium* tablets of a known concentration were added to calculate pollen concentrations. After chemical and physical treatment, between 518 and 231 pollen grains (excluding non-pollen microfossils) were identified under a light microscope using the reference collection of the Laboratory of Palynology at the University of Murcia. Identification criteria for regional

pollen types have been detailed in previous papers (Carrión and van Geel, 1999; Carrión et al., 2000b). Identification of non-pollen microfossils was aided by the descriptions and microphotographs of Pals et al. (1980), van Geel et al. (1981, 1986, 1989), Jarzen and Elsik (1986), and Carrión and van Geel (1999).

Pollen diagrams (Figs. 3, 5 and 6) were constructed using the computer program PSIMPOLL (Bennett, 2000), and are based on counts averaging 430 pollen grains and spores. Hydroseral pollen (*Potamogeton*, *Myriophyllum*, *Ranunculus*, *Typha*, Cyperaceae, Asteraceae, Lamiaceae, and *Polygonum aviculare* type), algal (*Closterium* and other desmids, *Botryococcus*, and Zygnemataceae), bryophytic (*Riccia lamellosa* and *R. sorocarpa*), and fungal spores (*Thecaphora*, Sordariaceae, and *Puccinia*), and other non-pollen palynomorphs (*Pseudoschizaea* shells and eggs of the whipworm *Trichuris*) were excluded from the pollen sum. The delimitation of Siles "microfossil" (SM) and "pollen" (SP) assemblage zone boundaries was obtained from an optimal division of the sequence using the information content criterion (Bennett, 2000). SP zones were based on the values of types that exceeded 2% in any sample. SM zonation was determined using non-pollen palynomorphs and pollen from aquatic and littoral vegetation (Fig. 3), excepting *Puccinia*, *Riccia*, *P. aviculare* type, Sordariaceae, *Thecaphora*, and *Trichuris*, which were neither utilized for SM or SP zonation. They were, nevertheless, represented within the SP zonation for comparison purposes (Figs. 5 and 6). A synthetic diagram including selected microfossil curves, the sums of xero- and mesophytes, and microscopic charcoal abundance is shown in Fig. 6. Regional (R-) pollen zones were depicted by visualization of correlative changes in ecologically significant pollen groups (pines, deciduous trees, Mediterranean elements, and xerophytes) along three pollen diagrams of the Segura mountains: Siles, Villaverde (Carrión et al., 2001a),

and Cañada de la Cruz (Carrión et al., 2001b) (Figs. 8 and 9).

The total number of charcoal particles longer than 10 μm was counted on the slides prepared for pollen analysis and their concentrations calculated with reference to the *Lycopodium* counts. The number of charcoal particles can be taken as an indication of regional fire occurrence (MacDonald et al., 1991). Rate of change between adjacent subsamples, with calibrated radiocarbon dates, was calculated using the chord distance (0 smoothed) through the program PSIMPOLL (Bennett, 2000) (Fig. 6). Spearman correlation coefficients were calculated through the program SPSS 7.0, using as variables the main pollen and microfossil taxa percentages, the sums of xero- and mesophyte pollen, and microcharcoal concentrations (Table 2). Nomenclature for plant vascular species follows Valle et al. (1989).

4. Siles environmental record

4.1. Chronology

The Siles environmental record spans from c. 20,300 to after 505 cal yr BP. The chronology was established on the basis of 12 radiocarbon dates. Samples consisted of bulk organic sediment, dated by the AMS method where necessary because of low carbon content in the organic extracts (Table 1). Dates were calibrated using CALIB 4.3 (Stuiver et al., 1998). Calibrated ages BP were taken as the mid-point of the 95.4% (2σ) probability interval. The probability that the dates are affected by hard-water error cannot be excluded. In that case, the dates would be probably affected in the same way, as suggested by the internal consistency of the series (Fig. 2). Because the basal sediment is very poor in organic matter and relatively clastic, some possibility

Table 1
Radiocarbon age determinations on bulk sediment from the Siles sequence

Depth (cm)	Laboratory code	^{14}C age (yr BP)	Calibrated age (cal yr BP) (range, 2σ)	Analysis
6–8	Pta-8152	430 ± 90	505 (640–290)	Conventional
28–30	Beta-141045	1580 ± 40	1470 (1550–1390)	AMS
34–36	GrA-17550	1685 ± 40	1566 (1700–1520)	AMS
39–41	Beta-141043	1900 ± 40	1815 (1910–1720)	AMS
45–47	Pta-8152	2280 ± 80	2270 (2480–2060)	Conventional
60–62	GrA-15998	3125 ± 35	3357 (3410–3310)	AMS
81–83	GrA-17552	4520 ± 45	5180 (5310–5040)	AMS
91–93	GrA-16000	5160 ± 40	5916 (6000–5870)	AMS
105–107	Pta-8148	6350 ± 130	7267 (7490–6940)	Conventional
135–137	Beta-155405	9120 ± 80	10,238 (10,510–10,150)	Conventional
143–145	Beta-155406	$10,300 \pm 80$	12,110 (12,410–11700)	Conventional
170–172	GrA-16119	$17,030 \pm 80$	20,276 (20,930–19,650)	AMS

Calibrations were carried out following Stuiver et al. (1998) (CALIB 4.3). The calibrated age BP was taken as the mid-point of the 95.4% (2σ) probability interval.
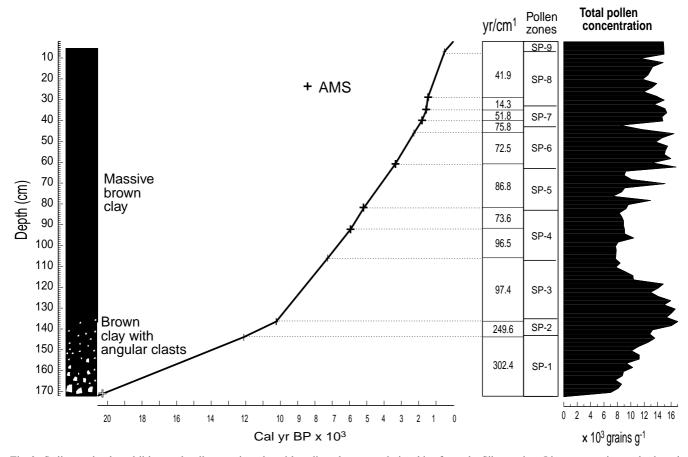
Fig. 2. Sediment depth and litho- and pollen stratigraphy with radiocarbon age relationships from the Siles section. Lines connecting each plotted point are interpolated sediment accumulation rates.

remains that the date at c. 20,300 cal yr BP is in error, although the pollen (prevailing xerophytes) and microfossil record (absence of Zygnemataceae) supports the view that this sample pertains to the Last Glacial Stage, before the Late Glacial amelioration observed in the sequence (Fig. 6). Although there is no sedimentary evidence, hiatuses cannot be excluded, especially at the beginning of the sequence. An age–depth model based on interpolated ages between adjacent pairs of dates (sediment top assumed as age 0) was obtained (Fig. 2).

4.2. Palaeolimnological changes

It is difficult to infer a unique explanation of changes in aquatic ecology because the lithology seems to be rather insensitive and sedimentary, geochemical, and biological indicators other than microfossils lack at the moment (Fig. 3). Except for the deposition of clasts in the bottom, the studied core corresponds to an uniform clayey bed without signs of erosive contacts or internal changes in colour, texture, and structure (Fig. 2). The interpretation of the microfossil changes given in this paper (Fig. 4) will be coherent with the assumption that

local drainage patterns have not been substantially altered during the sequence and, consequently, water-level changes were due principally to rainfall water input and evaporation.

In agreement with previous palaeoecological studies from Spain, the microfossil assemblage of Type 128 (Pals et al., 1980), and Desmidiaceae is suggestive of comparatively poor-nutrient water stages in the context of low water temperatures (Carrión and van Geel, 1999; Carrión et al., 2001b; Carrión and Navarro, in press). Zygnemataceae suggests meso- to eutrophic stagnant shallow water under milder climate and longer snow-free periods (van Geel et al., 1986). *Botryococcus* suggests a rise of the water table to still more limnic conditions (Mateus, 1992, Carrión et al., 2001b). *Debarya* behaves often as pioneer, but as most representatives of the Zygnemataceae, needs a relatively high water temperature to sporulate (van Geel et al., 1989). *Potamogeton* and *Myriophyllum* develop in similar conditions to Zygnemataceae, but under less temporary water bodies. Advances of marginal vegetation are indicated by increases of Cyperaceae and *Typha*. Stages of seasonal desiccation associated with
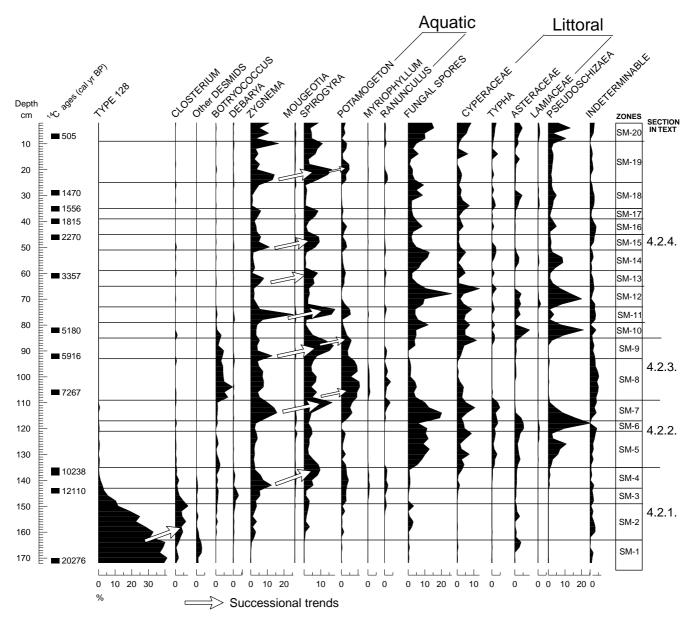
Fig. 3. Pollen diagram of Siles for hydro- and hygrophyte pollen, and non-pollen microfossils including algal and fungal spores, *Pseudoschizaea* shells and Type 128 (Pals et al., 1980). All taxa excluded from pollen sum. SM assemblage zone boundaries determined according to the information content criterion (Bennett, 2000) for all types. SM zones represent hydroclimatic variation in the lake (see Fig. 4). Ages are given in calibrated radiocarbon years BP (CALIB 4.3, Stuiver et al., 1998).

decomposing activity are suggested by peaks of fungal spores (*Polyadosporites, Pluricellaesporites*) and, especially, *Pseudoschizaea* cysts (Scott, 1992) (Fig. 4). The absence of peaty layers and preserved macroremains suggests, however, that some desiccation of the basin, organic matter decomposition and mineralization occurred throughout the whole sequence.

The palaeolimnological sequence of Siles consists of 20 SM assemblage zones (Fig. 3). The recurrence of several intrazonal patterns must be emphasized. Thus, *Zygnema* is usually rising earlier than *Spirogyra* and

Potamogeton, *Mougeotia* correlates to *Zygnema* peaks, *Myriophyllum* and *Ranunculus* correlate to *Potamogeton* peaks, Cyperaceae precedes *Typha*, and Asteraceae does *Pseudoschizaea* (Figs. 3 and 4).

4.2.1. Glacial to early Holocene microphyte succession (c. 20,300–10,100 cal yr BP)

Zones SM1–SM4 mark a Late Glacial–early Holocene warming trend defined by increased Zygnemataceae, and the following succession: Type 128—other desmids (*Cosmarium/Euastrum*) in zone SM1 (c. 20,300–
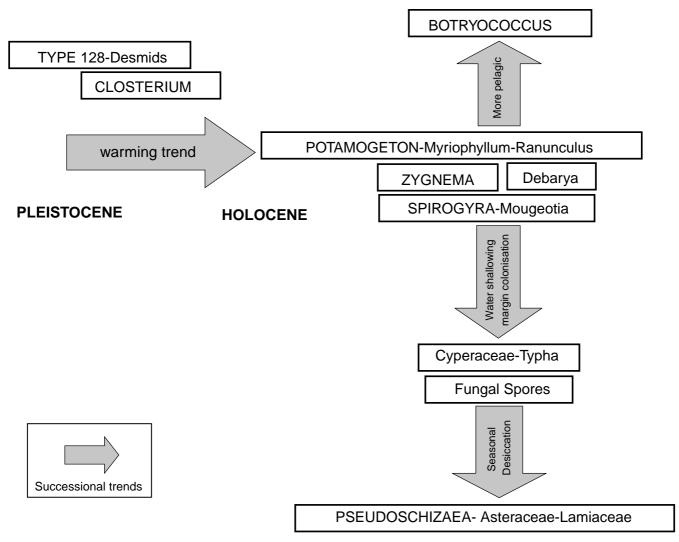
Fig. 4. Palaeolimnological relationships and successional trends based on hydroseral pollen and microfossil changes observed in Fig. 3. See van Geel et al. (1981, 1986, 1989), Scott (1992), Carrión and van Geel (1999), and Carrión and Navarro (2002) for background about the ecological indication of these palynomorphs. Capitals are used for the main palaeolimnological indicators.

18,300 cal yr BP), Type 128—*Closterium–Zygnema–Spirogyra* in zone SM2 (c. 18,300–13,500 cal yr BP), *Zygnema–Debarya–Potamogeton–Closterium* in zone SM3 (13,500–11,900 cal yr BP), and *Zygnema–Spirogyra–Mougeotia–Potamogeton–Myriophyllum–Ranunculus* in zone SM4 (c. 11,900–10,100 cal yr BP) (Figs. 3 and 4). This colonization by thermophilous microphytes correlates a reduction in cryoclastic scree content and particle size, and its disappearance from the lake sediment (Fig. 2), which plausibly results from slope weathering under periglacial conditions.

4.2.2. Early-Holocene hydrological crises (c. 10,100–7600 cal yr BP)

Zones SM5–SM7 involve shallowing of the lake (c. 10,100–8100 cal yr BP), including two events of maximum drying up characterized by *Pseudoschizaea*

peaks at about 9300 and 8400 cal yr BP. The zone SM7 (c. 8100–7600 cal yr BP) shows a return to less-dry conditions characterized by *Zygnema*, *Spirogyra*, and *Potamogeton*.

4.2.3. Mid-Holocene pelagic phase (c. 7600–5400 cal yr BP)

A depositional environment of relatively deeper water is inferred for the period SM8–SM9 (c. 7600–5400 cal yr BP). This is characterized by abundance of the pelagic *Botryococcus* (especially between c. 7500 and 7000 cal yr BP), maxima in aquatic angiosperms, moderately high values of Zygnemataceae, retreats of littoral vegetation, and minimum incidence of *Pseudoschizaea*, Asteraceae, Lamiaceae, and fungal spores. The zone SM9 (c. 5800–5400 cal yr BP) implies lower lake levels, with sequenced

rises of *Zygnema* (c. 5700 cal yr BP), *Spirogyra* (c. 5600 cal yr BP), and Cyperaceae (c. 5500 cal yr BP).

4.2.4. Alternance of desiccation and shallow-water stages (c. 5400–after 500 cal yr BP)

Since c. 5400 cal yr BP, the lake seems to have experienced episodic oscillations in the body of water. The most prominent desiccation phases define the zones SM10 (c. 5400–4800 cal yr BP) and SM12 (c. 4300–3800 cal yr BP), with two main peaks of *Pseudoschizaea* at c. 5200 and 4100 cal yr BP, respectively. Although less pronounced, additional hydrological crises become manifest in the zones SM14 (c. 3100–2600 cal yr BP), SM16 (c. 2200–1700 cal yr BP), SM18 (c. 1450–1300 cal yr BP), and SM20 (c. 700–after 500 cal yr BP). *Pseudoschizaea*, Asteraceae, and fungal spores are relatively abundant during the modern phase SM20, which represents average lake desiccation periods of 1–2 months a year. The intermediate zones SM11 (c. 4800–4300 cal yr BP), SM13 (c. 3800–3100 cal yr BP), SM15 (c. 2600–2200 cal yr BP), SM17 (c. 1700–1450 cal yr BP), and SM19 (c. 1300–700 cal yr BP) involve returns to conditions of longer water permanence (Fig. 4).

4.3. Pollen stratigraphy and vegetation history

The pollen sequence of Siles may allow insights into the vegetation history of the supramediterranean areas of the Segura mountains from c. 20,300 cal yr BP to nearly present (Fig. 5). As in topographically similar mountain sites of Spain, the pollen catchment is likely to include a lower-altitude, mesomediterranean signal caused by ascending air flow along slopes (Vázquez and Peinado, 1993).

4.3.1. Glacial steppe, Juniperus colonization, and survival of forest (c. 20,300–11,900 cal yr BP)

During SP1 (c. 20,300–11,900 cal yr BP) a steppe grassland of Poaceae, *Artemisia*, *Ephedra nebrodensis*, and scattered junipers and pines, with Chenopodiaceae, Caryophyllaceae, Brassicaceae, and *Helianthemum*, was the characteristic vegetation (Fig. 5). This assemblage partially has a counterpart in the modern high-elevation, xerocryophilous communities of *Festuca hystrix*, *Poa ligulata*, *Juniperus sabina*, *Dianthus subacaulis*, *Arenaria tetraquetra*, *Vella spinosa*, and *Helianthemum croceum*. At the expense of *Artemisia*, *E. nebrodensis*, and Chenopodiaceae, a gradual expansion of junipers within the steppe grassland is shown throughout SP1, culminating at c. 12,100 cal yr BP, and paralleling slight increases of *P. pinaster* and evergreen *Quercus*.

During the full glacial (c. 20,000–17,000 cal yr BP), *P. pinaster* percentages reach 6%, deciduous *Quercus* 3%, evergreen *Quercus* 2.5%, Ericaceae 2.1%, *Corylus* 2%, *Betula* 2.9%, and *Fraxinus* 1.8% (Fig. 5). At the Late Glacial (c. 17,000–11,900 cal yr BP), these taxa slightly

increase up to 7.8%, 3.6%, 3.9%, 2.8%, 3.5%, 2.8%, and 3%, respectively. Zone SP1 is also characterized by constant occurrences of *Acer*, *Taxus*, *Arbutus*, *Buxus*, *Salix*, *Ulmus*, *Phillyrea*, *Pistacia*, and *Olea*. These pollen spectra suggest the proximity of glacial refugia of temperate and Mediterranean trees.

4.3.2. Spread of Pinus (c. 11,900–7400 cal yr BP)

Zone SP2 (c. 11,900–10,100 cal yr BP) is characterized by early-Holocene expansion of *Pinus* within the grassland (Fig. 5). Based on the current ecology of Iberian pines, *P. nigra* is the most likely pine-pollen producing species at these altitudes in the calcareous Betics (Carrión et al., 2001b). The invasion of *P. nigra* in zone SP2 is relatively sudden, and presumably marks upslope movement in the position of the forest-steppe ecotone to above the site and establishment of its present position east and south of the study site. Zone SP2 is also characterized by slight increases of thermophytic pollen such as *Phillyrea*, *Olea*, Ericaceae, and evergreen *Quercus* (Fig. 5).

During zone SP3 (c. 10,100–7400 cal yr BP), the main pollen contributor continues to be *P. nigra*, with average percentages of ∼50%. Gradually, there is a partial replacement of *P. nigra* by *P. pinaster*, which peaks at c. 8100 and 7700 cal yr BP, and slight rises of *Juniperus*, Poaceae, *Artemisia*, *E. nebrodensis*, Chenopodiaceae and other heliophytes. A mesophytic component of *Betula*, *Fraxinus*, deciduous *Quercus*, *Corylus*, and *Acer* starts increasing after c. 8100 cal yr BP.

4.3.3. Mid-Holocene development of angiosperm forests (c. 7400–5300 cal yr BP)

During zone SP4 (c. 7400–5300 cal yr BP), the pine forests are initially replaced by deciduous-*Quercus* forests with important components of mesophilous trees such as *Betula*, *Corylus*, *Fraxinus*, *Acer*, *Salix*, and *Ulmus*, and constant occurrence of *Taxus*, *Arbutus*, *Buxus*, *Hedera*, and *Ilex* (Fig. 5). *Juniperus* and xerophytes attain their minimum, and Caryophyllaceae, Brassicaceae, and *Helianthemum* are absent from this zone. *Ephedra fragilis* occurs for the first time at c. 6000 yr BP and will be found continuously throughout successive zones. The presence of *Juglans* pollen since c. 7000 cal yr BP is also noticeable, supporting the view that the walnut did not disappear from Iberia during the Last Glaciation (van den Brink and Janssen, 1985; Carrión and Sánchez-Gómez, 1992; Franco et al., 2001), although this does not contradict the idea that present distribution of walnut is due principally to arboriculture in historical times.

Zone SP4 also marks the spread of Mediterranean vegetation characterized by *Q. ilex-rotundifolia* forest with understorey of Ericaceae, *Phillyrea*, *Rhamnus*, *Pistacia*, and *Olea* (Fig. 5). However, the maximum of Mediterranean forest-scrub (c. 5900 cal yr BP) is time-
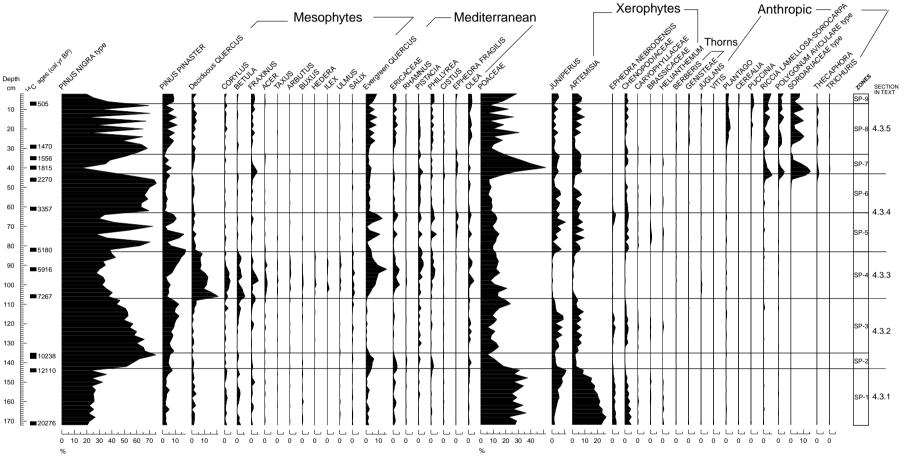
Fig. 5. Pollen diagram of Siles for terrestrial vegetation. SP assemblage zone boundaries determined according the information content criterion (Bennett, 2000) for pollen taxa displaying curves, excepting *Polygonum* and non-pollen microfossils. Points indicate pollen frequencies below 2%. Ages in calibrated radiocarbon years BP (CALIB 4.3, Stuiver et al., 1998).

transgressive with respect to those of deciduous *Quercus* and *Betula* (c. 7300 cal yr BP), *Acer* (c. 6600 cal yr BP), *Fraxinus* (c. 6500 cal yr BP), and *Corylus* (c. 6400 cal yr BP). This successional pattern culminates with new increases of *P. nigra* and *P. pinaster*.

4.3.4. Pinus–Quercus interactions (c. 5300–2000 cal yr BP)

The zone SP5 (c. 5300–3500 cal yr BP) is characterized by rapid alternances of *P. nigra* vs. *P. pinaster* and Mediterranean elements (Fig. 5). *P. pinaster* peaks initially at c. 5200 cal yr BP, *P. nigra* attains two maxima at c. 4900 and 4200 cal yr BP, while *P. pinaster*, evergreen *Quercus*, Ericaceae, *Pistacia*, *Phillyrea*, *E. fragilis*, and *Olea* increase synchronously at c. 4500 and 3800 cal yr BP. Deciduous *Quercus* and other mesophilous trees decline, and *Juniperus* and xerophytic taxa

(*Artemisia*, Chenopodiaceae, *E. nebrodensis*) increase again (Fig. 6). After a new peak at c. 3350 cal yr BP, *P. nigra* remains dominant during SP6 (c. 3500–2000 cal yr BP). Additional characteristics of this zone include the disappearance of *E. nebrodensis* at c. 3000 cal yr BP, and continuous occurrences of *Cistus* and *Pistacia*.

4.3.5. Recent episodes of forest decline (c. 2000–after 500 cal yr BP)

Abruptly during SP7 (c. 2000–1550 cal yr BP), *P. nigra* decreases, and Poaceae becomes dominant, showing a maximum of ∼50% at c. 1800 cal yr BP (Fig. 5). Characteristic taxa of this zone include *Fraxinus*, *Pistacia* (peaks at c. 1900 cal yr BP), *E. fragilis*, *Juniperus*, and *Artemisia*. Significantly, the first peak of Poaceae (c. 1800 cal yr BP) is preceded (c. 2200–2000 cal yr BP) by rising curves of *P. aviculare* and
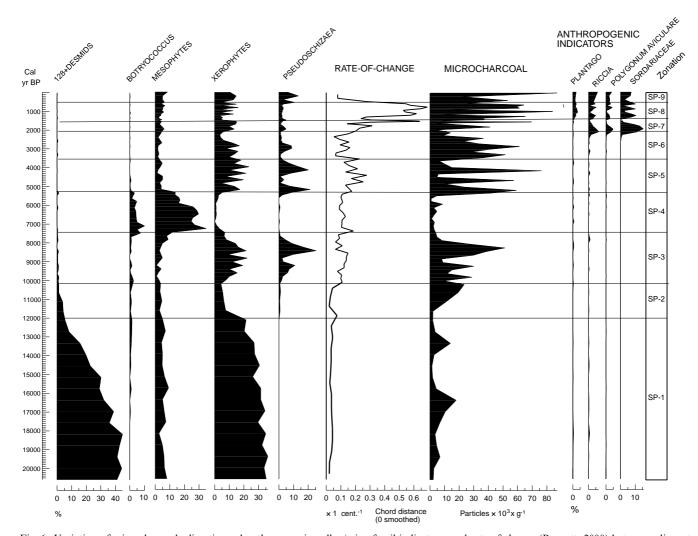

Fig. 6. Variation of microcharcoal, climatic, and anthropogenic pollen/microfossil indicators, and rate of change (Bennett, 2000) between adjacent samples throughout the Siles SP sequence. The number of charcoal particles can be taken as an indication of regional fire occurrence, which is principally related with hydroclimatic variation, although human-set fires could have occurred from SP-7 onwards. Peaks of *Riccia* spores, *P. aviculare*-type pollen, and Sordariaceae ascospores are interpreted as increases of local grazing pressure.

Riccia, and the first occurrences of Sordariaceae, *Thecaphora*, and *Trichuris* (Figs. 5 and 6).

The zone SP8 (c. 1550–500 cal yr BP) is characterized by rapid alternances of *P. nigra* and Poaceae (Fig. 5). Increases in grass pollen occur synchronously with small rises of *P. pinaster*, evergreen *Quercus*, *Fraxinus*, Ericaceae, *Juniperus*, *Phillyrea*, *Artemisia*, and Chenopodiaceae. In contrast, increases of *P. nigra* correlate with slight peaks of deciduous *Quercus* and *Corylus*. This zone also shows continuous occurrences of *Berberis*, *Olea*, *Cistus*, *Rhamnus*, Genisteae, and *Juglans*, and the first pollen records of *Vitis* at c. 800 cal yr BP. The zone SP9 (after c. 500 cal yr BP) marks the establishment of current local landscape, characterized by mixed open forests of *P. nigra*, *P. pinaster*, and *Q. rotundifolia*, and open, grazed areas dominated by grasses, junipers, and spiny shrubs.

4.4. Hypotheses about controls of vegetation sequence

The pollen record of vegetation (Fig. 5) can be compared with the microfossil record of lacustrine hydrological variation (Figs. 3 and 4), microcharcoal indication of fire activity (Fig. 6), and palynological record of anthropogenic disturbance (Figs. 5 and 6) to create a picture of vegetation change for the Siles sequence (Fig. 7).

4.4.1. Relationships between the records of vegetation, fire, and hydroclimatic variation

The most direct evidence for climatic changes is the palaeolimnological record, which was seen to reflect the Late Glacial–Holocene warming trend and water-level variations during the Holocene (Figs. 3 and 4). Although less steadfast, the pollen record itself provides palaeoclimatic information through the variation of mesophytes (wet climate), xerophytes (aridity), Mediterranean component (summer drought), and thermophytes such as *Olea*, *Pistacia*, *Cistus*, and *E. fragilis* (Figs. 5 and 6). The relationship between mesophytic vegetation and maximum lake water levels is assessed by the Spearman correlation coefficient, which is significantly positive between "mesophytes", *Botryococcus*, and deciduous *Quercus* (Table 2). The microcharcoal record (Fig. 6) suggests that fire activity is principally related with hydroclimatic variation. Microcharcoal particles are relatively abundant during the zone SP3, with three peaks, and still more abundant during the zones SP5–SP9, with more than a dozen peaks. This pattern of low occurrence in the mid-Holocene, preceded and followed by stages of more fire occurrence fits with the pollen record of meso- and xerophytes, and the microfossil record of deep- and shallow-water indicators (Fig. 6). Burning periods may have therefore occurred during dry climatic phases. This is supported by the significant positive correlations between microcharcoal,

and *Artemisia*, xerophytes, *Juniperus*, and *Pseudoschizaea*, and the negative correlations between microcharcoal, and mesophytes and *Botryococcus* (Table 2). It is likely that, during the Holocene, late spring–summer precipitation has controlled regional fire occurrence, while lake levels may have been controlled by autumn–winter precipitation (Carcaillet and Richard, 2000).

4.4.2. Palynological evidence of human activity

In the last c. 2500 years, the rises of sordariaceous ascospores may be linked to increases of grazing in the lake surroundings as Sordariaceae often are coprophilous (Lundqvist, 1972). *Thecaphora* and *Trichuris* can also be related with dung input (Carrión et al., 2000c). The spore curve of the liverwort *Riccia* is similarly significant (Fig. 5). *R. lamellosa* and *R. sorocarpa* grow abundantly in the emergent surfaces of mountain water bodies within areas of grazing. The spores found in our samples must have been dislocated by water running off towards the sampling site, or, alternatively, during the wet seasons, the area where sporulating *Riccia* specimens were present became inundated and spores spread with the water throughout the inundated area. *P. aviculare* and *Plantago lanceolata* can be also related to pastoralism, and even arable agriculture in conjunction with Cerealia, *Vitis*, and *Puccinia* (Carrión and van Geel, 1999) (Figs. 5 and 6).

4.4.3. A contingent picture of vegetation dynamics and the causes of late-Holocene forest vulnerability

Periglacial climate would preclude forest development during SP1 (c. 20,300–11,900 cal yr BP). The gradual expansion of *Juniperus* within the steppe grassland appears to be a response to the Late Glacial warming manifested in the lake by increased water temperature and nutrients (Fig. 4). The first spread of *P. nigra* within the grassland (c. 11,900–10,100 cal yr BP) (Fig. 5) implies the introduction of a warmer climate than that of the previous period, which reduced both wind severity and persistence of snow cover at this altitude, and permitted *Pinus* to grow near the lake (Fig. 7). The preceding increase of Zygnemataceae suggest climate warming might have occurred several centuries earlier, so that the sudden invasion by *Pinus* may be conceived as a threshold response to climatic change.

The partial replacement of *P. nigra* by *P. pinaster* during the zone SP3 (c. 10,100–7400 cal yr BP) (Fig. 5) is preceded by increases in charcoal abundance and synchronous of high values in xerophyte pollen and indicators of lake desiccation (Fig. 6). Current ecological studies in the Segura mountains (Martínez-Sánchez et al., 1996), and palaeoecological data from elsewhere in the Mediterranean (Carcaillet et al., 1997; Carrión et al., 2000b) support the view that fire could stimulate some expansion of *P. pinaster* within *P. nigra* forests (Fig. 7).
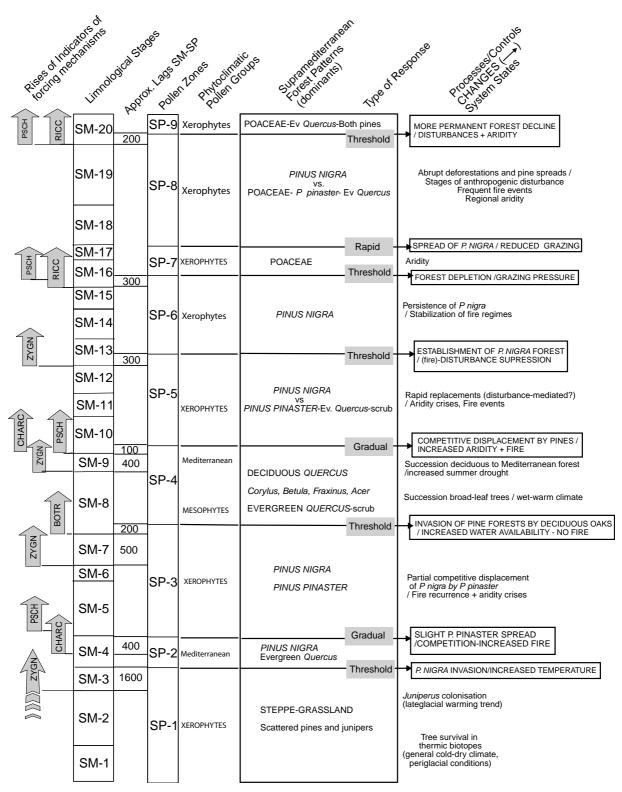
Fig. 7. Temporal relationships between limnological (SM) and terrestrial vegetation (SP) zones, and hypotheses for the main processes and controls of vegetational developments in the Siles sequence (Figs. 5 and 6). Arrows indicate increases in the following palaeoecological indicators: ZYGN = Zygnemataceae, CHARC = microcharcoal, PSCH = *Pseudoschizaea*, BOTR = *Botryococcus*, and RICC = *Riccia*. Starting curves of these microfossils (Fig. 3) are represented by arrow basal lines. Climatically influenced changes occur often as threshold responses to competitive interactions, aridity crises, increased water availability, grazing pressure, and fire disturbance. Lags in vegetational developments occur at the centurial scale. Biotically induced changes of vegetation are mainly shown at the intrazonal variation level (Fig. 5). See Section 4.4.3 for further explanation of these contingencies.

Table 2
Spearman correlation coefficient for pollen and microfossil taxa percentage values and microcharcoal concentration at Siles

	P. nigra	Dec. *Quercus*	*Artemisia*	*Botryococcus*	Mesophytes	Xerophytes	*Juniperus*	*Pseudosch*
Dec. *Quercus*	0.373							
Ev. *Quercus*	−0.412							
Artemisia		−0.514						
Botryococcus	−0.329	**0.643**	−0.436					
Mesophytes	−0.475	**0.929**	−0.542	**0.686**				
Xerophytes		−0.566	**0.920**	−0.487	**−0.611**			
Juniperus		−0.559	**0.793**	−0.413	−0.585	**0.933**		
Pseudoschizaea		−0.315	0.374		−0.344	0.505	0.554	
Microcharcoal			0.379	−0.408	−0.340	0.351	0.332	0.376

See Fig. 5 for definition of "mesophytes" and "xerophytes". Only values meaningful at the 0.01 level are represented. Bolds for the highest correlations.

The invasion of pine forests by mesophilous species after c. 7400 cal yr BP is envisaged as a threshold response to increased water availability (Fig. 7). Zygnemataceae and *Botryococcus* rise respectively about 500 and 200 yr before the SP4–SP5 transition (Fig. 3). Particular-species developments might have been shaped by previous availability of local populations and competitive adjustments. The expansion of Mediterranean vegetation after c. 5900 cal yr BP coincides with limnological indication at SM8–SM9 towards more pronounced summer drought (Fig. 3). Hydrological stress would have diminished the competitiveness of broad-leaf trees against evergreen oaks and scrub (Fig. 7).

As suggested by the records of abrupt shifts of *Pseudoschizaea* and microcharcoal during SP5 (Fig. 6), the balance between *P. nigra* and *P. pinaster* could have been episodically broken by dry spells, perhaps associated to fire disturbance. The cause for a longer persistence of *P. nigra* during SP6 remains controversial. Is it perhaps due to the stabilization of fire regimes? (Fig. 7). The role of other internal biotic factors such as fuel availability is non-testable.

The palynological record (Sordariaceae, *Riccia*, *Thecaphora*, *Trichuris*, and *P. aviculare*) coincide to suggest overgrazing in the lake catchment since c. 2400–2300 cal yr BP (SP7–SP9), and arable agriculture (*Plantago*, *Cerealia*, *Vitis*, and *Puccinia*) since c. 1400 cal yr BP (Fig. 5). The *Riccia* curve starts several hundred years before the grass expansion/ forest decline at SP7, and therefore, the continuous occurrences of *Berberis*, *Rhamnus*, and Genisteae in phase with those anthropogenic indicators since SP8 suggest they may be related with expansion of thorny scrub following historical overgrazing on the grassland.

This anthropogenic phase corresponds with maximum fire activity and great sensitivity in the vegetation, as can be deduced from the rate-of-change curve (Fig. 6). During at least seven times throughout SP7–

SP8, supramediterranean pine forests may have been pushed over a threshold by anthropogenic disturbance leading to the spread of grassland, thorny scrub, junipers, and nitrophilous communities (Fig. 7). Natural fires alone may have not been sufficient to maintain the grassland within the natural area of *P. nigra* forests. Fire events are indeed recorded long before this period of forest depletions, during which, for the first time in the sequence, xerophytes and anthropogenic indicators rise synchronously with fire-tolerant species (*P. pinaster*, evergreen oaks, Ericaceae, *Phillyrea*, and *Cistus*), while the more fire-sensitive deciduous oaks decline (Fig. 5). Plausibly, the vulnerability thresholds of supramediterranean *P. nigra* forests would be crossed by the combined action of dry climate, fire activity, and critically, pastoralism (Fig. 7).

5. Late Quaternary environmental history of the Segura region

5.1. Glacial refugia for temperate and Mediterranean trees

The incidence of temperate and Mediterranean forest taxa in the full glacial of Siles (Fig. 5) is important in the context of Iberia, where similar findings have been only reported from lower altitudes (Stevenson, 1985; Pons and Reille, 1988; Pérez-Obiol and Julià, 1994; Allen et al., 1996; Carrión et al., 2000a; Valero et al., 2000; Muñoz et al., 2001), as in other southern European pollen sites (Tzedakis, 1994; Willis, 1994; Leroy et al., 1996; Tzedakis et al., 1997; Follieri et al., 1998; Magri, 1999; Allen and Huntley, 2000; Willis et al., 2000). Pollen from temperate vegetation is more abundant in cave sites from eastern and southeastern Spain (Dupré, 1988; Carrión et al., 1999), but also nearer the coast.

The forest belt zone during full glacial times must have been generally narrower and less continuous than

it is today. Very likely, temperate and Mediterranean trees were confined to protected habitats. It is not necessary to invoke for long-distance transport to explain tree pollen percentages during SP1 at Siles (Fig. 5) because the site is only 5–15 km from the thermic gorges of the Guadalimar, Tus, Navalperal–Acebeas, Carrizas, Orcera, and Madera watercourses (López Vélez, 1996), which provide a plausible scenario for tree survival under a regionally colder and drier climate. It is worth stressing that, between 1100 and 1350 m a.s.l., these sites support today one of the most southerly *C. avellana* forests in Europe, as well as relic populations of *Ilex aquifolium*, *Betula celtiberica*, *T. baccata*, *Fraxinus angustifolia*, *A. granatense*, *Sorbus torminalis*, and *Ulmus glabra* (Valle et al., 1989).

The Siles sequence provides support for the view that tree species could survive in southern European mountains at relatively elevated locations during the Last Glacial Stage. This hypothesis was put forward by Bennett et al. (1991), who contended that tree survival would have been especially important in those mountain ranges that, like the Balkans (Willis, 1994), allowed rapid altitudinal displacements of tree populations in response to climatic pulses. As the Balkans, the Segura mountains could also permit latitudinal movements of tree populations owing to their more or less north–south orientation. Other data suggesting that the Betic Cordillera included important tree reservoirs during the Last Glacial Stage derive from the present genetic structure of European tree populations (Herrán et al., 1999; Jiménez, 2000; Salvador et al., 2000).

5.2. Holocene developments

The palaeoecological records of Cañada de la Cruz, Siles, and Villaverde, situated across elevational and latitudinal gradients (Fig. 1), can be correlated to produce a picture of Holocene environmental history in the Segura region (Figs. 8 and 9), in concurrence with the examination of forcing mechanisms of vegetation change in the Siles sequence (Fig. 7). Cañada de la Cruz (38°04′N, 2°42′W, 1595 m a.s.l.) is an intramontane, temporary shallow lake lying in the south of the Sierra de Segura, at the boundary between supra- and oromediterranean vegetation (Carrión et al., 2001b). Villaverde (2°22′N, 38°48′W, 870 m a.s.l.) is a tufaceous peat deposit lying north of Sierra de Alcaraz within a well-defined catchment that represents boundary conditions for semi-arid, plateau, and mountain vegetation (Carrión et al., 2001a).

5.2.1. Climatic control of early Holocene pine forests

Since there is no additional pollen record to Siles for glacial vegetation in the Segura mountains, the possibility cannot be rejected that angiosperm forest developments occurred during the Late Glacial and early

Holocene in other parts of the mountains. However, the presence of pine forests in Siles during the regional zone R1 (c. 11,500–10,100 cal yr BP), and their persistence in Siles and Villaverde during R2a and R2b (c. 10,100–7600 cal yr BP) seems to reflects a regional pattern (Fig. 8). The consistent abundance of xerophytes and microcharcoal until c. 7300–7400 cal yr BP (Fig. 9) suggests that pine dominance is related with aridity, a process being also plausible in the southern slopes of the Iberian System (Carrión and van Geel, 1999), Montes Universales (Stevenson, 2000), Central System (Franco et al., 1998), and most continental areas of the Meseta (Franco et al., 2001). These data confirm the hypothesis of underlying climatic control for the Siles zones SP2 and SP3 (Fig. 7). It is likely that *P. nigra* was the dominant species in high and mid-elevations, where it would enter in competition with *P. pinaster*. Interestingly, the cluster pine is absent in the Villaverde pollen record (Carrión et al., 2001a), which suggests that its modern distribution in the northern Sierra de Alcaraz is the result of recent migration (e.g. the last millennium) and/or introduction by humans in historical times. *P. pinaster* would be, however, native to the southern and central Segura mountains (Fig. 5), and the Iberian System (Carrión et al., 2000b).

5.2.2. Altitudinal displacements of vegetation belts

The Cañada de la Cruz pollen record shows that the ecotones between high-elevation pine forests and xerophytic grassland-scrub have changed in altitude at least five times over the last 10,000 years, and do appear to be sensitive to temperature change, although this must be strongly related with wind exposure, continentality, and average climate xericity (Carrión et al., 2001b). The cryo-xerophilous character of grassland communities with dwarf junipers with respect to pine woodlands is well established (Valle et al., 1989). Comparison between the main vegetation shifts in Cañada de la Cruz and Siles depicts climatically induced altitudinal displacements of vegetation belts. Advances of grassland and junipers in Cañada de la Cruz during the regional zones R2a (c. 10,100–8500 cal yr BP), R4 (c. 3600–2700 cal yr BP), and R6 (c. 1300–650 cal yr BP) correlate both to declines of local woodlands, and forested stages of *Pinus* in Siles.

The upper altitudinal limit of angiosperm forests in the region is also strongly influenced by mean annual temperatures (Valle et al., 1989). The expansion of pine forests above 1600 m would have involved upward displacements of deciduous forests, and expansions of evergreen oak forests and scrub during the mid-Holocene zone R3 (c. 7600–3600 cal yr BP). Altitudinal correlation of these taxa is complicated by species interactions, mainly competitive and successional processes among *P. nigra*, *P. pinaster*, deciduous and evergreen *Quercus*. Plausibly, *Q. ilex* may have occurred
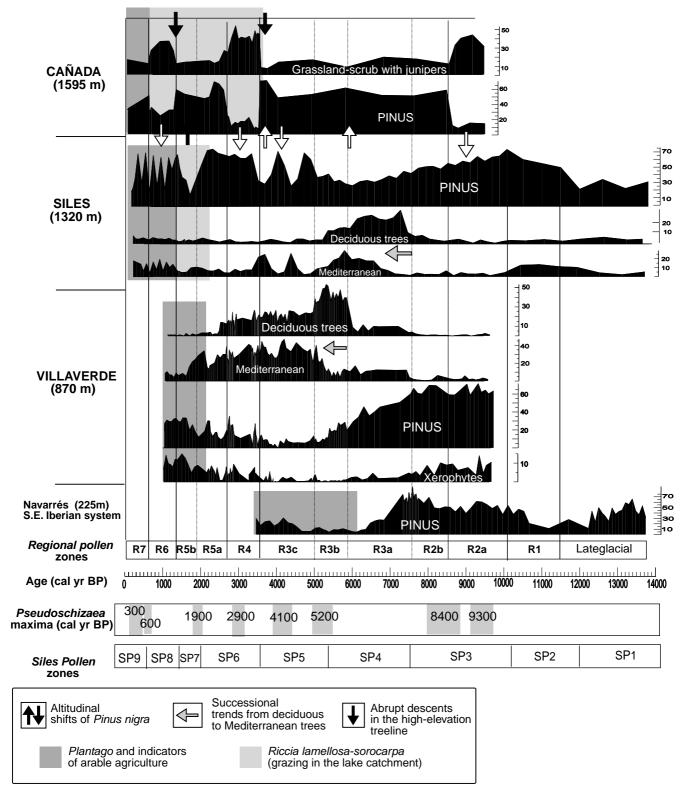
Fig. 8. Relationships between shifts in the most important pollen types and ecological groups in the Segura region since c. 14,000 cal yr BP. This picture is based on the assumption that centurial-scale lags are not due to dating errors (e.g. hard-water effect). On that assumption, increases of xerophytic scrub-grassland in high-elevation areas are associated with displacements of *P. nigra* forests from oro- to supramediterranean positions. Expansions of deciduous trees and Mediterranean forest would appear time-transgressive from supra- to mesomediterranean. Deciduous trees are better competitors than evergreen oaks and Mediterranean scrub in the first stages of the Holocene mesophytic optimum (R3a–b). The early Holocene pine forest dominance in the Segura mountains coincides with expanded semi-arid vegetation in the lowlands, and is not exclusive to the Betics (see e.g. Navarrés, in the southern slopes of the northernmost Iberian system, Carrión and van Geel, 1999).
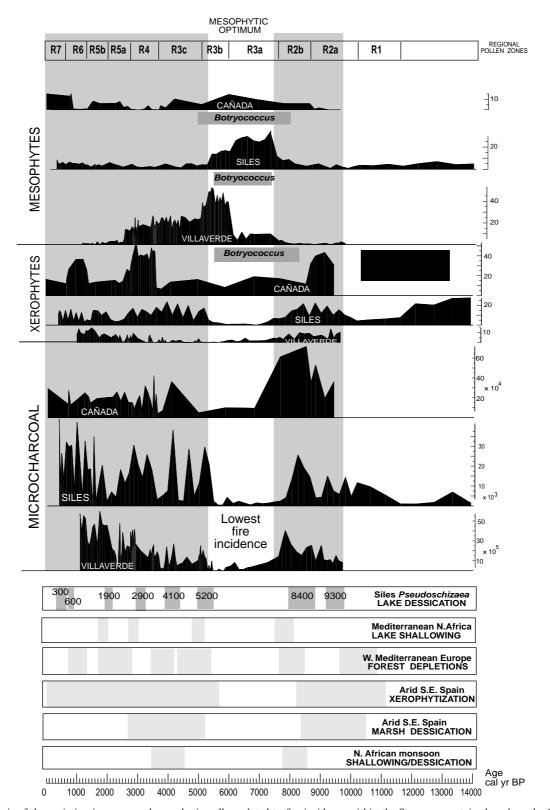
Fig. 9. Synthesis of the variation in meso- and xerophytic pollen related to fire incidence within the Segura mountains based on the Cañada de la Cruz, Siles, and Villaverde palaeorecords. A regional picture is depicted of a generally wet mid-Holocene (c. 7500–5200 cal yr BP) characterized by spread of mesophilous vegetation, between drier conditions characterized by greater abundance of xerophytes and higher fire incidence. This interpretation is coherent with the chronology of desiccation phases in the Siles sequence at this study and in other sequences outside the study region.

during the earlier mesophytic stages, becoming introgressively replaced by *Q. rotundifolia* throughout the late Holocene. This species is better adapted to continental climate and summer drought while the former, characteristic of mesic, periferal areas of Spain, is threatened with extinction in the study region (Sánchez-Gómez et al., 1995).

While remaining clear that the succession from deciduous to Mediterranean forest takes place under a context of increased aridity, it is worth wondering why developments of angiosperm trees occurred earlier in Siles than Villaverde (Fig. 8). Both climatic, edaphic, and ecological factors, and perhaps the proximity of preexisting populations derived from glacial reservoirs, may have influenced this dynamic. There are significant physiographic differences between Siles and Villaverde. Siles lies within wetter, orographically more complex territory. Villaverde is located in a high plain near the semi-arid Murciano–Almeriense phytoprovince, and La Mancha steppic region (Carrión et al., 2001b). Mountain to high-plain displacement of forest trees can be expected in the context of increased moisture following the same gradient. Another possibility is, simply, that time lags are due to radiocarbon dating errors such as hard-water effect. The chronology of these sites, as with other regional pollen sequences, is based on radiocarbon dating of bulk organic matter. In addition, most of these sites are shallow lakes subject to periodic desiccation and experiencing slow rates of sedimentation. Century-scale hiatuses in the sedimentary record cannot be excluded, despite the ecological coherence of these pollen changes and the absence of sharp contacts in the stratigraphies.

5.2.3. Human impact on the Segura mountains vegetation

The late Holocene has been a time of great environmental variability in the Segura mountains, probably due to the spatial heterogeneity of anthropogenic impacts. In high and mid-elevation areas, human activities would have taken place well before the occurrence of conventional anthopogenic pollen indicators (Fig. 8). High grazing pressures may have promoted local increases in the proportion of grasses. *Riccia* rises earlier in the oromediterranean Cañada (c. 3700 cal yr BP) than in the supramediterranean Siles (c. 2400 cal yr BP), probably because extensive pastures are natural above the treeline. In contrast, *Plantago* and other indicators of agriculture and arboriculture (e.g. Cerealia, *Vitis*, *Papaver*, *Centaurea aspera* type, *Puccinia*, *Tilletia*, Spore Types 984, 985, and 988, increases of *Olea*, *Fraxinus*, and *Juglans*), and indicators of forest degradation stages (*Berberis*, Genisteae, increased *Cistus* and *Rhamnus*), occur or start rising first in the pollen record of lowland Villaverde (c. 2200–1600 cal yr BP), then in Siles (c. 1400 cal yr BP), and finally in Cañada de la Cruz (c. 670 cal yr BP) (Fig. 8). In general, human impact on vegetation would have come relatively late. Documentary and pollen evidence of clearance and agriculture are found in the peripheral sites of Navarrés (Carrión and van Geel, 1999) (Fig. 8) and Elx since Neolithic and Chalcolithic times (Burjachs et al., 1997). It is clear that the intensity and timing of the human impact on vegetation varied from one part of the southeastern peninsula to another.

Archaeological and documentary sources can shed any light about palaeoecological hypotheses in the Segura region. It is unclear when prehistoric hunting communities adopted a more sedentary pattern of resource use. Archaeological data from the Neolithic to the Bronze Age suggest that settlement was sparse (Jordán, 1992). Seed and charcoal data are fragmentary and there is no firm evidence concerning intensification of agriculture before Roman times (Buxó, 1997). Documentation of woodlands has been available only since the Cadastre of Marquis of Ensenada, which was produced 250 years ago. The first urban expansion took place during Islamic times, after c. AD 950. The flanks of the Segura mountains were dotted by a string of villages practising irrigation but the agricultural perimeter of these villages and towns was small and did not intersect with that of other communities, from which they were separated by large areas of pasture (De la Cruz, 1980). After AD 1238, when the region became under Christian domination, Muslim and Christian armies regularly pillaged the countryside and most of the original inhabitants emigrated. The region lacked the demographic resources for repopulation. This has caused a major lag in the expansion of agriculture in the area. Only in the last centuries population growth and the improvement of agricultural technologies appear to have caused transformation of forests into croplands at low- and mid-altitudes, although many areas were left uncultivated or reverted to grazing until the present, and much of the forested territory was managed exclusively for timbering (Merino-Alvarez, 1915). Numerous reports point to an extensive brush and forest cover in the eastern Sierras de Segura only a century ago (Sánchez-Gómez et al., 1995).

5.2.4. Correlation with extra-regional climatic proxies and the significance of abrupt events

The period from c. 7500 to 5200 cal yr BP in the region represents the mesophytic optimum, xerophytic minimum, the period of lowest fire activity, and according to *Botryococcus* records, a phase of relatively high lake levels (Fig. 9). This is confirmed in the Villaverde tufa system by the formation of sapropels (Carrión et al., 2001a). Palaeoecological records from the most arid province of southeastern Spain show relatively low frequencies of *Pseudoschizaea* and *Artemisia*, and a forest optimum between 8200 and 5700 cal yr BP (Pantaleón, 1997). Other relatively

synchronous, mid-Holocene angiosperm forest developments have been recorded in the eastern coast of the Mediterranean (Burjachs and Riera, 1995). Records of water-level variation and spring activity in northern Africa and the Sahel show that maximum wetness occurred during a synchronous phase to the mid-Holocene in a number of sites (Hassan, 1997; Gasse, 2000). A return to widespread eolian sediment mobilization after 5000 cal yr BP is recorded in the Sahara (Swezey, 2001). In contrast, Alborán offshore pollen sequences (Targarona, 1997), and the Mediterranean Spanish sites of Padul (Pons and Reille, 1988), and Elx and Salines (Burjachs et al., 1997) show the expected early Holocene (c. 11,500–8500 cal yr BP) maxima of mesophytic pollen in phase with mesocratic forest developments in northern Europe (Birks, 1986; Huntley, 1990) and the eastern and central Mediterranean region (Willis, 1994; Tzedakis et al., 1997; Roberts et al., 2001).

Several oscillations and transitions in the Siles, Cañada de la Cruz, and Villaverde palaeoecological records coincide with established chronologies for abrupt climatic changes in Mediterranean Europe, north Africa and the Sahel. The main peak of *Pseudoschizaea* in Siles at c. 8100–8500 yr BP correlates to the European and Greenland cooling event at c. 8200 cal yr BP (Peteet, 2000), and a consistent lowering of lake levels in the northern monsoon domain of Africa ∼8000–8400 cal yr BP (Gasse, 2000). The most recent *Pseudoschizaea* maxima at c. 5200 and 4100 cal yr BP correlate to the beginning of a long phase of reiterated dry spells in Mediterranean areas of Europe and north Africa. In particular, aridification phases inferred from pollen ratios in western Mediterranean palynological sequences have been established at c. 8400–7600, 5300–4200, 4300–3400, 2850–1730, and 1300–750 cal yr BP (Jalut et al., 2000), while arid intervals at Tigalmamine were established by Lamb et al. (1995) around >7860–7500, 5010–4860, 2990–2830, and 1880–1660 cal yr BP. In contrast, there is no signal in Siles for the Younger Dryas cold spell. Correlating these and other Holocene sequences of climate proxies across the Mediterranean (Valero and González, 1999) is not simple because chronological control is often imprecise and estimated ages rely often upon disparate models. So the possible relationships between abrupt climatic events and the transitions at Siles, Cañada de la Cruz, and Villaverde, although thought-provoking, remain tentative.

6. Conclusion

The mid-Holocene emerges in the Segura region of southern Spain as the time of maximum forest development and highest lake levels, the early Holocene as a generally dry, pyrophytic period of pine forests, with grassland scrub at high altitudes, and the late Holocene as a period of protracted vegetation sensitivity, with return to development of pine forests, spread of xerophytic communities, and increased fire activity and anthropogenic disturbance, under the context of dry spells, and shallowing and desiccation of lakes. As expected from its high spatial complexity, and notwithstanding the existence of several significant correlations, the Segura region has shown a particularly high amount of response variability to climatic change. Environmental contrasts across this region today are a hint of the challenging heterogeneity found in palaeoenvironmental records from the Mediterranean basin.

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