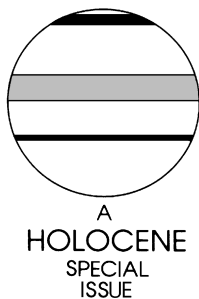


Crossing forest thresholds: inertia and collapse in a Holocene sequence from south-central Spain

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Abstract: A Holocene palaeoecological sequence from Villaverde, south-central Spain, is presented. The pollen stratigraphy is used to infer past vegetation changes within a catchment area that represents the boundary between semi-arid, plateau and mountain vegetation. From c. 9700–7530 cal. yr BP, *Pinus* is dominant, probably as a result of a combination of a relatively dry climate and natural fire disturbance. From c. 7530–5900 cal. yr BP, moderate invasion by *Quercus* appears to be a migrational response following increased moisture and temperature, but in part shaped by competitive adjustments. From c. 5900–5000 cal. yr BP, the pine forests are replaced by deciduous-*Quercus* forests with an important contribution from *Corylus*, *Betula*, *Fraxinus* and *Alnus*. Mediterranean-type forests spread from c. 5000 to 1920 cal. yr BP coincident with expansions of *Artemisia*, *Juniperus* and other xerophytes. From c. 1920–1160 cal. yr BP, *Pinus* becomes dominant after a disturbance-mediated invasion of the oak forests. Human impact upon the regional landscape was negligible during the Neolithic, and limited in the Bronze and Iron Ages. Local deforestation and the expansion of agro-pastoral activities occur after c. 1600 cal. yr BP.

Key words: Holocene, vegetation change, palaeoecology, pollen analysis, climatic change, Spain.

Introduction

The Iberian peninsula has been under-investigated in palaeo-vegetation research. The present study sets out to fill this gap, at least partially, by presenting a Holocene palaeoecological sequence from Villaverde, a site located on the southeastern La Mancha Plain in Albacete province, in the southeastern part of the peninsula (Figure 1). The site lies in a region of wide environmental gradients, characteristic of alternating basin and mountain-range topography, and is an excellent example system with which to address several palaeoecological issues.

Attempts to establish generalities in plant dynamics in Mediterranean Iberia have absorbed much attention in recent years (Burjachs *et al.*, 1997), but few proposed patterns have survived the weight of accumulated exceptions. A basic outline of the vegetational history of the region still eludes us (Carrión *et al.*, 2000a). It is important to emphasize that much scientific work

has yet to see the light of international publication, so current understanding may well be an incomplete impression. In this paper, we aim primarily to establish Holocene vegetation changes and to examine the record in its own right before broader generalizations are attempted.

A second palaeoecological issue addressed here is the identification of the causes of vegetation change. The first step is to examine the potential of the palaeolimnological record to provide independent evidence of past climate. As part of an ongoing research project (Carrión, 1998), the work described here represents the increasing availability of basic information. This will be used to help distill those arguments that are of interest for exploring current hypotheses. Specific topics relate to: (i) the overriding importance of pine forests during the early Holocene in Mediterranean Spain; (ii) their local persistence after the arrival of mesophilous trees; (iii) the mid-Holocene spread and decline of deciduous forests; (iv) the establishment of mediterranean-type forests; (v–vi) the late-Holocene spread of *Juniperus* and *Pinus* and their relationship to the regional history of fire; (vii–viii)

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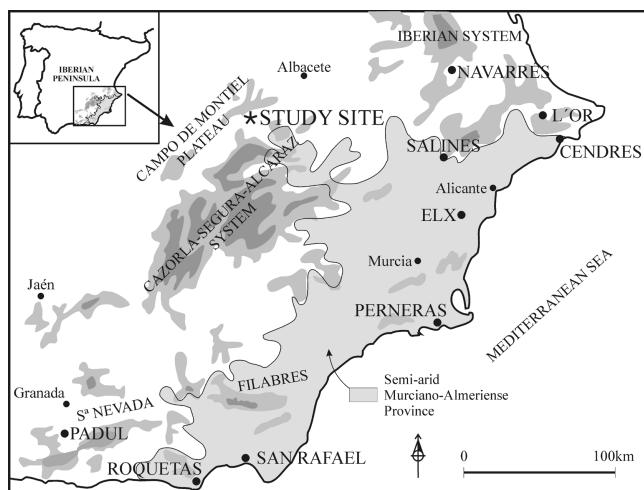


Figure 1 Location of the study site and other pollen sites in southeastern Spain. The site lies within boundary conditions for semi-arid (Murciano-Almeriense province), plateau (Campo de Montiel) and mountain vegetation (Cazorla-Segura-Alcaraz system).

current hypotheses about the existence of regional 'cultural landscapes' during prehistoric times, and since the onset of Roman colonization; (ix) the conflicts between the present palaeoecological record and existing ecologically based concepts of vegetation change in the field area.

Study site and geographical setting

The study site ($2^{\circ} 22'W$, $38^{\circ} 48'N$, 870 m a.s.l.) is a tufaceous peat deposit developed on an old lake bed adjacent to the Cubillo River, 1 km south of a permanent freshwater lake, the Laguna Ojos de Villaverde (Figure 2). The site lies in the Campo de Montiel within the El Bonillo-Lezuza-El Ballestero karst wetlands, near the small village of Villaverde, municipality of Robledo, 57 km west of the city of Albacete. The Cubillo valley has locally a semi-endorheic character related to the dynamics of alluvial fans and, consequently, the creation of lake and marsh conditions. The sedimentary context includes detrital marls interbedded with peats and sapropels overlying basal conglomerates. A relatively high water table is maintained in the permeable carbonates by the presence of gypsiferous siltstone within the underlying Triassic marls (González-Beserán *et al.*, 1991). Water withdrawal for irrigation purposes and various forms of drainage,

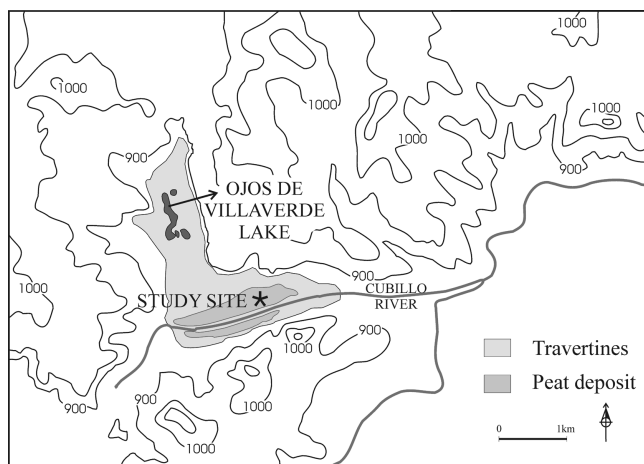


Figure 2 Detailed location of the study site in the Cubillo Basin. Surface travertines are characteristic of the whole interfan area with accumulation of peaty tufas nearby the Cubillo river.

especially trench excavation, have provoked basin desiccation during the nineteenth century. The land has been cultivated for maize, sunflower, alfalfa and other legumes. Recently, interest was shown in peat exploitation and a legal application for permission to do this is in progress.

The following hydrosere is found at Laguna de Villaverde and other regional lakes (from open water to shore): (1) *Chara major*; (2) submerged *Myriophyllum-Potamogeton* communities; (3) thick emergent littoral vegetation of *Phragmites australis*; *Cladium mariscus* and *Typha dominguensis*; (4) Cyperaceae-*Juncus* communities; and (5) hygro-nitrophilous communities dominated by Poaceae and Asteraceae (Cirujano, 1990).

Local vegetation of the Campo de Montiel plateau is dominated by patches of *Quercus rotundifolia* forest with scattered *Juniperus thurifera*, and *Berberis hispanica* on well-drained shallow soils (González-Beserán *et al.*, 1991). The adjacent mountains of the Alcaraz-Segura-Cazorla range are renowned for their magnificent *Pinus nigra* and *P. pinaster* forests, but a number of deciduous trees such as *Quercus faginea*, *Q. pyrenaica*, *Corylus avellana*, *Acer granatense*, *A. monspessulanum*, *Sorbus domestica*, *S. torminalis*, *S. aria* and *Fraxinus angustifolia* are also present. Other communities include *Q. rotundifolia* forests, *Q. coccifera-Rhamnus lycioides* scrub, and upland *Pinus nigra-Juniperus communis* communities (Valle *et al.*, 1989). In contrast, portions of the semi-arid southeastern province, where trees are growing near their physiological tolerance to summer drought, are dominated by *P. halepensis*.

The climate of the area is dry continental Mediterranean. The nearby stations of Munera, El Bonillo, Lezuza, Casas de Lázaro and El Ballestero have a mean annual temperature of 13–14°C and a mean annual rainfall of 400–450 mm. In the Alcaraz-Segura mountains, precipitation exceeds 1100 mm, but 30 km to the south, at Villaverde, in the semi-arid bioprovince, the observatory of Minateda has 225 mm. The absolute temperature range at 59°C is one of the widest in the Iberian peninsula (González-Beserán *et al.*, 1991).

Methods

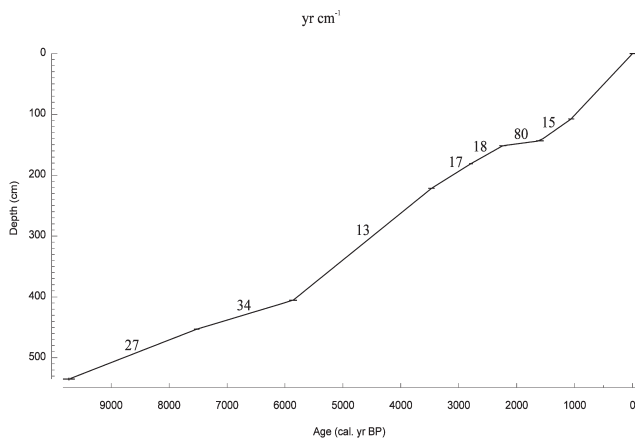
The valley deposit was selected in preference to the lake because of the predominantly organic nature of the former, relative thickness and simpler basin geomorphology (Figure 2). The Ojos de Villaverde basin is a typical karstic lake system with travertine sediment, heavily fissured bedrock, and a number of substantial concentrated flows of groundwater ('Ojos'), which makes it difficult to obtain a stratigraphically coherent record with acceptable analytic potential.

A sediment core (total depth 550 cm) was obtained with a piston corer at the eastern part of the fan using the land-owner's recommendations and unpublished exploitation projects. This information was vital to avoid areas that had been subject to intensive trenching. The drilling ended at a calcareous conglomerate bedrock. The uppermost 1 m of the core was a greyish disturbed horizon, palynologically sterile.

A chronology was established on the basis of eight radiocarbon dates obtained from bulk organic sediment (Table 1) and calibrated using BCal (<http://bcal.cf.ac.uk>), based on the INTCAL98 dataset (Stuiver *et al.*, 1998). The calibrated age is taken as the midpoint of the 95% probability interval, and the error values included on the diagrams are for one standard deviation. The probability that the dates are affected by hardwater error cannot be excluded, but the internal consistency of the series provides no evidence that this has in fact occurred (Figure 3). An age-depth model based on interpolated ages between adjacent pairs of dates (sediment top assumed as age 0) was obtained (Figure 3). The variation of sediment type within the sequence means that it

Table 1 Radiocarbon ages of bulk sediment samples from Villaverde (ages calibrated using CALIB 4.12, Stuiver *et al.*, 1998)

Lab. ref.	Depth (cm)	Conventional age (^{14}C years BP)	Calibrated age range	Calibrated age (years BP)	Material
Pta-7964	107–108	1230 \pm 35	1260–1065	1160	Peat
Pta-7962	143–144	1680 \pm 50	1710–1490	1600	Peat
Pta-7693	151–152	2260 \pm 60	2355–2125	2240	Peat
Pta-7958	180–182	2650 \pm 45	2850–2730	2790	Organic marl
Pta-7954	221–222	3240 \pm 50	3573–3360	3470	Organic marl
Pta-7951	405–406	5140 \pm 60	5994–5732	5860	Peat
Pta-7959	452–454	6670 \pm 60	7615–7435	7525	Peat
Beta-125960	533–537	8720 \pm 80	9930–9530	9730	Lime marl

**Figure 3** Age-depth curve for the Villaverde sequence. The model was based on interpolated ages between adjacent pairs of dates (sediment top assumed as age 0).

would be inappropriate to fit more complex models to the entire data set.

Samples for the analysis of microfossils were taken at intervals of 4–8 cm throughout the core except where pollen results prompted closer intervals of up to every 1 cm. As a control of modern pollen deposition of the whole range of neighbouring plant communities, five surface samples were studied, each consisting of a mixture of ten soil surface subsamples. The pollen spectrum showed in the uppermost part of the pollen diagrams represents average percentages of pollen taxa from these surface subsamples (Figures 5–11). The extraction of pollen follows standard procedures (Moore *et al.*, 1991). Exotic *Lycopodium* tablets of a known concentration were added in order to calculate pollen concentrations. Mineral separation with Thoulet heavy liquid of specific density 2.0 was used for all the samples. Identifications were aided by the use of reference material at the Pal-MUB collection, Murcia University. Identification of algal, fungal and other non-pollen microfossils was aided by the descriptions and microphotographs in Van Geel *et al.* (1981; 1986; 1989), Jarzen and Elsik (1986) and Carrión and Van Geel (1999) (Table 2; Figure 5). Several ecological groups have been considered (Figure 11). ‘Other xerophytes’ include *Artemisia*, *Chenopodiaceae*, *Ephedra fragilis*, *Asteroidae* and *Cichorioideae*. ‘Other mesophilous trees’ include *Betula*, *Fraxinus*, *Salix*, *Corylus*, *Alnus*, *Ulmus*, *Acer* and *Sorbus*. ‘Other Mediterranean’ include *Pistacia*, *Phillyrea*, *Erica arborea*, *Olea*, *Cistus*, *Rhamnus* and *Myrtus*. Nomenclature for vascular plants follows Tutin *et al.* (1964–80).

The delimitation of pollen (VP) and ‘microfossil’ (VM) assemblage zone boundaries was obtained from an optimal division of the sequence using the information content criterion, after exploration of four other methods. The number of the zones was determined using the method of Bennett (1996). Pollen zones

were based on the values of pollen types that exceeded 5% in any sample. ‘Microfossil’ zones include non-pollen palynomorphs and pollen from aquatic and littoral vegetation (Figure 5). Pollen diagrams were constructed using Tilia and TiliaGraph programs (Figures 6–10). Pollen concentration curves show that most increases observed in these diagrams are not artifacts of percentage data (Figure 10). A synthetic diagram including selected pollen curves and microscopic charcoal abundance is shown in Figure 11. The total number of charcoal particles longer than 10 μm were counted on the slides prepared for pollen analysis and their concentrations calculated as for pollen concentration (Figure 11). No pieces exceeded 100 μm , and most were less than 60 μm . No macroscopic charcoal (>140 μm) was found with the microfossil samples. By excluding the finest and coarsest particles, the total number of charcoal particles can be taken as an indication of regional fire occurrence.

Further examination of the main directions of variation in the data was facilitated by means of a principal components analysis (PCA) of the main pollen types (Figure 4). The pollen types included were all the main pollen taxa that exceeded 5% within the sequence, with the exception of *Equisetum*, omitted because it is not likely to have been a significant component of the terrestrial vegetation. The PCA was implemented on a covariance matrix after square-root transformation (to reduce the bias towards abundant taxa), using algorithms of Press *et al.* (1992) within the computer program ‘psimpoll’ (Bennett, 2000).

Samples for microfossil analysis, one per lithological unit, were boiled in 5% KOH for 5–10 minutes and strained through a 140 μm mesh sieve. Counting was undertaken on a cross-ruled petri-dish using a stereo microscope. Plant macroremains were poorly preserved but included a few seeds of *Cyperaceae*, *Juncus* and *Potamogeton*. Macrocharcoal was absent. Characeae gyrogonites and ostracod valves were, however, abundant and well preserved (Figure 5). Identification criteria follow Haas (1994) for Characeae, and Henderson (1990) and Baltanás *et al.* (1996) for Ostracoda.

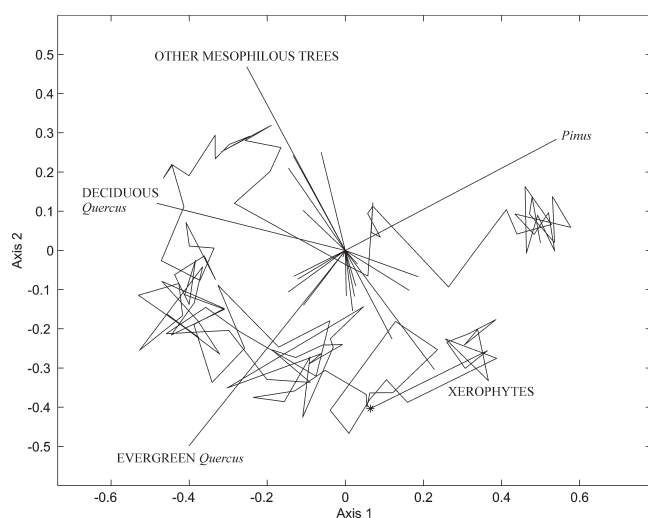
Results

Palaeolimnological changes

The lithostratigraphy (VL) can be combined with the microfossil (VM) and macrofossil changes to infer past hydrological conditions of the basin (Figure 5). The lithology comprises pale-brown organic marls (VL1, VL3, VL5) and black organic sediments of varying states of humification (‘peats’: VL6, VL7) or decomposition (‘sapropels’: VL2, VL4) (Figure 5). Macrofossil analyses, mainly from VL2, VL4, VL6 and VL7, reveal the occurrence of poorly preserved seeds, scales, rootlets, rhizome fragments (up to 10 mm) of cormophytes and moss leaflets. Characeae detritus is, however, the main component of plant macrofossils throughout the core from VL2 upwards, although the detritus

Table 2 Non-pollen microfossils with stratigraphical value at Villaverde sequence. Reference literature for original descriptions and palaeoecological indication

Type	Indication	Relevant references
128 119 304 <i>Closterium</i>	Mainly mesotrophic oxygen-rich fresh water (lake and pool deposits)	Pals <i>et al.</i> (1980) Carrión and Van Geel (1999)
<i>Zygnema</i> <i>Spirogyra</i> <i>Mougeotia</i> <i>Tetraedron</i>	Meso- to eutrophic Stagnant shallow open water	Van Geel (1976) Van Geel <i>et al.</i> (1981; 1983; 1989)
181 179	Eutrophic stagnant shallow open water	Van Geel <i>et al.</i> (1989)
224 359 <i>Pseudoschizaea</i>	Peaty deposits in lakes Temporal desiccation	Van Geel <i>et al.</i> (1981; 1989) Scott (1992)
222	Sandy deposits in lakes	Van Geel <i>et al.</i> (1989)
984 985 988	Sandy peat deposits in lakes Irrigation agriculture? Runoff?	Carrión and Van Geel (1999)
<i>Glomus</i>	Root activity (terrestrial vegetation)	Van Geel <i>et al.</i> (1989)
<i>Polyadosporites</i> <i>Pluricellaesporites</i> <i>Dictyosporites</i>	Organic matter decomposition (fungal activity)	Jarzen and Elsik (1986)
Sordariaceae <i>Chaetomium</i> <i>Gelasinospora</i>	Fungal activity (dung?)	Van Geel (1972; 1978) Jarzen and Elsik (1986) Carrión <i>et al.</i> (1999a)
<i>Tilletia</i> <i>Puccinia</i>	Anthropogenic phase (agriculture)?	Carrión and Van Geel (1999)

**Figure 4** Principal component analysis biplot of the Villaverde Holocene pollen spectra. The first (horizontal) and second (vertical) axes of the ordination account for approximately 46% and 18% of the variation in the data set, respectively. The ordination presents: (i) loadings of the important pollen taxa; and (ii) scores of the fossil pollen spectra, connected in sequence. The top sample is marked with an asterisk. See MacDonald (1987) for details of interpretation.

component is better preserved in marl layers. This detritus consists of branchlets, fragments of axial internodes with the typical diplostichous-anisostichous cortex, clusters of spine cells attached to axial fragments, and gyrogonites. Charophyte encrustation by calcite is likely to provide an important part of the marl, although calcium carbonate may also have been precipitated from the water by aquatic angiosperms.

These variations suggest fluctuating water levels with the deposition of marls during periods of higher lake levels and the deposition of peats associated with advances of littoral emergent vegetation during lower lake levels. Overall, charophyte-rich facies throughout the core confirms the presence of permanent, albeit relatively shallow, water conditions. The abundance of *Chara hispida* gyrogonites in VL3 and VL5 indicates *in situ* deposition as well as submersion for at least three months, which is the time required for the plant to complete a full cycle of growth including calcification of the reproductive organs (Soulié-Märsche, 1993). *Chara hispida* today forms spectacular extensive communities at the bottom of permanent freshwater lakes (4–9 m) of the region, where it solidifies directly into a soft marl layer in lake depocentres (Cirujano, 1990).

Granular lime marl of the kind observed in VL2, VL3 and VL5 is found today in static or sluggish flow waters with abundant dissolved and particulate calcium carbonate, an environment favourable for the abundant ostracod *Ilyocypris bradyi* to construct its valves. Associated microfossil assemblages (VM3, VM5) fit into this picture. They include the spore types 128 and

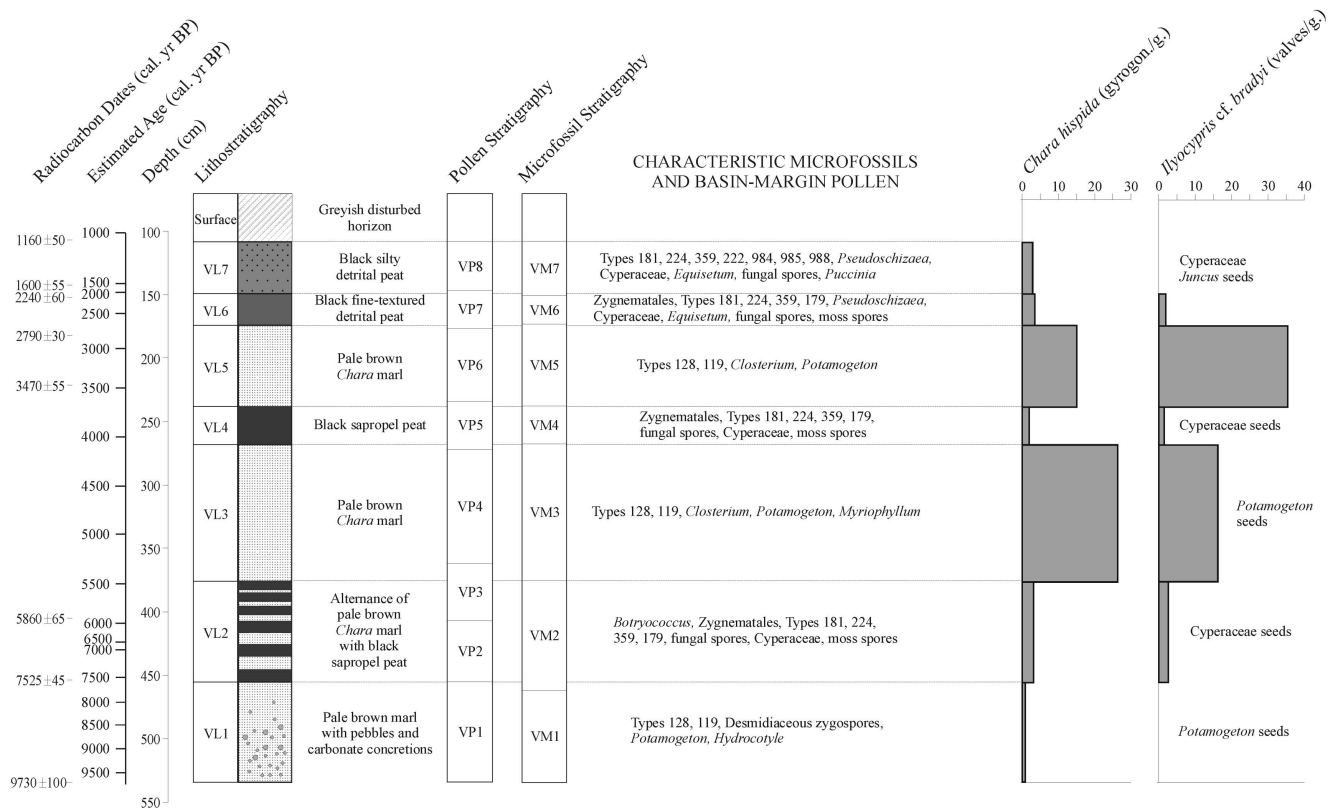


Figure 5 Lithostratigraphy (VL), and pollen (VP), microfossil (VM) and macrofossil stratigraphies (*Chara*, *Ilyocypris*) in the sequence of Villaverde. There is good correlation between VL and VM zones, but VP zones are out-of-phase below c. 350 cm depth. See Table 2 for relevant literature and ecological indication of microfossil types.

119, zygospores of *Closterium*, and pollen of *Potamogeton* and *Myriophyllum* (Figures 5, 8 and 9; Table 2). In particular, *Closterium*-type 128 are characteristic of mesotrophic stages in lake hydrospheres of the region (Carrion and van Geel, 1999). Physico-chemical precipitation, in addition to biogenic, must have taken place during the initial VL1 stage because lime marls are not associated with charophyte-rich facies and gyrogonites are almost absent. A conglomerate of rounded heterometric pebbles is deposited in a calcreted matrix, which suggests an increased, although probably intermittent, flow regime, perhaps associated with degassing points at resurgences (Pedley *et al.*, 1996). Higher flow velocities would have prevented biofilm colonization and *Chara* growth. A higher abundance at VM1 of the microfossil assemblages characteristic of VM3 and VM5 supports this hypothesis. In addition, *Hydrocotyle* pollen may also be indicative of groundwater input (Moore, 1986), while *Ceratophyllum* leaf-spines and type 304 may be indicative of deeper-water stages (Van Geel *et al.*, 1989).

During short periods in VL2, and stages VL4, VL6, and VL7, there must have been increased organic input associated with lower water levels. Increased turbidity would have diminished the reproductive capability of aquatic angiosperms and charophytes carpeting the ground. Characteristic microfossil assemblages include Zygnematales (*Zygnema*, *Spirogyra*, *Mougeotia*, *Tetraedron*), *Rivularia*, types 181, 224, 359 and 179, Cyperaceae, *Lythrum*, *Epilobium*, ferns, decomposing fungi and moss spores. Together these palynomorphs suggest advances of peat- and sapropel-producing marsh environments, areas of temporary stagnant water and lake eutrophication. Changes in wetness are further attested by *Arcella*, which, like other rhizopods, responds to falling lake levels by encysting rather than migrating (Van Geel *et al.*, 1989). Ostracod valves are infrequent during peat levels, presumably because of reduced calcium carbonate availability or lack of habitat. In comparison with the sapropelic VL2 and VL4 zones, the peats VL6 and VL7 appear to be formed under more terrestrial

conditions, as is further indicated by the occurrence of *Equisetum* spores, *Pseudoschizaea* cysts and spore types 222, 984, 985 and 988, among other fungal palynomorphs (*Glomus*, *Polyadosporites*, *Pluricellaesporites*, *Sordariaceae*) (Figures 8 and 9). The presence of *Tilletia* and *Puccinia*, mainly grass-parasitizing fungi, coupled with siltation, may be related to increased agriculturization, clearance and devegetation of floodplains, and moderate catchment erosion.

It is clear that the initiation of the lacustrine sequence must have been connected with some kind of drainage impedence, perhaps associated with increased water input. It is also clear that biological and geological changes are coupled with water-level variation. However, pinpointing the prime source of the hydrological events is difficult since there must have been alterations in local drainage patterns caused by karst dynamics and groundwater input. This would explain why there is no good correlation between limnological and pollen events (Figure 5), and suggests that this basin is not a suitable model for multi-proxy palaeoclimate reconstruction studies.

Pollen stratigraphy and vegetation history

The pollen sequence of Villaverde can be used to establish the vegetation history of the region from c. 9700 to 1160 cal. yr BP (Figures 6–7). Unfortunately no detailed studies of the pollen rain of the area have been made, but taking into account the location of the basin and its altitude and diameter, and the dispersal mechanisms of individual species (Markgraf, 1980), the expected pollen source area should include not only the valley mostly dominated today by cultivars and cleared oak and juniper woodlands but also the surrounding hills at the Campo de Montiel (Figure 1), and northern slopes of Alcaraz-Segura mountains, and semi-arid region (Figure 2). Surface samples studied here confirm this view. The average pollen spectrum shows predominance of

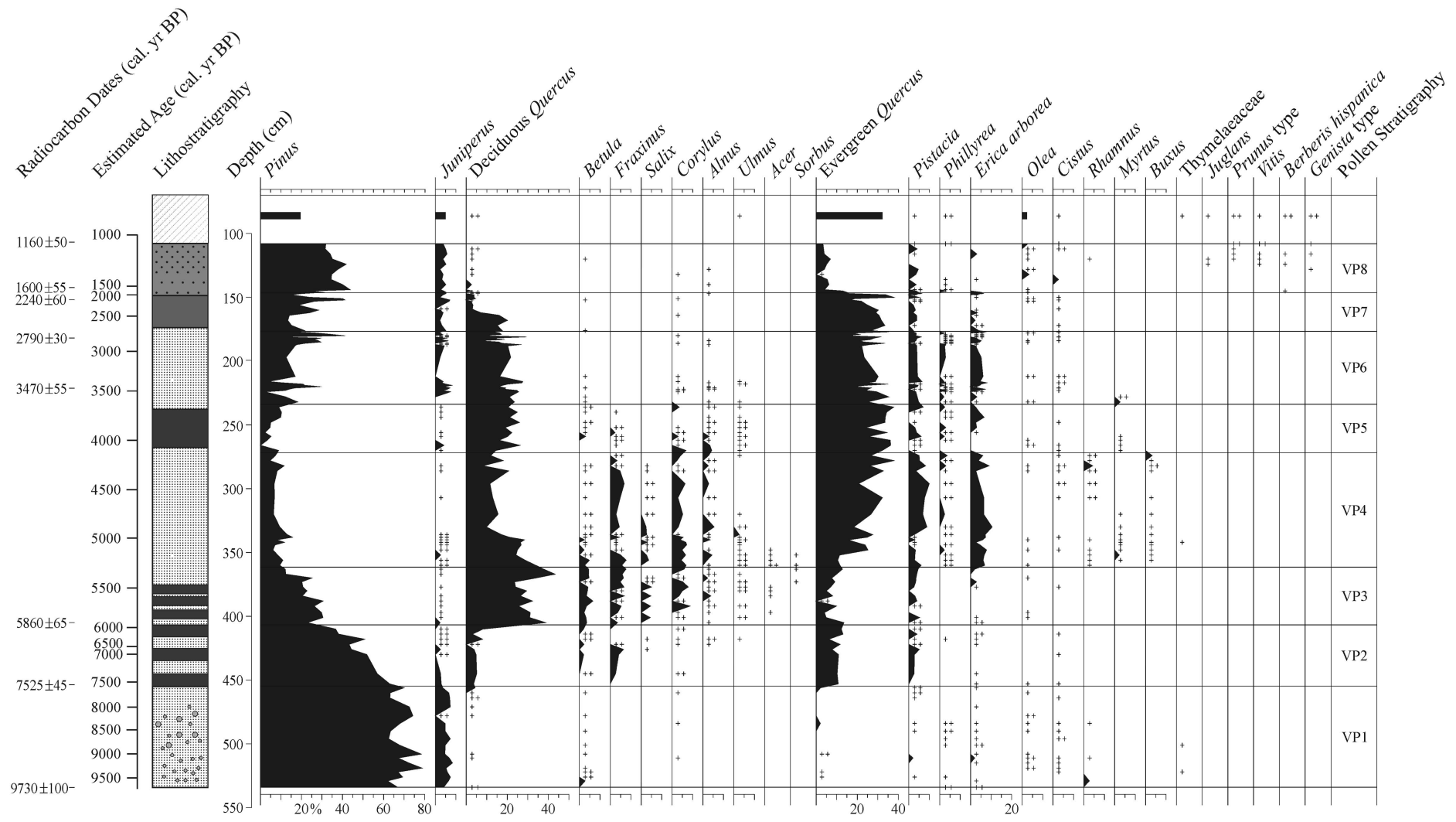


Figure 6 Villaverde sequence. Arboreal pollen percentages.

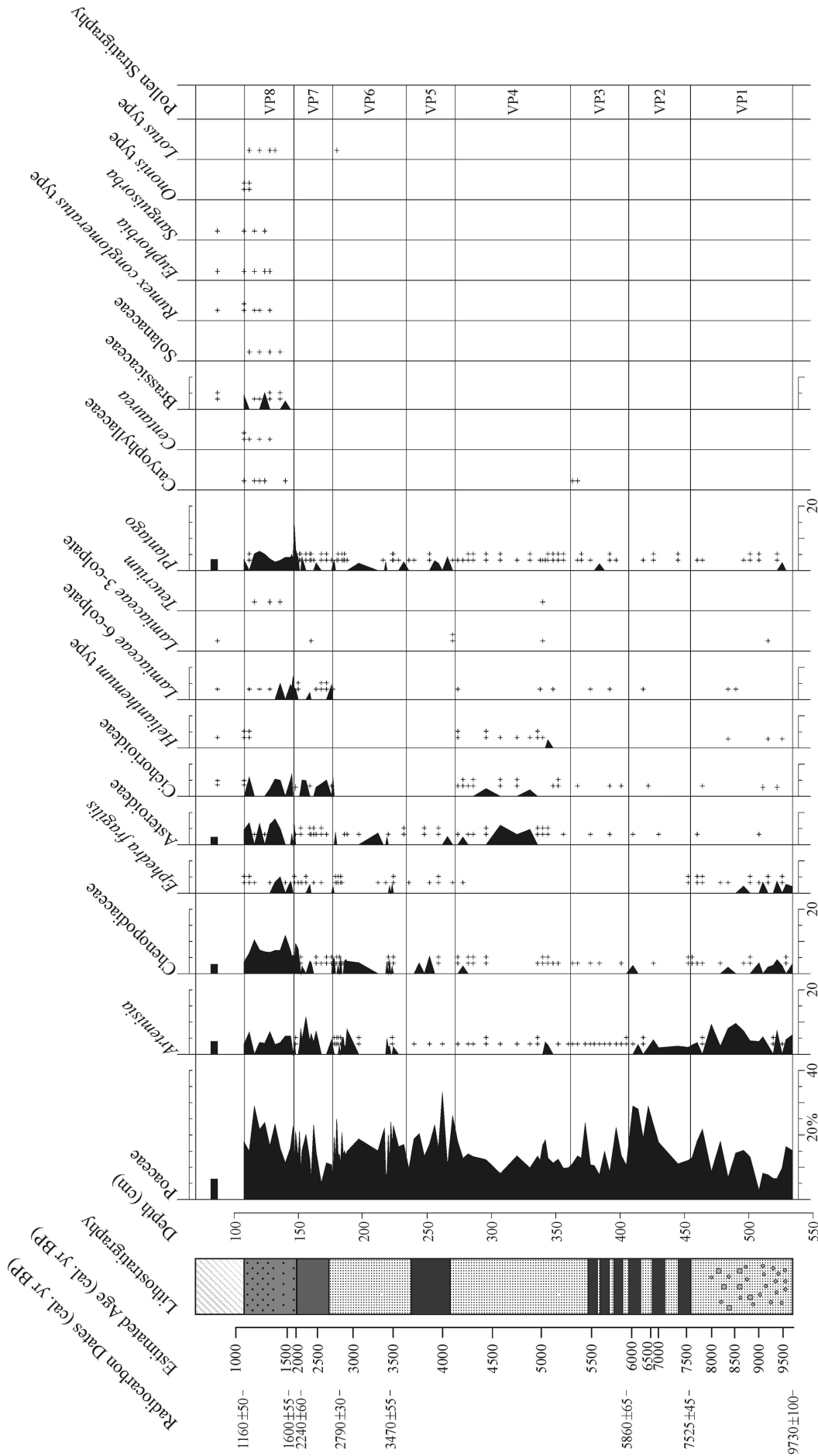


Figure 7 Villaverde sequence. Non-arboreal pollen percentages.

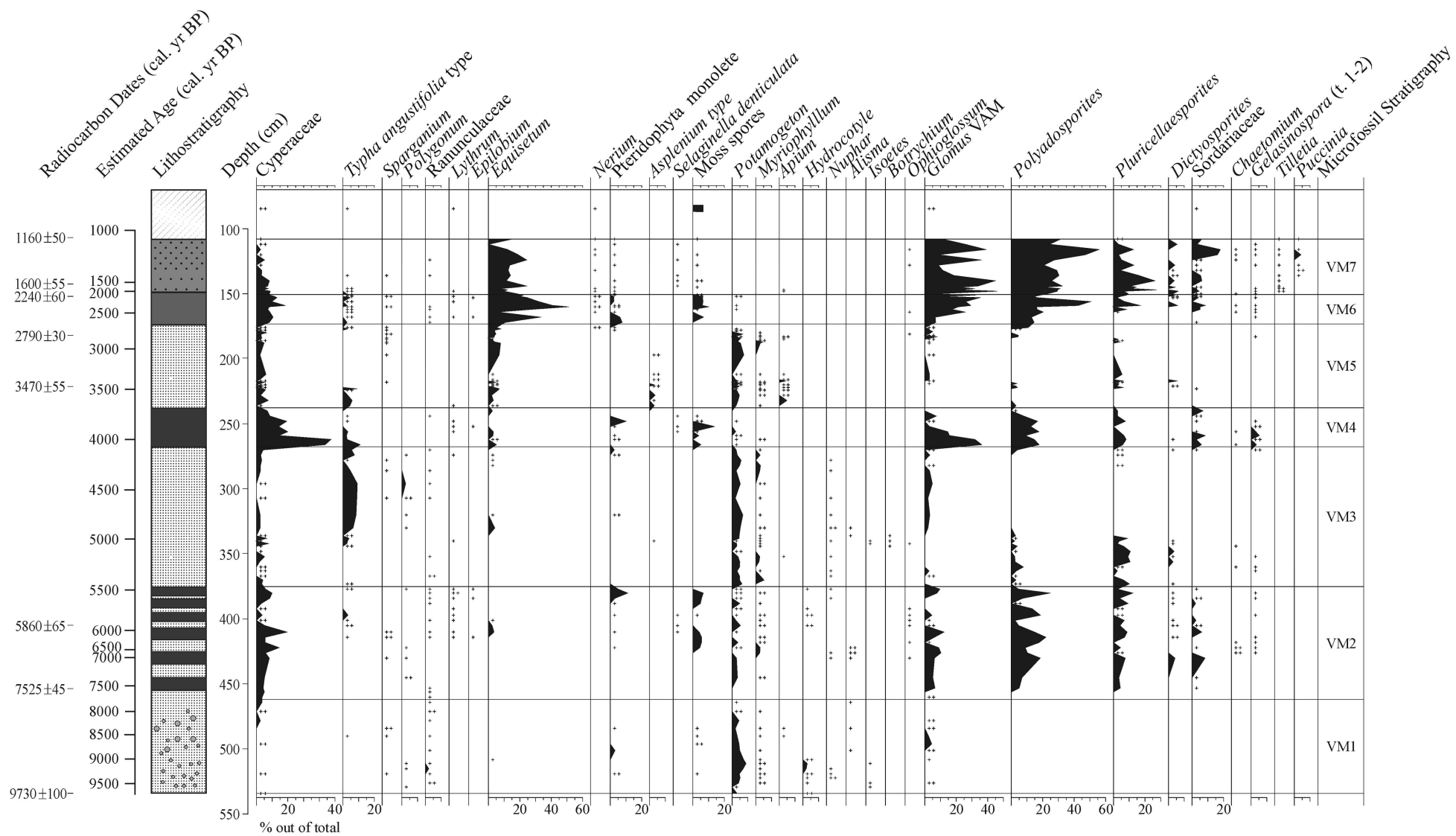


Figure 8 Villaverde sequence. Basin-margin pollen, and fern and fungal palynomorphs.

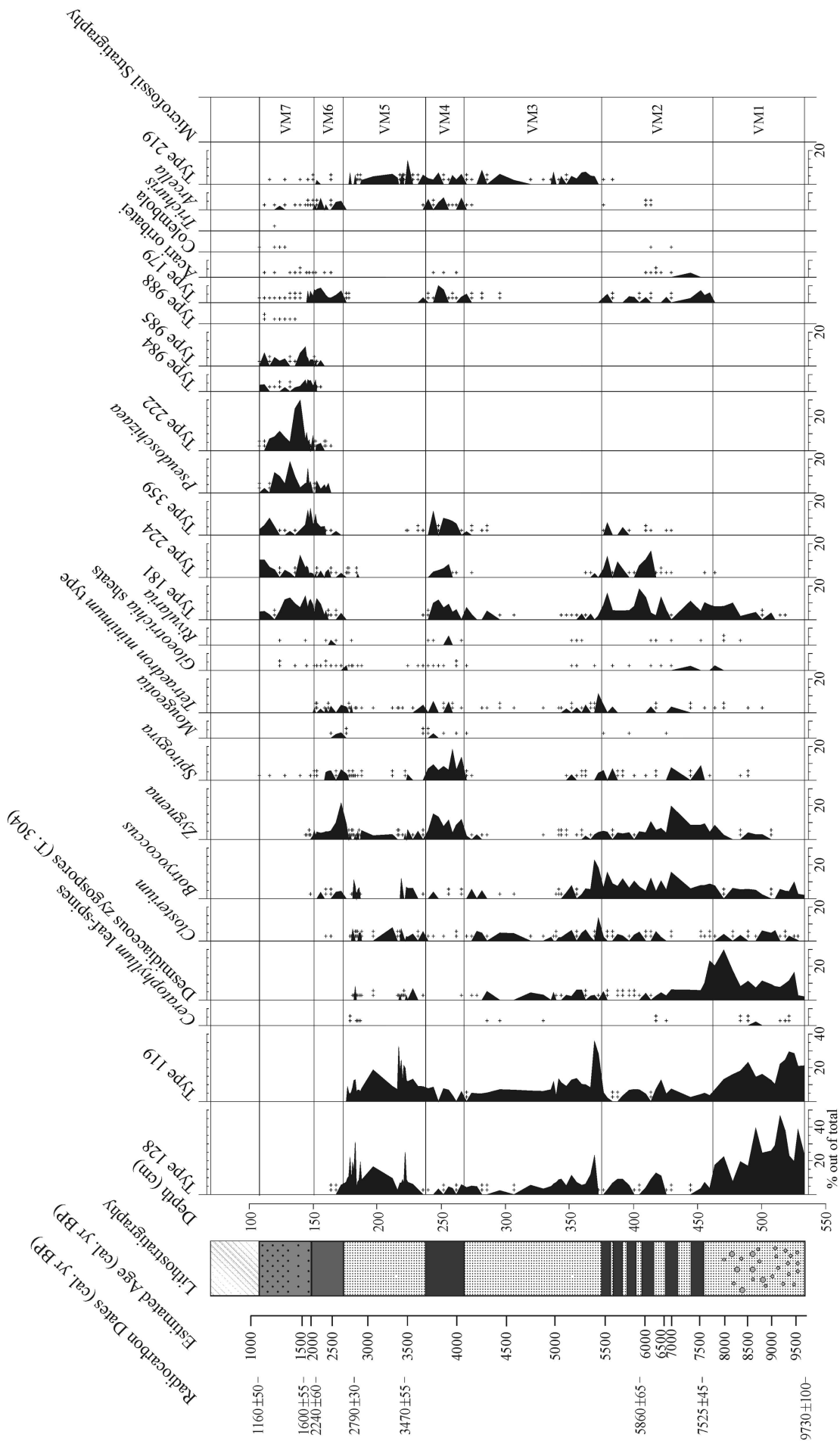


Figure 9 Villaverde sequence. Algal and other non-pollen microfossils.

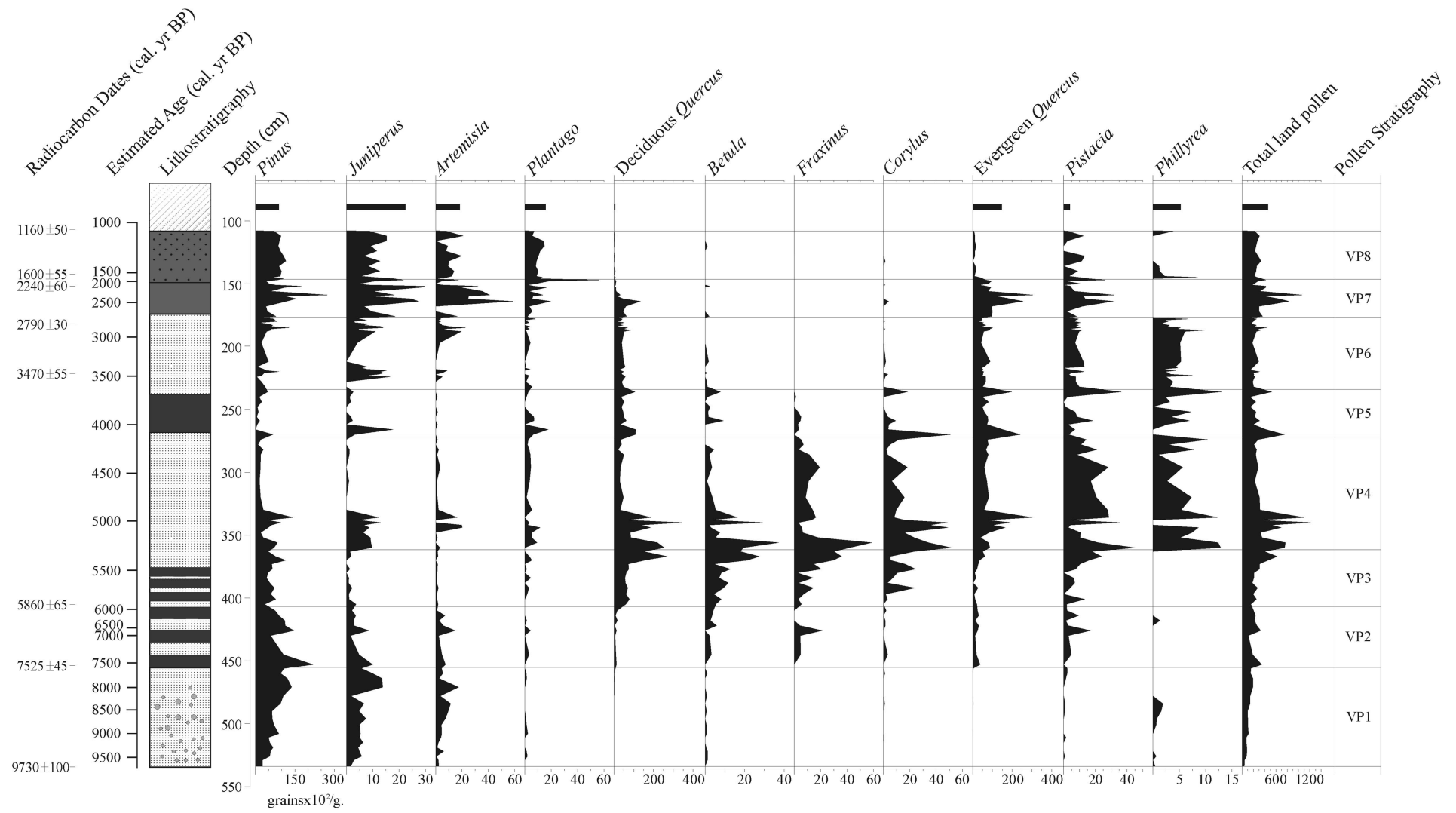


Figure 10 Villaverde sequence. Pollen concentration diagram of selected types.

evergreen *Quercus* (33%), and important values of *Pinus* (18%) and *Juniperus* (5%). Other relevant taxa are Poaceae (6%), *Artemisia* (4%), *Plantago* (3.5%), Chenopodiaceae (3%) and *Olea* (2%). With lesser occurrences there are *Juglans*, *Prunus*, *Vitis*, *Berberis* and *Genista* type.

During VP1 (c. 9700–7530 cal. yr BP) pine forests were the dominant vegetation, with *Juniperus* cf. *thurifera* probably occupying the shallowest soils and most continental biotopes. A notable semi-arid pollen signal of *Artemisia*, Chenopodiaceae and *Ephedra fragilis* is recorded.

During VP2 (c. 7530–5940 cal. yr BP), the dominant pollen contributor continues to be *Pinus*, with mean percentages of about 50%. There is a partial replacement of *Pinus* by evergreen *Quercus*, and, to a lesser extent, deciduous *Quercus*, *Fraxinus* and *Betula*. *Pistacia* increases above 2%, while *Juniperus* and *Artemisia* decrease, and Chenopodiaceae and *Ephedra* almost disappear.

Zone VP3 (c. 5940–5290 cal. yr BP) marks the arrival and spread of deciduous forests. Pine forests are replaced by deciduous-*Quercus* forests with important contributions from mesophilous trees such as *Corylus*, *Betula*, *Fraxinus*, *Alnus* and *Salix*, and occurrence of *Ulmus*, *Acer* and *Sorbus*. Xerophytes, such as *Artemisia* and Chenopodiaceae, and *Juniperus* attain a minima, and *Ephedra* is absent during this zone. Evergreen *Quercus* and *Pistacia* continue to be secondary.

During VP4 (c. 5290–4120 cal. yr BP), deciduous *Quercus* is replaced by evergreen *Quercus*. The sclerophyllous Mediterranean component (*Pistacia*, *Phillyrea*, *Erica arborea*, *Cistus*, *Rhamnus*, *Myrtus*, *Buxus*) reaches its maximum as evergreen *Quercus* increases. This expansion of Mediterranean forest and scrub parallels a considerable reduction in the broad-leaved forests dominated by deciduous *Quercus*, while other mesic pollen types such as *Corylus*, *Fraxinus* and *Alnus* persist above 5%. *Pinus* decreases to frequencies of less than 10%.

During VP5 (c. 4120–3630 cal. yr BP), the evergreen *Quercus* forest reaches its maximum. This zone marks the final declines of the deciduous taxa *Betula*, *Fraxinus*, *Corylus*, *Alnus* and *Ulmus*, although deciduous *Quercus* increases slightly from VP4. Mediterranean scrub types decline. Local vegetation during this period was probably a mixed *Quercus rotundifolia/ilex-Q. faginea* forest with deciduous trees growing mostly along north-facing slopes, mountain gullies and watercourses. Unfortunately, the evergreen oak species involved is not known. It could be *Q. ilex*, characteristic of peripheral mountain sites and threatened with extinction in the study region, or *Q. rotundifolia*, better adapted to continental climates and summer drought. Plausibly, *Q. ilex* may have occurred during the mesophytic VP3 phase, becoming introgressively replaced by *Q. rotundifolia* from VP4 onwards.

Zone VP6 (3630–2740 cal. yr BP) shows no major change in the forest dominants, but *Pinus* plays a major role in forest dynamics by experiencing abrupt short-lived oscillations at c. 3470 cal. yr BP and 2790 cal. yr BP. Additional characteristics of this zone include rises of *Juniperus*, *Artemisia*, Chenopodiaceae and *Ephedra*. A Mediterranean-forest understory of *Pistacia*, *Phillyrea* and *Erica arborea* is also characteristic of this zone.

Conspicuously during VP7 (c. 2740–1920 yr BP), deciduous *Quercus* declines, and evergreen *Quercus* becomes the main forest dominant. *Pinus* again shows distinct oscillations, with a main peak at c. 2240 cal. yr BP, followed by a maximum of evergreen *Quercus* at about 2000 cal. yr BP. *Phillyrea* and *Erica arborea* diminish, but *Pistacia* is still recorded above 2%. *Artemisia* reaches 9%, and Chenopodiaceae, *Ephedra* and *Juniperus* are noteworthy.

At the base of VP8 (c. 1920–1160 yr BP), there is a major vegetation shift including a change in the forest dominance and the expansion of herbaceous taxa. After a new *Pinus* peak at c. 1600 yr BP, evergreen *Quercus* falls to percentages below 10%, while *Pinus* prevails dominant. Characteristic taxa of this zone

include *Olea*, *Pistacia*, *Cistus*, *Juglans*, *Prunus* type, *Vitis*, *Berberis*, *Genista* type, Asteroideae, Cichorioideae, *Plantago*, Lamiales, Brassicaceae, Caryophyllaceae, *Centaurea*, Solanaceae, *Rumex*, *Euphorbia*, *Sanguisorba* and Fabaceae, in addition to *Juniperus*, *Artemisia*, Chenopodiaceae and *Ephedra fragilis*.

The PCA synthesizes this pollen stratigraphy concisely (Figure 4). The dominant pollen types are *Pinus*, evergreen *Quercus*, deciduous *Quercus* and other mesophilous trees. The sequence begins with pollen spectra dominated by *Pinus*, then moves through a mesophilous/deciduous *Quercus* phase towards spectra dominated by evergreen *Quercus*, and finally to the modern xerophytic-dominated spectra. It is clear that the pollen spectra, and hence vegetation, have been changing continually, but have never returned to any intermediate state.

Discussion

Previous studies

Pollen and mollusc records have been reported from the Cubillo interfan by Taylor *et al.* (1998). This study is based on the analysis of 13 samples of organic-rich sediments from a 6 m depth core dated from c. 6800 cal. yr BP at the bottom to c. 3150 cal. yr BP at c. 170–180 cm depth. Although the sequence has a similar alternation of peats and lime muds, it does not correlate with the VL sequence (Figure 5), which suggests that individual cores are of little value in elucidating past hydrological changes at the scale of the entire basin. The pollen sequence of Taylor *et al.* (1998) shows similar tendencies in the *Pinus* and *Quercus* variations to Villaverde. Their paper also includes a pollen record from sapropel horizons of a barrage tufa deposit at the nearby locality of Alcaraz. This record, beginning at 6000 cal. yr BP, shows overall dominance of *Pinus*, and an expansion of *Quercus* at c. 3400 cal. yr BP, which also roughly matches the Villaverde sequence. It is finally worth mentioning the consistent abundance of *Pinus* throughout the mid- to late-Holocene cave sites of Cueva del Calor, Cortijo de Andrevía, Cueva del Milano and Los Molinos, in northwestern Murcia (López, 1991), and the relative abundance of mesophyte pollen in the Neolithic rockshelter Cueva del Nacimiento, Jaén, Sierra de Segura (López, 1981).

Other pollen diagrams help us to elucidate the nature of Holocene vegetation to the west and the north in La Mancha. The Daimiel II (Menéndez-Amor and Florschütz, 1968) and Castillo de Calatrava (García Antón *et al.*, 1986) pollen records show slightly fluctuating co-dominance by *Pinus* and *Quercus* from c. 7100 cal. yr BP to after 1650 cal. yr BP. The Guadiana river-basin CC-17 pollen record (Dorado *et al.*, 1999) shows a regional abundance of *Pinus* from c. 11200 to 7650 cal. yr BP, and the dominance of *Pinus* and *Quercus* from c. 9450 to c. 2360 cal. yr BP. This chronology is based on radiocarbon dates of c. 10200 cal. yr BP at the bottom, and c. 7050 cal. yr BP in the middle part of the sequence. Clearly improved dating is required to assess patterns and allow full comparison. The authors also suggest that they found pollen signals for arid phases at about 10500–9200, 6600–5150 and 2550–1950 cal. yr BP. However, it appears that the suggested pollen changes are conditioned by site-specific pollen taphonomy, because none of these arid events is demonstrable by increases in both percentage and concentration values of xerophyte types. Climatic control for the observed changes in the water level is suggested (Dorado *et al.*, 1999), but this should be confirmed through a more extensive, multi-core study. These kinds of karstic landscapes may show great sensitivity to disturbance, and small-scale events can result in a basin-wide change in regime (Goudie *et al.*, 1993).

Were early-Holocene pine forests (c. 9700–7500 cal. yr BP) keeping pace with climate?

Following climate warming from the Lateglacial into the Holocene, angiosperm trees invaded wide parts of the low- and mid-altitude last-glacial conifer forests and steppes of Mediterranean Spain (Watts, 1986; Pons and Reille, 1988; Yll and Pérez-Obiol, 1992; Peñalba, 1994; Pérez-Obiol and Julià, 1994; Allen *et al.*, 1996; Targarona, 1997). The pollen records from Villaverde, and also from Navarrés (Carrión and Dupré, 1996; Carrión and Van Geel, 1999), suggest that the permanence of pine forests during periods of the Holocene was not restricted to the highest mountain belts, steep topographies and shallow-soil biotopes. Rather more, it is common in Mediterranean Iberia throughout mountain valleys and continental areas (García-Antón *et al.*, 1997; Andrade, 1994; Peñalba, 1994; Franco *et al.*, 1998; Taylor *et al.*, 1998; Carrión *et al.*, 2000b), and coastal territories (Stevenson and Moore, 1988; Dupré and Renault-Miskovsky, 1990; Riera, 1993; Carrión *et al.*, 1999a). The possible causes of this phenomenon need discussion.

Initially, we focus on the Villaverde region. To the north and east of Villaverde, the pollen records CC-7 (Dorado *et al.*, 1999) and Elx and Salines (Burjachs *et al.*, 1997), respectively, show earlier development of *Quercus* than Villaverde, but pine pollen is abundant (Figure 1). The submontane L'Or and Navarrés and the littoral Cendres sites show a clear dominance of *Pinus* pollen (Dupré, 1988; Carrión *et al.*, 1999a). Unpublished pollen records from Cañada de la Cruz and Siles in the Segura mountains suggest that pines were the main forest components at this time. Thus, independent of particular site-specific dominants, and the equally puzzling landscape dynamics, there is a regional pollen signal for the abundance of *Pinus* during the early Holocene.

A prevailing dry climate during the first Holocene millennia could explain the abundance of pines in these regions. High percentages of xerophyte pollen during VP1 indicate the proximity of semi-arid vegetation, while the relatively high concentrations of microcharcoal (Figure 11) suggest that episodic fires occurred regionally and may have been important in giving *Pinus* the competitive advantage over deciduous *Quercus* at sites where the former remained dominant. The positive correlation found at Villaverde between microcharcoal and *Pinus*, xerophytes and *Juniperus* suggests a relationship between fire disturbance, vegetation and climate (Table 3). The abundance of *Artemisia* until c. 8500 cal. yr BP at San Rafael and Antas pollen records, Almería (Pantaleón-Cano, 1997), supports this hypothesis. Using the best modern analogues method, Cheddadi *et al.* (1998) have reconstructed annual precipitation from Tigalmamine, in the Middle Atlas of Morocco. They suggest that dry conditions affected the early Holocene of Mediterranean North Africa. A plausible scenario for Villaverde is therefore a combination of relatively dry climate and fire disturbance.

The difficult question, however, concerns local dominance, because the absence of macrocharcoal in VP1 makes the local occurrence of fires unlikely. Initial conditions and local-species interactions in addition to the influence of nearby mountain pine forests may also have played their role. Small differences in cold-stage tree distributions may have become magnified as tree populations increased and spread (Bennett and Willis, 1995). The Iberian Peninsula was a vast Pleistocene reservoir of pine forests (e.g., Dupré, 1988; Bennett *et al.*, 1991; Burjachs and Julià, 1994; Pérez-Obiol and Julià, 1994; Carrión *et al.*, 1995a; 1995b; 1999a), which, from the Holocene onset, must have been influential in determining the pattern of events within the Holocene (Carrión *et al.*, 1999b).

Arrival of oaks and permanence of pine forests (c. 7500–5900 cal. yr BP)

Moderate invasion of the catchment area by *Quercus*, *Fraxinus*, *Betula* and *Pistacia* appears to be a migrational response follow-

ing increased moisture and temperature, but in part shaped by competitive adjustments. *Pinus* remained locally dominant for more than a millennium, even though there was a rich pool of available potential free colonists from c. 7800 cal. yr BP. There are regional pollen signals between 7800 and 5700 cal. yr BP for deciduous and evergreen *Quercus*, *Alnus*, *Betula*, *Corylus*, *Ulmus*, *Fraxinus*, *Acer*, *Salix*, *Sorbus*, *Ilex*, *Arbutus*, *Buxus*, *Pistacia*, *Phillyrea*, *Olea*, *Myrtus*, *Sambucus*, *Viburnum*, *Rhus*, *Erica arborea*, *Coriaria* and *Rhamnus* (Dupré, 1988; Burjachs *et al.*, 1997; Dorado *et al.*, 1999; Carrión and Van Geel, 1999). *Pinus* dominance may again relate to a prevailing dry climate, but also to the inertia of established tree populations, which can modify environments in ways that perpetuate forest patches, for instance through allelopathic mechanisms. Species that have stayed in place for great periods of time may also survive climate change and invasion by possessing large genetic plasticity (Bradshaw and McNeilly, 1981). At first, inertial mechanisms might explain the permanence of existing tree populations for ecologically sensitive scales of decades to centuries (Bennett and Willis, 1995). Interestingly, at the evolutionary tempo (i.e., millions of years), the so-called 'home-field advantage' can also explain resistance to invasion of specific niches (DiMichele and Bateman, 1996). Frustratingly, the gap in our knowledge is that at the millennial scale.

'Atlantic forests' in Mediterranean Spain (c. 5900–5000 cal. yr BP)

The optimum of deciduous trees at Villaverde (5900–5000 cal. yr BP) occurs later than mesocratic phase of forest development in northwestern Europe, which extends from about 10200 until 5700 cal. yr BP (Birks, 1986). Neither does it coincide with maximum development of mesophyte pollen in terrestrial records or the most recent sapropel in the eastern Mediterranean, deposited between 10200 and 6800 cal. yr BP (Rossignol-Strick, 1999). However, mesophyte maxima in other sites of eastern and southeastern Spain also occur at c. 6800–4400 cal. yr BP (Carrión and Van Geel, 1999; Pantaleón-Cano, 1997). There is abundant evidence in North Africa for a warm moist maximum from c. 6800 to 4400 yr BP, apparently as a delayed consequence of early- to mid-Holocene northward extension of monsoonal rains and subsequent arid-belt contraction (Gasse, 2000; Lamb *et al.*, 1995). It should not be expected that any single climatic parameter will be the responsible controlling factor over the whole catchment. However, vegetational development at Villaverde is most likely a long-term response to increasing available moisture, which would have allowed species such as *Quercus faginea* and *Corylus avellana* to have reached their real forest potential. This hypothesis is substantiated by decreased frequencies of xerophytes and *Juniperus* (Figure 11), and the negative correlation between microcharcoal and both deciduous *Quercus* and mesophytes (Table 3).

The abrupt shift towards deciduous *Quercus* dominance is more difficult to explain. Interpolation of radiocarbon dates from boundary pollen samples suggests that this shift occurred within c. 10–30 years (Figure 12), which seems too rapid to be climatically controlled, although it is of course a threshold response which could be ultimately mediated by climate. It remains possible that the pollen-stratigraphical change is due to a sedimentary hiatus, but a change at century scale is unquestionable. Hypotheses involving senescence, nutrient shortage and the intervention of a pathogen are non-testable. Deciduous oaks, being shade-tolerant species, might have invaded closed stands of pines quite rapidly. We remain nevertheless unaware of the ultimate mechanisms by which oaks stayed subordinate for so long, and by which they suddenly expanded into existing pine forests.

Aridification and spread of mediterranean-type forest (c. 5000–1600 cal. yr BP)

A change towards dominance by evergreen *Quercus* communities is observed within VP4 over a period of 300–400 years. This

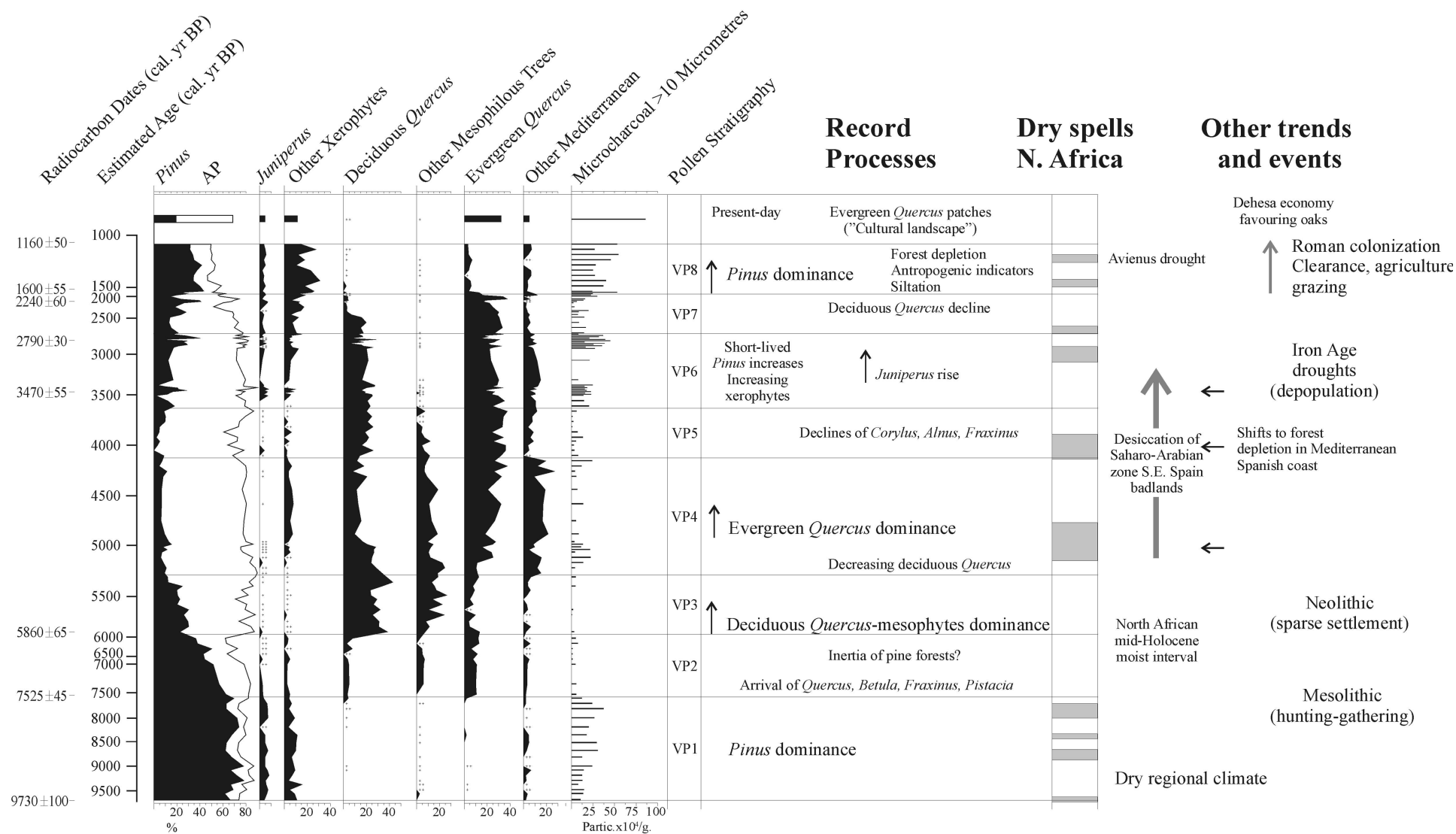


Figure 11 Villaverde sequence. Synthetic diagram with past vegetation changes in climatic and cultural contexts.

Table 3 Spearman correlation coefficient for pollen taxa percentage values and microcharcoal concentration at Villaverde (see text in 'Methods' for definition of 'other xerophytes', 'other mesophilous trees' and 'Mediterranean woods')

Pollen taxa percentage	Microcharcoal
<i>Pinus</i>	+0.245**
<i>Juniperus</i>	+0.550**
Other xerophytes	+0.525**
Deciduous <i>Quercus</i>	-0.426**
Other mesophilous trees	-0.63**
Evergreen <i>Quercus</i>	-0.055
Mediterranean woods	+0.071
AP	-0.292**

** = meaningful correlation.

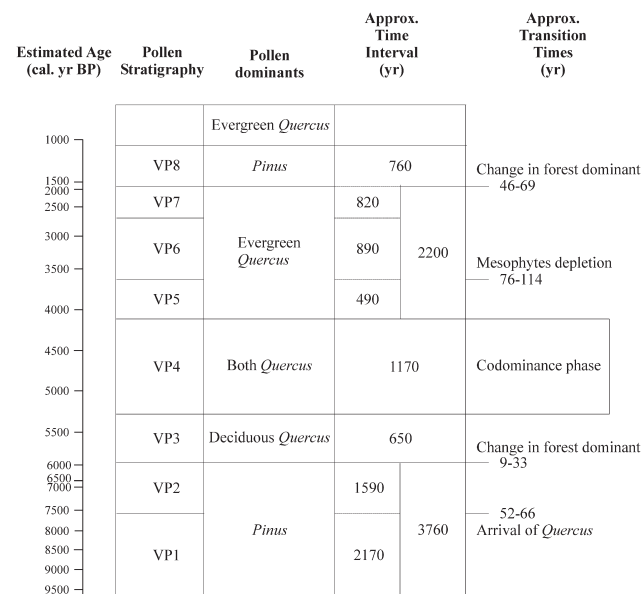


Figure 12 Vegetation stages and changes in the sequence of Villaverde. Transitions in the pollen record occur at the multi-decadal to centennial scale.

change can be viewed as the consequence of competitive interactions following a trend of increased aridity, which would have been critically manifested in the pollen record at *c.* 5000, 3650, 2400 and 1600 cal. yr BP. This climatic trend can be inferred from declines of mesophilous vegetation and expansions of xerophytes, *Juniperus* and *Pinus*. Palynological data from Mediterranean Spain suggest subhumid forest depletions after *c.* 5200 cal. yr BP (Dupré, 1988; Riera, 1993; Parra, 1994; Burjachs *et al.*, 1997; Yll *et al.*, 1997; Carrión *et al.*, 1999a), after *c.* 4000–3400 cal. yr BP (Esteban-Amat, 1995; Burjachs and Riera, 1995), and again after *c.* 2550 yr BP (Targarona, 1997) (Figure 11). These events correspond to expansions of *Artemisia* and/or *Chenopodiaceae* in arid Almería (Pantaleón-Cano, 1997). Other pollen records from elsewhere in the Mediterranean show evergreen oaks and progressive matorralization during the last four millennia at the expense of subhumid forests (Huntley and Birks, 1983; Bottema and van Zeist, 1991; Willis, 1994; Reille *et al.*, 1996; Magri, 1999). The arid tendency is also supported by palaeoanthracological information relative to species composition (Badal *et al.*, 1994), and wood anatomy (Terral and Arnold-Simard, 1996).

Geomorphological evidence of badlands in southeastern Spain is also abundant since 5200 cal. yr BP (Wise *et al.*, 1982). Lake-water levels fell abruptly while peatbog formation ceased in a number of western and central Mediterranean sites from *c.* 5200

cal. yr BP and again 4000–3750 cal. yr BP (Pons and Reille, 1988; Magri, 1999), and there were important changes in the hydrological regimes of tropical lakes of Africa (Roberts, 1998; Gasse, 2000). At 5300–5000 cal. yr BP, there is a dramatic drop in Nile water discharge which matches with arid conditions in Morocco, the Sahel and Mesopotamia (Hassan, 1997). During the 4200–3900 cal. yr BP interval, and again at *c.* 2600 cal. yr BP and 1370 cal. yr BP, droughts influenced many lakes in the Sahara and the Sahel (Mees *et al.*, 1991; Lamb *et al.*, 1995). The pollen signal at *c.* 5200 cal. yr BP parallels a global-magnitude event of decline in methane at Greenland ice cores (Bradley, 1999).

The return of *Juniperus* (*c.* 3530 cal. yr BP)

Juniperus is an important pollen contributor at Villaverde during the early-Holocene VP1 zone, and again from *c.* 3500 cal. yr BP to present (Figures 6 and 11). From its present-day local abundance, it appears plausible that *J. thurifera* is the main species involved. Given its low dispersal potential, *Juniperus* must have developed abundantly locally for both periods. A relationship between dry climate and *Juniperus* abundance is suggested, first, by the significant positive Spearman correlation between *Juniperus*, xerophytes and microcharcoal concentration (Table 3) and, second, by the fact that *Juniperus* rises as mesophyte pollen drops and vice versa. Although Rivas-Martínez (1969) suggests that the existing *J. thurifera* communities are in decline, the data presented here support the former hypothesis of Ceballos (1934) that *J. thurifera* has increased recently due to a suggested xerothermic trend. Auspiciously, Ceballos (1934) also suspected that current communities were invaders of former deciduous forests.

Species-interactions and late-Holocene expansion of pines (*c.* 1600–1150 cal. yr BP)

The spread of *Pinus* at *c.* 1600 cal. yr BP appears to be a threshold response to some kind of environmental pressure beginning at *c.* 3500 cal. yr BP, from which six short-lived peaks of *Pinus* are recorded. We infer from the age-depth model (Figure 3) that these expansions did not exceed 120 years. The main three peaks occurred at *c.* 3500 cal. yr BP, 2800 cal. yr BP and 2250 cal. yr BP, with *Pinus* values of *c.* 27%, 36% and 39% successively. At the base of VP8, there is a new relative maximum of 43% and *Pinus* becomes dominant of a semi-forested landscape. Altogether these observations envisage a disturbance-mediated invasion of mixed and evergreen oaks forests by *Pinus*. This spread of *Pinus* brought about a permanent modification of the ecosystem (a plastic response), while previous episodic expansions were temporary (elastic).

The pattern of microcharcoal abundance in Villaverde (Figure 11), and the correlations observed between *Pinus*, *Quercus* and microcharcoal (Table 3), suggest that fire is the main disturbance. Using diffusion-reaction equations to model the spatio-temporal pattern of plant succession, Shigesada and Kawasaki (1997) have shown that, under random fire disturbance, a competitively weaker species is able to adapt and, at times, even displace a potential competitor to become the sole surviving species. It is worth mentioning that peaks of *Pinus* at *c.* 3500, 2800 and 1550 cal. yr BP are preceded by charcoal increases. At the 160–190 cm depth interval, it has been roughly estimated that *Pinus* increases for about 60–120 yr after microcharcoal first surpasses the critical value of 25×10^4 particles/g. If values of microcharcoal concentration of $2 \times$ the mean value are considered to be significant in terms of fire occurrence, a fire event can be considered to have occurred every 20–60 years during VP6. A more accurate picture is not possible because we cannot obtain fire-history information at the patch level (MacDonald *et al.*, 1991).

Using simulation experiments, Pausas (1999) has predicted changes in the relative abundance of *Q. rotundifolia*, *P. halepensis* and *Cistus salvifolius* with changes in the fire recurrence in eastern

Spain ecosystems. Their model predicts mature *Q. rotundifolia* forests in areas with low fire recurrence (less than 100 yr), pine/oak woodlands in areas with higher fire recurrence (40–100 yr) and shrublands in the highest fire recurrence areas (5–20 yr). Similar patterns of increasing shrublands and decreasing *Quercus* communities due to increasing fire recurrence are found in other Mediterranean Basin systems (Trabaud, 1980; Martínez-Sánchez *et al.*, 1996). This model predicts the coexistence of *Pinus* and *Quercus* during the above-mentioned interval at VP6, and suggests that the establishment of *Pinus* may have been the result of increased fire frequency from VP4 to VP8. In addition, these results suggest that *P. halepensis* may well have been involved in the forest dynamics since VP6. This species is extremely resistant to climatic stress and its recruitment is stimulated by fire (Pausas, 1999). Furthermore, charcoal analyses suggest a regional spread of *Pinus halepensis* during this time (Rodríguez, 1992; Badal *et al.*, 1994). It remains unclear whether the microcharcoal record during VP8 is the result of slash-and-burn practices, because the balance between human-set fires and climate is problematic.

A prehistoric cultural landscape?

Human disturbance has been suggested as a major forcing of vegetation change in Spain and other Mediterranean areas during the last 4500 years or earlier (Barbero *et al.*, 1990; Reille and Pons, 1992; Stevenson and Harrison, 1992), but direct evidence for these activities, such as cereal pollen, macrocharcoal and independent archaeological remains, is not uniform within the region. It is, of course, possible that in some areas the effects of climatic change since the mid-Holocene have been accentuated by increasing anthropogenic pressure whereas in other cases it is anthropogenic forces alone that are responsible for these changes. However, in the study region, we suggest that there are problems with the anthropogenic argument.

First, there is an absence of archaeological evidence. It is not clear when prehistoric hunting communities at the region adopted a more sedentary pattern of resource use, but archaeological data from the Neolithic to the Bronze Age suggest that settlement was still sparse (Jordán, 1992). Certainly, regional settlement become more systematic in the Bronze Age, when cattle and pigs assumed greater importance, but it was still comparatively uneven (Nájera and Molina, 1977). Agriculture and domesticated animals were only prominent in the Iberian periphery, while hunting-gathering remained important in the interior plains (Butzer, 1988). For southwestern Albacete, it has been suggested that there were malarial areas which would have been avoided as places for settlement (Bauer, 1980; Jordán, 1992). Historical documents describe wide marsh extensions until the sixteenth century (López-Bermúdez, 1978). During the Iron Age, the region even experienced extensive depopulation, possibly due to intense droughts (Jordán, 1992).

The palaeoecological record of Villaverde suggests that impact of societies upon the regional landscape was negligible in the Neolithic, and probably slight even in the Bronze and Iron Ages (Figure 11). As far as disturbances by these societies is concerned, this record provides little evidence which may be distinguished from non-anthropogenically induced phenomena. *Plantago* does not show a continuous curve before c. 1900 cal. yr BP, although a first increase is already noticed at c. 4050 cal. yr BP (Figure 7). The indicative value of this increase and subsequent peaks is unclear. Additionally, the observed pollen type, typically, is not *P. lanceolata*, nor are all the possible regional species ruderals.

Second, no other plausible indicator of human activity apart from *Plantago* is found in the pollen record prior to c. 1600 cal. yr BP (Figure 7). The curves of *Artemisia*, Chenopodiaceae, Asteraceae and Lamiaceae pollen could be regarded as indicators of ruderalization and therophytization in other geographical con-

texts (Barbero *et al.*, 1990), but not at the fringes of the semi-arid region where most species of these genera and families are xerophytes. In addition, *Artemisia*, Chenopodiaceae, *Ephedra* and, to a lesser extent, *Plantago* show pollen increases during VP1, when human influence on the pollen record is unlikely. At a regional level, none of the other regional pollen diagrams (Menéndez-Amor and Florschütz, 1968; García-Antón *et al.*, 1986; Dorado *et al.*, 1999) show anthropogenic indicators before c. 1950 cal. yr BP. Seed and charcoal data are fragmentary and there is no firm evidence concerning any intensification of agricultural exploitation before Roman times (Buxó, 1990, 1997; Bernabeu *et al.*, 1993). Our argument is strengthened by comparative evidence from other pollen diagrams in which a very clear phase of forest regression is associated with pollen of cultivated trees and crops, such as Gölhisar in Turkey (Eastwood *et al.*, 1998; 1999).

We cannot clearly detach humans from the environment and, hence, the question concerning how to factor out the relative roles of natural and human ignitions in vegetation is open to debate. However, since there is no clear indication of extensive human impact on the region before historical times, and because of the existence of overwhelming evidence for increased aridification since 5200 cal. yr BP, we provisionally assume that at least fire-disturbance regimes prior to c. 1600 cal. yr BP were largely controlled by climate and vegetation traits. Although the deliberate destruction of wildwood in order to make farmland might have begun in the Neolithic at about 5700–6850 cal. yr BP, as in Levant and littoral Andalusia, it seems that the wildwood of Iberian interior areas retreated late.

Landscape during the historical expansion of agriculture

The palaeoecological record of Villaverde indicates local deforestation and the expansion of pasture plants and arable agriculture since c. 1600 cal. yr BP. Several observations support this picture: (i) continuous pollen curve of *Plantago*; in addition to (ii) the occurrence of pasture-land indicators (e.g., *Rumex conglomeratus* type); (iii) weeds and agriculture indicators (Brassicaceae, Solanaceae, *Centaurea*, *Euphorbia*, *Sanguisorba*, Fabaceae, *Juglans*, *Prunus* type, *Vitis*, increased *Olea* values, *Tilletia*, *Puccinia*, spore types 984, 985, 988); (iv) indicators of forest degradation stages (*Berberis hispanica*, *Genista* type, *Prunus* type, increased *Cistus* values); (v) increase of NAP; (vi) increased flux of inorganic material; and (vii) increased microcharcoal input suggesting larger and more frequent fires.

No quantitative data on agriculture in La Mancha and Sierras de Segura exist for the Roman period. References to livestock are given by the accounts of Strabo (c. 20 BC) and Pliny (c. AD 75). Black-fleeced sheep and cattle herding were prominent starting in the Middle Ages in the upper basins of Castilian rivers (Butzer, 1988), related to a more continuously open agricultural landscape, deforestation and subsequent soil deterioration. Classical literary sources, however, do not give us any measurement of ecological decline; but they inform of many wooded regions in eastern Spain which are not barren (Bauer, 1980). Numerous reports point to an extensive shrub and forest cover in southeastern Albacete and northwestern Murcia only a century ago (Sánchez-Gómez *et al.*, 1995).

Landscape openings after c. 1600 cal. yr BP do not have to be primarily determined by increased agriculturization, a climatic explanation also being plausible. Historical sources, alarmed about the spread of sub-desertic areas towards La Mancha, describe catastrophic droughts, floodings, epidemics and locust plagues in the southeast during Roman and early Mediaeval times (Merino-Alvarez, 1915; Barceló, 1978; Bauer, 1980). A fascinating document by Rufus Avienus (c. AD 385) provides landscape information of Mediterranean coastal areas from Gadir (current

Cádiz) to north Valencia, describing 'desolated landscapes of once populous towns, ruins, no inhabitants, abandoned towns...' (Bryson, unpublished data). Romans referred to the southeastern coast as 'the coast of the rabbits' (González, 1999), which suggests open shrubby landscape, while the northern fringes of the so-called *Campus Spartarius* Province ('*Stipa* fields': Pliny: *Historia Naturalis*) were only *c.* 20 km away from the present study area (Vila-Valentí, 1961). There is palaeolimnological evidence for shallow-water phases in north Africa between *c.* 1910 and 1650 cal. yr BP (Lamb *et al.*, 1995), while monsoonal climate appears to show increased frequency variability from 1710 to 1060 cal. yr BP (Sirocko *et al.*, 1996).

It must be stressed that both the classical literary sources and much of the archaeological evidence hitherto used are so imprecise and lacking in quantitative measurement that contradictory conclusions may have been drawn from the same set of data. In particular, the agricultural developments of the Roman period may have been much exaggerated by modern writers. The sequence of Villaverde suggests that any anthropogenic forest disturbance merely facilitated a change in forest composition that might have occurred naturally given the increased dryness of climate ever since 5200 cal. yr BP.

Is there anything worth calling 'potential natural vegetation'?

Although both modern vegetation and pollen rain at the site are characterized by evergreen *Quercus*, the most recent available pollen record at 1150 cal. yr BP suggests the local dominance of pines (Figure 6). In other parts of La Mancha, oaks and pines co-exist at this time (Dorado *et al.*, 1999) while pines clearly prevail in the southeastern mountains of Murcia (López, 1991). The floristic-phytosociological approach of vegetation science establishes a 'potential' forest vegetation of *Q. rotundifolia* for most of this territory (Peinado *et al.*, 1992; Escudero *et al.*, 1995). This hypothesis comes to see this forest as dominant in the theoretical absence of anthropogenic disturbance.

Apart from the obvious fact that there is no vegetation in the field area today which has not been affected by human interference, it must be mentioned that historical sources suggest that *Q. rotundifolia*, which produces a valuable acorn crop traditionally used to feed free-range pigs, has been historically protected along La Mancha, Campo de Montiel and northeastern Murcia (Merino-Alvarez, 1915; Rodríguez de la Torre, 1985). The study area is recorded in the local land register under the denomination of 'Dehesa Villaverde', which connotes a particular agro-sylvo-pastoral tradition protecting oaks (Marañón, 1988). Landscape descriptions and toponyms from Islamic times to the late nineteenth century outline a diverse regional landscape including forested and open areas, pine, mixed and oak forests (Sánchez-Gómez *et al.*, 1995). Most sources, including the 'Archivo Histórico Provincial de Albacete', reiterate the existence of wide areas of 'dehesa' ever since the fourteenth century (Rodríguez de la Torre and Cano, 1987). The amount of public punishments following tree-cutting has been traditionally much heavier when dealing with oaks than pines, while oak planting was rewarded (De la Cruz, 1980).

Connected with the former is that, for different reasons, including the eventual lack of demographic resources for repopulation, there has been a major lag in the expansion of regional agriculture, which left many areas uncultivated until the nineteenth century (Rodríguez de la Torre, 1985; Jordán, 1992). Pastoral transhumance and dehesa economy have prevailed for most of the last millennium, and, from the pastoralist's point of view, a dehesa conferred far more benefits than irrigation agriculture. Finally, there is also historical documentation supporting the fact that deforestation focused largely on pine forests. Especially important, and continuous until the end of the nineteenth century,

was the pine demand for naval shipbuilding (González, 1999). In the region, the main species affected appears to have been *P. nigra* (Sánchez-Gómez *et al.*, 1995), as *P. sylvestris* was in the Central mountain system (Pardo and Gil, 1997). The antiquity of the dehesa economy in the region remains open to debate, and whether the prehistoric oak-pine/fire dynamics together with the sporadic appearance of ruderal pollen are somewhat connected with human activities. We need spatially orientated palaeoecological studies to address this issue.

We conclude that present-day *Q. rotundifolia* forests, allegedly remnants of the natural potential vegetation, cannot be conceived to be out of the reach of human interference. It is to be questioned whether, in the absence of last-millennium human activity, potential natural vegetation might not be dominated by one or several *Pinus* species. Moreover, it is questionable whether there is something worth calling potential natural vegetation. There are inherent difficulties in transferring models and methods from the floristic-phytosociological approach to the ecology, which has created more than a little confusion (Blanco *et al.*, 1997; Carrión *et al.*, 1999b).

Conclusions

The pollen stratigraphy at Villaverde can be used to infer past vegetation changes within a well-defined catchment area that represents boundary conditions for semi-arid, plateau and mountain vegetation. At the millennial scale, climate appears to have been a major control of the species pool. The picture is of a generally wet mid-Holocene stage characterized by spread of mesophilous vegetation, anteceded and followed by drier conditions, which are inferred from a higher abundance of xerophytes, pines, evergreen oaks and Mediterranean scrub.

At the centurial and decadal scale, we challenge the overriding problem of spatial scale (Prentice, 1986). Here it is hypothesized that initiating factors and the inertia of established tree populations, as well as migrational processes interconnected with competition adjustments, have been responsible for timelags in the response of local vegetation to climate amelioration from the early to mid-Holocene (*c.* 9700–5200 cal. yr BP). Fire disturbance would have been a major factor shaping interspecific relationships and vegetation change from *c.* 5200 cal. yr BP onwards. There is also, at this scale, the possibility of seeing vegetation as being in a state of non-equilibrium, stochastically changing in time and space (Moore *et al.*, 1996; Bennett and Willis, 1995). Apparent trends could be, in this context, generated as side consequences of expansions and contractions in the amount of variability within the system, and not by anything actually moving anywhere.

Several changes in the pollen record coincide with established times for abrupt oscillations and rapid transitions in the climates of north Africa and the Sahel (Lamb *et al.*, 1995; Hassan, 1997; Gasse, 2000). The possible relationships between these events and the transitions at Villaverde (Figure 11) remain obscure and need further research. We might search for parallelisms, but in so doing risk confusing correlation and causality.

Several transitions in the pollen record occur over decades, apparently as ecological crises during which key thresholds were crossed (Figure 12). We come to see some kind of permanence as the norm for most of the time, and change as a relatively rapid event, as a sort of collapse bringing the system to a new state. There are no two identical phases throughout the Villaverde sequence (Figure 4), so that it appears that every stage is contingent. Overall, this model alerts us that the successful application of palaeoecological transfer functions for climate reconstruction may be conditioned by system states. Clearly, we need to puzzle out the palaeoecological database within the context of a contin-

gent ecology in addition to, and interacting with, traditional deterministic approaches.

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