# Past distribution and ecology of the cork oak (Quercus suber) in the Iberian Peninsula: A pollen-analytical approach

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**4 authors:**

José Carrión
University of Murcia

Igor Parra
Fundación Atapuerca

Cadine Navarro
Massachusetts Institute of Technology

Manuel Munuera
Universidad Politécnica de Cartagena - UPCT

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**BIODIVERSITY RESEARCH**

# Past distribution and ecology of the cork oak (*Quercus suber*) in the Iberian Peninsula: a pollen-analytical approach

J. S. CARRIÓN*, I. PARRA†, C. NAVARRO* and M. MUNUERA§ **Departamento de Biología Vegetal, Facultad de Biología, Universidad de Murcia, 30100 Campus de Espinardo, Murcia, Spain; †Institut des Sciences de l'Evolution and Montpellier 34060 PL. E. Batailon, France; and §Departamento de Producción Agraria, ETS de Ingeniería Agronómica, Universidad Politecnica de Cartagena, 30203 Cartagena, Murcia, Spain. E-mail: carrion@fcu.um.es*

**Abstract.** This study presents pollen-analytical data from continental and offshore Iberian Peninsula sites that include pollen curves of *Quercus suber*, to provide information on the past distribution and ecology of the cork oak (*Q. suber*). Results centre on a new pollen record of Navarrés (Valencia, eastern Spain), which shows that the cork oak survived regionally during the Upper Pleistocene and was important during a mid-Holocene replacement of a local pine forest by *Quercus*-dominated communities. This phenomenon appears linked to the recurrence of fire and reinforces the value of the cork oak for reforestation programmes in fire-prone areas. In addition to Navarrés, other Late Quaternary pollen sequences (Sobrestany, Casablanca-Almenara, Padul, SU 8103, SU8113, 8057B) suggest last glacial survival of the cork oak in southern and coastal areas of the Peninsula and North Africa. Important developments also occur from the Late Glacial to the middle Holocene, not only in the west but also in the eastern Peninsula. It is suggested that, in the absence of human influence, *Q. suber* would develop in non-monospecific forests, sharing the arboreal stratum both with other sclerophyllous and deciduous *Quercus* and *Pinus* species.

**Key words.** cork oak, historical biogeography, Iberian Peninsula, palaeoecology, pollen.

## INTRODUCTION

The large gaps in the palaeoecological dataset for Iberia mean that our understanding of the history of major trees in the Mediterranean Basin is incomplete. This limitation becomes critical in the case of the cork oak (*Quercus suber*), since we need information on both the past distribution and ecology to establish management and conservation strategies.

In the course of recent investigations in the Late Quaternary site of Navarrés, Valencia, eastern Spain, a well-differentiated oak pollen curve, assigned to *Q. suber*, was seen in phase with a mid-Holocene replacement of pine forests by sclerophyllous *Quercus*-dominated assemblages (Carrión & van Geel, 1999). In view of these findings, we felt encouraged to review the major continental and marine sequences close to the Iberian Peninsula that include pollen curves of *Q. suber* (Fig. 1). A preliminary point is to know the degree of confidence with which one can identify *Q. suber* in the pollen record. This paper relies on the conviction that palynological discrimination of *Q. suber* is often possible, and based on this assumption, our goals are to know:

1. Whether pollen-analytical data provides evidence of changes in the past distribution of *Q. suber* and how they interplay with the present distribution of this species in the Iberian Peninsula. Although cork oak forests generally occur in areas of maritime influence on siliceous substrates, humans must have played a significant role in controlling the distribution and abundance of *Q. suber* since it has

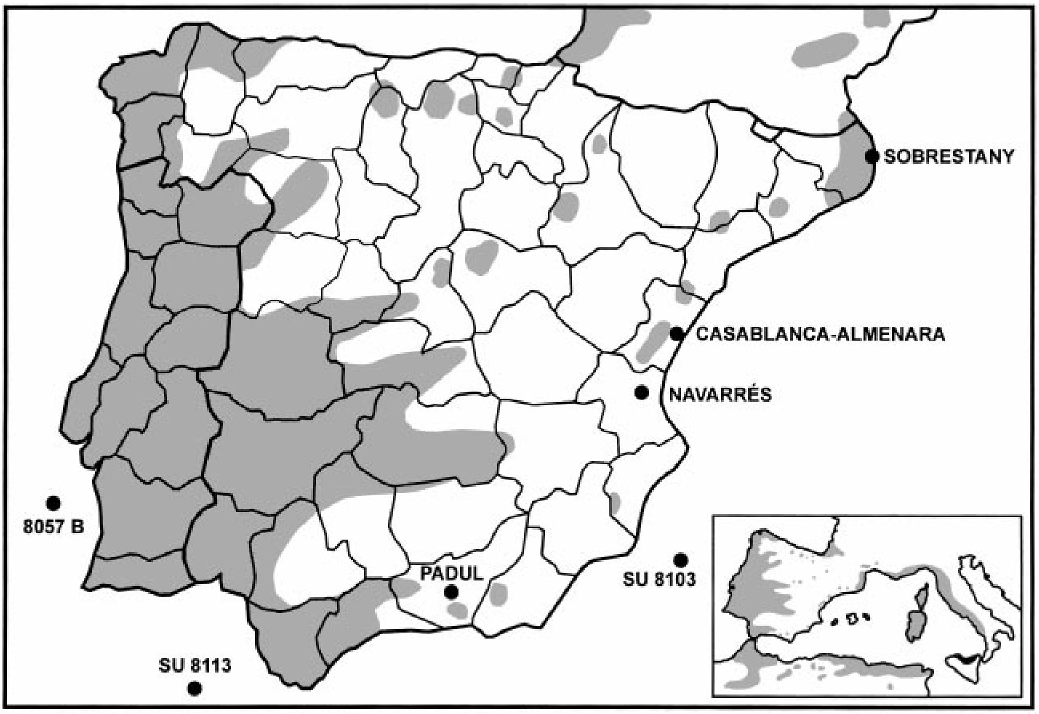

**Fig. 1** Present-day distribution of *Quercus suber* [redrawn from Blanco *et al.* (1997)]. Within Iberia, its distribution is centred in the western part. Location of pollen record sites.

been traditionally used as a source of cork and has provided acorns for pigs and boars (Parsons, 1962).

2. In connection with the former, whether past analogues of the present mono-specific cork oak forests can be found. There is significant overlap between the areas of cultural landscape named *dehesa* in Spain and *montado* in Portugal, and the peninsular distribution of *Q. suber* (Blanco *et al.*, 1997). This system, composed of mono-specific cleared oak woodlands (*Q. suber*, *Q. rotundifolia*) with an annual grassland understorey (Marañón, 1988), has been suggested to be the result of selective planting or increased human pressure (e.g. cutting) on the accompanying species (Pérez-Latorre, 1996). Nowadays, the denser and best-structured *Q. suber* forests (≈ 75% of the total) are not mono-specific, and this species co-exists with *Q. canariensis*, *Q. ilex*, *Q. rotundifolia*, *Q. lusitanica*, *Q. faginea* and pine (largely *Pinus pinaster*) (Montero *et al.*, 1994; Blanco *et al.*, 1997; Marañón & Ojeda, 1998).
3. Finally, whether there is palaeoecological support for a relationship of *Q. suber* with after-fire dynamics such as postulated by experimental studies (Cabezudo *et al.*, 1995; Pausas, 1997).

## ON THE PALYNOLOGICAL DISCRIMINATION OF *QUERCUS SUBER*

*Quercus* pollen shows a characteristic pattern of granulate sculpturing elements over the underlying carpet of collumelae (Moore *et al.*, 1991). These elements are irregularly arranged in most species, but the sharpness of uneven distribution at light microscopy is crucial to distinguish oak species groups. For Navarrés-3, the most detailed sequence at this study (Fig. 2), three oak groups were palynologically distinguished according to the criteria shown in

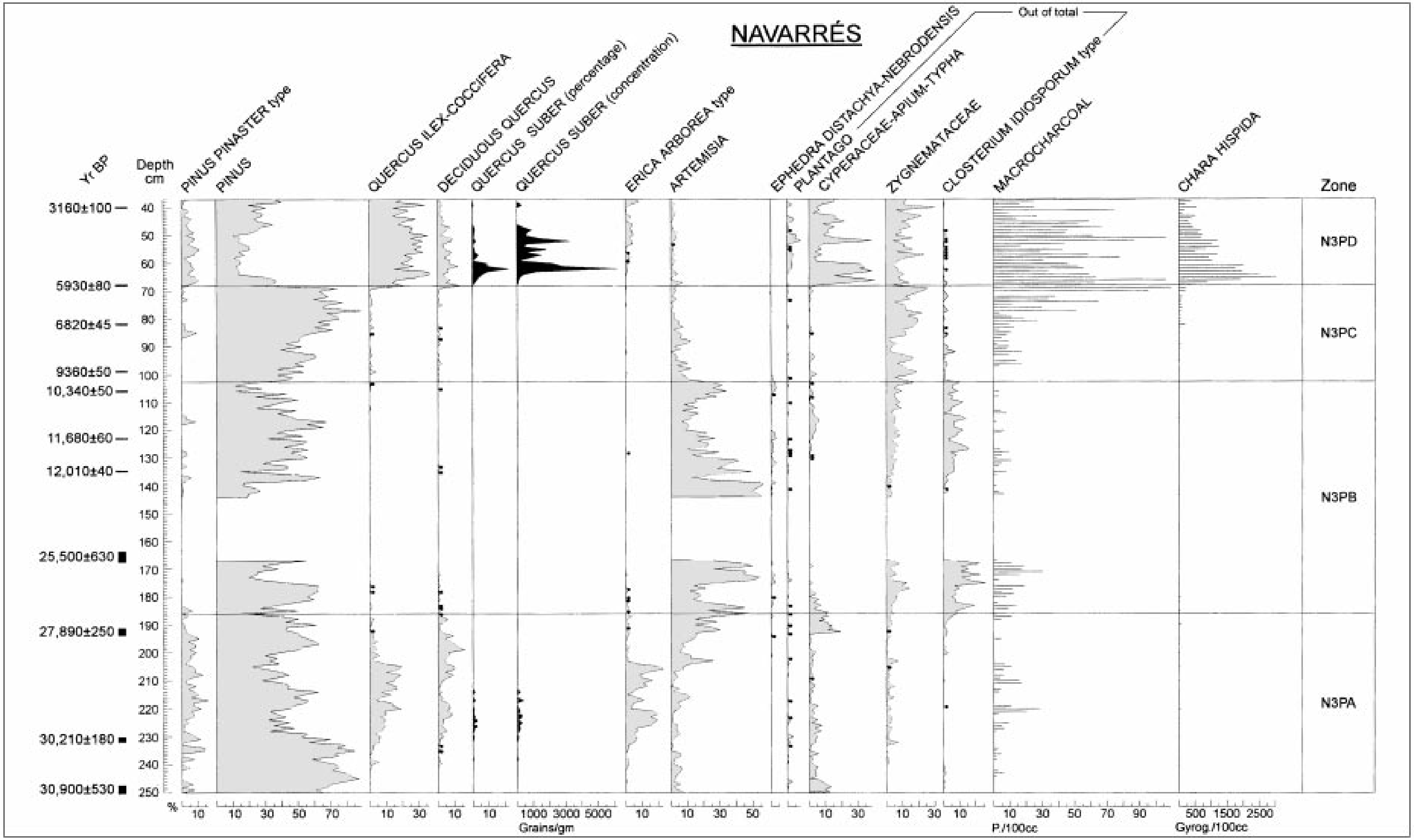

**Fig. 2** Navarrés-3 pollen diagram. Selected types. *Q. suber* is involved in Last Glacial and mid-Holocene partial replacements of *Pinus* by evergreen and deciduous *Quercus* and *Pinus pinaster*. Dots indicate percentages below 2%. Ages are given in uncalibrated radiocarbon years. Identification criteria for palynomorph types were discussed in Carrión & van Geel (1999). Other important pollen types recorded in zone N2PD are *Corylus*, *Arbutus*, *Olea*, *Phillyrea*, *Pistacia*, *Viburnum*, *Sambucus nigra*, *Myrtus*, *Hedera helix*, *Coriaria myrtifolia*, *Rhamnus*, *Ruta*, *Ulex parviflorus*, *Lamiaceae*, *Cistaceae* and *Asphodelus fistulosus*.

Table 1. Those features are clearly illustrated in Reille's (1992b) pollen atlas, and mainly follow the work by Planchais (1962), who established that pollen of *Q. suber* have a relatively large apocolpium, circular amb, and continuous colpi in equatorial view together with a slight ornamentation. Needless to say, these criteria are not universal, and we have occasionally observed that some herbarium and modern collections of *Q. suber* have some grains that are more heavily ornamented than observed by Planchais (1962). These grains would normally be included under the fossil type customarily named 'deciduous *Quercus* type' (Reille, 1990). However, according to our experience, the appearance of pollen characteristics shown in Table 1 is a reliable indication of the presence of *Q. suber* in a fossil assemblage. The presence of this species in Navarrés-3 is definitive since there were not many transitional palynomorphs and the pollen assigned to *Q. suber* constitutes a curve of well-differentiated palynomorphs. A few doubtful pollen grains were not included in this curve, which represents a conservative estimate of the past occurrence of *Q. suber* in the Navarrés core (Fig. 2).

Considering the present distribution and ecology of the Spanish oaks, *Q. faginea* is the most likely species relative to 'deciduous *Quercus*' in Navarrés-3 (Table 1), Casablanca-Almenara, and SU-8103 (Fig. 2). In the remaining sequences, other species apart from *Q. faginea* may be involved; these include: *Q. pubescens* and *Q. robur* in Sobrestany; *Q. pubescens* and *Q. pyrenaica* in Padul; and *Q. canariensis*, *Q. pyrenaica*, and *Q. lusitanica* in the SU-8113 and 8057B cores (Fig. 1). We suggest that, among the Iberian Mediterranean oak species, the most likely to be palynologically confused with *Q. suber* are *Q. canariensis* and *Q. pubescens*, although these deciduous species show generally more heavily ornamented grains (Reille, 1992b).

Occurrences of *Q. suber* are not customarily reported in the palynological literature, since discrimination of this pollen taxon from other *Quercus* types becomes difficult in certain pollen assemblages that show important quantities of intermediate palynomorphs between the groups shown in Table 1. Nevertheless, several authors have produced pollen curves of *Q. suber* from sites around the western Mediterranean Basin (e.g. Reille, 1977, 1990; Ben Tiba & Reille, 1982;

**Table 1** Palynological criteria for the oak groups in the Navarrés-3 pollen sequence (Fig. 2)

| | Oak types | | |
|---|---|---|---|
| | Ilex-coccifera | Deciduous | Suber |
| Relative pollen size | Small | Medium to large | Large |
| Sculpturing density | Slight | Heavy | Medium |
| Distribution of tectum processes | Non-distinguishable from the underlying carpet of finer columellae | Unevenly scattered over the tectum | Almost regularly spaced |
| Apocolpium | Small | Generally small, side rarely > *ca.* 8 µm | Large, side > *ca.* 8 µm |
| Colpi | Elbowed to straight | Straight to slightly curved | Elbowed |
| Colpi margins | Variable | Thin | Thick |

Planchais & Parra, 1984; Bernard & Reille, 1987; Pons & Reille, 1988; Peñalba, 1989; Brun, 1991; Salamani, 1991; Stevenson *et al.*, 1993; Marret & Turon, 1994; Parra, 1994; Reille *et al.*, 1996; Sánchez-Goñi & Hannon, 1999). Because of identification problems, it is possible that cork oak in the Iberian Peninsula may have occurred more widely in the past than is suggested from the bulk of the palaeobotanical data. Consequently, although this paper focuses mainly on past distribution of *Q. suber*, it is obvious that little can be concluded from the absence of *Q. suber* in a pollen record, and this will be kept in mind.

## REMARKS ON THE PRESENT DISTRIBUTION AND ECOLOGY OF THE CORK OAK IN THE IBERIAN PENINSULA

The cork oak (*Q. suber*) is a western Mediterranean sclerophyllous oak present in Portugal, Spain, North Africa, south France, the Italian coast and some Mediterranean islands such as Corsica, Sardinia and Sicily (Fig. 1). Within Iberia it occupies ≈ 600 000 ha, ranging from sea level to 800 m a.s.l., seldom extending above 900 m a.s.l. The optimum mean annual temperature and precipitation regimes experienced by *Q. suber* are ≈ 15 °C and 600–1000 mm, respectively. The main limiting factors are frost and a requirement for siliceous soils, although it can exist on decalcified limestone (Blanco *et al.*, 1997). Its distribution is centred principally in the western part of the Iberian peninsula with its largest extent in Portugal (Fig. 2). An important disjunct area exists in north-eastern Spain (La Selva, Baix Ampurdá) and many other minor localities throughout the rest of the country, which strongly suggests a larger, more continuous range in the past.

In the dehesas and montados, the cork oak bark is stripped off every 7–9 years. Besides producing cork and acorns, the cork oak is utilized for fuelwood, charcoal and browse, and the trees modify the microenvironment for the herbaceous understorey and serve as a shelter for livestock. This agro–sylvo–pastoral system maintains a high biological diversity and represents a model for the management of renewable natural resources, flexible and adapted to the Mediterranean climate (Marañón, 1988). However, while traditional economies seem not to have represented a major stress factor for *Q. suber*, a present-day uncontrolled recurrence of cork extraction has resulted in a situation where cork oak forests have clearly reduced their natural ability to resprout (SPAN, 1995). In some cases, cork oak trees have been cut down and dehesas re-planted with eucalypts to produce low-quality wood and pulp, or transformed into cereal cropland areas with intensive farming. Due to emigration of the rural area population, abandoned dehesas have become fire-hazard shrublands (Marañón, 1988). Hopefully, initiatives of sustainable use and rural eco-development are to be successful, such as proven in the Alcornocales Natural Park, Gibraltar Strait region (Ojeda *et al.*, 1995; Marañón *et al.*, 1999).

## POLLEN-ANALYTICAL DATA

Among the pollen sequences reporting *Q. suber* in continental and offshore Iberian Peninsula, we have selected seven of interest for this paper. Four are from peat bogs and the remainder are from marine cores (Fig. 1). The most detailed pollen sequence included at this study is Navarrés-3 (Fig. 2). It is assumed that the four littoral peat bogs studied in this paper reflect the past coastal vegetation while the three marine pollen records reflect the integrated vegetation of southern Spain and northern Africa.

The late Quaternary pollen sequence of Navarrés-3 (39°06′N, 0°41′W), Valencia province, has been subdivided into four biozones, two for the last glacial (N3PA-N3PB) and two for the Holocene (N3PC-N3PD) (Fig. 2) (Carrión & van Geel, 1999). During zone N3PA (≈ 31 000–27 000 BP), both evergreen and deciduous oaks, *P. pinaster* and *Erica arborea* attain, relatively high percentages (generally higher than 25%). The occurrence of *Q. suber* does not exceed 2% although it appears continuously in the middle part of this zone. Together with oaks, a number of trees (*Abies*, *Taxus*, *Alnus*, *Betula*, *Corylus*, *Ulmus*, *Salix*, *Fraxinus*, *Arbutus*, *Olea*) and shrubs (*Pistacia*, *Myrtus*, *Viburnum*, *Sambucus*, *Phillyrea*, Cistaceae, *Buxus*, *Coriaria*, *Myrica*, *Rhamnus*) were identified (Carrión & van Geel, 1999). The zone N3PB (≈ 27 000–10 000 BP) embraces the last glacial maximum and the Late Glacial. *Q. suber* and other thermophyllous taxa disappear. During the early Holocene N3PC zone (≈ 10 000–6000 BP), *Q. suber* remains absent from

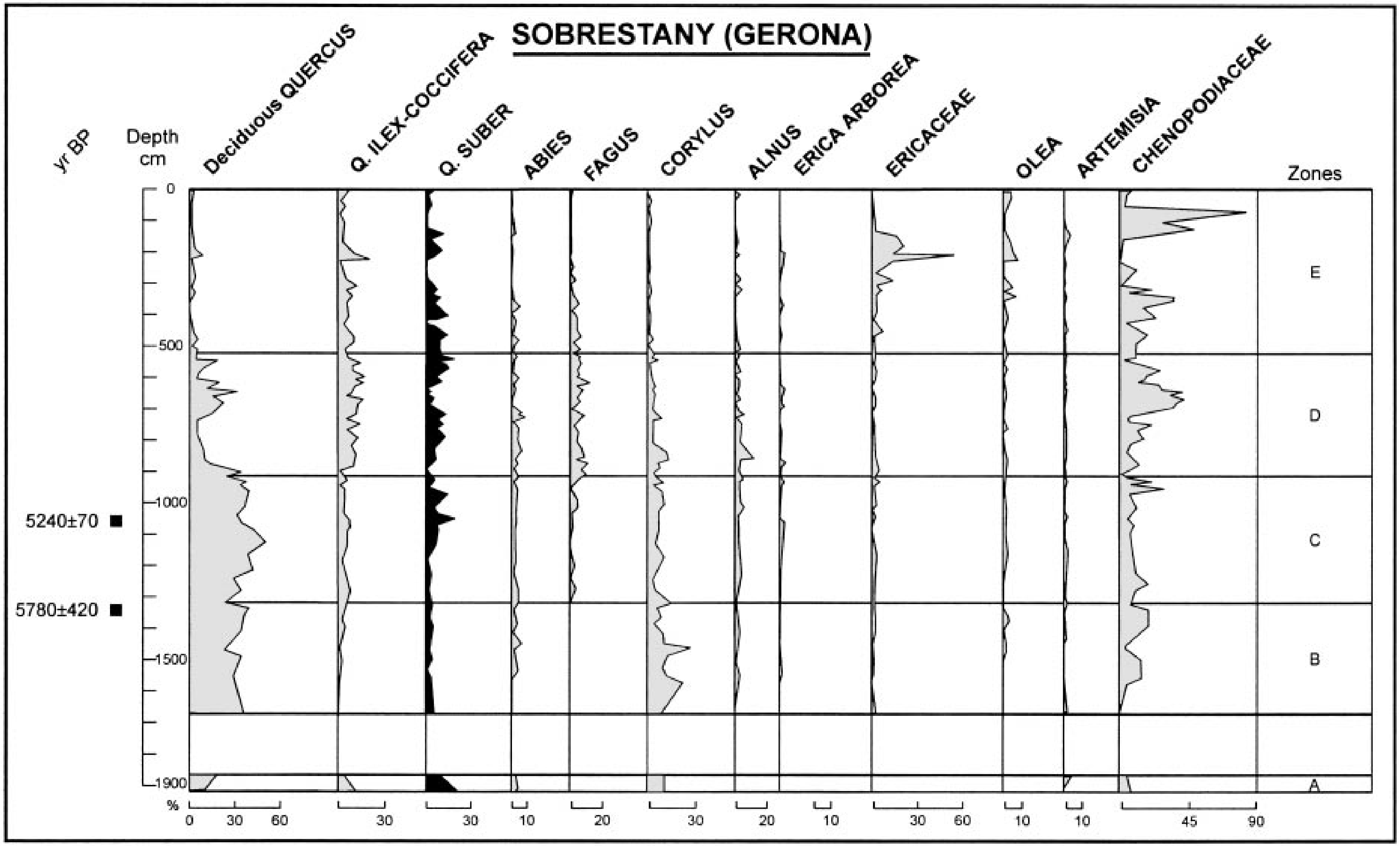

**Fig. 3** Pollen diagram from the site of Sobrestany, Gerona. Redrawn from Parra (1994). *Q. suber* parallels *Q. ilex-coccifera* pollen curve.

the pollen record and the appearance of other oaks, trees and shrubs is scarce and sporadic. The area remained occupied by dense pine forests. During N3PD (*c.* 6000–3000 BP), there is an abrupt replacement of *Pinus* by *Quercus*, including evergreen, deciduous oaks and *Q. suber*. This vegetation change (around *ca.* 5930 BP) has been demonstrated to occur synchronously all over the Navarrés basin (Carrión & Dupré, 1996). The basin shows signs of progressive eutrophication (Zygnemataceae, *Chara hispida*), and the curve of *Plantago* indicates human activity, although it must be stressed that this taxon increases only after the onset of the *Quercus* curve (Fig. 2). *Q. suber* appears in the first sample of the zone N3PD, increases suddenly, and attains its maximum values around 60 cm depth. Afterwards, it declines to below 2%. The peak seems, therefore, to correspond with the conventional Holocene humid warm phase, which has been well documented from pollen records from offshore marine cores in the western Mediterranean (Hooghiemstra, 1988) and from terrestrial pollen sequences in Italy (Magri, 1997), but not clearly from Spain. Due to its calcifuge character, *Q. suber* may have developed in gullies and ravines of the Navarrés area on calcium-depleted soils, such as can be observed today in several eastern localities of the Málaga, Granada, Almería and Murcia provinces.

The site of Sobrestany (42°06′N, 3°06′E), Gerona province, north-eastern Spain (Fig. 3) (Parra, 1993, 1994), shows a continuous mid-Holocene curve of *Q. suber* which, together with *Fagus*, *Alnus* and *Quercus ilex-coccifera*, attains its maximum values after *ca.* 5240 BP (zones D–E). The previous phases (zones A–C) are dominated by deciduous *Quercus* and *Corylus*. At the end of zone E, there are peaks in Chenopodiaceae, *Olea* and Ericaceae suggesting increased aridity and/or anthropogenic disturbance. It is also plausible that the peaks in Chenopodiaceae may reflect a change in the marine influence into the area. Although *Q. suber* is present throughout the whole sequence of Sobrestany, it behaves as a typical evergreen sclerophyllous oak paralleling a decline of broadleaf forests.

Casablanca–Almenara (39°45′N, 0°12′W), Castellón, lying north of Navarrés and south of Sobrestany along the eastern coastline (Fig. 4) (Planchais & Parra, 1984; Parra, 1994), is similar to the former site in showing a continuous Holocene curve of *Q. suber*. There are indicators of human influence (*Juglans*) and a decline of deciduous *Quercus* during the late Holocene. In general, broadleaf trees are less abundant in Casablanca–Almenara than Sobrestany at equivalent times during the Holocene which, as postulated by Parra (1993), agrees with a picture of past vegetation along the Spanish Mediterranean coast controlled by latitudinal differences in summer drought.

The uppermost Padul-3 pollen diagram of the Pleistocene pollen record from Padul (37°N, 3°40′W), Granada, south-eastern Spain (Fig. 5) (Pons & Reille, 1988) shows a *ca.* 4000-year-long, continuous pollen curve of *Q. suber* beginning at *ca.* 8200 BP. Paralleling the curve of *Pistacia*, the cork oak appears episodically since ≈ 12 080 BP. Pons & Reille (1988) suggested the establishment of *Q. suber* towards 8000 BP to mark the onset of the conventional Holocene temperature maximum. As for Sobrestany and Casablanca–Almenara, the cork oak variation at Padul parallels relatively well that of Mediterranean taxa. Furthermore, although occurring at different times during the Holocene, the pollen assemblages accompanying *Q. suber* are very similar to those found in Navarrés postdating the *Pinus* decline (e.g. other *Quercus*, *Coriaria*, *Viburnum*, *Arbutus*, *Rhamnus*, *Phillyrea*, *Fraxinus*, *Ulmus*, *Taxus*, *Corylus*, *Acer*, *Olea*).

The SU 8103 marine pollen diagram (37°58′N, 0°05′E), offshore at Murcia (Fig. 6) provides evidence for the Late Glacial and early Holocene presence of *Q. suber* in south-eastern Spain, since ≈ 13 550 BP (Parra, 1994). As mentioned for continental sequences, the cork oak covaries with other sclerophyllous oaks while *Pinus* decreases. Nevertheless, *Pinus* is abundant throughout the sequence and not only during the Pleistocene, supporting the view that oak colonization due to interglacial climatic improvement cannot be ruled out in southern Spain (Carrión *et al.*, 1999). The SU 8103 pollen sequence contains probably an important pollen signal originated in North Africa (Parra, 1994), and interpretation of the pollen curves in terms of past distribution must be cautious.

The SU 8113 marine pollen diagram (36°0′N, 7°40′W), offshore SW Spain, covering ≈ 19 000 BP

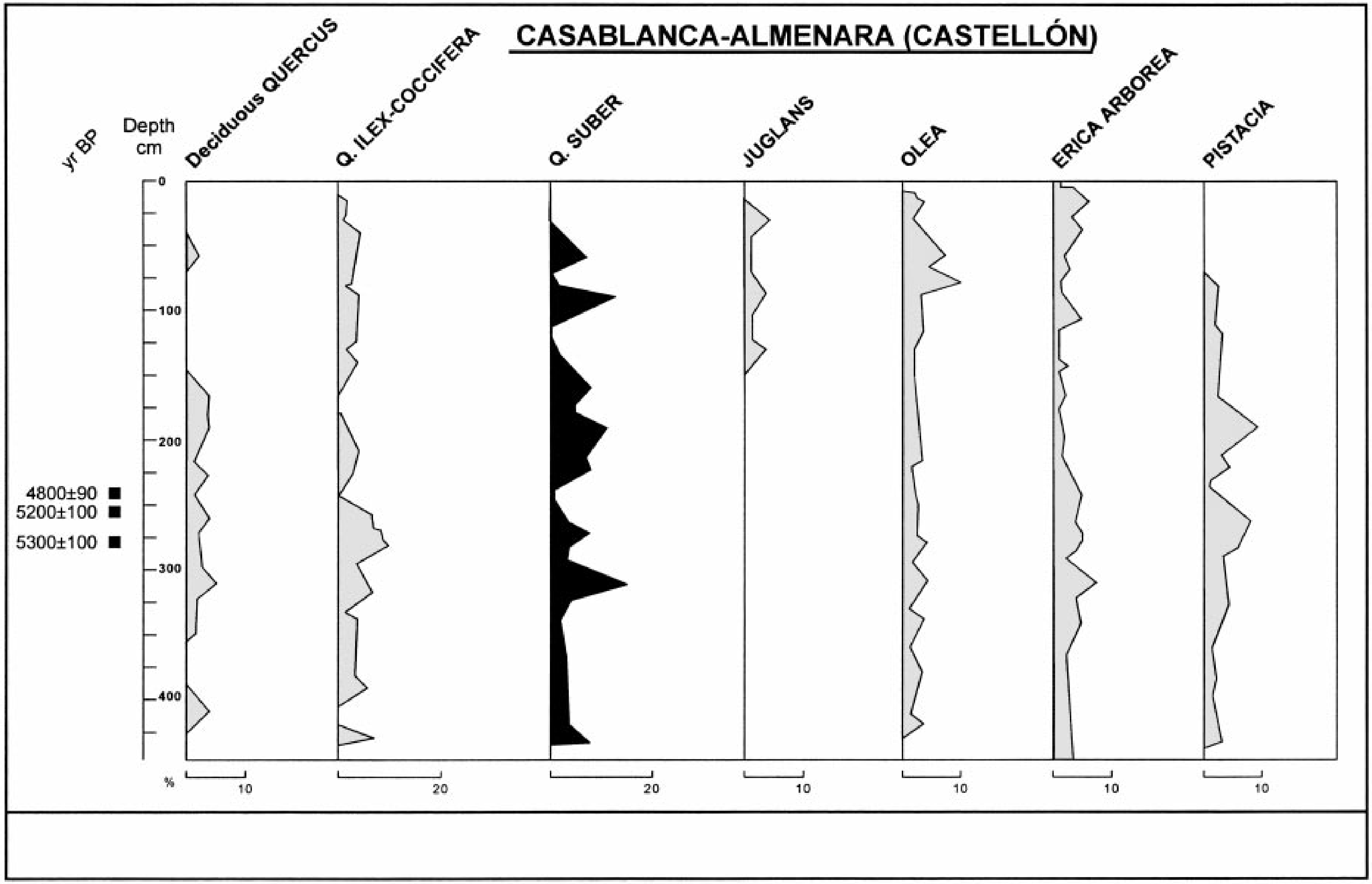

**Fig. 4** Pollen diagram from the site of Casablanca–Almenara, Castellón. Redrawn from Parra (1993). *Q. suber* is relatively abundant along the sequence.

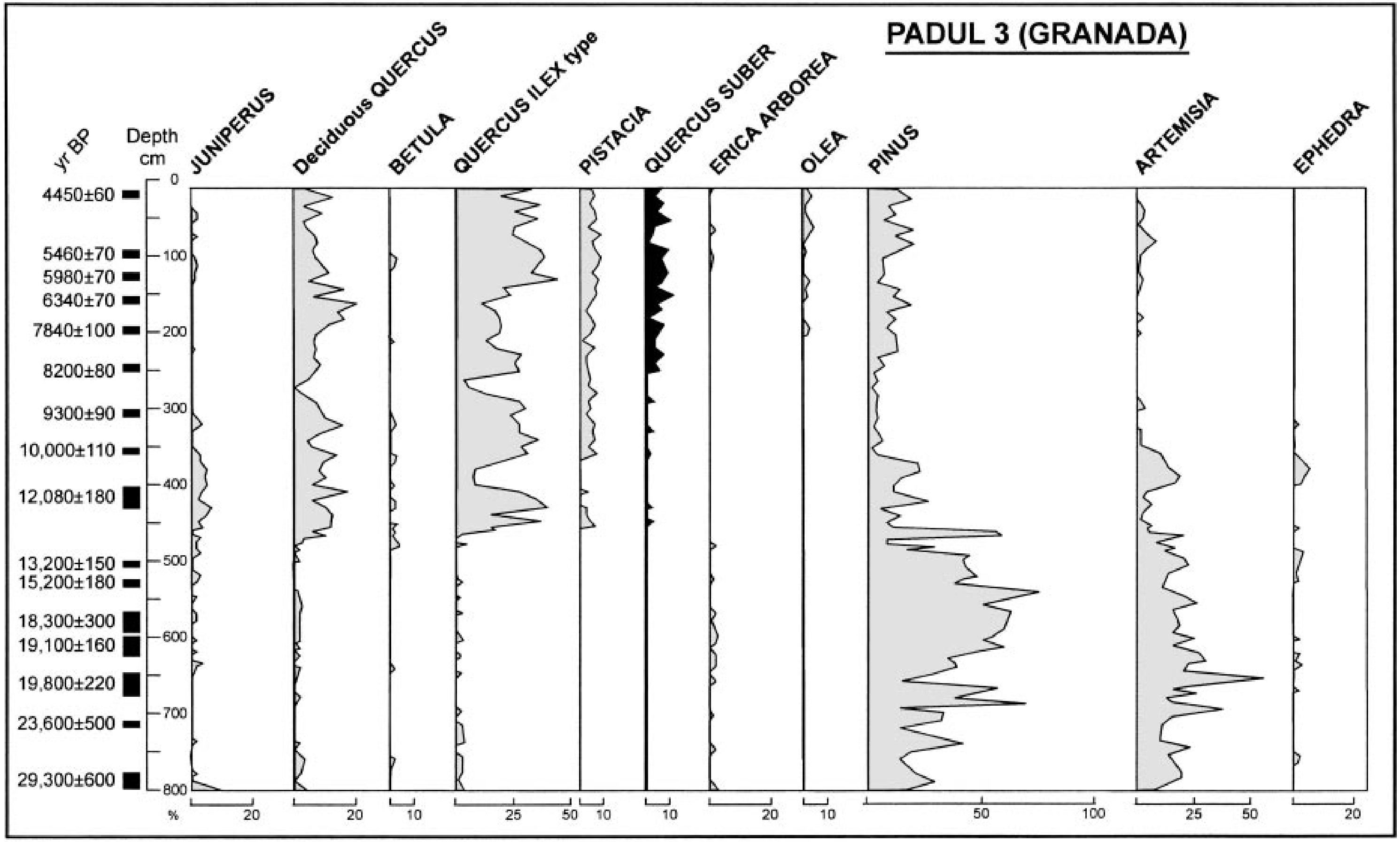

**Fig. 5** The late Pleistocene and Holocene Padul-3 pollen record (Granada). Redrawn from Pons & Reille (1988). *Q. suber* covaries with *Q. ilex* type.

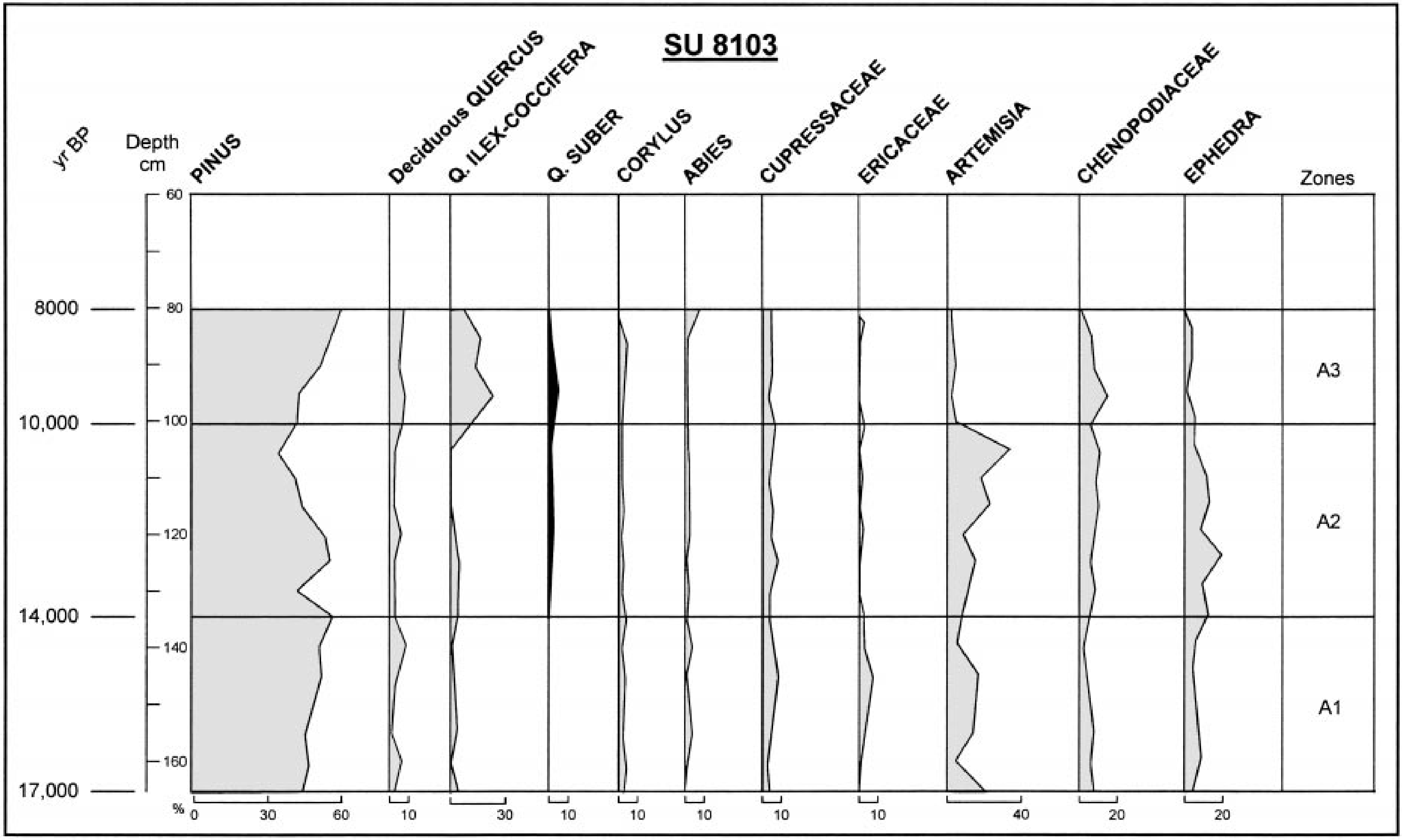

**Fig. 6** SU 8103 pollen record, offshore south-eastern Spanish coast. *Q. suber* appears from ≈ 14 000–8000 BP. Redrawn from Parra (1994). Total sum excluding *Pinus* counts.

to the present (Fig. 7) (Parra, 1994), shows the expected Late Glacial and Holocene *Quercus* invasion of the last-glacial pine forests and *Artemisia*–Chenopodiaceae steppes, as shown at Padul (Fig. 8). *Q. suber* is relatively abundant during the whole sequence, reaching maximum values during the Holocene. Again, the variation of the cork oak correlates better with other evergreen than the deciduous *Quercus* curve, and does not experience a decline when deciduous *Quercus* values diminish after *ca.* 8000 BP. As in the former sequence, a certain amount of the pollen signal must proceed from North Africa.

The 8057B marine pollen diagram (37°41′N, 10°05′W), offshore SW Portugal, covering the period from ≈ 19 100–2900 BP (Fig. 8) (Hooghiemstra *et al.*, 1992), shows a similar pattern of *Q. suber* variation to that seen in SU 8113 (Fig. 7), although the relative percentages are lower. The last glacial *Pinus*–*Artemisia*–Chenopodiaceae–*Ephedra* pollen assemblages are progressively replaced by deciduous and sclerophyllous *Quercus*, *Corylus*, *Pistacia*, *Erica* and *Cistus*, among others.

## DISCUSSION

### Past and present distribution of *Quercus suber*

Considering the available palynological data in conjuction with present distribution, *Q. suber* must have varied its distribution somewhat in the Iberian Peninsula during the late Quaternary. It appears to have existed for significant periods not only in the west but also in the eastern peninsula. There is palynological evidence of a last glacial survival of *Q. suber* in North Africa and the eastern and southern coasts of the Iberian Peninsula. Isolated pollen grains of *Q. suber* have been reported for the Late Glacial and Holocene periods in Quintanar de la Sierra and Las Pardillas sequences from the Iberian Mountain Chain, north-central Spain (Peñalba, 1989; Sánchez-Goñi & Hannon, 1999). In addition, charcoal analyses from archaeological sites in Portugal (Figueiral, 1995) demonstrate the occurrence of the cork oak during the late Pleistocene in western Iberia. Cork oak has been a constant and significant component in the mountain regions of North Africa since at least 33 700 BP (Ben Tiba & Reille, 1982). If one takes into account the bioclimatical requirements outlined earlier, it is to be expected that glacial refugia for the cork oak were located in littoral areas and intra-mountainous valleys, preferably, but not necessarily, on siliceous substrates. The floristic composition of current forests supports the view that south-western Spain may have been a key refugial region for *Q. suber* together with other Mediterranean, mesophilous and even humid subtropical elements (Arroyo, 1997), while south-eastern Spain would have been important for the survival of thermo–xerophytic Ibero–Mahgrebian flora. This hypothesis finds further support in pollen analysis of cave deposits at middle and upper Palaeolithic sites located at low and middle altitudes (Carrión *et al.*, 1995).

The first noteworthy occurrences of *Q. suber* pollen account during the Late Glacial and reach maxima values during the early and middle Holocene (Fig. 2). Apart from the data presented here, a Late Glacial expansion of *Q. suber* can be seen in other pollen diagrams such as Atlantic KS 78007 core (34°19′N, 7°01′W), offshore Morocco (Marret & Turon, 1994). Little can be concluded from the regression that can be seen in Navarrés after *ca.* 4000 years and, although it seems that eastern populations are relicts, more research on the issue must be still given to elucidate the reasons for the onset of a possible decline. On the other hand, economic activities in the late Holocene could have protected and even increased the range of the species in particular areas such as the western Peninsula (Montero *et al.*, 1994; Cabezudo *et al.*, 1995). Other palynological evidence suggests that this phenomenon also occurred beyond the Iberian Peninsula. For example, on Corsica (Reille, 1990; 1992a) and in the Rif (Reille, 1990), *Q. suber* and *Q. ilex* often replace deciduous *Quercus* forests after the first evidence of human action. At Garaet el Ichkeul, north-west Tunisia, it can be detected as an anthropogenically induced succession towards *Q. suber* and *P. pinaster* and its fire-derived understorey *Phillyrea* (Stevenson *et al.*, 1993).

### On the floristic composition of the *Quercus suber* forests

The critical role of Pleistocene and early Holocene climate in shaping modern plant distributions is widely recognized. A debate among scholars dealing with vegetation science is whether plant

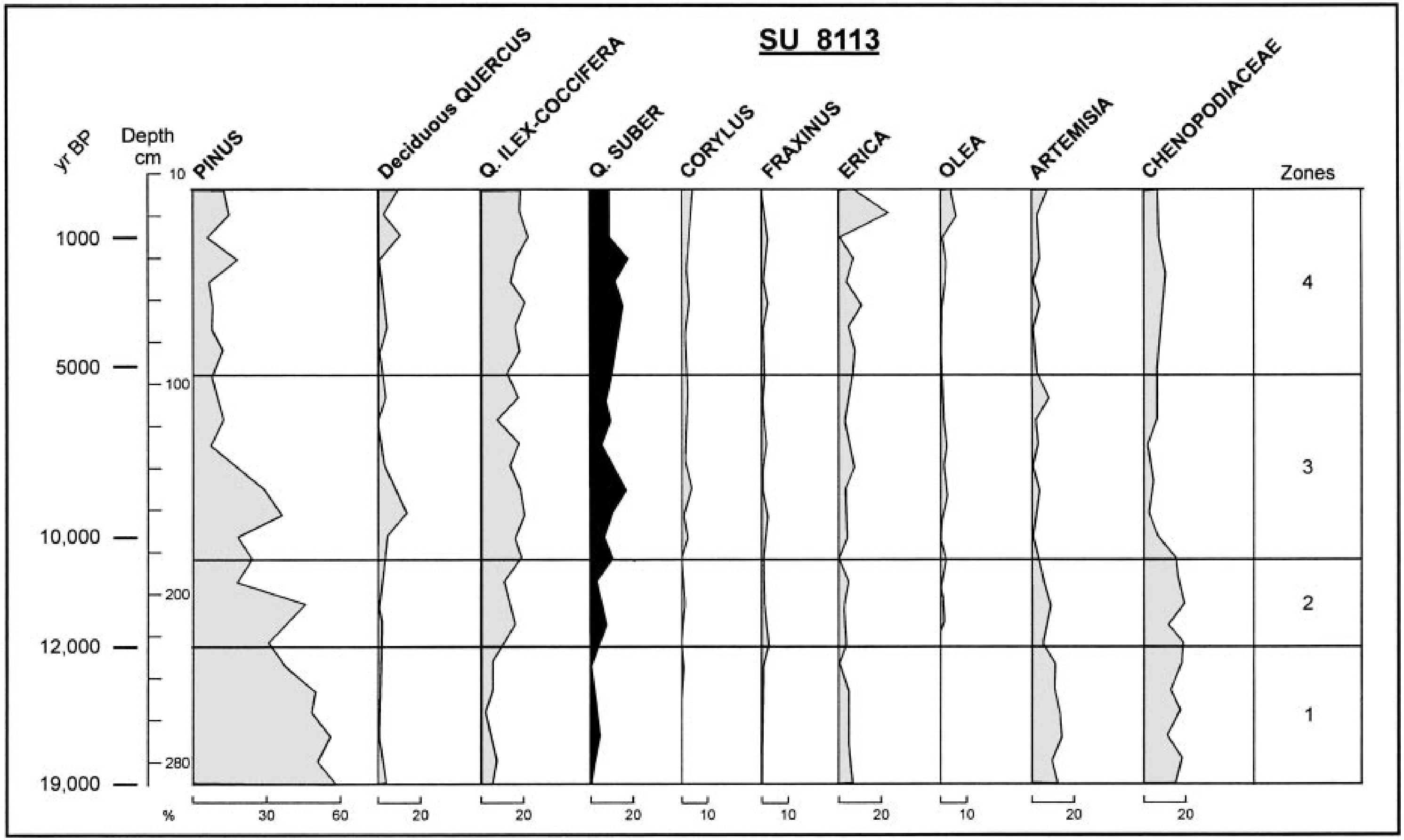

**Fig. 7** SU 8113 pollen record, offshore south-western Spanish coast. *Q. suber* is abundant during the Holocene. Redrawn from Parra (1994). Total sum excluding *Pinus* counts.

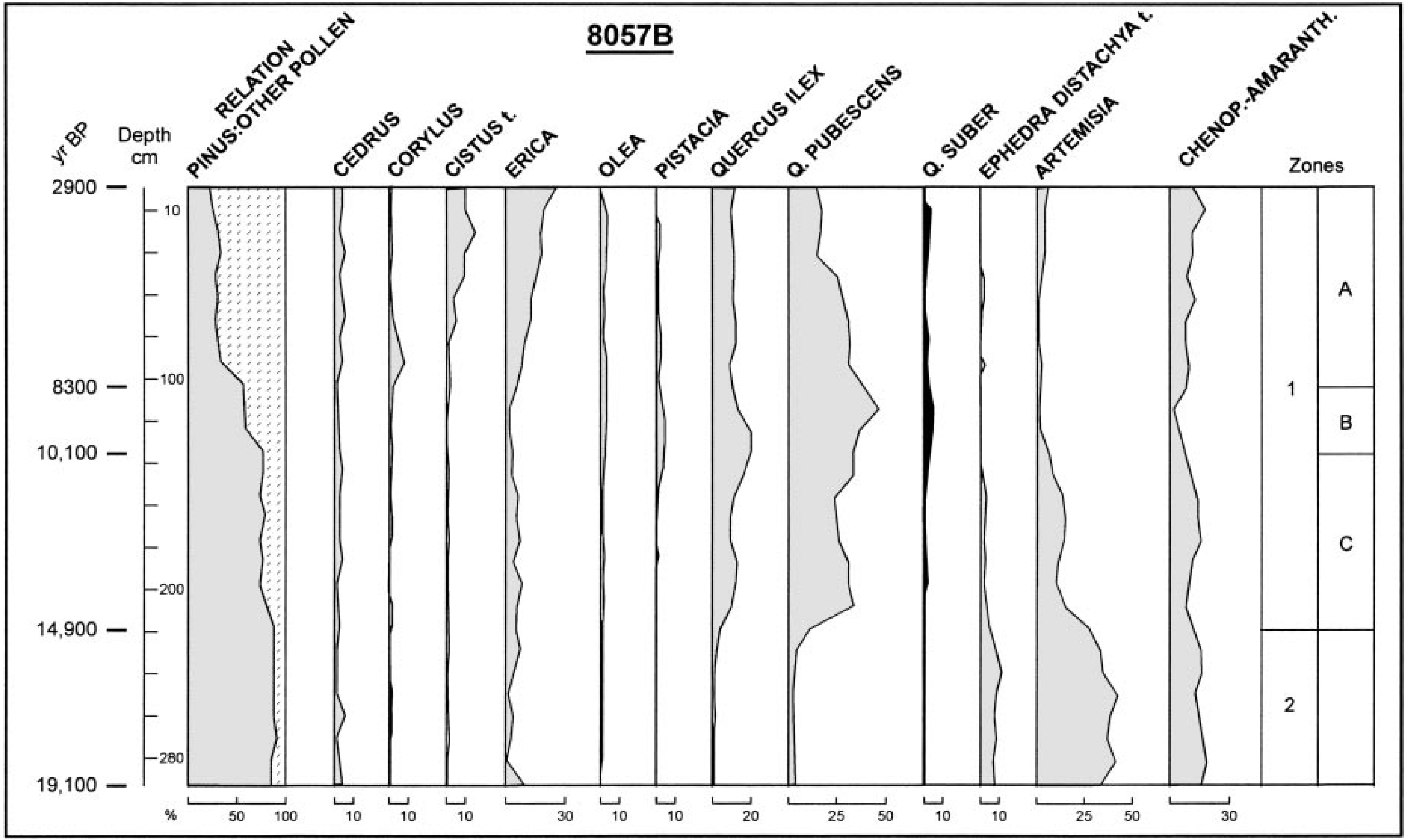

**Fig. 8** 8057B pollen record, offshore south-western Portugal coast. *Q. suber* is recorded since ≈ 14 000 BP. Redrawn from Hooghiemstra *et al*. (1992).

communities can be traced through time with continuity or if they are chance assemblages of species in space and time (Gleason, 1917; Clements, 1936). A number of palaeoecological data show that several Holocene changes of vegetation in temperate latitudes are a consequence of individualistic responses of plant species (Huntley, 1990; Bennett, 1997). For prolonged periods of time, tree taxa do not appear to have responded synchronously to environmental change. However, the Navarrés-3 pollen record suggests that, although not as much as interdependence in species responses, we can expect plant assemblages to have arisen fortuitously at meeting points in time and space of a series of different migration pathways (Tallis, 1991). Pollen assemblages including *Q. suber* in Navarrés-3 (Fig. 2) match the floristic composition of the present-day *Q. suber* forests, where the tree stratum is shared with other oaks and pines, and the understorey is dominated by *Phyllirea angustifolia*, *Viburnum tinus*, *Rhamnus* sev. sp., *Olea europaea*, *Coriaria myrtifolia*, *Myrtus communis*, *Pistacia lentiscus*, *P. terebinthus*, Ericaceae (*Erica arborea*, *E. scoparia*, *Arbutus unedo*), *Cistus*, Genisteae (*Ulex parviflorus*, *Cytisus triflorus*, *Calicotome spinosa*, *Genista linifolia*) and Lamiaceae (*Lavandula stoechas*, *Teucrium chamaedrys*) (Nieto *et al.*, 1991; Ojeda *et al.*, 1996a; Pérez Latorre, 1996). Similarly, there are frequent lianas such as *Hedera helix* and ferns (*Asplenium onopteris*, *A. adiantum-nigrum*, *Pteridium aquilinum*), especially in the coastal forests, which are generally richer in understorey and epiphytic species than those in continental situations.

The antiquity of human influence ensures that there are no pristine cork oak forests in the Iberian Peninsula. The Navarrés pollen sequence (Fig. 2) supports that, in the absence of human intervention, *Q. suber* would develop in non-monospecific forests, sharing the arboreal stratum with other sclerophyllous and deciduous *Quercus*, and also *P. pinaster*. Most dense monospecific forests of cork oak in the Iberian Peninsula must be a result of human selection.

## *Quercus suber* and fire dynamics

A striking feature of the Navarrés-3 pollen record is the mid-Holocene replacement of a pine forest by *Quercus*-dominated communities including *Q. suber* (Fig. 2). Macro- and microcharcoal counts strongly suggest a previous stage of local severe fires and it is plausible that there is a relationship between both processes. The very presence of such taxa as *Q. suber*, *P. pinaster*, *Phyllirea* cf. *angustifolia*, *Ulex parviflorus*, *Erica arborea*, *Cistus salviifolius*, *Asphodelus fistulosus*, *Pteridium aquilinum* and *Ruta* cf. *angustifolia*, (Carrión & van Geel, 1999), among others, conforms with a picture of fire disturbance (Trabaud, 1980; Trabaud & Outric, 1989; Ojeda *et al.*, 1996b).

There are several species within the Mediterranean scrub that resprout after disturbance using subterranean structures but it must be stressed that *Q. suber* is the only European tree with above-ground sprouting capability, which is a well-known fact in eucalypts (Strasser *et al.*, 1996). Experimental studies (Pausas, 1997) have shown a very low mortality of *Q. suber* by fire. The bark-stripping for cork production increases the water stress and reduces the ability of the tree to recover from fire. The insulating capability of the bark is as a key factor of survival. Cabezudo *et al.* (1995) have studied the dynamics of cork oak forests of south Spain and demonstrated that, on average, 50% of the individuals survive after fire with a number of understorey shrubs. It seems that the survival rates and phytodiversity of the matorral increase noticeably in the absence of after-fire grazing.

It must be noticed that *Q. suber* maximum at Navarrés is only reached ≈ 300–400 years after the onset of zone N3PC (Fig. 2), which suggests the existence of successional processes where other oaks antecede the cork oak. In this context *Q. suber* would have its optimum after fire recurrence, but not immediately to the main vegetation change. Interestingly, there are other studies where relative maxima of different oaks can be seen out of phase, such as in the Holocene pollen sequence of Besós, north-eastern Spain and southwards at Sobrestany (Riera, 1993). During the late Holocene *Q. suber* invades progressively deciduous *Quercus* formations in the sites of Sobrestany (Fig. 3), Casablanca–Almenara (Fig. 4) and Padul (Fig. 5). In Dar Fatma (Ben Tiba & Reille, 1982), *Q. suber* and *E. arborea* invade a middle Holocene forest of *Q. canariensis.* A possible role of fire in these cases has not been demonstrated.

Palaeoecological information provided here agrees with the observation that the cork oak exhibits multiple adaptive traits to fire and supports the idea that, independently of the role of human activity, episodic fires may have been critical in shaping the present distribution and ecology of the species. If consideration is given to cork exploitation, *Q. suber* may represent one of the best Mediterranean species for reforestation programmes in fire-prone areas.

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