The distribution of cluster pine (Pinus pinaster) in Spain as derived from palaeoecological data

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The distribution of cluster pine (*Pinus pinaster*) in Spain as derived from palaeoecological data: relationships with phytosociological classification

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Abstract: New pollen-analytical data from the Navarrés peatbog (Valencia, eastern Spain) show a synchronous Late-Quaternary fluctuation of *P. pinaster*- (cluster pine) and *Quercus*- (oak) dominated assemblages. During glacial times, *P. pinaster* survived in refugia together with other trees such as *Corylus*, *Fraxinus Quercus*, and a number of Mediterranean shrubs such as *Arbutus*, *Erica arborea*, *Olea*, *Phyllirea*, *Pistacia terebinthus*, *Myrtus communis* and *Viburnum tinus*. These nuclei of vegetation expanded around *c*. 30 000–27 000 BP invading areas formerly occupied by pine forests. *P. pinaster* retreated considerably during the last glacial maximum and the Younger Dryas event, but not as much as *Quercus*. During *c*. 10 000–6000 BP, a local pine forest resisted possible oak and *P. pinaster* invasion. Around 6000 BP, *P. pinaster* was involved in a post-fire change towards oak-dominated vegetation. This work supports the contention that *P. pinaster* is native to the Iberian Peninsula and that well-developed *P. pinaster* forests, particularly if mixed with oaks, are a natural feature of the landscape. The data presented here disagree with the floristic-phytosociological assumption that considers that the forest patches of *P. pinaster* and other Mediterranean species of pines are incidental and mainly derived from afforestation.

Key words: Cluster pine, *Pinus pinaster*, phytosociology, palaeoecology, vegetation history, Spain, Late Quaternary, Holocene.

Introduction

At a time of increasing concern over the management and biological conservation of natural resources, a knowledge of the history of the main forest trees is of paramount importance. *Pinus pinaster* Aiton (cluster, maritime pine) is a western Mediterranean species reaching the High Atlas and Tunisia in North Africa (Figure 1). It is particularly abundant in Spain where it attains a cover of over 1 300 000 ha (Gil *et al*., 1990). *P. pinaster* has been traditionally used for timber and as a source of turpentine (Devesa, 1997). Although some authors favour its segregation into two subspecies, namely *P. pinaster* subsp. *atlantica* H. del Villar (*P. maritima* s.str. Lamk) and *P. pinaster* subsp. *pinaster* (*P. hamiltoni* Ten), their supposed traits do not seem to be fixed enough to support such a taxonomic discrimination (Do Amaral, 1986).

P. pinaster is versatile ecologically. While particularly successful on sandstone and in climates with only a weak summer

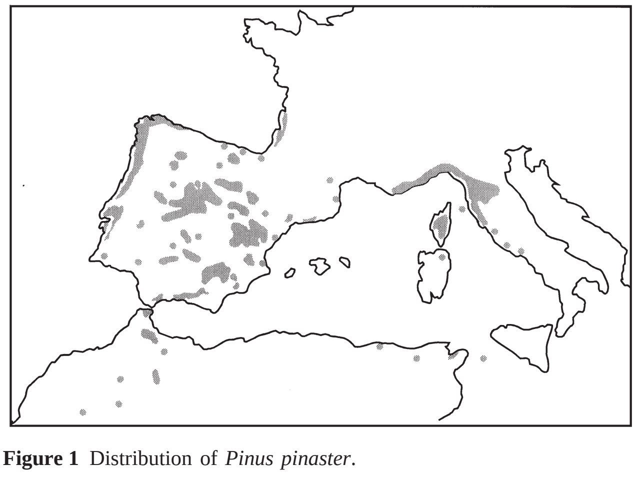

Figure 1 Distribution of *Pinus pinaster*.

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drought, this species actually occurs on a variety of substrates (i.e., limestone, granite, schist, marly limestone, peridotite) and under a range of Mediterranean climate regimes (semi-arid to humid). It grows most commonly with an open forest physiognomy, a situation that permits the development of a dense maquis that is highly combustible (Brosse, 1977). However, *P. pinaster* can also form closed forests that are either monospecific or mixed with different evergreen or deciduous trees and a varied understorey (Blanco *et al.*, 1997).

As for other European pines, the historical biogeography of *P. pinaster* has been a matter of controversy. Some botanists have explicitly mentioned the indigenous nature of *P. pinaster* in the Iberian Peninsula (Agostini, 1968; Destremau *et al.*, 1982; Gil, 1991) and a few natural communities have been described (Nieto *et al.*, 1989; 1991), but most often it is described as an invasive species of sclerophyllous scrub or deciduous forest (Izco, 1984). The floristic-phytosociological literature does not support the idea of self-established populations and suggests that they are a result of recent afforestation (Costa, 1974; 1987; Bellot *et al.*, 1983; Peinado and Martínez-Parras, 1985; Sánchez-Mata, 1989), even in some parts of the Iberian cordillera (Bellot, 1978), where genetic marker studies postulate its centre of origin (Alia, 1989). From an ecological perspective, Rivas-Martínez (1987) argues that the planting of this pine is inappropriate and that stand development is therefore expected to be unsuccessful. Even when considered indigenous, its populations are in most cases associated with ‘particularly unstable and/or immature topographic or soil conditions’ and treated as ‘paraclimax’ (Quèzel and Barbero, 1990) or ‘disclimax’ stages (Bellot, 1978) of disturbed *Quercus* forests.

It is clear, however, that afforestation with *P. pinaster* was unimportant in the peninsula before 1887 (Gil, 1991), and there is no documentary evidence to support the extension through planting of this pine in a number of pre-existing populations. On the contrary, ethnobotanical and toponymic information contained in historical reports, dictionaries and a multitude of chronicles and legal papers indicate the common occurrence of *P. pinaster* woodlands throughout Spain (Gil, 1991; Sánchez-Gómez *et al.*, 1995). Charcoal analyses from a number of prehistoric settlements in central and northern Portugal (Figueiral, 1995) demonstrate the presence of *P. pinaster* in coastal and inland areas since *c.* 33 000 BP. Palaeoecological studies suggest a continual presence and provide further support for native populations of *P. pinaster* in Portugal (Mateus, 1989; Mateus and Queiroz, 1993), northwestern Spain (Aira *et al*., 1989; Ramil, 1992), the Pyrenees (Reille, 1990; 1991) and, sporadically, on the eastern coast (Dupré, 1988).

The question of the Iberian origin of *P. pinaster* seems therefore no longer disputable. However, it is likely that recent afforestation must have partially reshaped its current distribution. This paper presents new pollen-analytical data from the peatbog of Navarrés (Valencia), a locality that not only exhibits the native character of *P. pinaster* in eastern Spain but also presented here its ecological importance as a well-developed Mediterranean woodland both in the absence and the presence of human activity.

Site description

The peatbog of Navarrés is located in a tectonic valley (39° 06′N, 0° 41′W), *c.* 2 km wide, lying at 225 m a.s.l. in Valencia province, eastern Spain (Figure 2). Today, the valley is cultivated with almond and olive trees, tobacco, vegetables, willow and alfalfa. Along the flanks is a garrigue of *Quercus coccifera*, *Pistacia lentiscus*, *Chamaerops humilis*, *Rhamnus alaternus*, *Juniperus oxycedrus*, a number of chamaephytic Lamiaceae, Cistaceae and Fabaceae, and scattered stands of *Pinus halepensis*. Although *P. pinaster* is not locally present, it is found in most of the adjacent mountains. This higher-altitude vegetation is reported to be a degradation stage of a native or ‘potential’ *Quercus rotundifolia* forest (called *Rubio-Quercetum* in the floristic-phytosociological terminology of Rivas-Martínez, 1987). This degradation is thought to have occurred as a consequence of anthropogenic disturbance, mainly in the form of livestock grazing. Like *P. pinaster*, *P. halepensis* is thought to have spread following disturbance, benefiting from being tolerant to unstable substrates or expanding from nearly afforestation (Costa, 1987).

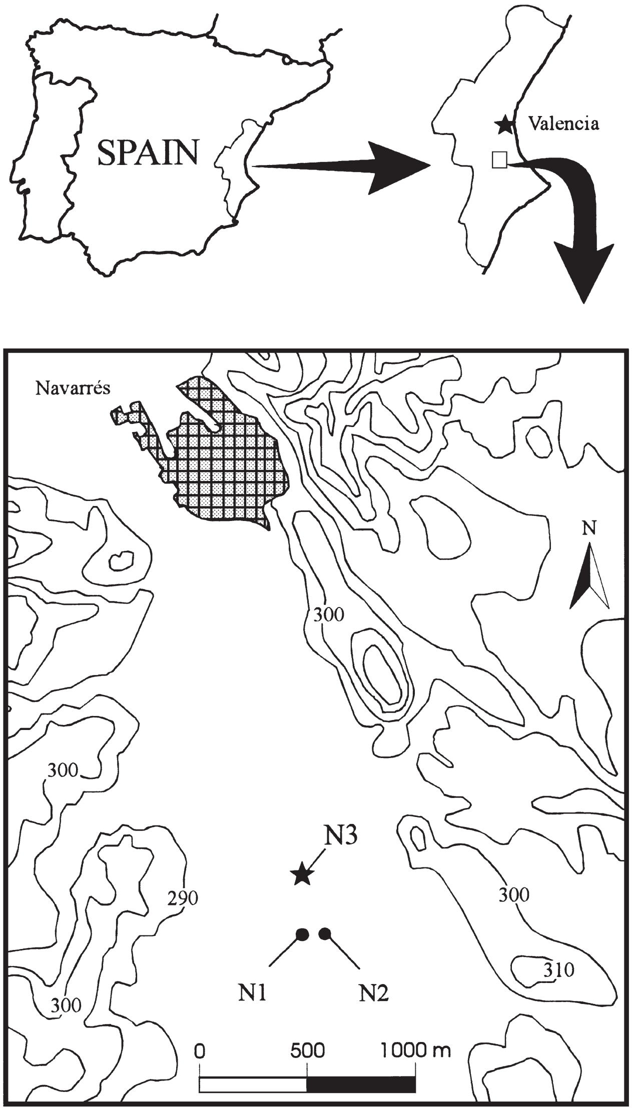


Figure 2 The site of Navarrés indicating the location of cores N1 and N2, and the section studied in this paper (N3).

Methods

The centre of the valley has been the subject of several palaeoenvironmental studies which show the existence of an ancient endorrheic area with a patchy distribution of small lakes eventually developing into marsh (Dupré *et al*., 1999). The palaeoecological investigation presented here was undertaken on one of these palaeolakes. The sedimentary sequence spans 25 m depth, but only the topmost 250 cm are fossiliferous and are classified as a sandy peat. A two-core pollen analytical investigation approach was initially reported by Carrión and Dupré (1996) but no distinction was made between different pine pollen types. A more detailed survey of pollen and macroscopic remains has been submitted elsewhere. Here we will summarize those parts of that study which specifically apply to *P. pinaster*.

The sedimentary sequence was retrieved using metal boxes $50 \times 20 \times 10$ cm that were pushed into a 2.5 m deep profile. In the laboratory, the sections were subsampled at 1 cm intervals. The uppermost 36 cm are a recent soil and they were not analysed further. Pollen preparation and macrofossil sampling followed the techniques most recently described by van Geel *et al.* (1989). Microscopic charcoal was measured and counted using the same slides as for microspores. Macroscopic charcoal (larger than 150 μm was counted from samples previously kept in water in a cross-ruled petri dish. A summary pollen percentage diagram (Figure 3) is presented, including curves for total concentration and charcoal counts. Pollen percentage zone boundaries were determined from the results of constrained incremental sum-of-squares cluster analysis (CONISS; Grimm, 1987) using a square-root transformation and chord-distance dissimilarity measure of the data for pollen types exceeding 2% abundance.

Identification criteria and variation of pine pollen size along the sequence

Pinus pinaster can be palynologically separated from other pine pollen by its larger pollen body, shorter alveoli and thicker proximal exine (Table 1). This differentiation is often possible under 40× microscopic magnification, although experience with reference collections shows that these criteria fail for some grains. Such undifferentiated pine pollen has been included in a general *Pinus* type, which may include one or several of the following species: *P. sylvestris*, *P. nigra*, *P. pinea* and *P. halepensis*. In biozone N3PD (Figure 3), we have observed some pollen grains with particularly large sac alveoli and thick proximal exine. These are identified as *P. halepensis*-type according to the criteria published by Roure (1985).

Statistical analysis of the pine pollen dimensions in the Navarrés-3 sequence supports the presence and variation of *P. pinaster* as shown in the pollen diagram (Figure 3). The equatorial diameter variable does not follow a normal distribution as demonstrated by a P-value tending to zero in the Anderson-Darling normality test and illustrated in the corresponding probability plot (Figure 4). The equatorial diameter distribution of the entire pine pollen sequence indicates a multimodal distribution of this attribute, suggesting the presence of several distinct pine pollen types (Figure 5). If we compare this frequency histogram (Figure 5) with those obtained by analysing the data from each pollen zone separately (Figure 6), two patterns of frequency distribution are observed: a size group around *c.* 80 μm and another one around *c.* 60 μm. The variation between pollen zones in the large-sized group (Figure 6) corresponds well with the pollen curve of *P. pinaster* (Figure 3). On the other hand, the small-sized group is only nearly unimodal in N3PC (Figure 6c) while showing great heterogeneity in the other zones (Figure 6, a, b and d). Taphonomical and ecological differences may have contributed to this pattern, together with a plausible contribution from other species of pine, at least during N3PA and N3PB. In light of both the pollen sizes (Roure, 1985) and the present-day biogeography and ecology of Spanish pines in the region, these contributing species could be *P. nigra* and *P. sylvestris*.

The Navarrés-3 pollen record

Results from the pollen analysis are presented in Figure 3. The uppermost 36 cm are recent soil and, therefore, not treated in the laboratory. For the remaining sequence, the section between 145 and 166 cm depth is palynologically sterile. All the remaining samples contained pollen, algae, fungi and other palynomorphs. Radiocarbon dating of the sequence suggests that the pollen profile covers the period between *c.* 31 000 and 3000 ^{14}C yr BP (Table 2). This Late-Quaternary sequence has been subdivided into four pollen zones, two covering the last glacial (N3PA and N3PB) and two covering the Holocene (N3PC and N3PD) (Figure 3). During the zone N3PA (*c.* 31 000–27 000 yr BP), *Pinus* is dominant and oaks (evergreen, deciduous and *Q. suber*) attain high percentages (generally higher than 25%), which, together with the presence of a number of mesothermophilous taxa (*Abies*, *Taxus*, *Alnus*, *Betula*, *Corylus*, *Arbutus*, *Pistacia*, *Myrtus*, *Viburnum*, *Olea*, *Phillyrea* and *Cistus*), suggest the nearby presence of glacial refugia for temperate and Mediterranean taxa. The continuous curve for *P. pinaster-type* in this zone should be noted, which covers a similar but longer span than the oak curve. The site is partially invaded by hygrophilous communities of Cyperaceae, *Typha* and *Apium*. Zone N3PA represents the most clear evidence for an expansion of a Mediterranean-type vegetation in Spain during the last glacial.

During zone N3PB (*c.* 27 000–10 000 yr BP), the pollen spectra reflect cold arid conditions, as can be seen from the abundance of xerophytic types with *Artemisia,* Chenopodiaceae and *Ephedra distachya-nebrodensis*, together with a marked reduction in deciduous trees and thermophytes which eventually disappear from the pollen record. At times, *Pinus* is abundant. *P. pinaster* disappears at the onset of this zone and occurs episodically thereafter. The sequence is interrupted between 145 and 166 cm, seemingly corresponding with the last glacial maximum, during which erosion and subsequent deposition of sands occurred through the basin. A regional Younger Dryas signal is noticed at the end of N3PB, centred around 10 340 yr BP. The last important peak of *Artemisia* is coeval with the latest appearance of *Ephedra*.

During zone N3PC (*c.* 10 000–6000 yr BP) *Pinus* increases and continues to be the most important pollen taxon. This unusual pattern of pine dominance shows a clear-cut correlation with early-Holocene pollen zones of two previously studied cores (N1 and N2) in the vicinity of the study site (Figure 2) (Carrión and Dupré, 1996). *P. pinaster* does not show a continuous curve. At the top of this zone, there is a notable increase in charcoal particles suggesting fires since *c.* 6310 yr BP.

During N3PD (*c.* 6000–3000 yr BP), a sharp change in the pollen assemblages is recorded. *Pinus* is mostly replaced by *Quercus*, with the evergreen oaks and *P. pinaster* becoming relatively abundant together with the presence of Mediterranean-type indicators and a diversity of broad-leaf trees. There is a progressive development of fens (Cyperaceae, *Typha*) indicating marsh infilling. The water bodies experience progressive eutrophication as can be deduced from increased Zygnemataceae and the abundance of *Chara* gyrogonites. Anthropogenic disturbance is suggested by the curve of *Plantago*, but it must be emphasized that this pollen taxon increases only after the formation of a continuous *Quercus* curve, as was previously shown in other parts of the basin (Carrión and Dupré, 1996). Both micro- and macrocharcoal are prominent throughout N3PD, which strongly suggests the occurrence of relatively frequent fires.

Discussion

Pinus pinaster in relation to glacial refugia

Results from this study indicate that *P. pinaster* survived during the last glacial in eastern Spain alongside other trees such as *Corylus*, *Fraxinus*, *Quercus faginea* and Mediterranean evergreen oaks such as *Quercus ilex-rotundifolia* and *Q. coccifera*. Shrub vegetation included *Arbutus*, *Erica arborea*, *Olea*, *Phyllirea*, *Pistacia terebinthus*, *Myrtus communis* and *Viburnum tinus*. In times

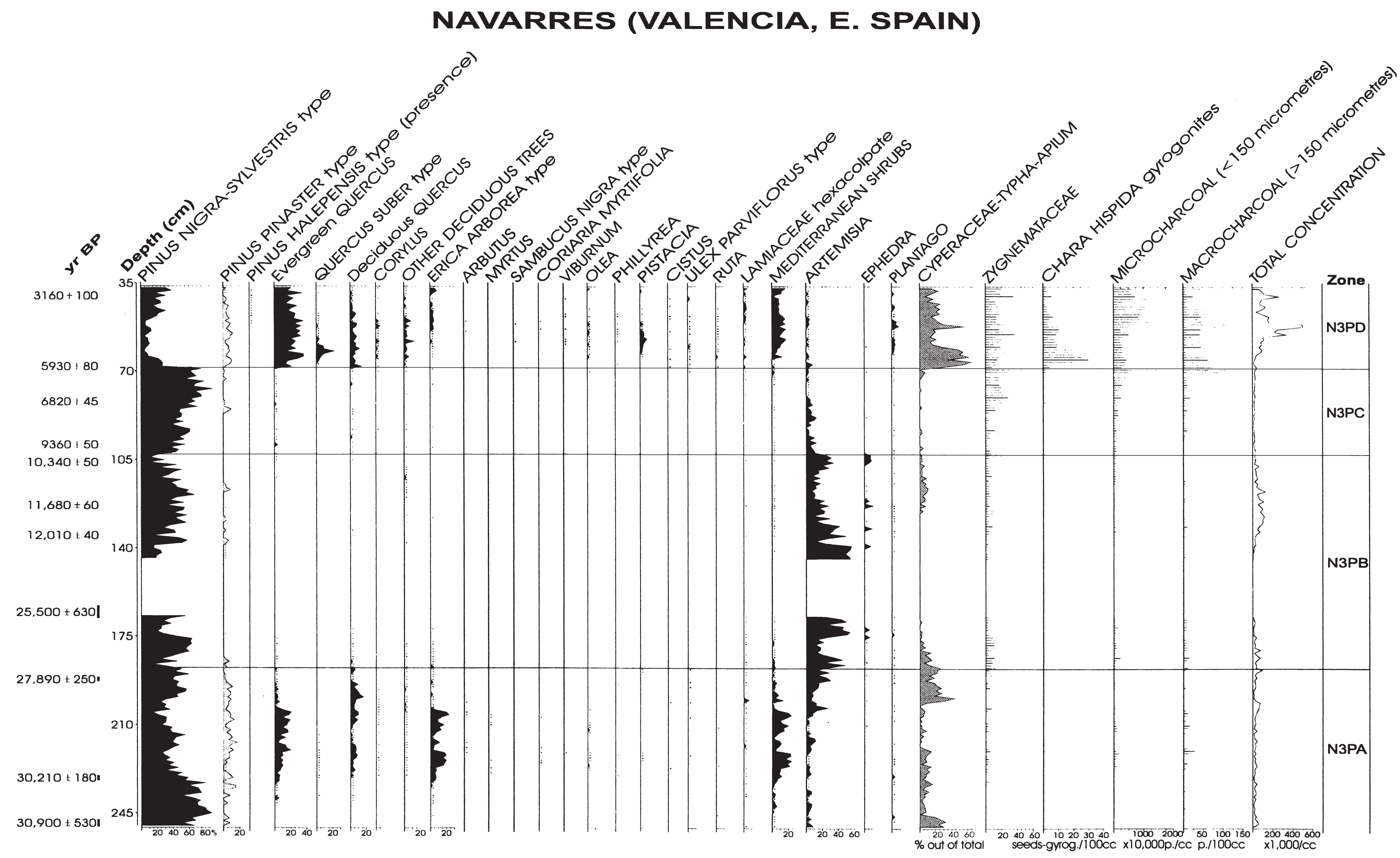


Figure 3 Summary pollen diagram of Navarrés-3. Dates are quoted in radiocarbon years BP and have not been calibrated.

Table 1 Distinctive pollen characteristics of Spanish pines according to Roure (1985)

	Mean equatorial diameter (μm)	Proximal exine	Alveoli
Pinus sylvestris	41–55	Thin	Short
Pinus nigra	45–65	Thick	Short
Pinus halepensis	43–65	Thick	Long
Pinus pinea	47–65	Thick	Long
Pinus pinaster	50–75	Thick	Short

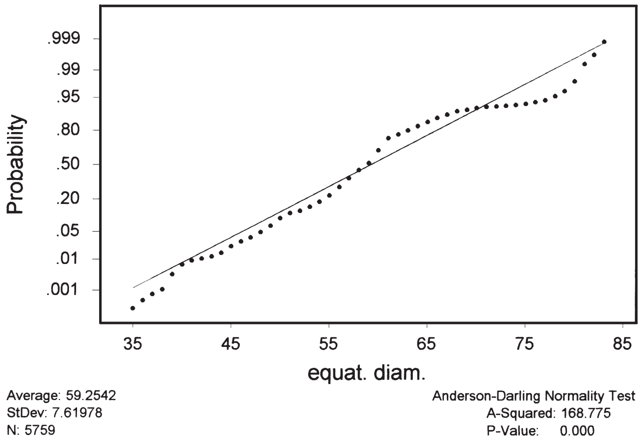


Figure 4 Normal probability plot and Anderson-Darling normality test for the equatorial diameter of pollen grains of pines in the Navarrés-3 sequence.

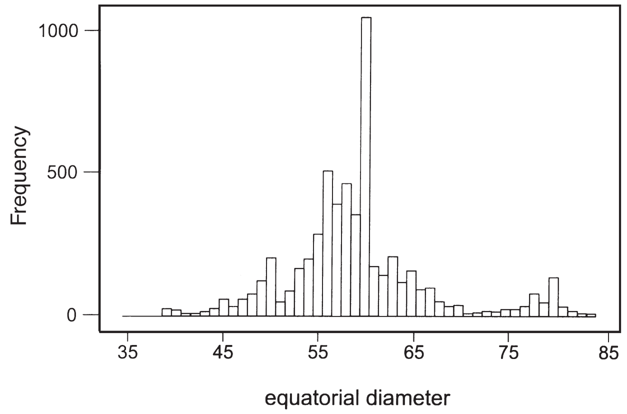


Figure 5 Frequency histogram for the equatorial diameter values (μm) of pollen grains of pines in the Navarrés-3 sequence.

of locally favourable climatic, edaphic or authogenic conditions, it would appear that these nuclei of vegetation expanded and reached the Navarrés area, partially invading areas occupied formerly by pine forests of cf. *P. nigra* and/or *sylvestris*. Both *P. pinaster* and the *Quercus*-dominated communities retreated considerably during the last glacial maximum and the Younger Dryas event, when *Artemisia* expanded. Although we lack a pollen record for the peak of the last glacial, for most of that period pines may have been (relatively) locally abundant. This fact is worth emphasizing because in studies of European refugia the fact that pines must also have been markedly restricted in their distribution during the Pleistocene stadials is often overlooked. *P. nigra* and *P. sylvestris* currently mainly occupy high-altitude forest belts in the Iberian peninsula, a distribution that suggests a degree of cold-tolerance (Figure 7). *P. nigra* is also renowned for its resistance to xeric conditions (Blanco *et al.*, 1997).

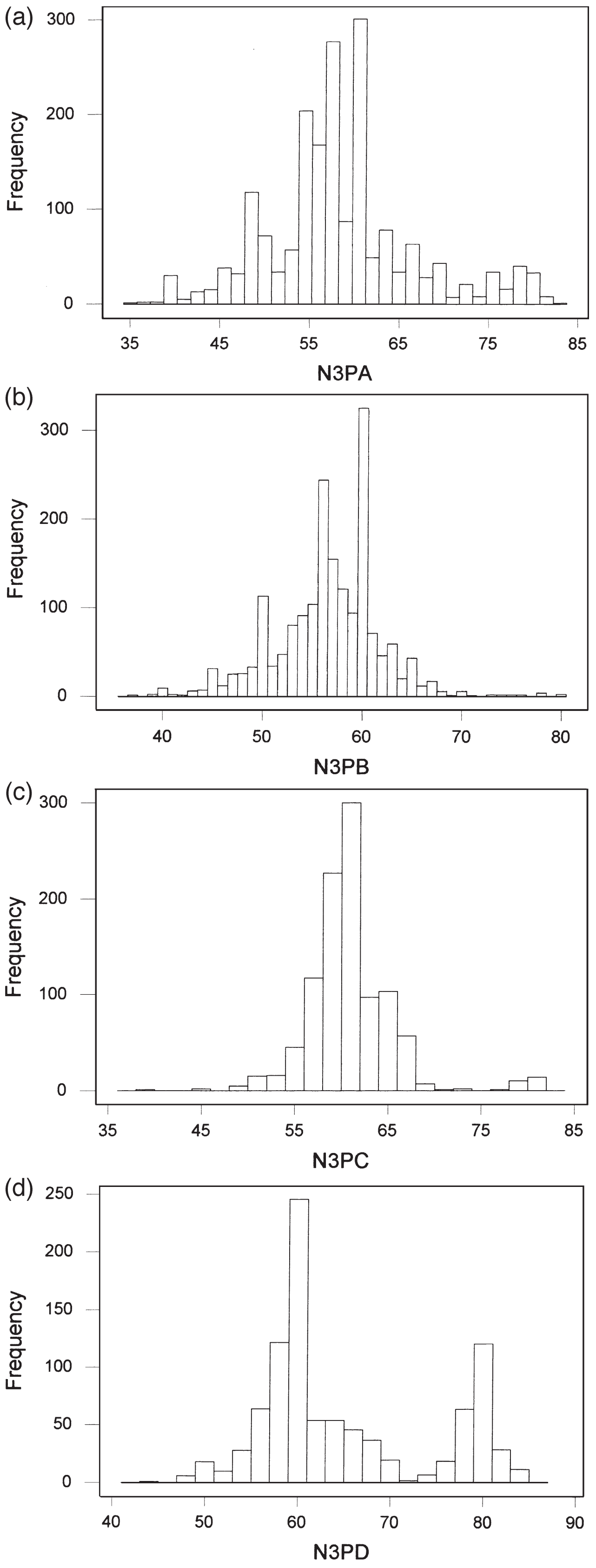


Figure 6 Frequency histogram for the equatorial diameter values (μm) of pollen grains of pines in zones N3PA (a), N3PB (b), N3PC (c) and N3PD (d).

Pinus pinaster seems to have been slightly less sensitive to thermic and/or hydric stress than the different *Quercus* species, as can be deduced from the fact that it precedes the *Quercus* colonization during N3PA and displays a higher resilience thereafter (Figure 3). Even during the glacial phase N3PB, *P. pinaster* still occurs

Table 2 Radiocarbon age determinations for the Navarrés-3 sedimentary sequence

Lab. no.	Depth (cm)	Conventional ^{14}C age (yr BP)	Analysis
Beta-102170	40	3160 ± 100	Extended counting
Beta-102171	68	5930 ± 80	standard
Pta-7438	69	6310 ± 70	standard
Pta-7204	82	6820 ± 45	standard
Beta-1052021	103	9360 ± 50	AMS
Beta-102172	106	10 340 ± 50	AMS
GrA-9008	123	11 680 ± 60	AMS
Beta-105205	135	12 010 ± 40	AMS
Pta-7442	166	25 500 ± 630	standard
Beta-102173	193	27 890 ± 250	standard
Pta-7205	197	26 600 ± 350	standard
Beta-102174	230	30 210 ± 180	AMS
Pta-7207	249	30 900 ± 530	standard

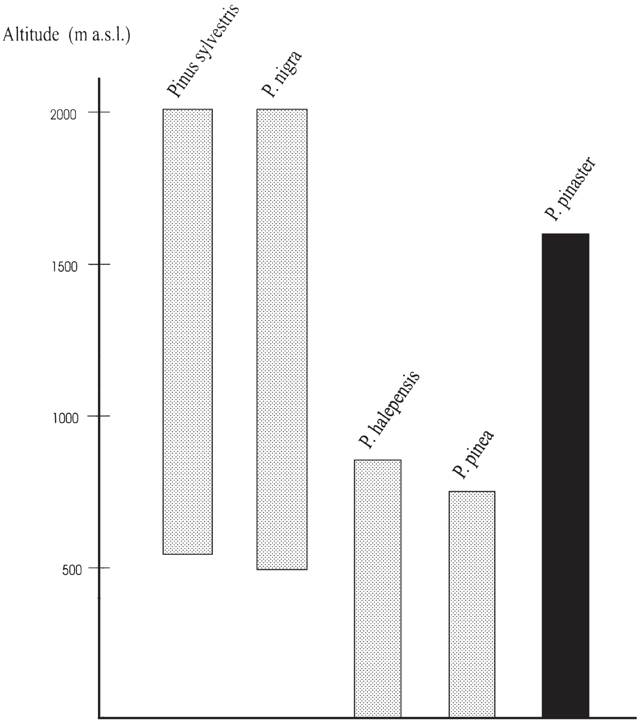


Figure 7 Altitudinal distribution of different pine species in the Iberian Peninsula.

episodically, suggesting that it was less resistant to the glacial conditions than the dominant pine type.

Refugial areas must have been situated not far from the study site, probably in intramontane valleys of the nearby Caroig, Sumacárcer, Martés, Mondúver and Espadán mountains (Figure 8). Pleistocene pollen finds of *P. pinaster* at the Mondúver site of Malladetes (Dupré, 1988) support this hypothesis. Nowadays, important populations of *P. pinaster* can still be seen in the Caroig and Espadán massifs (Figure 8). However, the most prominent regional forests are located in the central Iberian System, to the northwest of Navarrés (Figure 8).

Genetic studies on allelic traits in a number of Spanish populations postulate these mountains as a centre of origin and a source of migrational routes for *P. pinaster* (Alia, 1989), a hypothesis which had been suggested previously by Rikli (1943) and Destremau *et al.* (1982). Similar studies by Baradat and Marpeau (1988) on a number of populations from the entire distribution area concluded that the European populations were probably restricted to some enclaves in the southernmost Betic mountains of Málaga, with the highest degree of isolation after *c.* 35 000 BP (Figure 9). Whatever the case, the Navarrés valley is on the southernmost fringe of the Iberian System and represents a plausible migration route from or to the Betic System, where *P. pinaster* also forms impressive forests, particularly in the Segura and Alcaraz mountain ranges (Figures 8 and 9).

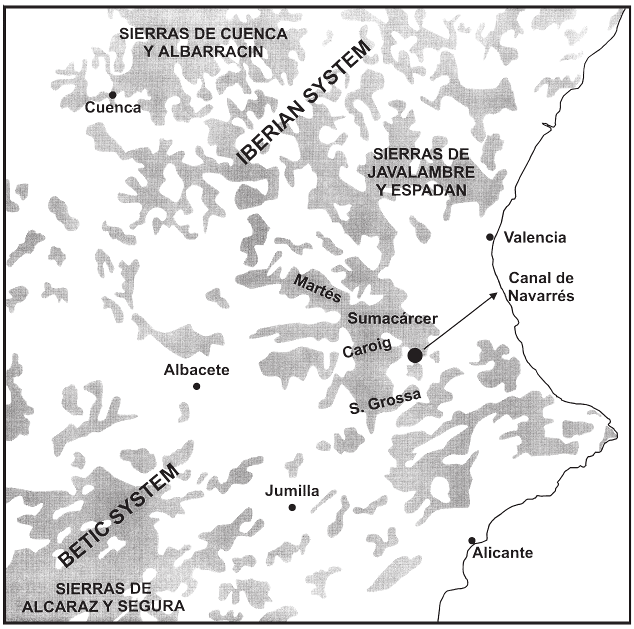


Figure 8 The main eastern Spanish mountain ranges and the site of Navarrés.

Climate is a possible factor that accounts for the synchronous variation in distribution of *P. pinaster* and *Quercus* during glacial times. The genus *Quercus*, as a whole, and *P. pinaster*, in particular, compare well in their present-day bioclimatic distribution. In north Africa, the distribution overlap between *P. pinaster* and *Q. faginea* and *Q. pyrenaica* is very close (Mikesell, 1960). In Spain, *P. pinaster* exists across a wide spectrum of precipitation zones, from subhumid biotopes suited to deciduous forests of oaks and *Q. suber* to dry environments suited to *Q. rotundifolia*,

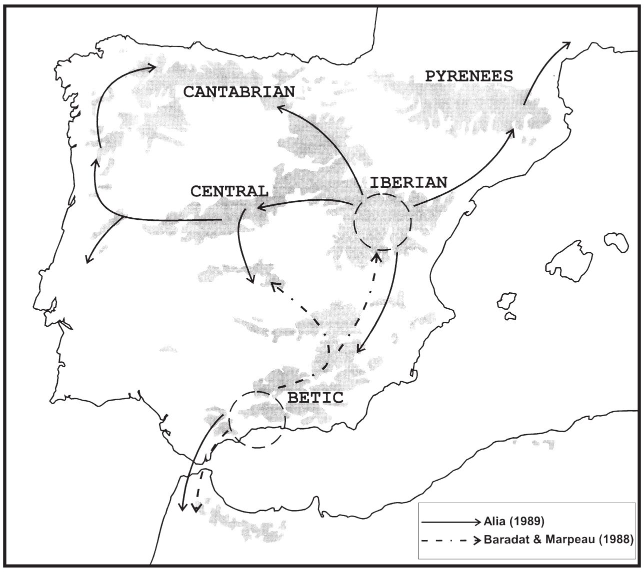
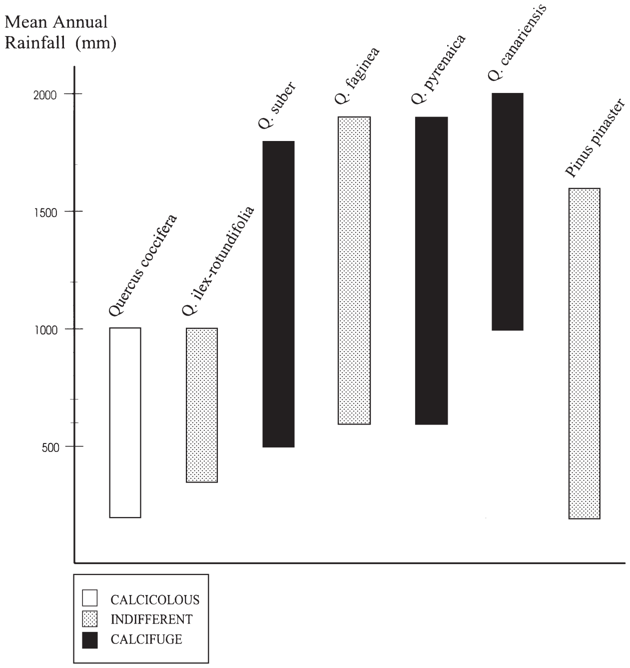


Figure 9 Two hypothesized migrational routes for *Pinus pinaster*.

Q. suber and *Q. coccifera* (Figure 10). Thus, thermically, *P. pinaster* is highly versatile and occurs throughout the range of *Quercus* (Figure 11).

In contrast to the general disregard of *P. pinaster* by floristic-phytosociological studies, Barkman's (1990) structural classification has described a *Pinus-Phyllirea* woodland type characterized by *P. pinaster* and a shrub layer of *Viburnum tinus*, *Phyllirea*, *Pistacia* and *Erica arborea*. It is interesting to note the similarity between these modern communities and the pollen assemblages described for zones N3PA and N3PD (Figure 3). As indicated by the palaeobotanical data, these communities appear to have been recurrent in the past. Figueiral (1995) showed the Pleistocene coexistence in Portugal of *P. pinaster* with *Q. ilex*, *Q. suber*, *Fraxinus*, *Arbutus unedo* and *Erica arborea*, among others. The hypothesis of a restricted distribution of glacial refugia in southeastern Spain (Baradat and Marpeau, 1988) (Figure 9) is therefore discarded and replaced by that of the existence of a larger number of refugia in the western Mediterranean. Additional palaeoecological records are needed to verify this hypothesis.

Figure 10 Mean annual rainfall tolerance of *Pinus pinaster* compared to different Spanish oak species and their associated soil features.



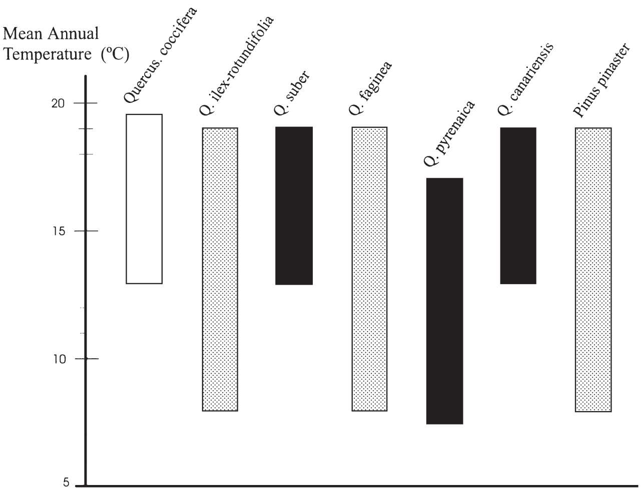


Figure 11 Mean annual temperature tolerance of *Pinus pinaster* compared to different Spanish oak species and their associated soil features.

Postglacial expansion and fire history

The parallel between *Quercus* and *P. pinaster* extends towards the Holocene zones N3PC and N3PD. During the former zone, while the local forest of cf. *P. nigra/sylvestris* resists a possible oak invasion, *P. pinaster* continued to be subordinate. Thereafter, it was involved in the vegetation shift already described for zone N3PD. The resistance of the original pine forest to invasion by *Quercus* and other thermophytes following the start of the Holocene can be related to the phenomenon known in population ecology as 'home-field advantage' (Pimm, 1991), This describes how a population will tend to resist invasion by similar phenotypes, and how competition will only become critical after removal of the original population by extrinsic forces or authogenic decline. With regard to *P. nigra*, resilience is conferred by longevity and a marked intra-populational genetic variability (Blanco *et al*., 1997).

From charcoal evidence, it appears that the vegetational change recorded in N3PD may have been a consequence of intensifying fire regimes. Many pine species are well adapted to fire disturbance and the location of present-day pine forests in the Iberian Peninsula coincide with areas of high lightning frequency and thus fire occurrence. In Navarrés, recurrent severe fires may have led to pine forest destruction, thus favouring oaks and a number of Mediterranean shrubs. Moreover, due to its serotinous cones, *P. pinaster* itself can take advantage of the high-frequency fire perturbation experienced by *P. nigra* forests (Alexandrian, 1992). Other studies suggest that *P. pinaster* and *P. halepensis* are related to post-fire dynamism (Thanos *et al*., 1996). However, more commonly a relationship between fire and invasions by sclerophyllous oaks can be observed (Reille, 1992; Willis *et al.*, 1995). In particular, the Navarrés data show a most striking similarity with pedoanthracological data collected in Corsica (Carcaillet *et al.*, 1997) which show a late-Holocene expansion of *Quercus ilex, Pinus pinaster* and *Erica arborea* after burning of a *Pinus nigra* forest. It is plausible that in Navarrés fires could have destroyed the remaining toxic humus that had accumulated during the millennia preceding the arrival of oaks, so facilitating expansion of *P. pinaster*. Furthermore, fires would have removed allelopathic inhibitions through the destruction of the litter (Mallik and Roberts, 1994).

The main factor initiating burning at the study site is not known. The fires may have been anthropogenically induced, since the first important charcoal peaks coincide with the arrival of Neolithic people in the area. Another possibility is that the first fires were natural, with occurrence thereafter being heavily influenced by local inhabitants. Although less intense or more distant from the sampling site, small charcoal peaks during N3PA (Figure 3) indicate fire events during glacial times. It is therefore likely that fire has played a role in the vegetation dynamics of this region over the Quaternary. Periodically, fire would have had a localized catastrophic impact on vegetation, although species would have persisted within the region as a whole through the presence of a mosaic of suitable habitats. Post-fire community dynamics will, however, be dependent upon specific site conditions, and both site history and the presence of source individuals or populations would have been critical. Mid-Holocene anthropogenic intervention could well have changed the predominant pathway of community development by increasing both fire frequency and intensity. An analogous situation may be seen with present-day macchia and garrigues with scattered *P. halepensis* stands that appear to be associated with anthropogenic activity in conjunction with the increased aridity of the last 1000 years (Parra, 1993).

However, climatic change cannot be overlooked. Sclerophyllous oaks may develop as a result of fire disturbance, but the presence of the deciduous tree, *Q. suber,* and some shrubs such as *Arbutus, Ilex, Buxus, Erica arborea, Pistacia terebinthus* and *Coriaria myrtifolia* suggest increased humidity in some areas during N3PD (Figure 3). Additionally, the effects of fire may have been accentuated by a warmer climate. In this context, it is interesting to examine the pollen content of offshore sediments at latitude 21°N which document climate displacements over the last 20 ka throughout the Mediterranean region (Hooghiemstra, 1988). In particular, the onset of the warm moist climatic phase of the Sahara around 6.5 ka ago coincides with the shift towards the dominance of evergreen *Quercus*, not only in Navarrés but also in many other sites within the Mediterranean (Pons and Reille, 1988; Willis, 1994; Magri, 1997).

Implications on the palaeoecological role of pines during the Quaternary

The palaeoecological data presented here show a synchronous development of the *P. pinaster* with *Quercus*-dominated assemblages during last glacial and Holocene times in eastern Spain and, therefore, support both the native character of *P. pinaster* in the eastern Iberian Peninsula and the naturalness of some present-day forests in which it occurs with oaks.

The phytosociological interpretation of the *P. pinaster* also encompasses other pine species represented within the Iberian Peninsula, in particular *P. pinea*, *P. halepensis* and, to a lesser extent, *P. nigra* and *P. sylvestris*. However, anthracological studies demonstrate the indigenous character of each species (Badal *et al.*, 1994; Figueiral, 1995) and palaeoecological studies document a number of peninsular sites where pines formed dense forests during the late Quaternary (Pons and Reille, 1988; Peñalba, 1989; Carrión *et al.*, 1998; García Antón *et al.*, 1997; Franco Múgica *et al.*, 1998). Of particular interest are the nearby Neolithic sequences of Cova de les Cendres and Cova de l'Or (Dupré, 1988; Carrión *et al*., 1999), where pines were extremely abundant in the Holocene when a *Quercus* development occurs synchronously in the Navarrés zone N3PD (Figure 3).

The floristic phytosociological model disagrees with both palaeoecological evidence and with field observations that show *P. pinaster* to form structurally well-developed monospecific and mixed forests under a number of physiographic conditions, not necessarily related to low water and nutrient availability. In the Segura mountains of the Betic system, for instance, *P. pinaster* and *P. nigra* often appear in the most favourable biotopes while several sclerophyllous oaks are clearly subordinate. This disagreement necessitates a consideration of the possible causes of the long-standing prevalence in many Mediterranean countries of an approach that does not fit well with observational or historical data. In our view, there are four underlying reasons.

First, there is a recurrent difficulty in separating natural from anthropogenic events since they often overlap in historical records and have similar effects on the present-day landscape. Certainly, it is difficult to define the impact of ancient afforestation on the modern vegetation cover. Because of this, there is no firm basis for separating communities into categories such as climax, paraclimax, potential, permanent or anthropogenically induced formations. This is illustrated by the assertion that very few, if any, present-day forests can categorically be said to be free from past human influence. Indeed, during the last decades, more and more allegedly 'virgin' forests have been shown to be subject to past anthropogenic disturbance. For instance, the suitability of *Q. ilex* forests under dry and subhumid ombroclimates has been discussed by Reille and Pons (1992). More recently, it has been demonstrated that many silicicolous *Q. suber* forests of the western Iberian Peninsula are the result of selection pressure exerted by man in order to utilize cork, acorns and other products (Pérez Latorre, 1996).

Second, it is the assumption that, since pines are adapted initially to a seasonal climate and dry sites (Taylor and Taylor, 1993), they must also be opportunistic and xerophytic. On this basis, most Mediterranean pines would represent paraclimatic stages of angiosperm mature forests. This is, for instance, the role assigned by Quèzel and Barbero (1990) for *P. halepensis*, *P. brutia* and *P. pinaster* regarding, respectively, to *Q. ilex-rotundifolia*, *Q. calliprinos* and *Q. suber*. An underlying premise is that the tolerances of modern species are similar to those of their fossil relatives, an assumption that ignores possible evolutionary changes in tolerance. In the Tertiary floras, however, pines were members of a variety of forests including mixed conifer, conifer hardwood and sclerophyllous woodlands (Axelrod, 1986) and there is no reason why they could not occur in present-day natural, well-developed forests not subject to successional competition.

Third, there is a common belief that the structure and dynamics of the vegetation are invariably the result of habitat conditions such as soil and climate (Braun-Blanquet, 1979). According to this, one should be able to predict actual ranges of species using physical characteristics of the sites. This argument ignores the importance of Stochastic processes (such as random colonization and extinction events) in determining the distribution of pines (Bergeron *et al.*, 1997). Furthermore, it does not take into account the importance of site-history factors, such as disturbance and intra-populational genetic processes.

A fourth assumption is that, after an initial period of competitive exclusion under site-specific deterministic factors, distribution will reach a stable equilibrium with the environment. This is the very crux of the proposition that only 'stable' associations should be included in the plant population dynamic studies as only they are the 'real' associations. This highlights a major problem with this approach, namely that the concepts of syntaxonomy and syndynamics are combined. Phytosociological classification should not impede research into plant population dynamism. As Mucina (1997) sharply pointed out, 'stability of a syntaxonomic system is an illusion, in particular when floristic-genetic processes, disturbance history, past management and other facets controlling the pathways of vegetation dynamics are neglected'. To avoid these problems, we suggest that palaeoecological data set interpretation is both independent of inferences based on modern plant relatives and that it is as far as possible conducted without reference to floristically orientated databases of vegetation types.

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